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FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY
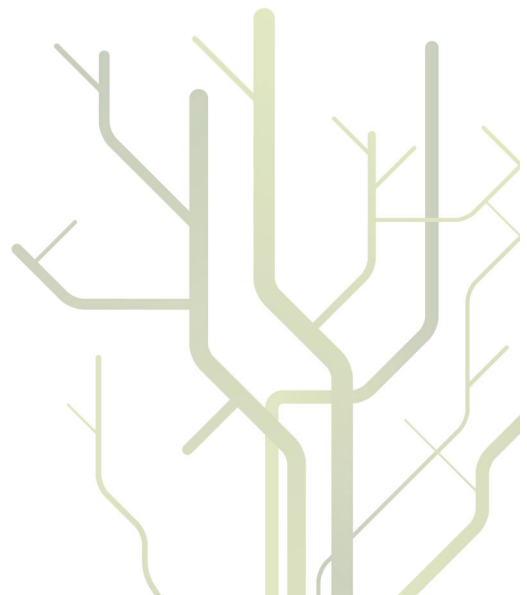
Converting sub-Arctic birch forests to spruce plantations

- responses of predators and prey

Åshild Ønvik Pedersen

A dissertation for the degree of
Philosophiae Doctor

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Åshild Ønvik Pedersen (all other photos)

Illustrations

Tove Midtun (p. 6, 8, 12)

List of papers

This thesis is based on the following original publications and submitted manuscripts which are indicated in the text by their roman numerals I - V below.

I   Pedersen, Å.Ø., Yoccoz, N.G., Ims, R.A. and Sigurdsen, T.
Effects of non-native spruce plantations on small mammal communities in sub-Arctic birch forests.
Submitted to Journal of Forest Ecology and Management, February 3, 2010.

II   Sigurdsen, T., Pedersen, Å.Ø., Yoccoz, N.G., Haukisalmi, V. and Ims, R.A.
Are endoparasites of common shrew indicators of tree species conversion from sub-Arctic birch forest to spruce plantations?
Submitted to Ecological Indicator, March 5, 2010.

III   Pedersen,Å.Ø., Ims, R.A., Yoccoz, N.G., Hausner V.H. and Juell, K.H.
Scale-dependent responses of predators and their prey to spruce plantations in sub-Arctic birch forests in winter.
Accepted Ecoscience, February 15, 2010. To be published in June 2010 issue 17 (2), doi.10.2980/17-2-3333

IV   Pedersen, Å.Ø., Yoccoz, N.G. and Ims, R.A. 2009.
Spatial and temporal patterns of artificial nest predation in mountain birch forests. *European Journal of Wildlife Research* 55: 371-384.

V   Klausen, K.B., Pedersen, Å.Ø., Yoccoz, N.G. and Ims, R.A.
Prevalence of nest predators in a sub-Arctic ecosystem.
European Journal of Wildlife Research.
Online first doi.10.1007/s10344-009-0304-1.

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Abstract

In northern Norway large areas of sub-Arctic coastal birch forests have gradually been replaced by non-native spruce plantations during the last century. Spruce planting changes the forest floor vegetation and soil conditions, increase the amount of artificial edges and alter the forest landscape mosaics. Such tree species conversions are likely to reduce or increase suitable wildlife habitat, alter animal space use patterns, habitat selection and population and community dynamics. In a spatially extensive study design using live-trapping, snow tracking and baited track boards, I studied responses of individual predator species (red fox, pine marten, stoat, least weasel, lynx and corvids) and prey species (mountain hare, voles, common shrew and gallinaceous birds) and their interactions at three spatial scales ranging from within forest stands to landscape mosaics. I also included a study along the birch forest – alpine tundra ecotone to compare nest predation in native landscapes with those impacted by tree species conversion.

In a 10 year observational trapping study of small mammals, I found much lower abundances of common shrew, red vole and field vole in spruce plantations compared to four birch forest types at stand scale. Autumn abundances were most impacted indicating that growth rates in the reproductive season were more influenced than winter declines. Species associated with productive forest habitats were most negatively impacted. Prevalence of endoparasites (helminths) in common shrew was highest in the rich birch forests and lowest in spruce plantations.

In a 3 year observational study of an assemblage of ground dwelling vertebrates in winter, scale- and time dependent responses to spruce plantations were documented for the dominating species (red fox, stoat, mountain hare and voles). Small-scale affinity to plantation edges was found for most species. Habitat selection for and against spruce plantations at stand scale alternated profoundly among the years and species, however, in qualitatively similar patterns among the dominant species. At landscape scale only red fox was negatively related to amount of spruce plantations, while mountain hares exhibited annual shifts in occurrence relative to the amount of spruce. Predators and prey were related in time and space at the two smallest scales which may be explained by year- and stand-specific snow conditions affecting the predator-prey interactions within the community.

In two experimental nest predation studies of 1 and 3 years, respectively, the omnipresent corvids were the dominant predators. The effects of spruce plantation edges and stands on predator prevalence were consistent with those of Einarsen et al. (2008), who concluded that edges and stand types had limited influence on spatial distribution of nest predators (Paper IV). Predator prevalence along the birch forest –

alpine tundra ecotone was remarkably consistent among locations and habitats. These results suggest that man-made and natural edges were not able to explain the overall high levels of predation observed.

A decade of research on different wildlife species has documented clear responses to spruce plantations. Among the strongest effects is the pervasive negative impact on small mammal abundances and passerine bird communities in the studies of Hausner et al. (2002; 2003). Common for these species are their responses to habitat qualities at small spatial scales and they serve as prey for the predator communities. Reduction in abundance of key functional species, in particular the small mammals, is expected to influence the overall community structure and dynamics of vertebrates in this boreal forest ecosystem. The relatively weak responses documented at landscape scale (except for red fox) might change when young spruce plantations matures into old closed canopy monocultures. The findings emphasise the importance of maintaining a mix of tree species and high spatial heterogeneity of forest stands to prevent negative impacts on prey species abundances.

The studies in this thesis have also shown that modern forestry can reinforce the effects of climate change. Changes in winter climate may modify snow conditions which in turn alter the role of forest stand mosaics in determining the structure of vertebrate communities. Moreover, the most probable cause of long-term declines in small mammal populations is changes in winter climate (Ims and Fuglei, 2005). These results comply with other studies reporting that modern forestry contribute to long-term declines of small mammal populations (Christensen and Hörnfeldt, 2006; Hörnfeldt *et al.*, 2006; Christensen *et al.*, 2008).

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VI

1. Introduction

1.1. Spruce plantations in sub-Arctic birch forest ecosystems

Habitat loss, fragmentation and introduction of exotic species are among the major threats to global biodiversity (Chapin *et al.*, 2000). Currently forests ecosystems cover one third of the land area worldwide. Deforestation and degradation of forest habitats still progress at an alarmingly high rate causing declines in biodiversity (Food and Agriculture Organization of the United Nations, 2006). As a consequence conservationists and foresters have over the last decades developed silvicultural practises that integrate protection of habitats and biodiversity in forest ecosystems (Sayer *et al.*, 2005).

Northern boreal birch (*Betula pubescens*) forest ecosystems have a rather limited distribution worldwide with their core areas in northern Fennoscandia and Kamchatka peninsula (Wielgolaski, 2001). The coastal birch forests in northern Norway are naturally fragmented into narrow belts and patches by fjords, mires and the ecotone between forest and alpine tundra. In this forest ecosystem large areas of birch forests have gradually been converted to non-native spruce (*Picea abies*) plantations during the last century (Hausner, 2001). Presently spruce plantations cover around 10 % of the productive forest areas in northern Norway (Sandnes, 2009). The ongoing conversion of native birch forests to non-native spruce plantations has received recent attention from conservationists because this type of silvicultural practise threaten biodiversity of boreal forest ecosystems (Directorate for Nature Management, 2006; Living Forest 2006; Living Forest Board, 2009). At the same time national forest authorities have emphasised the importance of spruce planting as a management action to reduce atmospheric CO_2 (Ministry of Agriculture and Food, 2009). Emerging debates and conflicting interests have called for a better understanding of impacts on biodiversity from tree species conversion in sub-Arctic birch forest ecosystems.

In recent years there has been focus on how introduction of non-native tree species have led to major changes in habitat quality, species assemblages, habitat use and population dynamics of different species (i.e. Baguette *et al.*, 1994; Gjerde and Saetersdal, 1997; Saetre *et al.*, 1997; Saetre, 1999; Sjöberg and Danell, 2001; Gjerde *et al.*, 2005; Einarsen *et al* , 2008). More specifically, in sub-Arctic birch forests one study documented more variation in passerine bird species composition in birch forests than spruce plantations. This effect was not evident for species richness estimates of birds between spruce plantations and the different birch forest types (Hausner *et al.*, 2002). Differences were related to habitat qualities within the forest stand such as lack of dead trees, snags and understory vegetation in the spruce plantations (Hausner *et*

al., 2002). At the landscape level only bird species sensitive to reduction in rich birch forests responded to fragmentation effects (Hausner *et al.*, 2003). Species traits (i.e. ground nesters, cavity nesters, flycatchers etc.) were promising indicators of land use impacts (Hausner *et al.*, 2003). A companion nest predation study to Paper IV of the present thesis, concluded that spruce plantation edges and stand types had relatively little influence on the spatial distribution of nest predators (Einarsen *et al.*, 2008).

1.2.   Rationale and objectives

The overall objective of this thesis was to investigate responses of an assemblage of vertebrate predators and prey species to large scale tree species conversion from native birch forests to non-native spruce plantations in a sub-Arctic ecosystem (Paper I – IV). A nest predation study along a native birch forest - alpine tundra ecotone was also conducted for comparative purposes (Paper V). Since predator and prey relations are influential in the overall community structure and dynamics in boreal forest ecosystems, I chose to study both responses of individual species and their interactions (Angelstam *et al.*, 1984; Lindström, 1989). Changing tree species composition is expected to influence forage resources and shelter for boreal herbivores (Thirgood and Hewson, 1987; Trebaticka *et al.,* 2008; Wegge and Kastdalen, 2008). Spatio-temporal distribution of herbivores inevitably affects their predators because habitat selection of predators is related to prey availability (Ryall and Fahrig, 2006). Thus, predator spatial distribution is expected to also be affected by spruce plantations.

The "appropriate" study scale depends on the questions of interest, and since this thesis has been more exploratory than testing of specific hypothesis, I choose to study the responses of individual species at three different spatial scales in which different aspects and extents of tree species conversion were expressed: (1) within forest stands (i.e. affinity to edges; Papers III - V), (2) within landscapes (i.e. among forest stands; Paper I - V) and (3) among landscapes with different amounts and configuration of forest stands (i.e. landscape mosaics; Paper III) (see also Box 1). This spatial scale hierarchy made it possible to assess if small scale responses propagated to larger scales, which is important for understanding how different responses are linked across spatial scales (Wiens, 1989).

Specific objectives addressed in my papers (I – V) were to:

I   Contrast seasonal estimates of small mammal population abundances in spruce plantations with four birch forest varieties in a landscape block design over a 10 year time period. Specifically, I explored which of the present small mammal species were most affected in terms of abundance and in which season the effect was strongest.

II   Assess prevalence and species richness of endoparasites in common shrew (*Sorex araneus*). This permitted investigation of whether endoparasites responded to spruce plantations in a manner that could be indicative of community level changes.

III   Investigate responses of predators and their prey to spruce plantations in a three-level spatial scale hierarchy. I focused on (a) species' distances to spruce stand edges to identify possible affinities, (b) species' selection for or against spruce plantations among forest stands and (c) whether species' abundances could be explained by different amounts and configurations of spruce plantation among landscapes.

IV   Assess if nest predator species showed affinities to specific forest types and artificial man-made edges by expanding the temporal scale from Einarsen et al. (2008). This enabled me to investigate the degree of temporal consistency of the spatial pattern of predation.

V   Investigate how nest predator species were distributed along a natural birch forest – alpine tundra ecotone and whether certain species showed affinities to specific habitats along the ecotone.

1.3. Impacts on wildlife from tree species conversion

For individual species inhabiting birch forest habitats, planting of non-native spruce stands can lead to: (a) loss or increase of suitable habitat, (b) change in space use patterns and (c) habitat selection and (d) altered population and community dynamics. Spatial scale-dependent responses of individual species, community processes (i.e. predator and prey interactions and inter-specific competition) and mobility of the different species, will likely influence these effects (Angelstam *et al.,* 1984; Senft *et al.*, 1987; Wiens, 1989; Hobbs, 2003).

1.3.1. Fragmentation and new edges

Habitat fragmentation is generally viewed as a combination of three processes: (a) habitat loss, (b) true fragmentation resulting in decreased patch area and increased isolation of patches and (c) changes in habitat quality of patches and amount of habitat edges (Andrén, 1994, 1996; Fahrig, 2001). Fine-grained fragmentation is a sub-division of habitat into patches smaller than the home range and territory of a species, whereas coarse-grained fragmentation happens when habitat patches are larger than the home range and territory (Rolstad, 1991). Planting of non-native spruce in this ecosystem is an example of large scale land-use changes that may lead to habitat fragmentation and habitat shredding (Hausner, 2001). Moreover, the new spruce stands, intermixed with the birch forests, create a highly heterogeneous forest landscape mosaic. Size, successional stage and spatial distribution of the spruce stands are likely to influence how the species respond to the landscape mosaic (fine vs. coarse grained). Similarly, these stand characteristics will influence availability of prey for carnivores and forage resources for herbivores, which are determinants of species habitat selection at different scales (Rolstad, 1991; Andrén, 1994; Mayor *et al.*, 2009; Paper I – III).

A characteristic feature of this new forest mosaic is numerous new high-contrast man-made edges between spruce plantations and birch forests (Paper III & IV). Elevated predation rates, inflicted by generalist species such as red fox and hooded crow (*Corvus cornix*), have been documented when forest landscapes become fragmented and mixed with agricultural land (Andrén, 1992; Yahner and Delong, 1992; Kurki, 2000; Storch *et al.*, 2005). Similarly higher predation rates have been documented in edge habitats between agricultural fields and forests compared to interior forest habitats (Gates and Gysel, 1978; Andrén, 1988; Møller, 1989; Donovan, 1997). However, research on nest predation in forested landscapes is characterised by inconsistent evidence regarding the ecological trap hypothesis (i.e. elevated predation rates along edges) (Paton, 1994; Lahti, 2001; Paper III – V).

### 1.3.2.   Compositional and structural diversity of the stands

Conversion of birch forests to spruce plantations affects the vertical penetration of light into a forest stand and lead to structural and compositional changes in the different vegetation layers (Saetre *et al.*, 1997; Saetre, 1999). Besides shading, spruce plantations lead to acidification of the soil which affects forest floor vegetation and soil fauna (Hågvar, 1989; Saetre, 1999). Such changes of environmental conditions may result in a shift in plant species composition and spatial distribution of food resources for herbivorous and insectivorous vertebrates (Paper I - III).

Compositional and structural changes in the forest stands may to some extent improve suitability as habitat for wildlife. Monoculture spruce plantations, not maintained by pre-commercial thinning, develop very dense understory layers (Hausner, 2001) providing shelter for ground dwelling herbivores like mountain hare and black grouse (Thirgood and Hewson, 1987; Svobodova *et al.*, 2004). Herbivores forage under risk of predation and habitats that provide protective cover may be incorporated in their home ranges due to reduced risk of predation (Hik, 1995; Svobodova *et al.*, 2004; Trebaticka *et al.*, 2008; Paper I – III).

In winter the dense spruce plantations affect snow conditions both in terms of snow depth and snow hardness (Paper III). Such conditions can impact access to forage resources for herbivores and hunting success of predators, and thus lead to changes in habitat use (Pruitt, 1959; Stenseth *et al.*, 2004; Boonstra and Krebs, 2006; Korslund and Steen, 2006; Sanecki *et al.*, 2006). Shifts in habitat use are likely to be important for population level processes because the temporal dynamics of boreal herbivores to a large extent are driven by predator-prey interactions (Angelstam *et al.*, 1984; Boutin *et al.*, 1995).

2. Study area

The general study area (Paper I - IV) was located in sub-Arctic birch forests in the municipalities of Evenens and Skånland (68º30 N, 16º40 E) in Nordland and Troms Counties, northern Norway (Figure 1). A comparative study area to the north (Paper IV) was located in sub-Arctic birch forests in the municipalities of Troms, Karlsøy and Balsfjord (69º N, 18-19º E) in Troms County (Figure 1). The main differences between these two study areas were related to the nature of habitat edges; the southern one representing man-made high-contrast edges between birch forests and spruce plantations in different successional stages and the northern one representing natural high-contrast edges between birch forests and low-alpine tundra.
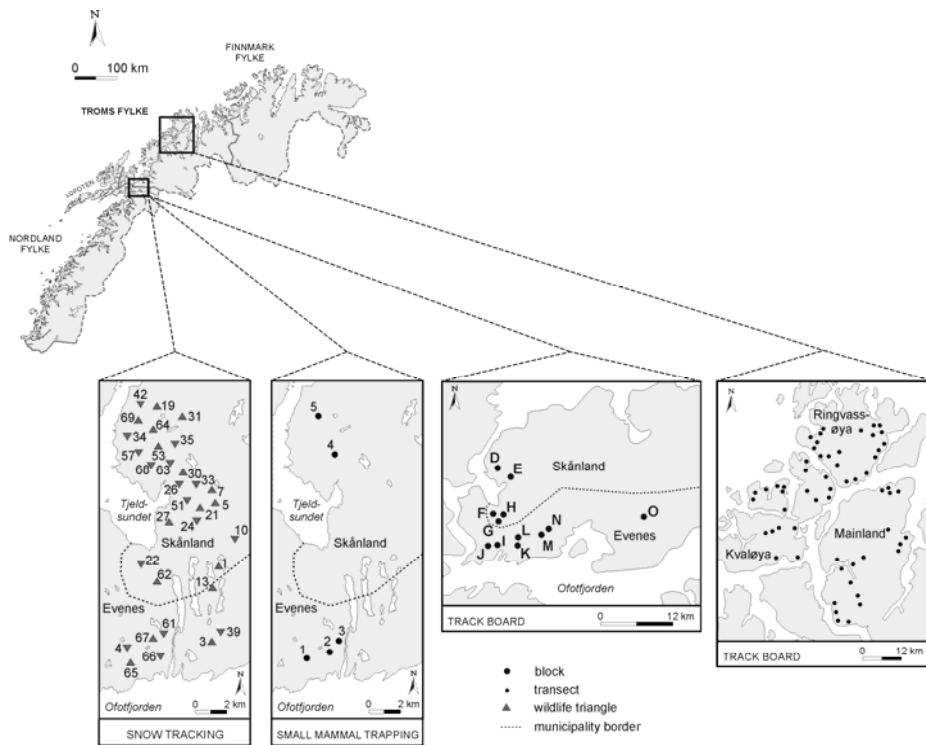
Figure 1. Map of northern Norway with insets showing the study areas with approximate placement of (from left to right): 32 equilateral triangular transects for snow tracking, 5 study blocks for small mammal trapping, 12 study blocks for baited tracks boards and 60 transects for baited track boards. Numbers or letters indicate sampling units.

2.1. Ecosystem characteristics

2.1.1. Study species

In sub-Arctic birch forest ecosystems the vertebrate community is characterised by relatively few herbivorous and carnivorous species (Henttonen and Wallgren, 2001). Small mammals, especially voles, play a key functional role in northern boreal forest ecosystems since they have major impact on the dynamics of their foraging resources and predators (Hansson and Henttonen, 1988; Ims and Fuglei, 2005).

In my studies the mammalian predators were mainly the generalists, red fox *(Vulpes vulpes),* European pine marten *(Martes martes)* and lynx *(Lynx lynx)*, and the small rodent specialists, stoat *(Mustela erminea)* and least weasel *(M. nivalis)* (Johansson, 1990a; Einarsen *et al.*, 2008). Avian predators were magpie (*Pica pica*), hooded crow (*Corvus cornix)* and raven (*Corvus corax)* (Einarsen *et al.* 2008). Important prey species were mountain hare (*Lepus timidus*), voles (field vole *Microtus agrestis,* red vole *Myodes rutilus,* grey-sided vole *M. rufocanus*), gallinaceous birds (willow grouse *Lagopus lagopus*, black grouse *Tetrao tetrix*) and insectivorous shrews (common shrew *Sorex araneus*, pygmy shrew *S. minutus,* water shrew *Neomys fodiens)* (Johansson, 1990b) (Figure 2, Box 1). For a more detailed description of the avian and mammalian vertebrate community, including ungulates and birds of prey, see Paper III.

For most of the predators in this study the spruce plantations were smaller than their home ranges and territories, hence creating a fine-grained forest mosaic landscape (Rolstad, 1991; Brainerd and Rolstad, 2002; Frafjord, 2004). In contrast the spruce plantations were for some of the prey species, such as voles and shrews, generally larger than individual home ranges and territories, hence creating a coarse-grained forest mosaic (Viitala, 1984; Rolstad, 1991).
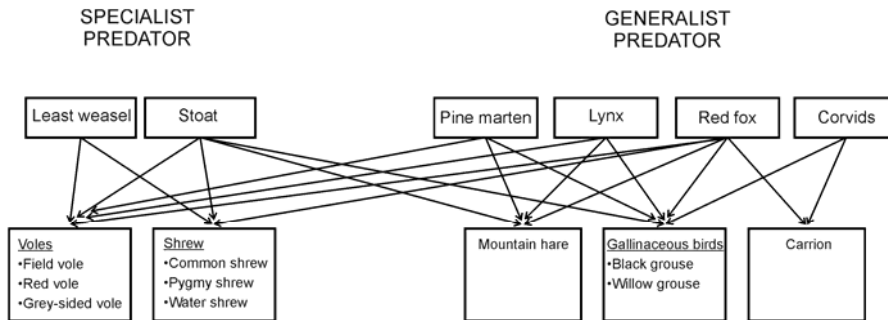
Figure 2. Trophic relations between predator and prey study species. Intra-guild predation is not indicated in the illustration.

| Box 1.	Study species and spatial and temporal study scales of research in this thesis.		
Paper	**Study species**	**Spatial scale**	**Temporal scale**
I	Field vole, red vole, grey-sided vole, common shrew	Stand	1997 – 2006 2 primary trapping periods in spring and autumn
II	Common shrew and their associated endoparasites	Stand	1997 3 primary trapping periods in spring, summer and autumn
III	Red fox, pine marten, lynx, stoat, least weasel, mountain hare, voles willow grouse, black grouse	Edge Stand Landscape	2003 – 2005 2 sampling periods each winter
IV & V	Red fox, pine marten, stoat, least weasel, hooded crow, raven, magpie, willow grouse, black grouse (other ground breeding birds of prey were waders, ducks and passerines)	Edge Stand	IV: 2003 – 2005 2 - 3 sampling periods each summer V: 2007 2 sampling periods

2.1.2. Spruce plantations in birch forests

Planting of non-native spruce in northern Norway was initiated around 1910, and prior to the 1950's planting was restricted to small patches (< 1 ha). Most plantations were established after 1950 and planting of spruce accelerated in the 1960-70's to supplement small scale agricultural households. Presently, approximately 10 % of the study area is cultivated by spruce, amounting to about 25 % of the productive area below the tree line (Ø. Kanstad, pers. comm. 2003). Most plantations are small in size (range 0.8 -17.1 ha, average 5.7 ha), relatively young in succession (around 50 – 60 years) and intermixed within the birch forest landscape, hence creating a relatively fine-grained forest mosaic (Hausner 2001) (Figure 3). Spruce plantation edges were either low-contrast edges between spruce plantations and mixed spruce-birch forests of different successional stages or high-contrast edges between spruce plantations and native birch forests, mires, agricultural fields or clear cut areas (Figure 3).

Figure 3. *Upper left:* Spruce plantations are often found in the most productive areas as illustrated here by plantations located on the south-west facing hillsides on relatively rich and most soils. *Upper right*: Coastal birch forest with a field layer dominated by ferns and herbs which in many stands were strongly influenced by grazing. *Down left:* A typical high-contrast artificial habitat edge between a spruce plantation and birch forest. *Down right*: Unthinned spruce plantation dominated by spruce litter and dead branches (predation board, Paper IV in the middle).

Analysis of compositional and structural diversity between spruce plantations and four different birch forest varieties, showed distinct differences between the spruce plantations (including the spruce section of the ecotone) and the birch dominated forest types (including mixed spruce-birch plantations) (Paper I; Figure 4). More specifically, the differences were related to lack of forest floor vegetation cover in the spruce plantations which were dominated by moss, spruce litter, roots and coarse woody debris. In contrast the birch forest varieties which dominated by ferns, herbs, grasses and juniper (Figure 4).
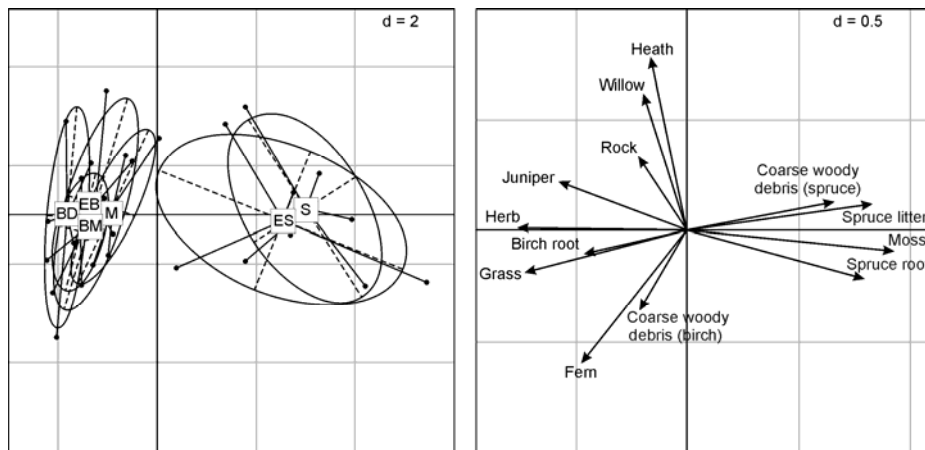
Figure 4. The degree of similarities and dissimilarities among 5 forest types (*left panel*) and their relation to 13 vegetation variables (*right panel*) derived from PCAIV ordination (Jongman *et al.,* 1995) (Paper I). *Panel left*: Positions of the forest types in the ordination space are indicated by line-connected dots. Ellipses are approximate 67% confidence limits for the bivariate distribution in the ordination space. BD = birch dry, BM = birch moist, EB = ecotone birch part, ES = ecotone spruce part, M = mixed spruce-birch plantation and S = spruce plantation *Panel right*: Correlations between the vegetation variables, mapped as coverage (%) in a circle of 2.5 m in diameter with a small mammal live-trap in the middle, and the first and second axes of PCAIV. The lengths of the arrows indicate the strength of the correlations. The first axis of the PCA on the 13 vegetation variables explained 35.7 % and the second axis 13.5 % of the variation in the dataset. The first axis of the PCAIV explained 54.0 % (R^2 = 86.2) and the second axis 17.8 % (R^2 = 87.7) of the variation of the vegetation variables.

3. Methods

3.1. Study designs and field methods

Choosing the appropriate study scale to cover ecological responses of interest, is crucial in inferential studies of spatio-temporal responses of vertebrates to landscape heterogeneity (Wiens, 1989; Orians and Wittenberger, 1991). Spruce is typically planted in stands and configuration of these stands influences the forest mosaics at landscape scale, thus allowing data sampling in a three-level spatial scale hierarchy ranging from within forest stands to landscape mosaics (see also section 1.2).

A wide variety of field methods have been developed in order to assess population state variables such as density or abundance of species (reviewed in Seber, 1986, 1992; Schwarz and Seber, 1999). In this thesis I used both observational (snow tracking, Paper III & V; live-and removal trapping, Paper I & II) and experimental (baited track boards, Paper IV & V) study methods to sample data for estimation of different abundance indices of the study species.

3.1.1. Snow tracking

Counting tracks on snow provide reliable indices of spatial and temporal relative abundance and distribution of species (i.e. Thompson, 1989; Linden *et al.*, 1996). In a spatially extensive study design of 32 permanent equilateral triangular sampling units of 3 km (termed transects), tracks of mammals and ground dwelling gallinaceous birds crossing transect lines were sampled over 3 consecutive winters (Figure 1; Paper III). Similarly, snow tracks were sampled along transects lines in native birch forests just below the tree-line as background information on relative abundance of predators and prey (Paper V). Species-specific relative track abundance was calculated as $NT / (D * NN)$ where NT is the number of tracks crossing the transect lines, D is the number of km and NN is the number of nights since last snowfall.

3.1.2. Small mammal trapping

Small mammal trapping (paper IV & V) was carried out in a block design with 5 contrasting habitat types (spruce plantations and four different birch forest varieties) within 5 replicate study blocks over 10 consecutive years (Figure 1) (Hausner *et al.*, 2002). The seasonal primary trapping period consisted of 3 trap secondary checks in spring and autumn (Pollock, 1982). One trapping grid, consisting of 16 live-traps, was placed in each habitat type in the blocks (Yoccoz and Ims, 2004; Ehrich *et al.*, 2009).

3.1.3. Prevalence of nest predators - baited track boards

To assess prevalence of nest predators in landscapes with man-made (Paper IV) and natural (Paper V) edges and habitats, baited track boards in a block design (Paper IV)

and a transect design (Paper V) were used as artificial nests (Figure 1 and Figure 5). The ecotones encompassed three habitat types in which artificial nests were placed (Figure 5). Each artificial nest consisted of one track board (0.6 x 0.6 m), smeared with non-toxic grease so that predators would leave tracks when removing the bait (Paper IV, one domestic hen egg, Figure 3; Paper V, one common quail *Coturnix coturnix* egg) (Angelstam 1986). Nests were exposed to predators for 2-3 consecutive trial periods of 10 days, coinciding with incubation of the most common birds.

3.1.4. Prevalence of endoparasites in common shrew

Prevalence of endoparasites (i.e. whether a species was present or absent in host) was recorded in juvenile common shrews trapped in autumn (1997). Host specimens were dissected and the contents of the stomachs and intestines were investigated separately with a microscope, and helminths were identified to species when possible (Paper II).
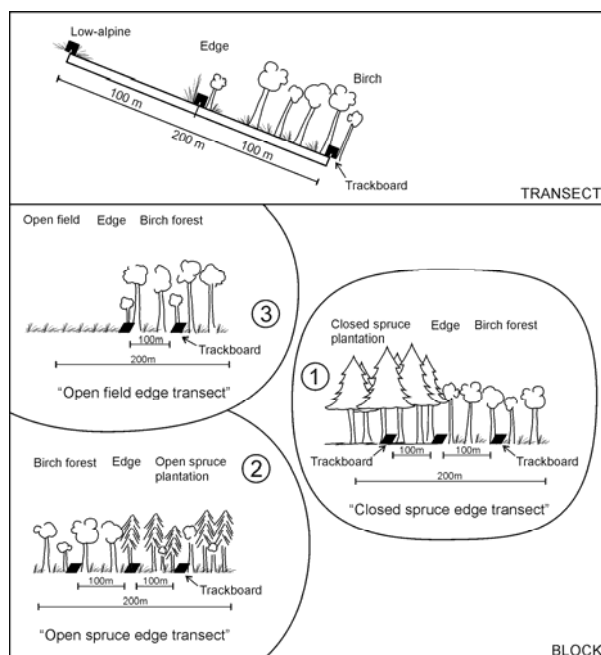
Figure 5. *Upper panel*: Transect design with placement of baited track boards along the birch forest – alpine tundra ecotone. *Lower panel*: Block design with three types of "edge transects" where the edge was defined according to type of spruce plantation (i.e. open mixed spruce-birch plantation vs. closed monoculture spruce plantation) or agricultural land the natural birch stand was bordering.

3.2. Analytical approaches

Different statistical approaches implemented in the software R (R Development Core Team, 2009) were used to analyse responses of the vertebrate community to spruce plantations at different spatial and temporal scales. In the statistical analyses I used: (a) Linear models (Paper II, abundance and body conditions of common shrews and species richness of endoparasites), (b) linear mixed effect models (Paper I, abundance of small mammals; Paper II, prevalence of helminth community; Paper III, relative track abundance and species affinity to edges), (c) logistic regression models (Paper I, sex ratio and prevalence of species-specific helminths; Paper IV & V, prevalence of nest predators) and (d) Manly's habitat selection index (Paper III; Manly, 2002). Population abundance and species richness, based on individual capture histories of red vole, field vole and helminths in common shrew, were estimated by probabilistic capture-mark-recapture models (Otis *et al.*, 1978; Manning *et al.*, 1995; Boulinier *et al.*, 1998; Rexstad and Burnham, 2000). See papers I – V for details regarding the analyses and Box 2 for sampling and analysis of vegetation variables describing composition and structure of the forest habitats.

Box 2. Summary of sampling design, field measurements and analytical approaches of compositional and structural vegetation variables used to describe habitat characteristics of the forest stands.

Sampling design: Vegetation variables describing composition and vertical structure of the forest habitats were commonly collected at sampling stations with regular intervals at or along the sampling units (i.e. around the live-traps for micro habitat composition (Paper I), along the triangular sampling units for studies of vertebrate community dynamics (Paper III) and along transect lines for studies of nest predators (Paper V)).

Field measurements: Vegetation variables were classified in the following layers: bottom- (ground level), field- (< 1 m), shrub- (0 - 2 m) and tree layer (0 - 2 m, 2 - 4 m and 4 - 10 m). The dominant vegetation variable intersecting a pre-defined measuring unit was recorded.

Analytical approaches: Different types of multivariate statistics, i.e. fuzzy correspondence analysis, principal component analysis (PCA) and PCA with respect to instrumental variables (PCAIV) were used to investigate habitat characteristics of the forest stands (Chevenet *et al.*, 1994; Jongman *et al.*, 1995; Chessel *et al.*, 2004).

4. Results

4.1. Responses to edges

In winter consistent affinity to artificial spruce stand edges was found for most of the study species, in particular among the common ones like red fox, stoat and mountain hare. Non-significant or weak responses typically coincided with limited data. In general the strength of edge affinity did not differ depending on whether tracks were set inside or outside spruce plantations (Paper III). Small scale (i.e. fine-grained) responses related to edge habitat between spruce plantations and birch forests was also documented for common shrew in autumn where the number of shrews in the birch section of the ecotone was 3 times higher than in the spruce section (Paper II).

In summer the corvids dominated among the nest predators and the effect of man-made high-contrast edges and stands on predator prevalence were consistent with those of Einarsen et al. (2008) who found that the influences of such edges and stand types on predator spatial distribution were limited (Paper IV). Similarly, along the birch forest – alpine tundra ecotone, corvids dominated and the predator prevalence was remarkably consistent among locations and habitats (Paper V).

4.2. Responses at stand scale

4.2.1. Abundance of small mammal

There was a rapid population growth of small mammals from few individuals in early summer to higher abundances in autumn in all landscape blocks and forest types (Paper I & II). None of the voles seemed to exhibit temporal dynamics resembling population cycles (Ims *et al.*, 2008). The three most common species (common shrew, red vole and field vole) were clearly less abundant in the spruce plantations compared to the birch forest types. The negative effect on abundance was larger in autumn than in spring, and field vole in the peak year was most negatively impacted by spruce plantations (i.e. around 6 times higher abundance in birch forest compared to spruce plantations) (Paper I). Shrews trapped in spruce plantations had significantly lower body weight than those caught in the forest types (Paper II).

4.2.2. Abundance of predators and prey

Highly dynamical relative track abundance patterns were detected at stand scale and the patterns were clearly consistent among numerically dominant species. There was a pervasive tendency for annual variation in Manly's habitat selection index for closed and mixed spruce plantations for the dominating species, red fox, stoat, mountain hare and voles. Spruce plantations were clearly selected some winters, while there was statistical evidence for avoidance in others. Despite this the temporally variable

selection patterns showed consistency among some of the species. Specifically, for mountain hare and voles the pattern was almost congruent both in closed and mixed spruce plantations. Moreover, habitat selection of the two most common predators for and against closed spruce plantations was similar to the two herbivorous prey species. For the less numerous species only least weasel showed significant avoidance of spruce plantations (Paper III).

4.2.3.   Prevalence and species richness of endoparasites in common shrew

In total 15 helminths, within the cestodes, nematodes and trematodes, were identified in the juvenile autumn sample of common shrew (Paper II). Prevalence of helminths, when analysed by species, showed almost no significant differences between spruce plantations and the other forest types. When analyzing prevalence in all species jointly, prevalence of helminths was around 1.5 times higher in moist birch forests compared to spruce plantations. Estimates of species richness tended to be lowest in the spruce plantations, however, differences between spruce plantations and other forest types were not significant (Paper II).

4.3.   Responses at landscape scale

The two most common species, red fox and mountain hare, were the only species with significant responses to spruce plantations at landscape scale. Red fox track abundance was negatively influenced by increasing coverage of closed spruce plantations. Mountain hare track abundance showed temporally inconsistent preference of spruce plantations, and this response was also reflected in the habitat selection index at stand scale (Paper III).

5. Discussion

5.1. Responses to edges

In winter there was a clear evidence for consistent edge affinity among both predator and prey during the study years (Paper III). In summer influences on predator prevalence from man-made and natural edges were few and weak (Paper IV). Predators affinity to edges are commonly related to increased availability of prey as demonstrated by elevated predation rates associated with edge habitats in many studies (Paton, 1994; Lahti, 2001; Ries *et al.*, 2004). Herbivores affinity to edges is often linked to availability of forage resources and shelter (Thirgood and Hewson, 1987; Hik, 1995). The contrasting results regarding edge effects may be related to differences in habitat use between seasons or more likely differences in predator species sampled and inherent biases in the field methods. Omnipresent corvids, which were not possible to survey by snow tracking in winter, dominated among the nest predators. Red fox and mustelids, which were difficult to capture on the track boards, dominated among the predators in winter.

Limited variation in predator prevalence at the scale of the edge transects, may also be attributed to the small scale of the edge transects relative to the mobility and territory sizes of the dominant predators species in the study (Smedshaug, 2002; Frafjord, 2004). Several studies have recorded edge effects in nest predation rates at roughly 50 meters, but there is evidence that this effect may reach as far as up to 4 km into forests landscapes (Storch *et al.*, 2005). In addition visual detection distances for birds are likely to be much greater and this may have accentuated the difference in prevalence of avian and mammalian predators. Moreover, the high consistent predation pressure from corvids may result from development of search images and learning abilities (Sonerud and Fjeld, 1987).

5.2. Responses at stand scale

The strongest and most consistent responses were found at stand scale for species with small home ranges and territories (Paper I & II). The voles, field vole and red vole, and common shrew were clearly less abundant in spruce plantations and species associated with productive forest habitats were most negatively impacted (Viitala, 1977; Hanski, 1984). Hausner et al. (2002) documented differences in species composition between spruce plantations and different birch forest types and a tendency for rich birch forests to host a higher number of species than spruce plantations. Common for our studies was that responses were related to structural and functional habitat qualities within the stand at a relatively small scale (Hausner *et al.*, 2002). Lack of dead trees, snags and understory vegetation influenced passerine bird

communities (Hausner *et al.*, 2002; Hausner *et al.*, 2003), whereas in my studies (Paper I & II) lack of forest floor vegetation and changes in soil fauna probably impacted both food resource and shelter for herbivorous and insectivorous small mammals (Ecke *et al.*, 2001; Ecke *et al.*, 2002; Hansson, 2002; Hagar, 2007; Trebaticka *et al.*, 2008). This implies that conversion of birch forests to spruce monocultures, in particular the richest ones, will have a major negative impact on vertebrates at stand scale (Paper I – III; Hausner *et al.*, 2002; Hausner *et al.*, 2003).

In winter there was a highly dynamical habitat selection pattern among the dominant study species and years (Paper III). This indicate that species with large home range or territory requirements such as red fox, stoat and mountain hare (Frafjord, 2004; Dahl and Willebrand, 2005; Hellstedt and Henttonen, 2006) showed a less consistent response at stand scale to spruce plantations compared to species with small home ranges (see above). The temporal habitat selection pattern for the dominant predator and prey species showed, however, correspondence at stand scale emphasising the importance of predator-prey interactions in this forest ecosystem (Paper III). Temporal variation in habitat selection of herbivores may be related to predation risk (i.e. Hik, 1995; Brainerd *et al.*, 1995; Trebaticka *et al.*, 2008) or that there is a bottom-up effect following from temporal variation in access of forage resources that propagate to the predator level. Still, the highly dynamical pattern was in need for an explanation. Thus, I proposed spatio-temporally variable snow conditions, verified by an interactive effect of habitat and year on snow depth with generally less snow in spruce plantations compared to other habitat types (see Paper III, Appendix II), to underlie such mechanisms of temporally changing habitat selection. Snow depth and quality of snow cover impact access to forage resources in herbivores and predator hunting success, and this have previously been emphasised in several papers (Pruitt, 1959; Hansson, 2002; Aars and Ims, 2002; Stenseth *et al.*, 2004; Boonstra and Krebs, 2006; Korslund and Steen, 2006; Sanecki *et al.*, 2006; Forchhammer *et al.*, 2008). Such conditions are expected to influence spatial distribution of small ground dwelling herbivore prey and their predators in this sub-Arctic birch forest ecosystem.

Monitoring of biological indicators can provide early warnings of ecological changes and loss of biodiversity (Heink and Kowatik 2010). Indicators should facilitate cost-effective methods to monitor biodiversity at forest stand scales (Similä *et al.* 2006; Hausner *et al.* 2003). Small mammals are suggested as indicators of sustainable forest management (Carey and Harrington, 2001; Pearce and Venier, 2005) and species traits of passerine birds as indicators of land use changes due to tree species conversion (Hausner *et al.* 2003). In Paper II, my results suggest that monitoring of common shrew abundances at stand scale is a suitable method to detect

changes in forest floor and soil fauna, rather than laborious sampling and analysis of endoparasites in common shrew. The suitability of small mammals as indicators are even enhanced in sub-Arctic ecosystems where they play a key role in food webs both as consumers and as prey (Ims and Fuglei, 2005). Reduced abundance of small mammals is expected to impact populations of predators dependent on small mammals as prey (Klemola *et al.*, 1999; Brandt and Lambin, 2007). Specialist vole predators, such as stoat and least weasel (Henttonen *et al.*, 1987; Norrdahl and Korpimäki, 1995), and the forest dwelling avian predators, such as Tengmalm's owls (*Aegolius funereus*) (Hörnfeldt *et al.*, 2005), are in particular expected to be negatively impacted (Paper I). The tight relations between small mammal prey species and predators in boreal forest ecosystems (Angelstam *et al.* 1984) may imply that monitoring of small mammal populations is likely to be more efficient than monitoring species traits of passerine bird communities to detect ecological community level changes due to tree species conversion.

5.3. Responses at landscape scale

Distribution patterns of predator and prey at landscape scale showed few significant relations to the area coverage of spruce plantations and the amount of spruce edges (Paper III). Clear small-scale responses, such as affinity to spruce edges, did not translate to a positive effect of amount of spruce edge at the landscape level for any species, thus limiting the ability to generalize conclusions across scales in this sub-Arctic birch forest landscape (Wiens, 1989; Mayor et al. 2009). Only the habitat generalist red fox was negatively related to amount of closed spruce plantations at landscape scales, but this was not reflected in occurrence of prey such as the mountain hare (Dell'Arte *et al.*, 2007). None of the genuine forest dwelling species, like pine marten or lynx (Pulliainen, 1984; Sunde *et al.*, 2000; May *et al.*, 2008) responded to spruce plantations at stand or landscape scales. This indicates that species with large home ranges and territories may be less affected by the present amount of spruce plantations since they operate on much larger spatial scales. Responses at landscape scale may change when the currently young spruce plantations (i.e. < 60 years) at stand scale mature to old closed canopy monocultures with different structural and functional characteristics that are expected to negatively influence spatial dynamics of both predator and prey.

6. Conclusions and management implications

A decade of research on avian and mammalian wildlife species has documented clear responses to tree species conversion from sub-Arctic birch forests to spruce plantations. Responses were strongest for species with small home ranges and territories and at the two smallest spatial scales. The most pervasive negative impact was on small mammal abundances and passerine bird communities in the studies of Hausner et al. (2002; 2003). Common for these species are their responses to changes in habitat qualities at stand scale which may, over time, propagate to predator communities.

Animal-habitat relations were highly scale-dependent and temporally consistent small-scale responses were not reflected on larger scales, thus limiting the possibility to generalize conclusions across spatial scales. Vertebrate responses at landscape scale were few and weak, however, their responses may change when the young spruce plantations (i.e. presently < 60 years) mature to old closed canopy monocultures with different structural and functional habitat characteristics at stand scale, which in turn will negatively influence spatio-temporal dynamics of predator and prey. Moreover, predicting future responses of vertebrates at landscape scale is a challenging task since the forest landscape mosaic is changing with succession of the forest stands. This possibility calls for long-term monitoring of vertebrates and their interactions with the forest habitats and mosaics in this birch forest ecosystem. Monitoring passerine bird communities allow for detecting changes both at the forest floor and in the over- and understory vegetation of the stand as well as on larger scales, though most of them are migratory and respond to spruce plantations only in the summer season. Monitoring of key functional species such as the small mammals (i.e. common shrew) is likely more efficient than monitoring species traits of passerine bird communities or endoparasites in common shrew to indicate ecological community level changes due to tree species conversion.

The studies in this thesis have also shown that modern forestry can reinforce the effects of climate change. Changes in winter climate may modify snow conditions which in turn alter the role of forest stand mosaics in determining the structure of vertebrate communities. Moreover, the most probable cause of long-term declines in small mammal populations is changes in winter climate (Ims and Fuglei, 2005). These results comply with other studies reporting that modern forestry contribute to long-term declines of small mammal populations (Hörnfeldt 2004; Christensen and Hörnfeldt, 2006; Hörnfeldt *et al.*, 2006; Christensen *et al.*, 2008).

In this thesis I have pointed out some management actions that are summarized below as recommendations for nature- and forestry management authorities.

- Abundance of small mammals was clearly much higher in both dry and moist birch forests compared to spruce plantations (Paper I & II). This implies, that tree species conversion independently of birch forest type, will negatively impact the small mammal community and their predators (Paper I).

- The abundance of small mammals in spruce plantations mixed with birch trees, and in the ecotones between spruce plantations and birch forests, was not significantly lower than in the native birch stands (Paper I). This indicates that the negative impacts of spruce plantations can be mitigated by managing spruce plantations to maintain a mix of different tree species in polycultures instead of monocultures and by high spatial heterogeneity of forest stands.

- Forestry practices such as pre-commercial and commercial thinning are recommended to modify stand density of spruce plantations to favour development of understory vegetation, hence reducing the negative effects on small mammal abundances when the spruce plantations age and become closed canopy monocultures covering more of the original birch forests (Paper I).

- Monitoring abundance of small mammals, in particular common shrews, is likely to be an efficient way of detecting changes in the forest floor and soil fauna resulting from tree species conversion (Paper I & II).

- Corvid predation on ground nesting birds was habitat independent (Paper IV & V). This implies that ground nesting birds may not be selective with respect to nesting habitats. However, due to the high abundance of the omnipresent hooded crow, this important nest predator should be considered for management actions to increase nesting success of game species such as willow grouse in coastal sub-Arctic birch forests.

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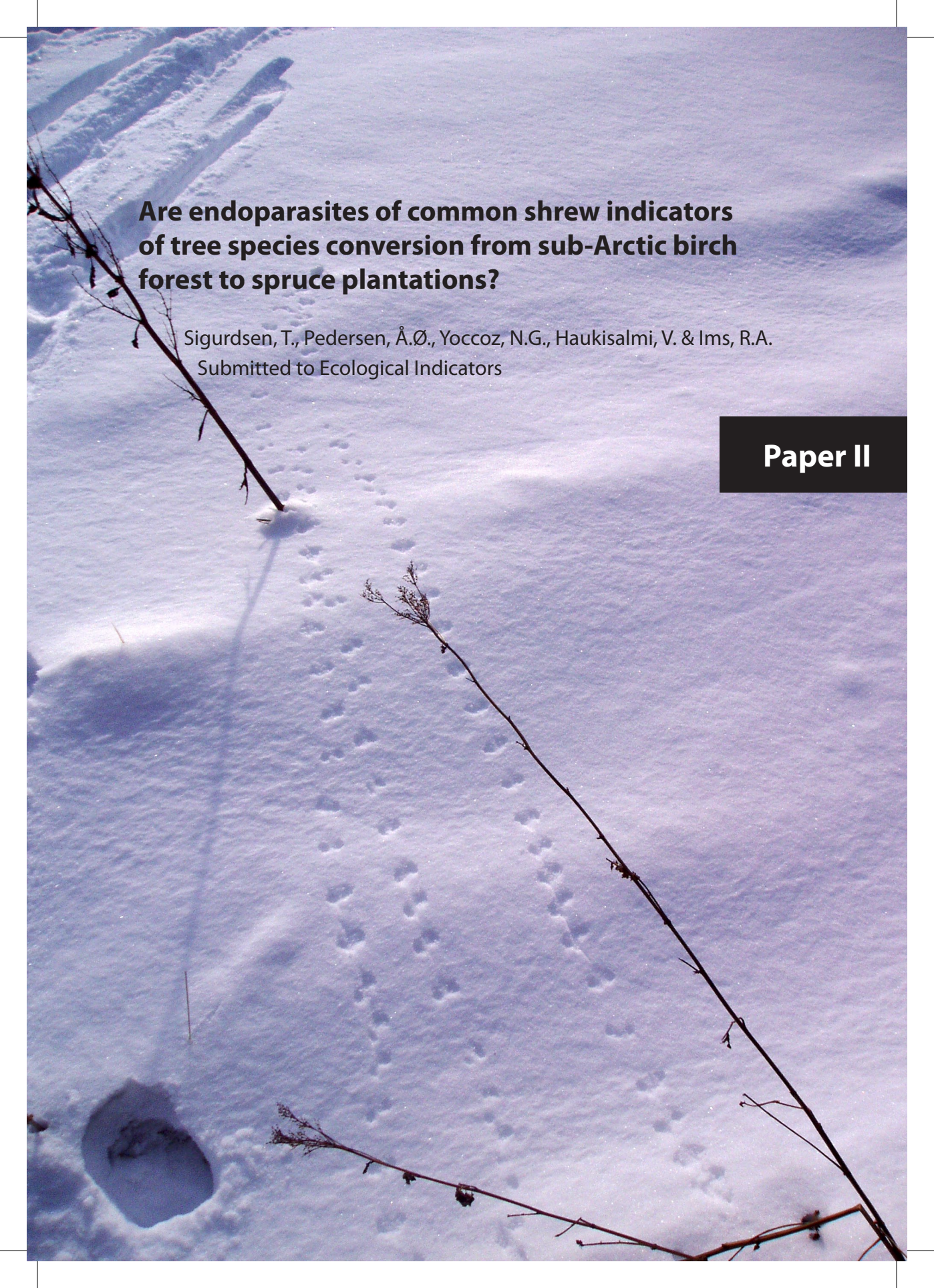
Effects of non-native spruce plantations on a small mammal community in sub-Arctic birch forests

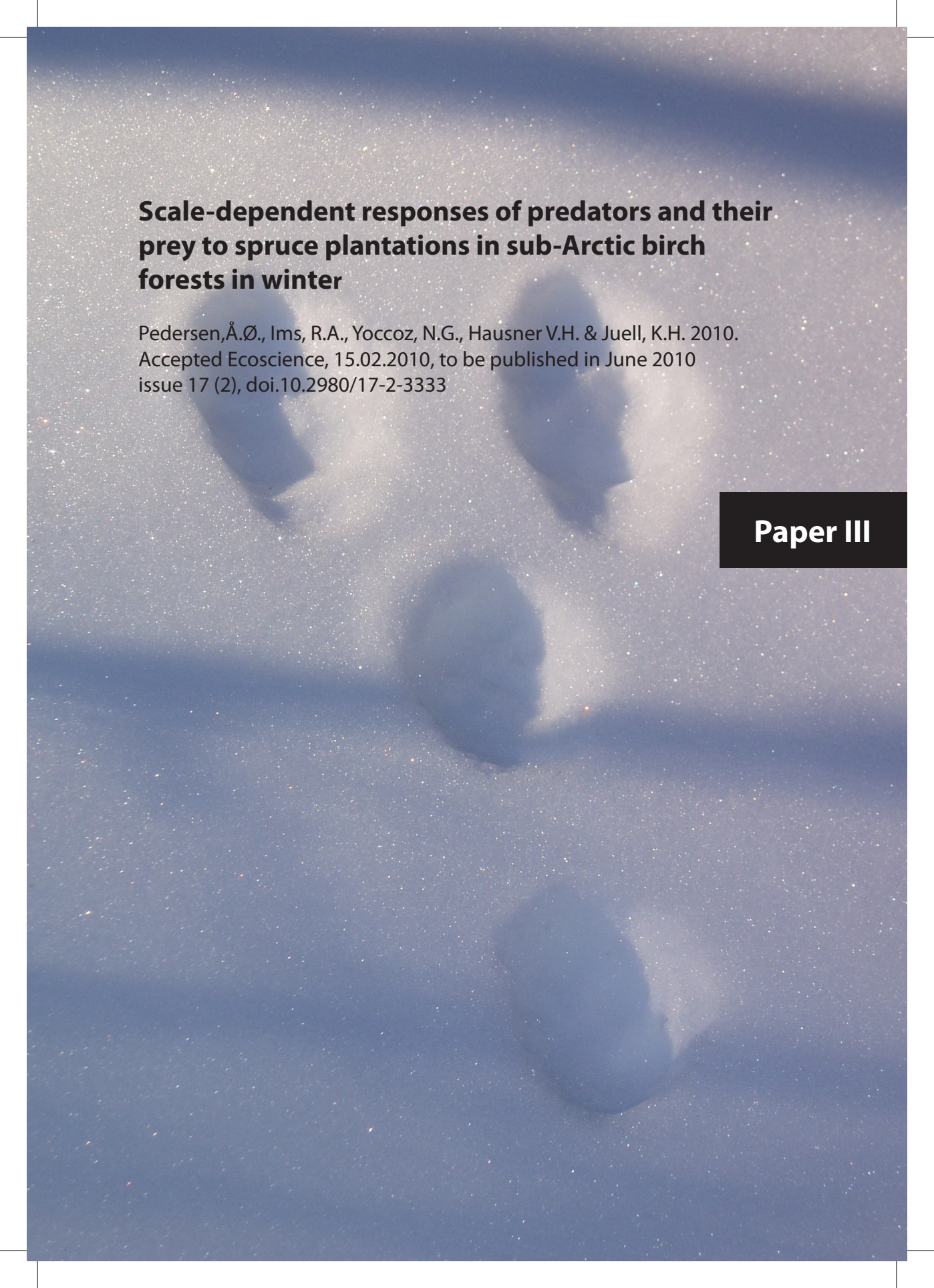Pedersen, Å.Ø., Yoccoz, N.G., Ims, R.A. & Sigurdsen, T

Paper I

Are endoparasites of common shrew indicators of tree species conversion from sub-Arctic birch forest to spruce plantations?

Sigurdsen, T., Pedersen, Å.Ø., Yoccoz, N.G., Haukisalmi, V. & Ims, R.A.
Submitted to Ecological Indicators

Paper II

Scale-dependent responses of predators and their prey to spruce plantations in sub-Arctic birch forests in winter

Paper III

Spatial and temporal patterns of artificial nest predation in mountain birch forests

Paper IV

Prevalence of nest predators in a sub-Arctic ecosystem

Paper V