

Science Plan for COAT: Climate-Ecological Observatory for Arctic Tundra



FRAM – High North Research Centre for Climate and the Environment



Fram Centre Report Series No. 1

Science Plan for COAT: Climate-Ecological Observatory for Arctic Tundra

Editors:

Rolf A. Ims, Jane U. Jepsen, Audun Stien & Nigel G. Yoccoz



Science plan for COAT: Climate-ecological Observatory for Arctic Tundra

| Editors: | Rolf A. Ims, Jane U. Jepsen, Audun Stien & Nigel G. Yoccoz |
|----------------------|--|
| Publisher: | Fram Centre by the University of Tromsø |
| Year of publication: | 2013 |
| Number of pages: | 177 |
| Cover photo: | Geir Vie |
| Cover layout: | Ingrid Jensvoll and Jane U. Jepsen |
| Typesetting: | Jane U. Jepsen |
| Printing: | Troms Produkt, Tromsø, Norway |
| ISBN: | 978-82-999253-0-3 |

The publication should be cited as follows:

| Ims, R.A., Jepsen, J.U., Stien, A. & Yoccoz, N.G. 2013. Science plan for |
|--|
| COAT: Climate-ecological Observatory for Arctic Tundra. Fram Centre |
| Report Series 1, Fram Centre, Norway, 177 pages. |

Notes:

| The Fram Centre is the short name for FRAM– High North Research Centre for Climate and the Environment. The Fram Centre is based in Tromsø and consists of 21 institutions involved in interdisciplinary research in the field of natural science, technology and social sciences. The following Fram Centre institutions are involved in COAT: University of Tromsø, Norwegian Institute for Nature Research, Norwegian Polar Institute, University Centre in Svalbard and Norwegian Meteorological Institute. |
|---|
| The science plan is coordinated by the University of Tromsø, and financienced with contributions from: The Ministry of Education and Research The University of Tromsø Norwegian Polar Institute Norwegian Institute for Nature Research |

The Fram Centre

TABLE OF CONTENTS

| FOREWORD | 5 |
|---|-----|
| EXECUTIVE SUMMARY | 7 |
| 1. BACKGROUND AND RATIONALE | 9 |
| 1.1. Arctic tundra ecosystem | 9 |
| 1.2. Long-term research and monitoring | 23 |
| 2. COAT MODULES | 29 |
| 2.1. Monitoring targets and conceptual climate impact path models | 29 |
| 2.2 Tundra-forest ecotone module (Varanger) | 31 |
| 2.3 Tall shrub (Varanger) | 41 |
| 2.4 Small rodent module (Varanger) | 51 |
| 2.5 Ungulate module (Varanger and Svalbard) | 65 |
| 2.6 Ptarmigan module (Varanger and Svalbard) | 77 |
| 2.7 Goose module (Svalbard) | 89 |
| 2.8 Arctic fox module (Varanger and Svalbard) | 97 |
| 2.9. Monitoring design and methods | 111 |
| 2.10. Data management and analysis | 137 |
| 3. ORGANIZATION | 141 |
| 4. INTERNATIONAL COLLABORATION | 143 |
| 4.1. Pan-arctic perspectives | 143 |
| 4.2. Links to other established ecosystem-based observatories | 144 |
| 4.3. COAT Russia | 144 |
| 5. SOCIETY INVOLVEMENTS, EDUCATION AND OUTREACH | 147 |
| 5.1. Management issues and stakeholder fora | 147 |
| 5.2. Education | 148 |
| 5.3. Outreach | 151 |
| Literature cited | 153 |

FOREWORD

In connection with the opening of Fram - High North Centre for Climate and the Environment in fall 2010, the centre was tasked to initiate a planning project for a *Climate ecological Observatory* for Arctic Tundra (COAT). The planning project was funded by the Ministry of Science and the University of Tromsø and Professor Rolf A. Ims was appointed as the leader. A task force was established in January 2011 with members from Department of Arctic and Marine Biology at the University of Tromsø, (Kari Anne Bråthen, John-André Henden, Dorothee Ehrich, Vera H. Hausner, Rolf A. Ims, Ingrid Jensvoll, Siw Killengreen, Virve Ravolainen, Nigel G. Yoccoz), Department of Arctic Ecology of the Norwegian Institute of Nature Research (Martin Biuw, Per Fauchald, Jane U. Jepsen, Audun Stien, Ingunn Tombre, Torkild Tveraa), Norwegian Polar Institute (Eva Fuglei, Jack Kohler, Åshild Ø. Pedersen), University Centre of Svalbard (Steve Coulson, Pernille B. Eidesen. Eike Müller). Ole Einar Tveito (Norwegian Meteorological Institute), Elisabeth Cooper (AMB, UoT) and Jesper Madsen (University of Aarhus) later joined the task force. The scientific scope and overall approach for COAT was agreed on during the course of a series of internal meetings during the spring of 2011. During these meetings the main responsibility for writing the module chapters was allocated to the different specialist members of the task force. It was also agreed that all the main modules of the COAT science plan should be thoroughly presented and discussed in workshops in which external referees were invited. Eight workshops were held during May - December 2011. The following colleagues kindly acted as referees during these workshops: Anders Angerbjörn, Tom Edwards, Heikki Henttonen, Greg Henry, Annika Hofgaard, Jesper Madsen, Jim Nichols, Carl Mitchell, Erling Solberg and Rene van der Wal. The overall approach of COAT was also presented and discussed at the AMINOR workshops in Tromsø and at the Terrestrial Monitoring Expert Group (TMEG) of the Circumpolar Biodiversity Monitoring Program (CBMP) in Denmark in November 2011 Finally, two meetings have been held with members of reindeer herding districts on Varanger Peninsula in May and November 2011 and the mayors of the municipalities at the Varanger Peninsula were informed about the project in a meeting in the Ministry of Environment in February 2011.

A draft of the science plan for COAT was submitted for review by an expert panel administrated by the Division for Energy, Resources and the Environment of The Research Council of Norway in June 2012. Their consensus review report was ready in November 2012. The review provided full support for the COAT science plan and concluded that "the original approach will make a worldclass contribution", "making this well-conceived and major initiative operational will simply rely on resources as all the necessary components, particulary concepts and experience, are present" and that it was their opinion "that the project should be funded appropriately and encouraged into the long -term [...] with all due haste". The 10-page review report provided also a set of contructive suggestions about additional scientific issues to be included in the plan as to make COAT even more comprehensive and, moreover, good advices on organizational issues that could make COAT more robust. The present version of the science plan, which is published as the first issue of the Fram Centre's report series, represents a revision of the draft plan submitted for review. It should, however, not be considered as a final product. According to COAT's paradigm of adaptive longterm science, its plan should also be an "adaptive entity" frequently subjected to revisions and improvements.

Tromsø June 25th, 2013

Rolf H. Emg

On behalf of the COAT team

EXECUTIVE SUMMARY

The arctic tundra comprises of the terrestrial ecosystems north of the continuous boreal forest and is one of the earth's largest terrestrial biomes. Owing to its remoteness, the arctic tundra still harbors vast stretches of pristine wilderness with intact ecosystem functions and endemic biodiversity of great fundamental and societal significance. Yet the arctic tundra is predicted to become more challenged by climate change than any other terrestrial biome. Global circulation models (GCMs) project an average temperature increase in the Arctic as large as 10 °C by the turn of the century. Given such an extensive and rapid change, the impacts on the ecosystems will be large and have pervasive implications locally and globally. The rapid shift to new climate regimes is likely to give rise to new ecosystems with unknown properties, making science unable to accurately predict the associated outcomes and long-term consequences. The large internal uncertainties of the GCMs added to the limitations of ecological projection models, will hinder society from responding to the changes by means of appropriate adaptive and mitigating actions. It therefore becomes crucial to establish scientifically robust observation systems to enable real time detection, documentation and understanding of climate impacts on arctic tundra ecosystems. In the light of this background it is paradoxical that our observing capacity of the arctic tundra is very low. In context of the vastness of the circumpolar biome and its large internal variability there are very few sites devoted to longterm research and monitoring and in particular which adopt an adequate ecosystem-based approach that accommodate the range of impacts and consequences that can be anticipated.

In response to these concerns, the Fram Centre hereby launches a science plan for a Climateecological Observatory for Arctic Tundra (COAT). COAT will be implemented at two sites representing the Norwegian sector of the tundra biome – low-arctic Varanger peninsula and higharctic Svalbard. However, the plan also describes initiatives for circumpolar collaborations and extensions, in particular, plans for the establishment of "sister observatories" in arctic Russia. The goal of COAT is to become the world's most comprehensive and management relevant longterm research and monitoring enterprise for arctic terrestrial ecosystems.

COAT aims to be a fully ecosystem-based system for long-term adaptive monitoring based on a food web approach. A food web approach in context of adaptive monitoring confers several advantages. First, the food web concept is strongly embedded in fundamental ecological theory. This allows the formulation of conceptual climate impact prediction models for tractable modules (compartments) of the food web which will act as a guide for defining adequate monitoring targets and state variables. Second, the comprehensive food web approach taken by COAT, with 7 modules and derived prediction models, accommodate the anticipated climate change impact on tundra ecosystems. Anticipated impacts include (1) "Arctic greening" due to encroachment of forest and tall shrubs and its resultant feedback to the ecosystem and climate system, (2) disrupted dynamics and changed abundance levels of arctic key-stone herbivores and the resultant trophic cascades likely to compromise main ecosystem functions and endemic arctic diversity, and (3) emergence of pest species outbreaks, zoonoses and invasive southern species and assessment of the consequent impacts. Third, the adopted food web approach of COAT should be sufficiently comprehensive to also accommodate early detection of unforeseen events (surprises) that follow the development of new climates and ecosystems. COAT has a special focus on targets that provide important provisioning and cultural ecosystem services locally (e.g. game), as well as supporting services (e.g. for the climate system) and iconic value (e.g. endemic arctic species) globally. Finally, by embracing the novel paradigm of adaptive monitoring, COAT meets the dual requirements of scientific robustness and societal relevance. Consequently, COAT includes routines for involving policy makers and managers in order to provide a scientifically robust basis for decision making and implementation of

actions, and to ensure their feedback into COAT. According to the adaptive protocol COAT will iteratively adjust prediction models and monitoring designs as new scientific knowledge and new research and monitoring technologies become available.

The present science plan provides a thorough review of the knowledge status of tundra food webs in context of present and future climate impacts. The review leads to the formulation of conceptual climate impact prediction models and identification of monitoring targets and state variables. These state variables include key components of the ecosystem (i.e. species and functional groups), the climate (variables quantifying the weather patterns and the cryosphere) and possible management actions (e.g. harvesting strategies). Following the identification of monitoring targets and state variables the plan outlines for each of the two focal ecosystems (Varanger peninsula and Svalbard) a hierarchically designed monitoring protocol that includes temporally frequent measurements (seasonal and annual) at relatively small spatial scales (i.e. landscape level) and more infrequent measurements (multi-annual intervals) at regional scales. The measurements are mostly field-based, but are designed to leave minimal environmental footprints. In addition, state-ofthe art remote sensing techniques will be applied, in particular, for measurements at the regional scale.

The amount of data generated by COAT will be substantial, which demands a stringent system for data assimilation, storage and access with a specifically dedicated data manager in charge. The COAT plan proposes solutions to the analytical challenges involved in translating heuristic conceptual climate impact path models into operational statistical models (e.g. dynamical structural equation models) based on the measurements of the state variables. Also in context of quantitative analyses and predictive modeling COAT will be adaptive in the sense that that the newest developments in the field of ecological statistics will be implemented. Moreover, COAT aims to be a contributor to this development. Finally, the COAT plan includes a structured scheme for involving stakeholders, policy makers and management authorities, as well as a protocol for monitoring changes in the public perception and use of ecosystem services and nature. This monitoring system of the socio-ecological system will partly be web-based and partly be based on observations and interviews. The society involvement will be aided by 1) the establishment of collaborative groups composed of major stakeholders and management authorities, 2) through workshops at regular intervals, 3) a dedicated school project (TUNDRA schoolnet) and 4) a specific set of outreach activities that aim at local, national and international audiences.

The COAT task force that has developed the present science plan consists of 23 scientists from four Fram Centre institutions and two external institutions. The task force encompasses a diverse and high level of competence on the subject matter, making it well qualified for running COAT. An explicit ambition of the Fram Centre is to promote Norway's position as an international leader in research and management of the arctic environment in the face of climate change. COAT will make a significant contribution to this goal by means of the implementation of this ambitious science plan. The scientific framework and protocols outlined in the plan will make COAT the most comprehensive and management relevant enterprise concerning arctic terrestrial ecosystem worldwide.

Key-words:

adaptive monitoring, adaptive management, Arctic greening, disrupted interaction cycles, circumpolar biodiversity monitoring (CBMP), ecosystem services, endemic biodiversity, forest-tundra transition, pest species outbreaks, plant-based food webs, long-term ecological research (LTER), marine subsidies, phenological mismatches, school project, socio-ecological systems (SES), stake-holder involvement, structural equation models (SEM), trophic cascades, zoonoses.

1. BACKGROUND AND RATIONALE

1.1. Arctic tundra ecosystem

1.1.1. Structure and function

The arctic tundra is the northernmost of earth's 10 terrestrial biomes. It is defined by a key climatic control on vegetation – the lower temperature limit for development of forest at 10-12°C mean for July (Jonasson et al. 2000). Consequently, the tundra biome forms a circumpolar zone with the southern boundary set by the extent of sub-arctic forest and the northern boundary by the margins of the arctic oceans (Figure 1.1.1). The southern boundary is not sharp however. It constitutes rather a gradual transition from continuous forest that becomes increasingly fragmented towards the north to be eventually entirely replaced by tree-less landscapes – i.e. tundra. The width of this forest-tundra transition

is geographically variable depending on topography, hydrology, herbivory and human exploitation in interaction with climate - i.e. temperature, wind and precipitation. The width of the circumpolar tundra zone is also highly variable, mainly depending on geographically variable forest-tundra transition and the position of the arctic coast line (Figure 1.1.1). At one extreme the tundra zone is only 10-40 km wide such as on the Varanger peninsula of northern Norway, where fringes of sub-arctic forests extends to 70°N. At the other extreme the tundra belt is close to 1000 km wide in Siberia and Canada. Considerable areas of tundra are found north of the continents on the high arctic islands, including Svalbard (Figure 1.1.1). Areas defined as arctic tundra amounts globally to 7 667 000 km²

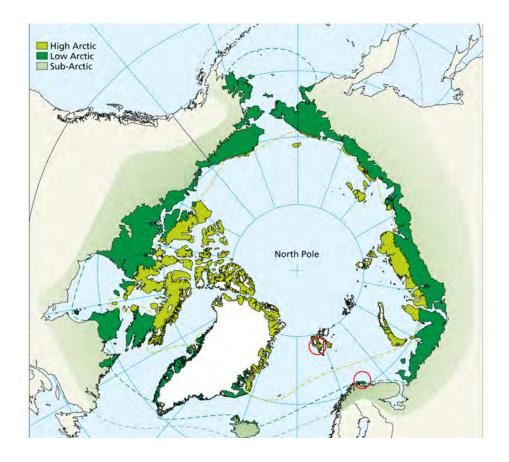


Figure 1.1.1. Circumpolar extents of low- and high-arctic tundra as well as a tentative demarcation of the sub-arctic region covered by boreal forests (ABA 2013). The two Norwegian COAT sites in focus of the present plan – Varanger peninsula in the low-arctic bordering sub-arctic forest and the Nordenskiöld Land and Brøgger peninsulas in the high-arctic Svalbard archipelago - are encircled in red.

(Bliss and Matveyeva 1992) which represents about 5% of the earth's land area.

Tundra plant communities may exist at mean July temperatures down to 1-2°C in the northernmost sites free of permanent surface ice. The annual mean temperatures for tundra ecosystems are in the range of -15°C to 1.5°C. Although permafrost is commonly associated with tundra, presence of permafrost is not a condition that defines the biome. Large areas with permafrost protrude deep into the boreal forest in continental areas of Siberia and North America while there are parts of coastal low-arctic tundra (i.e. areas north of the latitudinal tree-line) with no or only discontinuous permafrost (Callaghan et al. 2004a). The latitudinal temperature gradient across the arctic tundra zone is considerably steeper than equivalent gradients in southern biomes such as boreal and temperate forests (Callaghan et al. 2004b). Moreover, there are distinct longitudinal gradients determined by maritime influences (ACIA 2004).

The wide range of climatic and other environmental conditions within the tundra biome give rise to large spatial variation in structural characteristics of the ecosystems (Callaghan et al. 2004c, Ims and Ehrich 2013). In terms of vegetation structure the coarsest distinction is that between low- and higharctic tundra (Figure 1.1.1; cf. Bliss 1997). The Circumpolar Arctic Vegetation Map team (CAVM Team 2003) classifies tundra vegetation further in five bioclimatic subzones (A-E). The low-arctic tundra (subzones D-E) holds closed, often shrub-dominated vegetation that in the warmest and most productive southern parts (subzone E) has canopies of erect Salix and Alnus exceeding heights of 2 meters. The high arctic is characterized by low-statured and patchy vegetation that in the very north (subzone A) consists of mainly mosses and lichens and less than 5% of the ground covered by vegetation (Chernov and Matveyeva 1997). Creeping prostrate vascular plants enters subzones B and C to provide more vegetation cover. Within each bioclimatic subzone topography shapes a mosaic of plant communities and habitats at different spatial scales (Callaghan et al. 2004a, Callaghan et al. 2004c). Altitudinal (orographic) temperature gradients are important sources of this variation together with terrain shape affecting drainage (hydrology) and snow accumulation patterns. Ecosystem disturbances are characteristic of the arctic tundra and contribute to the structural diversity (Bliss 1997, Callaghan et al. 2004a). Major abiotic disturbances include freeze-thaw processes and erosion caused by wind, snow and flooding water, while herbivores,

either through natural periodic population outbreaks or anthropogenic induced overabundance, may regionally and/or temporally impose important disturbances shaping vegetation patterns.

The structure and composition of tundra vegetation and the forest-tundra transition have implications for crucial bio-physical functions in tundra ecosystems (Callaghan et al. 2004d). In particular, the vertical vegetation structure in terms of height of shrub canopies in tundra, and spatial extent of forest patches in the forest-tundra transition, affect a host of processes that determine internal ecosystem dynamics as well as ecosystemclimate system interactions, the latter mainly through heat and greenhouse gas exchange (Chapin et al. 2005, Sturm et al. 2005b, Sturm 2010). Also the composition of vegetation in terms of the presence and abundance of different functional types influences a host of below- and above-ground processes including greenhouse gas emission and nutrient cycling (Wookey et al. 2009).

Species richness in arctic tundra is generally low and decreases towards the north (Callaghan et al. 2004d, Ims and Ehrich 2013). Species with strongholds in sub-arctic forest systems contribute substantially to the species richness in the low-arctic, while species endemic to the Arctic become proportionally more important towards the north. There is also an increase in so-called superabundant species that may occupy a wide range of habitats towards the north (Chernov and Matveyeva 1997). These super-abundant species are key components of tundra food webs that relative to more southern ecosystems have a simple structure and usually no more than three trophic levels (Krebs et al. 2003, Ims and Fuglei 2005).

Tundra species have adapted substantial resilience to harsh climatic conditions with extreme seasonal and annual variation (Callaghan et al. 2004c, Callaghan et al. 2004e). Different strategies of coping with the severe environmental constraints in terms of physiological, morphological and life history adaptations may underlie a high diversity of functional species types (Wookey et al. 2009). The combination of low diversity of species and high diversity of functional types yields little functional redundancy in the sense that changes in the abundance of single species may cause major alterations of the functioning of the whole ecosystem (Post et al. 2009, Gilg et al. 2012). Since arctic species appear to have experienced only weak selection for traits that enhance success in interspecific interactions with competitors and natural enemies (Callaghan et al. 2004f), tundra ecosystems are predicted to have poor resistance and resilience to invasive species (Post et al. 2009).

Owing to low summer temperatures and short growing seasons, primary production is low in arctic tundra (Bliss 1997). However, decomposition rates of dead plant tissue are also low and tundra ecosystems typically accumulate organic materials in soils and peat. Thus, at least parts of the tundra biome functions as a sink for atmospheric carbon (Callaghan et al. 2004b). The low primary productivity imposes a (bottom-up) limitation of secondary and tertiary productivity (Oksanen et al. 1981). However, although there is ecological theory that predicts that terrestrial primary productivity may be too low to sustain a plant-based terrestrial food web in the northernmost parts of the tundra biome (Oksanen and Oksanen 2000), herbivores and predators appears to be omnipresent in the high arctic (Krebs et al. 2003).

A thorough understanding of the functioning of food webs has been highlighted as a key for predicting the response of tundra ecosystems to drivers of change (Post et al. 2009). To what extent

higher trophic levels exert top-down regulation of plant biomass is a matter of controversy in the literature (Oksanen and Oksanen 2000, Aunapuu et al. 2008, Oksanen et al. 2008, Gauthier et al. 2011). A source of this controversy is that the role of herbivores in tundra food webs varies geographically. For instance arctic breeding geese can in extreme cases cause massive destruction of wetland vegetation (Jano et al. 1998). Significant vegetation impacts of ungulates are in particular known from regions where reindeer have come under domestic control (Bråthen et al. 2007a, Forbes et al. 2009), while wild reindeer and caribou is thought to have relatively minor impacts (Jefferies et al. (1994), but see van der Wal (2006)). Small rodents (voles and lemmings) are with few exceptions key-stone herbivores in tundra ecosystems (Ims and Fuglei 2005). However, to what extent small rodents exert control on vegetation structure and growth differs geographically, apparently depending on amplitude (the magnitude of peak abundances) and species composition in their 3-5 year population cycles. Lemming plant consumption is very low relative to primary production in sites where this has been studied in



Figure 1.1.2. Lemmings have significant ecosystem impact in terms of grazing, digging and deposition of excreta. The photo shows a thick litter layer on snow in late June, composed of mainly clipped vegetation mixed with soils and lemming faecal pellets, resulting from intense activity of the Norwegian lemming during one peak density winter on Varanger peninsula. This litter, which some arctic indigenous people term "lemming hay" (Chernov and Matveyeva 1997), is often flushed by melt water in spring and may appear (as in the photo) on the top of remaining snow patches. Photo: Rolf A. Ims.

the Canadian high Arctic, where peak densities of lemmings normally do not exceed 10 individuals/ha (Gauthier et al. 2004, Legagneux et al. 2012b). On the other hand, the role of lemmings in shaping plant communities (Fig. 1.1.2) is considered to be substantial in tundra sites of Fennoscandia (Virtanen 2000), Alaska (Batzli et al. 1980) and Siberia (Chernov and Matveyeva 1997), where peaking lemming populations sometimes exceed 100 individuals/ha. The geographically variable amplitude of the lemming cycle, and consequently its role in determining trophic flows in tundra ecosystems is likely to be caused by a combination of local climate and the extent of top-down predator control (Ims et al. 2011).

1.1.2. Humans in tundra ecosystems and ecosystem services

Some of the functions of arctic tundra ecosystems described above are considered to play a significant role in regional and global climate systems – in particular those processes involving arctic vegetation that regulate exchange of heat and greenhouse gasses between the atmosphere and earth's surface (Chapin et al. 2005, Sturm 2010, Swann et al. 2010). Thus, tundra ecosystems provide important *regulating ecosystem services* far beyond the arctic regions (ACIA 2004).

Locally tundra ecosystems have provided people with harvestable terrestrial resources for subsistence (provisioning ecosystem services) for millennia. Already 12 000 years BP, human settlements were found along the coasts of northernmost Norway (Thommessen 1996). The impact of the long-term human exploitation on the tundra ecosystem is difficult to assess. One longterm anthropogenic influence that may have altered tundra ecosystems is human exploitation of large herbivores. While the extinction of the Pleistocene mega-herbivore fauna may have had an anthropogenic origin, causing an ecosystem state-shift from steppe to tundra (Zimov et al. 1995, Alroy 2001, Zimov 2005), more recent impacts are those connected to harvesting and domestication of caribou/reindeer (van der Wal 2006, Bråthen et al. 2007a, Ims et al. 2007b). However, whereas terrestrial ecosystems in large parts of the world are substantially shaped by humans, the arctic tundra is still relatively pristine across vast territories. Residents of the circumpolar arctic regions comprise many different groups of indigenous people. They often live in

small resource dependent communities and rely to various degrees on local ecosystem services to sustain their life (AHDR 2004, Aslaksen and Glomsrød 2009, Larsen et al. 2010). Semidomesticated reindeer herds, including the nutritious pastures they feed upon, provide services important for consumption and sharing in arctic communities, as well as for the cultural identity and quality of life (Kruse et al. 2009). Besides direct effects of climate on the abundance and productivity of such resources, climate change may also influence resource access by changing regulating services such as flood regulation by riparian vegetation, protection of the active soil layer against wind erosion, or water purification. Most arctic communities are also dependent on cash income and is as such influenced by indirect effects of climate change and market economy (Aslaksen and Glomsrød 2009). Increased access to the Arctic and the prospects of growth in mining activities and nature-based tourism could change human activities as well as the ecosystem services that are demanded by people. The arctic nature and species of the tundra carry values of importance to people of the arctic regions and beyond. Indeed, arctic species and landscapes have attained positions as icons for some of the earth's last large wildernesses with intact ecosystems and endemic biodiversity (ABA 2013). Partly also for this reason, arctic ecosystems can provide a particularly unambiguous and visible case for the impact of climate change in terms of loss of biodiversity and ecosystem services.

1.1.3. Climate change and projections

The Arctic, and the Norwegian Arctic is no exception, is a region with large climatic variability and observed historical changes (Overland et al. 1997, Miller et al. 2010). Temperature increases during the last decades have been largest on land in northernmost Canada and northern Siberia, with relatively smaller changes around south Greenland and northern Norway (Fig. 1.1.3). Precipitation changes are less consistent, and are strongly linked to decadal changes in teleconnection patterns (AO/NAO) as well as, more recently, changes in seasonal sea ice cover (Macdonald et al. 2005, Stroeve et al. 2011, Liu et al. 2012). In addition to these decadal changes, inter-annual variability is very large, particularly so in winter (Yoccoz and Ims 1999, Beaumont et al. 2011, Førland et al. 2011). The expected climate changes obtained from Global Circulation Models (GCM) are faster and larger for the Arc-

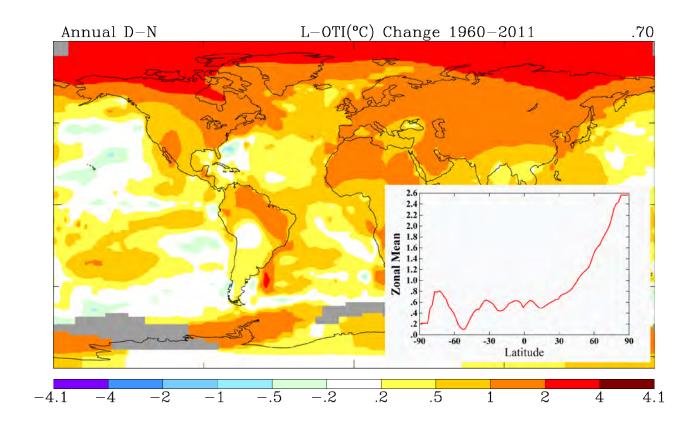


Figure 1.1.3. Trends in annual mean temperature for the period 1960–2011, based on the NASA GISS analysis (http:// data.giss.nasa.gov/gistemp). The inset shows linear trends over the 52-year analysis period averaged by latitude showing the warming amplification at polar latitudes.

tic than non-polar regions because of various feedbacks (e.g. loss of sea ice and changes in albedo) described in the concept of "Arctic amplification" (Fig. 1.1.3) (Serreze and Barry 2011). Average temperatures are expected to increase by up to 10 °C before the end of the century. Precipitation is also expected to increase. However, these projected climate changes show very large intermodel and regional variability, with a large difference in the models' predictions of recent patterns and trends (Overland et al. 2011a). This is in part due to varying ability to model seasonal sea ice, with the most recent GCM simulations from CMIP5 having smaller bias than the simulations from CMIP3 that have been used in regional climate projections so far. The large internal variability in climate model regional predictions (Deser et al. 2012) and the uncertainty associated to regional mechanisms such as aerosols, the Atlantic circulation and the connection between sea ice and weather patterns (Overland et al. 2011b, Stroeve et al. 2011, Booth et al. 2012, Liu et al. 2012), make the uncertainty associated with predicted patterns of regional climate change in the Arctic high, particularly so for the next decades.

1.1.4. Climate change impacts

The scientific focus on tundra ecosystems, their functioning and biodiversity, has increased tremendously along with the awareness that climate has already warmed in the Arctic and is likely to continue warming the Arctic at a high rate (§1.1.3). The Arctic Climate Impact Assessment (ACIA 2004) provided a comprehensive syntheses regarding arctic tundra ecosystems a decade ago as they then were observed, interpreted and projected. More recent studies, reviews and assessments (ABA 2013, IPCC 2007, Post et al. 2009, SWIPA 2011) have supported and reinforced, but also nuanced the conclusions from ACIA. Below we briefly summarize the main points, while detailed accounts of the status of knowledge and identification of knowledge gaps concerning climate impacts on tundra ecosystems is to be found in \$2 of this plan.

1.1.4.1. Vegetation and primary productivity

Changes in tundra vegetation consistent with the expectations under longer and generally warmer growing seasons have been recorded (§2.2 and

2.3). Vegetation seasonality in the arctic region has had a 4-6° latitudinal shift equator-ward during the last 30 years (Xu et al. 2013). Remote sensing studies show that plant biomass has been increasing ("Arctic greening") over the last decades. However, as yet these phenomena are spatially heterogeneous, with large areas still without changes detectable from space (Figure 1.1.4). Ground-based studies and high resolution aerial photos have demonstrated expansion of erect shrubs, which for this reason has been interpreted to be the main process underlying the greening of the tundra (§2.3). In contrast to the tundra, subarctic forests as far north as the forest-tundra ecotone have recently become browner in satellite images. Reduced vitality and even death of forests is predominantly resulting from droughts and insect pest outbreaks (§2.2). These impacts on large parts of sub-arctic forests, have largely come as a surprise, and alter the premises for the conventional projections of northern forest zone encroachment into tundra.

1.1.4.2. Herbivores and secondary productivity

The observed forest insect pest outbreaks are probably the only examples that abundances of high-latitude herbivores have increased as a result of a warmer arctic (§2.2). Cases of increased abundance of other herbivores are attributed to other causes. For instance, changed land use and management on their overwintering ground in the south is the main cause of increasing populations of the migratory arctic breeding geese (§2.7), while increasing herds of domestic reindeer is due to reduced harvesting (§2.5). Other arctic herbivore populations, such as wild ungulates (§2.5) and ptarmigans (§2.6), have shown decreasing trends and tundra rodents have got dampened or lost population cycles (§ 2.4). In the case of rodents, a compelling connection to climate has been made in terms of shorter and milder winters (§2.4).

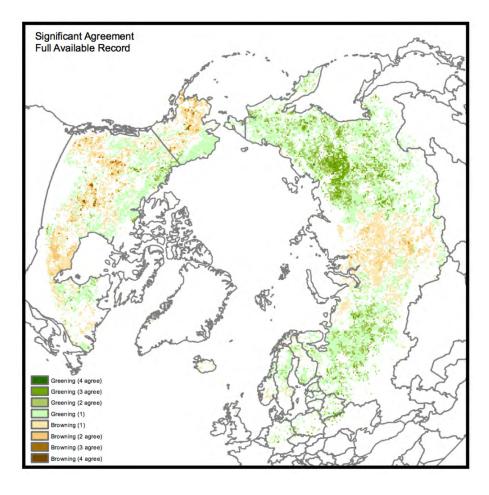


Figure 1.1.4. Recent temporal trends in growing season NDVI observed over high northern latitudes (> 50°N) by Earth-orbiting satellites dating back to 1982. Four different long-term satellite-derived NDVI products were analyzed for statistically significant trends using Mann-Kendal and Theil-Sen tests ($\alpha = 0.05$): GIMMS 3g (since 1982), SPOT VGT D10 (since 2002), MODIS (since 2002), and SeaWiFS (since 1998). Green colors represent trends of increasing NDVI, indicating increased gross vegetation productivity, and brown colors indicated declines, with colors becoming darker as more data sets indicate similar changes in vegetation productivity (updated from Beck & Goetz 2011).

1.1.4.3. Trophic interactions and cascading impacts

It is yet not known to what extent the decreased abundance of key-stone herbivores like lemmings and ungulates contributes to the expansion of shrubs in tundra (§2.3). There is, however, now evidence for that these herbivore groups may have the capacity to control abundances of shrubs (§2.4 and 2.5). Overabundant semi-domestic reindeer may even eliminate thicket forming shrubs in riparian habitats with significant cascading impact on game populations and general biodiversity (§2.5). Moreover, knock-on effects of population irruptions of arctic geese have been documented (§2.7). Different pathways for climate impacts from altered food web interactions are now beginning to be underpinned by empirical results. Examples are population declines of specialist predators on lemming and ptarmigan following collapsed or dampened populations cycles (§2.4, 2.6 and 2.8), emerging matches (§2.2) or mismatches (§2.6) between trophic interactants due to shifting phenologies, and enhanced resource subsidies to generalists predators due to increased or changed human land use in the Arctic (§2.5 and 2.8). Climate impacts mediated through trophic interaction in the food webs is typically difficult to predict because they often involve unknown nonlinear relations (e.g. thresholds).

1.1.4.4. Invasive species and increasing human activity

A rather safe prediction is that as the Arctic warms up new species from more southern ecosystems are likely to enter the tundra. As yet, however, there are still few documented cases, in particular to the extent that structure and the functioning of ecosystems have been affected (cf. §2.2 and 2.8). Incidences of species invasions with significant ecosystem impacts are, however, expected to take on momentum as a result of increased warming, especially in combination with increased human presence as a warmer Arctic will open for new settlements and industries. The effect of increased human activity is likely to cause more introductions of exotic species as well as new habitats and food resources for southern species that are facilitated by human presence (§2.6 and 2.8).

1.1.4.5. Uncertainties and knowledge gaps

Although the making of model-based projections has become an increasingly important enterprise

in context of climate impact on arctic ecosystems (e.g., Jensen et al. (2008)), there are some issues that severely limit their applicability. One issue is the extreme range of the projections from GCMs (§1.1.3) and how this should be accounted for when taking the next step to model how ecosystems are likely to respond. There are both technical and conceptual challenges involved. For the most extreme GCM projections, in terms of unprecedented rates of change and evolution of "novel climates" with no modern analogue (Williams et al. 2007), there will be little empirical basis for formulations of quantitative projection models. Furthermore, ecological projection models are often mechanistically naïve in the sense that they assume that trophic interactions will constrain the species niche in the future as it does today (Guisan and Thuiller 2005, van der Putten et al. 2010). It is increasingly recognized that new or strongly modified trophic interactions resulting from climate change may dominate the overall response of ecosystems (Post et al. 2009), sometimes in quite unexpected ways (Lindenmayer et al. 2010). Such insights typically come from welldesigned long-term empirical studies (Olofsson et al. 2011, Martin and Maron 2012). Thus there are good reasons for increasing the capacity for making precise and informed observations that embrace the many ways by which climate change impacts may be mediated and expressed in ecosystems (Dawson et al. 2011).

For arctic tundra - the terrestrial biome where climate is expected to change the most in absolute terms - it is hence paradoxical that the empirical basis for assessing climate impacts is the poorest due a scarcity of long-term empirical studies and monitoring. Considering the vastness of the circumpolar tundra and its large inherent spatial variability, the currently few tundra sites with long-term measurements of ecological variables provide an extremely poor geographic coverage. This implies an acute deficiency in our ability to detect and act upon climate change impact in the Arctic - a major concern that has been repeatedly pointed out in recent assessments such as the (ACIA 2004, MEA 2005, IPCC 2007, ABA 2013). Moreover, among on-going ecological monitoring activities in the Arctic there are only a handful that employ an ecosystem approach (§1.2). The aim of COAT is to substantially improve on this matter for the Norwegian sector of the arctic tundra biome.

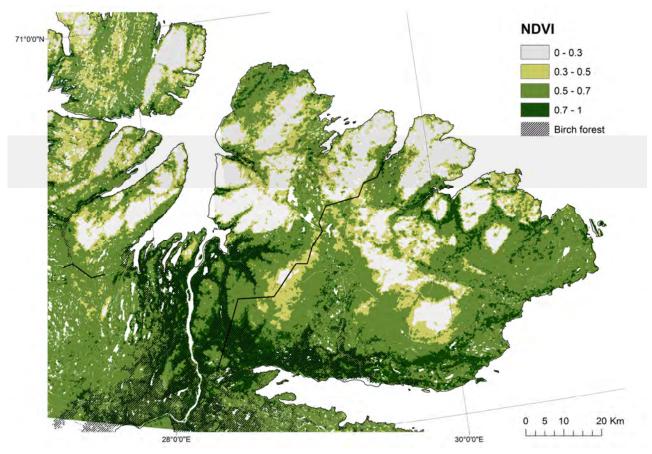


Figure 1.1.5.1. A map of vegetation productivity expressed as summer NDVI in low-arctic Varanger peninsula. NDVI values were derived from MODIS 16-d NDVI for 2011 starting day 225 (August 16th). Full black lines show the fenced border between the two reindeer herding districts on the peninsula.

1.1.5. Norwegian arctic tundra

The Norwegian sector of the Arctic belongs to sub -region 1 of the Arctic Climate Impact Assessment (ACIA 2004). Sub-region 1 corresponds to the proper arctic parts (i.e. tundra) of the Barents region including the north-eastern tip of Norway and north-western Russia. Climatically this arctic sub-region is characterized by oceanic climate with rather mild and variable winters. The weather pattern is particularly susceptible to variability and changes in the North Atlantic Oscillation determining the strength of the eastern airflow from the north Atlantic onto land. The Barents Region has condensed climatic gradients with shorter distances between boreal and tundra biomes than anywhere in the Arctic (Callaghan et al. 2004e). The Barents region with over 6 million people is the most densely populated area in the circumpolar Arctic with heavy industry and developed infrastructure at places. Fisheries, mining and oil and gas extraction are important to the economy of the region. Reindeer husbandry is practiced in most of the region, primarily important to the economy of local and indigenous peoples.

1.1.5.1. Low-arctic Varanger peninsula

Ecosystem characteristics: At 70-71°N, 30 °E the Varanger peninsula harbors the westernmost fringe of the vast continental Eurasian arctic tundra (Figure 1.1.1). Bordering the ice-free southern part of the Barents sea the outer low-lying coastal areas have annual average temperatures above zero (0-2°C), while the interior of the peninsula with highland rising to 600 m above sea level have below zero annual temperatures (-3 - 0°C) and wide-spread low-arctic permafrost (Farbrot et al. 2013, Isaksen et al. 2008). Annual precipitation is highest in the coastal areas facing the Barents Sea and in the central highlands. The northern and eastern coastal low-lands as well as the interior highlands have mean July temperatures ≤ 10 °C and belong to the CAVM bioclimatic tundra zone E (low-shrub tundra). The south-western low lands with higher July temperatures (11-13°C) are mostly forested by birch Betula pubescens (Figure 1.1.5.1). Thus there is an extensive forest-tundra transition zone that cuts through the peninsula mainly in the west-east direction. However, topographic variation creates climatically benign conditions allowing for isolated patches of forest in some of the north-eastern valleys (Karlsen et al. 2005).

Within the area classified as tundra, the most extensive vegetation is dwarf-shrub heaths (Killengreen et al. 2007, Ravolainen et al. 2010). However, local variation in bedrock and topography creates considerable gradients and spatial contrasts in local climate, nutrient levels, moisture run-off and snow deposition over short distances that causes a spatial mosaic of vegetation types in terms of structural complexity and primary productivity. Structurally complex and highly productive vegetation types are in particular found in the bottom of the main riparian valleys with thickets of tall shrubs and lush meadow vegetation. Productive habitats are also found in some lee-sides and moderate snow beds. On the other hand, large areas in the inland highlands (more than 350-450 m above sea level) consist of low productive barrens (Figure 1.1.5.1) with sparse cover of prostrate vascular plants and cryptogams that can be considered to be low-arctic orographic equivalents to high-arctic polar deserts.

Steep climatic gradients, the high diversity of vegetation types/habitats within the tundra and the close neighborhood of forested ecosystems give rise to a rather complex tundra food web that is composed by a mixture of boreal and truly arctic species (Figure 1.1.5.2). Key-stone herbivore species, linking the main plant functional groups and the species rich assemblage of predators at the top of the food web, are two ungulates (semi-domestic reindeer and moose), a guild of small rodents (two species of voles and the Norwegian lemming) and two species of ptarmigan (rock and willow ptarmigan). Beside the inevitable effects of climatic seasonality, food web dynamics is driven by seasonal migrations of in particular reindeer (for which the Varanger peninsula constitute pastures during the snow-free seasons) and a guildlevel multi-annual abundance cycle of rodents. Detailed accounts of the structure and functions of the food web and relation to climate and climate change are given in §2.

Human presence, land and resource use: The coasts of Varanger peninsula were among the first areas in Fennoscandia to be colonized by humans after the last ice age (Hirsti 1979). Thus natural resources have been exploited in this region for millennia. Although marine resources always have provided the bulk of the subsistence, also terrestrial resources were important (Hirsti 1979). Presently, marine fisheries constitute the main industry for several smaller cities and villages along the coast, and the total human population is at present 15 148 people. The largest city Vadsø hosts the administrative center of Finnmark County. There is well developed infrastructure with roads along the southern and eastern coast, as well a road that crosses the interior western tundra plateau connecting the two communities at northwestern coastal section of the peninsula. Four of the cities have small airports.

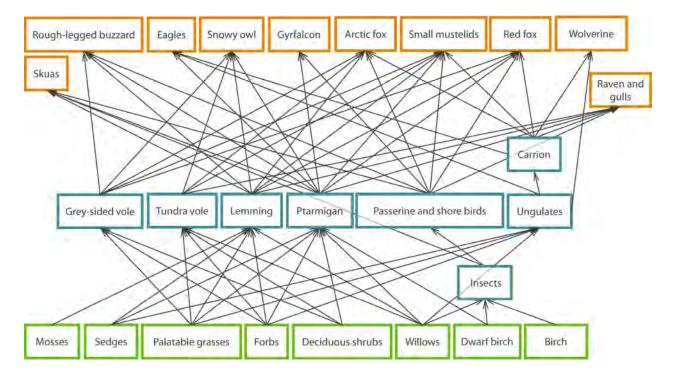


Figure 1.1.5.2. The plant based food web for low-arctic tundra including the tundra-forest ecotone on Varanger peninsula.

Reindeer herding is presently the most important human land use across the tundra and foresttundra ecotone to which the indigenous Sámi people have exclusive rights. The peninsula holds two spatially separated reindeer herding districts (a western and an eastern; Figure 1.1.5.1) that use the peninsula as summer and spring/autumn grazing pastures for an average of 14 000 animals (Anonymous 2011). The eastern district holds double the density of that in the western district, creating a contrast of reindeer grazing impacts that has persisted for several decades (Ravolainen et al. 2010). Among wild game open to be harvested by all citizens of the region, moose and ptarmigan are the most important in terms of the number of people participating (350 moose and 650 ptarmigan hunters in 2010-2011 season) and the amounts harvested (300 moose and approximately 3050 ptarmigan, www.ssb.no). Also recreational fishing of anadromic salmonoids in the larger rivers attracts people to the interior parts the peninsula from which these rivers originate.

In 2006 Varanger Peninsula National Park was established. With an area of 1806 km² the national park covers most of the interior of the peninsula as well as coastal tundra, especially in the eastern and northern parts. A key motive for the establishment of the park was to protect the only large area with terrestrial arctic biota and landscape features in mainland Fennoscandia. The fact that the Varanger peninsula hosts the most diverse set of arctic species for any accessible locality in Europe makes the region and its natural park attractive for many naturalists. Based on this there has recently been initiated several local enterprises aiming to making a living out of "nature based tourism".

Climate change and impacts: During the last three decades mean annual temperature and precipitation patterns have shown significant deviations from 1961-1990 standard normal values (Benestad et al. 2009). On the Varanger peninsula, only a single year since 1989 has been colder than the 1961-1990 normal (Fig. 1.1.5.3 left). Also, mean monthly precipitation show positive deviations from normal in the majority of years since 1990 (Fig. 1.1.5.3 right). The clearest and most extensive ecological effect of climate warming so far in the Varanger region is the eastward spread of the outbreak range of the winter moth Operopthera brumata. This insect pest species has contributed to defoliation and death of large tracts of the birch forest and a comprehensive vegetation state shift throughout the forest-tundra ecotone (§2.2). Moreover, climate warming appears to have reduced the outbreak amplitude of the Norwegian lemming Lemmus lemmus, which have contributed to dampening of the guild level rodent dynamics, which nevertheless is still cyclic (§2.4). Cascading impacts of dampened small rodent cycles may have contributed to severe popu-

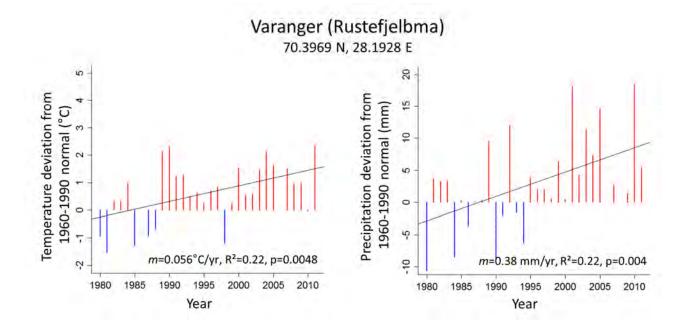


Figure 1.1.5.3. Observed trends in mean annual temperature (left) and mean monthly precipitation (right) expressed as deviations from 1961-1990 standard normal values for the climate station Rustefjelbma in low-arctic Varanger.

lation declines of lemming-dependent predators of which some now are red listed (§2.4 and 2.8).

Key site-specific assets for COAT: The positioning of the Varanger peninsula at the southern edge of the low arctic tundra provides excellent opportunities for monitoring the changes across and close to the transition zone between sub-arctic forest and arctic tundra which is expected to represent a hot spot for climate change impacts in particular in terms of species range changes and structural aspects of vegetation with feed-backs to the climate system. The Varanger peninsula also harbors other highly climate sensitive vegetation strata within the tundra zone and 'warm' low-arctic permafrost in its highlands with low resilience to increasing temperatures (Farbrot et al. 2013). In particular, the peninsula provides excellent opportunities for investigating the dynamics of tall shrub habitats as influenced by the opposing effects of changed levels of herbivory and climate warming and how management can influence the dynamics. The peninsula provides also a test bed for trials of actions aimed at conserving vulnerable fringe populations of arctic endemics and one project of this kind is already running (§2.8). With its ice-free coast relatively densely populated by human settlements the Varanger peninsula provides a case for how the arctic ecosystems can be managed rationally *under increased stress from anthropogenic impacts* as large tracts of the Arctic opens up to human settlements and industries in a warmer climate.

1.1.5.2. High-arctic Svalbard

Ecosystem characteristics: At 74-81°N, 15-30 °E the archipelago of Svalbard harbors one of the northernmost terrestrial ecosystems of the world. The archipelago consist of numerous islands, whereof the largest is Spitsbergen (37 700 km²). The North Atlantic Current has a strong effect on Svalbard's climate. While the sea north and east of Svalbard in general is ice covered for at least 8 months of the year, the warm North Atlantic Current keep the west coast of Svalbard ice free for most of the winter. This warm sea water results in up to 20 °C higher average winter temperatures than what is found at similar northern latitudes elsewhere. Still permafrost is found in all nonglaciated areas. Long term meteorological records are mainly available from the west coast of Spitsbergen where the annual average temperature was -6.7 °C for the period 1961-1990 (Longyearbyen Airport). Precipitation is low (on average 190-525 mm annually), and tends to decrease from the outer parts of the fjords on the west coast (~500 mm annually) to the inner eastern parts of these

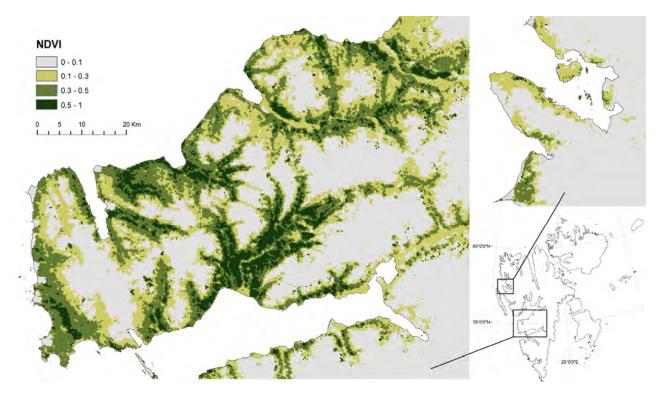


Figure 1.1.5.4. A map of vegetation productivity expressed as summer NDVI on Nordenskiöld Land (left) and Brøggerhalvøya (top right) in high-arctic Svalbard. NDVI values were derived from MODIS 16-d NDVI for 2011 starting August 16th. Relatively high primary productivity is found in coastal near areas and at the bottom of the main valleys, while elevated areas have sparse vegetation and low primary productivity. The position of the two areas is indicated by rectangles on the inset map of Svalbard (bottom right).

fjords (~200 mm annually). The vegetation on Spitsbergen covers bioclimatic tundra zone A (Arctic polar desert), B (Northern arctic tundra) and C (Middle arctic tundra) (CAVM Team 2003). In the most productive parts of Spitsbergen a topography dominated by alpine mountains separated by deep broad valleys generates steep altitudinal gradients, and associated steep gradients in vegetation structure. Large areas with relatively high primary production are found in the bottom of the valleys, while sparse vegetation covers of arctic polar desert type, are commonly found at altitudes above 200 m (Fig. 1.1.5.4). At an average July temperature of 6 °C, the vegetation in the most productive valleys is dominated by prostate dwarf shrubs (Salix polaris and Dryas octopetala), grasses and sedges, forbs and mosses.

As on the Varanger peninsula, local variation in bedrock and topography creates considerable gradients and spatial contrasts in local climate, nutrient levels, moisture and snow depositions that cause a small scale spatial mosaic of vegetation types in terms of structural complexity and primary productivity. In addition, extensive permafrost and freeze – thaw processes in the active soil layer cause unstable soils in many areas. Productive wet marsh vegetation is often present in wet areas in the bottom of the valleys, while heath vegetation, dominated by *Luzula sp.*, covers a large part of the drier areas. In addition, productive patches dominated by graminoids (e.g. *Poa sp.*) are found in moderate snow beds, and may appear up the sides of the valleys until arctic polar desert vegetation takes over at higher altitudes (Elvebakk 1997, van der Wal et al. 2000a).

The relatively low overall productivity of the higharctic tundra and the isolated geographical position of the archipelago are probably the main reason for the relatively low complexity of the tundra food web on Svalbard (Figure 1.1.5.5). The keystone herbivore species are one ungulate (the endemic Svalbard reindeer), one species of ptarmigan (the endemic Svalbard rock ptarmigan) and two species of migrating geese (the pink-footed and the barnacle goose). The predator/scavenger guild is also depauperate with the main species being the arctic fox and the glaucous gull, species that also make extensive use of marine food sources (Figure 1.1.5.5). Migrating passerines (e.g. snow bunting) and shore birds (e.g. purple sandpipers) add to the species diversity and abundance of prey in the summer season. Contrary to what is found in most tundra food webs, small rodents

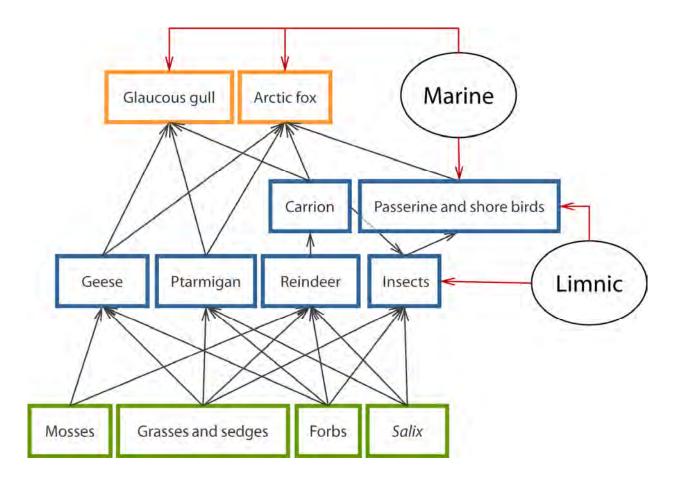


Figure 1.1.5.5. The plant based food web for high-arctic tundra on Svalbard.

are functionally absent on Svalbard. The only population that exist on the archipelago is spatially restricted to the area around a sea bird colony on Nordenskiöld Land peninsula (Henttonen et al. 2001). Detailed accounts of the structure and functions of the food web and its relation to climate and climate change are given in §2.5-2.8. The whole terrestrial food-web and all main vegetation types are present at Nordenskiöld Land peninsula on Spitsbergen (Fig. 1.1.5.5). Nordenskiöld Land was therefore chosen as the intensive (cf. §2.9.1) COAT study area on Svalbard, whereas some state variables also will be targeted according to a more extensive protocol at Brøgger peninsula.

Human presence, land and resource use: After the discovery of Svalbard at the end of the 16'th century, whaling, sealing and trapping were the main activities on Svalbard for three centuries (Arlov 1996). Thus, the terrestrial ecosystem on Svalbard has been exploited by humans for the last four centuries. Today, the economy on the archipelago is based on mining, tourism and research. There are only two towns on the archipelago, both located on the Nordenskiöld Land peninsula on Spitsbergen. The main town Longyearbyen is the administrative center and hosts about 2000 people out of the total population of 2400 people on Svalbard (SSB 2012a). There is very little infrastructure outside the main towns, where transport therefore is predominantly by boat, helicopter or snowmobiles. The main airport is in Longyearbyen making this town the main point of entry and departure from the archipelago.

Well into the 20th century, trappers were main exploiters of the terrestrial ecosystem, as well as marine species, on Svalbard. The trappers harvested polar bears and arctic foxes for their fur, collected eider down, and harvested seals, reindeer, geese and ptarmigans for their meat. However, it was probably the increase in mining in the late 19th and early 20th century that led to overharvesting of the reindeer population for food. The Svalbard reindeer became protected in 1925, but in 1983 a regulated reindeer hunt was reopened. Polar bears became protected from hunting in 1973. Today, only 2-5 trapping stations are in use, and the hunting of reindeer, geese and ptarmigans, and trapping of arctic foxes, is increasingly becoming a recreational activity of the local community. Only the pink-footed goose and ptarmigan hunt is open for people living outside the archipelago. Today nature-based tourism is the main economic exploitation of the terrestrial ecosystem on Svalbard. In addition, Svalbard has become an important arena for arctic environmental research.

In 2002 the Svalbard environmental protection act came into effect. The purpose of the protection act is to minimize the human footprint on the marine and terrestrial ecosystems on and around Svalbard, while allowing for environmentally sound settlement, research and commercial activities. At present 65 % of the archipelago is protected as national parks or nature reserves.

Climate change, projections and impacts: During the last three decades the mean annual tempera-

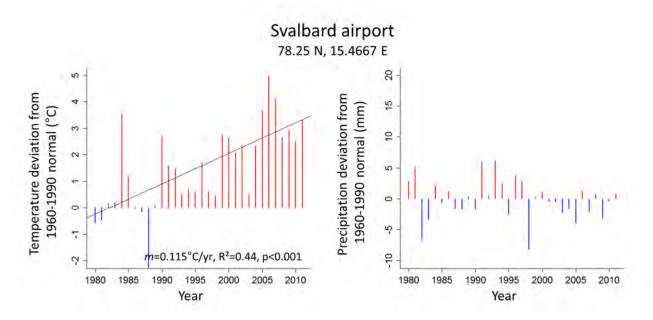


Figure 1.1.5.6. Observed trends in mean annual temperature (left) and mean monthly precipitation (right) expressed as deviations from 1961-1990 standard normal values for the climate station at Svalbard airport.

ture on Svalbard has shown a significant increase (Fig. 1.1.5.6 left). In the period 1981-2010 the annual temperature was, depending on the location of the weather station, on average 1-2 °C higher than the 1961-1990 standard normal values (Førland et al. 2011). Since 1989, no year has been colder than the 1961-1990 normal (Fig. 1.1.5.6 left). The increase in temperature has been particularly prominent in the autumn and winter temperatures (Førland et al. 2011). Annual mean monthly precipitation has not shown a similar strong increasing trend over the last three decades (Fig. 1.1.5.6 right). However, the seasonal pattern of precipitation seems to have changed with less precipitation in the spring and summer, and more precipitation in the autumn and winter when compared with the 1961-1990 normal (Førland et al. 2011). The combination of milder winters and more precipitation in the winter has also resulted in an increasing amount of precipitation falling as rain in the winter period the last three decades (Hansen et al. 2011).

The clearest ecological effect of climate warming so far on Svalbard is due to the increase in the frequency of rain-on-snow in the winter. Rain-on -snow cause ground ice, which has significant negative effects on the population growth of Svalbard reindeer (§2.5), and may become a threat to the viability of Svalbard reindeer populations. Ground ice cause elevated reindeer mortality and the carcasses improve food availability for arctic foxes in the winter with subsequent positive effects on arctic fox reproductive rates (§2.8). In addition, climate warming has led to an increase in plant primary productivity (van der Wal and Hessen 2009), that is likely to benefit herbivore species (§2.5).

Key site-specific assets for COAT: The position of Svalbard provides excellent opportunities for monitoring climate change effects in a high arctic ecosystem. The close proximity between vegetation communities ranging from the middle arctic type to arctic desert type will allow vegetation transitions to be monitored at local to regional spatial scales, and imply that transitions between these vegetation communities may respond quickly without a need for stochastic immigration events. Furthermore, the simple food-web provides excellent opportunities for disentangling the direct and indirect effects of climate change on high-arctic ecosystems. Finally, monitoring efforts and a better understanding of high-arctic trophic interactions will lead to a better foundation for the management of high-arctic terrestrial ecosystem in general, and more specifically the terrestrial ecosystem on Svalbard with two vertebrate endemics of special conservation concern, the Svalbard reindeer and Svalbard rock ptarmigan. As the most accessible site in the high-arctic there are decades of research and monitoring on key components of the terrestrial ecosystem that COAT Svalbard can utilize and expand on.

1.2. Long-term research and

monitoring

1.2.1. Origins and directions

The importance of long-term ecological research (LTER) and monitoring is now recognized by scientists, decision-makers and the public. This recognition has developed from an: i) acknowledgement of long-term studies at levels from individuals to ecosystems as a main approach to understand patterns and processes in ecological science (Peters 2010), and ii) acknowledgement of a need for data repositories that secure long-term data and make them available to a broad audience, including environmental managers and the general public, as well as scientists. It is of course with accumulation of data that the value of longterm research has become substantial (Clutton-Brock and Sheldon 2010). The Park Grass Experiment at Rothamsted (Silvertown et al. 2006) was started in 1856 and is the oldest ongoing ecological experiment in the world. Some of the LTER sites in the US have now been running for more than 50 years, with major results obtained under way (e.g. the short-term and long-term ecosystem consequences of acid rain; Likens (2004)).

Formal organizational structures implemented to improve integration and synergistic effects from multiple long-term research and monitoring sites are of more recent origin. The US Long Term Ecological Research Program was established in 1980 (Gosz et al. 2010, Hobbie et al. 2003), while the European Long-Term Ecosystem Research (http://www.lter-europe.net/) network was launched in 2007. As a network of networks the International Long-Term Ecological Research Network (ILTER; http://ilternet.edu/), was founded in 1993 and had its strategic plan written in 2006. Norway is not yet a member of either network, but has been active through the alter-net network (Europe's biodiversity research network; van Dijk et al. (2011)) and TOV (Terrestrial Nature Monitoring Program; Framstad 2011, Ims et al. 2010), and is currently actively involved in the planning of SIOS - a new infrastructure facility for earth system monitoring at Svalbard (www.sios-svalbard.org). There exist other networks of long-term research focusing on more specific topics (e.g. vegetation changes on mountain summits - GLORIA; Pauli et al. (2012)), but as these networks do not have strong ecosystem components we do not discuss them further. The LTER networks have different requirements. The US LTER is more integrated and has a strong focus on questions, whereas other networks often are less question-focused, often have requirements restricted to data availability and may focus on some form of measurement standardizations. The US LTER network is reviewed by the National Science Foundation (NSF) every 10 years, whereas each LTER site has to apply to NSF every 6 years. The last review of the network has just been published (Michaels and Power 2011). It was considered as "one of the jewels in the NSF crown" (p. 5).

The approach of COAT (§1.2.5) is close to the US LTER in the sense that it focuses strongly on questions and predictions based on conceptual models of how the system works. In addition, COAT embraces the new paradigm of adaptive monitoring (see §1.2.2). COAT differs from US LTER as it does not include all the core areas of US LTER primary production, trophic structures, organic matter accumulation and decomposition, inorganic inputs and movements of nutrients, and disturbances (Hobbie et al. 2003) - but is restricted to a trophic (food web) framework for understanding and managing ecosystem structure, function and services and with an emphasis on the impact of one major driver of change - i.e. climate change (see §1.2.5 for a justification of the trophic framework). The scientific scope of different programs has also implications on the degree of footprints on the environment (Box 1.2.1).

The LTER program, as well as related global change research aiming at projecting future state of ecosystems at 10 to 100 year time scales (Luo et al. 2011), has naturally a strong focus on longterm, slow processes, and how these processes interact with short-term, fast processes. Typically one can think of vegetation changes as a slow process, whereas population abundance of single species may be characterized by fast short-term fluctuations or sudden irruptions. The importance of considering interactions between fast and (presumed) slow ecosystem processes will be exemplified by the forest-tundra ecotone dynamics subjected to scrutiny in \$2.2 of the present plan. The focus on question-based research and interaction between long-term and short-term changes can arguably be seen as the reason why many of the major surprises of ecological research has been obtained through such long-term studies (Doak et al. 2008, Lindenmayer et al. 2010), since a surprise (i.e. something unexpected) is defined with regards to an expectation (i.e. question/ model).

1.2.2. Adaptive monitoring

Expanding on earlier calls for making ecological monitoring programs question/hypothesis/model -driven so as to become more powerful tools for scientific inferences and management decisions (Legg and Nagy 2006, Nichols and Williams 2006, Yoccoz et al. 2001b). Lindenmayer and Likens (Lindenmayer and Likens 2009, 2010, Lindenmayer et al. 2011) have been advocating for their paradigm of *adaptive monitoring*. The term *adaptive* have several connotations in this context.

One relates closely to the concept adaptive management (Walters 1986) in the sense that management actions can enter the design of the monitoring program in an experimental fashion so as provide strong inferences about how management strategies could be adapted to become maximally rational/effective. Other kinds of experimental treatments than those relevant in a management setting could potentially also be invoked to allow for causal inferences about what are the drivers of change of the focal system. For instance, ecologi-

Box 1.2.1. COAT: Minimizing the footprint on the environment

The extent of infrastructure developments associated with long-term research and monitoring programs differs widely depending on the remoteness of the region, the scientific focus of the program and, not the least, the extent to which priority is given to minimizing the added impact to the environment in the initial design and planning of the monitoring program. While ecological monitoring programs tend to have low demands for heavy instrumentation compared for instance to geo-chemical and atmospheric monitoring, there are still striking contrasts between the added impact to the environment between sites (Figure B.1.2.1 for an example).

COAT will operate according to *a minimizing footprint principle*. The two geographical regions targeted in COAT (low-arctic Varanger and high-arctic Svalbard) share a great advantage, in that they are inhabited regions with a reasonably well-developed infrastructure, leaving little need for additional developments. The approach taken in COAT (adaptive monitoring of food web components, § 1.2.5) rely for the most parts on non- or little invasive sampling techniques and we will, according the adaptive protocol, prioritize to develop new techniques that minimize the impacts of sampling. The minimizing footprint principle will also be an integral part in the design and planning of individual COAT activities both with respect to field instrumentation, activities in sensitive areas/seasons (for instance reindeer calving periods) and transportation of personnel.



Figure. B.1.2.1. A contrast in infrastructural development associated with two long-term ecological monitoring sites, Toolik lake LTER and Bylot Island field station (see § 1.2.6). COAT will operate according to a minimizing footprint principle comparable to Bylot Island. Image sources: http://toolik.alaska.edu/gis/maps/index.php and http://www.cen.ulaval.ca/bylot/intro.htm.

cal climate effect research can involve experimental manipulation of climatic variables - at least at small spatial scales (cf. ITEX, see §1.2.5). However, adaptive monitoring programs need to be adaptive not only with respect to "learning by doing" through management interventions or other experimental manipulations, but also through the insight that can be gained by analysis of the effects of non-manipulated drivers. Most notably, climate change will be a driver that cannot be subject to manipulations in most climate effect monitoring programs, yet climate variables will naturally be key predictors. Climate effect monitoring programs can be adaptive in terms of optimizing their design with respect to which climate predictors and ecological responses that are in focus and how they are measured in time and space. For instance, invoking geographical climatic gradients in the design can provide a spatial dimension in the analysis of temporal change that can significantly strengthen inferences (Ims et al. 2011, Johnson et al. 2010). Finally, with respect to how measurements should to be done, monitoring programs ought to adapt to and use new technologies and methods as they are developed. The main aspects of the adaptive protocol as applied to monitoring of climate change impacts on ecological systems are summarized in Figure 1.2.2. In effect the protocol of adaptive monitoring is congruent with the general protocol of hypotheticodeductive long-term science.

1.2.3. Ecosystem-based monitoring and food webs

As briefly reviewed in \$1.1.4, some of the strongest climate change impacts on tundra ecosystems are expected, and also increasingly observed, to be mediated by trophic cascades in the food web. This fact motivates ecosystem-based monitoring based on a food web approach. There are two further arguments for the usefulness of the food webs as a focal target for adaptive monitoring of climate change impacts on tundra ecosystems. First, a conceptual model of the functioning of the monitoring target constitutes the baseline for adaptive monitoring (Figure 1.2.2). Within the field of ecology the functioning of food webs has been conceptualized in terms of models all the way back to Charles Elton's pioneering work on Svalbard (Pimm 1982 for a review). Thus there is generally an appropriate theoretical underpinning for developing conceptual food web models and especially in plant-based tundra food webs (Aunapuu et al. 2008). Second, humans often affect ecosystems by their involvement in food webs (Strong and Frank 2010). Thus the essential role of management interventions in the framework of adaptive monitoring also makes the food web an appropriate target in this context.

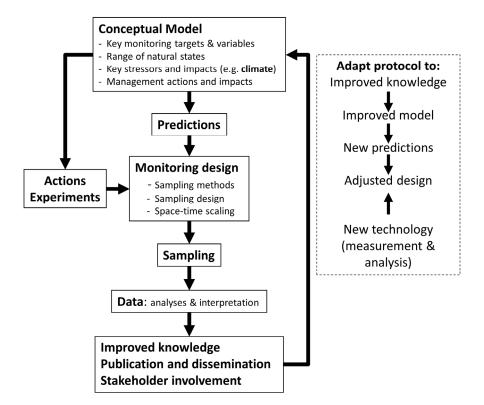


Figure 1.2.2. The protocol for adaptive monitoring of Lindenmayer and Likens (2010), here modified to be tailored to climate change impact monitoring.

1.2.4. The COAT approach

As argued above COAT will be developed according to the principles of adaptive monitoring (§1.2.2) and a food web approach (§1.2.3). Thus it follows that a central task of the present plan is to develop conceptual models that specify climate and management relevant targets in the plantbased tundra food web (see §2). In general, relevant management targets are either key species in the food web that are subjected to harvesting, or species that can be (or should be) controlled to preserve arctic endemic diversity (e.g. invasive/ expansive species). The management actions, when possible, are typically attempting to mitigate or build up ecosystem resilience against "undesired" climate impacts, where the decision of what is "undesired" is defined by collaborative groups composed of management authorities and other stakeholders (§2.9.4 and §5.1).

Hypothesis/model driven monitoring programs are sometimes criticized for being narrow minded in the sense that they invoke relatively few targets and variables so that unforeseen changes (surprises) are missed (as opposed to the "laundry list approach" criticized by Lindenmayer and Likens (2009)). However, by spanning most key components of the plant-based food web and the involvement of a team of researchers with a broad competence we find it unlikely that major ecological surprises will escape the attention of COAT (Lindenmayer et al. 2010).

In context of climate warming much current interest within tundra ecosystem research is devoted to elucidating biophysical processes that induce positive feed-backs on the climate system (Chapin et al. 2005, Wookey et al. 2009, Swann et al. 2010). Some of these processes are strongly influenced by components of the plant-based food web; i.e. albedo, snow accumulation and soil temperature/ permafrost that are affected directly by vegetation structure and indirectly by manageable herbivore populations. According to its aim of being immediately management relevant, COAT will emphasize research related to such biophysical processes that potentially are within the realm of ecosystemlevel management actions. Thus COAT can provide input to larger "Earth Science Perspectives" on these premises, but will generally not emphasize fundamental research and monitoring on biogeochemistry and ecohydrology (Schimel et al. 2011). COAT will however, encourage and collaborate with whatever external research and monitoring that can be connected to its core program. This regards also experimental research projects with more short-term perspectives and funding.

1.2.5. Current long-term research and monitoring in arctic tundra ecosystems

The Terrestrial Expert Monitoring Group of the Circumpolar Biodiversity Monitoring Program (CBMP-TEMG) has just compiled and reviewed the existing monitoring activities within the circumpolar tundra region (Christensen et al. 2011) and a final plan for the CBMP-Terrestrial is due to be published in 2013. Although there are many monitoring activities that are listed by the Arctic Council Nations most of them appear to fall into the categories criticized by Lindenmayer and Likens (2009, 2010) for being passive, mandatory and/or haphazard in motivation and design (see also Nichols and Williams 2006, Yoccoz et al. 2001b, Yoccoz 2012). Moreover, there is a scarcity of truly ecosystem-based programs for monitoring or long-term research with the following notable exceptions.

Toolik Lake LTER has been under review by the NSF in 2010, and while it continues to have as overarching goal to develop a predictive understanding of the North Alaska landscape, it will have a special focus for the period 2010-16 on the interactions between climate warming and changes in disturbance regimes, which for Toolik lake are thawing of permafrost, increased frequency of wildfires, and changes in the seasonality and synchrony of ecosystem processes (Shaver 2010). The Toolik lake LTER site is seen as an "excellent model system" to address theoretical and empirical questions related to the role of disturbance, and furthermore how responses of tundra ecosystems to environmental change can feed back on the factors driving the change. Research addresses societal issues by analyzing climate change impacts on the delivery of key ecosystem services to local communities. Research at Toolik Lake started in 1975, and the site became a member of the LTER network in 1987. The core, long-term activities at Toolik Lake are supported by NSF (with a budget for the 6 year period 2010-16 of 5.6 M \$). An additional 30+ projects are currently running at Toolik Lake, with diverse funding sources. This represents up to 100 scientists working at a given time on the site, and 6000 user days/year.

A new large initiative, the National Ecological Observatory Network (NEON) has just been launched in the USA, with some financial hurdles still remaining. This network has a strong site overlap with the LTER network: for example, the two tundra sites, in the Arctic and the Rocky Mountains, are also LTER sites (Toolik Lake and Niwot Ridge, respectively). While NEON mentions long-term research in its strategic plan, it is strongly focused on large, continental scale ecology. The main goal is to "Enable understanding and forecasting of the impacts of climate change, land use change, and invasive species on aspects of *continental-scale ecology* such as biodiversity, biogeochemistry, infectious diseases, and ecohydrology" (Schimel et al. 2011; our italics). NEON is very focused on setting up a very large number of sensors (>15,000 over ca 20 sites), complemented by aerial and satellite surveys. The overall cost is planned to be 434 M \$ over the next decade (Tollefson 2011), i.e. ca 2 M \$ per site per year.

The International Tundra Experiment (ITEX: http://www.geog.ubc.ca/itex; (Henry and Molau 1997)) was launched in 1990. ITEX has a strong vegetation focus, relying on small scale temperature manipulation through the use of ~ 1 m² open -top chambers (OTC). Not all of the ~50 sites are in the Arctic, with Norwegian sites being located at Dovre, Finse (both are alpine) and Longyearbyen and Ny Ålesund (Svalbard). There are also sites at Kilpisjärvi and Abisko in Finland and subarctic Sweden. The long-term results have just been published (Elmendorf et al. 2012), showing large between-sites heterogeneity: shrubs have increased at sites with high ambient temperature, whereas graminoids have increased at cold sites. Because of the small scale of temperature manipulations, ITEX does not involve an ecosystem perspective besides soil responses (Lamb et al. 2011).

Greenland has two "Ecological Research Operations", one at Zackenberg in the high Arctic (ZERO, started in 1995), and one at Nuuk in the low Arctic (NERO, started in 2007). Both are organized around 4 "basis" monitoring programs on climate, snow-ice-glaciers, terrestrial and marine ecosystems - to which additional research projects make short-term contributions (Jensen and Rasch 2011b, 2011a, Meltofte et al. 2008). The terrestrial ecosystem component of ZERO covers the different trophic levels, with a strong focus on vegetation dynamics, mammalian herbivores, carnivores, and birds. NERO is focusing on vegetation, arthropods and birds (mammalian herbivores are absent from Nuuk), with an emphasis on phenology. ZERO has a rather large research station, with 73 scientists visiting the site in 2010 and 1869 bed nights. NERO had 36 scientists visiting the site with 360 man days. Turnover for ZERO and NERO in 2010 were 9.0 and 5.5 million DKK respectively.

Bylot Island represents the main study site for long-term tundra ecosystem research in Canada. It started in the 1980s as a research project on Greater Snow Geese – the large colony breeding on the island was rapidly growing then and there was concern about negative impacts on tundra vegetation. While the snow goose research is still going on (Legagneux et al. 2012a), the last 20 years has seen the research move to a study of trophic interactions in the context of global (http://www.cen.ulaval.ca/bylot/ change intro.htm). Vegetation, geese, foxes, lemmings and birds, together with climate change are monitored. The ecological studies are strongly question -driven, and focus in particular (Gauthier et al. 2011, Legagneux et al. 2012b) on assessing if the dynamics of ecosystem components (e.g. lemmings, geese) are mainly driven by bottom-up interactions (with vegetation and climate) or by top-down interactions (with arctic fox, skuas). The effort on Bylot Island amounts to 1100 man days/year, with 35 scientists visiting the site. The minimum turnover is estimated at 0.65 M \$/year (Dominique Berteaux pers. comm.)

In Svalbard the environmental monitoring program MOSJ (Sander et al. 2006) includes selected populations of several terrestrial species and >10 year time series are presently available for Svalbard reindeer (§2.5), Svalbard rock ptarmigan (\$2.6), and arctic fox (\$2.8). The aim of MOSJ is to elucidate drivers of change of the Svalbard ecosystem (including climate change) and advocates that the list of species mandated to be monitored serves as appropriate indicators in this respect. The indicator approach to monitoring has been severely criticized by Lindenmayer and Likens (2010). MOSJ is presently due to be evaluated by an appointed committee (Ims, Alsos, Fuglei, Pedersen & Yoccoz in prep). Besides MOSJ the terrestrial ecosystem at Svalbard has during the last two-three decades hosted a series of more short-term research projects that have also involved trophic interactions (Fox et al. 2007, Hansen et al. 2009, Hansen et al. 2013, Speed et al. 2010b, Stien et al. 2010a). Some of these projects have been extended into more long-term monitoring however, mostly without any secure funding. COAT will build on what is found relevant of the activities of MOSJ and other projects towards its aim of implementing adaptive monitoring and climate impact research on the plant-based food web in Nordenskiöld land and Brøgger peninsulas (§1.1.5.2). COAT will also utilize whatever infrastructure that will be suitable for its purpose through the development of SIOS (www.siossvalbard.org).

For partly unknown reasons the many assets of the Varanger peninsula as a site for elucidating climate change impact on low-arctic tundra ecosystem (§1.1.5.1) has not yet been exploited in terms of long-term monitoring. However, there is a set of more short-term research projects initiated during 2005-2006 presently approaching their term that COAT can build on. An arctic fox project financed by the Directorate of Nature Research employs a food web perspective and adaptive management approach to unravel the causes of decline in the arctic fox at the fringe of its distribution (Killengreen et al. 2007, Killengreen et al. 2011, Killengreen et al. 2012, Killengreen et al. 2013). In addition, there are two projects funded by the Research Council of Norway that focuses on herbivore – vegetation interactions in a climate change perspective. EcoFinn focuses on reindeersmall rodent-tall shrub interactions (Ravolainen et al. 2010, Ravolainen et al. 2011), while ClimMoth focuses on the effect of the recent outbreak range expansion of a geometrid moth on the tundra-forest ecotone (Jepsen et al. 2008, Jepsen et al. 2011, Jepsen et al. 2013).

2. COAT MODULES

2.1. Monitoring targets and conceptual climate impact path models

In this chapter we develop the set of conceptual models that outlines how the tundra food webs of low-arctic Varanger peninsula and high-arctic Svalbard are expected to be impacted by climate change. These models define the framework for what shall be monitored in COAT (i.e. the monitoring targets) and *how* (i.e. monitoring design). The monitoring targets, being the biotic components of the conceptual models, are species or species assemblages (e.g. vegetation strata, trophic guilds and functional groups) with known or expected key functions in the food web. Such functions include processes that can act to maintain tundra ecosystem integrity, arctic biodiversity, ecosystem services or other aspects of ecosystems with societal relevance. Moreover, known or expected sensitivity to climate change and scopes for management interventions to mitigate undesired effects are other key criteria for prioritizing monitoring targets. Although some aspects of the targets certainly will be specific to the two focal ecosystems of this plan (i.e. higharctic Svalbard and low-arctic Varanger peninsula) we emphasize those attributes that make them suitable for highlighting what can be expected to be generic climate change impacts on tundra ecosystems in an overall circumpolar perspective.

A major aim of COAT is to identify pathways for which climate change may exert strong impacts on the prioritized monitoring targets. Such pathways can be both direct and indirect, the latter in the sense that climate impacts may cascade through several components (i.e. targets) of the food web. While food webs by nature are complex entities, potentially open for a multitude of indirect effects and cascades, we will strive to arrive at relatively simple (parsimonious) climate impact path models. This is because simple conceptual models are more likely to guide efficient monitoring designs and powerful (statistical) analyses of monitoring data than complex models. Of course, simple models will often prove to be inadequate or even wrong, but they are still likely to provide useful points of departure for developing better models according to the modus of adaptive monitoring.

We have approached the challenge of arriving at simple models by specifying conceptual climate impact models for separate modules (i.e. com-

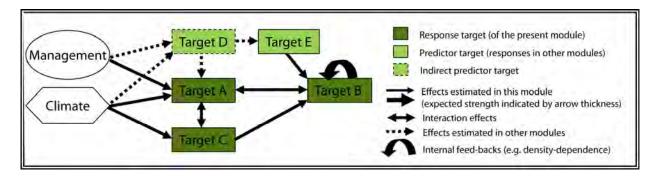


Figure 2.1. Outline of the principle structure and standardized notations used in the conceptual *climate impact path models* developed in separate modules in the COAT plan. Management actions (e.g. harvesting) and climate (change) represent the two main external drivers of food web interactions to be addressed. The arrows define the predicted climate and management impact paths onto the monitoring targets (species and functional species groups) of the module. To analyze monitoring data to obtain quantitative estimates of effects, statistical versions of the climate path models will be developed (see § 2.10). In the statistical path models each monitoring target, climate and management will be represented by quantitative state variables (e.g. abundance of a species, number harvested, climatic variables). The monitoring targets (and their state variable) are of two kinds: Response targets that are focal to the present module, and predictor targets that are focal responses of other food web modules. Likewise, impacts (broken arrows) pointing at predictor targets denote effects that are estimated in other models, while whole arrows pointing at response targets are focal impacts to be estimated as effects in the present model. Two-headed arrows denote interaction effects between response targets and loop-arrows denote feed-back effects within response targets (e.g. density-dependence).

partments; Holt and Polis 1997) of the plant based food web in tundra. Each food web module, and an associated climate impact path model, consists of a small set of monitoring targets that are expected to be mutually linked by strong biotic interactions (i.e. competitive or trophic) in the food web. This implies that the targets' responses to climatic impacts or management interventions also will be linked by those biotic interactions. Food web topology studies (e.g. Pimm et al. 1991, Montoya et al. 2003, Montoya et al. 2006) support the view that the dynamics and structures of ecosystems indeed can be ruled by the kind of "tight interaction clusters" among species or functional groups that in the context of COAT is defined as intra-module interactions. Moreover, the relative simplicity and small degree of functional redundancy in arctic ecosystems (Post et al. 2009) argue for that such a modular (reductionist) approach is likely to be justified for ecosystem-based climate impact modelling in the case of tundra food webs. Figure 2.1 outlines the principle structure and notations of the climate impact path models of the COAT plan. Below we present the seven food web modules that will form the core of the COAT science plan. Each module is, for simplicity, named by one of its response targets that often have immediate management relevance, although all modules include several targets from different trophic levels (Figure 2.2). Four modules are specific for either low-arctic Varanger (3 modules) or high-arctic Svalbard (1 modules), while three modules are common for the two ecosystems, although with different climate impact path models for each ecosystem. Importantly, the different modules are also to varying extents linked (Figure 2.2), in the sense that what is defined as a response target in one module may serve as a predictor target of other modules (Figure 2.1). These sorts of linkages across modules demand that monitoring and analyses of the different modules are well coordinated (cf. \$3).

Each of the module chapters provides a fairly thorough review of the knowledge basis and criteria used to select and define the module and its focal monitoring targets. The selection is based on consideration about the module's (and targets') ecosystem functions, sensitivities to climate impacts, as well as its management options and societal relevance (i.e. arguments for why the module should be included in COAT). In arriving at climate impact path models for each module and focal ecosystem, critical judgments have been made to arrive at simple models that focus on what is expected to be the most influential impact pathways in terms of strong and rapid responses in targets, and the sort of management options that could be considered to mitigate climate impacts. Specification of the set of state variables that will represent (quantify) each monitoring target, as well as the design and methods of monitoring, will be presented in §2.9. Each module chapter closes with a short presentation of the COAT team's competence with regard to the subject matters to be addressed in the module. For the sake of providing brief overviews, each of the module chapters starts out with a summary which defines the monitoring targets in terms of functions and relevance aspects. The climate impact path model(s) arrived at in the module chapters is also shown in the summary, along with its main predictions.

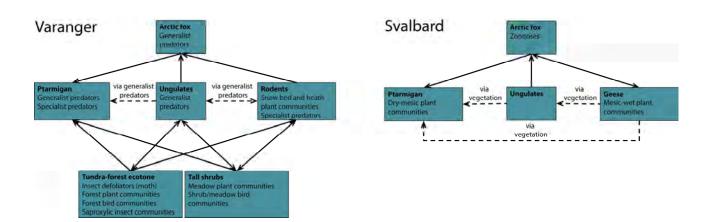


Figure 2.2. An outline of the seven food web modules in COAT (blue boxes) and the linkages within the two focal ecosystems (Varanger and Svalbard). Each modul's *response targets* are listed within the boxes and the target giving the module names is written in bold. Arrows indicate direct (full line) and indirect (broken line) linkages between modules explicitly addressed in COAT.

2.2. Tundra-Forest ecotone module (Varanger)



Functions and relevance:

Changes in the location and characteristics of the *Tundra-forest ecotone* is of key significance for the global climate system due to strong feedback mechanisms. *Sub-arctic forests* are expected to encroach on northern and alpine tundra as a result of climate warming *threatening the integrity of tundra habitats*. Climate-induced changes in the *natural disturbance regime* in sub-arctic forest have been documented and are likely to have profound implications for forest ecosystem functioning.

Response targets:

Tundra-forest transition zone with relevant associated vertical vegetation strata and plant functional groups.

Insect defoliators (geometrid moth) exhibiting *population outbreaks* in the transition zone.

Sub-arctic birch forest: plant community state changes and succession following *insect defoliator out-breaks*.

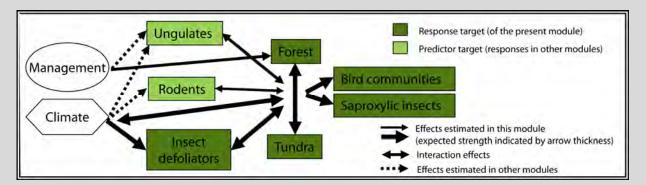
Communities of *saproxylic insects* and *birds*: changes in community structure of birds associated with birch forest and invertebrates associated with deadwood following insect outbreaks.

Predictor targets:

Ungulates and rodents as key herbivores influencing seedling establishment and forest succession.

Climate impact path model and its main predictions:

Two main climate impact paths are expected with contrasting process rates: i) rapid changes in the extent and severity of insect outbreaks may results from changes in spring and winter temperatures, causing reduced growth and increased die-back of the mountain birch and associated state shifts in forest floor vegetation with cascading effects on other ecosystem components such rodents, ungulates, birds and saproxylic invertebrates. ii) Woody species encroachment into tundra and ultimately changes of the location of the tundra-forest ecotone are expected long term results of improved growth conditions for woody vegetation under increased summer and winter temperatures. Climate-mediated encroachment as well as the succession after insect outbreaks may be modified by the effects of herbivores such as rodents and ungulates that are themselves likely to be impacted by climate (cf. §2.4 and §2.5).



Management options:

Ungulate management (cf. ungulate module) will influence natural regeneration and encroachment rates. Forestry practices such as clear cutting may influence regeneration rates locally following insect outbreaks.

2.2.1. Functioning

The tundra-forest ecotone is the largest vegetation transition on the planet, stretching for more than 13.000 km around the northern hemisphere (Callaghan et al. 2002a, Fig. 2.2.1.1 left). It encompasses the transition from northern boreal forests to treeless tundra. Through most of the ecotone the transition from forest to tundra is dominated by coniferous tree species (pine, larch, fir and spruce), while in Fennoscandia and northwest Russia it is formed by birch. The Fennoscandian tundra-forest ecotone includes a number of valuable natural habitats listed in the European Habitats Directive, Annex 1 (EEC 1992).

Ultimately, the location of the tundra-forest ecotone is climatically determined; above a certain altitudinal or latitudinal limit tree sized growth is prevented by adverse climatic conditions (Sveinbjornsson et al. 2002, Holtmeier 2003). As a result of climate warming these limits are expected to move upwards and northwards, and sub -arctic forests are consequently expected to encroach on northern and alpine tundra areas (Harding et al. 2002, Skre et al. 2002, Kaplan et al. 2003, ACIA 2004, Fig. 2.2.1.1 right), with substantial implications for the local and global functions of the ecotone. The tundra-forest ecotone is therefore an important target for long-term monitoring (Holtmeier and Broll 2005). However, several fundamental conceptual and logistical challenges remain before we can arrive at a unified and operational definition of the tundra-forest ecotone, and hence at unbiased estimates of changes in its location. One obvious reason for this is the immense heterogeneity and complexity of the ecotone caused by differences in climate, topology, vegetation, and historic and present land use across the northern hemisphere. Much of the challenge, however, lies with the fact that what is traditionally described and depicted (Fig. 2.2.1.1) as a line is in reality a heterogeneous gradient of decreasing tree cover along which local conditions related to topography, permafrost, soil, moisture, past and present land use and herbivory either favor or inhibit the growth of trees (Moen et al. 2008, Olofsson et al. 2009, Hofgaard et al. 2010, Speed et al. 2010a).

On the Varanger peninsula, the northernmost outpost of deciduous forest in Europe, this is particularly evident. In Varanger, mountain birch stands are found at elevations as high as 250-280 m in the southwest, while occurrence in the exposed northeast is limited to protected localities below 50 m, or lacking altogether. Even in the southern lowlands, however, tree cover is frequently discontinuous, interrupted by variations in small-scale topography and moisture. A low polycormic growth form of mountain birch is dominating in all but the richest areas. The entire forested area in Varanger, along with many other flat northern low-lands, can hence be appropriately viewed as being part of a spatially extended

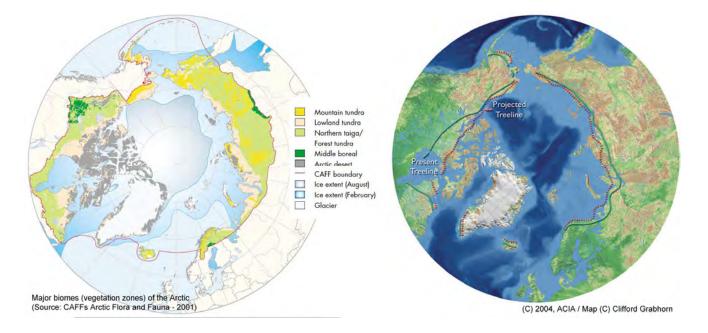


Figure 2.2.1.1. Vegetation zones in the arctic and sub-arctic regions (*left*) and an illustration of projected changes in the northern tree line within the 21st century (*right*). Sources: UNEP/GRID-Arendal, 'Vegetation zones in the Arctic' (*left*) and 'Tree line in the Arctic' (*right*), *UNEP/GRID-Arendal Maps and Graphics Library*, http://maps.grida.no/go/graphic/ (Accessed 20 September 2011).

transition zone from continuous forest to tundra. This calls for a terminology and methodology capable of capturing and quantifying gradients (Callaghan et al. 2002b).

2.2.1.1. Regional and global climate feedbacks

Changes in the location and characteristics of the tundra-forest ecotone are of key significance for the global climate system, due to potentially strong feedback mechanisms and the vast geographical expansion of the tundra and northern boreal forest biome. Climate regulation at the tundra-forest ecotone is dominated by feedbacks between processes affecting mainly regional climate (changes in albedo of the land surface and water flux), and processes with feedback effects on global climate (net emission of long-lived greenhouse gasses; Chapin et al. 2000, Fischlin et al. 2007). Tundra areas play an important role in keeping the planet cool, owing to the high albedo of snow covered surfaces, low evapotranspiration and low decomposition and mineralization rates, leading to a net accumulation of carbon in the soil (Callaghan et al. 2004f). Shrub-land and forest have much lower winter and spring albedo and higher evapotranspiration than tundra, and hence transfer more heat and water to the lower atmosphere. On the other hand, trees and tall shrubs store large amounts of carbon in living tissue, and forested areas are crucial in regional and global carbon sequestration (Nabuurs et al. 2007). Recent estimates suggest that northern boreal and tundra ecosystems hold one-third of global terrestrial carbon, the majority of which is bound in soil organic matter (McGuire et al. 2009, Tarnocai et al. 2009). Although there may still be uncertainties with respect to the relative contribution of the different processes associated with the transition between forest and tundra, recent models suggest that the net effect of more deciduous forest will provide a positive feedback to climatic warming (Swann et al. 2010).

2.2.1.2. Productivity and importance for biodiversity

Compared to more southern ecosystems, the tundra-forest ecotone is characterized by low productivity and relatively simple food webs, with a strong gradient running from the least productive tundra through dwarf shrub and tall shrub tundra to forests (Callaghan et al. 2004f). Food webs of the tundra-forest ecotone are often dominated by species with strong multiannual cyclic dynamics,

cies

34

providing regular but transient boosts of resources that cascade through the ecosystem (Ims and Fuglei 2005, § 2.4). Such cyclic dynamics are essential for the integrity of the ecosystem, both in terms of structure (e.g. maintenance of biodiversity and trophic relationships) and functioning (energy conversion and nutrient cycling). The tundra-forest ecotone also provides habitats supporting biodiversity values and resources. Large and medium-sized carnivores and omnivores such as hooded crow (Corvus corone), golden eagle (Aquila chrysaetos), wolverine (Gulo gulo), lynx (Lynx lynx) and red fox (Vulpes vulpes) are typically associated with forested areas, but frequently hunt (and occasionally breed) far into tundra areas (Killengreen et al. 2012). Valued and economically important game species such as moose and willow ptarmigan also have their strongholds in the forest or the tundra-forest ecotone. In northeastern Fennoscandia and northwest Russia the tundra-forest ecotone to some extent also separates the forest winter grounds of semi-domestic reindeer from the tundra summer pastures (cf.§ 2.5).

2.2.1.3. A limit to invasions

Certain boreal forest species are potentially important players also in the tundra ecosystem. For instance, in Fennoscandia the red fox has expanded its distribution range northwards in recent decades (Hersteinsson and Macdonald 1992, Post et al. 2009). It now represents a real threat to the continued existence of the smaller and competitively weaker arctic fox in the more productive parts of the tundra (cf.§ 2.8). A continued advance northwards of the more energy-demanding red fox can be expected to be tied in parts to shifts in productivity of the habitat (Hersteinsson and Macdonald 1992, see also Killengreen et al. 2011). Changes in the location and characteristics of the tundra-forest ecotone will contribute to this. Similarly, outbreaks by forest insect pests which, along with wild fires, constitute the most important agents in the natural disturbance regime of northern boreal forests across the hemisphere, are generally limited upwards and northwards by the altitudinal and latitudinal tree line. Insect pest outbreaks may extend far into the shrub tundra, as witnessed during a recent massive outbreak by geometrid moth in Fennoscandia (Karlsen et al. 2013). Such outbreaks can hence affect vegetation function and structure across the entire ecotone. It remains to be shown whether these 'alpine' moth outbreaks result from spillover of larvae transported by wind from nearby birch forest

habitats, or from self-sustained moth populations in dwarf birch habitats. However, the extent to which moth outbreaks can expand above the climatic tree line is probably limited.

2.2.2. Ecosystem services and other aspects of societal relevance

The subarctic birch forest and the tundra-forest ecotone harbour (endemic) biodiversity and provide crucial provisional ecosystem services locally and regulatory ecosystem services globally. Habitat provisioning for the native flora and fauna and the maintenance of biodiversity values are among the most important services provided by the tundra-forest ecotone. The three economically and recreationally most important game species in the region, willow ptarmigan (cf. §2.6), moose (cf.§ 2.5) and hare, are tied to forested areas and tall shrub tundra (cf.§ 2.3). Sub-arctic birch forests and the tundra-forest ecotone provide winter grazing grounds for a large stock of semidomestic reindeer. Finnmark County, the total stock is about 178.000 animals, of which roughly Varanger peninsula 14.000 are on the (Anonymous 2011). There is a clear gap of knowledge, however, with respect to the use of forested versus non-forested areas by reindeer at any time of year, which at present makes it difficult to judge the actual importance of the mountain birch forest as a resource for reindeer (cf. \$2.5). The birch forest is an important source of firewood, which constitutes a locally valued source of income. Harvesting of berries, in particular cloudberries (Rubus camaemorus), but also cowberries (Vaccinium vitis-ideae), bilberries (Vaccinium myrtillus) and black crowberries (Empetrum nigrum) has traditionally been a valued subsistence income for many. Today berry harvesting is no less valued, but for mostly recreational reasons.

Sub-arctic birch forests contribute significantly to the total carbon budgets of northern regions through their role in carbon sequestration (Aurela et al. 2001, Christensen et al. 2007, Heliasz et al. 2011). Christensen et al. (2007) report mean carbon uptake rates of -50 g C m⁻² yr⁻¹ for subarctic birch forests, as opposed to -3 g C m⁻² yr⁻¹ for heathland in the same region. The large seasonal differences in albedo and transpiration of water vapor between birch forest and the tundra (cf.§ 2.2.1.1) means, however, that an expansion of sub -arctic birch forests into tundra areas is expected to result in a positive feedback amplifying the global warming process (Chapin et al. 2000, McGuire et al. 2009, Swann et al. 2010).

2.2.3. Sensitivity

2.2.3.1. Increased productivity and coverage of tall woody vegetation

According to conventional projections in climate warming scenarios, northern boreal forests, including sub-arctic birch forest in Fennoscandia, will become more productive (greener) and expand into the arctic tundra (Grace et al. 2002, Lucht et al. 2002, Kaplan et al. 2003, Fischlin et al. 2007, Fig. 2.2.1.1). For instance, a moderate 2°C increase in global mean temperature above preindustrial levels is projected to cause a reduction in tundra areas by 42% globally and as much as 88.1% in northern Fennoscandia and northwest Russia (Kaplan and New 2006, 'Robust mean' scenario), and a corresponding increase in forested areas by 55.8% and 37.2%, respectively. While reconstructions of ecotone dynamics based on historical maps and recent remote sensing data suggests that such projections from dynamical global vegetation models (DGVMs) may be overestimates (Aune et al. 2011, Hofgaard et al. 2013) an increasing trend in productivity across the northern tundra and boreal forest region is already evident (Stow et al. 2007, Hudson and Henry 2009, Beck et al. 2011b) and can be at least partially attributed to an increase in shrub cover (§2.3) in tundra areas (Sturm et al. 2001b, Chapin et al. 2005, Tape et al. 2006, Rundqvist et al. 2011, Sturm 2010). These prospects are dramatic for the northern tundra, which could be facing a biodiversity crisis with extensive loss of habitat and biodiversity, including a host of endemic species (e.g. §2.4 and 2.8). The projected shifts in the tundra-forest ecotone would also reduce the quality and quantity of forage for caribou and reindeer, as well as force changes in the use of seasonal grazing grounds. This could threaten the foundation for traditional reindeer husbandry as practiced in northern Fennoscandia today.

The good news is that native herbivores may also act as 'ecosystem engineers' in ways that could potentially counteract the climate-driven encroachment process (Suominen and Olofsson 2000, Post and Pedersen 2008, Olofsson et al. 2009, Speed et al. 2010a, Aune et al. 2011). For instance, Olofsson et al. (2009) showed that reindeer are effective in limiting the spread of shrubs in tundra regions, while voles and lemmings have larger effects in the forest. This offers a potential opening for management to mitigate the local effects of climate change. Careful management of large grazers which exert such limiting effects can effectively provide means to preventing, or even reversing, the local effects of climate change on vegetation changes. Moreover, the limiting effect of grazing by native herbivores may also interact with disturbances caused by forest pests such as geometrid moth (see below). While such interactions between grazing and pest outbreaks may control encroachment, they may also have negative effects by magnifying and prolonging the disturbances (die-offs) of natural forest systems caused by pest outbreaks.

2.2.3.2. Changes in the natural disturbance regime

Most projections of vegetation responses to climate change based on DGVMs focus on positive growth effects, but the predicted transitions could also be moderated by factors not yet included in the models (Volney and Fleming 2000, Fischlin et al. 2007, Chapin et al. 2010, Seidl et al. 2011). For instance, recent empirical discoveries have sparked doubts whether projected vegetation changes are consistently linear processes. Indeed, coniferous forests have been observed to abruptly become less vital (browner) in Alaska (Sturm 2010, Beck et al. 2011b). In northernmost Fennoscandia large tracts of birch forest, including

the sensitive tundra-forest ecotone, have died during the last decade (Jepsen et al. 2009a, Figure 2.2.3.1). In both instances outbreaks by forest pest insects have been decisive. Indeed, intensified insect outbreaks in sub-arctic forests may represent fast, non-linear responses to climate (Hagen et al. 2008b), that have received relatively little attention in predictions of vegetation response to climate change. Cyclic outbreaks by geometrid moths occur at roughly decadal intervals in the sub-arctic birch forest in northern Fennoscandia, but vary greatly in both spatial extent and amplitude. The controlling mechanisms on moth outbreaks are still to some extent an enigma and a target for further research. Extreme winter colds kill the overwintering eggs, and therefore represent a definite mechanism for outbreak control (Tenow and Bylund 1989, Virtanen et al. 1998, Ammunét 2011). Even if winter temperatures do not reach these extremes, outbreaks may still be controlled by other factors. Since close temporal synchrony between egg hatching in spring and budburst of the host tree is a prerequisite for a population build-up of larvae during summer (Feeny 1970, van Dongen et al. 1997), spring temperatures and their control over the timing of both moth and birch phenology are likely decisive for whether outbreaks occur.

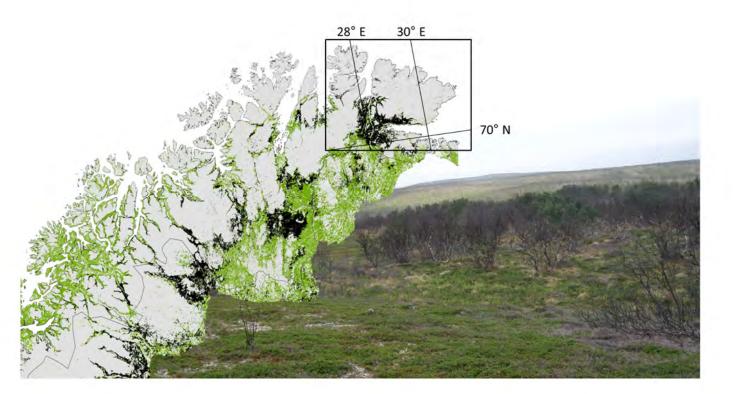


Figure 2.2.3.1. Defoliated birch forest in Varanger following severe moth outbreaks. Overlaid map show the birch forest belt of northern Fennoscandia with the Varanger focal area in the northeast. Black shaded areas show birch forest affected by severe defoliation as detected by satellite during the most recent outbreak (2002-2008), while green areas show forest with no or moderate defoliation (modified from Jepsen et al. 2009a). Photo: Ole Petter L. Vindstad.

Under normal circumstances the birch forest regenerates after moth outbreaks, albeit slowly (Lehtonen 1987). However, the most recent massive moth outbreak in the region has received international attention, as it is the first documented insect outbreak that appears to have become intensified as a result of a climate-induced northern range expansion of a non-native species as far north as the tundra-forest ecotone (Post et al. 2009). It has been shown how the winter moth (Operophtera brumata) has recently expanded its outbreak range along altitudinal (Hagen et al. 2007) and latitudinal-longitudinal (Jepsen et al. 2008) gradients into the outbreak range of the native autumnal moth (Epirrita autumnata), while a potential new pest species, the scarce umber moth (Agriopis aurantiaria) has spread as far north as 70°N in coastal regions (Jepsen et al. 2011). This has resulted in greatly extended moth outbreaks, both in terms of spatial coverage and duration (Jepsen et al. 2009b), and extensive forest death. Given the current trend of intensified outbreaks, it is of concern whether the resilience of the birch forest's cyclical succession after moth outbreaks have been exceeded (Chapin et al. 2004), and result in permanent state changes in the subarctic birch forest. Severe moth outbreaks cause distinct shifts in forest floor vegetation due to defoliation of shrubs and fertilization effects of larval excretion (Jepsen et al. 2013, Karlsen et al. 2013). Although moth larvae in outbreak years may provide insectivorous species (passerine birds) with an ephemeral pulse of overabundant resources, general habitat degradation can be expected for many species over time due to adverse changes in resource availability. As tree decay advances there will be an accumulation of dead wood which may provide another resource pulse, this time for saproxylic insects and fungi. The nature and implications for the birch forest ecosystem of cascading effects initiated by moth outbreaks represent a central gap in our understanding of the drivers of the dynamics in the tundraforest ecotone in northern Fennoscandia. In many respects, the impact of birch forest moths on the ecosystem resembles the impact of intense wildfires in boreal coniferous forest further south, but covers a much greater spatial extent than modern time forest fires in the region. Swedish colleagues have recently quantified the reduction in carbon sink capacity of an area affected by severe moth outbreaks to be as much as 89% compared to healthy birch forest (Heliasz et al. 2011).

There are also several unknowns related to invasions of new species of defoliators into the tundraforest ecotone. For instance, the invasive winter moth appears to be more versatile in choice of host plants than the native autumnal moth. In temperate regions of Europe there are strains of winter moth that utilize vastly different plants, such as heather (Calluna vulgaris) and Sitka spruce (*Picea sitchensis*). During the last outbreak of the winter moth also tracts of dwarf birch (Betula nana) in tundra areas were defoliated, but it is not known whether this is due to a spill-over of larvae from mountain birch or whether the winter moth manages to persist in dwarf birch. If the winter moth evolves to establish reservoir populations in different plant species it could possibly both increase the duration and frequency of outbreaks in the tundra-forest ecotone.

2.2.3.3. Competition from southern tree species

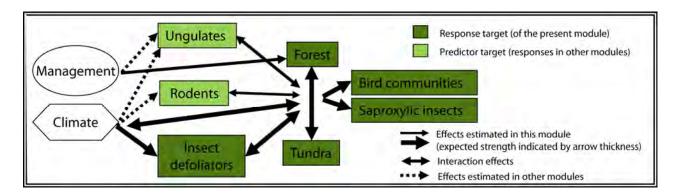
Northernmost Europe (i.e. Fennoscandia, Kola, Iceland, Greenland) is the only place where the sub-alpine vegetation belt is dominated by mountain birch, and where this species forms the tree line. The reason for this is most likely related to the high degree of oceanity (high precipitation, humidity and ice-free oceans; Oksanen 1995, Wielgolaski 2003, Wielgolaski et al. 2005). Similar to the process of tall shrub, dwarf shrub and forest encroachment into tundra in response to a warming climate, the birch system may be exposed to increased competition from more southern species. There are still substantial gaps in our knowledge of the importance of competition for a potential northward expansion of boreal forest species at the expense of birch, and how this interacts with other controlling mechanisms. The response of species to climate change is likely affected by many factors in addition to competition (Callaghan and Johansson 2009), leading to nonlinear responses and associated departures from simple predictions of the effects of climate change on vegetation. Herbivory and pest outbreaks are two important controlling factors on recruitment and growth, and may influence the competitive balance between species. For instance, aspen (Populus tremula) and also rowan (Sorbus aucuparia) are relatively common components of boreal forests with great potential for rapid colonization and growth (Worrell 1995). While such species therefore represent potent competitors to the lower recruiting and slower growing birch, van Bogaert et al. (2009) showed that aspen expansion was effectively restricted by heavy browsing by moose. However, if continued climate warming leads to increased frequency and severity of moth outbreaks, and therefore reduced birch forest resilience, the competitive balance may shift, thus facilitating the expansion of aspen, and possibly also other species such as rowan and pine (but see Young et al. 2011). Climate change may also affect the resilience of birch in other ways. For instance, birch bud burst may gradually occur earlier in spring as the warming trend continues, but this may increase the risk of buds suffering frost damage (Bennie et al. 2010), thereby lowering the resilience of the birch forest.

2.2.4. Climate change impact predictions

We outline two primary pathways for climate change effects on the tundra-forest ecotone on Varanger peninsula (*Climate impact path model 2.2.4.1*). The strength of the different pathways will ultimately determine the location of the ecotone and hence the feedback to regional and global climate.

The first pathway (Model 2.2.4.1) is through a climate-mediated increase in erect shrub cover in tundra habitats (encroachment), which could be followed also by altitudinal and/or latitudinal advances of forest. This will negatively impact the extent and integrity of tundra habitats. We hypothesize that an increase in shrub cover will be dominant in the short term since many shrub species are already widespread in the Varanger peninsula tundra habitats and may thus respond rapidly to changing conditions (Macias-Fauria et al. 2012). Indeed, spread of tall Salix shrubs can be rapid in riparian tundra habitats, in particular when released from grazing (cf. §2.3 for specific predictions). However, in contrast to Salix shrubs, encroachment by dwarf birch and birch (and other woody species such as rowan, aspen, spruce and pine) into tundra habitats can occur also in dry and mesic habitats. It has been suggested (Sturm et al. 2005b) that a gradual temperature driven shrub encroachment of the tundra can induce a positive feedback loop in which shrub growth is further improved as a result of increased soil microbial activity and hence nutrient availability, in turn caused by the insolating effect of snow accumulating in the shrub layer during winter. This highlights the importance of monitoring not only processes related to the growth season, but also winter processes, in particular snow accumulation and melt-off.

The second pathway (Model 2.2.4.1) acts through a change in the natural disturbance regime related to outbreaks of geometrid moths at the alpine and arctic tree lines. We hypothesize that a decrease in the occurrence of extreme winter cold and a general increase in temperatures will permit further range expansions of the native moth species, as well as the invading southern moth species, into more continental and northern areas. Given that the required phenological match between moth larvae and birch is maintained (§2.2.3.2 for details) this could mean more extensive and possibly also more severe moth outbreaks in the future with negative consequences for the birch forest and associated habitats. The cascading impacts of pulsed resources generated by moth outbreaks on the community composition of small birds and saproxylic insects are also investigated in this module. Note that either pathway may be modified by the other. With increased density of dwarf birch above the tree line we predict that moth outbreaks, when occurring, will be able to advance further into shrub tundra areas, even in absence of a general forest advance. At the same time grazing by rodents (cf. §2.4) and large ungulates (cf. §2.5), as well as the episodic damage to trees and shrubs caused by moth outbreaks, have the capacity to counter-act the climate-driven



Model 2.2.4.1. Climate impact path model for the Tundra-Forest ecotone module. Details regarding expected transitions are provided in the text.

encroachment in the ecotone. It is hence vital that patterns of encroachment and ecotone dynamics are studied in context of the natural disturbance regime. The effects of insect disturbance and the two functional groups, ungulates and rodents, may even be expected to interact. For instance, moth induced changes to the understorey vegetation can have cascading effects on both rodent and ungulates (Jepsen et al. 2013). The species composition of the small rodent community may shift following habitat changes induced by insect outbreaks, which in turn affect the severity of their browsing impacts on saplings of woody plants (Ravolainen et al. 2011), including tall Salix shrubs (cf.§ 2.3). However, the impact of rodents is expected to diminish as rodent cycles become dampened due to warmer and more unstable winters (cf. §2.4), so the net outcome of the direct and the indirect (through insect outbreaks) effects is difficult to predict. Moreover, as the abundance of shrub and tree-layer browse diminish drastically in the tundra-forest ecotone following moth outbreaks, moose may move further into tundra areas with increased impact on Salix shrubs in riparian habitats (cf. §2.3).

It is important to be aware of the large differences in the rate of change according to the different climate-driven pathways. The drastic ecosystemstate changes caused directly by insect outbreaks are very rapid. For instance, during the last outbreak in the Varanger-Tana region forest death and ground vegetation state changes that impacted more than 1500 km² occurred within a period of 5-6 years. Forest regrowth, shrub encroachment and, most noticeably, forest expansion (Hofgaard et al. 2013) are, by comparison, much slower (decadal to multi-decadal) processes.

2.2.5. Management options

Given the critical importance of the location of the tree line, both locally in terms of biodiversity and ecosystem stability, and globally in terms of feedbacks into the climate system, it is worth discussing management options that may be available to control its location and/or counteract the effects of encroachment. In this context it is important to define what is considered a desirable outcome prior to the adoption of any management scheme. For instance, the objective may be to prevent any further encroachment into the tundra, and to maintain the current ecotone location. On the other hand, it may be desirable, in some regions or under certain circumstances, to attempt a reversal of historical encroachment, and to re-establish some historical location. Regardless of the desired outcome, which is to be decided on by stakeholder for a (cf. §2.9.5 and §5.1), the two main drivers that can be relatively readily controlled are grazing and forest management.

2.2.5.1. Grazing

The most important grazer in this region is the semi-domestic reindeer, and changing reindeer husbandry practices probably constitute the most effective management option for controlling the encroachment process (cf. §2.5). Grazing by sheep is much less common in northern Fennoscandia, but sheep grazing has been shown to efficiently limit recruitment and adversely affect growth in mountain birch, even at moderate sheep densities (Speed et al. 2010a, 2011). Sheep grazing can hence potentially complement reindeer grazing in particular regions. A third grazing species which is increasing in importance in the tundra-forest ecotone in northern Fennoscandia is moose (cf. §2.5). In the 1950's and 1960's moose was a rare sight in Finnmark county, and the few individuals harvested were shot in the coniferous forest areas in the east. During the last two decades, however, the moose has spread across the county, and moose harvesting increased from <200 animals in 1990 to 830 in 2010 (SSB 2012a).With the increasing importance of moose as a game species in the region comes new management options, such as quotas set preferentially to control encroachment. Moose show strong forage selectivity and feed on aspen and rowan in disproportional amounts compared to birch (Wam and Hjeljord 2010). It may therefore also provide a management tool for controlling the birch/aspen dynamics in the region.

2.2.5.2. Forest management

As has been discussed previously, logging can be locally important, both for subsistence firewood and as a source of income. It may also be a very effective forest management tool, and tree felling in areas affected by moth outbreaks is believed to stimulate the re-establishment of healthy birch forest stands. A long-term experiment aimed at investigating the role of logging as a management tool in moth damaged mountain birch forest in Varanger has recently been initiated in collaboration between ecologists at UoT and NINA, Tromsø, the Finnmark Property (FeFo) and the Governor of Finnmark. While logging in theory can be used to directly control the tree line location and to counteract encroachment, in practice it is unlikely to be an effective tool over large areas.

2.2.6. COAT team competence

The tundra-forest ecotone module will be led by the Norwegian Institute for Nature Research (NINA). Team member in charge is Jane Uhd Jepsen (NINA) with contributions from Virve Ravolainen (UoT), Kari Anne Bråthen (UoT), John-André Henden (UoT), Rolf A. Ims (UoT), Torkild Tveraa (NINA) and Audun Stien (NINA). NINA and UoT researchers are jointly responsible for the monitoring of moth population outbreaks in northern Norway, with a focus on climate (Ims et al. 2004, Hagen et al. 2008b, Jepsen et al. 2008, Jepsen et al. 2009b, Jepsen et al. 2011, Jepsen et al. 2013) and are in charge of a work package in the Nordic Centre of Excellence "How to preserve the tundra in a warming climate" (NCoE-Tundra, www.ncoetundra.utu.fi). NCoE-Tundra targets specifically the role of herbivores, including large ungulates, rodents and moths, in controlling climate-driven expansions of woody vegetation into tundra areas. The NCoE -Tundra network includes a range of ecologists from Finland, Sweden and Norway with expertise

on Nordic tundra and forest ecosystems in addition to climatologists, geographers and social scientists, and provides an important international and cross-disciplinary platform. UoT researchers are responsible for the project "EcoFinn" (2008-2012) which focuses on plant-herbivore interactions, and in particular ungulate browsing mediated habitat alteration on the Varanger peninsula. The team of scientists contributing to the tundraforest ecotone module harbors extensive expertise in plant ecology, grazing responses and encroachment in tundra habitats and sub-arctic forest (Bråthen and Oksanen 2001, Bråthen et al. 2007a, Hagen et al. 2008a, Ravolainen et al. 2011), population dynamics and habitat use of large and small mammalian herbivores in sub-arctic forest and tundra habitats (Tveraa et al. 2007, Pedersen et al. 2010b, Stien et al. 2010a, Henden et al. 2011b) moth population ecology and outbreak dynamics in sub-arctic forest (Ims et al. 2004, Mjaaseth et al. 2005, Hagen et al. 2008b, Jepsen et al. 2008, Jepsen et al. 2009b, Jepsen et al. 2011), impact of forest structure changes on passerine birds and insect communities saproxylic (Sverdrup-Thygeson and Ims 2002, Hausner et al. 2003), trophic implications of herbivore-induced habitat changes (Ims et al. 2007b, Henden et al. 2010, Ims and Henden 2012, Jepsen et al. 2013) and remote sensing applications (Jepsen et al. 2009a).



2.3. Tall shrub module (Varanger)



Functions and relevance:

The *expansion of tall shrubs* in low-arctic tundra is *one of the most extensive and rapid changes induced by climatic warming* and appears to be the main process underlying the "greening of the Arctic". The expansion of tall shrubs has significant *positive feedback on climate at local, regional and global scales.* Furthermore, because tall shrubs represent habitats that are *biodiversity hot spots* in the tundra, climate warming is likely to have *cascading impacts in tundra food webs*. The extent of tall shrub expansion is, however, geographically variable and likely to be constrained, and possibly even *counteracted by herbivores*.

Response targets:

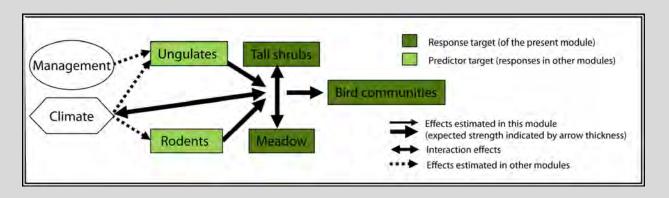
Tall willow shrubs (thickets) and *meadows* as two alternative vegetation states. Associated *bird community* sensitive to the extent and spatial configuration of willow thickets. Sensitivity of *meadows* to shrub encroachment is dependent on plant functional composition, and the presence of silicate rich grasses.

Predictor targets:

Ungulates (reindeer and moose) and *rodents* (Norwegian lemming and tundra vole) as key herbivores on both woody and herbaceous plants.

Climate impact path model:

The model predicts that the rate, and maybe even the direction, of the transition between tall shrub and meadow states in tundra depends on two major interacting climate impact paths; one due to direct effects of climate warming on the two vegetation states, while the other works through changed abundance and grazing/browsing impacts of ungulates and rodents. Following areal expansion and vertical growth of tall shrubs the tundra bird community is expected to change in favor of species with strongholds in boreal and sub-arctic forest.



Management options:

Management of ungulates (reindeer and moose) can possibly counteract the expansion of tall shrubs.

2.3.1. Functioning

2.3.1.1. Tall shrub tundra in the European lowand sub-arctic

Tall shrub tundra holds the tallest vegetation, is located in areas favorable for growth, and is among the most productive tundra types in the Arctic (Walker et al. 2005). Tall shrub tundra provides habitats to a wide range of plants and animals, and plays a central role in ecosystem functioning, including biotic (Ripple and Beschta 2004, Henden et al. 2011a, Ravolainen et al. 2011, Ehrich et al. 2012a) and abiotic processes (Blanken and Rouse 1994, Sturm et al. 2001a).

Tall shrub tundra is typically found in river valleys, along creeks and on moist slopes, where the shrubs become 0.5 to 3 m tall. Typically, the height of the shrubs declines with altitude, and tall shrubs disappear altogether at altitudes above 250 -300 m above sea level. Deposits of clay, silt, sand, and gravel left by flowing streams produce alluvium that makes fertile soils providing optimal conditions for establishment of tall shrub tundra. In the Eurasian Arctic, the dominant woody plants in these shrub-dominated vegetation types are willows (Pajunen et al. 2010), i.e. several species in the genus Salix and hybrids of these (see Box 2.3.1). Tall shrub tundra often exists in a two-state mosaic of open meadows and patches of shrubs (Kalliola 1939, Gabay et al. 2011, Ravolainen et al. 2013), where both the tall shrub understory and the meadows are rich in functional groups and typically made up of forbs, grasses, sedges, vascular cryptogams, and saplings of the willow shrubs (Schickhoff et al. 2002, Ravolainen 2013, Pajunen et al. 2010).

Plants in tall shrub tundra are palatable to the majority of tundra herbivores, and, apart from providing forage, tall shrubs also function as protection from predators, nesting and foraging habitat for a number of birds, and host plants for insects (Roininen et al. 2005). Which configuration of the tall shrub patches is best may vary among the associated organisms. All states of tall shrub tundra may provide good habitats for the tundra vole (Henden et al. 2011b) and forage for large ungulates, such as reindeer and moose, whereas willow ptarmigan prefer the tall shrub tundra in a state of larger tall shrub patches (Ehrich et al. 2012a). Finally, a number of bird species are confined to habitats where the shrub patches are present, as opposed to the open meadow state (Ims and Henden 2012).

Tall shrubs modify their physical environment in many ways. Enhanced nutrient cycling (Buckeridge et al. 2010, Chu and Grogan 2010), warmer soil temperatures through an insulating effect of thicker snow cover (Sturm et al. 2005a), and soil stabilization (Tape et al. 2011) are among



Figure 2.3.1.1. Tall shrub tundra in Komag valley, Varanger peninsula, Norway, in a two-state mosaic of open meadows and patches of shrubs. Photo: Kari Anne Bråthen.

the more prominent effects of tall shrubs on their physical environment.

2.3.1.2. Tall shrub tundra on the Varanger peninsula

Tall shrub tundra on Varanger peninsula is currently a mosaic of willow patches and meadows (Figure 2.3.1.1, Boxes 2.3.1 and 2.3.2), and represents hot spots in terms of productivity in an otherwise barren landscape with low-productive dwarf-shrub heath vegetation (Bråthen et al. 2007a). The meadows on Varanger peninsula cover extensive areas on riparian sediment plains and resemble willow understory plant communities in the Russian Arctic (Ravolainen 2009, Pajunen et al. 2010, Ravolainen et al. 2013). In Varanger, tall willow shrubs are browsed by both reindeer and moose, of which reindeer currently is by far the most numerous and important in terms of impact on the vegetation. Reindeer also impact the growth of willow saplings and, combined with bursts of sapling mortality caused by cyclic small rodent outbreaks, shrub expansion into the surrounding meadows appears currently to be controlled by the joint impact of the two groups of mammalian herbivores (Ravolainen et al. 2011, Ravolainen et al. unpublished).

Box 2.3.1. Shrub state in tall shrub tundra

Vegetation descriptions from the Arctic currently treat tall deciduous and evergreen shrub species within "low shrub tundra". These shrubs vary from low-growing plants just above 40 cm to shrubs that reach several meters in height (Walker et al. 2005). The mere height-variation in the shrubs, however, brings along differences in ecosystem function (e.g. Sturm et al. 2005a, Pomeroy et al. 2006). Moreover, species that typically form the tallest growing shrub patches, such as willow (*Salix*) and alder (*Alnus*), have different nutrition economics than the typically lower growing shrubs, such as the dwarf birch (*Betula nana*). Therefore the latter group of shrubs is not treated in the current module (but see § 2.4), even if some of the species can reach heights well above the 40 cm definition of Walker et al. (2005).

Existence of tall-growing shrubs is at biome scale defined by bio-climatic zonation, and they are particularly found in areas bordering the sub-arctic (Lantz et al. 2010, Pajunen et al. 2010). Quantifications of tall shrub extent indicate that the tall shrubs currently cover a relatively small proportion of the general tundra landscape (Beck et al. 2011a). On Varanger peninsula shrubs cover 20-30% of the landscape when measurement is centered on valleys with shrub patches. There is considerable variation in shrub patch size and perimeter of edge, giving variable present day configurations of shrubs (Henden et al. 2011b). Importantly, at river catchment scale, there are differences to whether shrub patches are present at all or completely fill their niche (Henden et al. 2010, Ims and Henden 2012). Likewise, abundance of shrub saplings varies (Ravolainen et al. 2013). This spatial variation suggests substantial variation in the driving processes in the past such as land use, as well as a potential for highly variable trajectories for shrub patch change in the future.

Shrub expansion happens in several ways. Shrub patches can change density, height or extent (Tape et al. 2006, Figure B.2.3.1). Whereas growth of existing shrub individuals is relatively well studied and known to be sensitive to summer temperatures (e.g. Tape et al. 2006, Forbes et al. 2010, Blok et al. 2011a), few studies have addressed factors influencing the processes of shrub areal expansion (e.g. Tape et al. 2006).

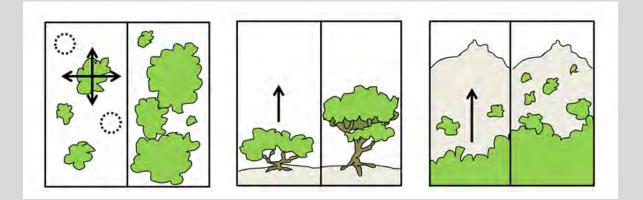


Figure B.2.3.1. Different ways of shrub expansion. From left to right; density growth or in-filling of existing patches (horizontal growth), height growth (vertical), and colonization of new areas or advancing shrub-line. (Figure from Myers-Smith et al. 2011).

The meadows are characterized by high, but between-years variable, standing crop. Standing crop variability in tundra meadows is as high as that of grasslands in temperate areas (Knapp and Smith 2001, Trasti 2010). Such variability indicates sensitivity to changing growing conditions and makes these habitats suitable as bellwethers of global change (Knapp and Smith 2001), suggesting that monitoring of the meadows should be conducted with high intensity (i.e. yearly intervals). Variability in standing crop also indicates high process rates. In fact, decomposition rates of these tundra meadows are the fastest documented in tundra ecosystems (Ancin 2012), although both pH (average 4.5) and temperatures (average for July: 10°C) are low. Despite expectations that the tall shrubs ameliorate the habitat in terms of soil temperature, microbial activity, and nutrient availability (Sturm et al. 2001a) decomposition rates do not differ between tall shrub tundra in the shrub or meadow state (Ancin 2012). Hence, high process rates seem to be governed by habitat characteristics independent of vegetation state.

Plants of the meadow state on Varanger peninsula also show high response rates to herbivory, the fastest documented in tundra ecosystems (Ravolainen et al. 2011). Both large ungulates and small rodents cause significant compositional changes of plant functional groups in these meadows. Importantly, saplings of willow shrubs respond fast to protection from herbivory (Ravolainen et al. unpublished). Such fast response rates indicate that the tall shrub tundra potentially has high resilience to herbivory, but it is not clear what governs this resilience. Plants in the meadows are predominantly perennial and clonal. Hence, resilience could be governed by the storage effect (sensu Chesson 2000) e.g. the ability of plants to survive several years as small individuals, clonal reproduction, or a substantial seed bank. Resilience could also be governed by plantsoil feedbacks (Ehrenfeld et al. 2005), causing high productivity in this habitat.

Box 2.3.2. Meadow state in tall shrub tundra

Tall shrub tundra is not formed by the shrub patches alone, but rather typically is configured as a mosaic of shrub patches and meadows. "Willow-characterized meadows" have long been recognized as distinct vegetation units (Kalliola 1939, Lyftingsmo 1965, Wielgolaski 1972), both in Alaska (Schickhoff et al. 2002) and in the Eurasian Arctic (Lyftingsmo 1965, Karlsen et al. 2005, Pajunen et al. 2010). Common to these descriptions is that they document meadows formed by a number of forbs, grasses, vascular cryptogams, and willow shrubs as recruits or small patches, while composition with respect to abundances of the species varies greatly.

In the larger river valleys of Varanger peninsula there appears to be three types or *phases of meadows* (Figure B.2.3.2): meadows characterized by saplings of willow shrubs and dwarf birch; meadows characterized by forbs such as *Rumex acetosa* coll. and grasses such as *Anthoxanthum odoratum*; and meadows dominated by silica-rich grasses, particularly *Deschampsia cespitosa* (Karlsen et al. 2005, Ravolainen et al. 2013). These meadow types occur across large land-scapes, and particularly meadows of the *Deschampsia-type* extend over tens of kilometers, either in a mosaic with shrub patches or without a tall shrub canopy.

While we have established that vegetation in tall shrub tundra meadows of Varanger peninsula is remarkably dynamic (Trasti 2010), what are decisive factors for their development and possible resilience differences between these different types of meadows is not established.



Figure B.2.3.2. Meadow phases identified on Varanger Peninsula. From left to right; shrub saplings phase, palatable forb and grass phase, silicate rich grass phase. Photo: Mette Nilsen, Pia Rännänen and Geir Vie.

2.3.1.3. Tall shrub vs. climate change: Forcing and feedbacks

The general observed trend for arctic vegetation is that productivity increases with climate change; i.e. "the greening of the Arctic" (Stow et al. 2004, Jia et al. 2006). Enhanced growth of tall shrubs has been suggested to be responsible for a considerable part of this "greening" (Sturm et al. 2001b, Tape et al. 2006, Forbes et al. 2010). Patches of tall deciduous shrubs, i.e. 0.5-3.5 m height, act as nuclei for climate-driven tall shrub expansion (Tape et al. 2006, Tape et al. 2012, Lantz et al. 2013). Warmer summer temperature is a primary factor associated to increasing shrub extent and growth (Tape et al. 2006, Forbes et al. 2010, Blok et al. 2011a). However, in a recent meta-analysis of experimental evaluation of both warming and increased precipitation, plant responses to warming are less pronounced than plant responses to increased precipitation (Wu et al. 2011). Studies investigating interactions among temperature and precipitation are still very few (Wu et al. 2011), and the relative importance of changes in temperature and water regime is not known.

A positive feedback loop for increasing shrub growth involves snow. That is, shrubs trap snow, soil temperature increases, microbial activity and nutrient availability increase, in turn promoting increased shrub cover (Sturm et al. 2005a, but see Wookey et al. 2009). Winter biological processes induced by the presence of shrubs are accordingly suggested to further contribute to conversion of tundra to shrubland (Sturm et al. 2001a, Sturm et al. 2005a). These positive feedback loops may also reinforce climate warming (Chapin et al. 2005), and the current prediction is that the increasing extent of tall shrubs will contribute to accelerate climate warming. Changes in surface reflectance (albedo) are considered to be a key vegetationclimate feedback, and shrub expansion has the potential to cause more than 70% of the predicted increase in atmospheric heating in Alaska (Chapin et al. 2005).

A feedback loop through which shrubs can mitigate impacts of climate change is via effects on soil erosion along rivers. Climate change also involves increased precipitation and increased run-offs in warmer springs. Hence more soil can be washed from valley slopes to the rivers and downstream. The largest rivers descending to the Arctic Ocean are increasingly discharging river detritus (Peterson et al. 2002, Dankers and Christensen 2005). However, recently, Tape et al. (2011) showed that shrub expansion along rivers in Alaska concurs with declined erosion, indicating that shrubs stabilize soil.

2.3.2. Ecosystem services and other aspects of societal relevance

Tall shrub tundra holds fast ecosystem processes, with high primary productivity and high nutrient cycling rates in otherwise low productive tundra. It is therefore likely that tall shrub tundra subsidizes (spatially) other parts of the Varanger peninsula where primary production is lower. The high productivity of the tall shrub tundra makes this habitat an important feeding habitat to herbivores, and thus important to reindeer husbandry and hunting of game species such as the willow ptarmigan, and moose.

The role of tall shrub tundra in the climate system, through its potential feedback on climate warming, has put its regulating ecosystem services high on the agenda in discussions of global consequences of greening of the Arctic (Sturm 2010).

2.3.3. Sensitivity

2.3.3.1. Tall shrub tundra sensitivity

Sensitivity of the tall shrub tundra depends on its resilience to the impacts of climate change and herbivory, where the extreme outcome may be loss of this tundra type (Figure 2.3.3.1). Tall shrub tundra is typically located in proximity to water sources and is therefore tightly coupled to the water regime of ecosystems, making this habitat vulnerable to altered river hydrology (Peinetti et al. 2002). Whereas catastrophic floods and landslides are a potential disturbance to arctic ecosystems from the thawing of permafrost (Lantz et al. 2009), this is not as yet a pronounced disturbance on the Varanger peninsula where permafrost is limited to high altitude and scarcely vegetated areas. Still, erosion from the actions of water may significantly reduce the extent of tall shrub tundra on riverbanks due to for instance severe flooding during the spring thaw, or to screes/avalanches along valley slopes. Whereas tall shrubs are protecting the habitat, maintaining (Tape et al. 2011), and perhaps even expanding, habitat extent along rivers and creeks, it is not clear whether herbaceous plants of the meadow state can have the same role. At the other extreme, tall shrub tundra is a habitat vulnerable to forest encroachment. Globally, a 2-3°C warming that is predicted for the time period of 2026-2060 would cause shrub tundra to disappear from the western European

Arctic, giving way to evergreen or deciduous forest (Kaplan and New 2006, Feng et al. 2012, see § forest-tundra ecotone.). On Varanger peninsula, mountain birch forest reach into shrub tundra in fringes along river valleys. The processes of forest encroachment are specifically dealt with in the forest-tundra ecotone module (cf. §2.2). However, at the same time tall shrubs are likely to expand to higher altitudes, at least in habitats with suitable edaphic and hydrological conditions for *Salix* spp. This expected altitudinal expansion of tall shrub tundra on Varanger peninsula parallels that of the latitudinal expansion of tall shrub tundra into presently more northern tundra zones elsewhere in the Arctic.

2.3.3.2. Tall shrub tundra state sensitivity

Previous descriptions of tall shrub tundra point to abiotic factors and plant succession as important drivers of vegetation development (Kalliola 1939, Schickhoff et al. 2002, Pajunen et al. 2010, McManus et al. 2012, Tape et al. 2012, Lantz et al. 2013). Under suitable abiotic conditions tall shrubs may expand spontaneously at the expense of open meadows dominated by herbaceous plants that eventually will develop into understory vegetation. Finally, a dense shrub canopy can outcompete these plants through processes such as shading and eventually limit plant growth and species richness (Totland et al. 2004, Pajunen et al. 2011). Climate warming is expected to enhance the rate of succession in the direction of increased extent of shrub patches (Figure 2.3.3.1). However, several taxa of herbivores, including insects, birds and mammals, modify this succession trajectory and may under certain circumstances even drive the succession in the opposite direction. For instance, intense herbivory is regarded as essential for keeping tall shrub tundra in the meadow state (Thing 1984). Herbivore effects may even be stronger than that of climate warming. Across gradients of reindeer grazing pressure and reindeer abundance in sub- and low-arctic Finnmark, reindeer impacts on shrub sapling size are more marked than the effect of a 2°C difference in summer temperature (Ravolainen et al. unpublished). Ungulates, such as reindeer, can furthermore reduce vertical growth and number of shoots for rejuvenated, mature willows (Olofsson and Strengbom 2000, den Herder et al. 2008), and cover of shrub patches at local scale (Pajunen et al. 2008, Kitti et al. 2009). Both large ungulates and small rodents can dramatically reduce growth and cause mortality of still small-statured saplings of

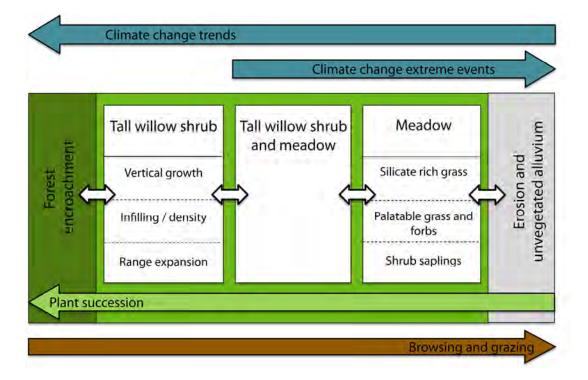


Figure 2.3.3.1. Conceptual model depicting possible transitions between shrub- and meadow-characterized states of tall shrub tundra. Hatched lines separate possible configuration changes in the tall shrub state (see Box 2.3.1) and possible phases within the meadow state (see also Box 2.3.2). The main drivers and the direction of change are indicated. Whereas plant succession and climate change are expected to cause tall shrub and, eventually, forest encroachment, herbivores (in particular ungulates and small rodents) are expected to counteract the encroachment processes. Climate extremes (high precipitation and fast run-offs of water in warmer springs) may cause severe erosion of river banks and a de-vegetated state.

tall-growing willow species (Ravolainen et al. unpublished). Ptarmigans have been found to reduce number of willow buds by their winter herbivory (Tape et al. 2010). Finally, willows support a wide variety of insects, especially herbivorous sawflies and beetles (Kouki et al. 1994, Sipura et al. 2002) and geometrid moths.

The tall shrub state on Varanger peninsula appears at present to be in a steady or even retarding state, due to the combined browsing pressure of reindeer and small rodents. However, the role of the different herbivores in the future is dependent on how climate change impacts each of them, and to what extent management can mitigate some of these impacts. As outlined in other modules (cf. in particular §2.2, 2.4 and 2.5) focusing on climate impacts and management options concerning herbivores, the abundance (and hence impacts) of some herbivore groups are expected to decline (i.e. small rodents; §2.4), while other herbivores' abundances are expected to increase (e.g. insect pests; cf. §2.2 and moose; cf. §2.5). There are however, large uncertainties as to what the cumulative effects of such changes could be.

Plant-plant interactions are likely one important and, as yet, little studied mediator of change in

Box 2.3.3. Tall shrub related bird community

Thickets of tall shrubs in low-arctic tundra hold many of the same structural and functional characteristics essential for birds as the tree-layer in forests. For this reason several bird species that have their strongholds in sub-arctic, boreal, and even temperate forests, are found breeding in tall shrub tundra. Examples are brambling *Fringilla montifringilla*, redwing *Turdus iliacus*, willow warbler *Phylloscopus trochilus*, and redpoll *Carduelis flammea*. A few low-arctic birds species, such as bluethroat *Luscinia svecica* and willow ptarmigan *Lagopus lagopus* (cf. § 2.6), can be considered to be tall shrub specialists. Even open tundra species, such as lapland bunting *Calcarius lapponicus* and golden plower *Pluvialis apricaria*, have been found to occur most frequently in dwarf-shrub heath close to riparian habitats with tall shrubs (Ims and Henden 2012). This is presumably owing to the higher insect abundance associated with the tall willow shrubs (den Herder et al. 2004) that spill over into open tundra. Due to the hot spot function of tall shrubs, bird species richness in a riparian habitat with presence of patches of willow shrubs is estimated to be more than twice compared to equivalent riparian habitats where such willow patches have disappeared due to intense reindeer browsing (Figure B.2.3.3). Moreover, habitat occupancy by the species that depend most on thickets, such as the willow ptarmigan, declines strongly with decreasing areal extent and increasing fragmentation of willow thickets (Henden et al. 2011a).

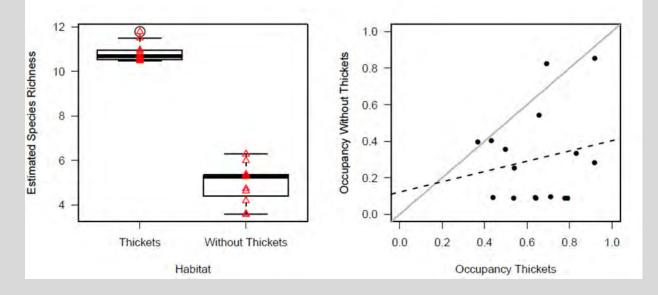


Figure B.2.3.3. Distributions of the plot-specific species richness estimates in riparian habitats with and without willow thickets, displayed by box plots. Right: Scatter plot of species-specific probabilities of occurrence (occupancy) in habitats with thickets vs. habitats without thickets. Dashed black line is the regression line based on the occupancy estimates whereas the solid grey line represents the expected relation based on same occupancy in the two habitats. The points are the occupancy estimates for each of 16 species observed. From Ims and Henden (2012).

shrub extent. Plant functional types of the meadow state, such as graminoids and forbs, increase their cover as much as do the deciduous shrubs when subjected to warmer temperatures (Walker et al. 2006, Elmendorf et al. 2012), and may mediate the ability of shrub saplings to grow and initiate shrub expansion. Particularly, we suspect that silica-rich grasses are important in this regard, potentially outcompeting both shrub saplings and more palatable forbs and grasses (see below).

2.3.3.3. Meadow state sensitivity

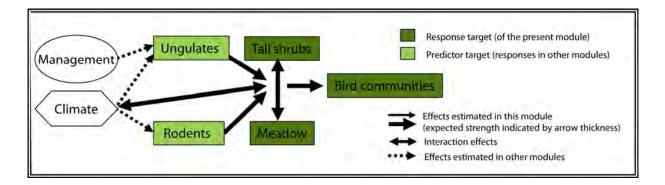
Variation in plant species composition in the meadow state can be recognized as different phases (Box 2.3.2), and resilience of the meadow state to shrub expansion may be dependent on the meadow phase. For instance, large turf-forming grasses typical of the silica-rich grass phase may suppress shrub growth more than forbs and grasses typical of the other meadow phases. Within the open meadows of tall shrub tundra small rodents and reindeer change the functional composition of plants and total standing crop (Ravolainen et al. 2011). Under no grazing, the abundance of forbs, vascular cryptogams, and deciduous shrubs (i.e. mostly Salix saplings) increases whereas abundance of more unpalatable, silica-rich grasses decreases. Hence, it seems that mammalian herbivory reduces availability of some of the most palatable plants, whereas meadows in the phase dominated by silica-rich grasses may be maintained or even promoted. Substantial dominance of silica-rich grasses on riparian sediment plains in several river catchments of Varanger peninsula has been observed half a century ago (Lyftingsmo 1965) and in recent time (Karlsen et al. 2005, Ravolainen et al. 2011, Ravolainen et al. 2013). However, it is unknown whether silica-rich grasses are

expanding with climate change or under the current grazing regime.

2.3.4. Climate change impact predictions

2.3.4.1. Climate effects on tall shrub tundra

Model 2.3.4.1 outlines predictor targets and impact paths for state shifts within the tall shrub tundra expressed in terms of state variables of two composite response targets of the tall shrub tundra; i.e. meadows state and tall shrub state. Predictions and impact paths concerning transitions between forest and tall shrub tundra in the foresttundra ecotone is dealt with in climate impact path model 2.2.4.1 (cf. §2.2). The most certain climate impact path is due the direct effect of warmer and longer summers (and possibly increased precipitation), causing the succession trajectory from the meadow to the shrub stage to be accelerated (see also Figure 2.3.3.1). The rate of this state transition within the shrub tundra could be from less than 5 years (Holland et al. 2005) to decadal timescales (Sturm et al. 2001b). Actual rates of expansion are, however, likely to depend upon meadow characteristics (i.e. the phases described in Box 2.3.2 and Figure 2.3.3.1), and most profoundly herbivory. Indeed, herbivore browsing of ungulates (mainly reindeer) and rodents (mainly tundra vole) seem presently to be able to counteract climate impact on shrub expansion on Varanger peninsula. However, the role of herbivores is also likely to be impacted by climate (i.e. the indirect pathway of model 2.3.4.1 and predictions deduced in climate impact paths models 2.4.4.1 and 2.5.4.1). The impacts of small rodents are predicted to become smaller due to dampened or lost tundra vole and lemming population peaks (cf. §2.4). The browsing impacts of ungulates will



Model 2.3.4.1. Climate impact path model for the tall shrub module. Details regarding expected transitions within the tall shrub tundra are given in figure 2.3.3.1, and for the bird community in Box 2.3.3.

be dependent on the sign and magnitude of climate impact on reindeer and moose, in conjunction with changes and adaptations in ungulate management regimes (cf. §2.3.5 and §2.5).

3.4.2. Climate feedbacks

Changes in shrub areal extent and height will modify winter surface reflectance (Chapin et al. 2005, Bewley et al. 2007), and in summer surface reflectance may also change depending on vegetation state (Blok et al. 2011b). However, changes in evapotranspiration may cause climatic feedbacks that can be even stronger than surface reflectance effects (Swann et al. 2010). It is not clear at what strengths different feedback mechanisms contribute to climatic feedback from tall shrub tundra, and it is even less clear how they are modified by the vegetation state of the tall shrub tundra.

2.3.4.3. Cascading impact on the bird community

Changes in extent and configuration of tall shrubs will impact the abundance, structure and species richness of bird communities in the tundra.

2.3.5. Management options

While the expectation following climate change is shrub expansion, and ultimately forest encroachment, the obvious possibility to mitigate or prevent this encroachment is ungulate management. Reindeer are at present using the Varanger peninsula as summer pasture, and are left to roam freely through the growing season. There is currently no data that can be used to predict how reindeer will actually use the peninsula as climate changes (§2.5). These animals are, however, owned and herded by the Sámi people, organized in herding units. If necessary, there may be a potential in the future for developing adaptive management targeted on keeping down encroaching shrubs and trees in co-operation with the herders (§5.1). Willows can respond very rapidly to release from herbivory, reaching similar levels to that of long-term exclosures in only 4 years (Holland et al. 2005). Hence, management actions likely need to be continuous. Prudent management of ungulates should, however, be balanced so as to avoid a state shift into less productive meadow phases (increase in unpalatable plants), erosion, and complete loss of tall shrub patches and associated biodiversity (i.e. bird species).

2.3.6. COAT team competence

The tall shrub tundra module will be led by the Northern Population and Ecosystem Unit at UoT. Team members in charge are Kari Anne Bråthen (UoT) and Virve Ravolainen (UoT) with contributions from Dorothee Ehrich (UoT), John-André Henden (UoT), Rolf A. Ims (UoT), Nigel Yoccoz (UoT), Jane Uhd Jepsen (NINA) and Audun Stien (NINA). The team members have experience from both research and monitoring. Team members have been responsible for developing the national monitoring plan for vegetation of protected alpine and arctic tundra areas in Norway (Norwegian Directorate for Nature Management). The team participates in the circumpolar "Shrub Hub" network (chaired by Isla Myers-Smith at University of Edinburgh, Scotland) where studies on response of woody arctic and alpine vegetation to climate warming will be coordinated. Team members have long research experience from studies on vegetation responses to herbivory (Bråthen and Oksanen 2001, Bråthen et al. 2007a, Ravolainen et al. 2010) with current emphases on tall shrub tundra (Ravolainen et al. 2011, Ravolainen et al. submitted), and have tight collaboration with equivalent activities on Iceland (represented by our partner Ingibjörg Svala Jónsdottir). Team members have considerable competence on vegetation attributes that will be affected by climate change, such as plant functional composition (Bråthen et al. 2007a), phenology (Iversen et al. 2009), plant diversity (Ravolainen et al. 2010) and role of silica rich grasses (Soininen et al. 2013), as well as remote sensing applications (Jepsen et al. 2009b). Furthermore, the team has considerable competence on trophic interactions, from studies on ungulate population dynamics and habitat use (Tveraa et al. 2007, Stien et al. 2010a), trophic cascades (Ims et al. 2007b) to the importance of tundra shrubs for the low-arctic food web (Henden et al. 2011a, Henden et al. 2011b, Ehrich et al. 2012a). The team competence has gained from experience in using large-scale, hierarchical study-designs (Bråthen et al. 2007a, Ravolainen et al. 2010), including landscape-scale experimental studies (Ravolainen et al. 2011), which are rare in the context of field-based vegetation studies. These study designs are made feasible by the use of an effective field method (Bråthen and Hagberg 2004) that will also be central to the continued research activities of COAT, where the competence on study design will be essential in the task of grasping complex, spatially heterogeneous responses of vegetation to climate change.



Photo: Rolf A. Ims

Summary of the rodent module

Functions and relevance:

Small rodents (lemmings and voles) constitute a guild of *key-stone species* in tundra ecosystems. Their cyclically high abundance cause *pulses of high grazing impacts on plant communities*, provides *subsistence prey for an endemic guild of specialist predators* and a host of *indirect food web interactions* likely to *maintain endemic arctic biodiversity* and *tundra ecosystem integrity*. Climate impacts on arctic rodents (in particular lemmings) are already indicated for some tundra ecosystems, but their wider ecological consequences have yet to be explored.

Response targets:

Rodents: Norwegian lemmings, Grey-sided voles and Tundra voles.

Plant communities: *snow beds* associated with lemming; *dwarf-shrub heaths* associated with grey-sided vole.

Specialist predators: *snowy owl* and *pomarine skua* mainly associated with lemmings, and *long-tailed skua, rough-legged buzzard*, and *mustelids (weasel and stoat)* associated with the entire small rodent guild.

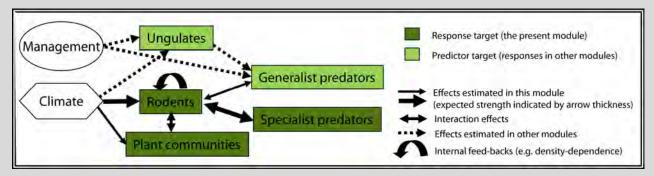
Predictor targets:

Plant community state changes in *Tall shrub module* interacting with lemming and tundra vole. *Plant community* state changes in the *Tundra-forest ecotone* module interacting with the rodent guild. *Generalist predators* in the *Ungulate, Ptarmigan* and *Arctic fox* modules interacting with rodents.

Climate impact path model and its main predictions:

The main impact path is expected to act through warmer winters causing dampened, irregular or lost rodent population cycles with the largest effects on the Norwegian lemming. Two major cascading impacts of the changed rodent dynamics and guild structure are expected: One acts on the guild of specialist predators of which in particular lemming-dependent species are predicted to be strongly negatively impacted. The other acts on plant communities for which reduced rodent grazing impacts will contribute to vegetation state changes.

The path model also addresses the potentially modifying effects of intra-specific and inter-specific density dependence within the rodent guild, predator-prey interactions (feedbacks on rodents and cascading impact on birds communities in tundra heath), plant-rodent interactions (feedbacks) including climate impacts on plant communities.



Management options:

Given strong impact of generalist predators, ungulate management (cf. ungulate module) and generalists predator control (cf. arctic fox and ptarmigan modules) are possible management options.

2.4.1. Functioning

2.4.1.1. Small rodent cycles

Small rodents are a key component of the terrestrial tundra ecosystem (Krebs 2011). They can consume considerably more plant material than large herbivores (Batzli et al. 1980) and are the most important prey for many terrestrial arctic predators (Gilg et al. 2003, Krebs et al. 2003). In many areas of the Arctic, lemmings are the dominant small rodent species, but several species of voles can also be important. Lemming populations exhibit multiannual density fluctuations, often called "lemming cycles", in most arctic regions (Stenseth and Ims 1993). Population cycles of arctic small rodents have typically a period of three to five years, but there is considerable variation in cycle period and amplitude (Angerbjorn et al. 2001, Krebs et al. 2002, Gilg et al. 2003, Gruyer et al. 2008). Where several species of lemmings and voles are sympatric, density fluctuations are generally synchronous (Krebs et al. 2002, Gruyer et al. 2008). Population density cycles create a boom and bust system which influences large parts of the tundra food web (Ims and Fuglei 2005). While many possible causes for the lemming cycles have been suggested (Stenseth and Ims 1993), there is at present a consensus that trophic interactions, either predator-prey interactions (Sittler 1995, Gauthier et al. 2009) and/or plant-herbivore interactions (Turchin et al. 2000, Oksanen et al. 2008) are involved. While small rodent cycles are a fundamental characteristic of the food web structure and dynamics on Varanger peninsula, Svalbard lacks native small rodents. An introduced population of sibling voles (Microtus levis) is present on Svalbard in a very local area (Fredga et al. 1990). Because this population does not (yet) assume a key function in the ecosystem, but is important for the life cycle of Echinococcus multilocularis, a parasite of arctic foxes and a human health risk, it will be addressed in §2.8.

2.4.1.2. Small rodents as plant consumers

The impact of lemmings on the vegetation is evident after winters with high densities (Moen et al. 1993), but also voles can exert strong impact on plants (Dahlgren et al. 2007, Olofsson et al. 2012). The impact of small rodents on the vegetation affects nutrient turnover, causes disturbance and influences species composition (Dahlgren et al. 2009a). Moreover, Oksanen et al. (2008) suggested that lemmings have evolved to be particularly efficient grazers under harsh conditions, and that their evolution during the Pleistocene may have played an important role for the evolution of arctic plants. Thus, certain states of vegetation may depend on the disturbance caused by lemmings during their episodic outbreaks (Oksanen et al. 2008). The impact of the Norwegian lemming (Lemmus lemmus) is particularly important in snow beds (Box 2.4.1), as they reside in these habitats in winter (Stenseth and Ims 1993, Virtanen et al. 1997, Virtanen 2000, Virtanen et al. 2002). Lemming exclosures have shown that grazing impacts both the biomass and species composition in snow beds. At high densities lemmings graze also considerably in the dwarf shrub tundra (Box 2.4.2), and destroy additional dwarf shrubs by clearing runways in the subnivean space. Greysided voles (Myodes rufocanus) graze as well intensely on dwarf shrubs at high densities and have a considerable effect on the vegetation (Dahlgren et al. 2007, Dahlgren et al. 2009a). Vaccinium myrtillus, their preferred food plant in winter, can experience serious reduction in biomass and postpone flowering after winters with high grey-sided vole densities. Of particular interest is the role of different species of small rodents as "predators" of ramets of tall shrubs, which may potentially counteract the encroachment of tall shrubs in tundra in a warmer climate (see § 2.3, Olofsson et al. 2009, Ravolainen et al. 2011).

2.4.1.3. Small rodents as prey

Small rodents, and in particular lemmings, are key prey for predators in tundra ecosystems (Wiklund et al. 1999). Resident specialist predators such as the stoat (Mustela erminea) or least weasel (M. nivalis) depend on small rodents year round, and hunt them intensively also during winter by tracking them into their tunnels under the snow. This leaves virtually no predator-free space for small rodents and can thus reduce populations to very low densities. Because of their slower reproductive rate, mustelid abundance follows the small rodent cycle with a lag of one year, creating delayed density dependence (Sittler 1995, Gilg et al. 2003). The interaction between small rodents and resident specialists has thus been put forward as a likely driver of the cycles (Stenseth 1999). Very little population data are, however, available from small mustelids, in particular in arctic regions. Specialized predators among birds are nomadic or migratory, such as snowy owls (Bubo scandiaca) (Gilg et al. 2006), pomarine skuas (Stercorarius pomarinus), rough-legged buzzards (Buteo lagopus) and long-tailed skuas (Stercorarius longicaudus). While the two first species only breed when lemmings are abundant, the rough-legged buzzard and long-tailed skua breed also in high vole density years. Snowy owls and pomarine skuas migrate over large areas to find places with high lemming densities suitable for breeding (Andersson and Erlinge 1977). Such nomadic predators may contribute to large scale synchrony of small rodent cycles (Ims and Steen 1990, Ims and Andreassen 2000). While rough-legged buzzards and snowy owls respond to the size of the rodents peaks in terms of increased clutch size (Figure 2.4.1.1), the reproductive output of the skuas is constrained to maximum 2 young.

The arctic fox (*Vulpes lagopus*) has been characterized as an opportunistic specialist (Elmhagen et al. 2000) and clearly prefers lemmings as prey in the parts of its range where lemmings occur. Although not as specialized as the species listed above, arctic fox densities have been strongly decreasing following the fading out of small rodent cycles in Scandinavia, showing the dependency of this species on high small rodent densities (Ims and Fuglei 2005, Henden et al. 2008, see § 2.8). In years of high small rodent abundance also generalist predators like red foxes (*Vulpes vulpes*), corvids (*Corvus* spp.) or gulls consume considerable amounts of these preys, contributing to decreasing their numbers.

Whereas the importance of small rodents for plants and predators is clear, there has been considerable controversy about the role of plants versus predators as the regulating mechanism behind

cyclic small rodent dynamics. Assuming a topdown control of food web dynamics, some researchers explain the rodent cycles as resulting from predator-prey interactions with small mustelids as key resident specialist predators (Gilg et al. 2003, Gauthier et al. 2009). The regulating impact of specialist predators is supported by time series analysis (Stenseth 1999), population dynamic modeling (Gilg et al. 2003) and some experimental evidence (Reid et al. 1995, Wilson et al. 1999). Others argues for a bottom-up regulation of tundra food web dynamics and attribute the main regulating role to plant-herbivore interactions, in particular in high-arctic/high-alpine situations were specialist predators are thought to be scarce and plant productivity low (Turchin et al. 2000, Oksanen et al. 2008).

2.4.1.4. Cascading impact of rodent cycles in food webs through alternative prey mechanisms

Generalist predator functional (and numerical) response to the rodent cycle may cause the predator-prey interaction cycle to cascade further to species that may serve as alternative prey to rodents (Ims and Fuglei 2005). It is well known that the recruitment rate in birds such as ptarmigan (see §2.6), waders and geese is sometimes well entrained to the population cycles of voles and lemmings. The reason is that eggs and young of these ground nesting birds are subject to increased predation rate in crash years of the rodent



Figure 2.4.1.1. Predators specialized on small rodents produce large clutches in lemming peak years on the Varanger peninsula. From the Norwegian lemming peak year of 2011: Young of rough-legged buzzard to the left and snowy owl to the right. Photo: R.A. Ims.

cycle. Hence their recruitment rate cycle in synchrony with rodent cycle, with high recruitment rates in rodent peaks and low rates in rodent crash years.

2.4.1.5. The small rodent guild on Varanger peninsula and its food web functions

Three species of small rodents are present on Varanger peninsula. They occupy different habitats and their population dynamics, as well as their role in the ecosystem, differ to some extent. Norwegian lemmings prefer hummocky bogs with Sphagnum spp. and Rubus chamaemorus in summer, but expand into most habitats in years of high densities. In winter they inhabit primarily snowbeds (Box 2.4.1) where they can feed on mosses and breed under the thick insulating snow layer. The main habitat of grey-sided voles is dwarf-shrub tundra (Box 2.4.2). They have a varied diet in summer (Soininen et al. 2009), while their most important food plant in winter appears to be Vaccinium myrtillus. Tundra voles (Microtus *oeconomus*) occupy the most productive parts of the landscape consisting of tall shrub tundra in states of shrub patches and meadows growing along river sediment plains (cf. §2.3). The tundra voles subsist on a diet of mainly herbs and graminoids (Tast 1966, Soininen et al. 2009). While the two vole species are cycling in inter-specific and spatial synchrony with a period of five years in north-eastern Fennoscandia (Ims and Yoccoz unpublished), lemming dynamics are considerably

less regular. After a period of two decades without lemming peaks, lemmings exhibited a large scale outbreak with relatively moderate amplitude in Finnmark in 2007 (Ims et al. 2011). A new, higher amplitude outbreak has taken place in 2011 in large tracts of Fennoscandia including Varanger peninsula (Figure 2.4.1.2). The dynamics of voles and lemmings differ also in the shape of population trajectories (Ims et al. 2011). Because lemmings breed under the snow, their densities can increase over the winter preceding a peak year, and reach high densities in spring, whereas vole populations usually decrease during winter, despite occasional winter breeding, and are highest in fall (Ims and Fuglei 2005). Lemming populations grow also more steeply previous to peak years and exhibit sharper peaks than vole populations, a difference which has been attributed to different population regulation mechanisms (Turchin et al. 2000, Oksanen et al. 2008) or to adaptations to winter breeding (Ims et al. 2011).

Lemmings play a key role in this ecosystem as prey for the exclusively arctic nomadic predators, the snowy owl and pomarine skua, both of which breed occasionally on Varanger pensinsula in high amplitude lemming outbreak years (Øien 2011, Ims unpublished). The Pomarine skua bred in 2011 about 200 m above sea level in flat, marshy areas with many small lakes (Øien 2011). Snowy owls breed in stony tundra above 250 m a.s.l. (Ims unpublished). Snowy owl is the only lemming-dependent bird that resides on Varanger peninsula in the winter. Both rough-legged

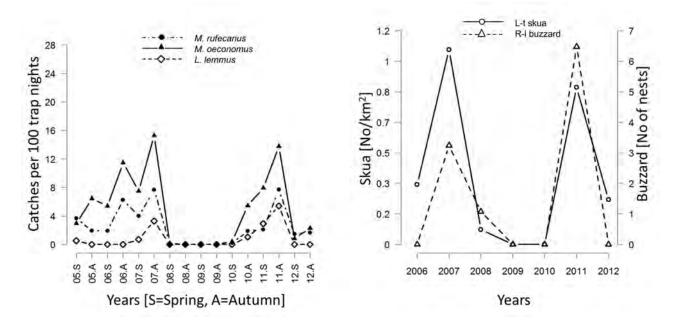


Figure 2.4.1.2. Trajectories of the three small rodents; grey-sided vole (*M. rufocanus*), tundra vole (*M. oeconomus*) and Norwegian lemming (*L. lemmus*), and two of specialist predators; Long-tailed skua and rough-legged buzzard. The time series are from the Komag valley intensive monitoring site on Varanger peninsula.

buzzards and long-tailed skuas breed from sea level to 350 m a.s.l. at traditional sites; the buzzards in slopes and cliffs while the skuas on flat tundra often close to bogs and mires. Long-tailed skuas reach breeding densities as high as > 1 pair per km² (Figure 2.4.1.2) and are clearly the numerically dominant small rodent predator among the birds (Ims et al. 2007a). Among the mammals least weasels, stoats, and both arctic (cf. § 2.8) and red foxes respond strongly both functionally and numerically to voles and lemmings. Corvids, specifically the hooded crow (Corvus corone) and common raven (Corvus corax) are present - the raven all over the peninsula, whereas the hooded crow only close to the tree-line (Killengreen et al. 2012). Both corvids are known to prey on small rodents (Haftorn 1971). However, it is unknown to what extent they respond functionally and numerically to rodent cycles. The functional and numerical responses of predators are known to affect many other components in the tundra food web through "the alternative prey mechanism" (Bety et al. 2002, Ims and Fuglei 2005). In this science plan these mechanisms will be dealt with in the ptarmigan module see §2.6).

Not much is known about the importance of direct competition between small rodent species in Varanger. Because the three species share the same predator guild, indirect relations mediated by shared predators can notably be expected. Whereas apparent competition is likely between tundra voles and grey-sided voles inhabiting heath adjacent to productive sediment plains (Henden et al. in prep.), apparent mutualism has been documented between grey-sided voles and lemmings (Ims et al. 2011). Concerning the potential effect small rodents can have on other tundra herbivores and vice versa, there are indications that Norwegian lemming grazing may facilitate better quality reindeer pastures, by removing mosses and promoting the growth of vascular plants, in particular graminoids in snow beds (Ims et al. 2007b). Moreover, the rodent community is likely to be affected by the massive impact of geometrid moth outbreaks on ground vegetation in the forest-tundra ecotone (cf. §2.2) and in Betula nana shrub tundra.

2.4.2. Ecosystem services and other aspects of societal relevance

Small rodents do not provide final ecosystem services themselves (Mace et al. 2012), but may have pervasive effects on many other components of the food web that provide such services. For this

56

reason small rodents are included as predictor targets in all of the other monitoring modules for COAT Varanger peninsula. A fading out of the cycles would lead to profound changes in ecosystem structure and function (Ims and Fuglei 2005), changes which would represent a loss of a typical component of Norwegian nature and lead to significant losses of arctic biodiversity, including the guild of specialists predators (cf. §2.4.1.4). The Norwegian lemming deserves special attention in this context. It is the only mammal endemic to Fennoscandia and the only mammal named "Norwegian" in English. Because of their conspicuous behavior at high densities, lemmings occupy a prominent place in Norwegian and Sámi culture and folklore. "To become angry as a lemming" is a common saying in Norwegian. In the Sámi folklore lemmings appear in the legend about Stallo, whose sledge is pulled either by reindeer or lemmings. The large lemming outbreak in northern Norway in 2011 received also considerable coverage in the media, reflecting public interest for this species.

2.4.3. Sensitivity

2.4.3.1. Winter climate During the last decades small rodent cycles have been fading out in several parts of the Arctic and these changes in dynamics have been related to climate change (Hörnfeldt et al. 2005, Ims and Fuglei 2005, Ims et al. 2008, Gilg et al. 2009). First indications that the typically northern high amplitude rodent cycles could be linked to winter climate were obtained from the analysis of geographic gradients (Hansson and Henttonen 1985, 1988). Fennoscandian vole cycles decrease in amplitude and period length from north to south (Bjørnstad et al. 1995, Henden et al. 2009a) and this pattern was related to the duration of winter and the increasing abundance of generalist predators (Hansson and Henttonen 1985). A similar pattern was observed in Hokkaido, Japan, and also attributed to a gradient in winter length (Saitoh et al. 1998). Starting in the 1980s the dynamics of voles in northern or alpine Fennoscandia has changed from the typical multiannual cycles to low amplitude or annual fluctuations with similar or lower multiannual average densities (Hörnfeldt 2004, Hörnfeldt et al. 2005, Kausrud et al. 2008). These changes may be caused by an increased frequency of meltingfreezing events in winter leading to ground icecrust formation in winter, which is detrimental for the survival of tundra voles (Aars and Ims 2002, Korslund and Steen 2006, Ims et al. 2008).

Kausrud et al. (2008) showed that the change in dynamics of Norwegian lemmings in the alpine tundra of southern Norway was correlated with snow hardness.

Dynamics have recently also changed in lemming -dominated arctic ecosystems. A modeling study showed that the changes in lemming dynamics observed in eastern Greenland were consistent with expectations for a longer snow-free season and less stable snow conditions (Gilg et al. 2009). This fading out of small rodent cycles has clear negative consequences for small rodent predators both in the Arctic (Ims and Fuglei 2005, Gilg et al. 2009, Schmidt et al. 2012) and in boreal northern Fennoscandia (Hörnfeldt et al. 2005).

Box 2.4.1. Snowbed habitats

Snowbed habitats are influenced by deposition of snow to such a degree that it much overrules other conditions. Often located in topographic depressions, snowbeds are covered with substantial depths of snow for much of the year, lasting long into the period of spring and summer. Consequently, the soil temperature of snowbed habitats is very stable during winter months, making these habitats an ideal place for lemmings to spend their winter. In summer snowbeds serve as important feeding habitats especially for reindeer (Skogland 1984, Edenius et al. 2003, Ims et al. 2007b). Late emergence from snow causes snowbeds to provide young, nutritious plants for an extended period of time into the summer season.

The plant community type in snowbed habitats depends on the amount of snow and the duration of the snow free season. In extreme snowbeds, that is snowbeds with large amounts of snow and a short snow free season, vascular cryptogams such as bryophytes (mosses) dominate. In late or moderate snowbeds, where the duration of the snow free season is longer, substantially more vascular plants such as small forbs, grasses and sedges are present. However, both small rodents and ungulates have a significant impact on plant community composition (e.g. Moen et al. 1993, Virtanen 2000, Olofsson et al. 2002, Olofsson et al. 2004), severely reducing plant biomass when abundant.

Because of their dependency on snow, snowbeds are likely to be highly sensitive to climate change. Monitoring snow beds has recently been highlighted as a priority issue by the Nordic Council of Ministers concerning climate impacts on Nature (Nordic Council of Ministers 2009). Studies in boreal forest show that a longer snow free season will facilitate growth of large pleurocarp mosses (Okland et al. 2004) and this effect combined with less frequent rodent outbreaks may cause a thicker and denser moss cover (Rydgren et al. 2007). Based on these results, we predict that mosses may be the growth form responding most substantially. Moreover, in tundra snow beds, earlier disappearance of snow with increased temperatures can cause invasion of shrubs and boreal species (Virtanen et al. 2003, Bjork and Molau 2007), severely transforming what characterizes these habitats. To what extent such vegetation transformations change the quality of snowbeds as habitats to small rodents is unknown, but is likely dependent on interactions between climate, herbivory, and plant species identity. For instance, mammalian herbivory may counteract effects of climate warming on the development of plant communities in snowbed habitats.



Figure B.2.4.1. Snowbed on the Varanger Peninsula. Here the snowbed habitats are mostly dominated by acrocarp bryophyte species of *Dicranum* and *Polytrichum*, along with vascular plants such as *Salix herbacea* and *Carex bigelowii*. Photo: L. E. Støvern

On Varanger peninsula, lemmings are the most climate sensitive small rodent species. Ims et al. (2011) showed that lemming population growth in winter increased with higher altitude, and explained this correlation with the orographic effect of lower temperatures and more stable snow cover. No such correlation was observed for sympatric grey-sided voles, indicating that the potential climate sensitivity of these voles is not due to the same factors as for lemmings. At present both tundra voles and grey-sided voles exhibit cycles with a period of five years on Varanger peninsula and have thus not been affected by the changes in dynamics observed in boreal and sub-arctic forests of northern Fennoscandia (Hörnfeldt et al. 2006). Vole population dynamics are characterized by population increase in summer and population decrease in winter. Little is known about how specific winter conditions affect the survival of these voles in the southern arctic tundra.

Lemmings experience irregular outbreaks, but in contrary to the pattern typical for the high arctic, their densities usually increase over the summer to reach a maximum in fall. The small rodent guild and their associated species and interactions in the food web can thus be considered to be in a transitional state between typically arctic lemming dominated dynamics and vole dominated dynamics (Ims and Fuglei 2005, see also figure 2.4.4.1). It is important to note, however, that the expected decrease in amplitude and regularity of small rodent cycles under climate change is not likely to result in smooth, monotonous trends as long as climate parameters themselves do not change monotonously. Analyses of long-term time series (>70 years) extending back to the late 1800s have shown evidence for non-stationary dynamics also during earlier times (Steen et al. 1990, Angerbjorn et al. 2001, Henden et al. 2009a). Periods with non -cyclic dynamics have tended to coincide with periods with warm winter climate (Henden et al. 2009a). Conversely, the recent emergence of a large-scale, high amplitude lemming and vole outbreak (2010-2011) throughout the Fennoscandian peninsula (including Kola Peninsula in Russia) coincided with two relatively cold winters and favorable snow conditions without ice layers (Rasmus and Henttonen pers. comm.). Thus we might expect that small rodent population fluctuations in boreal and arctic regions, at least for some decades, will continue to wink in and out of high amplitude cycles (in particular for lemmings). However, with the predicted longterm trend in arctic climate towards warmer winters with more thaw-freeze episodes, absence of proper rodent peaks are likely to prevail in the future.

Finally, it is important to be aware that temporal loss of high amplitude population cycles may result from transient dynamics of non-linear food web interactions, as has been shown by mathematical models and experimental work on simple laboratory model systems (Hastings 2004). Such an explanation for periods of non-cyclic dynamics has also been proposed for boreal rodents (Hanski and Henttonen 1996, Brommer et al. 2010). Thus, relative short-term alterations of cycle characteristics as such cannot be attributed to climate change unless convincing mechanistic relations between climatic variables and rodent population dynamics are established.

2.4.3.2. Sensitivity of dependent predator species

The anticipated shift in the small rodent guild and its spatio-temporal dynamics will have consequences for the composition of the guild of truly arctic predators. The different predator species appear to differ in their requirements for successful breeding in terms of abundance of rodent prey. Typically, arctic lemming specialists such as snowy owls (Gilg et al. 2003) and pomarine skuas appear to be most demanding and will not breed unless lemmings are very abundant (Pitelka et al. 1955, Wiklund et al. 1998). The lemming abundance threshold for arctic fox breeding seems to be lower, possibly because they also exploit other food resources than owls and raptors. Roughlegged buzzards and long-tailed skuas breed in all small rodent peaks (and sometimes in increase years; cf. Figure 2.4.4.1) probably because they also hunt in habitats where grey-sided voles and tundra voles are dominant. This may be a function of their hunting mode or of lower food requirement for bringing up young. Small rodent dynamics may change in different ways. Simulations showed that the growth rate of arctic foxes was highly sensitive to the temporal mean of small rodent densities, and to some extent to the variance, whereas the period of the cycles was not important (Henden et al. 2008). More knowledge about the requirements of other predators is needed to predict changes in predator guild with climate induced changes in small rodent dynamics. Among the predators, the snowy owl has been clearly declining in northern Norway during the last century (Jacobsen 2005) and has now the status endangered ("sterkt truet"). The arctic fox is critically endangered ("kritisk truet"). The roughlegged buzzard and the long-tailed skua are not

Box 2.4.2. Dwarf shrub tundra habitat

Dwarf shrub tundra is the most extensive vegetation type in the circumpolar Arctic (Walker and Gould 2002), covering heath, leeside and ridge habitats, and it is the most wide-spread vegetation type in Varanger. Dwarf shrub tundra is dominated by late successional species that often have strong impact on ecosystem processes. Graminoids and forbs are generally present only as a minor components, but may be more common where moisture availability increases, such as in leeside habitats.

The extensive coverage of dwarf shrub tundra makes it an important habitat to herbivores not being specialized on other vegetation types (e.g. reindeer). While grey-sided voles have this tundra type as their main habitat, lemmings may also be periodically abundant, particularly in the most mesic parts of dwarf shrub tundra. With their woody structures dwarf shrubs are important as cover for small rodents in summer and subnivean space in winter. Accordingly, in wintertime dwarf shrubs may be heavily impacted by small rodents, both through the loss of buds and other plant parts being grazed upon, but also by making paths (Dahlgren et al. 2009b, see figure below). Such winter activity may facilitate establishment of forbs and graminoids in summer. Caribou and reindeer, however, preferentially feed on forbs and graminoids (Skogland 1984, Thing 1984, Bråthen and Oksanen 2001, Bråthen et al. 2007b), potentially reducing their extent in dwarf shrub tundra (but see Olofsson et al. 2001). The berries of several dominating dwarf shrubs are readily consumed by herbivores, but survive the digestive tract of ungulates, germinate (Bråthen et al. 2007a) and may further facilitate dwarf shrub dominance.

Several dwarf shrubs typically have traits that cause them to have low growth rates and low nutrient content (Freschet et al. 2010). One of the perhaps most influential traits is the ability of these species to make soils more acidic at the same time as they have recalcitrant or even allelopathic effects on soil nutrient availability (Bardgett and Wardle 2003). Dwarf shrubs produce phenols that can greatly impair access to N for competing vegetation, but is accessible for themselves through their mycorrhizae (Kraus et al. 2003, Gundale et al. 2010). The phenols also have consequence for dwarf shrub palatability to small rodents. In winter, grey-sided voles prefer dwarf shrub tundra dominated by bilberry that is tall and have a low content of phenols (Hambäck et al. 1998, Hambäck et al. 2002). Also, modifications of the environment brought about by dwarf shrubs is likely to have consequences to the abundance and diversity of other forage plants available to herbivores (Bardgett and Wardle 2003, Bråthen et al. 2010).

With climate change, growth of graminoids (mainly sedges) and dwarf shrubs (both evergreen and deciduous) is predicted to increase in dwarf shrub tundra, whereas abundance of lichens and bryophytes will decrease (Walker et al. 2006). Herbivory by small rodents and reindeer may profoundly modify such development.



Figure B.2.4.2. Different types of dwarf shrub heath on Varanger peninsula. Left: Mesic type with dwarf birch (*Betula nana*) and bilberry (*Vaccinium myrtillus*) which provides a suitable habitat for Norwegian lemmings. Right: dwarf shrub heath dominated crowberry (*Empetrum hermaphroditum*) heavily impacted by small rodent winter activity. Photo: K. A. Bråthen.

on the national red list, but rough-legged buzzards have been declining during the late 1900s (Kjellen and Roos 2000). In the only long-term monitored population of long-tailed skuas in the Arctic (east Greenland) the reproductive success has recently collapsed (Schmidt et al. 2012). Skuas are, however, long-lived birds so that there will probably be a long time lag until the breeding population is affected (Barraquand et al. in prep). Indeed, the strikingly different life history tactics of the guild of rodent predators may render them differentially vulnerable to changes in rodent dynamics to the extent which is not presently known.

2.4.3.3. Small rodents and plant communities

With increasing temperature the length of the growing season and general plant productivity is likely to increase in the Arctic and shrubs are predicted to expand (Sturm et al. 2001b). Shrub expansion may, however, be counteracted by intense grazing of large and small herbivores (cf. §2.3). Whereas the impact of ungulates, notably of semidomestic reindeer, has received considerable attention, the role of small rodents may have been previously underrated (Olofsson et al. 2009, Ravolainen et al. 2011, Olofsson et al. 2012). Willow thickets and the adjacent productive meadows are the habitat of tundra voles, and climate- or grazing induced changes in this habitat could potentially affect the voles. Henden et al. (2011b) showed that although a clear positive effect of thicket fragmentation on the presence of voles was observed in the area with the overall highest density, there were no such effects of willow configuration on tundra voles in the low density areas. As tundra voles feed primarily in the meadow vegetation adjacent to willow thickets, a homogenous expansion of thickets overgrowing the surrounding meadows might be perceived as a reduction of their habitat. On the other hand, if tall shrub expansion is more heterogeneous (e.g. herbivore induced) and accompanied by the existence of the surrounding meadow vegetation, one could hypothesise that the habitat available to tundra voles may increase. Climate change is also likely to affect plant production, nutritious quality and species composition in other focal habitats for small rodents, such as snow beds and dwarf shrub tundra (see Boxes 2.4.1 and 2.4.2), and induce changes which may affect small rodents. Increased productivity and nutrient content of preferred food plants such as mosses or V. myrtillus may be favourable, whereas changes in species composition could be detrimental.

The relationship between vegetation structure, productivity, quality of preferred food plants and small rodent abundance is, however, complicated by the impact the small rodents themselves have on the vegetation. First of all, the direct impact of winter climate may override most indirect climate effects (such as those outlined above mediated by changed vegetation patterns). In that case it is more likely that changed small rodent dynamics, implying modified and possibly less intense grazing, may affect the vegetation. Second, there is potential for top-down trophic cascades to disconnect small rodent abundance from productivity of their food plants. For instance, Aunapuu et al. (2008) found plant productivity to be unrelated to vole abundance in low altitude tundra and attributed this to the top-down regulating impact of predators.

2.4.4. Climate change impact predictions

2.4.4.1. Impact of winter climate on rodent population dynamics and guild structure

Among various pathways in which climate may impact the tundra food webs mediated by altered small rodent population dynamics, we consider the direct impact of winter climate to be the most immediate and important. Among the three small rodent species present in Varanger, the Norwegian lemming is likely to be the most sensitive to climate, as outlined in §2.4.3. If winters become warmer and wetter, and in particular if winters with melting-freezing events and ice crust formation become more common, sizeable lemming outbreaks are expected to become even rarer than they have been during the four last decades in Fennoscandia. The small rodent community may then become dominated by the two vole species. Climate change will thus induce a shift in guild structure (see Figure 2.4.4.1). In a sense this will render the small rodent community and its associated functions in the food web more boreal than arctic (Ims and Fuglei 2005). Further climate change may lead to a transition from multiannual density fluctuations to mainly seasonal fluctuations and possibly lower overall vole densities, as has been observed further south in Fennoscandia. As lemmings are the truly arctic-alpine species in the rodent guild, COAT will in particular focus on the Norwegian lemming.

Although there are correlative data that presently support the direct connection to winter climate both for lemmings (Krebs et al. 2003, Ims et al.

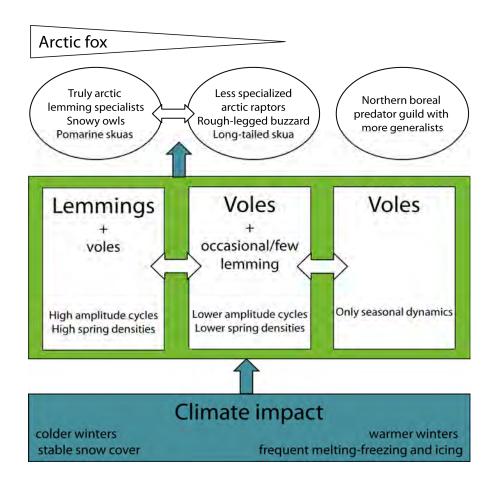


Figure 2.4.4.1. Predicted transitions in small rodent community composition with changing winter climate. Likely associated change in predator guild composition is also shown. Open arrows indicate ecosystem transitions and filled blue arrows indicate climate impact.

2011) and tundra voles (Aars and Ims 2002, Korslund and Steen 2006), we need to improve our ability to predict if, when and where lemming and vole cycles are still likely to occur in the near future. For this we need to establish, in quantitative how primary climate terms. parameters (precipitation, wind and temperature) affect small rodents though snow-cover characteristics. We will implement monitoring designs that allow for substantial spatio-temporal variation in such characteristics as we suspect they will be shaped by topographic, edaphic and vegetation variables at various spatial scales. We predict that there are certain combinations of climate state variables which will make regions, landscapes and habitats more or less prone to harsh snow conditions. It will be a goal for the rodent module of COAT to use data on climate, snow and rodent abundance to build predictive statistical models of such relations in time and space (§2.10). At the same time it will be necessary to get a better understanding of the processes by which snow pack structure limits lemming population growth and affects lemmings and voles differently: Detrimental winter climate could for instance reduce survival, possibly by limiting movements under the snow and access to food, an effect which could be more serious for lemmings that have high nutritious requirements (Batzli 1993, Korslund and Steen

2006), or it could prevent reproduction because of lack of suitably isolated sites for good winter nests (Reid et al. 2012). Such mechanisms for direct climate impact will be investigated experimentally in a possible spin-off project. As trophic interactions will certainly be involved in shaping rodent population and community dynamics (Hansson and Henttonen 1988, Ims et al. 2011), we need for the Norwegian lemming to estimate the recovery rate of mosses in snow beds after outbreaks (Virtanen 2000). The recovery of mosses and the plant community type will clearly also be affected by climate change (see Box 2.4.1). Finally, to develop good prediction models, we need to know to what extent space with benign winter conditions (in terms of snow and food resources) coincides with relative enemy-free space, in particular spatial distribution of small mustelids in winter (Henttonen et al. 1987). We predict that the prevalence of mustelids in lemming winter habitats will be dependent on both the general abundance of voles and the distance to vole patches. Indeed, the fate of lemmings is likely to depend on the impact of climate on the two sympatric vole species and their shared predators.

2.4.4.2. Predicted guild structure shift in specialist rodent predators

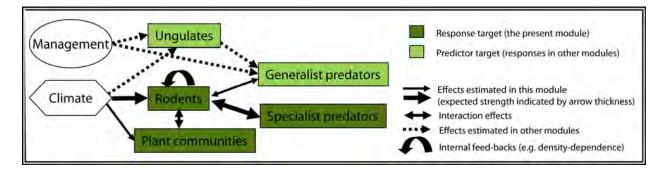
Based on the available knowledge about different rodent-dependent predators (see Figure 2.4.4.1) we predict that climate impact may shift the composition of the specialized predator guild, from the arctic, nomadic lemming specialists (snowy owls and pomarine skuas) to a guild which will be able to reside in tundra based on cycling voles and to some extent alternative prey (long-tailed skuas, rough-legged buzzards and small mustelids) (see Figure 2.4.4.1). There is, however, a need to better quantify the threshold for successful breeding of all predators and, to the extent it is possible, other demographic parameters. This information is needed to parameterize demographic models predicting long-term growth rates and thus extinction probabilities for the different predator species (Henden et al. 2008, Barraquand et al. in prep). Both for such models and as input to the ptarmigan module regarding alternative prey mechanisms (§2.6) there is a need to estimate functional responses for the main predator species.

2.4.4.3. Climate impact path model

Beyond the specific expectation in terms of transitions in rodent population dynamics and guild structure, and their likely knock-on effects on the specialist predator guild outlined above, the main pathways for climate impact on the focal food web module is depicted in Climate impact path model 2.4.4.1.

Besides the specialists predators (i.e. as response targets of the present module), we will in context of rodent dynamics also explore the link to generalist predators (e.g. corvids, red fox) which are monitoring targets focal also to the ptarmigan and arctic fox modules (see §2.6 and §2.8). These predators can be expected to respond numerically and functionally to rodents with possible feedbacks on the rodent dynamics, as well as cascading impact on alternative prey. The cascading impact on alternative prey is a key issue of the ptarmigan module (see §2.6), but will also be dealt with in the present module in terms of an assemblage of shore birds (ringed plower, golden plower, turn-stone and dunlin) which breeding densities will be monitored in survey transects for skuas.

Impact of changed rodent population dynamics and guild structure on major plant communities on Varanger peninsula is partially dealt with in the tall shrub module (§2.3) and forest-tundra ecotone module (§2.2). These modules need input from the present one in terms of seasonal abundance of the three rodent species in different strata of the tundra and forest-tundra ecotone. Among the possible feedbacks from climate induced changes in vegetation to rodents we predict the strongest and most immediate will be due to the dramatic shift in the ground vegetation from dwarf shrubs to graminoids (Jepsen et al. 2013, Karlsen et al. 2013), induced by the recent insect pest outbreak across the forest-tundra ecotone (see §2.2 for details). This has the potential to shift the rodent community in these areas from greysided vole to tundra vole dominance. Focal plant communities (i.e. response targets) of the present module will be snow beds (Box 2.4.1) and dwarf shrub tundra (Box 2.4.2). Snow beds are central because of their importance to lemming population growth during winter and the strong effect lemming grazing has on snow bed plant communities, as well as the expected climate sensitivity of snow beds in general (Bjork and Molau 2007). We predict in particular that mosses will be impacted by warmer climate and shorter winter seasons (Box 2.4.1), but how this balance against the effect of less lemming grazing on mosses is unclear.



Model 2.4.4.1. Climate impact path model for the rodent module. Details regarding expected transitions in rodent guild structure and population dynamics and their knock-on effects on specialist predators are provided in Figure 2.4.4.1 and \$2.4.4.1 and \$2.4.4.2).

Note that also a facilitating effect of lemming grazing on quality of reindeer pasture have been suggested to be centered on snow beds (Ims et al. 2007b). Dwarf shrub tundra is the key habitat of grey-side voles, and is also used by lemmings (Box 2.4.2). Note, however, that the impact of climate induced changes of the vegetation on small rodents is likely to be a much slower process than the immediate direct impacts of changes in winter climate on small rodent population growth.

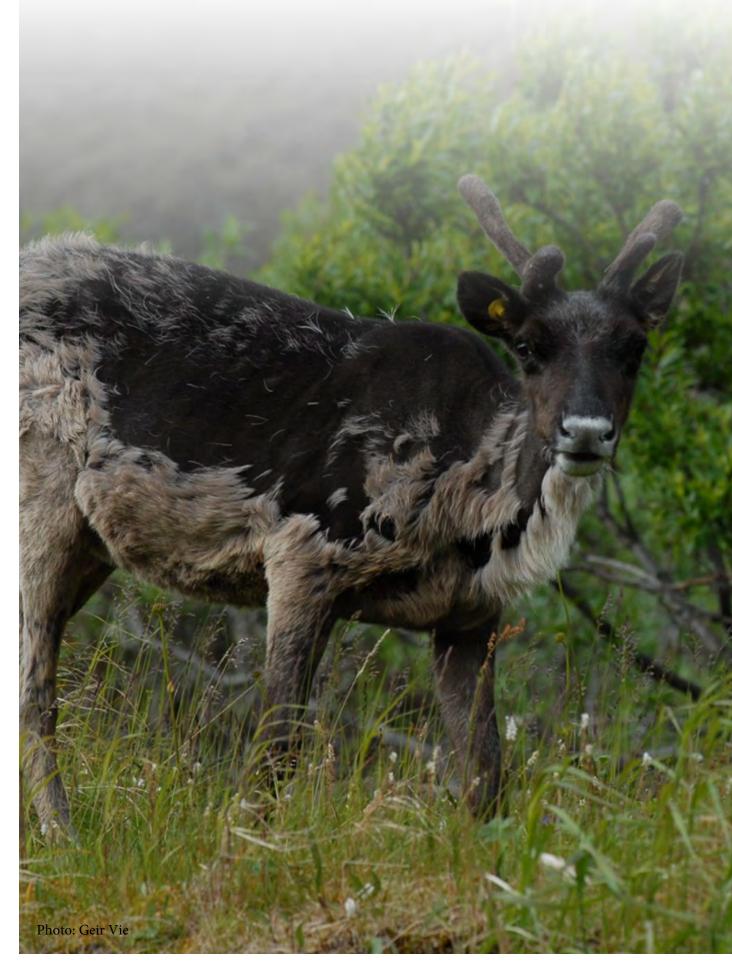
2.4.5. Management options

In contrast to temperate regions where small rodents can have seriously detrimental effects on agricultural production, they are not acting as pests in the arctic tundra (however, note the effect of invasive sibling voles in Svalbard addressed in §2.8). They are also not providing any final ecosystem services, and are therefore not directly targeted by any management actions. The small rodent community may, however, indirectly be affected by management actions directed at other ecosystem components. In term of grazing impacts there is presently no evidence that reindeer impact rodent abundance (Ims et al. 2007b). However, at high reindeer densities and especially in bad winters, numerous reindeer carcasses constitute significant subsidies for generalist predators such as red foxes or corvids (Killengreen et al. 2011, Killengreen et al. 2012). As generalist predators have a stabilizing effect on population dynamics, increased presence of such opportunistic generalists may be hypothesized to strengthen the impact of climate change on population cycles. Generalist predator control (red fox culling) might also potentially have an effect on small rodent dynamics.

2.4.6. COAT team competence

The small rodent module will be led by the Northern Population and Ecosystem Unit at UoT. Team members in charge are Dorothee Ehrich (UoT) and John-André Henden (UoT) with contributions from Kari Anne Bråthen, Rolf A. Ims, Siw T. Killengreen and Nigel G. Yoccoz. There is extensive competence within this team on all aspects of the ecology of arctic rodents relevant to COAT, including development of monitoring designs (Yoccoz and Ims 2004), assessment of climate impacts on demography (Aars and Ims 2002) and associated changes in population dynamics (Yoccoz et al. 2001b, Ims et al. 2008, Ims et al. 2011, Menyushina et al. 2012), rodent - habitat relations (Henden et al. 2011b), grazing impacts on plants (Ravolainen et al. 2011), rodentpredator interactions (Ims and Andreassen 2000) and impacts of changed rodent dynamics on specialists lemming predator guilds (Henden et al. 2008, Schmidt et al. 2012). The team is also engaged in active collaboration about climate change consequences for small rodent populations in Scandinavia and elsewhere, notably with Anders Angerbjörn, (University of Stockholm), Heikki Henttonen (METLA, Finland) and Xavier Lambin (University of Aberdeen).

2.5 Ungulate module (Varanger and Svalbard)



Functions and relevance:

Large ungulates constitute key-stone herbivorous species in tundra ecosystems and the tundra-forest ecotone and are main providers of ecosystem services in the form of meat and fur. They are abundant, have strong impacts on vegetation communities, are important prey for large predators, and provide carrion that supports the mesopredator guild of facultative scavengers.

Response targets:

Large ungulates: *reindeer* and *moose*.

Generalist predators: Lynx, Wolverine, Red fox, Golden eagle and White-tailed eagle

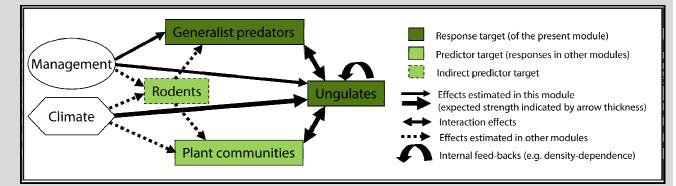
Predictor targets:

Plant communities: changes in the distribution of *forest-tundra ecotone*, and community state change in *tall shrub tundra* and *snow beds*.

Rodents: Changed impact of lemmings on snow bed plant communities

Climate impact path model predictions:

The main direct impact path is expected to act through warmer winters causing rain-on-snow and groundice that limit forage accessibility and cause starvation in reindeer, and through warmer and longer summers causing green forage available for a longer period of the year and thereby improved survival and reproductive rates in both moose and reindeer. Two major cascading impacts of changes in the abundance of large ungulates is expected: One acts on the guild of generalist predators, of which most also act as facultative scavengers. Elevated abundances of large herbivores are expected to contribute more carrion and thereby support larger populations of generalist predators, with a negative feedback effect on early calf survival in reindeer. The other acts on plant communities for which changes in large ungulate grazing pressure will contribute to vegetation state changes. The path model also addresses the potentially modifying effects of intra-specific and inter-specific density dependence among large ungulates and the modifying role of other herbivores on vegetation state changes.



Management options:

Large ungulates and many of the generalist predators are managed by adjustment of harvest levels.



Summary of the ungulate module (Svalbard)

Functions and relevance:

The *Svalbard reindeer is an endemic subspecies* and a *key-stone herbivore* in the high-arctic terrestrial ecosystem in Svalbard. It has *strong impacts on vegetation communities* and is *harvested by local people*. *Reindeer carrion* provides crucial *food resources for arctic fox* which may bring about *cascading impacts on other herbivores* (in particular ptarmigan and geese) in the food web.

Response targets:

Large ungulates: Svalbard reindeer

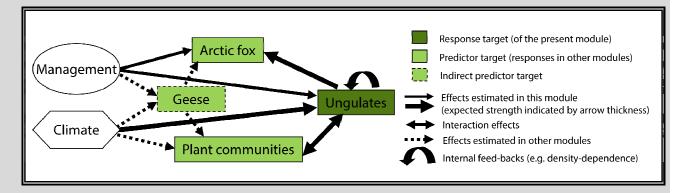
Predictor targets:

Plant community: Wet and mesic moss dominated fen vegetation.

Geese: Increasing population of pink-footed goose

Climate impact path model predictions:

The main direct impact path is expected to act through warmer winters causing rain-on-snow and groundice that limit forage accessibility and cause starvation in reindeer, and through warmer and longer summers causing green forage available for a longer period of the year and thereby improved survival and reproductive rates. Changed abundance of reindeer will impact plant communities through changed grazing pressure and may contribute to vegetation state changes. The path model also addresses the potentially modifying effects of geese on vegetation state changes.



Management options:

Svalbard reindeer is managed by adjustment of harvest levels.

2.5.1. Functioning

Large ungulates are found at high abundances in most terrestrial ecosystems of the world. They are often key species that have important effects on vegetation communities (Zimov et al. 1995, Augustine and McNaughton 1998, Oksanen and Oksanen 2000, van der Wal 2006), are important prey for large predators (Fuller and Sievert 2001, Hayward et al. 2007), and provide carrion that support the mesopredator guild of facultative scavengers (Killengreen et al. 2011, Eide et al. 2012). There are few species of large ungulates associated with the arctic tundra, but population densities can be high even though primary production is low. With its circumpolar distribution and often relatively high population densities, the reindeer (Rangifer tarandus) is the most abundant large herbivore in arctic tundra. In addition to reindeer, the moose (Alces alces) is widespread in the tundra-forest ecotone throughout the northern hemisphere, where it shows habitat overlap with reindeer. The specialist tundra herbivore, the muskox (Ovibos moschatus), is primarily found in parts of arctic North America and Greenland.

2.5.1.1. Large herbivores as plant consumers

Large herbivores have a significant impact on the vegetation community structure of the arctic tundra (Suominen and Olofsson 2000, van der Wal

2006). However, the impact may depend on several factors including the local species pool, local habitat productivity and grazing intensity (Austrheim and Eriksson 2001). Reindeer have a wide diet including sedges, grasses, willows and lichens. It is well known that lichens are sensitive to grazing and trampling (Manseau et al. 1996, Kumpula et al. 2000, van der Wal et al. 2001, Tømmervik et al. 2012), and at high reindeer densities preferred lichen species become depleted quickly (van der Wal et al. 2001, Hansen et al. 2007). The recovery of lichens after severe overgrazing is less predictable. In high-arctic Svalbard such recovery seems very slow or non-existent (Hansen et al. 2007), while reductions in reindeer densities seems to have resulted in a fast recovery of lichens on winter pastures in Finnmark (Tømmervik et al. 2012). In Svalbard a main effect of reindeer grazing is a reduction in the widespread moss layer. This has positive effects on vascular plants, in particular on grasses, and suggests that reindeer grazing facilitates the growth of preferred forage species (van der Wal et al. 2004, van der Wal and Brooker 2004, Gornall et al. 2007, Gornall et al. 2009, Gornall et al. 2011). In Finnmark, the moss layer is less extensive (Bråthen et al. 2007a, Tømmervik et al. 2012) and contrary to what observed on Svalbard, high reindeer densities seem to limit the biomass of palatable grasses and forbs on summer pastures (Bråthen and Oksanen 2001, Bråthen et al. 2007a, Ravolainen et



Figure 2.5.1.1. Moose are regularly using tall shrub tundra with patches of tall willow shrubs which is prime browse. The two moose in the photo (a cow and her calf) were found more than 20 km from the closest forest line on Varanger peninsula. Photo: Rolf A. Ims

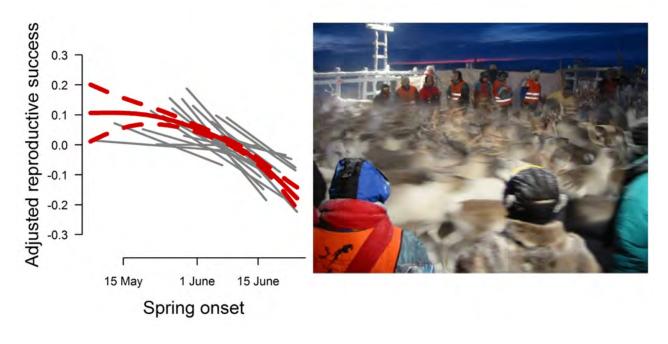


Figure 2.5.1.2. For semi-domesticated reindeer in Finnmark late spring is associated with reduced reproductive success in the data from 19 reindeer management districts over the last 10 yrs (left). Reproductive success (calves per female) have been adjusted for the effect of herd population size and peak plant biomass. Gray lines gives the linear regression line for each district, while the red line gives the overall non-linear smooth spline estimate (\pm 1 SE) (Tveraa et al. 2013). Winter corralling (right), Semi-domesticated reindeer in Finnmark are usually brought into a corral twice a year.

al. 2011) and facilitate non-palatable silica-rich grasses (Ravolainen et al. 2011), causing reduced habitat productivity (Bråthen et al. 2007a, Ravolainen et al. 2011). Non-palatable ericoid shrubs are dominant plants on reindeer summer pastures in northern Norway (Bråthen et al. 2007a), but the role of grazing in the development of this pattern is at present unclear (Bråthen et al. 2007a). Reindeer browsing has significant impact on the growth and expansion of tall shrubs (cf. §2.3), and can thereby counteract the ongoing greening in arctic ecosystems (den Herder et al. 2004, Post and Pedersen 2008, Olofsson et al. 2009). Moose are also browsers of shrubs (van Beest et al. 2010) and therefore have the potential to contribute to reduced shrub expansion, especially near (Figure 2.5.1.1) and in the tundra-forest ecotone. However, the importance of moose to vegetation in the subarctic tundra-forest ecotone is so far not well known.

The significant impact of reindeer on tundra plant communities and plant productivity suggest that the grazing pressure in many areas is high. Observed strong density dependent effects on the body mass growth of calves (Tveraa et al. 2007, Bårdsen and Tveraa 2012), on their fecundity (Solberg et al. 2001, Tyler et al. 2008, Bårdsen and Tveraa 2012) and reindeer population growth rates (Solberg et al. 2001, Tveraa et al. 2007, Tyler et al. 2008, Hansen et al. 2011) give strong support to the notion that reindeer populations are food limited at high densities. However, the impact of between year variability in plant productivity and changes in plant community composition on reindeer population dynamics is still largely unknown. This is to some degree due to difficulties in monitoring variability in plant productivity at the spatial scale of reindeer habitat use. The use of satellite derived indices of plant productivity (NDVI and EVI, see Pettorelli et al. 2005) have recently allowed such studies to be done, and has shown that between year variability in EVI integrated over the plant growing season has significant effects on reindeer body mass growth and fecundity (Bårdsen and Tveraa 2012). This effect of the integrated EVI on reindeer demography may be partly caused by variability in the length of the plant growth season (Garel et al. 2011), but both the timing of the onset of spring (Helle and Kojola 2008, Tveraa et al. 2013, Figure 2.5.1.2), and peak plant biomass seems to be of importance for reindeer population dynamics in northern Fennoscandia (Tveraa et al. 2013).

Also the fecundity of moose is affected by spring climate conditions (Grøtan et al. 2009). However, the availability of food throughout the winter is often suggested to be a main determinant of reindeer population growth (Solberg et al. 2001, Kohler and Aanes 2004, Hansen et al. 2011, Stien et al. 2012, Hansen et al. 2013). If so, the snow conditions and the presence of ice on ground may be more important for winter food availability than summer plant production, and reduce the impact of variability in plant productivity on reindeer population growth. The significant impact of reindeer on plant community composition and productivity may have knock-on effects on other herbivores in the tundra ecosystem. In particular, a negative effect of reindeer and moose browsing on the distribution and abundance of willow thickets (*Salix* sp.) in northern Fennoscandia (cf. $\S2.3$), has the potential to have significant negative effects on hare and willow ptarmigan population densities (Ims et al. 2007b, Ehrich et al. 2012a).

2.5.1.2. Large herbivores as prey

In ecosystems with large predators, predation can have important impacts on the population dynamics of large ungulates (e.g. Skogland 1991, Owen-Smith and Mills 2006). The terrestrial ecosystem on Svalbard contains no functional predators of reindeer. Predation events by polar bears (Ursus maritimus, Derocher et al. 2000) and the arctic fox (Vulpes alopex) on reindeer calves (Tyler 1986) are regarded as rare and of little significance. In northern Fennoscandia, the only obligate predator that preys on reindeer is the lynx (Lynx lynx). The lynx is closely associated with the forest ecotone, but may also enter the tundra in search of prey. In sub-arctic areas, where alternative prey is scarce, reindeer is the main prey species of lynx (Mattisson et al. 2011). The lynx is also regarded to be the main predator of reindeer (Direktoratet for Naturforvaltning 2010) while the wolverine (Gulo gulo) and golden eagle (Aquila chrysaetos), are the second most important predators of reindeer in northern Fennoscandia (Direktoratet for Naturforvaltning 2010). The latter two species are, however, facultative scavengers that also utilize available reindeer carcasses. Carcasses of reindeer killed by lynx, is a main food source for wolverine in areas where both species are present (Mattisson et al. 2011). While it has been documented that the golden eagle can kill adult reindeer, most reindeer killed by the golden eagle are taken as calves in the course of their first summer (Fauchald et al. 2004, Norberg et al. 2006, Nieminen et al. 2011). In addition, the brown bear (Ursus arctos) and the red fox (Vulpes vulpes) are known to kill reindeer calves (Fauchald et al. 2004, Nieminen et al. 2011).

Clearly, there are several potential predator species associated with the tundra biome, and reindeer herders in northern Fennoscandia report large losses of reindeer to predators. Still, our current understanding of the population dynamics of reindeer in Finnmark is that food limitation, caused by variability in spring climate and local reindeer densities, is the main determinant of these losses (Tveraa et al. 2013). An observed strong relationship between the body condition of reindeer, their fecundity and mortality is one pattern that lends support to this conclusion (Tveraa et al. 2003). Furthermore, the main objective of the Norwegian management regime for large predators (i.e. wolf Canis lupus, brown bear, lynx and wolverine), is to keep population sizes low, and reported losses in the reindeer industry are substantially higher than the losses expected to be caused by the relatively small predator populations found in the northernmost parts of Norway (Herfindal et al. 2011). In the current situation it is likely that reindeer have significant bottom-up effects on the population dynamics of intermediate sized predators and scavengers in northern Norway (Henden et al. 2013), while the top-down effects of predators on reindeer is likely to be weak and mainly affect early calf survival. Reindeer carcasses resulting from die-offs due to severe winter climate or density dependent food limitation is currently the most likely explanation for the observed meso-predator / scavenger release in Fennoscandian tundra ecosystems (Killengreen et al. 2011), and also play a significant role in the population dynamics of the arctic fox on Svalbard (Fuglei et al. 2003, Eide et al. 2012, Hansen et al. 2013). The impact of reindeer on the meso-predator / scavenger guild is likely to depend on the extent of the annual migration between summer and winter pastures since migratory behavior will reduce the availability of carcasses / prey for parts of the year (Fryxell and Sinclair 1988, Henden et al. 2013). Ground nesting birds, hares and rodents may all be affected by elevated meso-predator abundances (Fuglei et al. 2003, Gauthier et al. 2004). This suggests that reindeer may impact a range of tundra species through effects on the meso-predator / scavenger guild and the mechanism of alternative prey. These cascading impacts of ungulates, acting thought the guild of generalist predators, are key issues to be considered in the ptarmigan (§2.6), goose (§2.7) and arctic fox (§2.8) modules of COAT. In addition, elevated meso-predator abundances are expected to have negative feedback effects on the survival of reindeer, in particular the early survival of reindeer calves (Tveraa et al. 2003).

2.5.2. Ecosystem services and other aspects of societal relevance

Large ungulates are main providers of ecosystem services in the Arctic. Extensive hunting and harvesting of reindeer and moose provide provisioning services such as meat and fur. They provide supporting services as they are important in the nutrient cycling, nutrient dispersal and seed dispersal in the tundra. They provide regulating services through effects on the shrub expansion on the tundra. Finally, they provide cultural services, being a key component in the culture of many indigenous people, and through recreational experiences to hunters. In Fennoscandia, reindeer is the cornerstone in the Sámi reindeer herding culture. The Svalbard reindeer (Rangifer tarandus platyrhynchus) is endemic to Svalbard and the sub -species is only found there. This suggests that Norwegian governmental bodies should have a special focus on conservation issues regarding the sub-species.

2.5.3. Sensitivity

While the ongoing global warming has led to northwards expansion of shrubs (cf. §2.3), and greening of the arctic tundra (Sturm et al. 2001b, Tape et al. 2006) important herbivores, including reindeer, are some places on retreat (Ims et al. 2008, Vors and Boyce 2009). Climate change may

influence large herbivores through several mechanisms which may impact population dynamics differently in the different seasons of the year. Global warming is leading to an earlier onset of spring and longer and warmer plant growth seasons (Myneni et al. 1997). These changes has direct effects on plants, causing increased primary production and changes in the plant community structure (e.g. Chapin et al. 1995, Arft et al. 1999, Hudson and Henry 2009). Changes that are likely to allow herbivore populations to increase (Tews et al. 2007), and may alleviate at least some of the negative effects of a poorer winter climate (Helle and Kojola 2008, Tveraa et al. 2013). However, in the Arctic reproduction is typically timed to coincide with the short spring and summer season, and any mismatch between the spring-summer peak in food quality or availability, and the peak in food requirements associated with reproduction, may negatively impact individual performance. The ability of reindeer to adjust breeding according to shifts in the timing of the seasons may therefore become an important determinant of future population sizes (Post and Forchhammer 2008).

In the winter, climate change is expected to cause milder and wetter weather, leading to more compact and crusted snow, or ice, on the tundra that hinder herbivores' access to food (Kausrud et al. 2008, Hansen et al. 2011). This may induce migration to habitats less affected by crusted snow and

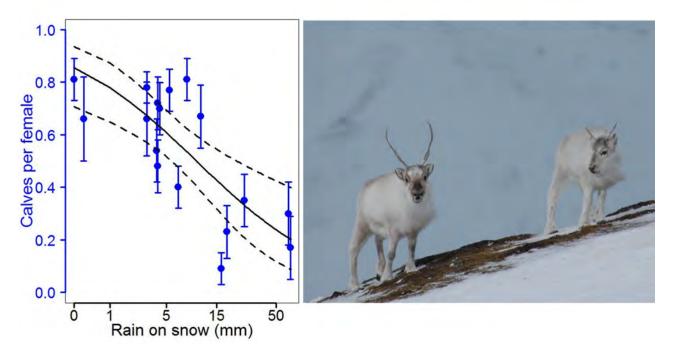


Figure 2.5.3.1. The relationship between the amount of rain-on-snow events in winter and calves per female Svalbard reindeer the following summer based on a 16-year monitoring series from Colesdalen-Reindalen area in Svalbard (left). The logistic regression line and 95% confidence envelopes (dotted lines) are given logistic regression (Stien et al. 2012). A female Svalbard reindeer with her calf in late winter (right, photo: Erik Ropstad).

icing (Stien et al. 2010a), and eventually die-offs and population collapses following extreme climatic events (Solberg et al. 2001, Kohler and Aanes 2004, Hansen et al. 2011, Hansen et al. 2013). In Svalbard inter-annual variation in reindeer fecundity can, in the present climate regime, to large degree be predicted by the frequency of rain-on-snow events in the winters (Figure 2.5.3.1), but it is unclear to which extent this relation will hold if winters become even warmer and shorter.

Climate change is implicated in changes in species overlap and northward and altitudinal species range shifts (Parmesan and Yohe 2003). We may therefore expect changes both in the abundance and species composition of the parasite fauna of large herbivores (e.g. Laaksonen et al. 2010), and the abundance and species of insects that cause significant harassment of large herbivores (Hagemoen and Reimers 2002, Laaksonen et al. 2010). The most pervasive shift in plant community structure is likely to result from a climate change induced elevation of the tree line (cf.§ 2.2), and expansion of coniferous forests (e.g. Wolf et al. 2008). Such a change may be slow, but will have significant negative effects on the extent of the tundra biome and thereby reduce the available habitat for reindeer in northern Norway. At the same time, such a change may have positive effects on species that have strong links to the forest biome, like moose, brown bear and lynx populations.

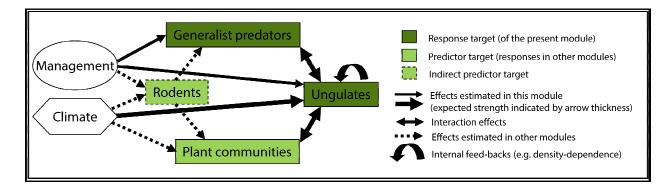
Based on what we know today, the responses to a changing climate are likely to differ significantly among sub-species and sub-populations of reindeer. First, persistent differences in prevailing climatic conditions among populations are likely to determine what weather component being the most important affecting food availability (Post 2005). While deep, compact or crusted snow might be most relevant for populations increasingly exposed to these conditions, variation in summer climate, notably spring onset and greenup, might be more significant for populations where deep snow and icing are rare (e.g. Grøtan et al. 2009). Second, the ability to cope with changes in climate seems to depend on the species ability to adapt to a changing climate. While reindeer in Fennoscandia benefit from an earlier onset of spring, caribou at Greenland fail to breed successfully when spring green-up is advanced (Helle and Kojola 2008, Post and Forchhammer 2008). The exact reasons for these differences are not fully known, but they may be linked to the fact

that Fennoscandian reindeer give birth to their calves earlier than caribou, and time delivery according to their nutritional status (Tveraa et al. 2013). Conversely, caribou appear to have evolved a fixed timing of reproduction (Post and Forchhammer 2008). Accordingly, we believe it is necessary to study reindeer in contrasting environments and disentangle the relative roles of changes in winter and summer climate on reindeer to understand its responses to climate change and predict reindeer's future role in the tundra ecosystem.

2.5.4. Climate change impact predictions

2.5.4.1. Moose and semi-domesticated migrating reindeer: Varanger model

On Varanger peninsula reindeer belonging to reindeer management district 6 (Varjjatnjarga), with a herd size in 2009 of 10000 reindeer, and management district 7 (Rakkonjarga), with a herd size in 2009 of 3800 reindeer, use the peninsula as summer pastures. Winter pastures are further south towards the border of Finland. However, at least in some winters a significant number of reindeer are left to overwinter on the peninsula (Henden et al. 2013), and the timing of the annual migration is likely to be determined by climate. The moose population on the Varanger peninsula was in 2011 estimated to 1200-1500 individuals (E.J. Solberg pers. comm.). The population is growing, and moose are found in most forested areas. Slaughter weights have shown a tendency to decrease over the last 10 years suggesting density dependent responses to the population increase (E.J. Solberg pers. comm.). For the Varanger peninsula, and other sub-arctic tundra ecosystems close to the forest ecotone, we outline a conceptual model that has two main pathways for climate change impacts on moose and reindeer. The first pathway acts through direct effects of climate change on snow and ice conditions in the winter, which determine winter food availability. We expect strong effects of poor winter snow and ice conditions on overwintering reindeer. These climate effects are expected to increase the mortality in winter, and elevated abundances of carcasses is expected to support elevated populations of generalist predators, which are important predators of many species in the tundra ecosystem, including reindeer calves. The impact of the abundance of reindeer carrion on the generalist predator guild will be monitored in conjunction with the arctic fox module (cf.§ 2.8). The second pathway

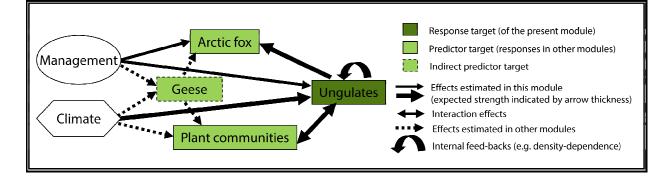


Model 2.5.4.1. Climate impact path model for low-arctic Varanger with ungulates (reindeer and moose) and generalist predators as response targets.

acts through effects of climate change on the plant growing season, with both improved plant growth in the summer and an extended growing season. We hypothesize that 1) an extended plant growth season with earlier springs and a later autumn will have a strong positive effect on both reindeer and moose by reducing the period with poor forage conditions in the winter, and 2) that positive effects of climate change on the seasonal peak biomass of palatable forbs, grasses and tall shrubs (§2.3) is likely to have a positive effect on both reindeer and moose. Furthermore, we hypothesize that a slow response to climate change in the elevation of the tree line and expansion of coniferous forests (§2.2) will have a negative effect on reindeer. Both through reductions in the area covered by tundra, and potentially through positive effects on the lynx population and a reduction in available predator free space. In contrast, an elevated tree-line is expected to have a positive effect on moose population sizes. We recognize that changed dynamics of other keystone herbivores, and in particular geometrid moths (§2.3) and rodents (§2.4), may have a modifying role in determining vegetation state changes and plant forage availability. In tundra, such effects are likely to be expressed in snow bed and tall shrub tundra plant communities, which are vegetation types preferred by reindeer in summer (Ims et al. 2007b). The development of these plant communities, will be monitored in conjunction with the tall shrub and rodent module (cf.§ 2.2. and 2.4). Reindeer responses to and impact on succession pathways of forest floor vegetation after geometrid moth outbreaks will be monitored in coordination with the forest-tundra ecotone module (cf. §2.2).

2.5.4.2. Wild reindeer in the high-arctic: The Svalbard model

Also for the high arctic ecosystem on Svalbard, we outline a conceptual model that has two pathways for climate change impacts on reindeer. As in the Varanger model, one pathway acts through direct effects of climate change on snow and ice conditions in the winter, which determine winter food availability. We expect strong negative effects of poor snow and ice conditions on reindeer. These climate effects are expected to increase the mortality in winter and data on the



Model 2.5.4.2. Climate impact path model for the high-arctic Svalbard for which the Svalbard reindeer is the ungulate response target.

mortality rates obtained from the present module will provide important input to the arctic fox module (cf. §2.8).

The second pathway acts through effects on the plant growing season, with improved plant growth in the summer and an extended growing season. As in the Varanger model, we hypothesize that an extended plant growth season with earlier spring and a later autumn will have a direct and strong positive effect on reindeer by reducing the period with poor forage conditions in the winter. Furthermore, we hypothesize that direct positive effects of climate change on the growth of palatable forbs and grasses is likely to have a positive effect on reindeer. We recognize that climate change has positive effects on the population size of pink-footed geese (§2.7). High densities of geese can cause habitat degradation and may therefore have a modifying role through effects on vegetation communities and negative effects on forage availability to reindeer. The reindeer plant community interactions will be monitored in conjunction with the goose and ptarmigan modules (cf.§ 2.6 and 2.7)

2.5.5. Management options

2.5.5.1. Varanger peninsula: Semi-domesticated reindeer

The population size of semi-domesticated reindeer is largely determined by the harvesting rate of the owners. It is therefore in principle possible to adjust herd sizes to counteract perceived negative effects of climate change, and to improve the fecundity of the reindeer in the case of density dependent negative effects on calf production. Similarly, the population size of moose and lynx may be regulated by adjusting hunting quotas. The potential development towards more forest may be counteracted by forest management or by manipulating grazing pressure from reindeer and moose.

2.5.5.2. Svalbard: Hunting

The Svalbard reindeer is harvested through recreational hunting. The number and spatial distribution of hunting licenses given to inhabitants of Svalbard is under the control of the Governor of Svalbard. Harvesting levels of Svalbard reindeer need to be considered closely in relation to the climate impact outlined in model 2.5.4.2 to ensure that harvesting is sustainable in new climatic settings. In addition, elevated harvesting levels of geese may be considered if the grubbing effects of a high goose population density cause habitat degradation.

2.5.6 COAT team competence

The large ungulate module will be led jointly by the Norwegian Institute of Nature Research (NINA) and Norwegian Polar Institute (NP). Team members in charge are Audun Stien (NINA) and Åshild Ønvik Pedersen (NP) with contributions from Torkild Tveraa (NINA), Per Fauchald (NINA), Erling J. Solberg (NINA), Olav Strand (NINA), Leif Egil Loe (UMB), Jack Kohler (NP), Steve Coulson (UNIS), John-André Henden (UoT), Siw T. Killengreen (UoT), Rolf A. Ims (UoT) and Nigel G. Yoccoz (UoT). NINA and NP are at present responsible for the annual monitoring of Svalbard reindeer populations with focus on climate impacts on population dynamics and demography. Furthermore, the NINA team is responsible for, or heavily involved in, individual based demographic studies and GPS based studies of habitat use, on moose and on reindeer both at Svalbard (with UMB) and on the Norwegian mainland. The UoT researchers were responsible for the project "EcoFinn" (2008-2012) which focuses on the interrelationship between reindeer and generalist carnivores and scavengers. The team has considerable competence in methods of monitoring and analyses of large ungulate population dynamics and demography (Tveraa et al. 2003, Tveraa et al. 2007, Grøtan et al. 2009, Bårdsen and Tveraa 2012, Tveraa et al. 2013), habitat selection (e.g. van Beest et al. 2010), and large ungulate - predator/scavenger interactions (Tveraa et al. 2003, Killengreen et al. 2007, Herfindal et al. 2010, Killengreen et al. 2012, Henden et al. 2013).

2.6. Ptarmigan module (Varanger and Svalbard)



Summary of the ptarmigan module (Varanger)

Functions and relevance:

Rock and willow ptarmigans are *the most popular small game in Fennoscandia* and constitute *subsistence prey for red listed raptors such as the gyrfalcon*. During the last decade ptarmigan populations have exhibited a *severe decline* over large geographic areas, including the Varanger peninsula and climate change has been suggested as a cause. However, the underlying mechanisms, and how management can eventually account for them, are unknown.

Response targets:

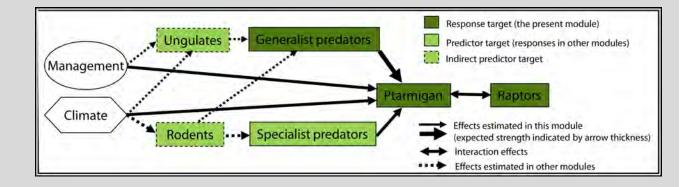
Willow and *rock ptarmigan, generalist predators* as ptarmigan egg and chick predators (see also Arctic fox module) and a *red listed raptor (gyrfalcon)* specialized on ptarmigan prey.

Predictor targets:

Facultative specialist predators on rodents exploiting ptarmigans as alternative prey. Both *rodents* and *ungulates* are to be considered as indirect predictors not entering the analysis of the present path model. *Rodents* are drivers of specialist and generalist predator numerical and functional responses, while *ungulates* (carrion) are key drivers of generalist predator abundance.

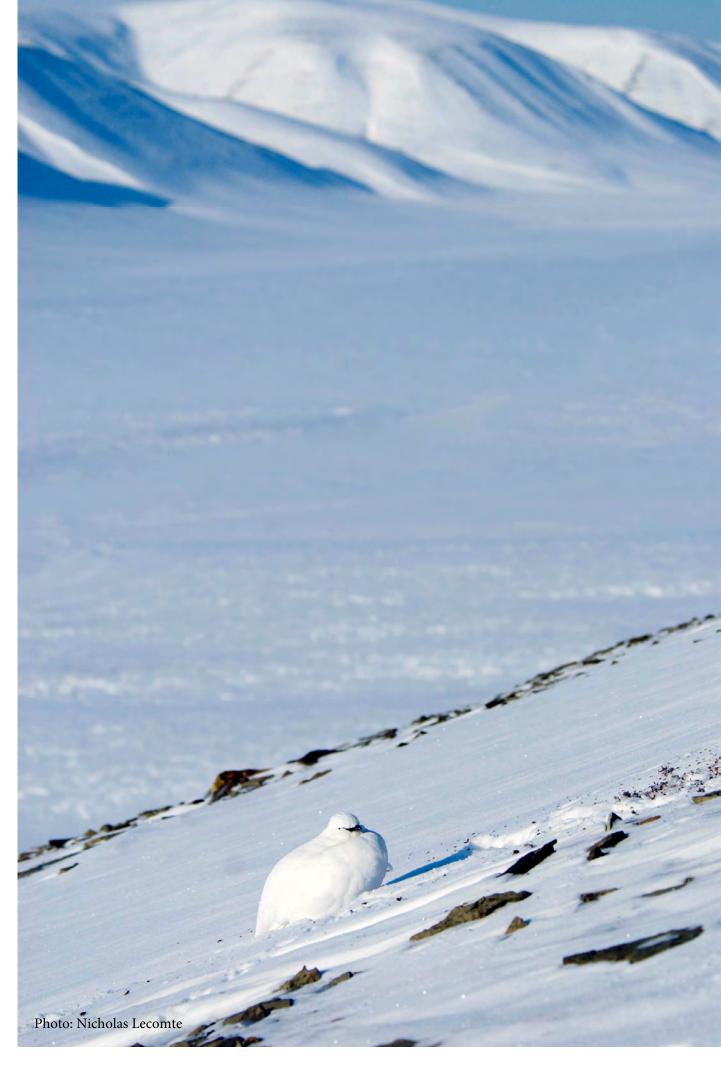
Climate impact path model predictions:

As predation appears to be the key driver of willow ptarmigan demography in Fennoscandia the model emphasizes two pathways for climate impacts on ptarmigan populations that involve predation; one works through specialist predators indirectly driven by changed rodent population dynamics, while the other is indirectly driven by ungulate carrion subsidies to generalist predators. Extreme weather events may also impact ptarmigan reproductive success directly, for instance, by inflicting high chick mortality.



Management options:

Ptarmigan harvesting regulations needs to be adjusted to new climate regimes and food web interactions impinging on ptarmigan population dynamics. Ungulate management could limit the carrion subsidies to generalist predators. Control of overabundant generalist predator populations (e.g. corvids and red fox) may be considered.



Summary of the ptarmigan module (Svalbard)

Functions and relevance:

The *Svalbard rock ptarmigan is an endemic sub-species* occurring as low population densities. As a highly specialized forager in the breeding season, the Svalbard ptarmigan could be hypothesized to be one of the arctic herbivores most *vulnerable to a phenological mismatch* with its preferred food plant under climate change. It is also likely to be affected by *interspecific competition* with other herbivores. The Svalbard rock ptarmigan is a *popular game bird*.

Response targets:

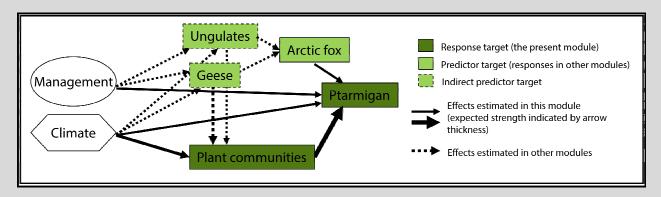
Svalbard rock ptarmigan and *associated plant communities* harboring essential forage plants (in particular *Bistorta vivipara*).

Predictor targets:

Arctic fox directly as a ptarmigan predator and *ungulates* and *geese* as indirect mediators of climate impacts either though predation (arctic fox) or inter-specific competition (geese) for selected food plants.

Climate impact path model predictions:

The model predicts three likely impacts. One is though reduced availability of food plants either resulting from a phenological mismatch between reproductive events in the ptarmigan and their food plants (in particular *Bistorta* bulbil production) or reduced abundance of forage due to increased grazing/grubbing by increasing populations of geese. A second impact is possible through increasing arctic fox predation resulting from more ungulate carrion subsidies. A third impact is extreme weather events in spring harming ptarmigan reproductive success.



Management options:

Reindeer, geese and arctic fox are under strict management regulations (harvesting) in Svalbard.

2.6.1. Functioning

Ptarmigans (Lagopus spp.) are among the most intensively studied birds worldwide (Storch 2007, Moss et al. 2010). The historic attractiveness of these herbivorous birds to research can both be explained by their role as important game species (Aanes et al. 2002), both for recreation and subsistence (Barth 1877), and their fascinating population dynamics, often characterized by multiannual density cycles (Moss and Watson 2001). Willow ptarmigan (Lagopus lagopus) and rock ptarmigan (Lagopus muta) have circumpolar distributions. The willow ptarmigan has its strongholds in the low-arctic tundra and sub-arctic tundra-forest ecotone, while the rock ptarmigan is a species belonging to rocky habitats of high-arctic or highalpine tundra. Arctic ptarmigans are among the few terrestrial birds that are year-round residents in the arctic region.

Different ptarmigan populations may exhibit highly contrasting dynamics depending on the ecosystem they are found. For instance, the endemic Svalbard rock ptarmigan (Lagopus muta hyperborea) occurs in low densities (up to 3 pairs per km²) with relatively little temporal variability (Pedersen et al. 2012). In contrast, sub- and lowarctic willow ptarmigan populations can exhibit highly fluctuating populations with densities that may reach > 100 pairs per km² (Storch 2007), whereas normal densities for Fennoscandia are 5-10 pairs per km² (Lindén and Pedersen 1997). At very high densities willow ptarmigan can impact their food plants, in particular shoots of erect shrubs protruding through the snow cover in winter (Tape et al. 2010). Although habitat quality, as determined by quality and quantity of food plants, certainly is an important determinant of spatial variation in population density, ptarmigans are not thought to be regulated by plantherbivore interactions (Moss and Watson 2001). However, there has been highly conflicting views, and to some extent strong controversy, concerning what regulate ptarmigan populations (Moss and Watson 2001). At least to some extent this can be attributed to the fact that ptarmigan populations are studied in very different food web contexts, climate- and management regimes. For instance, the most extensively studied Lagopus populations are found in the moorlands of northern England and Scotland. Here intensive ecosystem management is almost entirely directed towards the goal of maximizing red grouse (a subspecies of Lagopus lagopus) production – an economically and culturally important game species. Strong control of predators is considered to be crucial for

successful ptarmigan management, causing populations to reach such high densities (max 115 pairs per km2; Hudson and Rands 1988) that aggressive interactions and/or high parasite loads kick in as population regulatory mechanisms strong (Mougeot et al. 2005). The case of the British red grouse, and how it has been managed for centuries, is an implicit recognition of the often important role of predators as determinants of ptarmigan population dynamics (Fletcher et al. 2010). Predation has also been highlighted as a key factor underlying the dynamics of ptarmigan populations in several other ecosystems (Moss and Watson 2001).

The importance and outcome of the interaction between predators and ptarmigans is likely to be dependent on the complexity of the food web, and in particular, the structure and functioning of the predator guild. For instance, in the fairly simple terrestrial food web of Iceland, the 10-year population cycle of the rock ptarmigan appears to be driven by an interaction with its key predator the gyrfalcon (Falco rusticolus) (Nielsen 1999). The gyrfalcon acts on the ptarmigan population as a typical specialist predator both in terms of numerical and functional response (Clum and Cade 1994, Booms and Fuller 2003). In contrast, ptarmigan populations in Fennoscandia, including the Varanger peninsula, find themselves in a very complex setting with a host of predator species belonging to three guilds that all may potentially have significant impacts. The gyrfalcon is present as а ptarmigan specialist (Figure 1.1.5.2;Tømmerås 1993), partly along with the golden eagle (Aquila chrysaetos), which to some extent relies on ptarmigan as prey during the breeding season (Nyström et al. 2006). The golden eagle also partly belongs to a guild of generalists predators that to a large degree subsists on ungulate carrion in winter (c.f. §2.5 and 2.8; Killengreen et al. 2012). Other prominent members in the guild of generalists are raven (Corvus corax), hooded crow (Corvus cornix) and red fox (Vulpes vulpes), which are important ptarmigan predators, in particular on eggs and chicks (i.e. Erikstad et al. 1982, Parker 1984, Munkebye et al. 2003). The third predator guild of interest are facultative rodent specialists (cf. §2.4) of which small mustelids are probably the most important ptarmigan predators (Parker 1984). These specialist rodent predators, and to some extent those of the generalist predators that responds functionally and numerically to the cyclic rodent dynamics, have been proposed to cause 3-5-year cycles in Fennoscandian willow ptarmigan through the "alternative prey mechanism" (Hagen 1952,

Myrberget 1982, Moss and Watson 2001, Ims and Fuglei 2005). Synchronized cycles of small rodents and willow ptarmigan was very clear in time series data from Fennoscandia until the 1980s (Myrberget 1982, Steen et al. 1988), thereafter the synchrony/cyclicity has vanished (see§ 2.6.3.3). For mainland Fennoscandia there is a big discrepancy in the knowledge about population dynamics of the two ptarmigan species. Reliable population time series are not available for the rock ptarmigan so as to establish what kind of population dynamics it exhibits. Unfortunately, the official bag statistics that are reported for rock ptarmigan must be deemed unreliable, because such statistics is most likely "contaminated" by the more common willow ptarmigan.

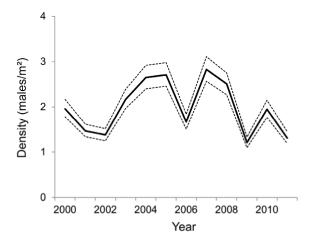


Figure 2.6.1.1. Time series depicting the temporal dynamics of Svalbard rock ptarmigan density (number of territorial males/ km^2 , mean \pm 95% C.I.) in Adventdalen and Sassendalen in Svalbard. Density estimates are obtained using distance sampling methods (modified after Pedersen et al. 2012).

High quality monitoring data is available for the Svalbard rock ptarmigan due to targeted monitoring during the last 12 years and application of proper statistical methods (Pedersen et al. 2012, Figure 2.6.1.1). Also its habitat affiliation and breeding biology is quite well known (Steen and Unander 1985, Pedersen et al. 2007, Pedersen et al. 2012). The Svalbard rock ptarmigan is found in an exceptionally simple terrestrial food web, probably only representative for a few isolated higharctic islands without small rodents and their associated guild of specialist predators. Even the gyrfalcon and other raptors are lacking (Strøm and Bangjord 2004). The only predator that is likely to be of importance to the Svalbard ptarmigan is the arctic fox (Steen and Unander 1985). Consistent with the lack of specialist predators of any kind, the Svalbard rock ptarmigan shows no signs of cyclicity in their generally low-density/ low-amplitude population dynamics (Figure 2.6.1.1).

2.6.2. Ecosystem services and other aspects of societal relevance

2.6.2.1. Harvesting and cultural value

On the Norwegian mainland willow ptarmigan and rock ptarmigan have historically been (Barth 1877) and are currently (SSB 2012b), the most important game species. Annually, approximately 100 000 hunters harvest between 200 000 and 500 000 ptarmigan (Aanes et al. 2002, SSB 2012b, Figure 2.6.2.1). This extensive hunting of ptarmigans was historically an important provisioning service for local people in the tundra region, whereas it presently is providing recreational experiences to hunters. In Finnmark ptarmigans have constituted an important cultural and provisional value to Sámi by means of traditional hunting and trapping. Bag statistics per ptarmigan species are currently reported per municipality.

The Svalbard rock ptarmigan has been hunted for hundreds of years (Løvenskiold 1964) and the species is the most popular small game for recreational harvesting around the local settlement, Longyearbyen (annual harvest range between 486 and 2069 ptarmigans).

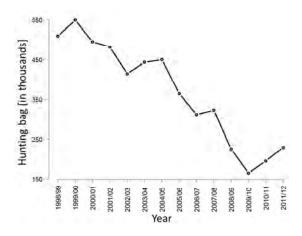


Figure 2.6.2.1. Ptarmigan harvest statistics from entire Norway for the period between 1999 and 2012 (Aanes et al. 2002, SSB 2012b).

During the last decades many species and populations of ptarmigan have been declining and some are even threatened with extinction (Connelly and Braun 1997, Storch 2007, Aldridge et al. 2008). For instance, while Storch (2007) refers to willow ptarmigan as a "non-problem" species, national hunting bag statistics (Figure 2.6.2.1) indicate that numbers of willow ptarmigan have dramatically decreased during the last decades in Norway (Kausrud et al. 2008, SSB 2012b, Henden et al. 2011a). Even though little is known about the dynamics and temporal trends of the rock ptarmigan in Norway, there are some indications of a temporal decrease similar to the willow ptarmigan (SSB 2012b). In contrast to the mainland species, the Svalbard rock ptarmigan has displayed quite low and stable densities during the last 10 years (Pedersen et al. 2012). However, its consistent low density and very restricted range of habitats, which only cover about 3% of the land areas (Pedersen et al. 2012) may render it particularly vulnerable to projected climate change. A recent study (Hansen et al. 2013) showed that extreme climatic events ('rain-on-snow') synchronized population fluctuations across the entire community of resident vertebrates, including the Svalbard rock ptarmigan. In the following we review what is likely to be sensitive aspects of the ecology of arctic ptarmigans that may render them vulnerable to climate change.

2.6.3.1. Intraguild competition

Increased interspecific competition due to facilitated growth of certain species is one of the main hypothesised consequences of climate change (Root and Schneider 2006, Hitch and Leberg 2007). Ptarmigans are herbivorous birds that share food plants with other herbivores both in high-arctic Svalbard and low-arctic Varanger, thus a potential for intra-guild competition is present. Two cases of increased abundance of competing herbivores may be of concern; semidomestic reindeer (cf. §2.3 and 2.5) and arctic geese (§2.7).

The potential impact of reindeer on ptarmigan populations has been addressed in context of reindeer browsing effects on willow shrubs (cf. §2.3). Den Herder et al. (2004) predicted the willow ptarmigan to be among the game species most sensitive to increased competition from high density ungulate populations due to its strong affiliation to willow shrubs as food and cover (Weeden 1969, Moss 1973, Pulliainen and Iivanainen 1981, Chernov 1985, Andreev 1988, Hakkarainen et al. 2007, Tape et al. 2010). In accordance with this prediction, Ims et al. (2007b) found ptarmigans less abundant in herding districts with high reindeer abundance in Finnmark, northern Norway. Moreover, Henden et al. (2011a) found that the spatial variation in willow ptarmigan habitat occupancy on Varanger peninsula was significantly related to browsing-related fragmentation and area reduction of willow thickets. However, the steep temporal decline in ptarmigan occupancy observed during this 4-year study of Henden et al. (2011a) was unrelated to the availability of willow shrubs. Hence, although willow shrubs are clearly important to the willow ptarmigans (providing cover and winter forage) there are certainly other drivers that are responsible for the recent changes in willow ptarmigan population dynamics. For instance, the decline of the ptarmigan populations appears to be equally strong in reindeer winter pastures in Finnmark, where the willow shrubs are not subjected to reindeer browsing (which mainly takes place in summer). Moreover, as shrubs are expected to increase under climate warming in most of the arctic region (cf. §2.3), it is unlikely that shrubs will be a limiting resource for willow ptarmigan in a wider perspective.

In contrast, rock ptarmigans prefer rocky ridges, diversely structured slopes and boulders offering good viewpoints and shelter (Watson 1972, Marti and Bossert 1985, De Juana 1994) where it forages on the often sparse vegetation composed of dwarf shrubs and herbaceous plants (Savory 1989). The transition zone between the heath and rocky ridges is heavily used by reindeer (Ims et al. 2007b), especially when temperatures and insect harassment peak during summer. Consequently, increased competition between reindeer and rock ptarmigans for limited food resources could potentially be a catalyst for population decline of rock ptarmigans, if reindeer grazing reduces the quality, configuration and forage of their preferred habitat. Although increased intraguild competition is a possible threat to the rock ptarmigan in Varanger, we find it to be more important in the Svalbard rock ptarmigan, where it also can be expected to be linked to climate change. In Svalbard the populations of pinkfooted geese (Anser brachyrhynchus) has increased substantially over the last decades, with climate change suggested as one of the major drivers, especially in recent years (§2.7; Madsen and Williams 2012). The impact of the rapidly increasing population of pink-footed geese on vegetation, which already is substantial, is a key subject of the Goose module of the COAT science plan (see

\$2.7). In context of the present module we address the impact of increased numbers of geese from the perspective of increased competitive pressures on the Svalbard rock ptarmigan. The necessary conditions for competition to take place are that the geese and ptarmigan overlap in habitat use, share food plants, and food availability is limited (van der Wal et al. 2000a). The pinkfooted goose share key food plants with the Svalbard rock ptarmigan (Unander and Steen 1985, Fox and Bergersen 2005), and it is well known that intensive goose grazing and grubbing may reduce plant biomass, and cause habitat degradation (Speed et al. 2009). Currently these effects are most profound in wetland habitats that are relatively unimportant to the rock ptarmigan. However, it is not known to what extent the two species will overlap in habitat use if the geese population continues to grow and/or have depleted their food plants in optimal goose habitats. In the Canadian population decline in ptarmigan arctic (Sandercock et al. 2005) have been attributed to expanding populations and severe habitat destruction impacts from snow geese (Anser caerulescens), which substantiate the possibility that a similar situation may develop in Svalbard.

2.6.3.2. Adverse effect of weather and trophic mismatch

Young chicks of ptarmigan are regarded to be highly sensitive to adverse conditions, and survival of chicks through the first few weeks is a critical component of demography in grouse and ptarmigan populations (Hannon and Martin 2006, Ludwig et al. 2006). Adverse weather conditions shortly after hatching can be detrimental for chick survival (Erikstad and Andersen 1983, Ludwig et al. 2006). If climate change involves an increased frequency of extreme weather events during this critical life stage, it may represent a strong direct impact on arctic ptarmigan populations.

Summer food availability has also been forwarded as one critical factor influencing grouse chick mortality (Ludwig et al. 2010). Ptarmigan might be affected through climate induced temporal asymmetry between the availability of important food resources and grouse reproduction, a phenomenon called trophic mismatch (Post and Forchhammer 2008). Both willow and rock ptarmigan chick survival appears dependent on protein-rich food during the first 1-2 weeks (Spidsø 1980, Wegge and Kastdalen 2008), highlighting the chicks as particularly vulnerable to changes in the timing of important food resources. Thus, a trophic mismatch would depend on the climate sensitivity of ptarmigan life-history events and/or food items that are particularly important. Young galliform chicks typically consume large quantities of invertebrates to meet growth and energetic demands (Ford et al. 1938, Spidsø 1980, Jørgensen and Schytte Blix 1985, Savory 1989). However, young ptarmigan (Lagopus spp.) chicks consume large amounts of plant material, using particularly the newly emerged and highly nutritious reproductive plant parts (Dixon 1927, Choate 1963, Weeden 1969, Savory 1977, Spidsø 1980, Williams et al. 1980, Pullianen and Eskonen 1982). In general, graminoids and forbs show larger variability in reproductive phenology than do shrubs (Molau et al. 2005). For instance, reproduction in the forb Bistorta vivipara (syn. Polygonum bistortum) (Figure 2.6.3.1) has been found to fail in the warmer parts of its distributional range (Doak and Morris 2010). On the other hand, Williams et al. (1980) found in a study from Alaska that willow ptarmigan chicks can alter food preference in consecutive years. Thus, as willow and rock ptarmigans seem capable of switching between different food sources depending on their availability, it seems unlikely that phenological mismatch can explain the Norway-scale decline (Henden et al. 2011a) currently observed in willow ptarmigan.



Figure 2.6.3.1. Bulbils of *Bistorta vivipara* is the main food plant of Svalbard rock ptarmigan chicks. Photo: Kari Anne Bråthen.

In Svalbard, however, with its less diverse plant communities and basically no access to aboveground macro-invertebrates, alternative food may be less available to ptarmigan chicks. Consequently, the Svalbard rock ptarmigan has been shown to hold a highly specialised diet during the early chick stage (Unander and Steen 1985). Newly hatched chicks feed almost entirely on protein rich *B. vivipara* bulbils (Unander et al. 1985). Hence, Svalbard rock ptarmigan may be more prone to trophic mismatch than mainland ptarmigans. Reported egg-laying dates in Svalbard span a limited range, coinciding with ambient temperatures above freezing (Steen and Unander 1985). The phenotypic plasticity in time of egg-lying is likely to be limited by a genetically determined photoperiodic effect on gonadal development (Stokkan et al. 1986). These factors suggest that the Svalbard rock ptarmigan may be vulnerable to rapid changes in climate that affect the phenology of its key food plants. With climate warming, soil temperature and soil nutrient availability likely increase in most habitats (Sjögersten et al. 2008) therefore, one might expect increased bulbil production. However, the amount of energy allocated to flower production rather than bulbil production has also been shown to increase with temperature along both altitudinal and latitudinal gradients (Bauert 1993, Fan and Yang 2009). Thus, climate warming may result in less bulbil production and higher seed production, with seeds available later in the growing season than bulbils, and reducing food availability for chicks. In conclusion, the highly specialised diet of the Svalbard rock ptarmigan especially in the chick stage, and the otherwise very simple food web setting in which this subspecies is found, makes it a very suitable case for exploring the likelihood that arctic ptarmigan populations will be impacted by climate change though a trophic mismatch.

2.6.3.3. Predation

The rodent cycle has been forwarded as a key community level process underlying the synchronous cyclic dynamics classically found within the community of small to medium-sized vertebrates in boreal and arctic ecosystems (Elton 1942, Hörnfeldt et al. 1986, Hansson and Henttonen 1988, Gauthier et al. 2004, Ims and Fuglei 2005, Gilg and Yoccoz 2010). However, as reviewed in §2.4 the classical small rodent population cycle with high amplitude peak densities has recently collapsed into non-cyclic low amplitude dynamics

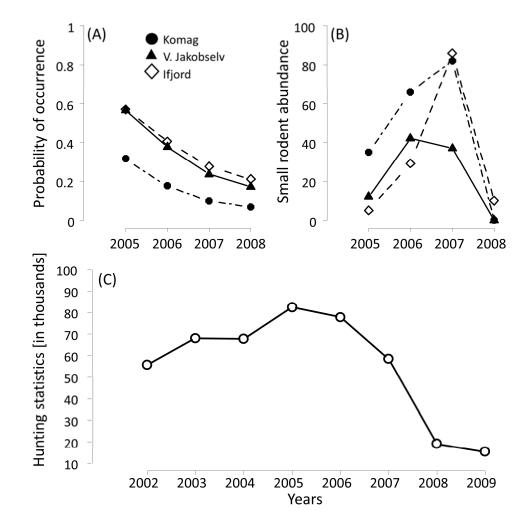


Figure 2.6.3.2. Temporal dynamics of willow ptarmigan habitat occupancy, small rodent population dynamics and hunting statistics. Panel (A) shows the predicted habitat occupancy of willow ptarmigan in autumn for three different regions in Finnmark (two on Varanger peninsula and one in the adjacent Ifjord) and year (2005-2008). Panel (B) depicts the total number of small rodents caught in autumn for each region. Panel (C) depicts the temporal trend in the hunting statistics for Finnmark.

in parts of Fennoscandia (Ims et al. 2008, Kausrud et al. 2008), attributed to increasing frequencies of freeze-melt events during winter (Korslund and Steen 2006). Kausrud et al. (2008) showed that willow ptarmigan populations rapidly declined and cyclicity was lost simultaneously with the sudden collapse of the small rodent cycle in this region. Based on the alternative prey hypothesis (c.f.§ 2.6.1) they attributed the decline of the willow ptarmigan to increased predation impact after the rodent population cyclicity collapsed. However, on Varanger peninsula where the rodent cycle still prevails, Henden et al. (2011b) could not find any effect of the different phases of the rodent cycle on temporal dynamics of willow ptarmigan. That is, the decline rate of the ptarmigan population appeared to be unaffected by the increase, peak and crash of the rodent population (Figure 2.6.3.3). This suggests that some other factor(s) than those predators that usually act to cause synchronous dynamics of rodents and ptarmigans are responsible for the long term depression of ptarmigan population growth. Specifically, there are reasons to propose that constant high abundance of generalists predators may be acting on willow ptarmigan populations. Generalist predators such as foxes and corvids have increased markedly in many places in the world in recent decades (Tapper 1992, Gregory and Marchant 1996, Tannerfeldt et al. 2002). Ground-nesting species are particularly susceptible to predation by avian and mammalian predators, and negative impacts of predation have been recorded for game birds and waterfowl on incubating adults, eggs and chicks (Marcström et al. 1988, Newton 1993, Fletcher et al. 2010, McKinnon et al. 2010). Recently, Fletcher et al. (2010) found that a large-scale reduction in abundance of carrion crow (Corvus corone) (-78%) and red fox (Vulpes vulpes) (-43%) led to an average threefold increase in breeding success of red grouse. Moreover, there are indications that corvids may play a similar role in the decrease of sage grouse in North America. With a warmer climate such predators may increase in tundra simply due to lower physiological demands at higher temperatures or even as a direct consequence of increased human settlements in the arctic region. More importantly in the case of northern Fennoscandia, is availability of reindeer carcasses, which is likely to have increased due to changed management policies in combination with more variable winters with ice-crust formation (Killengreen et al. 2012). Indeed, generalist predators have been shown to stabilise at high densities in response to high reindeer abundance, due to increased access to carcasses in the long

and limiting winter period (Henden et al. in prep). This, in turn, is likely to promote strong and continuous predation pressure on ground nesting species in the summer (Fletcher et al. 2010). Moreover, the fact that low-arctic ptarmigan populations are subjected to the simultaneous impacts of three guilds of predators (generalists, rodent specialists and ptarmigan specialists), with different numerical and functional responses as well as different responses to climate change, provides scope for complex cumulative impacts of ptarmigan populations that cannot be ignored.

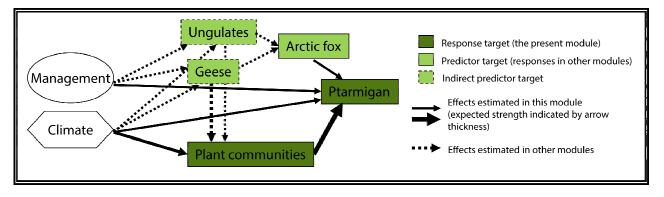
Compared to the complex impacts that may be implied by the functionally diverse predator community in low-arctic Varanger, the situation in terms of predator impacts on high-arctic Svalbard rock ptarmigan is likely to be simpler. This is due to predation from mainly one terrestrial predator species - the arctic fox. The impact of arctic fox predation on the Svalbard rock ptarmigan is not known. However, it has been proposed that, owing to the lack of lemming cycles, arctic fox predation rates on ground breeding birds is likely to be continuously high (Gilg and Yoccoz 2010). Still, temporal and spatial variability in predation rates on Svalbard rock ptarmigan may be caused by climate induced fluctuations in the abundance of alterative food sources for the arctic fox, such as reindeer carrion and breeding geese (Eide et al. 2004, Eide et al. 2012).

2.6.4. Climate change impact models

According to the review of the probable sensitivities of ptarmigan populations to climate change (§2.6.5) we develop climate impact path models that emphasise different mechanisms in higharctic Svalbard (model 2.6.4.1) and low-arctic Varanger (model 2.6.4.2).

2.6.4.1. Model for Svalbard rock ptarmigan

As argued above, the Svalbard rock ptarmigan provides a very suitable case for exploring the likelihood of climate induced trophic mismatch between ptarmigans and their forage plants. Thus the path model for Svalbard rock ptarmigan (model 2.6.4.1) includes plant community as a response target, represented by state variables describing the reproductive phenology and the abundance of a key forage plant. The key prediction regarding trophic mismatch is that increasingly advanced onsets of spring will lead to rapid phenological shifts in *Bistorta vivipara*, while the onset of reproduction in ptarmigan (i.e. egg-



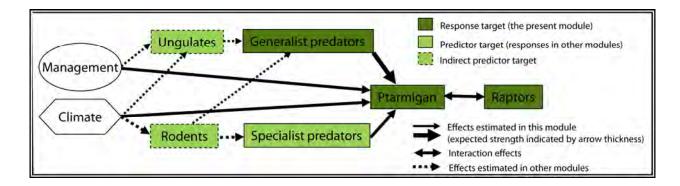
Model 2.6.4.1. Climate impact path model for the high-arctic Svalbard ptarmigan module.

laying) is predicted to be more conservative. Earlier springs is predicted to cause reduced production and quality of Bistorta bulbils with negative effect in terms of reduced growth and survival of ptarmigan chicks. The state variable of the plant community response targets will, in conjunction with monitoring directed by the goose module (cf. §2.7), provide opportunities to quantify a second impact pathway. This pathway is mediated by intensified competition from increasing populations of pink-footed geese (i.e. as an indirect predictor target). Increased abundance of geese is also involved in the third climate impact pathway through increased arctic fox predation (as a predictor target). The elevated arctic fox populations may result from climate-related increased abundances of geese and reindeer mortality. Finally climate may have direct effects on ptarmigan reproduction through adverse weather events during the breeding season.

2.6.4.2. Model for low-arctic ptarmigans

The conceptual path model developed for lowarctic Varanger peninsula focuses on the impacts of the three predator guilds on ptarmigan population dynamics, as well as the direct impact of cli-

mate (adverse weather events) on ptarmigan breeding success. The aim is to target both willow and rock ptarmigan in Varanger, as the degree of inter-specific synchrony in the two ptarmigan species' response to the various predictor targets is likely to provide important insights. However, whereas monitoring methods already have been developed and time series is currently running for willow ptarmigan, we have to adopt the COAT team's experience with monitoring the Svalbard rock ptarmigan, to initiate rock ptarmigan time series in Varanger. Assessment of the impact of specialist rodent predators (denoted specialist predators in model 2.6.4.2), and their connections to climate change, will be coordinated with the small rodent module (cf. §2.4). Generalist predators will be monitored both in conjunction with the present module (focussing on the abundance of corvids in the ptarmigan breeding season), the small rodent module (§2.4) and the arctic fox module (cf. §2.8) focussing on generalist predators utilizing ungulate carrion in the winter. Climate impact enters here through reindeer mortality patterns. Finally, the present module involves one specialist ptarmigan predator - the gyrfalcon (i.e. denoted as raptors in model 2.6.4.2.) as response target, as this species is the only predator that is likely to respond numerically to the ptar-



Model 2.6.4.2. Climate impact path model for the low-arctic Varanger ptarmigan module.

migan abundance. Not included in the path model 2.6.4.2 is the connection between tall shrubs and willow ptarmigan. This connection is highlighted in the tall shrub module (§2.3) where the willow ptarmigan will be monitored together with the entire bird community associated with willow thickets in low-arctic tundra.

2.6.5. Management options

Much focus has recently been devoted to the effect of hunting on willow ptarmigan populations in Fennoscandia (Pedersen et al. 2004, Sandercock et al. 2011). Hunting mortality has been found to act with a substantial additive component to natural mortality, especially when harvesting levels are high. Thus, data on harvesting levels need to enter as a predictor in the analysis of the path models. COAT will cooperate with the agencies that acquire and make use of hunting statistics for management purposes, i.e. The Governor of Svalbard and the Landowner agency in Finnmark (FEFO), in order to improve the quality and use of hunting statistics. The ptarmigan module of COAT aims to provide advice to these management authorities on harvesting regulations whenever such regulations are required. The regulations may take the form of bag-limits, i.e. limit on the number of ptarmigan shot each day by each hunter, restrictions on number of hunter-days in each hunting unit or by preserving high-productive areas from hunting in certain years altogether.

Systematic culling of corvids and red fox populations to release declining ptarmigan populations from predation has successfully been implemented as short term management actions in Northern England (cf. Gibbons et al. 2007, Fletcher et al. 2010). While the benefits of predator control for management and conservation are increasingly recognised (Gibbons et al. 2007), such actions can be contentious if predators and prey are valued differently by different stakeholders (Redpath et al. 2004). There are good reasons to believe that corvid and fox control may be a rational and uncontroversial management action, provided that COAT produces firm evidence that these generalist predators cause substantial pressures on ptarmigan populations and other ground nesting arctic birds, and since the expansion of these predators into tundra ecosystems may have anthropogenic origins (Killengreen et al. 2012). Actions that could be targeted directly at the drivers of such expansion should be considered. Harvesting statistics shows coincidences between increasing red fox and ungulate populations (Selås and Vik 2007). On Varanger peninsula red fox and corvid presence on the peninsula appear to be facilitated by reindeer carrion in winter (Killengreen et al. 2012). Reindeer management practice, in particular factors determining migration patterns and winter mortality, is thus likely to be important (c.f. §2.5). This also regards management of moose populations (harvesting practice) in tundra or in nearby subarctic forest, and management of large carnivores (Elmhagen and Rushton 2007, Elmhagen et al. 2010).

2.6.6. COAT team competence

The ptarmigan module will be led jointly by the Northern Population and Ecosystem Unit at UoT and Norwegian Polar Institute (NP). Team members in charge are Eva Fuglei (NP) and John-André Henden (UoT) with contributions from Rolf A. Ims (UoT), Åshild Pedersen (NP), Dorothee Ehrich (UoT), Nigel G. Yoccoz (UoT) and Pernille Bronken Eidessen (UNIS). The research and monitoring activity of rock ptarmigan in Svalbard are coordinated with equivalent activities on Iceland by Olafur K. Nielsen, Icelandic Institute of natural History, and in Sweden by Maria Hörnell-Willebrand at Hedmark University College, Norway/Grimsö Wildlife research Station, Sweden. NP is at present responsible for the annual monitoring of Svalbard rock ptarmigan with a focus on population dynamics, herbivore-guild and trophic interactions. The UoT researchers are responsible for the project "EcoFinn" (2008-2012) which focuses on research on impacts of ungulate browsing mediated habitat alteration on small to medium sized herbivores (including ptarmigan) on Varanger peninsula. The team harbors considerable competence on methods of monitoring and analyses of ptarmigan population dynamics (Pedersen et al. 2012), assessment of hunting impact (Pedersen et al. 2004), ptarmigan-habitat relations (Henden et al. 2011a, Ehrich et al. 2012a), predictive habitat models (Pedersen et al. 2007), and predation on ground nesting birds (Klausen et al. 2010, Pedersen et al. 2010a).

2.7. Goose module (Svalbard)



Summary of the goose module

Functions and relevance:

Geese constitute key-stone herbivorous species in tundra ecosystems. Their population sizes increase due to climate change and environmental factors on their staging and wintering grounds outside Svalbard. Increasing abundances cause high grazing pressure on plant communities and degradation of moss dominated fen vegetation. Geese and their eggs and goslings are important prey of Arctic foxes and avian predators.

Response targets:

Geese: Pink-footed goose and Barnacle goose.

Plant communities: wet and moist moss dominated fen vegetation with grasses, sedges and Bistorta

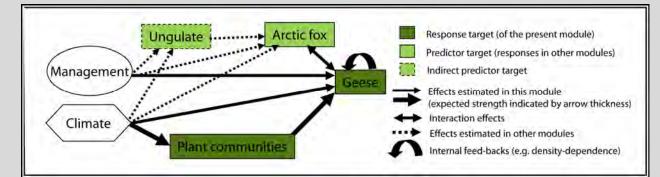
Predictor targets:

Plant community: state changes in moss dominated fens with sedges/grasses interacting with geese.

Predators: *Arctic fox, Arctic skua, Glaucous gull* and *Polar bear* (increasingly associated with island nesting barnacle geese)

Climate impact path model predictions:

For pink-footed geese the main direct impact path is expected to act through earlier onset of spring/snow melt opening suitable nesting habitat giving rise to increasing densities and wider altitudinal and geographic distribution. Earlier ice melt is expected to free nesting islands from foxes, leading to higher nest densities and reproductive output. Warming is expected to result in earlier plant growth and peak in quality which may result in a mismatch with timing of reproduction and impacting growth and survival of goslings. Increasing densities of geese is expected to result in increasing grubbing impact (pink-footed geese) on wet and moist fen vegetation with a resulting degradation of the habitat and biodiversity, and with a knock-on effect on ptarmigan and reindeer forage. Arctic fox predation affects the survival of adult geese, eggs and goslings and predation pressure is expected to increase if the fox population will increase due to better winter survival. The path model also addresses the potentially modifying effects of intra-specific and inter-specific density dependence in goose colonies (competition for good quality nest sites, food competition), predator-prey interaction (feedbacks on fox densities), plant-goose interactions (feedbacks) includ-ing grubbing impacts on plant communities.



Management options:

In case of increasing tundra degradation, intensified hunting pressure (in Svalbard and on staging and wintering grounds) is a possible measure but only for pink-footed goose (the only quarry species). Predator control and regulation of human intrusion are options in case conservation measures are needed.

2.7.1. Functioning

Arctic nesting geese are migratory; they spend approximately four months on the breeding grounds and the rest of the year on temperate staging and wintering areas (Madsen et al. 1999). Due to the shortness of the arctic summer, timing of breeding and moulting is crucial, and geese have to time their nesting to raise their young when food resources peak in quality and quantity. Hence, they start egg-laying when the tundra is still partly snow covered. To evaluate their dynamics and functioning in arctic ecosystems, it is necessary to understand the influence of processes affecting their fitness in a year-round perspective. Especially because high-arctic geese are dependent on endogenous body reserves built-up on the spring staging areas for their successful reproduction, factors affecting geese on their wintering or spring staging grounds may carry-over to their performance on the breeding grounds.

The Svalbard archipelago host three nesting goose species; pink-footed goose (*Anser brachyrhyn-chus*), barnacle goose (*Branta leucopsis*) and lightbellied brent goose (*Branta bernicla hrota*). The two first species have increased dramatically; from the 1970s until today, pink-footed geese increased from c. 15,000 to c. 80,000 (2011; Figure 2.7.1.1); barnacle geese from c. 5000 to 35,000 (Griffin and Mackley 2004, Wildfowl and Wetlands Trust, www.wwt.org.uk), while brent geese increased from c. 3000 to a stable number of around 9000 (Fox et al. 2010, P. Clausen unpublished). The brent goose is, however, highly vulnerable due to low reproductive rates and is a red-listed species in Svalbard.

The pink-footed goose winters in Denmark, The Netherlands and Belgium. In spring, the population migrate through Norway with Nord-Trøndelag (central Norway) and Vesterålen (northern Norway) as the main spring staging sites. The barnacle goose population winters in southwest Scotland/ northwest England, UK, with spring staging areas along the west coast of Norway (Helgeland in mid-Norway and Vesterålen in northern Norway). As the goose populations use different breeding and wintering areas (Madsen et al. 1999), they are a special case when it comes to monitoring and conservation. In this context we focus on monitoring in the breeding areas in Svalbard. Though, we give an overview of monitoring initiatives in the wintering and staging areas in Table 2.7.1.1. The size of most goose populations is estimated during winter, along with reproductive success; i.e. percentages of juveniles in the

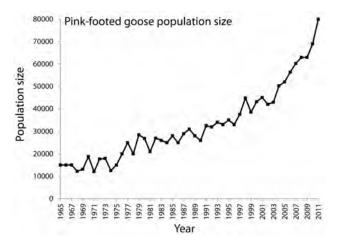


Figure 2.7.1.1. Population size of pink-footed goose estimated on the wintering grounds (Madsen et al. 1999, Fox et al. 2005, Madsen and Williams 2012, Madsen unpublished).

population (Madsen et al. 1989, Fox et al. 2010, Mitchell et al. 2010).

2.7.1.1. Geese as plant consumers

The goose species are all herbivores, but occupy different niches in Svalbard and are differently distributed, although with some overlap. Goose grazing affects the standing crop and composition of the tundra vegetation, in particular in fens. During the last decade, increasing signs of the impact of foraging pink-footed geese on tundra vegetation in Svalbard have been observed, partly due to grubbing for roots and rhizomes in the wet moss carpets whereby geese pull out moss and food plants. This may in some areas create holes or craters (see Figure 2.7.1.2), which appear to regenerate at variable rates depending on wetness, patch size and the plant community (Speed et al. 2010b). Regeneration is slowed down by the fact that geese year after year return to the same patches, grubbing on the edge of open patches. Geese are selective, and can remove large quantities of plant material, which has knock-on effects for net ecosystem exchange (van der Wal et al. 2007). Some plant species regrow immediately after grazing to replace grazed tissue, whereas others will not grow again until the following year; but this occurs at the expense of a reduction in their belowground reserves; and other species are completely removed by geese (Cooper et al. 2006, Cooper & Jonsdottir unpublished, Birkgit et al. unpublished). Geese are also floral herbivores (Alsos et al. 1998), which can lead to changes in the soil seed bank (Kuijper et al. 2006). Geese trample the moss layer in wetland systems, which

affect soil temperature in the rooting zone of vascular plants and can lead to enhanced graminoid growth (van der Wal et al. 2000c, Gornall et al. 2009). In this way goose grazing, as well as grubbing, can change vegetation community composition, structure and function. The barnacle goose colonies breeding in western Spitsbergen experience density dependence at the colony level due to an increased competition for food (Prop 2004, Black et al. 2007).

2.7.1.2. Geese as prey

Being the largest species, the pink-footed goose nests in the open tundra and is able to defend its nest against arctic foxes. Nevertheless, eggs, goslings and adults constitute important prey for the arctic fox (Loonen et al. 1998, Tombre et al. 1998a, Tombre et al. 1998b), which appears to be the most important goose predator. However, to some extent eggs and goslings are also taken by skuas and glaucous gulls (Dalhaug et al. 1996, Hübner et al. 2002, Madsen et al. 2007). The barnacle geese cannot defend themselves against the foxes, and they resort to nesting on islands as well as steep cliffs where foxes have no access. Nests and goslings may be predated by skuas and gulls, and during brood-rearing also the foxes may take goslings (Madsen et al. 1989, Dalhaug et al. 1996, Tombre and Erikstad 1996, Loonen et al. 1998, Madsen et al. 1998, Tombre et al. 1998a, Tombre et al. 1998b, Hübner et al. 2002). In seasons of late breakup of sea-ice, foxes have access to goose nests on islands. In such years foxes may depredate whole colonies for goose eggs (Tombre et al. 1998a). During the last decade, polar bears have become more frequent along west Spitsbergen, foraging to a large extent on barnacle goose eggs on the islands (J. Prop unpublished).

Table 2.7.1.1. Overview of national and international ongoing and or/planned monitoring activities related to the Svalbard nesting goose populations of the pink-footed goose *Anser brachyrhynchus* and the barnacle goose *Branta leucopsis*. The table summarizes area, methods, associated measurements and references.

| Area | Method | Measurement | Estimates | References |
|-----------------------------|---|---|--|--|
| Wintering (both species) | Field counts | Population counts Breeding success Brood size | Size of population Reproductive success Population reproductive output | Population monitoring since 1980 (Madsen et al. 1999) |
| | Marking-resightings | Survival Dispersal Migration schedule | Adult seasonal survival rate | Capture-resighting pro- gram; Pink-footed geese since 1990 (Madsen et al. 1999); barnacle geese since the 1970s (Black et al. 2007) |
| | Harvest estimate (pink-footed goose) | Bag statistics | Harvest mortality | Madsen et al. 2002 |
| Spring staging | Counts, ring resight- ings Abdominal profiles | Migration schedule Body condition | Timing of migration Individual fitness | Pink-footed geese: (Tombre et al. 2008, Mad- sen 2001) |
| | | | | Barnacle geese: (Prop et al. 1998, Prop 2004, Black et al. 2007) |
| Breeding | Field counts Remote sensing of snow cover | Population density Nest success Snow cover | No. of nests Reproduc- tive success Percentage snow cover at egg-laying | (Madsen et al. 2007, Prop 2004, Black et al. 2007) |



Figure 2.7.1.2. Wet moss fen grubbed by pink-footed geese; Sassendalen, Svalbard. Photo: Jesper Madsen

2.7.2. Ecosystem services and other aspects of societal relevance

Wild geese have traditionally been a valuable food source throughout Europe (Fox et al. 2010). Among the Svalbard breeding populations, only the pink-footed goose is currently hunted. Internationally it is hunted both in Svalbard, mainland Norway and Denmark, and bags have rapidly increased (DST 2011, SSB 2012a). In Svalbard, the harvest is very limited (around 200 SSB 2012a/ Governor of Svalbard). Additionally, the Governor of Svalbard can give permits to collect down from nests of both pink-footed geese and barnacle geese.

In Svalbard, there has been an increasing tourism activity during recent decades, both in terms of organised trips by tour boats and snowmobiles as well as more unorganised individual trips (Anonymous 2006). Geese are highly valued as natural assets in this relation and bird watching in general is also an activity increasing in Svalbard. Due to increasing goose foraging, there is a concern about longer term impacts on the tundra vegetation, ecosystem functions and the vulnerable biodiversity in Svalbard (see e.g. van der Wal et al. 2007). It has been suggested that migratory birds, such as the barnacle goose, may be the most important vectors bringing the zoonotic parasite *Toxoplasma gondii*, a coccidian protozoan, to Svalbard. In barnacle goose the prevalence is 7 % (Prestrud et al. 2007). Toxoplasmosis is highly prevalent in arctic foxes (43%) and suggested to sometimes cause mortality in arctic foxes (Sørensen et al. 2005, Prestrud et al. 2007).

2.7.3. Sensitivity

An increase in temperature (both in wintering, staging and breeding grounds), a shift towards earlier springs and extended summer seasons, has direct effects on plants, causing changes in phenology, increased primary production and changes in the plant community structure (Chapin et al. 1995, Arft et al. 1999, Hudson and Henry 2009). Earlier snow and sea ice melt will physically provide earlier access to food plants in the prenesting period, as well as islands or tundra patches suitable for nesting (Fox et al. 2007, Madsen et al. 2007). Furthermore, even a small increase in summer temperature will extend the frost free period to enable geese to breed over a wider area in the high Arctic. In Svalbard this will be most promi-

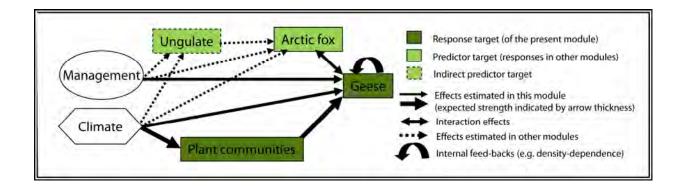
nent in the east and north of the archipelago, but also along an altitudinal gradient (Jensen et al. 2008). These climate driven changes are likely to allow geese population densities to increase and distributions to expand, with a corresponding influence on the tundra.

Consequences of herbivore impact on the structure/function of arctic ecosystems have been documented through strong top-down effects of key herbivores on plant productivity and vegetation community structure (van der Wal and Brooker 2004, Bråthen et al. 2007a, Post and Pedersen 2008) as well as bottom-up effects on the abundance and diversity of the predator guild (Ims and Fuglei 2005, Ims et al. 2008, Gilg and Yoccoz 2010). Therefore, direct climate effects on herbivore populations, as well as changes in trophic interactions determining herbivore population sizes, will play a crucial role in determining future vertebrate as well as plant community structure in arctic ecosystems (Post et al. 2009). Increased plant productivity will grossly be to the benefit to geese (Madsen et al. 2011). However, unless geese advance their arrival and egg-laying in accordance with a warming Arctic, there is a risk of a mismatch between the timing of breeding and the quality of the food plants available for the goslings. However, evidence for this is still limited (but see Sedinger and Flint 1991)

The increase in grubbing impact by geese has not yet been documented; potentially, this may become a factor affecting the availability of food resources during critical stages of pre-nesting and nesting. The extent of grubbed areas seems to be increasing with the increment in population size (Speed et al. 2010b), although monitoring of this development is currently lacking. With the rapid expansion in pink-footed goose numbers, the extent of grubbing should be carefully monitored along a climatic gradient. The foraging activity may also cause a shift in vegetation composition with a decrease in moss cover and an increase in graminoids (grasses and sedges) (van der Wal and Hessen 2009).

Earlier studies in east Svalbard have shown that polar bears caused a high nest predation in lightbellied brent geese (and most likely also for the other goose species nesting in the same area, although this is not documented) and that the breeding success of the population as a whole was negatively related to the presence of sea ice during the nesting period in the area, which was an indicator of polar bear presence (Madsen et al. 1989, Madsen et al. 1998). Whether this relationship still prevails is unknown, but there are signs that polar bears have changed behaviour, foraging more on land during summer. This is manifest in west Spitsbergen where polar bear predation of eggs in bird colonies, including barnacle geese, has increased dramatically during the last decade and strongly influences the breeding success of the west Spitsbergen colony of barnacle geese (Prop, unpublished data). Due to their dispersed breeding sites, often in inland habitats, pinkfooted geese can be expected to be much less vulnerable to polar bears.

Increasing tourism in Svalbard constitutes a potential problem to nesting, moulting and broodrearing geese, especially in certain areas with high goose concentrations or on nesting islands (Madsen et al. 2009). Long escape distances of the geese in some areas (open tundra in the brood rearing period) also involve that humans may not be aware of their disturbance. In a climate warming perspective, accessibility to new areas by tourists (cruise boats and smaller boats) will increase, which may have negative consequences for geese if the activity is not strictly regulated.



Model 2.7.4.1. Climate impact path model for the high-arctic Svalbard with geese and associated plant communities as response targets.

2.7.4. Climate change impact predictions

Climate change has been suggested as one of the major drivers for the significant increase in the pink-footed goose population, especially for the last decade (Madsen & Williams in prep.). Warmer springs are also suggested to be one of the main reasons for an expanded and more northerly distribution of the barnacle goose population at the spring staging sites on the Norwegian mainland (Prop et al. 1998). Climate induced effects are likely to influence several stages of the life cycle of geese in which the geese inhabit different distribution areas. Geese are likely to respond to climate in their migration phenology, breeding phenology, distribution and productivity, winter distribution, survival and carry-over effects (i.e. winter body condition effects on subsequent reproduction and survival). Furthermore, biotic interactions are likely to change with increasing interspecific competition and facilitation, and changes in predator guilds due to altered climatic conditions have been recognized. The potential impacts of climate on arctic breeding geese are listed below, categorized as either having a positive or a negative effect.

Positive effects:

Geese rapidly adjust their migratory behaviour to changing environmental conditions (Prop et al. 1998, Bauer et al. 2006, Tombre et al. 2008, Duriez et al. 2009, Eichhorn et al. 2009)

Plant productivity is improved by earlier snowmelt (Prop et al. 1984, Prop and de Vries 1993, Black et al. 2007, Madsen et al. 2007)

Potential nesting space will increase with only slightly elevated temperatures (Jensen et al. 2008); there are signs that east Svalbard is opening up to become more suitable as a breeding site

Capacity of moulting habitats for non-breeders may increase due to improved vegetation productivity (Madsen et al. 2011), but with possible increased inter-specific competition.

Negative effects:

Potential for mismatch between goose breeding phenology and plant growth (Sedinger and Flint 1991)

Increased predation pressure by in particular arctic foxes

Increased inter and intraspecific competition for

food during nesting (Fox et al. 2009) and for moulting sites like observed in East Greenland (Madsen and Mortensen 1987)

Increased grazing pressure may lead to decreased quality of grazing areas, including grubbingenhanced soil erosion. This may also have knockon effects on other herbivores (cf. §2.5 and §2.6).

The most important potential positive and negative impact on arctic breeding geese in Svalbard listed above are summarised in climate impact path model 2.7.4.1. The targeted goose species in context of COAT will be barnacle goose and pinkfooted goose, with most focus on the pink-footed goose because of its strongly increasing populations (Figure 2.7.1.1) and its potential for interaction with other herbivores. Beside the geese, plant communities likely to be most affected by geese will be in focus as a response target. The plant community monitoring will, however, be coordinated with the ungulate (§2.5) and ptarmigan modules (cf. §2.6). Input from the arctic fox module (cf. §2.8) is needed to obtain predictor variables to estimate the effect of changed predator pressures.

2.7.5. Management options

At present, no specific management plan exists for the three goose species in Svalbard. The general management follows the international legislations existing for each species. An international flyway plan for the pink-footed goose is in the process of implementation under the African-Eurasian Waterbird Agreement under the Bonn Convention. The objective is to maintain a viable and stable population size while taking into account economic and recreation interests, as well as avoiding further degradation of vulnerable tundra vegetation in Svalbard (Madsen and Williams 2012). A key action is to increase the hunting pressure on the population to stabilize the population size at around 60,000 individuals. However, the feasibility of this measure to reach the target will depend on the growth rate of the population which is hypothesized to be positively influenced by climate warming. In Svalbard, one management action could be to make incentives to increase the harvest level, although the probability for an increase in bag sizes more than a "moderate increase" is unlikely.

For barnacle geese, an international management plan was made in late 1990's (Black 1998), but it is not operational since both member countries

(Norway and UK) have not yet signed the plan. However, its main long-term objective - to maintain favourable conservation status throughout its geographical range - is in many respects fulfilled since there are different management schemes established at their wintering and spring staging sites (summarised in Black et al. 2007). The population is not harvested. Current population estimates, carried out in the autumn/winter in UK, are a challenge to quantify as the population has increased and distribution has become wider (see Tombre et al. 2008). In Svalbard, the colonies in the western parts of Spitsbergen face a new threat through disturbance, and thereby energetically trade-offs, and egg predation by the increasing density of polar bears (Prop, unpublished data). The egg predation rate may in some years be detrimental, and will be a central issue to monitor in the coming years.

2.7.6. COAT team competence

The goose module will be led jointly by Department of Bioscience, Aarhus University (AU) and Division of Arctic Ecology, Norwegian Institute for Nature Research (NINA). Team members in charge are *Jesper Madsen* (AU) and *Ingunn M. Tombre* (NINA), with contributions from Åshild Pedersen (NP), Eva Fuglei (NP), Audun Stien (NINA), Tony Fox (AU), Rene van der Wal (Aberdeen University) and Jouke Prop (NL and

University of Groningen). AU is at present responsible for monitoring the Svalbard population of pink-footed geese, with focus on population dynamics (capture-resighting), and effects of climate change and harvest. A breeding colony in Sassendalen in Svalbard has been monitored as part of the programme since 2003. J. Prop is responsible for long-term monitoring of barnacle geese at Nordenskiöldkysten. NINA has been responsible for compiling and presenting data on the distribution of geese in Svalbard (http:// goosemap.nina.no/Startside.aspx). The team has a solid experience with monitoring of geese on the breeding grounds (e.g. Prop 2004, Black et al. 2007, Madsen et al. 2007), analysis of population dynamics (Madsen et al. 2002, Kery et al. 2006), behavioural ecology of geese (e.g. Tombre and Erikstad 1996, Hübner 2010, Tombre et al. 2012), intra- and interspecific competition (Fox et al. 2009), diets (Fox et al. 2007), and food web interactions (van der Wal et al. 2007, Madsen et al. 2011). The team has also experience with predictive population modelling (Trinder and Madsen 2008), spatial modelling (Jensen et al. 2008, Wisz et al. 2008), remote sensing analyses (Madsen et al. 2007, Tombre 2010), as well as applied research in relation to impact assessments in Svalbard (Madsen et al. 2009).

2.8. Arctic fox module (Varanger and Svalbard)



Summary of the arctic fox module (Varanger)

Functions and relevance:

Over the past century the arctic fox has been retracting from the southern edge of its circumpolar range - a change attributed to global warming. The arctic fox is placed on the IUCN "*climate flagship species list*", as to "*highlight climate change's disruptive effects on interactions between species*". The arctic fox is *red listed as highly endangered* in low-arctic Varanger, where it is subjected to intense *conservation efforts*.

Response targets:

Arctic fox and interacting guild of meso-sized generalist predators (red fox, golden eagles and ravens).

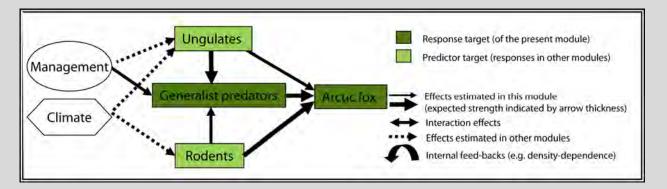
Predictor targets:

Norwegian lemming in rodent module as the key subsistence prey for the arctic fox.

Reindeer in the *ungulate module* as key driver of generalist predator abundance and intra-guild interactions.

Climate impact path model predictions:

Two potentially interacting paths, having their origin in warmer winters, is expect to impact arctic fox populations negatively; one works though decreased availability of lemming prey (cf. Rodent module), the other through increased abundance of generalist predators (natural enemies of arctic foxes) resulting from increased availability of ungulate carrion (cf. Ungulate module).



Management options:

Ungulate management to reduce climate and density-dependent mortality carrion subsistence for arctic fox natural enemies. Red fox culling (generalist predator control) as an arctic fox conservation effort (currently run on Varanger peninsula).



Summary of the arctic fox module (Svalbard)

Functions and relevance:

Without natural enemies on high-arctic islands, the arctic fox is an *abundant and functionally important apex predator* on both terrestrial and marine prey species, and it is *a reservoir for dangerous zoonoses*. The arctic fox is *harvested* as a furbearer although harvesting in Svalbard nowadays is mostly recreational.

Response targets:

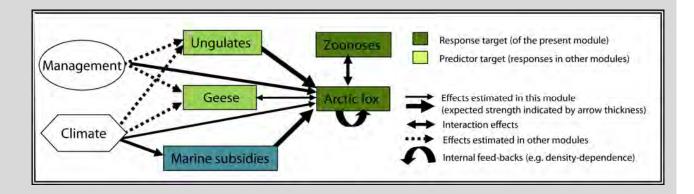
Arctic fox and the zoonoses rabies, toxoplasmosis and Echinococcus multilocularis.

Predictor targets:

Ungulates (reindeer carrion); *geese* and *marine subsidies* (sea birds and mammals) as arctic fox food resources.

Climate impact path model predictions:

The model predicts three climate impact paths. One works though decreased sea ice extents reducing arctic fox migration and exploitation of marine resources in winter. The two other pathways work indirectly though variable climate impact on availability of key terrestrial prey species, reindeer and geese (cf. Ungulate and goose modules). All changes in arctic fox population density, movements as well intermediate hosts are likely to influence the prevalence of zoonoses.



Management options:

Reindeer, geese and arctic fox is under strict management regulations (harvesting) in Svalbard.

2.8.1. Functioning

The arctic fox (Vulpes lagopus) is the only endemic mammalian predator to the arctic tundra. It is almost omnipresent in the tundra biome - from the polar deserts of the most northern arctic islands to southern shrub tundra close to the arctic forest line (Audet et al. 2002). The arctic fox is thus found in a wide variety of food web contexts, where it can take different roles (functions) as predator and/or scavenger. In large tracts of the tundra biome, in particular in the high arctic, the arctic fox can be considered as the dominant apex predator as larger terrestrial predators such as wolves (Canis lupus), wolverines (Gulo gulo), red fox (Vulpes vulpes) and golden eagles (Aquila chrysaetos) are either scarce or absent. However, the influence of these larger predators becomes increasingly important towards the southern border of the tundra (and the distribution range of the arctic fox). The influence of larger predators may also become more important in the future in different climate and ecosystem management regimes (see §2.8.4). In terms of functions in the food web there has been made a conventional dichotomous distinction between two arctic fox ecotypes - the "lemming fox" and "coastal fox" (Braestrup 1941).

2.8.1.1. Food webs ruled by rodent cycles: The functions of lemming foxes

The *lemming ecotype* resides in tundra ecosystems with distinct lemming cycles. The arctic fox specializes on lemmings as prey and their life history/ demography is shaped by the booms and busts of the lemming cycle (Braestrup 1941). Breeding takes place with large litter sizes (normally 8-12 pups) in the lemming peak years while the foxes do not even attempt to breed in lemming low years (Tannerfeldt and Angerbjorn 1998, Angerbjörn et al. 1999, Meijer et al. 2013). Also the survival rate of (especially) young foxes drops after lemming crashes. To the extent alternative food resources are available, arctic foxes perform prey-switching to other terrestrial small-medium sized bird or mammal prey (e.g. ptarmigan, waders, geese, passerines, hares) or carrion of large herbivores such as reindeer/caribou in lemming low (and crash) years (Roth 2003). Such preyswitching is known to impact the reproductive success and population dynamics of alternative prey populations substantially, such as shorebirds and geese (Bety et al. 2001, Gauthier et al. 2004, Ims and Fuglei 2005). It is unclear to what extent the arctic fox is able to shape/regulate lemming and arctic vole cycles. However, the arctic fox is a key predator transmitting the cascading impact of the lemming cycle throughout the terrestrial arctic food web. An important spillover-effect, mediated by the arctic fox in food webs with lemmings, of particular concern for humans, is canide-born zoonoses such as rabies and *Echinococcus multilocularis*.

2.8.1.2. Coast-near tundra food webs: The functions of coastal foxes

The other arctic fox ecotype – the *coastal fox* rely heavily on food resources from the marine food webs with sea mammals (often carrion) and/or sea -birds being the most important (Braestrup 1941). The coastal ecotype in its purest form is found on arctic islands where lemmings are lacking (e.g. Iceland and Svalbard, Hersteinsson 1989, Prestrud 1992, Fuglei et al. 2003) Compared to the lemming ecotype, costal foxes have a much more stable demography (e.g. yearly litters of small sizes) and population density (e.g. Tannerfeldt and Angerbjorn 1998). Depending on accessibility/ vulnerability of bird nests, coastal arctic foxes can exert strong controls on populations of seabirds and geese (Fuglei et al. 2003). In some cases the top-down impact can be so strong that it cascades down to vegetation and primary productivity of the terrestrial food web, by reducing the transport of avian born nutrient from the ocean to land (Maron et al. 2006).

2.8.1.3. Ecosystem switchers: mixed functions in arctic foxes

In many cases the arctic fox does not fall so clearly into the two archetypical ecotypes described above. Many coastal tundra regions harbor both lemmings and accessible marine food sources, so that arctic foxes may perform switching between lemmings and marine food over the lemming cycle (Roth 2002). This may act both to stabilize fox population dynamics and consequently their impacts on the food web. In some cases arctic fox populations may subsist on terrestrial resources other than lemmings, e.g. geese, ptarmigan and reindeer carcasses. At a small scale coastal arctic foxes in Svalbard can be found along a resource gradient from being dominated by a stable access to marine resources close to bird cliffs along the coast, to a more variable resource base determined by access to reindeer carrion inside the deep valleys (Jepsen et al. 2002, Eide et al. 2004, Eide et al. 2005, Eide et al. 2012). On Varanger peninsula the

arctic fox was found, according to the distribution of old dens, along the full gradient from coastline to the interior of the peninsula. However, nowadays the small arctic fox population in Varanger is mostly restricted to the interior of the peninsula where they depend on terrestrial resources (Killengreen et al. 2007, Ehrich et al. in prep).

2.8.2. Ecosystem services and other aspects of societal relevance

The arctic fox has traditionally been one of the most valuable furbearers in the Arctic. Following domestication and the industrial farming of the species, and declining demands and prices, the role of harvesting wild arctic fox populations has become substantially diminished throughout the circumpolar region (Angerbjörn et al. 2008). However, trapping is maintained by some indigenous people. In Svalbard traditional trapping is still conducted by 2-3 professional trappers at private trapping stations or stations administered by the Governor of Svalbard. Moreover, recreational harvesting is conducted by local people based in Longyearbyen, Svea or Ny-Ålesund. The total harvest amounts to 60-320 individuals per year (Figure 2.8.2.1).

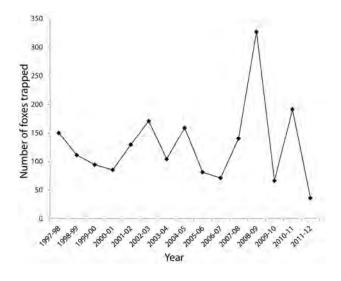


Figure 2.8.2.1. Yearly harvest statistics of arctic fox in Svalbard.

On the Norwegian mainland the arctic fox became protected in 1930 following a period of intense harvesting and steep population decline. Harvesting contributed to the decline, but also other factors likely have contributed. In Fennoscandia the arctic fox has become iconized as a symbol of vulnerable species/tundra nature to the extent that it could be regarded as *cultural service*.

The arctic fox is an important vector for zoonoses (animal born parasites/diseases that may spillover to humans), in particular rabies and the tape worm Echinococcus multilocularis (EM), and toxoplasmosis. These are of concern in cases where the arctic fox population is dense, in connection with high lemming peaks, and/or have contact though immigration pulses from such populations (Norén et al. 2011b). Rabies and EM are not prevalent in northern Fennoscandia, whereas EM recently has been found in red fox in southern Sweden. The status of toxoplasmosis in Fennoscandian arctic fox is unknown, whereas this parasite is highly prevalent in the red fox, also on the Varanger peninsula (Åsbakk et al. unpublished). Both rabies and EM is common in the NW arctic Russia. In Svalbard, EM is permanently present and associated with the introduced population of the sibling vole - the latter serving as the intermediate host for this parasite (Henttonen et al. 2001, Fuglei et al. 2008, Stien et al. 2010a). Toxoplasmosis is also highly prevalent (43%) and seems to sometimes cause mortality in foxes, specifically in juveniles (Sørensen et al. 2005, Prestrud et al. 2007). Rabies outbreaks are present in Svalbard (Prestrud 1992, Mørk and Prestrud 2004), however with so infrequent/erratic occurrence (the first observed in 1980 and the second in 2011) that it is likely introduced by immigrating pulses of lemming foxes from arctic Russia to Svalbard (Johnson et al. 2007, Mørk et al. 2011, Norén et al. 2011b). The prevalence of rabies in arctic foxes in Svalbard between the outbreaks is 0.3% (Mørk et al. 2011). In the latest outbreak (2011), 10 of 15 reindeer found dead were infected by rabies.

Box 2.8.1. Native arctic foxes, invasive voles and zoonotic *E. multilocularis* in Svalbard

Echinococcus multilocularis (EM) is a tapeworm having a life cycle with foxes as a definitive host, and small rodents as intermediate host (Figure B.2.8.1). The larval stage (cysts) of the parasite can infect humans if eggs shed in excreta of foxes are ingested. In humans EM causes the disease *Alveolar Echinococcosis* with 80-90 % mortality, if left untreated. The intermediate host of EM in Svalbard is the sibling vole *Microtus levis*, which accidentally was introduced to the former Russian mining settlements in Grumantbyen and spread to the nearby productive grassy vegetation associated with seabird colonies (Henttonen et al. 2001). The limit of the present core area of the vole population is approximately 10 km from the main human settlement in Svalbard – Longyearbyen. However, the vole population is exhibiting large fluctuations in density and spatial distribution (Yoccoz and Ims 1999), mainly driven by variation in winter temperature and precipitation (Hansen et al. 2013), and during population peaks the limits of the vole spatial range includes Longyearbyen (Henttonen et al. 2001). The risk of human infections is restricted to areas with continuous presence of both hosts (Fuglei and Ims 2008, Stien et al. 2010b). As the native arctic fox is omnipresent in Svalbard, monitoring the risk of EM infections should focus on monitoring the stability and eventual spread of vole occupancy in habitats associated with seabird colonies and human settlements at and beyond the limits of the sibling vole's present distribution range.

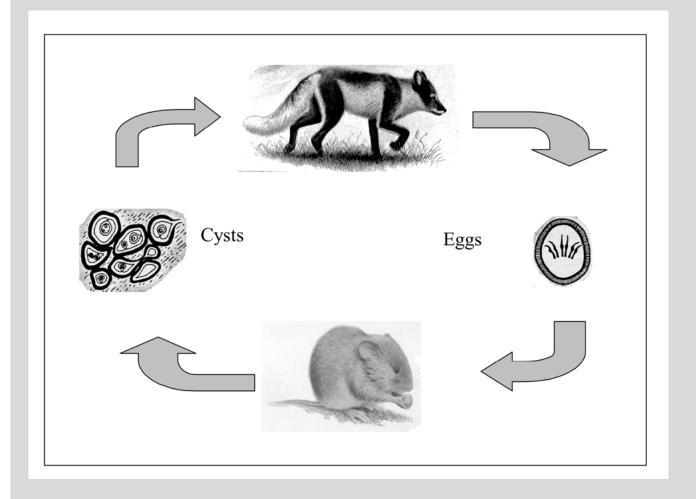


Figure B.2.8.1. The sibling vole – arctic fox – *Echinococcus multilocularis* (EM) system in Svalbard. The life cycle transitions of EM are indicated by the arrows. The arctic fox and the sibling voles are final and intermediate hosts, respectively.

2.8.3. Sensitivity

Because the arctic fox can be impacted by climate warming in several ways that involves fundamental changes in arctic ecosystems, it is on a red list of 10 species elected by the IUCN to highlight climate change worldwide. During the course of the last decennium the southern distribution limit of the arctic fox has moved northwards at a circumpolar scale (Hersteinsson and Macdonald 1992). This range contraction and decline in abundance is best documented in Fennoscandia, where only fragmented remnant sub-populations are now present (Angerbjörn et al. 2008, Herfindal et al. 2010). The arctic fox is presently extinct in Finland (last breeding in 1996), while the species is red listed as critically endangered in both Norway and Sweden (Angerbjörn et al. 2008). On Varanger peninsula the arctic fox population is also critically small with the maximum number of 4 breeding pairs in any year (2011) since the start of the monitoring series in 2001 (Figure 2.8.3.1). There has, however, been an increase in the production of pups during this period.

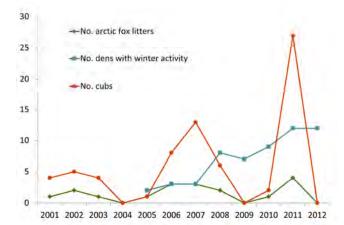


Figure 2.8.3.1. Arctic fox breeding population size during the period of systematic monitoring of known dens (N=33) on Varanger Peninsula.

2.8.3.1. Release of natural enemies

While overharvesting in the period 1910-1930 has been regarded as the main cause of the decline in Fennoscandia, the circumpolar nature of the decline in the southernmost part of the tundra, and the fact that the arctic fox has proved to be remarkably resilient to intense persecution on Island (Hersteinsson 1989, Angerbjörn et al. 2004), calls for other explanations. Specifically, Hersteinsson and MacDonald (1992) suggested, based on a circumpolar scale analysis of harvest statis-

104

tics, that climate warming throughout the last century was the main underlying cause of the range contraction. They hypothesized that increased primary productivity in the southern part of the tundra biome had paved the way for the more energy-demanding, larger-sized red fox (Vulpes vulpes), which has moved its distribution range northwards into the southern part of the arctic fox range. While there are presently several observations that are consistent with arctic fox being competitively subordinate of the red fox; i.e. expelling the arctic fox from breeding dens (Frafjord et al. 1989, Frafjord 2003, Rodnikova et al. 2011) and territories (Tannerfeldt et al. 2002), and from carrion in winter (Hamel et al. 2013), the vulnerability of arctic fox populations to competitive interaction with its larger congener in various ecological settings needs to be clarified. This regards also the role of other potentially expanding scavengers and predators such as corvids and eagles (Killengreen et al. 2011, Figure 2.8.3.2). The roles of these other competitors for carrion in winter are unknown. Moreover, the golden eagle has been documented as a predator on the arctic fox as well as other fox species (Sulkava et al. 1999, Meijer et al. 2011). In the case of the declining populations of the endangered Channel island fox (Urocyon littoralis), spill-over predation from the golden eagle plays a decisive role (Roemer et al. 2002). It is possible that reindeer carrion (cf. \$2.5 and below) may play an equivalent role as the "ecological pork" of Channel island food web (Courchamp et al. 2003). In general, food web structure/dynamics among predators and scavengers is likely to be of importance determining the extent of scramble competition for resources. In a modeling study Henden et al. (2010) found that the impact of red fox on arctic fox was highly dependent on the population dynamics of the red fox. Stable red fox populations had a larger negative impact on arctic fox numbers than cyclic populations.

It has been questioned whether the northwards expansion of the red fox is mediated by climate warming (Killengreen et al. 2011, Gallant et al. 2012). In fact there appears to be no evidence of increased terrestrial secondary productivity and thus more food resources for foxes due to increased primary productivity in the tundra (see §2.3; Killengreen et al. 2012). On the contrary, the recent incidences of collapses and dampening of arctic small rodent cycles indicates that the resource situation for foxes may have deteriorated, at least regionally, in the tundra. In addition, the population densities of shrub-dependent small- to medium sized herbivores like hares and ptarmigan in northern Fennoscandia is too low to compensate for dampening of rodent cycles (Ehrich et al. 2012b). Indeed, the intimate dependence of the arctic fox and other rodent specialists on regular, high amplitude lemming peaks probably represents the main climate threat to arctic predators and their associated functions in the tundra food webs (see §2.4).

In the long term natural enemies and competitors of the arctic fox may be decisive as red fox, eagles (golden and white-tailed eagles) and corvids (raven and hooded crow) move northwards along with the limit of the arctic forest. In the short term expansion of such species is more likely to result from altered human use and management of northern ecosystems (e.g. agriculture, ungulate management, urbanization, garbage management). For instance, red foxes in the interior Varanger peninsula appear to subsist on carrion from semi-domesticated reindeer (Killengreen et al. 2011). A similar connection to reindeer abundance and mortality rate, in particular during the winter, appear to be valid for the whole guild of generalist predators that reside on the tundra in winter (Killengreen et al. 2012, Henden et al. 2013). The fate of reindeer husbandry in a changing climate (cf. §2.5) is also likely to affect the arctic fox and many other components of the plant based tundra food web.

2.8.3.2. Changed dynamics of arctic small rodents

For the arctic fox lemming ecotype climate induced change in arctic small rodent dynamics (cf. \$2.4) will be decisive. Modeling have demonstrated how these various aspects of changed rodent dynamics is likely to impact arctic fox population viability (Loison et al. 2001) and long-term growth rate (Henden et al. 2008). In particular, collapse of cycles (i.e. loss of rodent peaks), either permanently or temporally (Ims et al. 2011), or severely dampened cycles (lower rodent peaks) will lead to arctic fox population extinction. Accordingly, the drastic decline of the arctic fox in Fennoscandia in the period 1910-1930 coincided with a period of climate warming and temporal loss of cycles regionally in Fennoscandia (Henden et al. 2009b). Similarly, regional extinctions of arctic fox populations in alpine tundra in southern Norway and northern Finland in the 1990s (Angerbjörn et al. 2013) coincided with a loss of cyclicity or severely dampened peak years (Ims et al. 2008). On this occasion the already small arctic fox population balanced on the verge of extinction at the scale of the entire Fennoscandia (Angerbjörn et al. 2013).

The arctic fox' strong reliance on lemmings (Elmhagen et al. 2002) makes the fate of lemmings particularly important. In presence of the red fox the arctic fox distribution on Varanger



Figure 2.8.3.2. The arctic fox and three of its main competitors for reindeer carrion in winter on Varanger peninsula; the golden eagle, common raven and red fox. The photos are taken at baited permanent monitoring stations equipped with time lapse cameras.

peninsula has become restricted to high altitude areas where only lemmings are common among the rodents (Killengreen et al. 2007, Ims et al. 2011). In habitats where voles are dominant these rodents seem anyhow unavailable in winters to predators that do not get access to the subnivean space (Killengreen et al. 2011).

2.8.3.3. The case of Svalbard: Arctic fox in absence of rodents and natural enemies

While the red fox has been able to colonize high arctic islands in Canada (Macpherson 1964, Berteaux et al. 2011) it is probably the remoteness of Svalbard that has made the archipelago inaccessible to the red fox. Svalbard does not harbor other potential terrestrial predators and competitors of the arctic fox, such as eagles and corvids. The decreasing extent of sea-ice (Serreze et al. 2007, Stroeve et al. 2007, Screen and Simmonds 2010) is expected to make Svalbard even less prone to natural colonization by competitors and enemies of the arctic fox in the future (Fuglei and Ims 2008). However, the decreasing extent of sea ice may cause other challenges. The arctic fox in Svalbard use the sea-ice as a habitat for feeding; ringed seals pups (Lydersen and Gjertz 1986) and remains from polar bear kills (Hiruki and Stirling 1989). Moreover, sea-bird colonies, which probably constitute the most important food resource and breeding habitat for the arctic fox in Svalbard, are linked to sea-ice related food webs (Mehlum and Gabrielsen 1993). The sea-ice is also a platform for long-distance arctic fox movements, as evident from ear tag returns (Fuglei and Øritsland 2003), population genetic studies that have included the Svalbard population (Dalen et al. 2006, Carmichael et al. 2007, Geffen et al. 2007, Norén et al. 2011a) as well from satellite telemetry from arctic America (Pamperin et al. 2008, Tarroux et al. 2010). It is unknown whether the different sub-populations on the various islands within the Svalbard archipelago are dependent on rescue-effects (Brown and Kodric-Brown 1977) to sustain viable populations. The vulnerability of the arctic fox and their related ecosystem functioning to reduced sea-ice extent in Svalbard is in need of better knowledge. One possible threat, specifically for coastal arctic foxes feeding from the marine ecosystem, is negative effects of high levels of persistent organic pollutants (Fuglei et al. 2007). Multiple stressors of diseases, parasites, pollutions and winter food depletion may have unknown consequences in arctic foxes.

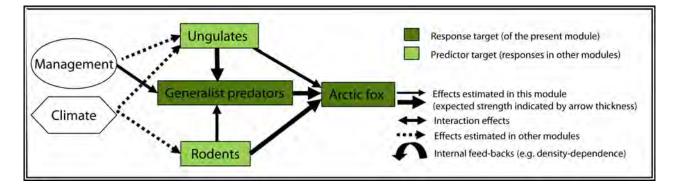
Studies of foxes in Svalbard indicate that at least a part of the population subsists on terrestrial resources among which reindeer carrion is crucial during winters (Eide et al. 2012) and geese are important in summer (Fuglei et al. 2003, Eide et al. 2005). Both of these food resources are expected to be sensitive to climate change (§ 2.5 and § 2.7). Such changes will, in turn, impact the spatial distribution and temporal dynamics of the arctic fox in Svalbard. In a recent study 'rain-on-snow' induced winter mortality in Svalbard reindeer was shown to cause a one-year delayed bottom-up effect on the arctic fox population (Hansen et al. 2013).

2.8.4. Climate change impact predictions

2.8.4.1. Rodent cycles and presence of natural enemies in the low-arctic: Varanger model

For the Varanger peninsula, and other arctic ecosystems with rodent population cycles and sympatric red fox populations, we outline a climate impact path model that has two pathways for climate change impacts on the arctic fox (Model 2.8.4.1). One pathway acts through changes of the rodent cycles (cf. § 2.4), for which we hypothesize that lemming dynamics are most influential. Specifically, we predict that the arctic fox population growth (mostly through breeding frequency and litter size) will be more dependent on the fate of lemmings than on that of voles, since arctic fox breeding is initiated when the tundra is still snow covered (and makes voles relatively inaccessible). As high amplitude lemming cycles may be present only in high altitude tundra, the range of the arctic fox may be increasingly restricted to these sections of the tundra.

The other pathway acts through the impact of increased intra-guild interactions (interference and scramble competition and predation) with red fox, golden eagles and corvids. We hypothesize that presence of these natural enemies on tundra to a large extent depend on presence of resource subsidies, either from large ungulates producing carrion on tundra (reindeer) or in the nearby forest (moose), or garbage from human settlements. The different possible sources of subsidies is likely to increase due to increased abundance and/or mortality of large ungulates and changed migration patterns, either related to climate change, altered management regimes (see § 2.5) or increased human populations. Stabilization of red fox dynamics will add to the negative impact of the arctic fox (Henden et al. 2010).



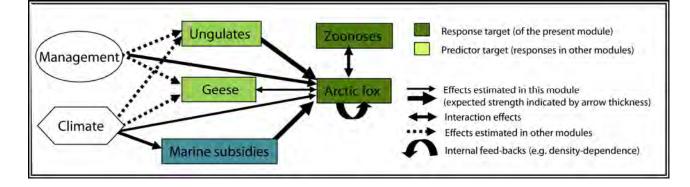
Model 2.8.4.1. Climate impact path model for the low-arctic Varanger with arctic fox and competing generalist predators as response targets.

2.8.4.2. High-arctic Svalbard model

There will be different impact pathways for coastal and inland foxes (Model 2.8.4.2). Inland foxes will depend on the fates of populations of geese and Svalbard reindeer. Geese populations are presently increasing for both climatic and other reasons (cf. §2.7), and may provide increasing abundance of prey for inland foxes in the breeding season. However, the arctic fox is known to be able to exert a sufficiently high predation pressure on breeding geese as to affect their distribution and abundance (Summers and Underhill 1987, Fuglei et al. 2003, Gauthier et al. 2004). Reindeer are most important in late winter through production of carrions, which have shown impact on arctic fox breeding (Fuglei et al. 2003, Eide et al. 2012, Hansen et al. 2013). Increased reindeer mortality owing to more icy winters (cf. §2.5) may produce more carrion to arctic foxes instead of harvestable reindeer for the local community in Svalbard.

Coastal foxes are especially dependent on the fate of colonial sea-birds. Change in sea bird populations can be relatively slow or fast, as exemplified by the sudden collapse of the common guillemot (*Uria alge*) along the coast of the Norwegian mainland and Bjørnøya (Barrett et al. 2006, Strøm 2006). Among additional marine resources the fate of ringed-seals (Freitas et al. 2009) and other ice-related animals will be influential as the extent of sea-ice is becoming even more limited. The arctic fox itself will be impacted by loss of sea-ice as habitat for foraging/prey and migratory movements. As a result the arctic fox in Svalbard will become more isolated with consequences for genetic structure (loss of variation and genetic drift), population dynamics (loss of rescue effect from immigrant foxes) and prevalence of zoonoses (halted influx of infected foxes).

Finally, changed arctic fox population dynamics, migration patterns as well as the dynamics of intermediate host of parasites are likely to affect the prevalence of zoonoses. Less sea-ice means less influx of rabid foxes from sources outside Svalbard. The prevalence of *E. multilocularis* will depend on the fate of the population of sibling voles in warmer climate (Box 2.8.1). One possible source of toxoplasmosis in arctic foxes in Svalbard is through migrating goose populations, which may thus be an additional way geese can impact arctic fox demography (cf. §2.7, Prestrud et al. 2007).



Model 2.8.4.2. Climate impact path model for the high-arctic Svalbard with the arctic fox and associated zoonotic deceases as response targets.

2.8.5. Management options

2.8.5.1. Varanger peninsula: Control of enemies and ungulate management

Systematic culling of red fox populations as an action to release endangered arctic fox populations from competition from red fox has been implemented both in alpine tundra in Sweden and Finland since the late 1990s (SEFALO), and on Varanger peninsula through the project "Arctic fox in Finnmark" since 2005 (Angerbjörn et al. 2013, Hamel et al. 2013). In the latter project, which is financed and practically operated by the Directorate of Nature Management, University of Tromsø is responsible for the project design, analysis and reporting of results. In "Arctic fox in Finnmark", there has been established three adjacent reference areas without red fox decimation, which serve as matching controls for the action. However, as there is no replication of the action area, we seek cooperation with our Swedish colleagues as to provide a more powerful analysis of the effect of the actions on the arctic fox demography and population dynamics (Angerbjörn et al. 2013). We are also conducting modeling studies as to provide guidelines on how the red fox reductions should be optimally administered in time and space (Henden et al. 2009a).

There are good reasons to think that red fox control may be a rational management action: The expansion of the red fox appear to have an anthropogenic origin, and moreover there is ample evidence that the red fox may outcompete arctic fox and that red fox culling have a positive effect on the arctic fox population (Angerbjörn et al. 2013, Hamel et al. 2013). In addition, it would be worth considering whether there are actions that could be targeted directly at the drivers of the red fox expansion. Harvesting statistics show coincidences between increasing red fox and ungulate populations (Selås and Vik 2006). On Varanger peninsula red fox presence in the interior of the peninsula appear to be facilitated by reindeer carrion in winter (Killengreen et al. 2011, Henden et al. 2013). Reindeer management practice, in particular factors determining migration patterns and winter mortality, is thus likely to be important. The same regards management of moose populations (harvesting practice) in tundra or in nearby sub-arctic forest, and management of large carnivores (Elmhagen and Rushton 2007, Elmhagen et al. 2011).

2.8.5.2. Svalbard: Arctic fox harvesting, management of reindeer and geese

Harvesting levels of arctic fox in Svalbard need to be considered closely in relation to the possible climate impacts outlined in model 2.8.4.2. This is both to ensure that harvesting is sustainable in new climatic settings and also to mitigate arctic fox impacts through predation on vulnerable prey (e.g. Svalbard rock ptarmigan; §2.6). As reindeer and geese are key food resources to arctic fox, the management of these two herbivores ought to be considered in context with the development of the arctic fox population. The arctic fox role as a vector for zoonoses is also an issue that involves management concerns. Arctic fox is the reservoir species of rabies in the arctic. As Svalbard has been the subject of two rabies outbreaks (1980 and 2011) action should be put on a screening for rabies in the annual trapping material. Factors important for spreading rabies or diseases are long-range migrations during winter. A study from the Canadian arctic showed that their use of sea-ice is highly influenced by food abundance (Tarroux et al. 2010).

2.8.6. COAT team competence

The arctic fox module will be led jointly by the Northern Population and Ecosystem Unit at UoT and Norwegian Polar Institute (NP). Team members in charge are Eva Fuglei (NP) and Siw T. Killengreen (UoT) with contributions from John-André Henden (UoT), Rolf A. Ims (UoT), Audun Stien (NINA) and Nigel G. Yoccoz (UoT). Research and conservation efforts on Varanger peninsula will be tightly coordinated with equivalent activities in sub-arctic mountain tundra in Fennoscandia, represented by partners in Sweden (Anders Angerbjörn, University of Stockholm), Finland (Heikki Henttonen, METLA) and Norway (Nina Eide, NINA). The research and monitoring in Svalbard are coordinated with equivalent activities on Bylot Island, Canadian Arctic represented by Dominique Berteaux, University of Quebec, Rimouski, and on Zackenberg Research Station, Greenland by Niels Martin Schmidt, Aarhus University, Denmark. NP is at present responsible for the annual monitoring of arctic fox in Svalbard with focus on population dynamics, epidemics of zoonotic parasites and diseases, environmental contaminants and harvesting. The UoT researchers are responsible for the project "Arctic fox in Finnmark" which focuses on research and management of the critically endangered arctic fox population on Varanger peninsula. The team

harbors considerable competence on methods of monitoring and analyses of arctic fox population dynamics and demography (Fuglei et al. 2003, Henden et al. 2009a, Eide et al. 2012, Hansen et al. 2013), diets (Lecomte et al. 2011), intra-guild interactions (Killengreen et al. 2012), trophic dynamics (Henden et al. 2008), food web connections (Killengreen et al. 2007) and the spread of zoonoses (Fuglei et al. 2008, Mørk et al. 2011, Norén et al. 2011b). The team has also experience with predictive modeling (Henden et al. 2009b) and statistical path model analysis of the effect of management actions on endangered arctic fox populations (Angerbjörn et al. 2013).



2.9. Monitoring design and

methods

In the following section, we describe the *monitor-ing design* selected for the ecosystems (high-arctic Svalbard and low-arctic Varanger peninsula) with respect to (1) the targets defined in the food web modules, (2) the climate observational network and (3) the monitoring of human use and valuation of those targets that are considered to provide ecosystem services. We further present a full set of *state variables* and the *measurement methods* applied to quantify them for each target, their use and valuation as ecosystem services and for climate.

2.9.1. Monitoring food web targets: A hierarchical design

In the previous chapters (§ 2.1-2.8) we have described a set of climate impact path models that defines a framework for what will be monitored in COAT. The monitoring targets defined by these models are species or species assemblages (i.e. trophic guilds and functional groups) and aspects of climate expected to be of particular importance for the specific response targets. However, the spatial scales at which the monitoring targets operate and respond to model pathways differ substantially between targets. Individuals of highly mobile species, like e.g. reindeer and many predators, will use large areas within a single year. For such monitoring targets synchronous large scale variation in environmental conditions are likely to be the important ones for individual fitness and population dynamics. Variation in environmental conditions at small spatial scales may, however, have strong effects on the distribution of individuals through effects on movement patterns and habitat selection. In contrast, the growth, survival and reproduction of individuals of sedentary species, like plants, will be strongly affected by local environmental conditions. The study of their population dynamics will therefore benefit from a study design that takes into account variability in environmental conditions at local spatial scales. The climate impact path models include interactions between monitoring targets that differ in their spatial response scales. To enable analyses and inferences at appropriate spatial scales we will employ a hierarchical monitoring design with three levels of spatial resolution.

The main structure of the hierarchical monitoring design will be shared by all modules. For processes

operating at small spatial scales we will use an intensive monitoring design with a high intensity of sampling within focal study sites, and an annual or higher sampling frequency. The focal study sites in the intensive monitoring design will be selected river valleys and the monitoring will be targeted at the climate impact pathways in which rapid responses and large inter-annual variability (i.e. population and trophic interaction cycles) are expected warranting frequent monitoring. This design will in particular be used in the detailed monitoring of plant response targets, but also in the monitoring of animal response targets, as well as food web interactions that can be expected to be localized and fast. The intensive design includes small scale spatial climatic variation by means of implementing altitudinal transects for several of the monitoring targets.

At a larger scale we will adopt a systematic extensive monitoring design. The regional coverage of the extensive monitoring design will i) allow extrapolation of the results from the intensive monitoring design to regional scales, ii) be targeted at monitoring large scale variability and trends in climate, vegetation and animal populations, and iii) be targeted at monitoring response targets implicated in slow climate impact pathways over long time intervals. For many monitoring targets we will adopt coarser monitoring methods and a lower sampling frequency in the extensive monitoring design than in the intensive monitoring design. Satellite based measurements (NDVI/EVI) and aerial photos of plant growth and vegetation structure have a relatively high spatial resolution and regional coverage. We have included such measurements in the extensive monitoring design.

Several monitoring targets have an "inherent" design given by their occurrence or space use which defies the extensive/intensive design categories defined above. We refer to these as *regional monitoring targets*. For instance, the monitoring of arctic fox reproduction is necessarily tied to the spatially dispersed occurrence of breeding dens (§ 2.8), and the natural unit for the monitoring of the demography and population size of semidomesticated reindeer (§ 2.5) is the herding district management unit.

2.9.2. Food web modules - low-arctic Varanger

2.9.2.1. Monitoring design

River valleys are characterized by more favorable edaphic and climatic conditions than the more exposed surroundings. In low-arctic Varanger they tend to form protruding frontiers for wooded vegetation into the tundra. Tall shrubs such as willow thickets are almost exclusively found in such riparian habitats. Moreover, mountain birch may be present as forest patches in the lowest parts and as single trees imbedded in thickets of shrubs further up in the valleys (Fig. 2.9.2.1). Meadows are predominantly found along the bottom of river valleys, while patches of snowbed and



Figure 2.9.2.1. Single birch trees extend above the layer of tall willow shrubs in the lower part of the valley Lavdnja-varjohka (Fig. 2.9.2.2, river no. 16) in the southern part of Varanger peninsula. Photo: Geir Vie

more extensive dwarf shrub heath communities are common along the sides. The relatively high primary productivity and the diversity of vegetation communities make river valleys a natural choice as the large spatial scale unit of replication in the intensive and extensive monitoring designs.

We have selected 11 river valleys for inclusion in the monitoring design in low-arctic Varanger. This includes 8 of the larger river valleys on the Varanger peninsula and 3 river valleys in the Ifjord area west of Varanger (Fig. 2.9.2.2). The river valleys are selected to cover the main climatic gradients (continental vs. oceanic), differences in geology (rich vs. mixed or poor bedrock) and differences in reindeer management regime across the region (Table 2.9.2.1). Based on this stratification the Varanger peninsula roughly divides into four sub-regions: two dryer, more continental regions in the south of which the eastern part have higher reindeer densities (Fig. 2.9.2.2, subregion III) and the western part lower densities (Fig. 2.9.2.2, sub-region II), and two wetter, more oceanic regions in the north with a similar contrast in reindeer densities between east (Fig. 2.9.2.2, sub-region IV) and west (Fig. 2.9.2.2, subregion I).

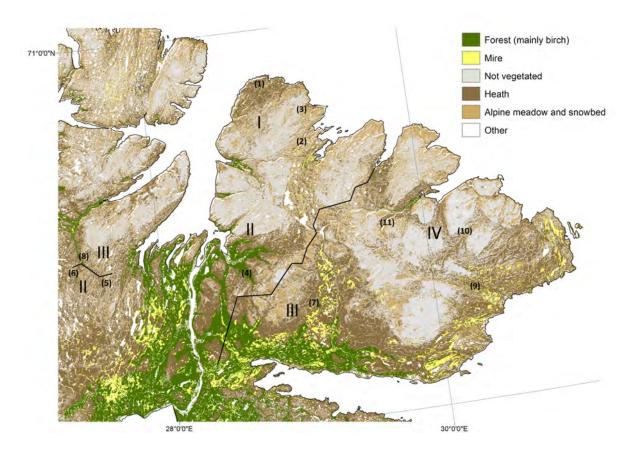


Figure 2.9.2.2. The location of the river valleys (numbered) included in the monitoring design for low-arctic Varanger. Numbers refer to table 2.9.2.1. Full black line show the fenced border between the two reindeer herding districts on the peninsula. Vegetation map reclassified from Johansen (2009).

Four river systems, distributed across all subregions, will be included in the intensive monitoring design. We use the term "river system" since the selections for the intensive design in most cases consist of more than the main river valley, but not entire catchments. Three of the four river systems selected for the intensive design contain long-term research study sites of the projects "Ecofinn" and "Arctic fox in Finnmark" with core relevance to COAT, while one river system has been added to ensure coverage of the main environmental gradients in the intensive monitoring design. The four river systems selected for the intensive monitoring design are Austre Risfjordelva (sub-region I, river no. 2, see Fig. 2.9.2.2, Table 2.9.2.1), Stuorrajohka with adjoining rivers (subregion II and III, river no. 5, 6 and 8), Bergebyelva with adjoining rivers (sub-region III, river no. 7) and Komagelva/Sandfjordelva_East (sub-region IV, river no. 9 and 10). The remaining rivers are included in the extensive monitoring design only.

2.9.2.2. Monitoring methods and state variables

Intensive monitoring state variables

In the intensive design the state variable are expected to exhibit rapid responses and hence also require frequent monitoring (seasonal to annual). Many targets monitored in the intensive monitoring design are also included in the extensive monitoring design, albeit at longer time intervals and with less detailed sampling. State variables in the intensive monitoring design describe the distribution, extent and configuration of relevant vegetation strata and the transitions between, abundances of herbivores and assessment of their grazing impacts, as well as the performance of the associated predator community (Fig. 2.9.2.3). This intensive design provides both a detailed monitoring of the state of each target in the climate impact path models, and the opportunity for indepth studies of the underlying processes driving observed changes. Ensuring partial overlap be-

Table 2.9.2.1. Overview of the river valleys included in the monitoring design in Varanger. Climate variables were extracted from gridded maps of normal (1961-1990) mean annual temperatures and annual precipitation (source: met.no) within a 1.5 km buffer around the main river (the hatched areas in Fig. 2.9.2.2). River valleys highlighted in bold belong to river systems selected for the intensive monitoring design.

| Locality (river number as in Fig. 2.9.2.2) | Region | Precip (mm) | Temp (°C) | Reindeer density | Geology | Approx. tree limit (m a.s.l.) |
|---|--------|----------------|--------------|---------------------|----------|-------------------------------------|
| Svanelva (1) | I | 530 | 0.60 | Low | Poor | 0 |
| Austre Risfjordelva (2) | I | 641 | 0.16 | Low | Poor | 0 |
| Sandfjordelva North (3) | I | 584 | 0.00 | Low | Mix | 0 |
| Austertanaelva (4) | II | 585 | -1.22 | Low | Rich | 200 |
| Upper Stuorrajohka (5) | II | 484 | -2.02 | Low | Rich | 200 |
| Estorjohka (6) | II | 520 | -1.40 | Low | Rich | 200 |
| Bergebyelva & tributaries (7) | ш | 595 | -1.16 | High | Mix | 200 |
| Lower Stuorrajohka & tributaries (8) | ш | 548 | -1.28 | High | Rich | 200 |
| Komagelva (9) | IV | 636 | 0.01 | High | Rich/Mix | 25-50 |
| Sandfjordelva East (10) | IV | 662 | 0.09 | High | Rich/Mix | 25-50 |
| Skogåselva (11) | IV | 687 | -0.30 | High | Rich/Mix | 100 |

Precip: Mean annual precipitation sum (mm). Temp: mean annual temperature. Reindeer density: Low = animals /km⁻² 1980-2003: 1.7, 2007-2010: 1.8, High = animals /km⁻² 1980-2003: 2.5, 2007-2010: 3. Geology: Rich = slate and limestone dominated types, Poor = mainly sand-stone, Mix = mixture of poor and richer types.

tween variables measured in experiments within the intensive design and variables in the extensive monitoring design will allow for linking the process-based and pattern-orientated studies. An important attribute of the spatial design of the intensive monitoring is strategic use of altitudinal (orographic) gradients both along the bottom of the river valleys and perpendicular to the rivers along the slopes of the valleys. These gradients will cover the main climatically determined transitions between plant communities. When experimental studies are conducted they will cover the same gradients as the intensive design. A full set of state variables and associated methods related to monitoring targets addressed in the intensive design are given in table 2.9.2.2.

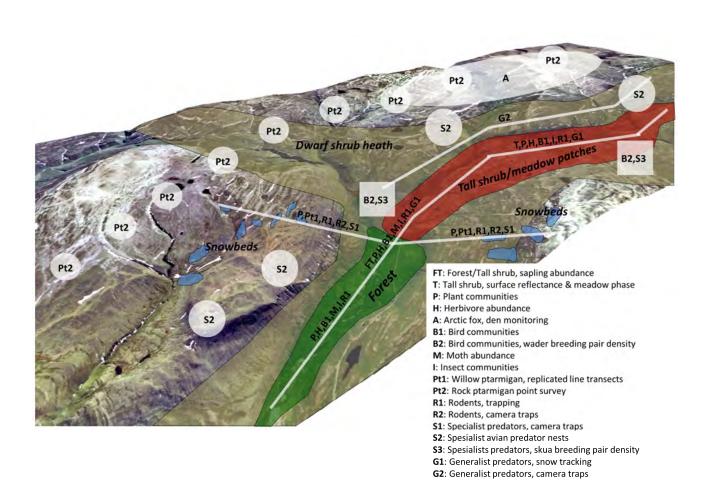


Figure 2.9.2.3. A simplified representation of the monitoring activities in river valleys selected for the *intensive monitoring design*. Targets are monitored either along transects from the coastline to the tundra parallel to the river, along (replicated) altitudinal gradients perpendicular to the river, or in specialized designs given by the occurrence of the target (for instance avian predator nests, S2). The selection of state variables addressed in any particular valley will differ depending on the presence of the relevant vegetation strata (e.g. forest is not present in all valleys). Transitions zones between the major vegetation strata (e.g. forest and tall shrub or dwarf shrub heath and snowbeds) are areas of intensified monitoring. Ortho photo obtained from www.norgeibilder.no.

Table 2.9.2.2. State variables and measurement methods used for monitoring targets included in the intensive design for Varanger. For state variables where time series already exist, we have indicated the start year of the time series in brackets in the interval column.

| Target | State variable | Interval | Methods (references) | Module |
|-------------------------|--|-----------------|--|----------------------------|
| | | | | relevance* |
| Forest/Tall shrubs | Shrub and tree sapling abun- dance | 1 yr | Survey transects along climatic gradients (Ravolainen et al. in prep.). Experimental establishment of shrub and tree saplings. Long-term herbivore exclosures (Ravolainen et al. 2011) in contrasting plant assemblages (Ravolainen et al. in prep) along environmental gradients. | 2.2, 2.3, 2.4, 2.5, 2.6 |
| Tall shrub tundra | Surface reflectance | 1 yr | Summer/winter albedo for major con- trasts in configuration of tall shrubs. Near infrared spectroscopy (NIRS) (Foley et al. 1998) | 2.3 |
| Meadows | Meadow phase. Functional group abundance, phenolo- gy, plant nutrient content, life history stage of silicate rich grasses | 1 yr (2005) | Survey transects (Ravolainen et al. in prep). Long-term exclosures (Ravolainen et al. 2011). Abundance estimates by point intercept methods (Jonasson 1988, Bråthen and Hagberg 2004). Plant quality by NIRS | 2.3 |
| Plant commu- nities | Plant community extent and configuration: | 1 yr (2006) | Survey transects along climatic gradients. Vegetation height, patch size and patch density (Ravolainen et al. 2010, Henden | 2.2, 2.3, 2.4, 2.5, 2.6 |
| | tall shrub vs. meadows, dwarf shrub heath vs. snow- beds | | et al. 2011a Ravolainen et al. in prep.) | |
| | Plant species abundance and community composition: forest, tall shrubs, meadows, dwarf shrub heath, snow- beds | 1 yr (2005) | Survey transects along climatic gradients. Abundance estimates by point intercept methods (Ravolainen et al. 2010) | 2.2, 2.3, 2.4, 2.5, 2.6 |
| | Norwegian lemming winter grazing impact and moss regrowth in snow beds | 1 yr (2009) | Abundance estimates by point intercept methods inside and outside of lemming exclosures (Ravolainen et al. 2011). | 2.4 |
| Insect defolia- tors | Abundance and species of Geometrid moth larvae in birch and dwarf birch | 1 yr | Survey transects along climatic gradients (forest to tundra) (Ims et al. 2004) | 2.2 |
| Ungulates | Reindeer habitat use | seasonal | GPS collared individuals | 2.2, 2.3, 2.5 |
| | Moose habitat use | seasonal | GPS collared individuals | 2.2, 2.3, 2.5 |
| | Abundance indices | 1 yr | Survey transects along climatic gradients. Abundance estimates by pellet counts (Killengreen et al. 2007) | 2.2, 2.3, 2.5 |

*2.2 Tundra-forest ecotone module, 2.3 Tall shrub module, 2.4 Rodent module, 2.5 Large ungulate module, 2.6 Ptarmigan module, 2.8 Arctic fox module

| Table | 2.9.2.2 | (cont.) |
|-------|---------|---------|
|-------|---------|---------|

| Target | State variable | Interval | Methods (references) | Module relevance* |
|--|---|--------------------|---|-----------------------|
| Rodents | Grey-sided vole and tundra vole abundance and demographic structure per season (spring/fall) and habitat (heath/riparian mead- ow) | Seasonal (2005) | Live trapping along climatic gradients (altitudinal and geo- graphical) (Yoccoz and Ims 2004) | 2.3, 2.4, 2.8 |
| | Norwegian lemming abundance and demographic structure per season (winter/spring/fall) and habitat | Seasonal (2009) | Camera traps (spring/fall) (Ims et al. in prep.), pellets counts (winter) along climatic gradients (altitudinal and geographical) (Ims et al. 2007b) | 2.3, 2.4, 2.8 |
| Ptarmigan | Willow ptarmigan and rock ptarmi- gan occupancy and abundance per season (spring/fall) and habitat (heath, riparian meadow and transi- tion heath/boulder fields) | Seasonal (2005) | Point-transects (spring), fecal counts (spring/fall), line tran- sects (summer/fall) (Henden et al. 2011a, Ehrich et al. 2012a, Pedersen et al. 2012) | 2.6, 2.8 |
| Bird communities | Assemblage of wader species breeding pair density in skua sur- vey transects | 1 yr (2006) | Survey transects, territory map- ping (Sokolov et al. 2012) | 2.4, 2.8 |
| | Community composition and diver- sity | 1 yr (2005) | Survey transects. Point counts of bird calls (Ims and Henden 2012) | 2.2, 2.3 |
| Specialist preda- tors (Rodents) | Stoat and least weasel abundance indices per rodent habitat and sea- son | Seasonal (2006) | Camera traps (spring/fall) (lms et al. in prep.), snow tracking transects (winter) (Oksanen et al. 1992) | 2.4 |
| | Skuas (long-tailed, arctic and poma- rine), snowy owl, rugged-legged buzzard breeding pair density and reproductive output | 1 yr (2006) | Survey transects. Breeding pairs/km², size of fledged clutch- es (Gilg et al. 2003) | 2.4 |
| | Diets of avian predators | 1 yr | Stable isotopes of feathers. Pel- let analysis (snowy owl, rough- legged buzzard) (Pokrovsky et al. in prep.) | 2.4 |
| Generalist preda- tors | Raven, hooded crow site-specific occupancy and abundance in sum- mer | 1 yr | Camera traps | 2.4, 2.6 |
| | Red fox relative abundance | 1 yr (2006) | Snow tracking transects in val- leys (Elmhagen et al. 2010) | 2.4, 2.5, 2.6, 2.8 |
| | Relative predation pressure on ptarmigan nests in summer | 1 yr (2005) | Artificial nests along altitudinal gradients (Thingnes et al. in prep.) | 2.6 |

*2.2 Tundra-forest ecotone module, 2.3 Tall shrub module, 2.4 Rodent module, 2.5 Large ungulate module, 2.6 Ptarmigan module, 2.8 Arctic fox module

Extensive monitoring state variables

State variables in the extensive design describe the distribution, extent and configuration of relevant vegetation strata, the transitions between them as well as the abundance of large ungulates as the main driver of vegetation state changes in the region in addition to climate (Fig. 2.9.2.4). Further,

the extensive design includes state variables obtained from remote sensing sources with regional coverage. A full set of state variables and associated methods related to monitoring targets addressed in the extensive design are given in table 2.9.2.3.

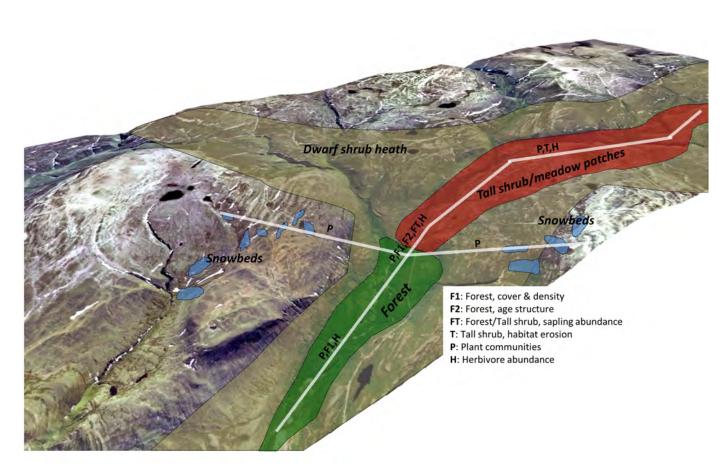


Figure 2.9.2.4. A simplified representation of the monitoring activities in river valleys selected for the extensive monitoring design in Varanger. Targets are monitored either along transects from the coastline to the tundra parallel to the river, or along (replicated) altitudinal gradients perpendicular to the river. As for the intensive monitoring design, the selection of state variables addressed in any particular valley will differ depending on the presence of the relevant vegetation strata, and transition zones between the major vegetation strata will be areas of intensified monitoring. Ortho photo obtained from www.norgeibilder.no.

Table 2.9.2.3. State variables and measurement methods used for monitoring targets included in the extensive design for Varanger. For state variables where time series already exist, we have indicated the start year of the time series in brackets in the interval column.

| Target | State variable | Interval (start) | Methods (references) | Module relevance* |
|--------------------------|--|---------------------|--|----------------------------|
| Tundra-Forest ecotone | Historical tree cover | once | Classification of historical (~1960- present) aerial photos | 2.2 |
| | Tree cover | 5 yrs | Classification of aerial photos and satel- lite images | 2.2, 2.3, 2.5 |
| | Tree density, species, height, diameter, growth form, health | 5 yrs | Survey transects along climatic gradi- ents. | 2.2, 2.3, 2.5 |
| | Tree age structure | 10 yrs | Survey transects along climatic gradi- ents. Age estimates by dendrochronolo- gy (Aune et al. 2011) | 2.2 |
| Forest/Tall shrub | Shrub and tree sapling abun- dance | 5 yrs (2010) | Survey transects along climatic gradi- ents. (Ravolainen et al. in prep.) | 2.2, 2.3, 2.4, 2.5, 2.6 |
| Tall shrub tundra | Habitat erosion in riparian tall shrub tundra. Extent of de-vegetated areas. | 5 yrs | Survey transects with permanently marked plots. Classification of aerial pho- tos and satellite images (Tape et al. 2011) | 2.3 |
| Plant communi- ties | Historical plant community extent | once | Classification of historical aerial photos and interpretation of written historical sources. | 2.2, 2.3 |
| | Plant community extent and configuration: tall shrub vs. meadows, dwarf shrub heath vs. snowbeds | 5 yrs (2010) | Survey transects along climatic gradi- ents. Classification of aerial photos and satellite images (Henden et al. 2011b) | 2.2, 2.3, 2.4, 2.5, 2.6 |
| | Plant species abundance and community composition: forest, tall shrubs, dwarf shrub heath, snowbeds | 5 yrs (2010) | Survey transects along climatic gradients (Ravolainen et al. 2010). Abundance esti- mates by point intercept methods (Jonasson 1988, Bråthen and Hagberg 2004) | 2.2, 2.3, 2.4, 2.5, 2.6 |
| | Vegetation greenness | 1 yr (2000) | Summer NDVI/EVI calculations from sat- ellite images (Bårdsen and Tveraa 2012) | 2.2, 2.3, 2.4, 2.5, 2.6 |
| Ungulates | Abundance indices | 5 yrs | Survey transects along climatic gradi- ents. Abundance estimates by pellet counts (Killengreen et al. 2007) | 2.2, 2.3, 2.5 |

*2.2 Tundra-forest ecotone module, 2.3 Tall shrub tundra module, 2.4 Rodent module, 2.5 Large ungulate module, 2.6 Ptarmigan module, 2.8 Arctic fox module

Regional monitoring state variables

The regional monitoring include state variables that are derived from regionally available statistics (e.g. hunting records, national monitoring programs) and state variables that have an inherent design given by their occurrence that defy the extensive and intensive designs otherwise adopted in COAT (Fig. 2.9.2.5). For most of the regional state variables, time series have been initiated during previous or ongoing research initiatives in Varanger during the last decade. They represent a valuable point of departure for the monitoring in COAT. A full set of state variables and associated methods related to monitoring targets addressed in the regional monitoring are given in table 2.9.2.4.

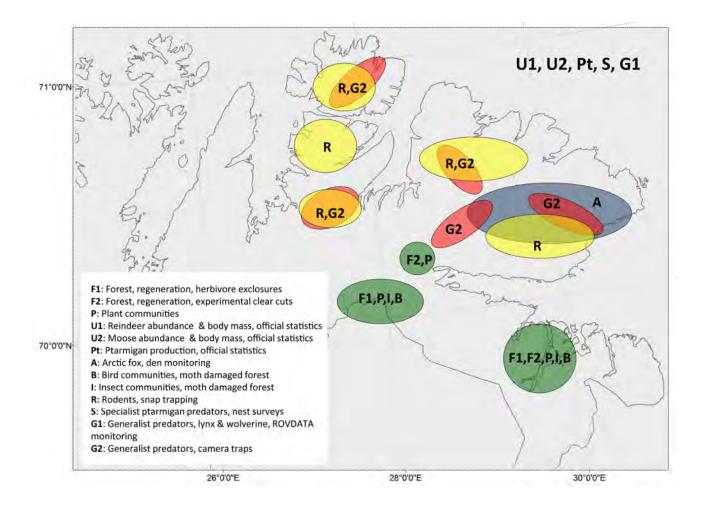


Figure 2.9.2.5. A simplified representation of the regional monitoring in Varanger. Monitoring targets listed in the upper right corner are based on official statistics available for the entire region.

Table 2.9.2.4. State variables and measurement methods used for the regional monitoring targets for Varanger. For state variables where time series already exist, we have indicated the start year of the time series in brackets in the interval column.

| Target | State variable | Interval | Methods (references) | Module |
|-------------------|---|--------------------|--|--------------------|
| | | (start) | | relevance* |
| Forest | Tree density, height, diameter, growth form, health | 5 yrs (2011) | Surveys in large ungulate exclosures and controls (Jepsen et al. in prep.) | 2.2, 2.5 |
| | Forest regeneration after moth outbreaks: Sapling species, sap- ling and basal shoot density | 5 yrs (2011) | Surveys in large ungulate exclosures and controls (Jepsen et al. in prep.) | 2.2, 2.5 |
| | Forest regeneration after moth outbreaks in cut and uncut for- est: Sapling species, sapling and basal shoot density | 5 yrs (2011) | Surveys in experimental clear cuts and uncut con- trols (Jepsen et al. in prep.) | 2.2 |
| Plant communities | Plant succession: species abun- dance and community composi- tion | 5 yrs (2011) | Surveys in large ungulate exclosures and controls. Point intercept methods (Jonasson 1988, Bråthen and Hagberg 2004) | 2.2, 2.5 |
| Ungulates | Reindeer abundance and demo- graphic structure | 1 yr (1980) | Official statistics (Tveraa et al. 2007) | 2.2, 2.3, 2.5 |
| | Reindeer body mass (fall) | 1 yr (1980) | Official statistics (Tveraa et al. 2007) | 2.5 |
| | Reindeer reproductive rates and body mass (spring/fall) | 1 yr | Individual based data (Bårdsen and Tveraa 2012) | 2.5 |
| | Moose relative abundance and demographic structure | 1 yr (1989) | 'Sett elg' monitoring program (Solberg et al. 2010) | 2.2, 2.3, 2.5 |
| | Moose body mass (fall) | 1 yr (2000) | Harvest statistics (www.fefo.no) | 2.5 |
| Rodents | Grey-sided vole and tundra vole abundance and demographic structure per season (spring/fall) | Seasonal (2004) | Snap trapping along cli- mate gradients (altitudinal and geographical) (Ims et al. 2011) | 2.2, 2.3,2.4, 2.8 |
| | Norwegian lemming abundance and demographic structure per season (winter/spring/fall) | Seasonal (2004) | Snap trapping along cli- mate gradients (altitudinal and geographical) (Ims et al. 2011) | 2.2, 2.3, 2.4, 2.8 |
| Ptarmigan | Willow and rock ptarmigan pro- duction | 1 yr | Wing samples from har- vested birds (fall) (Parker et al. 1985) | 2.6 |
| Bird communities | Community composition and diversity | 1 yr (2011) | Survey transects in moth damaged forest. Point counts of bird calls (Ims and Henden 2012) | 2.2 |

*2.2 Tundra-forest ecotone module, 2.3 Tall shrub tundra module, 2.4 Rodent module, 2.5 Large ungulate module, 2.6 Ptarmigan module, 2.8 Arctic fox module

| Target | State variable | Interval (start) | Methods (references) | Module rele- vance* |
|--|---|---------------------|---|------------------------|
| Insect commu- nities | Community composition and abundance of saproxylic in- sects | 1 yr (2011) | Survey transects in moth damaged forest. Flight interception traps (Sverdrup-Thygeson and Birkemoe 2009) | 2.2 |
| Generalist predators | Red fox, wolverine, raven, crow, white-tailed and golden eagle frequency and competi- tion on carcasses in late winter | 1 yr (2005) | Camera traps on carcasses along envi- ronmental gradients in areas with and without red fox decimation (Killengreen et al. 2012) | 2.4, 2.5, 2.6, 2.8 |
| | Lynx and wolverine relative abundance | 1 yr (1999) | The ROVDATA monitoring program (www.rovdata.no) | 2.5 |
| Specialist pred- ators (Ptarmigan) | Gyrfalcon breeding frequency, diet and reproductive output in terms of size of clutches | 1 yr (2012) | Nest surveys, nest pellet remains (Nielsen 1999) | 2.6 |
| Arctic fox | Size of breeding population and reproductive success | 1 yr (2004) | Inventories and camera traps at dens in summer (Meijer et al. 2011) | 2.4, 2.8 |
| | Disturbance on arctic fox dens by red fox and golden eagle | 1 yr (2012) | Camera traps at dens (Meijer et al. 2011) | 2.8 |
| | Genetic identity (species- and individual-level), genetic pop- ulation structure | 1 yr (2010) | Scat samples at dens, samples of fur (Ehrich et al. 2012b) | 2.8 |
| | Late summer/early autumn and winter diet | Seasonal (2007) | Stable isotope analysis of winter fur (Killengreen et al. 2011) | 2.4, 2.8 |

*2.2 Tundra-forest ecotone module, 2.3 Tall shrub tundra module, 2.4 Rodent module, 2.5 Large ungulate module, 2.6 Ptarmigan module, 2.8 Arctic fox module

2.9.3. Food web modules - high-arctic Svalbard

2.9.3.1 Monitoring design

On Nordenskiöld Land peninsula in high arctic Svalbard river valleys are characterized by more favorable edaphic and climatic conditions than the more exposed surroundings. Vegetation cover decrease rapidly at altitudes above 200 m.a.s.l. Swamps, wet moss and fen marsh communities are predominantly found along the bottom of river valleys, while meadows, snowbed and graminoid dominated communities are common along the sides (Johansen et al. 2012). Similar to the low arctic Varanger, the relatively high primary productivity and the diversity of vegetation communities make river valleys a natural choice as the large spatial scale unit of replication in the intensive and extensive monitoring designs. On Brøggerhalvøya penninsula, further north on Svalbard, vegetation cover decrease rapidly above 100 m.a.s.l. In contrast to high arctic Nordenskiöld Land peninsula and low arctic Varanger, favorable edaphic and climatic conditions for plants and wildlife are predominantly found along the coast on Brøggerhalvøya as inland the valleys tend to be covered by glaciers.

We have selected 5 river valleys on the Nordenskiöld Land peninsula for inclusion in the monitoring design in high arctic Svalbard (Fig. 2.9.3.1). The river valleys were selected, using our knowledge of the system, to cover the main climatic gradients (continental vs. oceanic) in the region and large variation in densities of breeding pink-footed geese and arctic foxes. The selected river valleys are: Reindalen and Semmeldalen with a continental winter climate, a low density of breeding arctic foxes and a low and relatively high, respectively, density of breeding pink-footed geese; Colesdalen and Adventdalen with a more oceanic climate and, respectively, low and medium densities of breeding pink-footed geese and foxes; and Sassendalen with a continental climate and high densities of breeding pink-footed geese and arctic foxes. Together these valleys cover about 40% of the densely vegetated ground on Nordenskiöld Land peninsula. On the Brøggerhalvøya peninsula we have selected 2 coastal areas for inclusion in the monitoring design (Fig. 2.9.3.1). One is the non-glaciated coastal area around Kongsfjorden and the other is the coastal plain of Sarsøyra.

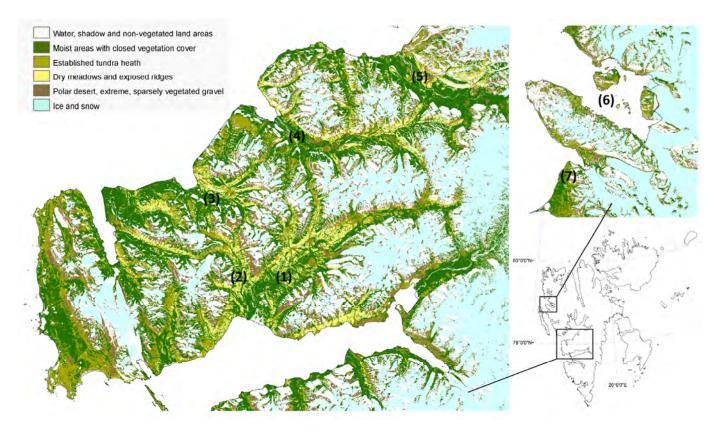


Figure 2.9.3.1. The location of the 5 river valleys included in the intensive monitoring design on high-arctic Svalbard. Reindalen (1), Semmeldalen (2), Colesdalen (3), Adventdalen (4) and Sassendalen (5). In addition two coastal sites are included on Brøggerhalvøya peninsula (6 and 7). Vegetation map reclassified from Johansen *et al.* (2009)

2.9.3.2. Monitoring methods and state variables

Intensive monitoring state variables

State variables in the intensive monitoring design describe the distribution and extent of relevant vegetation strata and herbivore abundances (Fig. 2.9.3.2). This intensive design provides both a detailed monitoring of the state of each target in the climate impact path models and the opportunity for in-depth studies of the underlying processes driving observed changes. All the seven selected areas in high arctic Svalbard are included in the intensive monitoring design. However, not all state variables will be monitored across all study areas. In particular, detailed plant and ptarmigan studies will be performed in Adventdalen and Sassendalen only. A full set of state variables and associated methods related to monitoring targets addressed in the intensive design are given in table 2.9.3.1.

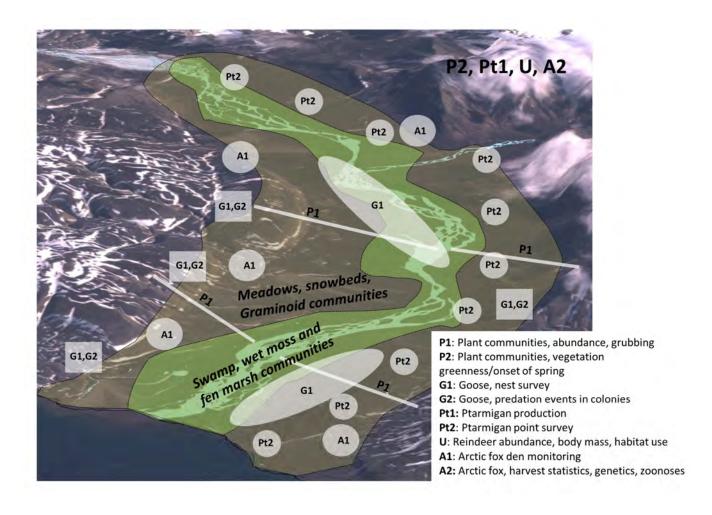


Figure 2.9.3.2. A simplified representation of the monitoring activities in river valleys selected for the intensive monitoring design. Targets are monitored either in replicated altitudinal transects, in systematic survey designs (e.g. ptarmigan point survey, Pt2) or in specialized designs given by the occurrence of the target (e.g. arctic fox dens, A1 and goose colonies, G1/G2). The selection of state variables in any particular valley in the intensive design will differ. Monitoring targets listed in the upper right corner are based either on official statistics available for the entire region, or on remote sensing sources with regional coverage.

Table 2.9.3.1. State variables and measurement methods used for monitoring targets included in the intensive design for Svalbard. For state variables where time series already exist, we have indicated the start year of the time series in brackets in the interval column.

| Target | State variable | Interval (start) | Methods (references) | Module |
|--|---|-------------------------------|--|----------|
| Plant commu- nities | Quantity and quality of goose and reindeer forage plants in marshes: | 1 yr | Biomass/leaf area index and pro- tein content in selected plants and plots at time of hatch (Pettorelli et al. 2011; ITEX Protocol, | 2.5, 2.7 |
| | Grasses/sedges | | www.geog.ubc.ca/itex; Madsen et al. in prep.) | |
| | Pink-footed goose grubbing impact on fen habitats | 1 yr (2003) | Quadrat and point-intercept sam- pling of vegetation cover and com- position on fixed transects along altitudinal transects (Madsen et al. 2011) | 2.6, 2.7 |
| | Abundance (biomass) and phe- nology of spring/summer herbi- vore forage plants: Altitudinal gradients: Polar willow (Salix | 1 yr | Abundance estimation by: point intercept method (Bråthen and Hagberg 2004) | 2.6, 2.7 |
| polaris) and Bistorta (Bistorta vivipara) | | | Estimation of phenology- temperature curves | |
| Geese | Pink-footed Goose (PG) and Barnacle Goose (BG) breeding pair density, timing of nesting, reproductive output in terms of numbers of nests hatching suc- cessfully: per habitat: altitudinal gradient (PG); islands vs. cliffs (BG) | 1 yr (PG 2003, BG 1980) | Colony surveys in selected plots (Madsen et al. 2007) | 2.7, 2.8 |
| | Predation events and rates in goose colonies | 1 yr (BG 1980) | Automatic cameras at selected goose colonies (Anthony et al. 2006, Liebezeit and Zack 2008) | 2.7, 2.8 |
| Jngulates | Svalbard reindeer abundance and demographic structure | 1 yr (1979) | Population surveys (Solberg et al. 2001, Aanes et al. 2003) | 2.5, 2.8 |
| | Svalbard reindeer body mass, pregnancy and calving rates (spring/summer) | seasonal (1995) | Individual-based measures (Stien et al. 2002, Stien et al. 2012) | 2.5, 2.8 |
| | Svalbard reindeer habitat use | Seasonal (2009) | GPS collared individuals (Stien et al. 2010a) | 2.5 |
| Ptarmigan | Svalbard rock ptarmigan yearly occupancy and abundance of territorial males in spring | Seasonal (2000) | Point-transect (spring) (Pedersen et al. 2012) Fecal counts (spring-summer) (Evans et al. 2007, Henden et al. 2011a) | 2.6, 2.8 |

*2.5 Large ungulate module, 2.6 Ptarmigan module, 2.7 Goose module, 2.8 Arctic fox module

Extensive monitoring state variables

For the extensive monitoring design we will rely on remote sensing methods (satellite and aerial photographs) (Table 2.9.3.2). Ground validation of the remote sensing techniques will be done based on data from the intensive monitoring design.

Regional monitoring state variables

For most of the regional state variables, time series have been initiated during the previous or ongoing research and monitoring initiatives in Svalbard (e.g. MOSJ http://mosj.npolar.no). They represent a valuable point of departure for the monitoring in COAT. The full set of state variables and associated methods related to monitoring targets addressed in the regional monitoring are given in table 2.9.3.3.

Table 2.9.3.2. State variables and measurement methods used for monitoring targets included in the extensive design for Svalbard. For state variables where time series already exist, we have indicated the start year for the time series in brackets in the interval column.

| Target | State variable | Interval (start) | Methods (references) | Module |
|------------------------|--|---------------------|---|---------------|
| Plant commu- nities | Vegetation greenness and onset of spring | 1 yr (2000) | Spring/summer NDVI/EVI calculations from satellite images (MODIS) (Madsen et al. 2007, Bårdsen and Tveraa 2012) | 2.5, 2.6, 2.7 |
| | Habitat erosion in wet and moist fen vegetation. Extent of de-vegetated areas. | 10 yrs | Classification of aerial photos and satel- lite images (Tape et al. 2011) | 2.5, 2.6, 2.7 |
| | Plant community extent and configuration: | 10 yrs | Classification of aerial photos and satel- lite images (Henden et al. 2011b) | 2.5, 2.6, 2.7 |
| | wet and moist fen, meadow, graminoid and polar desert vegetation | | | |

*2.5 Large ungulate module, 2.6 Ptarmigan module, 2.7 Goose module



Table 2.9.3.3. State variables and measurement methods used for the regional monitoring targets for Svalbard. For state variables where time series already exist, we have indicated the start year of the time series in brackets in the interval column.

| Target | State variable | Interval (start) | Methods (references) | Module |
|------------|--|-------------------------------|---|--------------------|
| Geese | Overall population size and productivity | 1 yr (BG 1950, PG 1980) | Autumn population counts and age counts, brood sizes in wintering areas (Madsen et al. 1999, Fox et al. 2005) | 2.7, 2.8 |
| Ungulates | Svalbard reindeer body mass (fall) | 1 yr | Harvest statistics (Hansen et al. 2012) | 2.5 |
| Ptarmigan | Ptarmigan production and abundance | 1 yr (1997) | Wing samples (fall), harvest statis- tics (Parker et al. 1985; Pedersen et al. in prep.) | 2.6, 2.8 |
| Arctic fox | Size of breeding population and reproductive success | 1 yr (1982) | Inventories and camera traps at dens in summer (Fuglei et al. 2003; Berteaux et al. in prep., Eide et al. 2012) | 2.5, 2.6, 2.7, 2.8 |
| | Genetic identity (species- and individual-level), genetic pop- ulation structure | 1 yr (1997) | Scat samples at dens, samples of fur and tissue from carcasses (Dalen et al. 2006, Norén et al. 2011b, Ehrich et al. 2012b) | 2.8 |
| | Late summer/early autumn and winter diet | Seasonal (2007) | Stable isotope analysis of fur and tissue from carcasses (Killengreen et al. 2011; Ehrich et al. in prep.) | 2.5, 2.6, 2.7, 2.8 |
| | | | Prey remains at dens in summer | |
| | Demographic structure and persistent organic pollutants | 1 yr (1982) | Harvesting statistics, autopsy of fox carcasses and organ analyses (Fuglei et al. 2007; Fuglei et al. in prep.) | 2.8 |
| | Change in prevalence of zo- onoses (rabies, toxoplasmo- sis, E. multilocularis) | 1 yr (1996) | Autopsy of fox carcasses (1990) Survey of sibling vole range limits (intermediate host of E. multilocu- laris) (Prestrud et al. 2007, Fuglei et al. 2008, Mørk et al. 2011) | 2.5, 2.8 |

*2.5 Large ungulate module, 2.6 Ptarmigan module, 2.7 Goose module, 2.8 Arctic fox module

2.9.4. Climate observational network

2.9.4.1. Monitoring design

Climate can be defined as the weather pattern in an area over some extended time period. The foundation for obtaining an estimate of climate is therefore repeated observations of the weather. The spatial and temporal scale of the meteorological measurements that are appropriate for estimating the weather pattern of interest, is in COAT determined by the response scale of the COAT monitoring targets and the climate drivers outlined in the climate impact path models (§ 2.1-2.8). The spatial and temporal scale and aspect of climate of interest vary between climate impact path models, and often vary between predictor and response targets within the same climate impact path model. In COAT we need to expand the current network of weather stations in order to i) measure weather parameters relevant to the prioritized climate impact path models at appropriate scales, and ii) provide a better basis for interpolating weather parameters and downscaling climate projections. To enable analyses and inferences at appropriate scales, the design of this climate observational network will follow the general framework of the COAT hierarchical monitoring design (see § 2.9.1).

The COAT climate monitoring network will be implemented using automatic weather stations

supplemented by the national weather observation network. In addition, measurements of snow and ice conditions need to be supplemented using manual observations, and remote sensing methods. We will use automatic weather stations of three types: Module stations (M), which acquires high resolution observations at the local scale for a small number of weather elements. Base stations (B), which are simplified weather stations that acquire observations of several basic climate elements, and Reference stations (R), which are complete meteorological stations observing all energy balance elements. The meteorological parameters measured by the different station types used in COAT are given in table 2.9.4.1. The synoptic stations in the national weather observation network are mostly equipped as reference stations except for radiation observations, but some observe only precipitation. The COAT climate monitoring network will have a high density of module stations in intensive monitoring sites, and base stations and reference stations at lower densities (for a similar approach see Kabas et al. 2011). The base and reference station network is intended to be permanent, to provide a robust platform for the long term monitoring program. The design of the module station networks will, however, be determined by the processes studied in the intensive monitoring sites and may change in response to changes in intensive monitoring targets.

| Target | State variable | Interval | Station type |
|----------------|---|----------|--------------|
| Weather | Air temperature (at 0.2 and 2 m above ground) | 1 hr | R, B, M |
| | Ground temperature (at surface and -0.1 m) | 1 hr | R, B, M |
| | Precipitation | 1 hr | R, B |
| | Humidity | 1 hr | R, B |
| | Wind (direction, force) | 1 hr | R, B |
| Energy balance | Radiation (shortwave and longwave) | 1 hr | R |
| Snow | Snow depth | 1 hr | R |

Table 2.9.4.1. State variables measured by the different types of automatic weather stations used in the COAT climate monitoring network. R=Reference stations, B=Base stations, M=Module stations.

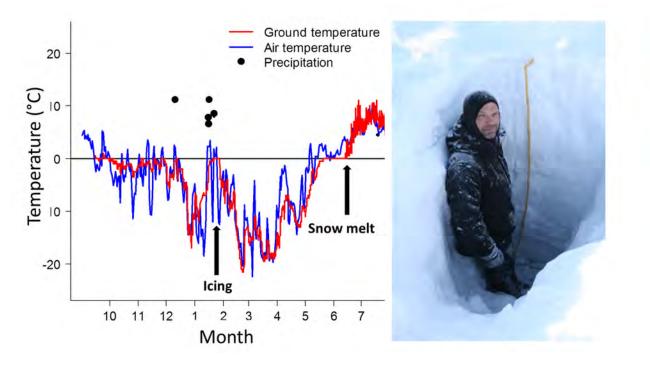


Figure 2.9.4.1. Time series of weather measurements (left) showing the signature of ground icing events where heavy rain (mm) cause zero degrees C ground temperatures, and the signature of snow melt when ground temperatures are released from the zero degrees state in spring. Manual measurements (right) of snow depth, snow structure and ground ice are time consuming when snow depths are substantial. Photo: Rolf A. Ims.

2.9.4.2. Monitoring methods and state variables

Summer temperatures and summer precipitation are expected to be important climatic drivers of variation in the quality and primary production of the vegetation (§ 2.2-2.8). Summer air temperatures are relatively easy to monitor and will be monitored at ground level and several distances above ground using all the weather station types (Table 2.9.4.1). The grid of measurements of precipitation be less dense and consist of the base stations, reference stations and some of the stations in the national weather observation network.

Snow is an important climatically determined driver in arctic tundra ecosystems (§ 2.2-2.8). Spatial variation in snow depths determine the patch structure of the length of the snow covered season and soil moisture, factors of critical importance for vegetation community structure. Between-year variation in the length of the snow free season is likely to be a main determinant of plant primary productivity. Also, the timing of snow melt is an important determinant of the food quality and availability, as well as nest site availability, in a critical period for reproduction in many herbivores (§ 2.5-2.7). Finally, snow depth and snow hardness, and in particular ice layers resulting from rain-on-snow events, are main determinants of herbivore food availability through the winter period (§ 2.4-2.5). A whole set of snow

parameters are therefore of critical importance to understand the impact of climate on arctic tundra food web interactions (§ 2.4-2.5). We will therefore use several methods for snow monitoring (table 2.9.4.2).

The timing of snow melt will be monitored locally using temperature loggers on the ground combined with measurements of air temperature. Ground temperatures stay at zero degrees when the snow is melting and change to the level of the air temperature when ground is snow free (fig. 2.9.4.1). In addition we will use satellite based measures of snow cover (MODIS) to monitor snow cover and snow melt at regional scales. The link between the local scale and regional scale measures will be investigated using the high intensity of ground temperature data obtained at the intensive monitoring sites.

The ground based temperature loggers will also be used to monitor the timing of ground ice development. Our experience from ongoing studies on Svalbard show that icing due to severe rain-onsnow events result in a clear ground temperature signature, causing the temperature to reach zero degrees during icing events caused by rain-onsnow (fig. 2.9.4.1).

Snow depths will be monitored automatically at the reference stations. At the intensive monitoring sites these observations will be supplemented by additional data from manual snow pit studies (fig. 2.9.4.1), and at larger scales using helicopterborne LIDAR (Grünewald and Lehning 2011). The latter give transect based snow depth measurements with 5 cm precision. The snow pit studies will in addition give information on the snow structure and ground ice thickness.

We will combine all these data in the development and testing of snow models that will construct maps of snow depth and hardness at regional scales. The SNOWPACK model (Lehning et al. 2002a, Lehning et al. 2002b, Rasmus et al. 2007) will be used to predict snow stratification, density and crystal structure based on measurements of air and ground temperature, air humidity, wind velocity, wind direction, shortwave and longwave radiation, and snow depth and precipitation. Given that these measurements will be available only from Reference stations, model predictions will be validated using snow pits located at different dis-

tances from the reference stations to assess the spatial variability in snow characteristics in the intensive and extensive monitoring regions. Data on the temperature, humidity and wind obtained at the Base stations will be used to assess if local predictions of snow characteristics can be improved using local temperature, precipitation and wind data. SnowModel (Liston and Elder 2006) will be used to predict snow accumulation, density, sublimation and melt, and redistribution by wind including interception by tall shrubs and forested areas. The model uses as input precipitation, wind speed and direction, air temperature and relative humidity, as well as topography and vegetation type. SnowModel has already been used to predict snow characteristics over catchments in the Arctic.

| Target | State variable | Interval | Station/measurement type |
|---------------------|--------------------|-------------|--------------------------|
| Timing of snow melt | Ground temperature | 1 hr | R, B, M |
| | Snow cover | 16 days | Satellite (MODIS) |
| Snow depth | Snow depth | 1 hour | R |
| | Snow depth | 1 day | Snow models |
| | Snow depth | 1 week-1 yr | Snow pits |
| | Snow depth | 1 yr | Remote sensing, LIDAR |
| Snow structure | Snow structure | 1 day | Snow models |
| | Snow structure | 1 week-1 yr | Snow pits |
| Ground ice | Ice thickness | 1 day | Snow models |
| | Ice thickness | 1 week-1 yr | Snow pits |
| Timing of icing | Ground temperature | 1 hr | R, B, M |

Table 2.9.4.2. State variables measured by the different types of methods used in monitoring snow conditions used in COAT climate monitoring network. R=Reference stations, B=Base stations, M=Module stations.

2.9.4.3. Design of the climate observational network in low arctic Varanger

One reference station will be set up for each monitoring area in the Varanger area. The network of base stations will be designed to support both the extensive and intensive monitoring design in COAT, and hence reflect the primary climatic gradients across the Varanger peninsula and the locations of the river systems selected for the intensive design. There will be an extensive use of temperature loggers in the intensive monitoring sites. In addition we will use the available national weather observation network (fig. 2.9.4.2). A significant development in the national weather observation network for the area is the placement of a precipitation radar on Varanger peninsula, expected to be built within the next 2-3 years. Snow depth, cover and hardness will be monitored once a year using in situ snow pit measurements as well as over larger areas using helicopter-borne LIDAR (Grünewald and Lehning 2011).

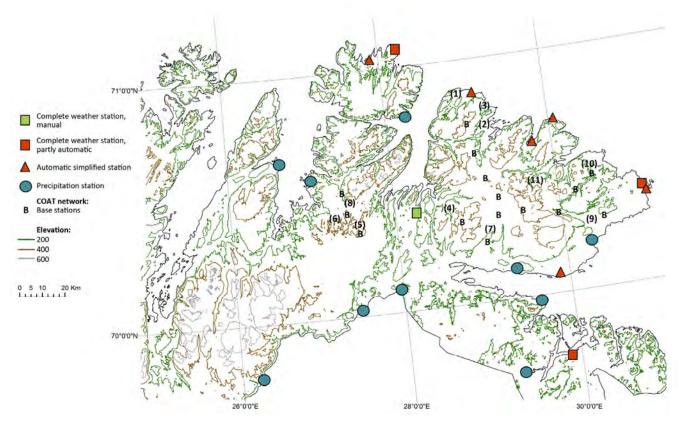


Figure 2.9.4.2. The existing national weather observation network in Varanger and adjoining regions, and the suggested COAT network of automatic base stations (B). In addition, one Reference station will be located in each of the four river systems selected for intensive monitoring and Module stations will be used for specific module components. Only two Meteorological Institute stations in Varanger (Tana and Vardø) acquire observations of all climate elements. Numbers (1-11) indicate the river valleys included in the monitoring design.

2.9.4.4. Design of the climate observational network in high arctic Svalbard

In Svalbard we will have one reference station in each of the extensive monitoring valleys Reindalen, Colesdalen and Sassendalen (valley no. 1, 3 and 5 in fig. 2.9.4.3). These will be supplemented by the national weather station at the mouth of Adventdalen and in Ny-Ålesund (fig. 2.9.4.3). The network of base stations will be designed to cover the river systems selected for the extensive design in COAT, with at least two weather stations of Base type or better in each river system and coastal site. Additional base stations will be added to improve the coverage of altitudinal gradients (fig. 2.9.4.3). There will be an extensive use of temperature loggers. In addition, snow depth and structure will be monitored once a year using in situ snow pit measurements across the extensive design, supplemented with weekly snow pit measurements along elevation gradients in Adventdalen, close to Longyearbyen. The climate observational network will be developed in close collaboration with SIOS (www.sios-svalbard.org).

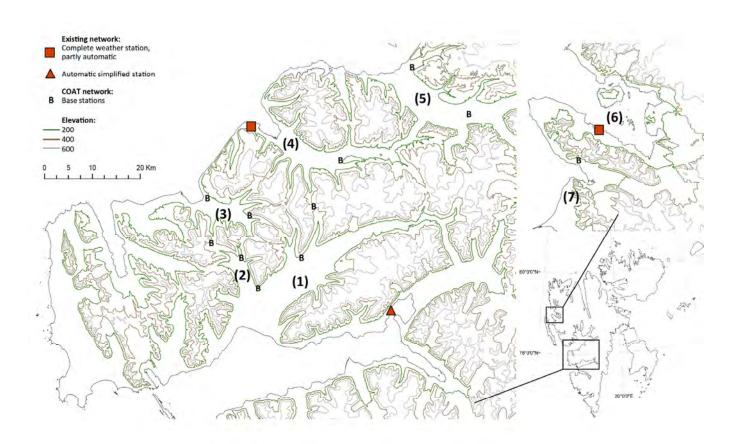


Figure 2.9.4.3. The existing national weather observation network on Nordenskiöld Land and Brøggerhalvøya and the suggested COAT network of automatic base stations (B). In addition, one Reference station will be located in each of the river valleys selected for intensive monitoring. Module stations will be used for specific module components. Only one Meteorological Institute station on Nordenskiöld Land (Longyearbyen airport) and one on Brøggerhalvøya (Ny-Ålesund) acquires observations of all climate elements. Numbers indicate the river valleys (1 – 5) and coastal sites (6-7) included in the monitoring design.

2.9.5. Human perception, use and management of ecosystem services

2.9.5.1. Monitoring design

The goal of COAT is to identify climate change impacts on ecosystems of relevance to society and to facilitate efficient information exchange of knowledge of the socio-ecological systems to society and institutions in charge of nature management and policymaking. The relevance to society of climate change impacts on ecosystems depends on the human perception and use of ecosystem services. Along with changes in climate, the ecosystem management and society in general, the human perception and use of ecosystem services is likely to change over time. COAT will therefore monitor human perception and use of ecosystem services and ecosystem management strategies in parallel with the monitoring of climate and foodweb dynamics. Ecosystem management strategies

and the human perception and use of ecosystem services are unlikely to fluctuate significantly at an annual scale. Changes are more likely to occur as a gradual process over several years, but with potential for infrequent sudden shifts in management strategies. The monitoring of these elements will therefore be done using an iterative 5 year task cycle. The establishment of an arena for communication of knowledge about the socioecological systems to society will be included in this 5 year task cycle. This arena will include decision making institutions to facilitate implementation of adaptive ecosystem management (cf. § 1.2).

The monitoring of feedbacks between humans and ecosystems (i.e. socio-ecological systems) and the impacts of climate and management actions on ecosystem services in space and time require an integrated design. Within the 5 year task cycle, a stepwise scheme for data collection and decision making will be employed (figure 2.9.5.1). The first



Figure 2.9.5.1. The iterative 5 year task cycle - a stepwise scheme for monitoring interactions between human and ecosystems that involve ecosystem service beneficiaries. 1y. Monitoring targets and predictive models for the socio-ecological system will be developed in the first year of the task cycle. 2y. The second year focuses on mapping of the activities of the general public, place values and monitoring of changes in the landscape as observed by the general public. The methods used will be web-surveys, brief visitor surveys and recordings of human traces along the river valley gradients coupled to the extensive monitoring design for the food-web targets. 3y. The perception and use of ecosystem services by key groups will be the monitoring target in the third year. The methods used will be local door-to-door surveys, hunter surveys and interviews associated with the linkage between knowledge, attitudes and place values. 4y. The fourth year will be devoted to integrated analyses by spatially coupling data from food web modules, surveys and official statistics (§2.10.2). 5y. Results from COAT will be presented on the workshop for the general public, which can comment on the findings. In addition focus groups will be invited to prioritize among ecosystem services by matrix-approaches and invited to contribute to the development of new targets and policy options in response to climate change. The collaborative groups will give input to the adjustments of protocols subsequent to the workshop.

year (1y) we define/re-define monitoring targets and derive predictions for the socio-ecological system. The 2y targets the general public and defines tasks for collecting data on public perceptions and use of ecosystem services, including recreation and nature-based tourism. The main activity is the web-based PPGIS (Figure 2.9.5.2 and \$2.9.5.2), which allow the public to map ecosystem services in a web-based internet survey. The 3y include tasks associated with key groups that are not well represented through the web-based PPGIS. A selection of the local community will be presented to the same survey by door-to-door visits. Hunters are surveyed as key ecosystem service beneficiaries and interviews will be designed to monitor the linkage between knowledge, attitudes and place values associated with a school project (§ 4.2). The 4y is devoted to data analysis (cf. § 2.10.2.2) and preparation for the workshop, which takes place in the fifth year (5y). The aim of the workshop is threefold and combine identification of policy options, ecosystem services weighting and outreach (§ 5.3). The outreach part includes results from the web-based PPGIS and will allow for feedback from the public. In addition we invite representatives of focus groups to the workshop that will work with ecosystem service weighting. Finally, the workshop should also be used to identify policy options, which is the responsibility of managers of the area. The development and adjustment of targets will be conducted together with the collaborative groups that are partners through the whole cycle. The collaborative group includes managers on national (Directorate of Nature Management), regional (Governor at Svalbard, FEFO and the County Governor in Finnmark) and local level (Sámi reindeer herders as well as the partners in the school project (see § 4.2)).

2.9.5.2. Methods

<u>Web-based PPGIS of public perceptions and use</u> of ecosystem services

The web-based PPGIS aims to capture the spatial heterogeneity of human activities, place values and observed changes by participants in the land-scape (see fig. 2.9.5.2). PPGIS using maps and markers has recently been used to measure change in place values, which is the values people assign to the landscape (Brown and Weber 2012). In addition, participants will record their spatial use of the landscape and the changes they have experienced the last 5 years. Points are preferred to polygons in order to increase the likelihood of participation and comparability over time (Brown and

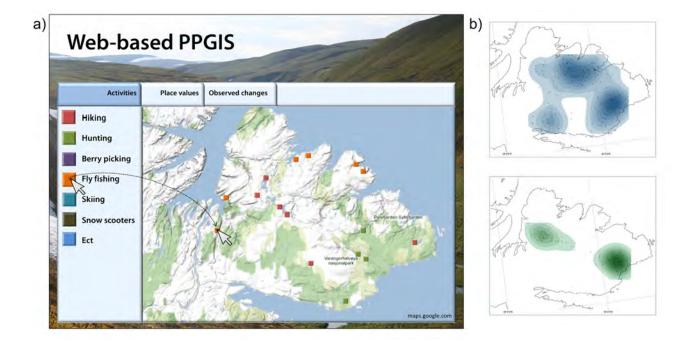


Figure 2.9.5.2. Illustration of the web-based PPGIS. The google maps interface allow participants to zoom, pan and view the maps as terrain, topographic maps or images. a) Participants will drag and drop markers belonging to different categories from the panel to the left onto the map. The categories above illustrate the method and need to be refined according to results from the ongoing PPGIS in the TUNDRA project (www.tundra.uit.no) (b) Point density mapping using kernel density estimation could be used to analyze spatial patterns of human activities, place values and changes in the landscape.

Table 2.9.5.2. Items and methods for monitoring human activities and ecosystem services.

| Target | ltem | Interval | Methods (references) |
|---------------------------------------|---|----------|---|
| Nature-based tourism | Place values | 5y | Web-based PPGIS (Alessa et al. 2008, Brown and |
| | Attitudes/beliefs | · | Weber 2012) |
| | Human activities | | |
| | #Visitors | 5y | Entry point visitor survey |
| | Socio-demographic char- acteristic | | Entry point visitor survey |
| | Spatial use of landscape | | Web-based PPGIS Physical traces/(Manning 1999) |
| | | | Distance sampling (Anderson and Buckland 2001) |
| Local recreational use | Place values | | Web-based PPGIS , |
| (incl. berries, mushroom, fishing) | Attitudes/beliefs | | Door-to door survey |
| | Human activities | | Focus group, Workshop |
| | #Local recreational users | | Entry point visitor survey |
| | Socio-demographic char- | | Entry point visitor survey |
| | acteristics | | Census data from SSB |
| | Socioeconomic data | | |
| Hunting | Spatial yields: | | |
| | Ptarmigan (incl. multi- species catch) | 1y | Self reports, GPS located |
| | Moose/predators | 1y | Self reports, GPS located |
| | Hunting | 5у | Hunters survey, workshop |
| | Attitudes/beliefs | | |
| | Socioeconomic data | | Census data from SSB |
| Reindeer herding | #Reindeer, harvest | | Harvest statistics |
| | Climate - Herding | | Collaborative group |
| | values/attitudes | | Workshop |
| Science/Education | Knowledge beliefs/value | | Focus group, workshop |
| | relationship | | TUNDRA school project (§4.2) |
| | | | Structured interviews |
| | Biodiversity | | |
| National | Biodiversity | | Collaborative group |

Pullar 2012). The internet page will include a brief questionnaire on demographics, general environmental attitudes and knowledge about tundra ecosystems of the participants.

Internet PPGIS reduces monitoring costs and increase precision in mapping, but tend to have lower response rates and a bias towards younger and educated participants (Pocewicz et al. 2012). To address some of these biases we will recruit participants by direct contact with visitors in the field and by door-to-door visits in local communities. The door-to-door visits will target groups that are poorly represented in the web survey. This will allow participants to choose between participation on the internet or by responding to a paper-based version of the same survey. The door-to-door survey will also expand the data collection by allowing the participants to draw in addition to using markers. A brief entry point visitor survey will be conducted on recreational trails including visitor counts and socio-economic characteristics. The reference to the web-based PPGIS will also be available on cabins, in selfregistration boxes and delivered by the fieldworkers involved in the extensive monitoring program. In the extensive monitoring of food web targets (§ 2.9.1), human traces will be recorded using distance sampling in the river valleys included in the extensive design.

Hunter's survey

The spatial pattern of hunting ptarmigan and moose will be recorded yearly by self-reports linked to GPS locations. Since public surveys could be biased with regard to hunters (Aas et al. 2010) we include questionnaires about hunting values and beliefs in addition to the web-based surveys. Hunters of moose and ptarmigan will participate in the workshop as focus groups.

School survey

The values and the perceived changes of ecosystem services are dependent on the baseline knowledge about ecosystems which change over time (Lewan and Soderqvist 2002, Papworth et al. 2009). The TUNDRA school project (§ 5.2) aim to increase the ecological knowledge of school children, and includes both areas where children participate as well as control areas. The relationship between knowledge, general beliefs (Dunlap et al. 2000), place values (e.g. Brown and Weber 2012) and ecosystem services will be monitored over time.



Workshop on adaptive monitoring and management

The ultimate goal of monitoring is to improve management and adaptive decision making. Different schools emphasize different degree of stakeholder engagement in the iterative monitoring process (Lindenmayer et al. 2011, McFadden et al. 2011). COAT mostly draws inspiration from the structured decision making framework and adaptive monitoring. The workshop will be the major arena for linking monitoring and management and will be based on three stages:

Stage 1: Open meeting: The goal is outreach and feedback from the general public on the management relevance of the monitoring objectives and results.

Stage 2: Focus group work: The goal is to let the different focus groups prioritize among ecosystem services independently through matrix-based ap-

proaches (Diaz et al. 2011). The results will be combined with the other data to identify bundles of ecosystem services (Raudsepp-Hearne et al. 2010).

Stage 3: Policy options: The goal is to identify alternative policy and management options to respond to changes.

In COAT the managers (Directorate of Nature Management, Governors in Svalbard and Finnmark, FEFO) will be encouraged to be responsible for i) identifying the focal groups which should participate in the workshop, ii) development of policy options based on the COAT findings from the food web modules and the socio-ecological surveys, and iii) providing inputs to revision of protocols based on findings in the workshop and iv) appointing a person who will function as a facilitator at the workshop.



2.10. Data management and

analysis

2.10.1. Data management and quality control

We follow here the policy of LTER sites (see LTER Niwot Ridge http://culter.colorado.edu/NWT/ data/datman_policy.html; LTER Toolik Lake; http://ecosystems.mbl.edu/arc/dataprotocol/

ArcticLTERIM.html; accessed 17 April 2013). One person (Data Manager) will be in charge of the Data management for COAT and will have a contact person for each module. The Data Manager will coordinate the transfer of data collected in the field to a digital form, ensuring that data quality issues are thoroughly documented. The Data manager will also coordinate the collection and documentation of remote sensing (RS) imagery and derived RS data products developed in COAT. Common data formats and variables will be used to ensure compatibility among modules. Welldocumented scripts written in R will be run systematically to plot raw data in order to identify potential outliers/errors. All data corrections will be documented, in order to make sure it is possible to trace back published data to the field observations. Data will be stored in a format guaranteeing long term archival (i.e., ASCII) and in at least two physical locations (in addition to scientists' personal computers). All data sheets/notebooks will be scanned and stored in a widely compatible format (pdf). If a COAT investigator leaves the COAT project, she/he must provide the Data Manager with copies of all data (notebooks and electronic files).All data collected in COAT will be described by detailed metadata. These metadata will be reassessed on a yearly basis to make sure that they describe current practices and that no information is getting lost as a consequence of changes in methods and designs, which must be thoroughly described. Metadata will be available on COAT web site, and freely available to everyone without restrictions. The Data Manager will take responsibility for making these metadata compatible with standards such as Ecological Metadata Language (EML).

Guaranteeing the long-term storage and documentation of the unreduced/unmanipulated and metadata is a challenge since how data will be stored electronically in 20 or 50 years is difficult to know. To make this possible, a complete listing of all data files will be updated every year, and a procedure will be set up to access all data files and ensure their continuing readability. In case changes are made with respect to the storage of data files (format, etc.), such a procedure should guarantee that no information is lost. The yearly assessment of raw and metadata by the Data manager and the contact persons for each module will be followed by a (yearly) meeting with all concerned COAT members to review the status of data storage and integration.

Time series of variables measured in COAT modules will be available on COAT web site at most 6 months after end of each field season (i.e., March for summer, October for winter-spring). Such a short time between data collection and archiving should contribute to reducing the occurrence of missing or erroneous data. However, it is important for COAT scientists to have enough time to make use of collected data. Therefore, data collected by COAT members are available either 1) with the permission of COAT board and members for specific scientific objectives, or 2) without restrictions 2 years after the collection of those data. Data cannot be redistributed without informing the COAT board. The exception is meteorological data which will be available without restrictions. Details as to how the use of COAT data should be acknowledged will be given on the COAT web site.

In addition individual COAT members who collected the data should be acknowledged. Researchers using COAT data must send the publications to the COAT board. All users of COAT data should be aware that data available on COAT web site or from individual researcher may contain errors and may be revised. Such revision will be documented for each data set.

2.10.2. Statistical analyses

2.10.2.1. Food web climate impact patch models

All COAT monitoring designs have two characteristics: 1) a hierarchical structure in the sense that the state variables are measured at more than one spatial scale; and 2) a path model or flow diagram (i.e. the climate impact path models; Figure 2.1) representing associations and causal relationships among those variables. Our goal is to implement statistical analyses which take these two characteristics into account, in order to accurately estimate parameters and their uncertainty, to distinguish between direct and indirect effects of different drivers, and assess how these effects vary within and among regions. Developing robust methods for analyzing spatial ecosystem models will be an important outcome of COAT. This will be done in three steps.

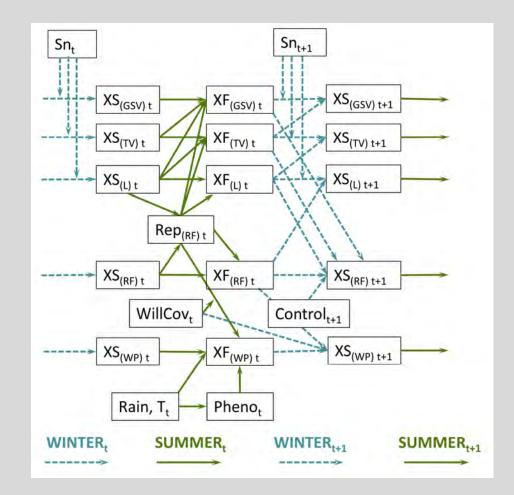
First, weather data will be interpolated in order to provide relevant predictors for the different modules. Interpolation will be done using different statistical approaches (in particular those used by the Norwegian Meteorological Institute at large spatial scales, such as first regressing observations against topographical variables, and then using kriging on residuals; for snow variables, Snow-Model (see §2.9.4.2) will directly provide spatial data). The interpolated data will be crossvalidated in order to assess the extent of measurement errors made by interpolation. The latter information is important since weather variables are used as predictors in other modules and measurement error in predictor variables lead to bias in regression coefficients (e.g. Reeves et al. 1998). A detailed knowledge of measurement error structure is needed in order to model it accurately in further analyses.

Second, direct relationships among food web target variables will be analyzed using mathematical and statistical models. Mathematical dynamical models will be developed to investigate specific trophic interactions, such as plant-herbivores (Turchin and Batzli 2001), predator-prey (e.g., arctic fox-small mammals (Henden et al. 2008, Henden et al. 2010); skua-lemming (Gilg et al. 2003, Barraquand et al. in prep.) and parasitoidhost-plant interactions (Yoccoz et al. in prep.)). Such models are needed to derive predictions related to direct and indirect impacts of climatic change, and to assess which functional relationships are most important in terms of sensitivity. Generalized linear mixed models (Bolker et al. 2009) provide a statistical framework for analyzing data collected with nested spatial structure, and will be used to estimate the shape and strength of associations among monitoring target variables. The diverse nature of response variables is taken into account through the flexibility of generalized linear modeling (i.e., proportions with a binomial distribution, counts with Poisson, continuous with Gaussian). Nonlinear relationships will be investigated using splines ('i.e., generalized mixed additive models', Wood 2006). Generalized linear mixed models will also be used to fit specific types of time series, state-space and structural models (Piepho and Ogutu 2007, Shipley 2009), so these models will play an essential role both as exploratory (e.g. to assess the shape of functional relationships, or the appropriate structure of random variation terms) and confirmatory tools (Shipley 2009). We have previously used such models in different ecological contexts. Diagnostic tools (residuals, influential values) will be used systematically to complement the data quality control process (cf. §2.10.1).

Third, we will use recent developments in the fields of structural equation models and statespace models (related or identical to latent, path and graphical models; e.g. Lee 2007, Chow et al. 2010, Pearl 2010, Højsgaard et al. 2012) to analyze the dynamical relationships between weather, management actions and ecological variables, and to test specific hypotheses about presence or absence of relationships between specific variables (Shipley 2009, Pearl 2010) as specified by the various climate impact models outlined in §2.2-2.8. Structural equation models allow to fit complex relationships among variables of different types (binary, categorical, ordinal, continuous), in particular the same variable can appear as a predictor in one equation and a response in another equation. They can also deal with measurement errors and complex error structure (e.g. autoregressive and/or moving average [AR/MA]: du Toit and Browne 2007). Structural equation/state space/ graphical models are extensively used in field such as economics, psychology and epidemiology, but are not yet common in ecology despite their great potential (e.g. Mysterud et al. 2008, Shipley 2009, Gimenez et al. 2012, Prugh and Brashares 2012). There are different approaches available to fit such models: a) Bayesian methods relying on numerical methods (MCMC) for estimation (e.g. Cressie et al. 2009, Song and Ferrer 2012), b) Maximum Likelihood/Restricted Maximum Likelihood and Least Squares (e.g. as implemented in OpenMx, Boker et al. 2011). Bayesian methods are increasingly used in ecology, in particular for hierarchical modeling (Cressie et al. 2009), but there are also concerns regarding the reliability of such methods for complex, nonlinear models (Hodges 2010, Fraser 2011). OpenMx provides a new and powerful framework for fitting complex structural equation models in R (including the multivariate autoregressive models with cross-lags as in Box 2.10.1). We will therefore use Bayesian as well as ML (and REML) approaches whenever possible, using simulated data in both cases to assess the reliability of estimated coefficients (Hamel et al. 2012, Song and Ferrer 2012). It is an open research question which approach is the most efficient and reliable so we do not commit ourselves to a specific tool.

The different modeling steps will be implemented yearly as soon as data have been entered and quality checked. This of course will not be done the

Box 2.10.1. Structural equation dynamic modelling



Example of structural equation dynamic model drawing on causal relations outlined in the conceptual climate impact models of the small rodent (§2.4) and ptarmigan modules (§2.6). Each arrow represents an assumed causal relationship between state variables (described by a regression-type model, which can be non-linear), and absence of an arrow means conditional independence. The model builds on previous models of small rodents time series (e.g., Stenseth et al. 2003; Kausrud et al. 2008) used to analyze seasonal dynamics (XS=Spring abundance, XF=Fall abundance), but incorporate interactions among small rodent species (direct competition – the model assumes that lemmings [L] dominate other vole species, greysided vole [GSV] and Tundra vole [TV], so there is an arrow connecting lemming to voles but not the other way around). Snow conditions (Sn) affect rates of change during the winter season (i.e., survival, and reproduction for L). Red fox (RF) population dynamics are described through Reproduction (Rep), a variable which will not be directly measured (i.e. a latent variable) but is related to other measured variables such as the proportion of juveniles in harvested RF (Control) and is dependent on small mammal spring densities. Willow Ptarmigan (WP) population dynamics are impacted by red fox reproduction (the model assumes here that intensity of predation by red fox depends on fox reproductive effort) and by summer climatic conditions, either directly (e.g., cold spring T negatively affects chick survival) or indirectly (through plant/insect phenology: Pheno). Removing the arrow between Summer weather (Rain,T) and ptarmigan fall abundance would imply conditional independence of Grouse abundance and summer weather conditional on phenology. Parameters describing WP summer or winter population dynamics might depend on vegetation variables with slow rates of changes, such as willow cover (WillCov), through their moderation of RF predation. All relationships include a random variation term, which is not shown to simplify the figure. Such random variation terms are not necessarily independent spatially or temporally (see text for more details).

first 2 years for the whole design, but only for those variables that have been monitored before 2012 (e.g. lemmings, Ims et al. 2011). The goal is to achieve what has been called data assimilation (Hobbs and Ogle 2011, Zobitz et al. 2011), i.e., a fusion of mathematical/statistical modeling with climatological and ecological data. For all mathematical and statistical analyses, associated scripts (in R) will be archived to guarantee the reproducibility of analyses (Reichman et al. 2011).

As an example of a structural equation dynamic model (Ferrer and McArdle 2003, Eichler et al. 2011), we use dynamics of small rodents, willow ptarmigan and one generalist predator, the red fox (Box 2.10.1).

2.10.2.2. Analysis of social-ecological surveys

Social-ecological surveys will be analyzed with 1) generalized linear models, and in particular logistic regression (when the response is binary), log-linear models and ordinal regression models (for contingency tables) (Højsgaard et al. 2012), 2) multivariate methods, such as multiple correspondence analysis (MCA; Greenacre and Blasius 2006) and non-linear PCA when variables are ordinal (de Leeuw 2006). Spatial analyses of use and values will be done using classical tools such as Moran's and Geary's coefficient for single variables (e.g. Dray 2011) and multivariate analyses taking into account spatial neighborhoods, such as developed in Griffith and Peres-Neto (2006) and Jombart et al. (2009).

2.10.2.3. Analysis of remote sensing data

Several state variables related to vegetation cover and productivity, in particular in the extensive monitoring design, will be monitored using remote sensing data in combination with field measured variables. The most important sources of RS data are orthophotos, moderate resolution satellite imagery (primarily MODIS) and high resolution color-infrared satellite imagery (for example SPOT). An analytical framework will be developed for quantifying changes in vegetation zonation along the established river valley gradients based on semi-automatic object-based image analysis (OBIA; Blaschke et al. 2008) of orthophotos and satellite imagery as well as data from field inventories (Stow et al. 2008, Wallentin et al. 2008). Both commercial (for instance 'Definiens') and open source (for instance i.smap in GRASS GIS) software packages are available for this task.

2.10.3. COAT team competence

The data management and analysis module will be lead jointly by the Northern Population and Ecosystem Unit at UoT and the Norwegian Institute for Nature Research (NINA). Team members in charge are Nigel G. Yoccoz (UoT) and Jane U. Jepsen (NINA), with contributions from Vera Hausner (UoT), Dorothée Ehrich (UoT), Rolf A. Ims (UoT), John-A. Henden (UoT), Audun Stien (NINA), Jack Kohler (NPI) and Ole Einar Tveito (DNMI). The team has considerable experience in statistical analyses of large data sets, at population, community and ecosystem levels. Nigel G. Yoccoz is Associate Editor of "Methods in Ecology and Evolution", has done statistical analyses of climate impacts on red deer and sheep populations, including two path analyses (Mysterud et al. 2001, Mysterud et al. 2008, Mysterud et al. 2009) and is working with Sandra Hamel (UoT) on developing and assessing generalized linear mixed models for analyzing longitudinal data (Hamel et al. 2012). Vera Hausner and Nigel G. Yoccoz have experience analyzing complex multivariate data sets (Hausner et al. 2003). Jane U. Jepsen has expertise in modeling of spatial dynamics (Jepsen and Topping 2004, Jepsen et al. 2005), GIS and remote sensing applications (Jepsen et al. 2009b). The team has moreover a strong tradition collaborating on different projects.

3. ORGANIZATION

Given the scenarios for greenhouse gas emissions and climate change trajectories provided by IPCC, impact monitoring of ecosystems must by necessity be planned as a long-term enterprise with adequate financing and organization. Moreover, the framework of adaptive monitoring to be adopted by COAT (\$1.2.2) requires an organization that is able to accommodate changes in the scientific program (models, targets and design) according to the iterative protocol outlined in figure 1.2.2. An organization that may fulfill this task is proposed in figure 3.1.

The COAT leadership consists of an overall leader, a vice-leader and a colloquium of module leaders (food web modules [§2.3-2.8], leaders for monitoring of the social-ecological system (SES) [§2.9.4]; data management and analysis [§2.10]). The identity of the personnel that will hold the various leadership positions and their responsibilities are given in Table 3.1and represent those people that have been responsible for developing the present science plan. Other personell may be included in the leadership structure depending on the potential integration of COAT with other national (e.g. MOSJ) and international monitoring initiatives (cf. §4).

For the modular approach of COAT to achieve

effective ecosystem-level integration it is important that the overall program is tightly coordinated. Integration is also facilitated by the fact that many of the COAT researchers take part in several modules. Indeed, as evident from the description of "COAT team competence" under each module there is already a great degree of collaboration among team members on subject matters covered by different modules. Moreover, there is an ambition of COAT to focus on comparative issues between high-arctic Svalbard and low-arctic Varanger whenever such issues are relevant. This is in particular the case for food web modules centered on key species present in both ecosystems (cf. §2.5, §2.6, §2.8). For these modules there are two module leaders with experience from either site that will collaborate on the development of the module.

The leadership of COAT will interact closely with the PhD school AMINOR. AMINOR was established in 2012 as an educational program for researchers in environmental sciences at University of Tromsø. The aim of AMINOR is to develop a general framework for bridging science, longterm monitoring and management within the FRAM - High North Centre for Climate and the Environment. COAT will provide opportunities

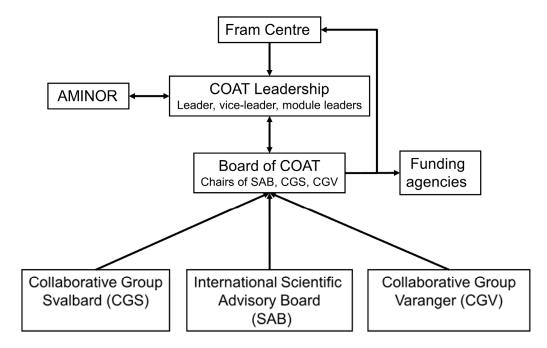


Figure 3.1. The organizational structure of COAT. The role of the collaborative groups in context of monitoring of the socioecological system is described in §2.9.4.

for PhD projects, either as an integral part of its long-term baseline program (e.g. analyses on baseline COAT data or development of new methods of sampling and statistical analyses) or based on short-term spinoff projects with external funding.

A scientific advisory board (SAB), composed of 5-6 internationally respected scientists covering the fields of food web dynamics, tundra ecology, climate impact research, long-term ecological research/motoring and management related research, will regularly review and give advice on the scientific development of COAT. Yearly meeting will be held between SAB and the leadership of COAT to provide SAB with updated results and progresses. SAB will make an overall written critical assessment of COAT every fifth year synchronized with the 5-yr cycle of the SES (§2.9.4). The report of SAB is taken to the board of COAT. The COAT board will be composed by the leader of SAB and the leaders of collaborative groups for COAT Svalbard and Varanger, respectively (cf. \$2.9.4). Thus the COAT board will have representatives that have first-hand knowledge of the scientific development of the observatory (i.e. the chair of SAB) and its relevance for the society (i.e. chairs of the two collaborative groups). The board reports both to the agencies that funds COAT as well as to the leadership of the Fram Centre which employs most of the staff of COAT. According the to this proposed schedule for reporting, review and governance of the COAT program, a funding cycle with a possibility for renewal at 5-year intervals will be appropriate. Accordingly, a complete update of the COAT science plan will be made every fifth year.

Table 3.1. The current leadership of COAT reflecting the responsibilities for the development of the present science plan. Other leaders may be involved pending potential integration between COAT and other national and international programs.

| Name | Affiliation* | Role in COAT | Task in COAT |
|---------------------|---------------------|---------------|--|
| Rolf A. Ims | Professor, UoT | Leader | Overall leadership & coordination |
| Audun Stien | Researcher, NINA | Vice-leader | Overall leadership & coordination with focus on Svalbard, leader of Ungulate module |
| Jane U. Jepsen | Researcher, NINA | Module leader | Leader of Forest-Tundra Ecosystem, |
| | | | Co-leader of Data Management & Analysis |
| Nigel G. Yoccoz | Professor, UoT | Module leader | Leader of Data management & Analysis |
| | | | Leader of AMINOR |
| Vera H. Hausner | Ass. Professor, UoT | Module leader | Leader Socio-ecological system monitoring |
| Ingrid Jensvoll | Advisor, UoT | Module leader | Leader Outreach and Society involvement |
| Kari Anne Bråthen | Ass. Professor, UoT | Module leader | Leader of Tall Shrub Module |
| Virve T. Ravolainen | Researcher, UoT | Module leader | Co-leader of Tall Shrub module |
| Dorothée Ehrich | Researcher, UoT | Module leader | Leader of Small rodent module |
| | | | Co-leader Socio-ecological system monitoring |
| John-André Henden | Researcher, UoT | Module leader | Leader of Ptarmigan Module |
| | | | Co-leader of Small rodent module |
| Åshild Ø. Pedersen | Researcher, NPI | Module leader | Co-leader of Ungulate module |
| Ingunn Tombre | Researcher, NINA | Module leader | Leader of Goose module |
| Jesper Madsen | Professor, AU | Module leader | Co-leader Goose Module |
| Eva Fuglei | Researcher, NPI | Module leader | Leader of Arctic fox module |
| | | | Co-leader of Ptarmigan module |
| Siw T. Killengreen | Researcher, UoT | Module leader | Co-leader of Arctic fox module |
| | | | Co-leader outreach and Society involvement |

* UoT: University of Tromsø, NINA: Norwegian Institute for Nature Research, NPI: Norwegian Polar Institute, AU: Århus University (Denmark)

4. INTERNATIONAL COLLABORATION

4.1. Pan-arctic perspectives

The circumpolar tundra biome is vast, and different geographic regions are subjected to different climatic domains, species pools, ecosystem complexity and anthropogenic impacts. Thus, no single site or ecosystem can be expected to be representative for the changes the biome will be facing in a warmer climate. The necessity of pan-arctic perspective and international collaboration underlies enterprises such as Arctic Climate Impact Assessment (ACIA), International Polar Year (IPY), Circumpolar Biodiversity Monitoring Program (CBMP), Arctic Biodiversity Assessment (ABA), Snow, Water, Ice and Permafrost in the Arctic (SWIPA), Arctic monitoring and Assessment program (AMAP; www.amap.no/), International Network for Terrestrial Research and Monitoring in the Arctic (INTERACT; www.euinteract.org), Svalbard Integrated Arctic Earth Observing System (SIOS; www.sios-svalbard.org) and Sustaining Arctic Observatory network (SAON: www.arcticobserving.org). COAT will take part in such pan-arctic initiatives whenever adequate. For instance, COAT leader Rolf A. Ims is lead author of the terrestrial ecosystem chapter of ABA and a member of CBMP's terrestrial monitoring expert group. However, the greatest challenge for truly ecosystem-based observatories in a pan-arctic perspective is that very few such observatories are presently placed in the Arctic (cf. §1.2.2 and Figure 4.1). The establishment of COAT at two sites will constitute a substantial improvement on this state of affairs.

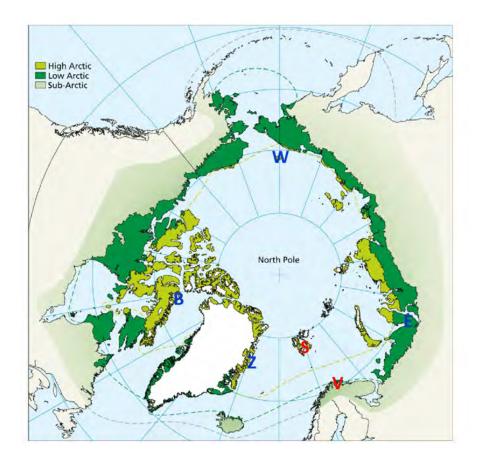


Figure 4.1. The sites of COAT (V-Varanger Penisula, S-Svalbard) and collaborating observatories (B-Bylot Island, E-Erkuta, Z-Zackenberg and W-Wrangel Island).

4.2. Links to other established ecosystem-based observatories

COAT shall maintain tight links with other ongoing monitoring/long-term research initiatives applied to tundra ecosystem that have adopted a comparable approach (i.e. based on a food web perspective); notably NERO/ZERO in Greenland and the Bylot Island ecosystem project in Canada. Indeed, collaboration between these initiatives and COAT researchers has already been established though the IPY projects ArcticWOLVES (http://www.cen.ulaval.ca/arcticwolves/

en_intro.htm) and Arctic Predators (http:// www.arctic-predators.uit.no/). There is presently an extensive exchange of PhD students, post docs and guest professors between the Bylot team and Department of Arctic and Marine Biology at UoT. Similar exchanges are underway in case of ZERO. Joint publications based on monitoring data are starting to emerge (Gilg et al. 2012, Schmidt et al. 2012). International collaboration with other researchers and institutions is also present within most of the COAT modules (cf. section on "COAT team member competence" in chapters on the different modules). There is a long tradition of collaboration within ecology between the Nordic countries and although only Norway and Denmark host research facilities in arctic tundra, COAT will aim to establish links to relevant activities in the sub-arctic research station in Sweden (Abisko: www.polar.se/en/abisko) and Finland (Kevo; www.kevo.utu.fi/en/ and Kilpisjärvi; www.helsinki.fi/kilpis/). Links to activities on these stations are already established through the Nordic Centre of Excellence – How to preserve the tundra in a warming climate (NCoE-Tundra. Cf. §2.2).

4.3. COAT Russia

Russia harbors almost all of the Eurasian arctic tundra. Although Russia has had a long-standing biological research tradition in the Arctic, Russian ecologists have often adopted different approaches than North American or European arctic ecologists. In particular, there have been relatively few activities within climate change impact research on terrestrial ecosystems and hence there has been little collaboration between Russian and western arctic ecologists on this matter. The International Polar Year (IPY), however, created an opportuni-



Figure 4.3.1. The Erkuta site in the shrub tundra of southern Yamal provides an interesting contrast to Varanger peninsula in terms of areal extent of tall shrubs which is presently larger in Erkuta (Ehrich et al. 2012a). Photo: Rolf A. Ims.



Figure 4.3.2. High-arctic landscape at Wrangel Island in eastern Siberia. Photo: Irina Menyushina

ty for remedying this state of affairs. The Norwegian IPY-project "Arctic Predators" (http:// www.arctic-predators.uit.no/) which had its origin in research conducted by COAT members in Svalbard and Varanger, aimed at establishing robust monitoring and assessment methods of tundra ecosystem functioning with the emphasis of the food web modules described in §2.4 and \$2.8 of the present plan. A main objective of the Arctic Predators project was to include study sites in Russia in order to cover the wide range of environmental conditions occurring in the Eurasian Arctic. Based on the experience from "Arctic Predators" we regard in particular two sites as suitable sister observatories to the two Norwegian COAT sites; Erkuta in Yamal Peninsula relative to Varanger peninsula in the low Arctic, and Wrangel Island in eastern Siberia relative to Svalbard in the high Arctic.

The Erkuta tundra monitoring site is located in the shrub tundra of southern Yamal in western Siberia (Figure 4.1). Starting with the Arctic Predators project in 2007 we are collaborating on ecosystem monitoring with Aleksander, Natalya and Vassiliy Sokolov (Ecological Research Station of the Institute of Plant and Animal Ecology, Ural

Branch of the Russian Academy of Science -ENIS). Presently the monitoring activities in Erkuta are focused on the issues outlined in the small rodent (cf. §2.4) and arctic fox (cf. §2.8) modules (e.g. Pokrovsky et al. 2010, Rodnikova et al. 2011). However, there are also good scopes for expanding on the activities in Erkuta to include the ungulate module (cf. §2.5) as southern Yamal is also grazed by large and increasing herds of domestic reindeer (Forbes et al. 2009). Yamal offers yet an interesting contrast to Varanger in the higher areal extent of tall shrubs (Figure 4.3.1, cf. \$2.3) which is likely to have consequences for at least willow ptarmigan populations (Ehrich et al. 2012a) and communities of passerine birds (Sokolov et al. 2012). Although boreal species are less prominent in Erkuta than in Varanger at present, the Erkuta site is close to the southern border of the tundra which offers an opportunity to focus on tundra-forest ecotone dynamics (cf. \$2.2). ENIS is at present developing a monitoring program for terrestrial biodiversity in Yamal which is likely to be financed by the regional government of Yamalo-Nenetsky AO. Erkuta is going to be a central site in this program, which will also include a more southern site in the forest tundra and a site in the high Arctic.

Wrangel Island is a high-arctic island located north of the coast of eastern Siberia (Figure 4.3.2). It harbors a unique ecosystem characterized by particularly high biodiversity for the Arctic and several endemic species (Gorodkov et al. 1987, Pulyaev 1988). The whole island is a nature reserve since 1976. It has a long history of biological investigations and ecosystem monitoring. Since the 1990s effects of climate change such as elongation of the frost free season have been observed on the island. Over the last 40 years the duration of the lemming cycles on Wrangel Island has shifted from a period of 5 years to 8 years, resulting in the longest period ever reported for lemming cycles (Menyushina et al. 2012). Our collaboration with Irina Menyushina and Nikita Ovsyanikov (Wrangel Island State Nature Reserve) was initiated during the IPY project Arctic Predators focussing on issues of the small rodent and arctic fox modules of the present plan. COAT Russia will develop the collaboration with Wrangel Island SNR, aiming at making the work carried out on Wrangel more comparable to the COAT framework. In relation to COAT Svalbard interesting

comparative issues with Wrangel island regard the changing role of marine subsidies to the terrestrial ecosystem (Killengreen et al. 2011) with decreasing sea ice extents (cf. §2.8), the impact of goose grazing on high arctic vegetation (cf. §2.7) and the dynamics of high arctic ungulates in a changing winter climate (cf. §2.5).

COAT Russia will investigate the possibilities for collaboration on ecosystem monitoring in additional regions of the Russian Arctic. We will specifically investigate the possibilities for such collaboration on Kola Peninsula, which is biogeographically very similar to Varanger peninsula, but has a very different history of settlement and land use. Furthermore, the Kanin Peninsula, the Pechora lowlands (Nenetsky Nature Reserve), Taimyr and the Lena Delta are sites COAT will explore as potential collaborating sites. Such collaboration is most likely to be based on the extensive monitoring design with 5-10-year intervals between the surveys as outlined in §2.9.

5. SOCIETY INVOLVEMENTS, EDUCATION AND OUTREACH

The overreaching aim of COAT is to produce knowledge about the impact of climate change on tundra ecosystems. Such knowledge becomes truly valuable only if it is made available and can be appreciated and used by society. Producing relevant knowledge and disseminating it in appropriate ways require a solid plan for outreach and societal involvement. In COAT we plan to formally involve stakeholders, local residents and decision makers in the adaptive monitoring scheme (§5.1, \$2.9.5.1). We are establishing a collaboration with schools in both regions to disseminate knowledge to school children (§5.2.2). University students at all levels will be primary targets for teaching activities, scientific results will be available to peer researchers through publishing in high ranking scientific journals, and wider dissemination will address the general public. This implies that we will implement our communication and contact in various channels. It is our goal to have an open two-ways communication about our progress, the value and relevance of our results, and our future plans.

5.1. Management issues and stakeholder fora

Well-designed adaptive monitoring programs that aim for more efficient decision making provide opportunities for learning about alternative models as well as model adjustments in response to new knowledge or values (i.e. double loop learning). In the iterative 5-year task cycle designed to monitor ecosystem management and human perception and use of ecosystem services (§2.9.4) we will learn about unanticipated shifts in values, institutions and climatic impacts which could demand changes in management targets and model adjustments. This will be facilitated by a structured decision making process in a workshop every 5th year. The workshop will be divided into three parts: **Part 1: Open meeting.** The goal of this first part is outreach and feedback from the general public on the management relevance of the monitoring objectives and results.

A document will be produced that briefly summarize the results for each food web modules.

Presentations will be given by the leaders of each food web module.

The COAT leader will synthesize these findings in relation to targets, alternatives, and predicted models.

The results from the web-based PPGIS will be presented as maps requesting feedbacks from the audience on outcomes.

Part 2: Focus group work. Representatives from focus groups will be invited that cover the diversity of interests associated with the two targeted ecosystems (Varanger peninsula and Svalbard). Each focus group will independently discuss and prioritize among ecosystem services guided by questions about their use. Ecosystem services will be listed and ranked by participants. The data will be analyzed and presented at the workshop to ensure feedback on site. The results will contribute partly to quality assurance of the PPGIS and partly to learning and adaptation of management targets and model adjustments (cf. §2.9.5.2).

Part 3: Policy options. The goal of this part of the workshop is to identify alternative policy and management options in response to changes. The managers on different levels will take the lead together with the focus groups to identify policy options in response to climate change.

The collaborative groups in COAT will through the open meeting, focus group work and policy option exercises provide input for the adjustment and changes of the monitoring targets and management options/actions for a new 5-year monitoring cycle (cf. §2.9.4 for details).

5.2. Education

5.2.1. University level

COAT aims to integrate the conducted research at different educational levels ranging from primary school to PhD courses. Through the university courses at UoT and UNIS, bachelor and master students will be offered research-based education and training within the COAT research program. In particular, COAT will provide a platform for a host of thesis projects based on monitoring data as well as projects aimed at developing and validating new methods of monitoring and data analysis. The FRAM centre based research school AMINOR (cf. §3) will provide integrated education in monitoring, research and management for PhD and Master students.

5.2.2. TUNDRA schoolnet

Teaching children is the best way to create environmental responsibility among people (Rivas and Owens 1999). Today children are highly influenced by the media, especially the internet when it comes to knowledge of wildlife, conservation and climate change. This limits their information to a few charismatic species while they often have little knowledge of their local fauna (Ballouard et al. 2011). The global perspective to climate change disseminated by the media can be difficult to relate to the effects on the local environment. Environmental education mediated through experience is an efficient way to learn ecology (Barker 2002, Lindemann-Matthies 2006), and especially in primary school the results from taking the teaching of biology out of the classroom are good (Kenney et al. 2003, Malone and Tranter 2003).

Teachers are the key players in order to create knowledge and enthusiasm in natural science education among students. One of the recommendations from an expert group, formed by the European commission to increase children's interest for science, was to form teacher's networks. Being part of a network allows the teachers to improve the quality of their teaching, support their motivation, as well as being an effective component to enhance the teachers' professional development (European Commission 2007). There are at present good examples of successful international initiatives using school networks and hands on experiments to stimulate the interest of school children for environmental science at the global scale (e.g. the GLOBE program www.globe.gov) or European scale (e.g. the

Beagle project - www.beagleproject.org), as well as at the more local scale (the Avativut project in Nunavik, arctic Canada - www.cen.ulaval.ca/ Avativut/en_accueil.aspx).

In the planning of COAT we have developed the school project TUNDRA schoolnet. Tundra Schoolnet is a research-based school project that seeks to promote curiosity and knowledge about local climate and ecology to students and teachers in the tundra region. The two main goals of TUNDRA schoolnet are:

- Promote awareness, curiosity and commitment for the arctic tundra ecosystem, through research-based education
- Establish a network for teachers and students, to create a common understanding of climate-related challenges in the North

TUNDRA schoolnet focuses primarily on the two COAT regions: Varanger Peninsula and Svalbard, but later we plan to extend the project to other tundra regions, in parallel with the development of international collaboration in ecosystem monitoring (§4). Contacts with some schools in Russia have already been initiated.

5.2.2.1. Activity plan

The project will be conducted at three levels from the 5th to 7th grade in the primary schools at Varanger peninsula and Svalbard.



Within the project we introduce three central activities, which will give an insight in species composition and important ecosystem processes in the arctic tundra (Fig. 5.2.2.1). The activities are research based and the recurring theme will be "how will climate change affect the ptarmigan?" The ptarmigan is a common game bird, and a species most children are familiar with, it is also climate sensitive to changes in different trophic levels (§2.6).

A) Winter activity: See the predators!

By using digital cameras positioned on bait it is possible to investigate which predators are present in the area. The obtained data can be compared with data gathered in other schools, as well as in on-going COAT studies, and the pupils can learn more about the temporal and spatial distribution of predators inhabiting the tundra.

Relevant questions: Which predators live in the vicinity of the local community? When are they active? What is the most common predator? Do they prey on ptarmigans?

B) Spring activity: The big bud burst!

To find the exact time of the yearly bud burst in the tundra biome each year, we plan to use digital cameras placed on dwarf birch at Svalbard and both dwarf birch and birch in Varanger. Timing of bud burst will be put in perspective with meteorological data gathered at each site to enable the pupils to see the connection between temperatures (e.g. monthly average, temperature sum) and the onset of spring.

Relevant questions: When is the onset of spring? Is there a difference from year to year? Is there a relationship between temperature and bud burst? How will early or late onset of spring affect the ptarmigan?

C) Autumn activity in Varanger: Herbivore habitat?

The pupils will learn which herbivores are present by identifying and counting their faecal pellets. The pellets count will be conducted each year at permanent sites in different habitats. In addition live trapping of small mammals will be conducted to illustrate small rodent dynamics, and to investigate whether the abundance of rodents is related to the abundance of ptarmigan.

Relevant questions: Which herbivores live in the vicinity of the local community? What habitats do they prefer? Why are peaks in the abundance of small rodents assumed to be favorable for the ptarmigan?

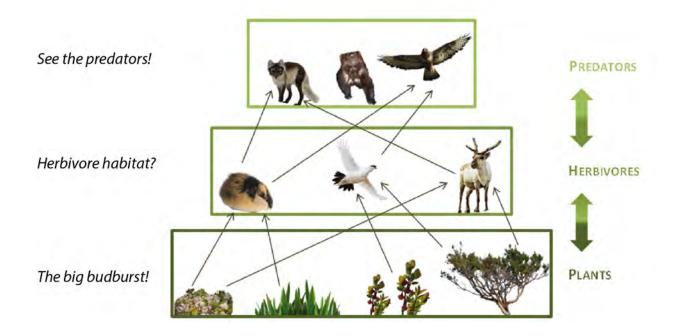


Figure 5.2.2.1. The activities in TUNDRA schoolnet illustrate the species composition and food web interactions at the arctic tundra.

5.2.2.2. Implementation

The Knowledge Promotion Reform in Norway (Kunnskapsløftet) emphasize that the schools and the school owners have the responsibility to develop a local curriculum to ensure that the students reach the national competence objectives (Pedlex Norsk Skoleinformasjon 2010). The planned activities in TUNDRA schoolnet are adapted to the competence objectives in several disciplines in the national curriculum; most importantly Natural science, but also Mathematics, Norwegian, English, Geography and Physical education.

Each of the different field studies will be supported by suitable learning material produced by the TUNDRA schoolnet. All educational material for pupils and teachers will be available at an interactive project website produced by the "Environmental Education Network" (Nettverk for miljølære). The participating classes will enter their observations and results on the website, making it possible for each school to compare their observations with results from other schools and other areas.

All Norwegian project schools will each year have a visit from one of the researchers working in COAT. The researcher will help in practical tasks during field studies, but also talk about recent results, and how the data collected by the schools are used in COAT. The experience that the data collected by the schools is of importance to scientists may be an additional motivation factor for the students to conduct the field studies and learn more about the local environment.

The teachers are an important factor in order to succeed with the implementation of the project. Through yearly seminars for teachers we will educate/update the teachers' knowledge in relevant topics in order to give them the competence and confidence to include the activities in their teaching. These yearly seminars will be a forum for teachers to meet, discuss and improve the different field studies and education plans, as well as strengthen the collaboration between schools in the tundra region.

TUNDRA schoolnet will seek to collaborate with existing school projects and networks both nationally and internationally. Environmental Education Network (Nettverk for miljølære) is a national network that facilitates cooperation between schools, environmental authorities, research institutions and NGOs that will provide the platform for the TUNDRA schoolnet website. For international collaboration we will collaborate with Polar Educators International and possibly the Globe project.



5.2.2.3. Evaluation

In Norway the project method will be evaluated. In 2012 we conducted a survey with basic questions in ecology, among 7th grades students in project schools and control schools in comparable regions of Finnmark. When the project has run for three years and all the different field studies described in the activity plan have been conducted we will again give the same questions to the 7th grade in 2015. By comparing the same cohort of students with different education regime in ecology, will make it possible to investigate the effect of the school project on the students' knowledge. To assess how well the implementation of the project works, an evaluation will also be carried out among teachers.

5.3. Outreach

The knowledge generated by the work planned in COAT will be disseminated to the scientific community and the wider public in and outside the monitoring regions through a variety of communication channels. In addition to traditional printed media such as scientific journals or popular science publications, we will use electronic channels, which are central for the information flow. Digital media create platforms for more rapid dissemination of information and is often delivered in short sections, for instance blog posts, webbased articles and digital video stories. These digital media also opens for potentially interesting communication and feed-back from readers. Below we outline how COAT plans to take advantage of these different information channels.

5.3.1. Scientific publications

The primary objective of COAT is to conduct research and it will be of foremost importance that scientific results are published in high ranking international scientific journals. The monitoring outlined in the science plan will result in new understanding of how climate impacts the functioning of the tundra ecosystem, and thus highlight fundamental aspects of ecology. The COAT plan outlines research that will be highly relevant for the ecosystem-based management of the terrestrial part of the Arctic. Results will thus be published both in high ranking general ecological journals and in journals with a more applied or management orientated focus. The researchers working in COAT will attend scientific conferences on diverse topics. They will present new results and participate actively in international discussions on climate change, ecological monitoring and ecosystem management in the Arctic. Several of the authors of this science plan are at present involved in international monitoring programs and assessments. The knowledge and experience gained through COAT will thus directly be made available to these international fora.

5.3.2. Popular science publication

Scientific knowledge created by state financed research has to be made available to the general public in forms which make the generated knowledge accessible. The monitoring planned in COAT addresses questions which are likely to be of interest for a substantial part of the population, making it particularly important to disseminate results appropriately. Moreover, scientifically founded information about the likely consequences of climate change is essential for people in order to get involved in discussions concerning management and political decision making. Knowledge generated by COAT will thus be presented to the general public through popular science publications.

The internet site forskning.no has specialized on communicating specialized research. COAT aims at communicating all new results to this web page. News from forskning.no is often disseminated further by the press, or by international popular science web pages.

As COAT will be an integral part of the Fram Centre, all communication channels established by the Fram Centre will be used actively by COAT researchers. News and discoveries will be published on the web site framsenteret.no. The Fram Centre has also launched a new communication platform: Fram shorts - instant arctic knowhow (framshorts.com). This site presents digital video stories about the research conducted by Fram centre scientists.

Moreover, COAT will create its own internet page where the public has the possibility to contact researchers and read more in depth about the findings in COAT. This web page will also contain presentations of all different modules, researchers, as well as short communications on everyday events within COAT. The goal of this web page is to make the communication between the public and scientists easier and facilitate exchange of in-

formation.

The COAT research will be presented in two Tromsø-based popular science journals; Fram Forum and Ottar. Fram Forum is an annual English journal that presents research highlights from the past year at the Fram Centre. Ottar is a popular science journal in Norwegian from the University Museum in Tromsø with topics from arctic environment and culture. One volume of Ottar in 2013 is reserved for COAT.

Museums and science centres are important places to disseminate science. We plan to collaborate with the science centre in Tromsø (Vitenskapsenteret) and the museums in Tromsø and Varanger in making exhibitions dealing with arctic tundra ecosystems. Today, the information and communication about northern ecosystems is limited, and by increasing the possibilities to learn more about these systems we hope to generate more interest for the arctic tundra ecosystem. Several of the modules in COAT focus on species and processes which are highly relevant to the local residents in Varanger and Svalbard. These people are indeed experiencing the impacts of climate change on the tundra ecosystem at first hand. Moreover, some of the endemic arctic species targeted by COAT are highly charismatic and their fates in a warming climate will certainly attract the attention of people for outside the arctic region. Researchers in COAT have a responsibility to contribute to the public debate with knowledge on climate change, management and ecosystem state. Increasing the public awareness of an environmental issue can enhance its perceived importance. Through the media we have the opportunity to increase people's awareness of, interest in and attention to the climate-ecological topics. We will therefore have an active contact with local and national newspapers and broadcasters to inform about our results, as well as contribute with knowledge to current topics related to COAT activities.



Literature cited

Aanes, R., B. E. Saether, E. J. Solberg, S. Aanes, O. Strand, and N. A. Oritsland. 2003. Synchrony in Svalbard reindeer population dynamics. Canadian Journal of Zoology-Revue Canadienne De Zoologie **81**:103-110.

Aanes, S., S. Engen, B. E. Saether, T. Willebrand, and V. Marcstrom. 2002. Sustainable harvesting strategies of Willow Ptarmigan in a fluctuating environment. Ecological Applications **12**:281-290.

- Aars, J. and R. A. Ims. 2002. Intrinsic and climatic determinants of population demography: The winter dynamics of tundra voles. Ecology **83**:3449-3456.
- Aas, Ø., H. Øian, R. Waaler, and M. Skår. 2010. Allmennhetens bruk av utmarka i Finnmark. Sammenstilling basert på skrevne kilder. NINA Rapport 642, Norwegian Institute for Nature Research, 94 p. (in Norwegian).
- ABA. 2013. Arctic Biodiversity Synthesis and Recommendations. CAFF International Secretariat, Akureiri, Iceland (in preparation).
- ACIA. 2004. Impacts of a warming Arctic. Cambridge University Press, New York, USA.
- AHDR. 2004. Arctic human development report. Stefansson Arctic Institute, Akureyri, Iceland.
- Aldridge, C. L., S. E. Nielsen, H. L. Beyer, M. S. Boyce, J. W. Connelly, S. T. Knick, and M. A. Schroeder. 2008. Range -wide patterns of greater sage-grouse persistence. Diversity and Distributions 14:983-994.
- Alessa, L., A. Kliskey, and G. Brown. 2008. Social-ecological hotspots mapping: A spatial approach for identifying coupled social-ecological space. Landscape and Urban Planning **85**:27-39.
- Alroy, J. 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. Science **292**:1893-1896.
- Alsos, I., A. Elvebakk, and G. W. Gabrielsen. 1998. Vegetation exploitation by Barnacle Gese *Branta leucopsis* during incubation on Svalbard. Polar Research 17:1-14.
- Ammunét, T. 2011. Trophic interactions of invasive forest herbivores and consequences for the resident ecosystem. University of Turku, Turku, Finland.
- Ancin, F. J. 2012. Fast decomposition rates in riparian meadows in the Norwegian sub-arctic tundra. MSc. Thesis. University of Tromsø, Tromsø, Norway.
- Anderson, D. R. and S. T. Buckland. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press.
- Andersson, M. and S. Erlinge. 1977. Influence of predation on rodent populations. Oikos 29:591-597.
- Andreev, A. V. 1988. Ecological energetics of Palaearctic Tetraonidae in relation to chemical composition and digestibility of their winter diets. Canadian Journal of Zoology **66**:1382-1388.
- Angerbjorn, A., M. Tannerfeldt, and H. Lundberg. 2001. Geographical and temporal patterns of lemming population dynamics in Fennoscandia. Ecography **24**:298-308.
- Angerbjörn, A., N. E. Eide, L. Dalén, B. Elmhagen, P. Hellström, R. A. Ims, S. Killengreen, A. Landa, T. Meijer, M. Mela, J. Niemimaa, K. Norén, M. Tannerfeldt, N. G. Yoccoz, and H. Henttonen. 2013. Carnivore conservation in practice: replicated management actions on a large spatial scale. Journal of Applied Ecology 50:59-67.
- Angerbjörn, A., P. Hersteinsson, and M. Tannerfeldt. 2004. Consequenses and resource predictability in the arctic fox- two life history strategies. In: D. W. MacDonald and C. Sillero- Zubiri, editors. The Biologi and Conservation of Wild Canids. Oxford University Press
- Angerbjörn, A., P. Hersteinsson, and M. Tannerfeldt. 2008. *Alopex lagopus*. In IUCN Red List of Threatened Species. Version 2010.4. (www.iucnredlist.org).
- Angerbjörn, A., M. Tannerfeldt, and S. Erlinge. 1999. Predator-prey relationships: Arctic foxes and lemmings. Journal of Animal Ecology **68**:34-49.
- Anonymous. 2006. Turisme og Friluftsliv på Svalbard. Utvikling, politiske føringer, rammebetingelser, utfordringer og strategier. Sysselmannens rapportserie 1, The Governor on Svalbard, Norway, 124 p. (in Norwegian).
- Anonymous. 2011. Ressursregnskap for reindriftsnæringen : for reindriftsåret 1.april 2009 31.mars 2010. Reindriftsforvaltningen, Alta (in Norwegian).
- Anthony, R. M., J. B. Grand, T. F. Fondell, and D. A. Miller. 2006. Techniques for identifying predators of goose nests. Wildlife Biology 12:249-256.
- Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G. H. R. Henry, M. H. Jones, R. D. Hollister, I. S. Jonsdottir, K. Laine, E. Levesque, G. M. Marion, U. Molau, P. Molgaard, U. Nordenhall, V. Raszhivin, C. H. Robinson, G. Starr, A. Stenstrom, M. Stenstrom, O. Totland, P. L. Turner, L. J. Walker, P. J. Webber, J. M. Welker, and P. A. Wookey. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. Ecological Monographs 69:491-511.
- Arlov, T. B. 1996. Svalbards historie. Aschehoug, Oslo (in Norwegian).
- Aslaksen, I. and S. Glomsrød. 2009. The Economy of the North 2008. Statistics Norway (www.ssb.no), Oslo.

Audet, A. M., C. B. Robbins, and S. Larivière. 2002. Alopex lagopus. Mammalian Species 713:1-10.

- Augustine, D. J. and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. Journal of Wildlife Management **62**:1165-1183.
- Aunapuu, M., J. Dahlgren, T. Oksanen, D. Grellmann, L. Oksanen, J. Olofsson, U. Rammul, M. Schneider, B. Johansen, and H. O. Hygen. 2008. Spatial patterns and dynamic responses of arctic food webs corroborate the exploitation ecosystems hypothesis (EEH). American Naturalist 171:249-262.
- Aune, S., A. Hofgaard, and L. Soderstrom. 2011. Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 41:437-449.
- Aurela, M., J. P. Tuovinen, and T. Laurila. 2001. Net CO2 exchange of a subarctic mountain birch ecosystem. Theoretical and Applied Climatology **70**:135-148.
- Austrheim, G. and O. Eriksson. 2001. Plant species diversity and grazing in the Scandinavian mountains patterns and processes at different spatial scales. Ecography **24**:683-695.
- Ballouard, J.-M., F. Brischoux, and X. Bonnet. 2011. Children prioritize virtual exotic biodiversity over local biodiversity. Plos One **6**:e23152.
- Bardgett, R. D. and D. A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84:2258-2268.
- Barker, S. 2002. More than a nature table and mobiles: Living ecology in the primary classroom. Environmental Education **71**:13-15.
- Barrett, R. H., S.-H. Lorentsen, and T. Anker-Nilssen. 2006. The status of breeding seabirds in mainland Norway. Atlantic Seabirds 8:97-126.
- Barth, J. B. 1877. Naturskildringer og Optegnelser fra mit Jæger- og Reiseliv. Kristiania. Cammermeyer. pp. 385.
- Batzli, G. O. 1993. Food selection by lemmings. In: N. C. Stenseth and R. A. Ims, editors. The biology of lemmings. Academic Press, London. Pages 201-301.
- Batzli, G. O., R. G. White, S. F. MacLean, F. A. Pitelka, and B. D. Collier. 1980. The herbivore-based trophic system.
 In: J. Brown, P. C. Miller, L. L. Tieszen, and F. L. Bunnell, editors. An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska. Dowden, Hutchinson and Ross, Stroudsburg, PA. Pages 335–410.
- Bauer, S., J. Madsen, and M. Klaassen. 2006. Intake rates, stochasticity, or onset of spring what aspects of food availability affect spring migration patterns in pink-footed geese *Anser brachyrhynchus*? Ardea **94**:555-566.
- Bauert, M. R. 1993. Vivipary in *Polygonum viviparum*: an adaptation to cold climate? Nordic Journal of Botany **13**:473 -480.
- Beaumont, L. J., A. Pitman, S. Perkins, N. E. Zimmermann, N. G. Yoccoz, and W. Thuiller. 2011. Impacts of climate change on the world's most exceptional ecoregions. Proceedings of the National Academy of Sciences 108:2306-2311.
- Beck, P. S. A. and S. J. Goetz. 2011. Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences. Environmental Research Letters 6:No. 045501.
- Beck, P. S. A., N. Horning, S. J. Goetz, M. M. Loranty, and K. D. Tape. 2011a. Shrub Cover on the North Slope of Alaska: a circa 2000 Baseline Map. Arctic Antarctic and Alpine Research **43**:355-363.
- Beck, P. S. A., G. P. Juday, C. Alix, V. A. Barber, S. E. Winslow, E. E. Sousa, P. Heiser, J. D. Herriges, and S. J. Goetz. 2011b. Changes in forest productivity across Alaska consistent with biome shift. Ecology Letters 14:373-379.
- Benestad, R. E., F. Flatøy, I. Hanssen-Bauer, J. E. Haugen, K. Isaksen, A. Sorteberg, and B. Ådlandsvik. 2009. Climate development in North Norway and the Svalbard region during 1900–2100. Norsk Polarinstitutt rapportserie, Norwegian Polar Institute, pp.
- Bennie, J., E. Kubin, A. Wiltshire, B. Huntley, and R. Baxter. 2010. Predicting spatial and temporal patterns of budburst and spring frost risk in north-west Europe: the implications of local adaptation to climate. Global Change Biology 16:1503-1514.
- Berteaux, D., A. Angerbjörn, D. Ehrich, N. E. Eide, E. Fuglei, D. Gallant, R. A. Ims, E. P. Kruchenkova, N. Lecomte, I. E. Menyushina, E. Noren, N. Ovsjanikov, A. Rodnikova, A. Tarrocux, and N. G. Yoccoz. 2011. Arctic and red foxes In: G. Gauthier and D. Berteaux, editors. ArcticWOLVES: Arctic Wildlife Observatories Linking Vulnerable EcoSystems. Final synthesis report Centre d'études nordiques, Université Laval, Quebec City, Quebec, Canada. Pages 76-88.
- Bety, J., G. Gauthier, J. F. Giroux, and E. Korpimaki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos **93**:388-400.
- Bety, J., G. Gauthier, E. Korpimaki, and J. F. Giroux. 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. Journal of Animal Ecology **71**:88-98.
- Bewley, D., J. W. Pomeroy, and R. L. H. Essery. 2007. Solar radiation transfer through a subarctic shrub canopy. Arctic Antarctic and Alpine Research **39**:365-374.
- Bjork, R. G. and U. Molau. 2007. Ecology of alpine snowbeds and the impact of global change. Arctic Antarctic and Alpine Research **39**:34-43.
- Bjørnstad, O. N., W. Falck, and N. C. Stenseth. 1995. Geographic gradient in small rodent density fluctuations a statistical modeling approach. Proceedings of the Royal Society of London Series B-Biological Sciences **262**:127-

133.

- Black, J. M. 1998. Flyway conservation and management plan for the Svalbard barnacle goose population. In: F. Mehlum, J. M. Black, and J. Madsen, editors. Research on arctic geese. Norsk Polarinstitutt Skrifter vol. 200, Oslo, Norway. Pages 29-40.
- Black, J. M., J. Prop, and K. Larsson. 2007. Wild goose dilemmas. Branta Press, Groningen, The Netherlands.
- Blanken, P. D. and W. R. Rouse. 1994. The role of willow– birch forest in the surface energy balance at Arctic treeline. Arctic and Alpine Research **26**:403–411.
- Blaschke, T., S. Lang, and G. Hay, editors. 2008. Object-based image analysis. Spatial concepts for knowledge-driven remote sensing applications. Springer, New York.
- Bliss, L. C. 1997. Arctic ecosystems of North America. In: F. E. Wielgolaski, editor. Polar and alpine tundra. Elsevier, Amsterdam. Pages 551-683.
- Bliss, L. C. and N. V. Matveyeva. 1992. Circumpolar arctic vegetation. In: F. S. III Chapin, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda, editors. Arctic ecosystems in a changing climate: An ecophysiological perspective. Academic Press, San Diego. Pages 59-89.
- Blok, D., U. Sass-Klaassen, G. Schaepman-Strub, M. M. P. D. Heijmans, P. Sauren, and F. Berendse. 2011a. What are the main climate drivers for shrub growth in Northeastern Siberian tundra? Biogeosciences **8**:1169-1179.
- Blok, D., G. Schaepman-Strub, H. Bartholomeus, M. M. P. D. Heijmans, T. C. Maximov, and F. Berendse. 2011b. The response of arctic vegetation to the summer climate: relation between shrub cover, NDVI, surface albedo and temperature. Environmental Research Letters **6**:035502.
- Boker, S., M. Neale, H. Maes, M. Wilde, M. Spiegel, T. Brick, J. Spies, R. Estabrook, S. Kenny, T. Bates, P. Mehta, and J. Fox. 2011. OpenMx: an open source extended Structural Equation Modeling framework. Psychometrika 76:306-317.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127 -135.
- Booms, T. L. and M. R. Fuller. 2003. Gyrfalcon diet in central west Greenland during the nesting period. The Condor **105**:528-537.
- Booth, B. B. B., N. J. Dunstone, P. R. Halloran, T. Andrews, and N. Bellouin. 2012. Aerosols implicated as a prime driver of twentieth-century North Atlantic climate variability. Nature **484**:228-232.
- Braestrup, F. W. 1941. A study on the arctic fox in Greenland. Immigration, fluctuations in numbers based mainly on trading statistics. Meddelelser om Grønland **131**:1-101.
- Brommer, J. E., H. Pietiainen, K. Ahola, P. Karell, T. Karstinen, and H. Kolunen. 2010. The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through 'climatic forcing'. Global Change Biology 16:577-586.
- Brown, G. and D. Weber. 2012. Measuring change in place values using public participation GIS (PPGIS). Applied Geography **34**:316-324.
- Brown, G. G. and D. V. Pullar. 2012. An evaluation of the use of points versus polygons in public participation geographical information systems using quasi-experimental design and monte carlo simulation. International Journal of Geographical Information Systems **26**:231-246.
- Brown, J. H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology **58**:445-449.
- Bråthen, K., C. H. Fodstad, and C. Gallet. 2010. Ecosystem disturbance reduces the allelopathic effects of *Empetrum hermaphroditum* humus on tundra plants. Journal of Vegetation Science **21**:786-795.
- Bråthen, K., V. González, M. Iversen, S. Killengreen, V. Ravolainen, R. Ims, and N. Yoccoz. 2007b. Endozoochory varies with ecological scale and context. Ecography **30**:308-320.
- Bråthen, K. A. and O. Hagberg. 2004. More efficient estimation of plant biomass. Journal of Vegetation Science 15:653-660.
- Bråthen, K. A., R. A. Ims, N. G. Yoccoz, P. Fauchald, T. Tveraa, and V. H. Hausner. 2007a. Induced shift in ecosystem productivity ? Extensive scale effects of abundant large herbivores. Ecosystems **10**:773-789.
- Bråthen, K. A. and J. Oksanen. 2001. Reindeer reduce biomass of preferred plant species. Journal of Vegetation Science 12:473-480.
- Buckeridge, K. M., E. Zufelt, H. Y. Chu, and P. Grogan. 2010. Soil nitrogen cycling rates in low arctic shrub tundra are enhanced by litter feedbacks. Plant and Soil **330**:407-421.
- Bårdsen, B.-J. and T. Tveraa. 2012. Density-dependence vs. density-independence linking reproductive allocation to population abundance and vegetation greenness. Journal of Animal Ecology **81**:364-376.
- Callaghan, T. V., B. R. Werkman, and R. M. Crawford. 2002a. The Tundra-Taiga interface and its dynamics: Concepts and Applications. Ambio Special Report, Tundra-Taiga Treeline Research 12:6-14.
- Callaghan, T. V., R. M. M. Crawford, M. Eronen, A. Hofgaard, S. Payette, W. G. Rees, O. Skre, J. Sveinbjornsson, T. K. Vlassova, and B. R. Werkman. 2002b. The dynamics of the tundra-taiga boundary: An overview and suggested coordinated and integrated approach to research. Ambio, Special Report **12**:3-5.
- Callaghan, T. V., L. O. Björn, Y. Chernov, F. S. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. C. Oechel, and G. R. Shaver. 2004a. Rationale, concepts and

approach to the assessment. Ambio 33:393-397.

- Callaghan, T. V., L. O. Björn, Y. Chernov, T. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, S. Schaphoff, S. Sitch, and C. Zockler. 2004b. Synthesis of effects in four Arctic subregions. Ambio 33:469-473.
- Callaghan, T. V., L. O. Björn, Y. Chernov, T. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, and H. Henttonen. 2004c. Effects on the structure of arctic ecosystems in the short- and long-term perspectives. Ambio 33:436-447.
- Callaghan, T. V., L. O. Björn, Y. Chernov, T. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, J. Elster, H. Henttonen, K. Laine, K. Taulavuori, E. Taulavuori, and C. Zockler. 2004d. Biodiversity, distributions and adaptations of arctic species in the context of environmental change. Ambio 33:404-417.
- Callaghan, T. V., L. O. Björn, Y. Chernov, T. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, J. Elster, I. S. Jonsdottir, K. Laine, K. Taulavuori, E. Taulavuori, and C. Zockler. 2004e Responses to projected changes in climate and UV-B at the species level. Ambio 33:418-435.
- Callaghan, T. V., L. O. Björn, Y. Chernov, T. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, and G. Shaver. 2004f. Effects on the Function of Arctic Ecosystems in the Short- and Long-term Perspectives. Ambio 33:448-458.
- Callaghan, T. V. and M. Johansson. 2009. The changing, living tundra: a tribute to Yuri Chernov. In: S. I. Golovatch, O. L. Makarova, and A. B. Babenko, editors. Species and Communities in Extreme Environments. Pensoft, Moscow. Pages 13-52.
- Carmichael, L. E., J. Krizan, J. A. Nagy, E. Fuglei, M. Dumond, D. Johnson, A. Veitch, D. Berteaux, and C. Strobeck. 2007. Historical and ecological determinants of genetic structure in arctic canids. Molecular Ecology 16:3466-3483.
- CAVM Team. 2003. Circumpolar Arctic Vegetation Map. Scale 1:7,500,000. Map No. 1. Conservation of Arctic Flora and Fauna (CAFF), U.S. Fish and Wildlife Service, Anchorage, Alaska.
- Chapin, F. S., T. V. Callaghan, Y. Bergeron, M. Fukuda, J. F. Johnstone, G. Juday, and S. A. Zimov. 2004. Global change and the boreal forest: Thresholds, shifting states or gradual change? Ambio **33**:361-365.
- Chapin, F. S., S. R. Carpenter, G. P. Kofinas, C. Folke, N. Abel, W. C. Clark, P. Olsson, D. M. S. Smith, B. Walker, O. R. Young, F. Berkes, R. Biggs, J. M. Grove, R. L. Naylor, E. Pinkerton, W. Steffen, and F. J. Swanson. 2010. Ecosystem stewardship: sustainability strategies for a rapidly changing planet. Trends in Ecology & Evolution 25:241-249.
- Chapin, F. S., A. D. McGuire, J. Randerson, R. Pielke, D. Baldocchi, S. E. Hobbie, N. Roulet, W. Eugster, E. Kasischke,E. B. Rastetter, S. A. Zimov, and S. W. Running. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. Global Change Biology 6:211-223.
- Chapin, F. S., G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Responses of Arctic tundra to experimental and observed changes in climate. Ecology **76**:694-711.
- Chapin, F. S., M. Sturm, M. C. Serreze, J. P. McFadden, J. R. Key, A. H. Lloyd, A. D. McGuire, T. S. Rupp, A. H. Lynch, J. P. Schimel, J. Beringer, W. L. Chapman, H. E. Epstein, E. S. Euskirchen, L. D. Hinzman, G. Jia, C. L. Ping, K. D. Tape, C. D. C. Thompson, D. A. Walker, and J. M. Welker. 2005. Role of land-surface changes in Arctic summer warming. Science 310:657-660.
- Chernov, Y. I. 1985. The living tundra. Cambridge University Press, Cambridge.
- Chernov, Y. I. and N. V. Matveyeva. 1997. Arctic ecosystems in Russia. In: F. E. Wielgolaski, editor. Polar and Alpine Tundra. Elvesier, Amsterdam. Pages 361-507.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics **31**:343 -366.
- Choate, T. S. 1963. Habitat and population dynamics of white-tailed ptarmigan in Montana. Journal of Wildlife Management **27**:684-699.
- Chow, S. M., M. H. R. Ho, E. L. Hamaker, and C. V. Dolan. 2010. Equivalence and differences between structural equation modeling and state-space modeling techniques. Structural Equation Modeling 17:303-332.
- Christensen, T., J. F. Payne, N. M. Schmidt, J. Madsen, J. J. Taylor, M. Doyle, M. Gill, J. Nymand, M. Svoboda, C. Rosa, B. Shuchman, M. Soloviev, M. Aronsson, E. Paakko, A. M. Fosaa, S. Heidmarsson, and B. Ø. Solberg. 2011. Terrestrial Expert Monitoring Plan – background paper. A Supporting Publication to the CBMP Framework Document. CAFF Monitoring Series Report Nr. 6, CAFF International Secretariat, pp.
- Christensen, T. R., T. Johansson, M. Olsrud, L. Strom, A. Lindroth, M. Mastepanov, N. Malmer, T. Friborg, P. Crill, and T. V. Callaghan. 2007. A catchment-scale carbon and greenhouse gas budget of a subarctic landscape. Philosophical Transactions of the Royal Society a-Mathematical Physical and Engineering Sciences 365:1643-1656.
- Chu, H. and P. Grogan. 2010. Soil microbial biomass, nutrient availability and nitrogen mineralization potential among vegetation-types in a low arctic tundra landscape. Plant and Soil **329**:411-420.
- Clum, N. J. and T. J. Cade. 1994. Gyrfalcon (*Falco rusticolus*). In: A. Poole and F. Gill, editors. The birds of North America. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union,

Washington, DC.

- Clutton-Brock, T. and B. C. Sheldon. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution **25**:562-573.
- Connelly, J. W. and C. E. Braun. 1997. Long-term changes in sage grouse *Centrocercus urophasianus* populations in western North America. Wildlife Biology **3**:229-234.
- Cooper, E. J., I. S. Jónsdóttir, and A. Pahud. 2006. Grazing by captive Barnacle geese affects graminoid growth and productivity on Svalbard. Memoirs of the National Institute for Polar Research **59**:1-15.
- Courchamp, F., R. Woodroffe, and G. Roemer. 2003. Removing protected populations to save endangered species. Science **302**:1532-1532.
- Cressie, N., C. A. Calder, J. S. Clark, J. M. V. Hoef, and C. K. Wikle. 2009. Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. Ecological Applications **19**:553-570.
- Dahlgren, J., L. Oksanen, T. Oksanen, J. Olofsson, P. A. Hamback, and A. Lindgren. 2009a. Plant defences to no avail? Responses of plants of varying edibility to food web manipulations in a low arctic scrubland. Evolutionary Ecology Research 11:1189-1203.
- Dahlgren, J., L. Oksanen, J. Olofsson, and T. Oksanen. 2009b. Plant defences at no cost? The recovery of tundra scrubland following heavy grazing by grey-sided voles, *Myodes rufocanus*. Evolutionary Ecology Research 11:1205-1216.
- Dahlgren, J., L. Oksanen, M. Sjodin, and J. Olofsson. 2007. Interactions between gray-sided voles (*Clethrionomys rufu-canus*) and bilberry (*Vaccinium myrtillus*), their main winter food plant. Oecologia **152**:525-532.
- Dalen, L., K. Kvaloy, J. D. C. Linnell, B. Elmhagen, O. Strand, M. Tannerfeldt, H. Henttonen, E. Fuglei, A. Landa, and A. Angerbjorn. 2006. Population structure in a critically endangered arctic fox population: does genetics matter? Molecular Ecology 15:2809-2819.
- Dalhaug, L., I. M. Tombre, and K. E. Erikstad. 1996. Seasonal decline in clutch size of the Barnacle Goose in Svalbard. Condor **98**:42-47.
- Dankers, R. and O. B. Christensen. 2005. Climate change impact on snow coverage, evaporation and river discharge in the sub-arctic Tana Basin, Northern Fennoscandia. Climatic Change **69**:367-392.
- Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. Science **332**:53-58.
- De Juana, E. 1994. The rock ptarmigan. New world vultures to guineafowl. In: J. Del Hoya, A. Elliott, and J. Sargatal, editors. Handbook of the birds of the world. Lynx, Barcelona. Page 403pp.
- de Leeuw, J. 2006. Nonlinear principal component analysis and related techniques. In: M. Greenacre and J. Blasius, editors. Multiple correspondence analysis and related methods. Chapman & Hall/CRC, London.
- den Herder, M., R. Virtanen, and H. Roininen. 2004. Effects of reindeer browsing on tundra willow and its associated insect herbivores. Journal of Applied Ecology **41**:870-879.
- den Herder, M., R. Virtanen, and H. Roininen. 2008. Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone. Basic and Applied Ecology **9**:324-331.
- Derocher, A. E., O. Wiig, and G. Bangjord. 2000. Predation of Svalbard reindeer by polar bears. Polar Biology 23:675-678.
- Deser, C., A. Phillips, V. Bourdette, and H. Y. Teng. 2012. Uncertainty in climate change projections: the role of internal variability. Climate Dynamics **38**:527-546.
- Diaz, S., F. Quetier, D. M. Caceres, S. F. Trainor, N. Perez-Harguindeguy, M. S. Bret-Harte, B. Finegan, M. Pena-Claros, and L. Poorter. 2011. Linking functional diversity and social actor strategies in a framework for interdisciplinary analysis of nature's benefits to society. Proceedings of the National Academy of Sciences of the United States of America 108:895-902.
- Direktoratet for Naturforvaltning. 2010. Rovbase 3.0. http://dnweb13.dirnat.no/Rovbase30Innsyn/Contentpages/ InnsynForsiden.aspx
- Dixon, J. S. 1927. Contribution to the life history of the Alaska Willow Ptarmigan. Condor 29:213-223.
- Doak, D. F., J. A. Estes, B. S. Halpern, U. Jacob, D. R. Lindberg, J. Lovvorn, D. H. Monson, M. T. Tinker, T. M. Williams, J. T. Wootton, I. Carroll, M. Emmerson, F. Micheli, and M. Novak. 2008. Understanding and predicting ecological dynamics: Are major surprises inevitable? Ecology 89:952-961.
- Doak, D. F. and W. F. Morris. 2010. Demographic compensation and tipping points in climate-induced range shifts. Nature **467**:959-962.
- Dray, S. 2011. A new perspective about Moran's coefficient: Spatial autocorrelation as a linear regression problem. Geographical analysis **43**:127-141.
- DST. 2011. Statistics Denmark, http://www.dst.dk.
- du Toit, S. H. C. and M. W. Browne. 2007. Structural equation modeling of multivariate time series. Multivariate Behavioral Research **42**:67-101.
- Dunlap, R. E., K. D. Van Liere, A. G. Mertig, and R. E. Jones. 2000. Measuring endorsement of the new ecological paradigm: A revised NEP scale. Journal of Social Issues **56**:425-442.
- Duriez, O., S. Bauer, A. Destin, J. Madsen, B. A. Nolet, R. A. Stillman, and M. Klaassen. 2009. What decision rules might pink-footed geese use to depart on migration? An individual-based model. Behavioral Ecology 20:560-569.

- Edenius, L., C. P. Vencatasawmy, P. Sandström, and U. Dahlberg. 2003. Combining satellite imagery and ancillary data to map snowbed vegetation important to reindeer *Rangifer tarandus*. Arctic Antarctic and Alpine Research **35**:150-157.
- EEC. 1992. Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (European Council). Brussels.
- Ehrenfeld, J. G., B. Ravit, and K. Elgersma. 2005. Feedback in the plant-soil system. Annual Review of Environment and Resources **30**:75-115.
- Ehrich, D., J. A. Henden, R. A. Ims, L. O. Doronina, S. T. Killengren, N. Lecomte, I. G. Pokrovsky, G. Skogstad, A. A. Sokolov, V. A. Sokolov, and N. G. Yoccoz. 2012a. The importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better? Oecologia 168:141-151.
- Ehrich, D., L. Carmichael, and E. Fuglei. 2012b. Age-dependent genetic structure of arctic foxes in Svalbard. Polar Biology **35**:53-62.
- Eichhorn, G., R. H. Drent, J. Stahl, A. Leito, and T. Alerstam. 2009. Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. Journal of Animal Ecology **78**:63-72.
- Eichler, M., G. Motta, and R. von Sachs. 2011. Fitting dynamic factor models to non-stationary time series. Journal of Econometrics 163:51-70.
- Eide, N. E., P. M. Eid, P. Prestrud, and J. E. Swenson. 2005. Dietary responses of arctic foxes *Alopex lagopus* to changing prey availability across an arctic landscape. Wildlife Biology **11**:109-121.
- Eide, N. E., J. U. Jepsen, and P. Prestrud. 2004. Spatial organization of reproductive arctic foxes *Alopex lagopus*: responses to changes in spatial and temporal availability of prey. Journal of Animal Ecology **73**:1056-1068.
- Eide, N. E., A. Stien, P. Prestrud, N. G. Yoccoz, and E. Fuglei. 2012. Reproductive responses to spatial and temporal prey availability in a coastal Arctic fox population. Journal of Animal Ecology **81**:640-648.
- Elmendorf, S. C., G. H. R. Henry, R. D. Hollister, R. G. Bjork, A. D. Bjorkman, T. V. Callaghan, L. S. Collier, E. J. Cooper, J. H. C. Cornelissen, T. A. Day, A. M. Fosaa, W. A. Gould, J. Gretarsdottir, J. Harte, L. Hermanutz, D. S. Hik, A. Hofgaard, F. Jarrad, I. S. Jonsdottir, F. Keuper, K. Klanderud, J. A. Klein, S. Koh, G. Kudo, S. I. Lang, V. Loewen, J. L. May, J. Mercado, A. Michelsen, U. Molau, I. H. Myers-Smith, S. F. Oberbauer, S. Pieper, E. Post, C. Rixen, C. H. Robinson, N. M. Schmidt, G. R. Shaver, A. Stenstrom, A. Tolvanen, O. Totland, T. Troxler, C. H. Wahren, P. J. Webber, J. M. Welker, and P. A. Wookey. 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecology Letters 15:164-175.
- Elmhagen, B., P. Hellström, A. Angerbjorn, and J. Kindberg. 2011. Changes in vole and lemming fluctuations in northern Sweden 1960-2008 revealed by fox dynamics. Annales Zoologici Fennici **48**:167-179.
- Elmhagen, B., G. Ludwig, S. P. Rushton, P. Helle, and H. Linden. 2010. Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. Journal of Animal Ecology **79**:785-794.
- Elmhagen, B. and S. P. Rushton. 2007. Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecology Letters 10:197-206.
- Elmhagen, B., M. Tannerfeldt, and A. Angerbjörn. 2002. Food-niche overlap between arctic and red foxes. Canadian Journal of Zoology **80**:1274-1285.
- Elmhagen, B., M. Tannerfeldt, P. Verucci, and A. Angerbjorn. 2000. The arctic fox (*Alopex lagopus*): an opportunistic specialist. Journal of Zoology **251**:139-149.
- Elton, C. S. 1942. Voles, mice and lemmings: problems in population dynamics. Clarendon Press, Oxford.
- Elvebakk, A. 1997. Tundra diversity and ecological characteristics of Svalbard. In: F. E. Wielgolaski, editor. Polar and alpine tundra. Elsevier, Amsterdam. Pages 347-399.
- Erikstad, K. E. and R. Andersen. 1983. The effect of weather on food intake, insect prey selection and feeding time in different sized willow grouse broods. Ornis Scandinavica 14:249-252.
- Erikstad, K. E., R. Blom, and S. Myrberget. 1982. Territorial hooded crows as predators on willow ptarmigan nests. Journal of Wildlife Management **46**:109-114.
- Evans, S. A., F. Mougeot, S. M. Redpath, and F. Leckie. 2007. Alternative methods for estimating density in an upland game bird: The red grouse *lagopus scotieus*. Wildlife Biology **13**:130-139.
- Fan, D. M. and Y. P. Yang. 2009. Altitudinal variations in flower and bulbil production of an alpine perennial, *Polygo-num viviparum* L. (Polygonaceae). Plant Biology **11**:493-497.
- Farbrot, H., K. Isaksen, B. Etzelmüller, and K. Gisnås. 2013. Ground thermal regime and permfrost distribution under a changing climate in northern Norway. Permafrost and Periglacial Processes Online Early:DOI: 10.1002/ ppp.1763.
- Fauchald, P., T. Tveraa, N. G. Yoccoz, and R. A. Ims. 2004. En økologisk bærekraftig reindrift. Hva begrenser produksjon og høsting? NINA Fagrapport, 35pp.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology **51**:565-581.
- Feng, S., C.-H. Ho, Q. Hu, R. Oglesby, S.-J. Jeong, and B.-M. Kim. 2012. Evaluating observed and projected future climate changes for the Arctic using the Köppen-Trewartha climate classification. Climate Dynamics 38:1359-1373.
- Ferrer, E. and J. J. McArdle. 2003. Alternative structural models for multivariate longitudinal data analysis. Structural Equation Modeling **10**:493-524.

- Fischlin, A., G. F. Midgely, J. Price, R. Leemans, B. Gopal, C. Turley, M. Rounsevell, O. Dube, J. Tarazona, and A. Velichko. 2007. Ecosystems, their properties, goods, and services. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, International Panel on Climate Change, Cambridge, 211-272 pp.
- Fletcher, K., N. J. Aebischer, D. Baines, R. Foster, and A. N. Hoodless. 2010. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. Journal of Applied Ecology 47:263-272.
- Foley, W. J., A. McIlwee, I. Lawler, L. Aragones, A. P. Woolnough, and N. Berding. 1998. Ecological applications of near infrared reflectance spectroscopy a tool for rapid, cost-effective prediction of the composition of plant and animal tissues and aspects of animal performance. Oecologia **116**:293-305.
- Forbes, B. C., M. M. Fauria, and P. Zetterberg. 2010. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. Global Change Biology **16**:1542-1554.
- Forbes, B. C., F. Stammler, T. Kumpula, N. Meschtyb, A. Pajunen, and E. Kaarlejärvi. 2009. High resilience in the Yamal-Nenets social–ecological system, West Siberian Arctic, Russia. PNAS **106**:no. 52 22041-22048
- Ford, J., H. Chitty, and A. D. Middleton. 1938. The food of partridge chicks (*Perdix perdix*) in Great Britain. Journal of Animal Ecology 7:251-265.
- Fox, A. D. and E. Bergersen. 2005. Lack of competition between barnacle geese *Branta leucopsis* and pink-footed geese *Anser brachyrhynchus* during the pre-breeding period in Svalbard. Journal of Avian Biology **36**:173-178.
- Fox, A. D., E. Bergersen, I. M. Tombre, and J. Madsen. 2007. Minimal intra-seasonal dietary overlap of barnacle and pink-footed geese on their breeding grounds in Svalbard. Polar Biology **30**:759-768.
- Fox, A. D., B. S. Ebbinge, C. Mitchell, T. Heinicke, T. Aarvak, K. Colhoun, P. Clausen, S. Dereliev, S. Faragó, K. Koffijberg, H. Kruckenberg, M. J. J. E. Loonen, J. Madsen, J. Mooij, P. Musil, L. Nilsson, S. Phil, and H. van der Jeugd. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and an assessment of trends. Ornis Svecica 20:115-127.
- Fox, A. D., N. E. Eide, E. Bergersen, and J. Madsen. 2009. Resource partitioning in sympatric arctic-breeding geese: summer habitat use, spatial and dietary overlap of Barnacle and Pink-footed Geese in Svalbard. Ibis 151:122-133.
- Fox, A. D., J. Madsen, H. Boyd, E. Kuijken, D. W. Norriss, I. M. Tombre, and D. A. Stroud. 2005. Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. Global Change Biology 11:881-893.
- Frafjord, K. 2003. Ecology and use of arctic fox *Alopex lagopus* dens in Norway: tradition overtaken by interspecific competition? Biological Conservation **111**:445-453.
- Frafjord, K., D. Becker, and A. Angerbjorn. 1989. Interactions between arctic and red foxes in Scandinavia Predation and aggression. Arctic **42**:354-356.
- Framstad, E. 2011. Natur i endring. Terrestrisk naturovervåking i 2010: Markvegetasjon, epifytter, smågnagere og fugl. NINA, Trondheim, 135 p.
- Fraser, D. A. S. 2011. Is Bayes posterior just quick and dirty confidence? Statistical Science 26:299-321.
- Fredga, K., M. Jaarola, R. A. Ims, H. Steen, and N. G. Yoccoz. 1990. The common vole in Svalbard identified as *Microtus epiroticus* by chromosome analysis. Polar Research **8**:283-290.
- Freitas, C., K. M. Kovacs, R. A. Ims, M. A. Fedak, and C. Lydersen. 2009. Deep into the ice: over-wintering and habitat selection in male Atlantic walruses. Marine Ecology-Progress Series **375**:247-261.
- Freschet, G. T., J. H. C. Cornelissen, R. S. P. van Logtestijn, and R. Aerts. 2010. Evidence of the 'plant economics spectrum' in a subarctic flora. Journal of Ecology **98**:362-373.
- Fryxell, J. M. and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology & Evolution 3:237-241.
- Fuglei, E., J. O. Bustnes, H. Hop, T. Mørk, H. Bjornfoth, and B. van Bavel. 2007. Environmental contaminants in arctic foxes (*Alopex lagopus*) in Svalbard: Relationships with feeding ecology and body condition. Environmental Pollution 146:128-138.
- Fuglei, E. and R. A. Ims. 2008. Global warming and effects on the arctic fox. Science Progress 9:175-191.
- Fuglei, E., N. A. Oritsland, and P. Prestrud. 2003. Local variation in arctic fox abundance on Svalbard, Norway. Polar Biology 26:93-98.
- Fuglei, E., A. Stien, N. G. Yoccoz, R. A. Ims, N. E. Eide, P. Prestrud, P. Deplazes, and A. Oksanen. 2008. Spatial distribution of *Echinococcus multilocularis*, Svalbard, Norway. Emerging Infectious Diseases 14:73-75.
- Fuglei, E. and N. A. Øritsland. 2003. Energy cost of running in an arctic fox (*Alopex lagopus*). Canadian Field-Naturalist 117:430-435.
- Fuller, T. K. and P. R. Sievert. 2001. Carnivore demography and the consequences of changes in prey availability. In: J. L. Gittleman, S. M. Funk, and D. W. Macdonald, editors. Carnivore conservation. Cambridge University Press, London, U.K. Pages 163-178.
- Førland, E. J., R. E. Benestad, I. Hanssen-Bauer, J. E. Haugen, and T. E. Skaugen. 2011. Temperature and precipitation development at Svalbard 1900-2100. Advances in Meteorology **2011**:Article ID 893790.
- Gabay, O., A. Perevolotsky, A. Bar Massada, Y. Carmel, and M. Shachak. 2011. Differential effects of goat browsing on herbaceous plant community in a two-phase mosaic. Plant Ecology **212**:1643-1653.

- Gallant, D., B. G. Slough, D. G. Reid, and D. Berteaux. 2012. Arctic fox versus red fox in the warming Arctic: four decades of den surveys in north Yukon. Polar Biology **35**:1421-1431.
- Garel, M., J. M. Gaillard, J. M. Jullien, D. Dubray, D. Maillard, and A. Loison. 2011. Population abundance and early spring conditions determine variation in body mass of juvenile chamois. Journal of Mammalogy **92**:1112-1117.
- Gauthier, G., D. Berteaux, J. Bety, A. Tarroux, J. F. Therrien, L. McKinnon, P. Legagneux, and M. C. Cadieux. 2011. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. Ecoscience 18:223-235.
- Gauthier, G., D. Berteaux, C. J. Krebs, and D. Reid. 2009. Arctic lemmings are not simply food limited a comment on Oksanen et al. Evolutionary Ecology Research 11:483-484.
- Gauthier, G., J. Bety, J. F. Giroux, and L. Rochefort. 2004. Trophic interactions in a high arctic snow goose colony. Integrative and Comparative Biology **44**:119-129.
- Geffen, E., S. Waidyaratne, L. Dalen, A. Angerbjörn, C. Vila, P. Hersteinsson, E. Fuglei, P. A. White, M. Goltsman, C. M. O. Kapel, and R. K. Wayne. 2007. Sea ice occurrence predicts genetic isolation in the arctic fox. Molecular Ecology 16:4241-4255.
- Gibbons, D. W., A. Amar, G. O. A. Anderson, M. Bolton, R. B. Bradbury, M. A. Eaton, A. D. Evans, M. C. Grant, R. D. Gregory, G. M. Hilton, G. J. M. Hirons, Hughes. J., I. Johnstone, P. Newbery, W. J. Peach, N. Ratcliffe, K. W. Smith, R. W. Summers, P. Walton, and J. D. Wilson. 2007. The predation of wild birds in the UK: a review of its conservation impact and management. RSPB Research report no. 23. RSPB, Sandy.
- Gilg, O., I. Hanski, and B. Sittler. 2003. Cyclic dynamics in a simple vertebrate predator-prey community. Science **302**:866-868.
- Gilg, O., K. M. Kovacs, J. Aars, J. Fort, G. Gauthier, D. Gremillet, R. A. Ims, H. Meltofte, J. Moreau, E. Post, N. M. Schmidt, G. Yannic, and L. Bollache. 2012. Climate change and the ecology and evolution of Arctic vertebrates. Ann. N.Y. Acad. Sci. 1249 166–190.
- Gilg, O., B. Sittler, and I. Hanski. 2009. Climate change and cyclic predator-prey population dynamics in the high Arctic. Global Change Biology 15:2634-2652.
- Gilg, O., B. Sittler, B. Sabard, A. Hurstel, R. Sane, P. Delattre, and L. Hanski. 2006. Functional and numerical responses of four lemming predators in high arctic Greenland. Oikos **113**:193-216.
- Gilg, O. and N. G. Yoccoz. 2010. Explaining Bird Migration. Science 327:959-959.
- Gimenez, O., T. Anker-Nilssen, and V. Grosbois. 2012. Exploring causal pathways in demographic parameter variation: path analysis of mark-recapture data. Methods in Ecology and Evolution **3**:427-432.
- Gornall, J. L., I. S. Jonsdottir, S. J. Woodin, and R. Van der Wal. 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia 153:931-941.
- Gornall, J. L., S. J. Woodin, I. S. Jonsdottir, and R. Van der Wal. 2009. Herbivore impacts to the moss layer determine tundra ecosystem response to grazing and warming. Oecologia 161:747-758.
- Gornall, J. L., S. J. Woodin, I. S. Jonsdottir, and R. van der Wal. 2011. Balancing positive and negative plant interactions: how mosses structure vascular plant communities. Oecologia **166**:769-782.
- Gorodkov, K. B., E. V. Siroechkovskyi, and N. G. Ovsyanikov. 1987. Fauna of Wrangel Island Nature Reserve. In: B. A. Yurtsev, editor. Flora and Fauna of Nature Reserves of the USSR. VINITI, Moscow (in Russian).
- Gosz, J. R., R. B. Waide, and J. J. Magnuson. 2010. Twenty-eight years of the US-LTER Program: experience, results, and research questions. In: F. Müller, C. Baessler, H. Schubert, and S. Klotz, editors. Long-Term Ecological Research. Springer Netherlands Pages 59-74.

Grace, J., F. Berninger, and L. Nagy. 2002. Impacts of climate change on the tree line. Annals of Botany 90:537-544.

- Greenacre, M. J. and J. Blasius, editors. 2006. Multiple correspondence analysis and related methods. Chapman & Hall/CRC Press, London.
- Gregory, R. D. and J. H. Marchant. 1996. Population trends of jays, magpies, jackdaws and carrion crows in the United Kingdom. Bird Study **43**:28-37.
- Griffin, L. and E. R. Mackley. 2004. WWT Svalbard Barnacle Goose Project Report 2003-2004. The Wildfowl and Wetlands Trust, pp.
- Griffith, D. A. and P. R. Peres-Neto. 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. Ecology **87**:2603–2613.
- Gruyer, N., G. Gauthier, and D. Berteaux. 2008. Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada. Canadian Journal of Zoology-Revue Canadienne De Zoologie **86**:910-917.
- Grünewald, T. and M. Lehning. 2011. Altitudinal dependency of snow amounts in two small alpine catchments: can catchment-wide snow amounts be estimated via single snow or precipitation stations? Annals of Glaciology 52:153-158.
- Grøtan, V., B. E. Sæther, M. Lillegard, E. J. Solberg, and S. Engen. 2009. Geographical variation in the influence of density dependence and climate on the recruitment of Norwegian moose. Oecologia **161**:685-695.
- Guisan, A. and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters **8**:993-1009.
- Gundale, M. J., J. Sverker, B. R. Albrectsen, M. C. Nilsson, and D. A. Wardle. 2010. Variation in protein complexation capacity among and within six plant species across a boreal forest chronosequence. Plant Ecology **211**:253-

266.

Haftorn, S. 1971. Norges fugler. Universitetsforlaget, Oslo (in Norwegian).

- Hagemoen, R. I. M. and E. Reimers. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. Journal of Animal Ecology **71**:883-892.
- Hagen, S. B., R. A. Ims, N. G. Yoccoz, and O. Sorlibraten. 2008a. Fluctuating asymmetry as an indicator of elevation stress and distribution limits in mountain birch (*Betula pubescens*). Plant Ecology **195**:157-163.
- Hagen, S. B., J. U. Jepsen, R. A. Ims, and N. G. Yoccoz. 2007. Shifting altitudinal distribution of outbreak zones of winter moth *Operophtera brumata* in sub-arctic birch forest: a response to recent climate warming? Ecography 30:299-307.
- Hagen, S. B., J. U. Jepsen, N. G. Yoccoz, and R. A. Ims. 2008b. Anisotropic patterned population synchrony in climatic gradients indicates nonlinear climatic forcing. Proceedings of the Royal Society B-Biological Sciences 275:1509-1515.
- Hagen, Y. 1952. Rovfuglene og viltpleien. Gyldendal Norsk forlag, Oslo.
- Hakkarainen, H., R. Virtanen, J. O. Honkanen, and H. Roininen. 2007. Willow bud and shoot foraging by ptarmigan in relation to snow level in NW Finnish Lapland. Polar Biology **30**:619-624.
- Hambäck, P. A., D. Grellmann, and J. Hjältén. 2002. Winter herbivory by voles during a population peak: the importance of plant quality. Ecography **25**:74-80.
- Hambäck, P. A., M. Schneider, and T. Oksanen. 1998. Winter herbivory by voles during a population peak: the relative importance of local factors and landscape pattern. Journal of Animal Ecology **67**:544-553.
- Hamel, S., N. G. Yoccoz, and J.-M. Gaillard. 2012. Statistical evaluation of parameters estimating autocorrelation and individual heterogeneity in longitudinal studies. Methods in Ecology and Evolution **3**:731-742.
- Hamel, S., S. Killengreen, J. A. Henden, N. G. Yoccoz, and R. A. Ims. 2013. Disentangling the importance of interspecific competition, food availability, and habitat in species occupancy: recolonization of the endangered Fennoscandian arctic fox. Biological Conservation in press.
- Hannon, S. J. and K. Martin. 2006. Ecology of juvenile grouse during the transition to adulthood. Journal of Zoology **269**:422-433.
- Hansen, B. B., R. Aanes, I. Herfindal, J. Kohler, and B. E. Saether. 2011. Climate, icing, and wild arctic reindeer: past relationships and future prospects. Ecology **92**:1917-1923.
- Hansen, B. B., V. Grøtan, R. Aanes, B.-E. Sæther, A. Stien, E. Fuglei, R. A. Ims, N. G. Yoccoz, and Å. Ø. Pedersen. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. Science 339:313-315.
- Hansen, B. B., S. Henriksen, R. Aanes, and B. E. Saether. 2007. Ungulate impact on vegetation in a two-level trophic system. Polar Biology **30**:549-558.
- Hansen, B. B., I. Herfindal, R. Aanes, B. E. Sæther, and S. Henriksen. 2009. Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore. Oikos **118**:859-872.
- Hansen, B. H., V. Veiberg, and R. Aanes. 2012. Material from harvested Svalbard reindeer. Evaluation of the material, the data and their areas of application for research and management. Norwegian Polar Institute Brief Report Series 024, Tromsø, Norway, 30 pp
- Hanski, I. and H. Henttonen. 1996. Predation on competing rodent species: A simple explanation of complex patterns. Journal of Animal Ecology **65**:220-232.
- Hansson, L. and H. Henttonen. 1985. Gradients in density variations of small rodents the importance of latitude and snow cover. Oecologia **67**:394-402.
- Hansson, L. and H. Henttonen. 1988. Rodent dynamics as community processes. Trends in Ecology & Evolution **3**:195-200.
- Harding, R., P. Kuhry, T. R. Christensen, M. T. Sykes, R. Dankers, and S. van der Linden. 2002. Climate feedbacks at the tundra-taiga interface. Ambio, Special issue **12**:47-55.
- Hastings, A. 2004. Transients: the key to long-term ecological understanding? Trends in Ecology & Evolution **19**:39-45.
- Hausner, V. H., N. G. Yoccoz, and R. A. Ims. 2003. Selecting indicator traits for monitoring land use impacts: birds in northern coastal birch forests. Ecological Applications 13:999-1012.
- Hayward, M. W., J. O'Brien, and G. I. H. Kerley. 2007. Carrying capacity of large African predators: Predictions and tests. Biological Conservation **139**:219-229.
- Heliasz, M., T. Johansson, A. Lindroth, M. Molder, M. Mastepanov, T. Friborg, T. V. Callaghan, and T. R. Christensen. 2011. Quantification of C uptake in subarctic birch forest after setback by an extreme insect outbreak. Geophysical Research Letters 38:L01704.
- Helle, T. and I. Kojola. 2008. Demographics in an alpine reindeer herd: effects of density and winter weather. Ecography **31**:221-230.
- Henden, J.-A., A. Stien, B.-J. Bårdsen, N. G. Yoccoz, and R. A. Ims. 2013. Guild-wide response in carnivores to disrupted seasonal migration in a large herbivore. Submitted manuscript.
- Henden, J. A., B. J. Bardsen, N. G. Yoccoz, and R. A. Ims. 2008. Impacts of differential prey dynamics on the potential recovery of endangered arctic fox populations. Journal of Applied Ecology **45**:1086-1093.
- Henden, J. A., R. A. Ims, and N. G. Yoccoz. 2009a. Nonstationary spatio-temporal small rodent dynamics: evidence

from long-term Norwegian fox bounty data. Journal of Animal Ecology 78:636-645.

- Henden, J. A., R. A. Ims, N. G. Yoccoz, P. Hellström, and A. Angerbjörn. 2010. Strength of asymmetric competition between predators in food webs ruled by fluctuating prey: the case of foxes in tundra. Oikos **119**:27-34.
- Henden, J. A., R. A. Ims, N. G. Yoccoz, and S. T. Killengreen. 2011a. Declining willow ptarmigan populations: The role of habitat structure and community dynamics. Basic and Applied Ecology **12**:413-422.
- Henden, J. A., R. A. Ims, N. G. Yoccoz, R. Sorensen, and S. T. Killengreen. 2011b. Population dynamics of tundra voles in relation to configuration of willow thickets in southern arctic tundra. Polar Biology **34**:533-540.
- Henden, J. A., N. G. Yoccoz, R. A. Ims, B. J. Bårdsen, and A. Angerbjörn. 2009b. Phase-dependent effect of conservation efforts in cyclically fluctuating populations of arctic fox (*Vulpes lagopus*). Biological Conservation 142:2586-2592.
- Henry, G. H. R. and U. Molau. 1997. Tundra plants and climate change: the International Tundra Experiment (ITEX). Global Change Biology **3**:1-9.
- Henttonen, H., E. Fuglei, C. N. Gower, V. Haukisalmi, R. A. Ims, J. Niemimaa, and N. G. Yoccoz. 2001. Echinococcus multilocularis on Svalbard: introduction of an intermediate host has enabled the local life-cycle. Parasitology 123:547-552.
- Henttonen, H., T. Oksanen, A. Jortikka, and V. Haukisalmi. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? Oikos **50**:353-365.
- Herfindal, I., H. Brøseth, M. Kjørstad, J. D. C. Linnell, J. Odden, J. Persson, A. Stien, and T. Tveraa. 2011. Modellering av risikobasert erstatning for tap av tamrein til rovvilt - En vurdering av ulike datasetts egnethet. NINA Minirapport **329**:24 pp.
- Herfindal, I., J. D. C. Linnell, B. Elmhagen, R. Andersen, N. E. Eide, K. Frafjord, H. Henttonen, A. Kaikusalo, M. Mela, M. Tannerfeldt, L. Dalén, O. Strand, A. Landa, and A. Angerbjörn. 2010. Population persistence in a landscape context: the case of endangered arctic fox populations in Fennoscandia. Ecography 33:932-941.
- Hersteinsson, P. 1989. Population genetics and ecology of different colour morphs of arctic foxes (*Alopex lagopus*) in Iceland. Finnish Game Research **46**:64-78.
- Hersteinsson, P. and D. W. Macdonald. 1992. Interspecific competition and the geographical distribution of red and arctic foxes, *Vulpes vulpes and Alopex lagopus*. Oikos **64**:505-515.
- Hirsti, R., editor. 1979. Finnmark. Gyldendal Norsk Forlag, Oslo.
- Hiruki, L. M. and I. Stirling. 1989. Population dynamics of the arctic fox (*Alopex lagopus*) on Banks Island, Northwest Territories. Canadian Field-Naturalist **103**:380-387.
- Hitch, A. T. and P. L. Leberg. 2007. Breeding distributions of North American bird species moving north as a result of climate change. Conservation Biology **21**:534-539.
- Hobbie, J. E., S. R. Carpenter, N. B. Grimm, J. R. Gosz, and T. R. Seastedt. 2003. The US Long Term Ecological Research Program. Bioscience **53**:21-32.
- Hobbs, N. T. and K. Ogle. 2011. Introducing data-model assimilation to students of ecology. Ecological Applications **21**:1537-1545.
- Hodges, J. S. 2010. Are exercises like this a good use of anybody's time? Ecology 91:3496-3500.
- Hofgaard, A., J. O. Løkken, L. Dalen, and H. Hytteborn. 2010. Comparing warming and grazing effects on birch growth in an alpine environment a 10-year experiment. Plant Ecology & Diversity **3**:19-27.
- Hofgaard, A., H. Tømmervik, G. Rees, and F. Hanssen. 2013. Latitudinal forest advance in northernmost Norway since the early 20th century. Journal of Biogeography **40**: 938-949.
- Holland, K. A., W. C. Leininger, and M. J. Trlica. 2005. Grazing history affects willow communities in a montane riparian ecosystem. Rangeland Ecology & Management **58**:148-154.
- Holt, R. D. and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist **149**:745-764. Holtmeier, F.-K. 2003. Mountain Timberlines: Ecology, Patchiness, and Dynamics. Springer.
- Holtmeier, F. K. and G. Broll. 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. Global Ecology and Biogeography 14:395-410.
- Hudson, J. M. G. and G. H. R. Henry. 2009. Increased plant biomass in a High Arctic heath community from 1981 to 2008. Ecology **90**:2657-2663.
- Hudson, P. J. and M. R. W. Rands. 1988. Ecology and management of gamebirds. BSP Professional Books, Oxford, UK.
- Hübner, C. E., I. M. Tombre, and K. E. Erikstad. 2002. Adaptive aspects of intraclutch egg size variation in the higharctic barnacle goose (*Branta leucopsis*). Canadian Journal of Zoology **80**:1180-1188.
- Hübner, C. E., Tombre, I.M., Griffin, L.R., Loonen, M.J.J.E., Shimmings, P., Jónsdottir, I. S. 2010. The connectivity of spring stopover sites for geese heading to arctic breeding grounds. Ardea **98**:145-154.
- Højsgaard, S., D. Edwards, and S. Lauritzen. 2012. Graphical models with R. Springer US.
- Hörnfeldt, B. 2004. Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses. Oikos **107**:376-392.
- Hörnfeldt, B., P. Christensen, P. Sandström, and F. Ecke. 2006. Long-term decline and local extinction of *Clethrionomys rufocanus* in boreal Sweden. Landscape Ecology **21**:1135-1150.
- Hörnfeldt, B., T. Hipkiss, and U. Eklund. 2005. Fading out of vole and predator cycles? Proceedings of the Royal Society B-Biological Sciences **272**:2045-2049.

- Hörnfeldt, B., O. Löfgren, and B. G. Carlsson. 1986. Cycles in voles and small game in relation to variations in plantproduction indexes in northern Sweden. Oecologia **68**:496-502.
- Ims, R., S. Killengreen, J. A. Henden, and N. Yoccoz. 2007a. Prosjekt "Fjellrev i Finnmark" Rapport for perioden 2004-2007. University of Tromsø, Tromsø, 39 p. (in Norwegian)
- Ims, R. A. and H. P. Andreassen. 2000. Spatial synchronization of vole population dynamics by predatory birds. Nature **408**:194-196.
- Ims, R. A. and E. Fuglei. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. Bioscience **55**:311-322.
- Ims, R. A. and J.-A. Henden. 2012. Collapse of an arctic bird community resulting from ungulate-induced loss of erect shrubs. Biological Conservation **149:**2-5.
- Ims, R. A., J. A. Henden, and S. T. Killengreen. 2008. Collapsing population cycles. Trends in Ecology & Evolution 23:79-86.
- Ims, R. A., B. M. Jenssen, M. Ohlson, and Å. Ø. Pedersen. 2010. Evaluering av 'Program for terrestrisk naturovervåking' (TOV 2000-2009). DN Utredning 9-2010, Norwegian Directorate for Nature Management, 32 pp.
- Ims, R. A. and H. Steen. 1990. Geographical synchrony in microtine population cycles: a theoretical evaluation of the role of nomadic avian predators. Oikos 57:381-387.
- Ims, R. A., N. G. Yoccoz, K. A. Brathen, P. Fauchald, T. Tveraa, and V. Hausner. 2007b. Can reindeer overabundance cause a trophic cascade? Ecosystems **10**:607-622.
- Ims, R. A., N. G. Yoccoz, and S. B. Hagen. 2004. Do sub-Arctic winter moth populations in coastal birch forest exhibit spatially synchronous dynamics? Journal of Animal Ecology **73**:1129-1136.
- Ims, R. A., N. G. Yoccoz, and S. T. Killengreen. 2011. Determinants of lemming outbreaks. Proceedings of the National Academy of Sciences of the United States of America 108:1970-1974.
- Ims, R. A. and D. Ehrich. 2013. Terrestrial Arctic Ecosystems. Arctic Biodiversity Assessment. Arctic Council (in press).
- IPCC, editor. 2007. Climate Change 2007. Impacts, Adaptation and Vulnerability, Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climatic Change. Cambridge University Press, Cambridge, UK, 976 pp.
- Isaksen, K., H. Farbrot, L. H. Blikta, B. Johansen, J. J. Sollid, and T. Eiken. 2008. Five-year ground temperature measurement in Finnmark, Northern Norway. In: Proceedings from the Ninth International Conference on Permafrost, Fairbanks, Alaska
- Iversen, M., K. A. Brathen, N. G. Yoccoz, and R. A. Ims. 2009. Predictors of plant phenology in a diverse high-latitude alpine landscape: growth forms and topography. Journal of Vegetation Science **20**:903-915.
- Jacobsen, K.-O. 2005. Snøugle (*Bubo scandiacus*) i Norge Hekkeforekomster i perioden 1968-2005. NINA Rapport 84. Norwegian Institute for Nature Research (in Norwegian)
- Jano, A. P., R. L. Jefferies, and R. F. Rockwell. 1998. The detection of vegetational change by multitemporal analysis of LANDSAT data: the effects of goose foraging. Journal of Ecology **86**:93-99.
- Jefferies, R. L., D. R. Klein, and G. R. Shaver. 1994. Vertebrate herbivores and northern plant communities reciprocal influences and responses. Oikos **71**:193-206.
- Jensen, L. M. and M. Rasch. 2011a. Nuuk Ecological Research Operations, 4th Annual Report, 2010. Aarhus University, DCE - Danish Centre for Environment and Energy, 84 pp.
- Jensen, L. M. and M. Rasch. 2011b. Zackenberg Ecological Research Operations, 16th Annual Report, 2010. Aarhus University, DCE Danish Centre for Environment and Energy, 114 pp.
- Jensen, R. A., J. Madsen, M. O'Connell, M. S. Wisz, H. Tømmervik, and F. Mehlum. 2008. Prediction of the nesting distribution of pink-footed geese (*Anser brachyrhynchus*) in Svalbard under a warmer climate scenario. Global Change Biology 14:1-10.
- Jepsen, J. U., J. M. Baveco, C. J. Topping, J. Verboom, and C. C. Vos. 2005. Evaluating the effect of corridors and landscape heterogeneity on dispersal probability: a comparison of three spatially explicit modelling approaches. Ecological Modelling **181**:445-459.
- Jepsen, J. U., M. Biuw, R. A. Ims, L. Kapari, T. Schott, O. P. L. Vindstad, and S. B. Hagen. 2013. Ecosystem impacts of a range expanding forest defoliator at the forest-tundra ecotone. Ecosystems **Online Early, DOI: 10.1007**/ s10021-012-9629-9.
- Jepsen, J. U., N. E. Eide, P. Prestrud, and L. B. Jacobsen. 2002. The importance of prey distribution in habitat use by arctic foxes (*Alopex lagopus*). Canadian Journal of Zoology-Revue Canadienne De Zoologie **80**:418-429.
- Jepsen, J. U., S. B. Hagen, K. A. Hogda, R. A. Ims, S. R. Karlsen, H. Tommervik, and N. G. Yoccoz. 2009a. Monitoring the spatio-temporal dynamics of geometrid moth outbreaks in birch forest using MODIS-NDVI data. Remote Sensing of Environment **113**:1939-1947.
- Jepsen, J. U., S. B. Hagen, R. A. Ims, and N. G. Yoccoz. 2008. Climate change and outbreaks of the geometrids *Oper-ophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. Journal of Animal Ecology 77:257-264.
- Jepsen, J. U., S. B. Hagen, S. R. Karlsen, and R. A. Ims. 2009b. Phase-dependent outbreak dynamics of geometrid moth linked to host plant phenology. Proceedings of the Royal Society B-Biological Sciences **276**:4119-4128.

- Jepsen, J. U., L. Kapari, S. B. Hagen, T. Schott, O. P. L. Vindstad, A. C. Nilssen, and R. A. Ims. 2011. Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. Global Change Biology **17**:2071-2083.
- Jepsen, J. U. and C. J. Topping. 2004. Modelling roe deer (*Capreolus capreolus*) in a gradient of forest fragmentation: behavioural plasticity and choice of cover. Canadian Journal of Zoology **82**:1528-1541.
- Jia, G. S., H. E. Epstein, and D. A. Walker. 2006. Spatial heterogeneity of tundra vegetation response to recent temperature changes. Global Change Biology 12:42-55.
- Johansen, B. E. 2009. Vegetasjonskart for Norge basert på Landsat TM/ETM+ data. Norut Rapport **4**:87 (in Norwegian).
- Johansen, B. E., S. R. Karlsen, and H. Tommervik. 2012. Vegetation mapping of Svalbard utilising Landsat TM/ETM plus data. Polar Record **48**:47-63.
- Johansen, B. E., H. Tømmervik, and S. R. Karlsen. 2009. Vegetasjonskart over Svalbard basert på satellittdata. Dokumentasjon av metoder og vegetasjonsbeskrivelse. NINA Rapport **456**, 54p. (in Norwegian).
- Johnson, D. M., U. Büntgen, D. C. Frank, K. Kausrud, K. J. Haynes, A. M. Liebhold, J. Esper, and N. C. Stenseth. 2010. Climatic warming disrupts recurrent Alpine insect outbreaks. Proceedings of the National Academy of Sciences 107:20576-20581.
- Johnson, N., A. Dicker, T. Mørk, D. A. Marston, A. R. Fooks, M. Tryland, E. Fuglei, and T. Müller. 2007. Phylogenetic comparison of rabies viruses from disease outbreaks on the Svalbard Islands. Vector-Borne and Zoonotic Diseases 7:457-460.
- Jombart, T., S. Dray, and A. B. Dufour. 2009. Finding essential scales of spatial variation in ecological data: a multivariate approach. Ecography **32**:161-168.
- Jonasson, S. 1988. Evaluation of the point intercept methods for the estimation of plant biomass. Oikos 52:101-106.
- Jonasson, S., T. V. Callaghan, G. R. Shaver, and L. A. Nielsen, editors. 2000. Arctic terrestrial ecosystems and ecosystem function. Harwood Academic Publishers, Newark, New Jersey.
- Jørgensen, E. and A. Schytte Blix. 1985. Effects of climate and nutrition on growth and survival of willow ptarmigan chicks. Ornis Scandinavica **16**:99-107.
- Kabas, T., A. Leuprecht, C. Bichler, and G. Kirchengast. 2011. WegenerNet climate station network region Feldbach, Austria: network structure, processing system, and example results. Advances in Science and Research 6:49-54.
- Kalliola, R. 1939. Pflanzensoziologische untersuchungen in der alpinen Stufe Finnisch-Lapplands. Annales botanici Societatis zoologicae botanicae Fennicae Vanamo:IX, 321pp.
- Kaplan, J. O., N. H. Bigelow, I. C. Prentice, S. P. Harrison, P. J. Bartlein, T. R. Christensen, W. Cramer, N. V. Matveyeva, A. D. McGuire, D. F. Murray, V. Y. Razzhivin, B. Smith, D. A. Walker, P. M. Anderson, A. A. Andreev, L. B. Brubaker, M. E. Edwards, and A. V. Lozhkin. 2003. Climate change and Arctic ecosystems: 2. Modeling, paleodata-model comparisons, and future projections. Journal of Geophysical Research-Atmospheres 108:No. 8171.
- Kaplan, J. O. and M. New. 2006. Arctic climate change with a 2 degrees C global warming: Timing, climate patterns and vegetation change. Climatic Change **79**:213-241.
- Karlsen, S. R., A. Elvebakk, and B. Johansen. 2005. A vegetation-based method to map climatic variation in the arcticboreal transition area of Finnmark, north-easternmost Norway. Journal of Biogeography **32**:1161-1186.
- Karlsen, S. R., J. U. Jepsen, A. Odland, R. A. Ims, and A. Elvebakk. 2013. Outbreaks by canopy-feeding geometrid moth cause state-dependent shifts in understory plant communities. Oecologia Online Early, DOI 10.1007/ s00442-013-2648-1.
- Kausrud, K. L., A. Mysterud, H. Steen, J. O. Vik, E. Ostbye, B. Cazelles, E. Framstad, A. M. Eikeset, I. Mysterud, T. Solhoy, and N. C. Stenseth. 2008. Linking climate change to lemming cycles. Nature **456**:93-U93.
- Kenney, J. L., H. P. Militana, and M. H. Donohue. 2003. Helping Teachers to Use Their School's Backyard as an Outdoor Classroom: A Report on the Watershed Learning Center Program. The Journal of Environmental Education 35:18-26.
- Kery, M., J. Madsen, and J. D. Lebreton. 2006. Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. Journal of Animal Ecology **75**:1172-1181.
- Killengreen, S. T., R. A. Ims, N. G. Yoccoz, K. A. Brathen, J. A. Henden, and T. Schott. 2007. Structural characteristics of a low arctic tundra ecosystem and the retreat of the arctic fox. Biological Conservation **135**:459-472.
- Killengreen, S. T., N. Lecomte, D. Ehrich, T. Schott, N. G. Yoccoz, and R. A. Ims. 2011. The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra. Journal of Animal Ecology **80**:1049-1060.
- Killengreen, S. T., E. Strømseng, N. G. Yoccoz, and R. A. Ims. 2012. How ecological neighbourhoods influence the structure of the scavanger guild in low arctic tundra. Diversity and Distributions **18**:563-574.
- Killengreen, S. T., R. A. Ims, J. A. Henden, N. G. Yoccoz, and D. Ehrich. 2013. Prosjekt "Fjellrev i Finnmark: Rapport for perioden 2008-2012. University of Tromsø, Tromsø, 50 pp.
- Kitti, H., B. C. Forbes, and J. Oksanen. 2009. Long- and short-term effects of reindeer grazing on tundra wetland vegetation. Polar Biology **32**:253-261.
- Kjellen, N. and G. Roos. 2000. Population trends in Swedish raptors demonstrated by migration counts at Falsterbo,

Sweden 1942-97. Bird Study 47:195-211.

- Klausen, K., Å. Pedersen, N. Yoccoz, and R. Ims. 2010. Prevalence of nest predators in a sub-arctic ecosystem. European Journal of Wildlife Research **56**:221-232.
- Knapp, A. K. and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science **291**:481-484.
- Kohler, J. and R. Aanes. 2004. Effect of winter snow and ground-icing on a Svalbard reindeer population: Results of a simple snowpack model. Arctic Antarctic and Alpine Research **36**:333-341.
- Korslund, L. and H. Steen. 2006. Small rodent winter survival: snow conditions limit access to food resources. Journal of Animal Ecology **75**:156-166.
- Kouki, J., P. Niemela, and M. Viitasaari. 1994. Reversed latitudinal gradient in species richness of sawflies (Hymenoptera, Symphyta). Annales Zoologici Fennici **31**:83-88.
- Kraus, T. E. C., R. A. Dahlgren, and R. J. Zasoski. 2003. Tannins in nutrient dynamics of forest ecosystems a review. Plant and Soil **256**:41-66.
- Krebs, C. J. 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. Proceedings of the Royal Society B-Biological Sciences **278**:481-489.
- Krebs, C. J., K. Danell, A. Angerbjorn, J. Agrell, D. Berteaux, K. A. Brathen, O. Danell, S. Erlinge, V. Fedorov, K. Fredga, J. Hjalten, G. Hogstedt, I. S. Jonsdottir, A. J. Kenney, N. Kjellen, T. Nordin, H. Roininen, M. Svensson, M. Tannerfeldt, and C. Wiklund. 2003. Terrestrial trophic dynamics in the Canadian Arctic. Canadian Journal of Zoology-Revue Canadienne De Zoologie 81:827-843.
- Krebs, C. J., A. J. Kenney, S. Gilbert, K. Danell, A. Angerbjorn, S. Erlinge, R. G. Bromley, C. Shank, and S. Carriere. 2002. Synchrony in lemming and vole populations in the Canadian Arctic. Canadian Journal of Zoology-Revue Canadienne De Zoologie 80:1323-1333.
- Kruse, J., B. Poppel, L. Abryutina, G. Duhaime, S. Martin, M. Poppel, M. Kruse, E. Ward, P. Cochran, and V. Hanna. 2009. Survey of Living Conditions in the Arctic (SLiCA). In: V. Moller, D. Huscka, and A. C. Michalos, editors. Barometers of quality of life around the globe: How are we doing. Springer, Dordrecht. Pages 107-134.
- Kuijper, D. P. J., J. P. Bakker, E. J. Cooper, M. J. J. E. Loonen, and I. S. Jonsdóttir. 2006. Intensive grazing by Barnacle geese depletes arctic seedbank. Canadian Journal of Botany 84:995-1004.
- Kumpula, J., A. Colpaert, and M. Nieminen. 2000. Condition, potential recovery rate, and productivity of lichen (Cladonia spp.) ranges in the Finnish reindeer management area. Arctic **53**:152-160.
- Laaksonen, S., J. Pusenius, J. Kumpula, A. Venalainen, R. Kortet, A. Oksanen, and E. Hoberg. 2010. Climate change promotes the emergence of serious disease outbreaks of filarioid nematodes. Ecohealth 7:7-13.
- Lamb, E. G., S. Han, B. D. Lanoil, G. H. R. Henry, M. E. Brummell, S. Banerjee, and S. D. Siciliano. 2011. A high arctic soil ecosystem resists long-term environmental manipulations. Global Change Biology **17**:3187-3194.
- Lantz, T. C., S. E. Gergel, and S. V. Kokelj. 2010. Spatial heterogeneity in the shrub tundra ecotone in the Mackenzie Delta region, Northwest Territories: Implications for arctic environmental change. Ecosystems **13**:194-204.
- Lantz, T. C., S. V. Kokelj, S. E. Gergel, and G. H. R. Henryz. 2009. Relative impacts of disturbance and temperature: persistent changes in microenvironment and vegetation in retrogressive thaw slumps. Global Change Biology 15:1664-1675.
- Lantz, T. C., P. Marsh, and S. V. Kokelj. 2013. Recent Shrub Proliferation in the Mackenzie Delta Uplands and Microclimatic Implications. Ecosystems 16:47-59.
- Larsen, J. N., P. Schweitzer, and G. Fondahl, editors. 2010. Arctic Social Indicators: a Follow-up to the Arctic Human Development Report. Nordic Council of Ministers, Copenhagen, 160 p.
- Lecomte, N., O. Ahlstrom, D. Ehrich, E. Fuglei, R. A. Ims, and N. G. Yoccoz. 2011. Intrapopulation variability shaping isotope discrimination and turnover: Experimental evidence in arctic foxes. Plos One 6:e21357.
- Lee, S.-Y. 2007. Structural equation modeling. Wiley.
- Legagneux, P., P. L. F. Fast, G. Gauthier, and J. Bety. 2012a. Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. Proceedings of the Royal Society B-Biological Sciences **279**:876-883.
- Legagneux, P., G. Gauthier, D. Berteaux, J. Bêty, M.-C. Cadieux, F. Bilodeau, E. Bolduc, L. McKinnon, A. Tarroux, J.-F. Therrien, L. Morissette, and C. J. Krebs. 2012b. Disentangling trophic relationships in a high arctic tundra ecosystem through food web modeling. Ecology 93:1707-1716.
- Legg, C. J. and L. Nagy. 2006. Why most conservation monitoring is, but need not be, a waste of time. Journal of Environmental Management **78**:194-199.
- Lehning, M., P. Bartelt, B. Brown, and C. Fierz. 2002a. A physical SNOWPACK model for the Swiss avalanche warning Part III: Meteorological forcing, thin layer formation and evaluation. Cold Regions Science and Technology **35**:169-184.
- Lehning, M., P. Bartelt, B. Brown, C. Fierz, and P. Satyawali. 2002b. A physical SNOWPACK model for the Swiss avalanche warning Part II: Snow microstructure. Cold Regions Science and Technology **35**:147-167.
- Lehtonen, J. 1987. Recovery and development of birch forests damaged by *Epirrita autumnata* in Utsjoki area, North Finland. Reports from the Kevo Subarctic Research Station **20**:35-39.
- Lewan, L. and T. Soderqvist. 2002. Knowledge and recognition of ecosystem services among the general public in a drainage basin in Scania, Southern Sweden. Ecological Economics **42**:459-467.

- Liebezeit, J. R. and S. Zack. 2008. Point counts underestimate the importance of arctic foxes as avian nest predators: Evidence from remote video cameras in Arctic Alaskan oil fields. Arctic **61**:153-161.
- Likens, G. E. 2004. Some perspectives on long-term biogeochemical research from the hubbard brook ecosystem study. Ecology **85**:2355-2362.
- Lindemann-Matthies, P. 2006. Investigating nature on the way to school: Responses to an educational programme by teachers and their pupils. International Journal of Science Education **28**:895-918.
- Lindén, H. and H. C. Pedersen. 1997. Willow grouse, *Lagopus lagopus*. In: W. J. Hagemeijer and M. J. Blair, editors. The EBCC Atlas of European Breeding Birds: Their distribution and abundance. T & AD Poyser, London. Pages 196-197.
- Lindenmayer, D. B. and G. E. Likens. 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. Trends in Ecology & Evolution **24**:482-486.
- Lindenmayer, D. B. and G. E. Likens. 2010. Effective ecological monitoring. CSIRO Publishing, Collingwood, Vic., Australia.
- Lindenmayer, D. B., G. E. Likens, A. Haywood, and L. Miezis. 2011. Adaptive monitoring in the real world: proof of concept. Trends in Ecology & Evolution **26**:641-646.
- Lindenmayer, D. B., G. E. Likens, C. J. Krebs, and R. J. Hobbs. 2010. Improved probability of detection of ecological "surprises". Proceedings of the National Academy of Sciences **107**:21957-21962.
- Liston, G. E. and K. Elder. 2006. A distributed snow-evolution modeling system (SnowModel). Journal of Hydrometeorology 7:1259-1276.
- Liu, J. P., J. A. Curry, H. J. Wang, M. R. Song, and R. M. Horton. 2012. Impact of declining Arctic sea ice on winter snowfall. Proceedings of the National Academy of Sciences of the United States of America **109**:4074-4079.
- Loison, A., O. Strand, and J. D. C. Linnell. 2001. Effect of temporal variation in reproduction on models of population viability: a case study for remnant arctic fox (*Alopex lagopus*) populations in Scandinavia. Biological Conservation 97:347-359.
- Loonen, M. J. J. E., I. M. Tombre, and F. Mehlum. 1998. The development of an arctic barnacle goose colony: Interaction between density and predation. . Norsk Polarinstitutt Skrifter **200**:67-79.
- Lucht, W., I. C. Prentice, R. B. Myneni, S. Sitch, P. Friedlingstein, W. Cramer, P. Bousquet, W. Buermann, and B. Smith. 2002. Climatic control of the high-latitude vegetation greening trend and Pinatubo effect. Science 296:1687-1689.
- Ludwig, G. X., R. V. Alatalo, P. Helle, H. Linden, J. Lindstrom, and H. Siitari. 2006. Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. Proceedings of the Royal Society B-Biological Sciences 273:2009-2016.
- Ludwig, G. X., R. V. Alatalo, P. Helle, and H. Siitari. 2010. Individual and environmental determinants of early brood survival in black grouse *Tetrao tetrix*. Wildlife Biology **16**:367-378.
- Luo, Y. Q., J. Melillo, S. L. Niu, C. Beier, J. S. Clark, A. T. Classen, E. Davidson, J. S. Dukes, R. D. Evans, C. B. Field, C. I. Czimczik, M. Keller, B. A. Kimball, L. M. Kueppers, R. J. Norby, S. L. Pelini, E. Pendall, E. Rastetter, J. Six, M. Smith, M. G. Tjoelker, and M. S. Torn. 2011. Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. Global Change Biology 17:843-854.
- Lydersen, C. and I. Gjertz. 1986. Studies of the ringed seal (*Phoca hispida* Schreber 1775) in its breeding habitat in Kongsfjorden, Svalbard. Polar Research **4**:57-63.
- Lyftingsmo, E. 1965. Oversyn over fjellbeite i Finnmark. Det kgl. selskap for Norges vel, Oslo (in Norwegian).
- Løvenskiold, H. L. 1964. Avifauna Svalbardiensis. Norsk Polarinstitutt, Skrifter. 129:155-169.
- Macdonald, R. W., T. Harner, and J. Fyfe. 2005. Recent climate change in the Arctic and its impact on contaminant pathways and interpretation of temporal trend data. Science of the Total Environment **342**:5-86.
- Mace, G. M., K. Norris, and A. H. Fitter. 2012. Biodiversity and ecosystem services: a multilayered relationship. Trends in Ecology & Evolution 27:19-26.
- Macias-Fauria, M., B. C. Forbes, P. Zetterberg, and T. Kumpula. 2012. Eurasian Arctic greening reveals teleconnections and the potentail for structually novel ecosystems. Nature Climate Change **DOI: 10.1038**/ **NCLIMATE1558**.
- Macpherson, A. H. 1964. A northward range expension of the red fox in the eastern Canadian Arctic. Mammology **45**:138-140.
- Madsen, J. 2001. Choice of spring migration strategies by pink-footed geese *Anser brachyrhynchus* and consequences for spring fattening and fecundity. Ardea **89**:43-55.
- Madsen, J., T. Bregnballe, J. Frikke, and J. B. Kristensen. 1998. Correlates of predator abundance with snow and ice conditions and their role in determining timing of nesting and breeding success in Svalbard light-bellied brent geese *Branta bernicla hrota*. Norsk Polarinstitutt Skrifter **200**:221-234.
- Madsen, J., T. Bregnballe, and F. Mehlum. 1989. Study of the breeding ecology and behaviour of the Svalbard population of Light bellied Brent Goose *Branta bernicla hrota*. Polar Research 7:1-21.
- Madsen, J., G. Cracknell, and A. D. Fox, editors. 1999. Goose population of the Western Palearctic. A review of status and distribution. Wetlands International and The National Environmental Research Institute, Denmark, Wageningen, The Netherlands.

Madsen, J., M. Frederiksen, and B. Ganter. 2002. Trends in annual and seasonal survival of pink-footed geese Anser

brachyrhunchus. Ibis 144:218-226.

- Madsen, J., C. Jaspers, M. P. Tamstorf, C. E. Mortensen, and F. R. Riget. 2011. Long-term effects of grazing and global warming on the composition and carrying capacity of graminoid marshes for moulting geese in East Green-land. Ambio **40**:638-649.
- Madsen, J. and C. E. Mortensen. 1987. Habitat exploitation and interspecific competition of moulting geese in East Greenland. Ibis **129**:25-44.
- Madsen, J., M. P. Tamstorf, M. Klaassen, N. E. Eide, C. M. Glahder, F. F. Riget, H. Nyegaard, and F. Cottaar. 2007. Effects of snow cover on the timing and success of reproduction in high-arctic pink-footed geese Anser brachyrhynchus. Polar Biology 30:1363-1372.
- Madsen, J., I. M. Tombre, and N. E. Eide. 2009. Effects of disturbance on geese in Svalbard: implications for management of increasing tourism activities. Polar Research **28**:376-389.
- Madsen, J. and J. H. Williams. 2012. International Species Management Plan for the Svalbard population of the Pinkfooted Goose *Anser brachyrhynchus*. AEWA Technical Series No. 48, Bonn, Germany, 53 p.
- Malone, K. and P. J. Tranter. 2003. School grounds as sites for learning: Making the most of environmental opportunities. Environmental Education Research **9**:283-303.
- Manning, R. E. 1999. Studies in outdoor recreation: search and reasearch for satisfaction. Oregon State University Press, Corvallis, Oregon.
- Manseau, M., J. Huot, and M. Crete. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: Community and landscape level. Journal of Ecology **84**:503-513.
- Marcström, V., R. E. Kenward, and E. Engren. 1988. The impact of predation on boreal tetraonids during vole cycles: An experimental study. Journal of Animal Ecology **57**:859-872.
- Maron, J. L., J. A. Estes, D. A. Croll, E. M. Danner, S. C. Elmendorf, and S. L. Buckelew. 2006. An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. Ecological Monographs **76**:3-24.
- Marti, C. and A. Bossert. 1985. Beobachtungen zur Sommeraktivität und Brutbiologie des Alpenschneehuhns (*Lagopus mutus*) im Aletschgebiet (Wallis). Ornithol Beob **82**:153-168 (in German).
- Martin, T. E. and J. L. Maron. 2012. Climate impacts on bird and plant communities from altered animal-plant interactions. Nature Climate Change 2:195-200.
- Mattisson, J., J. Persson, H. Andren, and P. Segerstrom. 2011. Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). Canadian Journal of Zoology-Revue Canadienne De Zoologie **89**:79-89.
- McFadden, J. E., T. L. Hiller, and A. J. Tyre. 2011. Evaluating the efficacy of adaptive management approaches: Is there a formula for success? Journal of Environmental Management **92**:1354-1359.
- McGuire, A. D., L. G. Anderson, T. R. Christensen, S. Dallimore, L. D. Guo, D. J. Hayes, M. Heimann, T. D. Lorenson, R. W. Macdonald, and N. Roulet. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. Ecological Monographs 79:523-555.
- McKinnon, L., P. A. Smith, E. Nol, J. L. Martin, F. I. Doyle, K. F. Abraham, H. G. Gilchrist, R. I. G. Morrison, and J. Bêty. 2010. Lower predation risk for migratory birds at high latitudes. Science **327**:326-327.
- McManus, K. M., D. C. Morton, J. G. Masek, D. D. Wang, J. O. Sexton, J. R. Nagol, P. Ropars, and S. Boudreau. 2012. Satellite-based evidence for shrub and graminoid tundra expansion in northern Quebec from 1986 to 2010. Global Change Biology 18:2313-2323.
- MEA. 2005. Ecosystems and human well-being: Current state and trends. Island Press, Washington.
- Mehlum, F. and G. W. Gabrielsen. 1993. The diet of high-arctic seabirds in coastal and ice-covered, pelagic areas near the Svalbard archipelago. Polar Research **12**:1-20.
- Meijer, T., K. Noren, and A. Angerbjorn. 2011. The impact of maternal experience on post-weaning survival in an endangered arctic fox population. European Journal of Wildlife Research **57**:549-553.
- Meijer, T., B. Elmhagen, N. E. Eide, and A. Angerbjörn. 2013. Life history traits in a cyclic ecosystem: a field experiment on the arctic fox. Oecologia **in press**.
- Meltofte, H., T. R. Christensen, B. Elberling, M. C. Forchhammer, and M. Rasch. 2008. High-arctic ecosystem dynamics in a changing climate - Ten years of monitoring and research at Zackenberg Research Station, Northeast Greenland - Introduction. Advances in Ecological Research, Vol 40. Elsevier Academic Press Inc, San Diego. Pages 1-12.
- Menyushina, I., D. Ehrich, J.-A. Henden, R. Ims, and N. Ovsyanikov. 2012. The nature of lemming cycles on Wrangel: an island without small mustelids. Oecologia **170**:363-371.
- Michaels, A. and A. G. Power. 2011. National Science Foundation's Long-Term Ecological Research Program. A report of the 30 year review committee.
- Miller, G. H., J. Brigham-Grette, R. B. Alley, L. Anderson, H. A. Bauch, M. S. V. Douglas, M. E. Edwards, S. A. Elias, B. P. Finney, J. J. Fitzpatrick, S. V. Funder, T. D. Herbert, L. D. Hinzman, D. S. Kaufman, G. M. MacDonald, L. Polyak, A. Robock, M. C. Serreze, J. P. Smol, R. Spielhagen, J. W. C. White, A. P. Wolfe, and E. W. Wolff. 2010. Temperature and precipitation history of the Arctic. Quaternary Science Reviews 29:1679-1715.
- Mitchell, C., K. Colhoun, A. D. Fox, L. Griffin, C. Hall, R. Hearns, C. Holt, and A. Walsh. 2010. Trends in goose numbers wintering in Britain & Ireland, 1995 to 2008. . Ornis Svecica **20**:128-143.
- Mjaaseth, R. R., S. B. Hagen, N. G. Yoccoz, and R. A. Ims. 2005. Phenology and abundance in relation to climatic vari-

ation in a sub-arctic insect herbivore-mountain birch system. Oecologia 145:53-65.

- Moen, J., D. M. Cairns, and C. W. Lafon. 2008. Factors structuring the treeline ecotone in Fennoscandia. Plant Ecology & Diversity 1:77-87.
- Moen, J., P. A. Lundberg, and L. Oksanen. 1993. Lemming grazing on snowbed vegetation during a population peak, Northern Norway. Arctic and Alpine Research 25:130-135.
- Molau, U., U. Nordenhall, and B. Eriksen. 2005. Onset of flowering and climate variability in an alpine landscape: A 10-year study from Swedish Lapland. American Journal of Botany **92**:422-431.
- Montoya, J. M., S. L. Pimm, and R. V. Solé. 2006. Ecological networks and their fragility. Nature 442:259-264.
- Montoya, J. M., M. A. Rodríguez, and B. A. Hawkins. 2003. Food web complexity and higher-level ecosystem services. Ecology Letters **6**:587-593.
- Moss, R. 1973. The digestion and intake of winter foods by wild ptarmigans in Alaska. Condor 75:293-300.
- Moss, R., I. Storch, and M. Muller. 2010. Trends in grouse research. Wildlife Biology 16:1-11.
- Moss, R. and A. Watson. 2001. Population cycles in birds of the grouse family (Tetraonidae). Advances in Ecological Research **32**:53-111.
- Mougeot, F., S. A. Evans, and S. M. Redpath. 2005. Interactions between population processes in a cyclic species: parasites reduce autumn territorial behaviour of male red grouse. Oecologia 144:289-298.
- Munkebye, E., H. C. Pedersen, J. B. Steen, and H. Brøseth. 2003. Predation of eggs and incubating females in Willow Ptarmigan *Lagopus l. lagopus*. Fauna Norvegica Serie C **23**:1-8.
- Myers-Smith, I. H., B. C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, K. D. Tape, M. Macias-Fauria, U. Sass -Klaassen, E. Lévesque, S. Boudreau, P. Ropars, L. Hermanutz, A. Trant, L. S. Collier, S. Weijers, J. Rozema, S. A. Rayback, N. M. Schmidt, G. Schaepman-Strub, S. Wipf, C. Rixen, C. B. Ménard, S. Venn, S. Goetz, L. Andreu-Hayles, S. Elmendorf, V. Ravolainen, J. Welker, P. Grogan, H. E. Epstein, and D. S. Hik. 2011. Shrub expansion at the forest tundra ecotone: spatial heterogeneity linked to local topography. Environ. Res. Lett. 6:No.045509.
- Myneni, R. B., C. D. Keeling, C. J. Tucker, G. Asrar, and R. R. Nemani. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature **386**:698-702.
- Myrberget, S. 1982. Fluctuations in Norwegian populations of willow grouse, *Lagopus lagopus*, 1932–1971 (in Norwegian, with English summary). Meddelser Norsk Viltforskning **3**:1-31.
- Mysterud, A., N. C. Stenseth, N. G. Yoccoz, R. Langvatn, and G. Steinheim. 2001. Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. Nature **410**:1096-1099.
- Mysterud, A., N. G. Yoccoz, and R. Langvatn. 2009. Maturation trends in red deer females over 39 years in harvested populations. Journal of Animal Ecology **78**:595-599.
- Mysterud, A., N. G. Yoccoz, R. Langvatn, N. Pettorelli, and N. C. Stenseth. 2008. Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. Philosophical Transactions of the Royal Society B-Biological Sciences **363**:2359–2368.
- Mørk, T., J. Bohlin, E. Fuglei, K. Asbakk, and M. Tryland. 2011. Rabies in the arctic fox population, Svalbard, Norway. Journal of Wildlife Diseases **47**:945-957.
- Mørk, T. and A. Prestrud. 2004. Arctic rabies A review. Acta Veterinaria Scandinavica 45:1-9.
- Nabuurs, G., K. Andrasko, P. Benitez-Ponce, R. Boer, M. Dutschke, L. Elsiddig, J. Ford-Robertson, P. Frumhoff, T. Karjalainen, O. Krankina, W. A. Kurz, M. Matsumoto, W. Oyhantcabal, N. H. Ravindranath, M. J. Sanz Sanchez, and X. Zhang. 2007. Forestry. Climate Change 2007: Mitigation of Climate Change (Contribution of Working Group III to the Intergovernmental Panel on Climate Change Fourth Assessment Report., Intergovernmental Panel on Climate Change, Cambridge.
- Newton, I. 1993. Predation and limitation of bird numbers. In: D. M. Power, editor. Current ornithology. Plenum Press, New York. Pages 143-198.
- Nichols, J. D. and B. K. Williams. 2006. Monitoring for conservation. Trends in Ecology & Evolution 21:668-673.
- Nielsen, O. K. 1999. Gyrfalcon predation on ptarmigan: numerical and functional responses. Journal of Animal Ecology **68**:1034-1050.
- Nieminen, M., H. Norberg, and V. Maijala. 2011. Mortality and survival of semi-domesticated reindeer (*Rangifer tarandus tarandus L.*) calves in northern Finland. Rangifer **31**:71-84.
- Norberg, H., I. Kojola, P. Aikio, and M. Nylund. 2006. Predation by golden eagle *Aquila chrysaetos* on semidomesticated reindeer *Rangifer tarandus* calves in northeastern Finnish Lapland. Wildlife Biology **12**:393-402.
- Nordic Council of Ministers. 2009. Signs of climate change in Nordic nature. TemaNord 551, Nordic Council of Ministers, Copenhagen, 52 p.
- Norén, K., L. Carmichael, L. Dalen, P. Hersteinsson, G. Samelius, E. Fuglei, C. M. O. Kapel, I. Menyushina, C. Strobeck, and A. Angerbjörn. 2011a. Arctic fox *Vulpes lagopus* population structure: circumpolar patterns and processes. Oikos 120:873-885.
- Norén, K., L. Carmichael, E. Fuglei, N. E. Eide, P. Hersteinsson, and A. Angerbjörn. 2011b. Pulses of movement across the sea ice: population connectivity and temporal genetic structure in the arctic fox. Oecologia **166**:973-984.
- Nyström, J., J. Ekenstedt, A. Angerbjörn, L. Thulin, P. Hellström, and L. Dalén. 2006. Golden Eagles on the Swedish mountain tundra diet and breeding success in relation to prey fluctuations. Ornis Fennica **83**:145-152.

- Okland, T., V. Bakkestuen, R. H. Okland, and O. Eilertsen. 2004. Changes in forest understorey vegetation in Norway related to long-term soil acidification and climatic change. Journal of Vegetation Science 15:437-448.
- Oksanen, L. 1995. Isolated occurrences of spruce, *Picea abies*, in northernmost Fennoscandia in relation to the enigma of continental mountain birch forests. Acta Botanica Fennica **153**:81-92.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118**:240-261.
- Oksanen, L. and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. American Naturalist 155:703-723.
- Oksanen, T., L. Oksanen, J. Dahlgren, and J. Ofsson. 2008. Arctic lemmings, *Lemmus spp.* and *Dicrostonyx spp.*: integrating ecological and evolutionary perspectives. Evolutionary Ecology Research **10**:415-434.
- Oksanen, T., L. Oksanen, and M. Norberg. 1992. Habitat use of small mustelids in North Fennoscandian tundra a test of the hypothesis of patchy exploitation ecosystems. Ecography 15:237-244.
- Olofsson, J., L. Ericson, M. Torp, S. Stark, and R. Baxter. 2011. Carbon balance of Arctic tundra under increased snow cover mediated by a plant pathogen. Nature Climate Change 1:220-223.
- Olofsson, J., P. E. Hulme, L. Oksanen, and O. Suominen. 2004. Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. Oikos **106**:324-334.
- Olofsson, J., H. Kitti, P. Rautiainen, S. Stark, and L. Oksanen. 2001. Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. Ecography **24**:13-24.
- Olofsson, J., J. Moen, and L. Oksanen. 2002. Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity. Oikos **96**:265-272.
- Olofsson, J., L. Oksanen, T. Callaghan, P. E. Hulme, T. Oksanen, and O. Suominen. 2009. Herbivores inhibit climatedriven shrub expansion on the tundra. Global Change Biology **15**:2681-2693.
- Olofsson, J. and J. Strengbom. 2000. Response of galling invertebrates on *Salix lanata* to reindeer herbivory. Oikos **91**:493-498.
- Olofsson, J., H. Tømmervik, and T. Callaghan, V. 2012. Vole and lemming activity observed from space. Nature Climate Change **DOI: 10.1038/NCLIMATE1537**.
- Overland, J. E., J. M. Adams, and N. A. Bond. 1997. Regional variation of winter temperatures in the Arctic. Journal of Climate 10:821-837.
- Overland, J. E., M. Y. Wang, N. A. Bond, J. E. Walsh, V. M. Kattsov, and W. L. Chapman. 2011a. Considerations in the selection of global climate models for Regional Climate Projections: The Arctic as a case study. Journal of Climate **24**:1583-1597.
- Overland, J. E., K. R. Wood, and M. Y. Wang. 2011b. Warm Arctic-cold continents: climate impacts of the newly open Arctic Sea. Polar Research **30**:No.15787.
- Owen-Smith, N. and M. G. L. Mills. 2006. Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. Ecological Monographs **76**:73-92.
- Pajunen, A., R. Virtanen, and H. Roininen. 2008. The effects of reindeer grazing on the composition and species richness of vegetation in forest-tundra ecotone. Polar Biology **31**:1233-1244.
- Pajunen, A. M., E. M. Kaarlejarvi, B. C. Forbes, and R. Virtanen. 2010. Compositional differentiation, vegetationenvironment relationships and classification of willow-characterised vegetation in the western Eurasian Arctic. Journal of Vegetation Science 21:107-119.
- Pajunen, A. M., J. Oksanen, and R. Virtanen. 2011. Impact of shrub canopies on understorey vegetation in western Eurasian tundra. Journal of Vegetation Science **22**:837-846.
- Pamperin, N. J., E. H. Follmann, and B. T. Person. 2008. Sea-ice use by arctic foxes in northern Alaska. Polar Biology **31**:1421-1426.
- Papworth, S. K., J. Rist, L. Coad, and E. J. Milner-Gulland. 2009. Evidence for shifting baseline syndrom in conservation. Conservation Letters 2:93-100.
- Parker, H. 1984. Effects of corvid removal on reproduction of willow ptarmigan. Journal of Wildlife Management **48**:1197-1204.
- Parker, H., H. Ottesen, and E. Knudsen. 1985. Age determination in Svalbard rock ptarmigan (*Lagopus mutus hyperboreus*). Polar Research **3**:125-126.
- Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421**:37-42.
- Pauli, H., M. Gottfried, S. Dullinger, O. Abdaladze, M. Akhalkatsi, J. L. B. Alonso, G. Coldea, J. Dick, B. Erschbamer, R. F. Calzado, D. Ghosn, J. I. Holten, R. Kanka, G. Kazakis, J. Kollár, P. Larsson, P. Moiseev, D. Moiseev, U. Molau, J. M. Mesa, L. Nagy, G. Pelino, M. Puşcaş, G. Rossi, A. Stanisci, A. O. Syverhuset, J.-P. Theurillat, M. Tomaselli, P. Unterluggauer, L. Villar, P. Vittoz, and G. Grabherr. 2012. Recent plant diversity changes on Europe's mountain summits. Science 336:353-355.
- Pearl, J. 2010. The foundations of causal inference. Sociological Methodology 40:75-149.
- Pedersen, H. C., H. Steen, L. Kastdalen, H. Broseth, R. A. Ims, W. Svendsen, and N. G. Yoccoz. 2004. Weak compensation of harvest despite strong density-dependent growth in willow ptarmigan. Proceedings of the Royal Society of London Series B-Biological Sciences 271:381-385.
- Pedersen, Å. Ø., B. J. Bårdsen, N. G. Yoccoz, N. Lecomte, and E. Fuglei. 2012. Monitoring Svalbard rock ptarmigan:

Distance sampling and occupancy modeling. Journal of Wildlife Management 76:308-316.

- Pedersen, Å. Ø., R. Ims, N. Yoccoz, V. Hausner, and K. H. Juell. 2010a. Scale-dependent responses of predators and prey to spruce plantations in sub-arctic birch forest in winter. Ecoscience **17**:123-136
- Pedersen, Å. Ø., J. U. Jepsen, N. G. Yoccoz, and E. Fuglei. 2007. Ecological correlates of the distribution of territorial Svalbard rock ptarmigan (*Lagopus muta hyperborea*). Canadian Journal of Zoology **85**:122-132.
- Pedersen, Å. Ø., N. G. Yoccoz, R. A. Ims, and T. Sigurdsen. 2010b. Effects of non-native spruce plantations on small mammal communities in subarctic birch forests. Forest Ecology and Management **260**:331-338.
- Peinetti, H. R., M. A. Kalkhan, and M. B. Coughenour. 2002. Long-term changes in willow spatial distribution on the elk winter range of Rocky Mountain National Park (USA). Landscape Ecology **17**:341-354.
- Peters, D. P. C. 2010. Accessible ecology: synthesis of the long, deep, and broad. Trends in Ecology & Evolution **25**:592-601.
- Peterson, B. J., R. M. Holmes, J. W. McClelland, C. J. Vorosmarty, R. B. Lammers, A. I. Shiklomanov, I. A. Shiklomanov, and S. Rahmstorf. 2002. Increasing river discharge to the Arctic Ocean. Science **298**:2171-2173.
- Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research **46**:15-27.
- Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution **20**:503-510.
- Piepho, H. P. and J. O. Ogutu. 2007. Simple state-space models in a mixed model framework. American Statistician **61**:224-232.
- Pimm, S. L. 1982. Food webs. University of Chigago Press, Chicago, Illinois.
- Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. Nature 350:669-674.
- Pitelka, F. A., P. Q. Tomich, and G. W. Treichel. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecological Monographs **25**:85-118.
- Pocewicz, A., M. Nielsen-Pincus, G. Brown, and R. Schnitzer. 2012. An evaluation of internet versus paper-based methods for Public Participation Geographic Information Systems (PPGIS). Transactions in GIS 16:39-53.
- Pokrovsky, I., N. Lecomte, A. Sokolov, V. Sokolov, and N. G. Yoccoz. 2010. Peregrine falcons kill a Gyrfalcon feeding on their nestling. Journal of Raptor Research **44**:66-69.
- Pomeroy, J. W., D. S. Bewley, R. L. H. Essery, N. R. Hedstrom, T. Link, R. J. Granger, J. E. Sicart, C. R. Ellis, and J. R. Janowicz. 2006. Shrub tundra snowmelt. Hydrological Processes **20**:923-941.
- Post, E. 2005. Large-scale spatial gradients in herbivore population dynamics. Ecology 86:2320-2328.
- Post, E. and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B-Biological Sciences **363**:2369-2375.
- Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Hoye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. van der Wal, J. Welker, P. A. Wookey, N. M. Schmidt, and P. Aastrup. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325:1355-1358.
- Post, E. and C. Pedersen. 2008. Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences of the United States of America **105**:12353-12358.
- Prestrud, A. 1992. Arctic foxes in Svalbard: Population ecology and rabies. Norwegian Polar Institute/University of Oslo, Oslo, Norway.
- Prestrud, K. W., K. Asbakk, E. Fuglei, T. Mørk, A. Stien, E. Ropstad, M. Tryland, G. W. Gabrielsen, C. Lydersen, K. M. Kovacs, M. Loonen, K. Sagerup, and A. Oksanen. 2007. Serosurvey for *Toxoplasma gondii* in arctic foxes and possible sources of infection in the high Arctic of Svalbard. Veterinary Parasitology 150:6-12.
- Prop, J. 2004. Food finding. On the trial to successful reproduction in migratory geese. University of Groningen.
- Prop, J., J. M. Black, P. Shimmings, and M. Owen. 1998. The spring range of barnacle geese *Branta leucopsis* in relation to changes in land management and climate. Biological Conservation **86**:339-346.
- Prop, J. and J. de Vries. 1993. Impact of snow and food conditions on the reproductive performance of Barnacle geese *Branta leucopsis* Ornis Scandinavica **24**:110-121.
- Prop, J., M. R. van Eerden, and R. H. Drent. 1984. Reproductive success of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds, western Spitsbergen. Norsk Polarinstitutt Skrifter 181:87-117.
- Prugh, L. R. and J. S. Brashares. 2012. Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. Journal of Animal Ecology **81**:667-678.
- Pulliainen, E. and J. Iivanainen. 1981. Winter nutrition of the willow grouse (*Lagopus lagopus* L.) in the extreme north of Finland. Annales Zoologici Fennici **18**:263-269.
- Pullianen, E. and H. Eskonen. 1982. Chemical composition of plant matter eaten by young chicks of the Willow Grouse *Lagopus lagopus* in northern Finland. Ornis Fennica **59**:146-148.
- Pulyaev, A. I. 1988. Flora of Wrangel Island Nature Reserve. In: B. A. Yurtsev, editor. Flora and Fauna of Nature Reserves of the USSR. VINITI, Moscow (in Russian)
- Rasmus, S., T. Gronholm, M. Lehning, K. Rasmus, and M. Kulmala. 2007. Validation of the SNOWPACK model in five different snow zones in Finland. Boreal Environment Research **12**:467-488.

- Raudsepp-Hearne, C., G. D. Peterson, and E. M. Bennett. 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. Proceedings of the National Academy of Sciences of the United States of America 107:5242-5247.
- Ravolainen, V. T. 2009. Tundra plant diversity as influenced by biotic interactions, PhD Thesis. University of Tromsø, Faculty of Biosciences, Fisheries and Economics, Department of Arctic and Marine Biology, Tromsø.
- Ravolainen, V. T., K. A. Brathen, R. A. Ims, N. G. Yoccoz, J. A. Henden, and S. T. Killengreen. 2011. Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. Basic and Applied Ecology 12:643-653.
- Ravolainen, V. T., K. A. Bråthen, R. A. Ims, N. G. Yoccoz, and E. M. Soininen. 2013. Shrub patch configuration at the landscape scale is related to diversity of adjacent herbaceous vegetation. Plant Ecology & Diversity Online early, DOI: 10.1080/17550874.2013.773104.
- Ravolainen, V. T., N. G. Yoccoz, K. A. Bråthen, R. A. Ims, M. Iversen, and V. T. Gonzalez. 2010. Additive partitioning of diversity reveals no scale-dependent impacts of large ungulates on the structure of tundra plant communities. Ecosystems 13:157-170.
- Redpath, S., B. Arroyo, F. Leckie, P. Bacon, N. Bayfield, R. Gutierrez, and S. Thirgood. 2004. Using decision modelling to resolve human-wildlife conflicts: a case study with raptors and grouse. Conservation Biology **18**:350-359.
- Reeves, G. K., D. R. Cox, S. C. Darby, and E. Whitley. 1998. Some aspects of measurement error in explanatory variables for continuous and binary regression models. Statistics in Medicine 17:2157-2177.
- Reichman, O. J., M. B. Jones, and M. P. Schildhauer. 2011. Challenges and opportunities of open data in Ecology. Science **331**:703-705.
- Reid, D. G., F. Bilodeau, C. J. Krebs, G. Gauthier, A. J. Kenney, B. S. Gilbert, M. C. Y. Leung, D. Duchesne, and E. Hofer. 2012. Lemming winter habitat choice: a snow-fencing experiment. Oecologia **168**:935-946.
- Reid, D. G., C. J. Krebs, and A. Kenney. 1995. Limitation of collared lemming population growth at low densities by predation mortality. Oikos **73**:387-398.
- Ripple, W. J. and R. L. Beschta. 2004. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. Forest Ecology and Management **200**:161-181.
- Rivas, J. A. and R. Y. Owens. 1999. Teaching conservation effectively: A lesson from life-history strategies. Conservation Biology **13**:453-454.
- Rodnikova, A., R. A. Ims, A. Sokolov, G. Skogstad, V. Sokolov, V. Shtro, and E. Fuglei. 2011. Red fox takeover of arctic fox breeding den: an observation from Yamal Peninsula, Russia. Polar Biology **34**:1609-1614.
- Roemer, G. W., C. J. Donlan, and F. Courchamp. 2002. Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. Proceedings of the National Academy of Sciences of the United States of America **99**:791-796.
- Roininen, H., T. Nyman, and A. G. Zinovjev. 2005. Biology, ecology, and evolution of gall-inducing sawflies (*Hymenoptera*: *Tenthredinidae* and *Xyelidae*). In: A. Raman, C. W. Schaefer, and T. M. Withers, editors. Biology, Ecology, and Evolution of Gall-inducing Arthropods. Science Publishers, Inc., Enfield, NH. Pages 467-494.
- Root, T. L. and H. Schneider. 2006. Conservation and climate change: the challenges ahead. Conservation Biology **20**:706-708.
- Roth, J. D. 2002. Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice. Oecologia 133:70-77.
- Roth, J. D. 2003. Variability in marine resources affects arctic fox population dynamics. Journal of Animal Ecology **72**:668-676.
- Rydgren, K., R. H. Okland, F. X. Pico, and H. de Kroon. 2007. Moss species benefits from breakdown of cyclic rodent dynamics in boreal forests. Ecology **88**:2320-2329.
- Saitoh, T., N. C. Stenseth, and O. N. Bjørnstad. 1998. The population dynamics of the vole *Clethrionomys rufocanus* in Hokkaido, Japan. Researches on Population Ecology **40**:61-76.
- Sander, G., I. Hanssen-Bauer, A. Bjørge, and P. Prestrud. 2006. The environmental monitoring of Svalbard and Jan Mayen MOSJ. Norsk Polarinstitutt, Tromsø.
- Sandercock, B. K., K. Martin, and S. J. Hannon. 2005. Demographic consequences of age-structure in extreme environments: population models for arctic and alpine ptarmigan. Oecologia **146**:13-24.
- Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Animal Ecology **80**:244-258.
- Savory, C. J. 1977. The food of Red Grouse chicks Lagopus l. scoticus. Ibis 119:1-9.
- Savory, C. J. 1989. The importance of invertebrate food to chicks of gallinaceous species. Proceedings of the Nutrition Society **48**:113-133.
- Schickhoff, U., M. D. Walker, and D. A. Walker. 2002. Riparian willow communities on the Arctic Slope of Alaska and their environmental relationships: A classification and ordination analysis. Phytocoenologia **32**:145-204.
- Schimel, D., M. Keller, S. Berukoff, B. Kao, H. Loescher, H. Powell, K. T., D. Moore, and W. Gram. 2011. 2011 Science strategy. Enabling continental-scale ecological forecasting. NEON inc.
- Schmidt, N. M., R. A. Ims, T. T. Høye, O. Gilg, L. H. Hansen, J. Hansen, M. Lund, E. Fuglei, M. C. Forchhammer, and

B. Sittler. 2012. Response of an arctic predator guild to collapsing lemming cycles. Proceedings of the Royal Society B-Biological Sciences **279**:4417-4422.

- Screen, J. A. and I. Simmonds. 2010. The central role of diminishing sea ice in recent Arctic temperature amplification. Nature **464**:1334-1337.
- Sedinger, J. S. and P. L. Flint. 1991. Growth-rate is negatively correlated with hatch date in Black Brant. Ecology **72**:496-502.
- SEFALO. The Sweedish-Finnish-Norwegian Arctic Fox Project, . http://www.zoologi.su.se/research/alopex/ homesefalo.html
- Seidl, R., M. J. Schelhaas, and M. J. Lexer. 2011. Unraveling the drivers of intensifying forest disturbance regimes in Europe. Global Change Biology 17:2842-2852.
- Selås, V. and J. O. Vik. 2006. Possible impact of snow depth and ungulate carcasses on red fox (*Vulpes vulpes*) populations in Norway, 1897-1976. Journal of Zoology **269**:299-308.
- Selås, V. and J. O. Vik. 2007. The arctic fox *Alopex lagopus* in Fennoscandia: a victim of human-induced changes in interspecific competition and predation? Biodiversity and Conservation **16**:3575-3583.
- Serreze, M. C. and R. G. Barry. 2011. Processes and impacts of Arctic amplification: A research synthesis. Global and Planetary Change 77:85-96.
- Serreze, M. C., M. M. Holland, and J. Stroeve. 2007. Perspectives on the Arctic's shrinking sea-ice cover. Science **315**:1533-1536.
- Shaver, G. R. 2010. Arctic LTER: Climate change and changing disturbance regimes in Arctic landscapes. The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA., pp.
- Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90:363-368.
- Silvertown, J., P. Poulton, E. Johnston, G. Edwards, M. Heard, and P. M. Biss. 2006. The Park Grass Experiment 1856-2006: Its contribution to ecology. Journal of Ecology **94**:801-814.
- Sipura, M., A. Ikonen, J. Tahvanainen, and H. Roininen. 2002. Why does the leaf beetle *Galerucella lineola* F. attack wetland willows? Ecology **83**:3393-3407.
- Sittler, B. 1995. Response of stoats (*Mustela erminea*) to a fluctuating lemming (*Dicrostonyx groenlandicus*) population in North-East Greenland - Preliminary results from a long-term study. Annales Zoologici Fennici **32**:79-92.
- Sjögersten, S., R. van der Wal, and S. J. Woodin. 2008. Habitat type determines herbivory controls over CO₂ fluxes in a warmer Arctic. Ecology **89**:2103-2116.
- Skogland, T. 1984. Wild reindeer foraging niche organization. Holoarctic Ecology 7:345-379.
- Skogland, T. 1991. What are the effects of predators on large ungulate populations. Oikos **61**:401-411.
- Skre, O., R. Baxter, R. M. M. Crawford, T. V. Callaghan, and A. Fedorkov. 2002. How will the tundra-taiga interface respond to climate change? Ambio, Special Report 12:37-46.
- Soininen, E., K. A. Bråthen, J. G. H. Jusdado, S. Reidinger, and S. E. Hartley. 2013. More than herbivory: levels of silica -based defences in grasses vary with plant species, genotype and location. Oikos **122**:30-41.
- Soininen, E. M., A. Valentini, E. Coissac, C. Miquel, L. Gielly, C. Brochmann, A. K. Brysting, J. H. Sonstebo, R. A. Ims, N. G. Yoccoz, and P. Taberlet. 2009. Analysing diet of small herbivores: the efficiency of DNA barcoding coupled with high-throughput pyrosequencing for deciphering the composition of complex plant mixtures. Frontiers in Zoology 6:No.16.
- Sokolov, V. A., D. Ehrich, N. G. Yoccoz, A. A. Sokolov, and N. Lecomte. 2012. Bird communities of the arctic shrub tundra of Yamal: habitat specialists and generalists. PLOS one 7: e50335.
- Solberg, E. J., P. Jordhoy, O. Strand, R. Aanes, A. Loison, B. E. Saether, and J. D. C. Linnell. 2001. Effects of densitydependence and climate on the dynamics of a Svalbard reindeer population. Ecography 24:441-451.
- Solberg, E. J., C. M. Rolandsen, M. Heim, J. D. C. Linnell, I. Herfindal, and B. E. Saether. 2010. Age and sex-specific variation in detectability of moose (*Alces alces*) during the hunting season: implications for population monitoring. European Journal of Wildlife Research **56**:871-881.
- Song, H. R. and E. Ferrer. 2012. Bayesian estimation of random coefficient dynamic factor models. Multivariate Behavioral Research 47:26-60.
- Speed, J. D. M., G. Austrheim, A. J. Hester, and A. Mysterud. 2010a. Experimental evidence for herbivore limitation of the treeline. Ecology **91**:3414-3420.
- Speed, J. D. M., G. Austrheim, A. J. Hester, and A. Mysterud. 2011. Browsing interacts with climate to determine treering increment. Functional Ecology 25:1018-1023.
- Speed, J. D. M., E. J. Cooper, I. S. Jónsdóttir, R. van der Wal, and S. J. Woodin. 2010b. Plant community properties predict vegetation resilience to herbivore disturbance in the Arctic. Journal of Ecology **98**:1002-1013.
- Speed, J. D. M., S. J. Woodin, H. Tømmervik, M. P. Tamstorf, and R. Van der Wal. 2009. Predicting habitat utilization and extent of ecosystem disturbance by an increasing herbivore population. Ecosystems 12:349-359.
- Spidsø, T. K. 1980. Food selection by Willow Grouse *Lagopus lagopus* chicks in northern Norway. Ornis Scandinavica **11**:99-105.
- SSB. 2012a. Statistics Norway, http://www.ssb.no.

SSB. 2012b. Småvilt og rådyrjakt. Statistics Norway, http://www.ssb.no/srjakt/. (in Norwegian).

Steen, H., N. G. Yoccoz, and R. A. Ims. 1990. Predators and small rodent cycles - an analysis of a 79-year time-series

of small rodent population fluctuations. Oikos 59:115-120.

- Steen, J. B., H. Steen, N. C. Stenseth, S. Myrberget, and V. Marcstrõm. 1988. Microtine density and weather as predictors of chick production in Willow ptarmigan, *Lagopus lagopus*. Oikos **51**:367-373.
- Steen, J. B. and S. Unander. 1985. Breeding biology of the Svalbard Rock Ptarmigan (*Lagopus mutus hyperboreus*). Ornis Scandinavica **16** 191–197.
- Stenseth, N. C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. Oikos **87**:427-461.
- Stenseth, N. C. and R. Ims. 1993. The biology of lemmings. Academic Press, London.
- Stien, A., R. A. Ims, S. D. Albon, E. Fuglei, J. Irvine, E. Ropstad, O. Halvorsen, R. Langvatn, L. E. Loe, V. Veiberg, and N. G. Yoccoz. 2012. Congruent responses to climate variability in high-arctic herbivores. Biology Letters 8:1002-1005.
- Stien, A., R. J. Irvine, E. Ropstad, O. Halvorsen, R. Langvatn, and S. D. Albon. 2002. The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies. Journal of Animal Ecology 71:937-945.
- Stien, A., L. E. Loe, A. Mysterud, T. Severinsen, J. Kohler, and R. Langvatn. 2010a. Icing events trigger range displacement in a high-arctic ungulate. Ecology **91**:915-920.
- Stien, A., L. Voutilainen, V. Haukisalmi, E. Fuglei, T. Mork, N. G. Yoccoz, R. A. Ims, and H. Henttonen. 2010b. Intestinal parasites of the Arctic fox in relation to the abundance and distribution of intermediate hosts. Parasitology 137:149-157.
- Stokkan, K. A., P. J. Sharp, and S. Unander. 1986. The annual breeding cycle of the high-arctic Svalbard ptarmigan (*Lagopus mutus hyperboreus*). General and Comparative Endocrinology **61**:446-451.
- Storch, I. 2007. Grouse Status Survey and Conservation Action Plan 2006-2010. WPA/BirdLife/SSC Grouse Specialist Group. IUCN, Gland and World Pheasant Association. Fordingbridge, UK. 112 pp.
- Stow, D., Y. Hamada, L. Coulter, and Z. Anguelova. 2008. Monitoring shrubland habitat changes through objectbased change identification with airborne multispectral imagery. Remote Sensing of Environment **112**:1051-1061.
- Stow, D., A. Petersen, A. Hope, R. Engstrom, and L. Coulter. 2007. Greenness trends of arctic tundra vegetation in the 1990s: comparison of two NDVI data sets from NOAA AVHRR systems. International Journal of Remote Sensing 28:4807-4822.
- Stow, D. A., A. Hope, D. McGuire, D. Verbyla, J. Gamon, F. Huemmrich, S. Houston, C. Racine, M. Sturm, K. Tape, L. Hinzman, K. Yoshikawa, C. Tweedie, B. Noyle, C. Silapaswan, D. Douglas, B. Griffith, G. Jia, H. Epstein, D. Walker, S. Daeschner, A. Petersen, L. M. Zhou, and R. Myneni. 2004. Remote sensing of vegetation and landcover change in arctic tundra ecosystems. Remote Sensing of Environment 89:281-308.
- Stroeve, J., M. M. Holland, W. Meier, T. Scambos, and M. Serreze. 2007. Arctic sea ice decline: Faster than forecast. Geophysical Research Letters **34**:L09501.
- Stroeve, J. C., M. C. Serreze, A. Barrett, and D. N. Kindig. 2011. Attribution of recent changes in autumn cyclone associated precipitation in the Arctic. Tellus Series a-Dynamic Meteorology and Oceanography **63**:653-663.
- Strong, D. R. and K. T. Frank. 2010. Human involvement in food webs. Annual Review of Environment and Resources **35**:1-23.
- Strøm, H. 2006. Common guillemot (*Uria aalge*). In: K. M. Kovacs and C. Lydersen, editors. Birds and Mammals of Svalbard. Norwegian Polar Institute Pages 159-162.
- Strøm, H. and G. Bangjord. 2004. The birds and mammal fauna of Svalbard. In: P. Prestrud, H. Strøm, and H. Goldman, editors. A catalogue of the terrestrial and marine animals of Svalbard. Norwegian Polar Institute Skrifter 201, Tromsø, Norway. Pages 123–137.
- Sturm, M. 2010. Arctic plants feel the heat. Scientific American 302:66-73.
- Sturm, M., T. Douglas, C. Racine, and G. E. Liston. 2005a. Changing snow and shrub conditions affect albedo with global implications. Journal of Geophysical Research-Biogeosciences **110**:G01004.
- Sturm, M., J. P. McFadden, G. E. Liston, F. S. Chapin, C. H. Racine, and J. Holmgren. 2001a. Snow-shrub interactions in Arctic tundra: A hypothesis with climatic implications. Journal of Climate 14:336-344.
- Sturm, M., C. Racine, and K. Tape. 2001b. Climate change Increasing shrub abundance in the Arctic. Nature **411**:546-547.
- Sturm, M., J. Schimel, G. Michaelson, J. M. Welker, S. F. Oberbauer, G. E. Liston, J. Fahnestock, and V. E. Romanovsky. 2005b. Winter biological processes could help convert arctic tundra to shrubland. Bioscience 55:17-26.
- Sulkava, S., K. Huhtala, P. Rajala, and R. Tornberg. 1999. Changes in the diet of the Golden Eagle *Aquila chrysaetos* and small game populations in Finland in 1957-96. Ornis Fennica **76**:1-16.
- Summers, R. W. and L. G. Underhill. 1987. Factors related to breeding production of brent geese *Branta-bernicla-bernicla* and waders (*Charadrii*) on the Taimyr peninsula. Bird Study **34**:161-171.
- Suominen, O. and J. Olofsson. 2000. Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: a review. Annales Zoologici Fennici **37**:233-249.
- Sveinbjornsson, J., A. Hofgaard, and A. Lloyd. 2002. Natural causes of the tundra-taiga boundary. Ambio, Special issue **12**:23-29.
- Sverdrup-Thygeson, A. and T. Birkemoe. 2009. What window traps can tell us: effect of placement, forest openness

and beetle reproduction in retention trees. Journal of Insect Conservation 13:183-191.

- Sverdrup-Thygeson, A. and R. A. Ims. 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. Biological Conservation **106**:347-357.
- Swann, A. L., I. Y. Fung, S. Levis, G. B. Bonan, and S. C. Doney. 2010. Changes in arctic vegetation amplify highlatitude warming through the greenhouse effect. Proceedings of the National Academy of Sciences of the United States of America 107:1295-1300.
- SWIPA. 2011. Snow, water, ice and permafrost in the Arctic. SWIPA 2011 Executive Summary. Arctic Monitoring and Assessment Programme (AMAP).
- Sørensen, K. K., T. Mørk, O. G. Sigurdardottir, K. Åsbakk, J. Åkerstedt, B. Bergsjø, and E. Fuglei. 2005. Acute toxoplasmosis in three wild arctic foxes (*Alopex lagopus*) from Svalbard; one with co-infections of *Salmonella enteritidis* PT1 and *Yersinia pseudotuberculosis* serotype 2b. Research in Veterinary Science 78:161-167.
- Tannerfeldt, M. and A. Angerbjorn. 1998. Fluctuating resources and the evolution of litter size in the arctic fox. Oikos **83**:545-559.
- Tannerfeldt, M., B. Elmhagen, and A. Angerbjörn. 2002. Exclusion by interference competition? The relationship between red and arctic foxes. Oecologia **132**:213-220.
- Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology **12**:686-702.
- Tape, K. D., M. Hallinger, J. M. Welker, and R. W. Ruess. 2012. Landscape Heterogeneity of Shrub Expansion in Arctic Alaska. Ecosystems 15:711-724.
- Tape, K. D., R. Lord, H. P. Marshall, and R. W. Ruess. 2010. Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska. Ecoscience 17:186-193.
- Tape, K. D., D. Verbyla, and J. M. Welker. 2011. Twentieth century erosion in arctic Alaska foothills: The influence of shrubs, runoff, and permafrost. Journal of Geophysical Research-Biogeosciences **116**:G04024.
- Tapper, S. C. 1992. Game Heritage: An ecological Review from Shooting and Gamekeeping Records. Fordingbridge: Game Conservancy.
- Tarnocai, C., J. G. Canadell, E. A. G. Schuur, P. Kuhry, G. Mazhitova, and S. Zimov. 2009. Soil organic carbon pools in the northern circumpolar permafrost region. Global Biogeochemical Cycles **23**:GB2023.
- Tarroux, A., D. Berteaux, and J. Bety. 2010. Northern nomads: ability for extensive movements in adult arctic foxes. Polar Biology **33**:1021-1026.
- Tast, J. 1966. The root vole *Microtus oeconomus* (Pallas), as an inhabitant of seasonally flooded land. Annales Zoologici Fennici **3**:127-171.
- Tenow, O. and H. Bylund. 1989. A survey of winter cold in the mountain birch/*Epirrita autumnata* system. Memoranda Societatis Pro Fauna Et Flora Fennica **65**:67-72.
- Tews, J., M. A. D. Ferguson, and L. Fahrig. 2007. Potential net effects of climate change on high arctic Peary caribou: Lessons from a spatially explicit simulation model. Ecological Modelling **207**:85-98.
- Thing, H. 1984. Feeding ecology of the West Greenland caribou (*Rangifer tarandus groenlandicus*) in the Sisimiut-Kangerlussuaq region. Danish review of game biology 12 (3), Game Biology Station, Rønde, Denmark, 52 pp.
- Thommessen, T. 1996. The early settlement of northern Norway. In: L. Larsson, editor. The Earliest Settlement of Scandinavia. Acta Archaeologica Lundensia 8. Pages 235-240.
- Tollefson, J. 2011. US launches eco-network. Nature 476:135-135.
- Tombre, I., K. Erikstad, and V. Bunes. 2012. State-dependent incubation behaviour in the high arctic barnacle geese. Polar Biology **35**:985-992.
- Tombre, I. M., J. M. Black, and M. J. J. E. Loonen. 1998a. Critical components in the dynamics of a barnacle goose colony: a sensitivity analysis. Norsk Polarinstitutt Skrifter **200**:81-89.
- Tombre, I. M. and K. E. Erikstad. 1996. An experimental study of incubation effort in high-Arctic barnacle geese. Journal of Animal Ecology **65**:325-331.
- Tombre, I. M., K. A. Høgda, J. Madsen, L. Griffin, E. Kuijken, P. Shimmings, E. Rees, and C. Verscheure. 2008. The onset of spring and timing of migration in two arctic nesting goose populations: the pink-footed goose *Anser brachyrhynchus* and the barnacle goose *Branta leucopsis*. Journal of Avian Ecology **39**:691-703.
- Tombre, I. M., F. Mehlum, and M. J. J. E. Loonen. 1998b. The Kongsfjorden colony of barnacle geese: Nest distribution and the use of breeding islands 1980-1997. Norsk Polarinstitutt Skrifter **200**:57-65.
- Tombre, I. M., Tømmervik, H., Gullestad, N., Madsen, J. 2010. Spring staging in the Svalbard-breeding Pink-footed Goose *Anser brachyrhynchus* population: site-use changes caused by declining agricultural management? Wildfowl **60**:3-19.
- Totland, O., J. A. Grytnes, and E. Heegaard. 2004. Willow canopies and plant community structure along an alpine environmental gradient. Arctic Antarctic and Alpine Research **36**:428-435.
- Trasti, V. N. 2010. Large temporal and spatial variation in standing crop of palatable and unpalatable growth forms in subarctic tundra. University of Tromsø, MSc. Thesis, Tromsø.
- Trinder, M. K. and J. Madsen. 2008. Predictive modelling of the Svalbard pink-footed goose population: an evaluation of the potential impacts of increased hunting pressure. Vogelwelt **129**:158-168.
- Turchin, P. and G. O. Batzli. 2001. Availability of food and the population dynamics of arvicoline rodents. Ecology **82**:1521-1534.

- Turchin, P., L. Oksanen, P. Ekerholm, T. Oksanen, and H. Henttonen. 2000. Are lemmings prey or predators? Nature **405**:562-565.
- Tveraa, T., P. Fauchald, C. Henaug, and N. G. Yoccoz. 2003. An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. Oecologia **137**:370-376.
- Tveraa, T., P. Fauchald, N. G. Yoccoz, R. A. Ims, R. Aanes, and K. A. Høgda. 2007. What regulate and limit reindeer populations in Norway? Oikos **116**:706-715.
- Tveraa, T., A. Stien, B.-J. Bårdsen, and P. Fauchald. 2013. Population densities, vegetation green-up, and plant productivity: impacts on reproductive success and juvenile body mass in reindeer. Plos One **8**:e56450.
- Tyler, N. J. C. 1986. Reinen i Adventdalen. In: N. A. Øritsland, editor. Svalbardreinen og dens livsgrunnlag. Universitetsforlaget, Oslo. Pages 143-159.
- Tyler, N. J. C., M. C. Forchhammer, and N. A. Oritsland. 2008. Nonlinear effects of climate and density in the dynamics of a fluctuating population of reindeer. Ecology **89**:1675-1686.
- Tømmervik, H., J. W. Bjerke, E. Gaare, B. Johansen, and D. Thannheiser. 2012. Rapid recovery of recently overexploited winter grazing pastures for reindeer in northern Norway. Fungal Ecology **5:**3-15.
- Tømmerås, P. J. 1993. The status of Gyrfalcon *Falco rusticolus* research in northern Fennoscandia 1992. Fauna Norvegica Series C 16:75-82.
- Unander, S., A. Mortensen, and A. Elvebakk. 1985. Crop content of the Svalbard rock ptarmigan (*Lagopus mutus hyperboreus*). Polar Research **3**:239-243.
- Unander, S. and J. B. Steen. 1985. Behavior and social structure in Svalbard rock ptarmigan (*Lagopus mutus hyperboreus*). Ornis Scandinavica **16**:198-204.
- van Beest, F. M., A. Mysterud, L. E. Loe, and J. M. Milner. 2010. Forage quantity, quality and depletion as scaledependent mechanisms driving habitat selection of a large browsing herbivore. Journal of Animal Ecology **79**:910-922.
- van Bogaert, R., C. Jonasson, M. De Dapper, and T. V. Callaghan. 2009. Competitive interaction between aspen and birch moderated by invertebrate and vertebrate herbivores and climate warming. Plant Ecology & Diversity **2**:221-U224.
- van der Putten, W. H., M. Macel, and M. E. Visser. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philosophical Transactions of the Royal Society B-Biological Sciences **365**:2025-2034.
- van der Wal, R. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. Oikos 114:177-186.
- van der Wal, R., R. D. Bardgett, K. A. Harrison, and A. Stien. 2004. Vertebrate herbivores and ecosystem control: cascading effects of faeces on tundra ecosystems. Ecography **27**:242-252.
- van der Wal, R., R. Brooker, E. Cooper, and R. Langvatn. 2001. Differential effects of reindeer on high Arctic lichens. Journal of Vegetation Science **12**:705-710.
- van der Wal, R. and R. W. Brooker. 2004. Mosses mediate grazer impacts on grass abundance in arctic ecosystems. Functional Ecology **18**:77-86.
- van der Wal, R., M. Egas, A. van der Veen, and J. Bakker. 2000a. Effects of resource competition and herbivory on plant performance along a natural productivity gradient. Journal of Ecology **88**:317-330.
- van der Wal, R. and D. O. Hessen. 2009. Analogous aquatic and terrestrial food webs in the high Arctic: The structuring force of a harsh climate. Perspectives in Plant Ecology Evolution and Systematics **11**:231-240.
- van der Wal, R., J. Irvine, A. Stien, N. Shepherd, and S. D. Albon. 2000b. Faecal avoidance and the risk of infection by nematodes in a natural population of reindeer. Oecologia **124**:19-25.
- van der Wal, R., N. Madan, S. van Lieshout, S. Dormann, R. Langvatn, and S. D. Albon. 2000c. Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. Oecologia **123**:108-115.
- van der Wal, R., S. Sjögersten, S. J. Woodin, E. J. Cooper, I. S. Jonsdóttir, D. P. J. Kuijper, A. D. Fox, and A. Huiskes. 2007. Spring feeding by pink-footed geese reduces carbon stocks and sink strength in arctic tundra ecosystems. Global Change Biology **13**:1-7.
- van Dijk, J., G. Ulateig, D. Terrasson, G. De Blust, A. Sier, L. Braat, R. Kanka, M. Mirtl, K. Török, E. Furman, M. Kertész, and J. Stadler. 2011. ALTER-Net, a long-term biodiversity, ecosystem and awareness research network – Year 7. NINA, Trondheim, 83 p.
- van Dongen, S., T. Backeljau, E. Matthysen, and A. A. Dhondt. 1997. Synchronization of hatching date with budburst of individual host trees (*Quercus robur*) in the winter moth (*Operophtera brumata*) and its fitness consequences. Journal of Animal Ecology **66**:113-121.
- Virtanen, R. 2000. Effects of grazing on above-ground biomass on a mountain snowbed, NW Finland. Oikos **90**:295-300.
- Virtanen, R., A. Eskelinen, and E. Gaare. 2003. Long term changes in alpine plant communities in Norway and Finland. In: L. Nagy, G. Grabherr, and C. Körner, editors. Alpine biodiversity in Europe. Springer-Verlag Pages 411-422.
- Virtanen, R., H. Henttonen, and K. Laine. 1997. Lemming Grazing and Structure of a Snowbed Plant Community: A Long-Term Experiment at Kilpisjärvi, Finnish Lapland. Oikos **79**:155-166.
- Virtanen, R., J. Parviainen, and H. Henttonen. 2002. Winter grazing by the Norwegian lemming (Lemmus lemmus) at

Kilpisjarvi (NW Finnish Lapland) during a moderate population peak. Annales Zoologici Fennici 39:335-341.

- Virtanen, T., S. Neuvonen, and A. Nikula. 1998. Modelling topoclimatic patterns of egg mortality of *Epirrita autumnata* (Lepidoptera : Geometridae) with a Geographical Information System: predictions for current climate and warmer climate scenarios. Journal of Applied Ecology 35:311-322.
- Volney, W. J. A. and R. A. Fleming. 2000. Climate change and impacts of boreal forest insects. Agriculture Ecosystems & Environment **82**:283-294.
- Vors, L. S. and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15:2626-2633.

Walker, D. A. and W. A. Gould. 2002. The Circumpolar Arctic Vegetation Map: AVHRR-derived base maps, environmental controls, and integrated mapping procedures. International Journal of Remote Sensing **23**:4551-4570.

- Walker, D. A., M. K. Raynolds, F. J. A. Daniels, E. Einarsson, A. Elvebakk, W. A. Gould, A. E. Katenin, S. S. Kholod, C. J. Markon, E. S. Melnikov, N. G. Moskalenko, S. S. Talbot, B. A. Yurtsev, and C. Team. 2005. The Circumpolar Arctic vegetation map. Journal of Vegetation Science 16:267-282.
- Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jonsdottir, J. A. Klein, B. Magnusson, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, O. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber, and P. A. Wookey. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America 103:1342-1346.
- Wallentin, G., U. Tappeiner, J. Strobl, and E. Tasser. 2008. Understanding alpine tree line dynamics: An individualbased model. Ecological Modelling **218**:235-246.
- Walters, C. J. 1986. Adaptive management of renewable resources. MacMillan, New York.
- Wam, H. K. and O. Hjeljord. 2010. Moose summer and winter diets along a large scale gradient of forage availability in southern Norway. European Journal of Wildlife Research **56**:745-755.
- Watson, A. 1972. The behaviour of ptarmigan. British Birds 65:6-26.
- Weeden, R. B. 1969. Foods of Rock and Willow Ptarmigan in central Alaska with comments on interspecific competition. Auk **86**:271-281.
- Wegge, P. and L. Kastdalen. 2008. Habitat and diet of young grouse broods: resource partitioning between capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*) in boreal forests. Journal of Ornithology **149**:237-244.

Wielgolaski, F. E. 1972. Vegetation types and plant biomass in tundra. Arctic and Alpine Research 4:291-305.

- Wielgolaski, F. E. 2003. Climatic factors governing plant phenological phases along a Norwegian fjord. International Journal of Biometeorology **47**:213-220.
- Wielgolaski, F. E., P. S. Karlsson, S. Neuvonen, and D. Thannheiser. 2005. Plant ecology, herbivory, and human impact in Nordic mountain birch forests. Springer, Berlin.
- Wiklund, C. G., A. Angerbjorn, E. Isakson, N. Kjellen, and M. Tannerfeldt. 1999. Lemming predators on the Siberian tundra. Ambio **28**:281-286.
- Wiklund, C. G., N. Kjellen, and E. Isakson. 1998. Mechanisms determining the spatial distribution of microtine predators on the arctic tundra. Journal of Animal Ecology **67**:91-98.
- Williams, J. B., D. Best, and C. Warford. 1980. Foraging ecology of ptarmigan at Meade River, Alaska. Auk **92**:341-351.
- Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences of the United States of America **104**:5738-5742.
- Wilson, D. J., C. J. Krebs, and T. Sinclair. 1999. Limitation of collared lemming populations during a population cycle. Oikos **87**:382-398.
- Wisz, M. S., M. P. Tamstorf, J. Madsen, and M. Jespersen. 2008. Where might the western Svalbard tundra be vulnerable to pink-footed goose (*Anser brachyrhynchus*) population expansion? Clues from species distribution models. Diversity and Distributions 14:26-37.
- Wolf, A., T. V. Callaghan, and K. Larson. 2008. Future changes in vegetation and ecosystem function of the Barents Region. Climatic Change **87**:51-73.
- Wood, S. N. 2006. Generalized additive models: an introduction with R. Taylor & Francis, CRC Press, London.
- Wookey, P. A., R. Aerts, R. D. Bardgett, F. Baptist, K. A. Brathen, J. H. C. Cornelissen, L. Gough, I. P. Hartley, D. W. Hopkins, S. Lavorel, and G. R. Shaver. 2009. Ecosystem feedbacks and cascade processes: understanding their role in the responses of arctic and alpine ecosystems to environmental change. Global Change Biology 15:1153 -1172.
- Worrell, R. 1995. European aspen (*Populus tremula* L) A review with particular reference to Scotland. 1. Distribution, ecology and genetic variation. Forestry **68**:93-105.
- Wu, Z. T., P. Dijkstra, G. W. Koch, J. Penuelas, and B. A. Hungate. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biology 17:927-942.
- Xu, L., R. B. Myneni, F. S. Chapin, T. V. Callaghan, J. E. Pinzon, C. J. Tucker, Z. Zhu, J. Bi, P. Ciais, H. Tømmervik, E. S. Euskirchen, B. C. Forbes, S. L. Piao, B. T. Anderson, S. Ganguly, R. R. Nemani, S. J. Goetz, P. S. A. Beck, A. G. Bunn, C. Cao, and J. C. Stroeve. 2013. Temperature and vegetation seasonality diminishment over northern lands. Nature Climate Change Online Early.

- Yoccoz, N. and R. Ims. 2004. Spatial population dynamics of small mammals; some methodological and practical issues. Animal Biodiversity and Conservation **27**:427-435.
- Yoccoz, N. G. 2012. Ecological Monitoring. Encyclopedia of Life Sciences (eLS). John Wiley & Sons, Ltd, Chichester.
- Yoccoz, N. G. and R. A. Ims. 1999. Demography of small mammals in cold regions: the importance of environmental variability. Ecological Bulletins **47**:137-144.
- Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001a. Monitoring of biological diversity in space and time. Trends in Ecology and Evolution **16**:446-453.
- Yoccoz, N. G., N. C. Stenseth, H. Henttonen, and A. C. Prevot-Julliard. 2001b. Effects of food addition on the seasonal density-dependent structure of bank vole *Clethrionomys glareolus* populations. Journal of Animal Ecology 70:713-720.
- Young, A. B., D. M. Cairns, C. W. Lafon, J. Moen, and L. E. Martin. 2011. Dendroclimatic relationships and possible implications for mountain birch and Scots pine at treeline in northern Sweden through the 21st century. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 41:450-459.
- Zimov, S. A. 2005. Pleistocene park: Return of the mammoth's ecosystem. Science **308**:796-798.
- Zimov, S. A., V. I. Chuprynin, A. P. Oreshko, F. S. Chapin, J. F. Reynolds, and M. C. Chapin. 1995. Steppe-tundra transitions a herbivore-driven biome shift at the end of the pleistocene. American Naturalist **146**:765-794.
- Zobitz, J. M., A. R. Desai, D. J. P. Moore, and M. A. Chadwick. 2011. A primer for data assimilation with ecological models using Markov Chain Monte Carlo (MCMC). Oecologia **167**:599-611.
- Øien, I. J. 2011. Polarjoen hekker på Varangerhalvøya i Finnmark. Vår fuglefauna: medlemstidsskrift for Norsk ornitologisk forening **34**:126-129 (in Norwegian).











CONTACT Professor Rolf Anker Ims Fram Centre, Tromsø, Norway Telephone: + 47 77 64 64 76 E-mail: rolf.ims@uit.no

- 11 A A 110 K Malaster Strates

ISBN: 978-82-999253-0-3