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Vegetation dynamics in semi-natural cultural landscapes. - Consequences of changed agricultural practices in Eastern Jotunheimen - Norway

Thesis for the degree philosophiae doctor

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Preface

This PhD thesis was started in 2003 as part of a larger European project: "BioScene, Scenarios for reconciling biodiversity conservation with declining agricultural use in the mountains of Europe". The overall objective of this project was to analyze and evaluate the biodiversity consequences of agricultural decline and restructuring in mountain areas of Europe. Case studies were taken part in six European countries where environmental, social and economic aspects were investigated and merged in sustainability assessments. I was lucky to take part in this project under the supervision of E. Gunilla A. Olsson, thanks Gunilla! During this project I have learned about both environmental problems and possibilities in various European countries, including Norway. In addition, I have learned about the importance of co-operations among disciplines. Therefore I would like to thanks all the BioScene partners during 2003-2005, especially the project's co-ordinator Jonathan Mitchley and my Norwegian partners E. Gunilla A. Olsson, Susanne K. Hanssen, Katrina Rønningen, Bjørn E. Flø, and Frank Egil Holm! Much of the work I have done is based upon the data collected by Synnøve N. Grenne and Anna Ekrem. I would therefore also like to thank them!

When Gunilla got a position in her childhood town and moved to Sweden, Bård Pedersen (main supervisor) and Lars Söderström had to take care of me. Thanks a lot to for all guidance during the last year and staying up to midnights and even longer the last month!

Additional funding from the Department of Biology and The Faculty of Natural Sciences and Technology at the Norwegian University of Science and Technology (NTNU) was received. This made it possible to sum up the results of the study when EU would not give more money to a person giving birth to two children and staying home for several moths. Therefore thanks to the institute and the faculty! (And for the benefits of being a Norwegian citizen….)

First Susanne K. Hanssen was doomed to share office with me, thereafter Line Johansen. Thanks to both of you, helping me to answer all kinds of questions! I would also like to thank the other colleges at the department and friends outside the working environment!

Last I would like to thank my family: Mom, dad and my sisters for helping me out looking after my children whenever necessary; My “parents in law” for answering all kinds of agricultural related questions; and Brage, Kajsa and Mickal.

Sølvi

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General introduction

Agricultural practices that had been used during several centuries were dramatically changed between the 1950s - 1960s in south-central Norwegian mountain areas (Kvamme et al. 1999, Nedkvitne et al. 1955, Olsson et al. 1998). New technologies, agricultural policies, and increasing globalised markets caused a restructure of the traditional agricultural practices (Green 2005, Statistics Norway 1999, 2006). Restructuring happened since the economic feasibility of the old practices decreased.

Studies have shown that transitions among vegetation classes and shifts in the forest line have occurred during the last decades in the mountain landscapes (Olsson et al. 1998, Olsson et al. 2000, Vandvik and Birks 2004). The vegetation changes observed have been linked to the changes in the agricultural practises. This thesis deals with the relations between human activity and vegetation changes in cultural landscapes in Eastern Jotunheimen, south-central Norway. It deals both with changes in forest line and in vegetation types below the forest line. In addition a red listed herb *Primula scandinavica* is studied as an example of how plants may react on the changes.

Mountain cultural landscapes

In the broadest sense cultural landscape is defined as a land area shaped by human use. This definition includes most areas in Norway (Framstad et al. 1998). The World Heritage Committee defined cultural landscapes as "the combined work of nature and of man" (UNESCO 2005) which narrows the consept to landscapes where some aspects of nature still remain. A city might therefore not be a cultural landscape since most landscape elements are strictly human made. In comparison, more remote araes will be more shaped by natural processes and less by human activities. Pyšek et al. (2002) defined a semi-natural cultural landscape as all aspects of a human influenced landscape except the areas strictly human made such as arable land, roads and buildings. Here this definition is applied and the dynamics studied in the mountain landscapes is restricted to the semi-natural cultural landscape.

Mountains have been used by humans since prehistoric times and are, to a great extent, cultural landscapes shaped by different farming systems (Jodha 1997, Parish 2002). In

Norway the history of land use is 10000 years, from the ice recession after the ice age (Norderhaug et al. 1999). During the first thousand years land use include only hunting and gathering (the pre-Neolithic phase), and the landscape can be defined as completely natural (Krönert et al. 2001). The Neolithic revolution in Norway began in 4000 BC, but only at lower altitudes (Myhre 2004). Semi-natural cultural landscapes were as a consequence of this formed in these areas. The area of semi-natural cultural landscapes expanded as human population increased and farm settlements were established also in the inland valleys. But as human population rose, the need for resources increased. Thus, more remote and climatically harsher mountain areas had to be used. In south-central Norwegian mountain areas transhumance practice evolved. Livestock was brought from main farm settlements to additional farm settlements (summer-farms) in regions of higher altitude to utilize pasture resources there. This mountain summer farming practice has been used more or less continuously since the 14th century (Reinton 1955, Fritsvold 1999, Lunden 2004). Summer-farm practices included free-range grazing by goats, cattle, and sheep, logging of timber for fuel and construction, and managing of land for food and/or fodder production. These systems formed semi-natural landscapes consisting of a mosaic of open grasslands, heaths, fens and bogs among forested habitats (Kvamme, 1988) – a heterogeneous landscape. Plant species originally distributed in low-alpine habitats as well as lower altitudinal regions have established in these open habitats. Today they are widely distributed in the mountain cultural landscape.

As a response to the industrial revolution in Europe there was a shift in patterns of employment also in Norway during the last century. During 1945 – 1950 more people became employees in the industrial sector compared to the agricultural sector (Almås 2002). The policy was that land use had to be modernized and rationalized. Agriculture also in the mountain areas were shifting from manually clearing and managing the cultural landscape to use of machines and fertilizers. The livestock that included different breeds and different species was replaced by livestock including only one cattle breed (Norsk Rødt Fe; NRF) that was bred for production of both milk and meat. As a consequence of the industrialization processes, free-range grazing of goat and cattle in south-central mountains was abandoned and NRF were let to graze in enclosed pastures. In addition increased regulations in accordance with hygiene (HOD 1995) have during the 1960s to present, forced many small-scale milk processors to abandon their practise. Some land close to the summer-farm settlements was converted to arable land allowing livestock to graze there only after harvesting. On the other hand, more economic feasible husbandry practices of livestock cooperatives including semi-natural reindeer and free-ranging sheep have established and increased during the last decades (data provided by Norway statistics and Reindriftsforvaltningen).

Modernization processes in agriculture have been claimed to alter the vegetation mosaic pattern of cultural landscapes (Asak 1974, Grenne 1998, Fjellstad and Dramstad 1999, Olsson et al. 2000, Hietala-Koivu 2002). These studies have shown that after decreased agricultural activities forest will establish in open semi-natural vegetation types both above and below the forest line. Semi-natural landscapes are of high historical value as they are important aspects of the cultural heritage (UNESCO 2005). The decrease of open vegetation types therefore threatens the (agri-) cultural heritage. Further, as a consequence of the loss of open habitats, species linked to them have decreased (Austrheim et al. 1999, Endels et al. 2002). Some species have even decreased at such levels that they have been assessed as threatened. 30% of the flowering species and 50% of the bird species on the Norwgian Red List 2006 are associated with habitats influenced and shaped by traditional human use (Kålås et al. 2006).

The Norwegian agriculture has in general relied on governmental subsidies (Almås et al. 2004). To compensate for the low subsidies given during the last decades the economy of some rural communities has moved from the less economic feasible animal husbandry towards the more profitable tourism industry (Solliva et al. 2008). Semi-natural cultural landscapes have been attractive areas for tourism and recreation activities. A recent perspective views farmers as multi-functional. Farmers are not only produce agricultural products but also maintain biodiversity and the common cultural heritage (Hanrahan and Zinn, 2005). Policy makers have increased their awareness and understanding of this multi-functionality of agricultural practices. WTO negotiations have indicated that subsidies to agricultural production has to be further decreased (WTO 2001, 2004). However, as a response to the WTO negotations and the awareness about other beneficial outcomes but food from the agricultural activities, a way of granting has been developed through "green" payments in agri-environmental programs. These grants subsidize not only food and agricultural products but maintenance of biodiversity, cultural heritage and rural viability. Members of the Norwegian government have stated that provisions for maintenance of the openness in the cultural landscape (Office of the Prime Minister 2007). Payments are given through measures such as SMIL (Forskrift om tilskudd til spesielle miljøtiltak i jordbruket) and RMP (Regionale miljøtiltak) to support managements that maintain both biological aspects as well as the cultural heritage in a cultural landscape. The aspects associated to a semi-natural cultural landscape includes the border between the boreal and the alpine zone, the vegetation mosaic, and rare species, If, all these aspects are to be maintained, however, detailed information about how agricultural practices relate to them have to be obtained.

List of papers

This thesis is based on five papers, which are referred to in the text by their Roman numerals.

I) Wehn, S. A map-based method for exploring responses to different levels of grazing pressure at the landscape scale. (Submitted)

II) Olsson, E.G.A., Hanssen, S.K., and Wehn, S. Forest line changes after 1960 in Norwegian mountains - implications for the future? (Submitted)

III) Wehn, S., Pedersen, B., and Hanssen, S.K. A comparison of influences by cattle, goat, sheep and reindeer on vegetation transitions in mountain cultural landscapes in Norway. (Manuscript)

IV) Olsson, E.G.A., Rønningen, K., Hanssen, S.K., and Wehn, S. The interrelationship of biodiversity and rural viability in mountain environments – sustainability assessment of land use scenarios. (Submitted)

V) Wehn, S., Olsson, E.G.A., and Söderström, L. Habitat preferences and population structure of the endemic herb *Primula scandinavica* in semi-natural landscapes. (Manuscript)

Objectives

The specific aims of the different papers in this thesis have been to

1) develop a method to construct indices of potential grazing pressure from domestic animals grazing in cultural landscapes (Paper I) .
2) assess transitions among five vegetation classes (grassland, heath, scrub, and pine- and birch forests) and displacement of the altitudinal position of the forest line (Paper I, III, IV).
3) spatially relate vegetation variables to the indices of grazing pressure, and thereafter investigate the influence of former and current livestock husbandry on spatial distribution of vegetation classes and altitudinal position of forest lines (Paper I, III, IV).
4) use the relations between changed agricultural practices and transitions among vegetation classes to construct scenarios of cultural landscapes given different agri-environmental policies (Paper V)
5) use scenarios of socio-economic variables given different agri-environmental policies to assess rural viability in south-central mountains in Norway (Paper V)
6) spatially relate spatial distribution and population structure of *Primula scandinavica* to the indices of present grazing pressure and other human related variables such as logging, fertilizing, paths, roadsides, and vegetation classes, and thereafter investigate the influence of agriculture and other human disturbance on *P. scandinavica* (Paper II).

Declaration of contributions

I contributed with ideas, planning of fieldwork, data collection, data analyses, and writing parts of II. Olsson contributed with ideas, planning of fieldwork, and leading the writing process. Hanssen contributed with ideas, planning of fieldwork, data collection, data analyses, and writing.

I came up with the idea as well as analyzed the data and wrote III. Pedersen contributed with planning and interpretation of the statistical analyzes as well as commenting on the paper. Hanssen contributed with data collection and commenting on the paper.

For paper IV I contributed with planning, data collection, data analyzes and writing. Olsson contributed with ideas, planning, and leading the writing process. Rønningen contributed with ideas, planning, data collection, data analyzes, and writing. Hansen contributed with planning, data collection, data analyzes and writing.

I contributed with ideas, planning, data collection, data analyzes, and wrote V. Olsson contributed with ideas, planning and commenting. Söderström contributed with ideas, planning and commenting.

Study area

The study area in the Eastern Jotunheimen is of special interest, since it is one of the few semi-natural mountain areas in Norway where summer farming still takes place. The area has a long history of human activity. After the deglaciation of the Jotunheimen mountain area that is estimated to have happened around 9500 yr BP (Barnett et al. 2001), there was a period without human influence. Archeological investigations in the area have, however, have found settlements as early as 4000 and 3000 years ago at altitudes of 850 and 1000 m a.s.l. (Asak 1975, Hougen 1944). Semi-nomads that followed the migration routes of reindeers are assumed to have used these settlements. Mountain farming has been practiced in the area since the 14th century. Decrease in the human population due to the Black Death in 1350 caused abandonment of many of the mountain farms. A new increase in farming took place in the 17th century, but now only as seasonal farms. However, the seasonal farms were used both during summer and winter (Asak 1981). Due to long distances from the main farms near the municipality centers to the seasonal farms in the mountains, it was more practical to bring the animals to the stored fodder at the seasonal farm also during winter, than bring the fodder to the main farm. Free-range grazing of goats and cattle has been practiced around the summer-farms during summer since the oldest summer-farms were established in

1630.

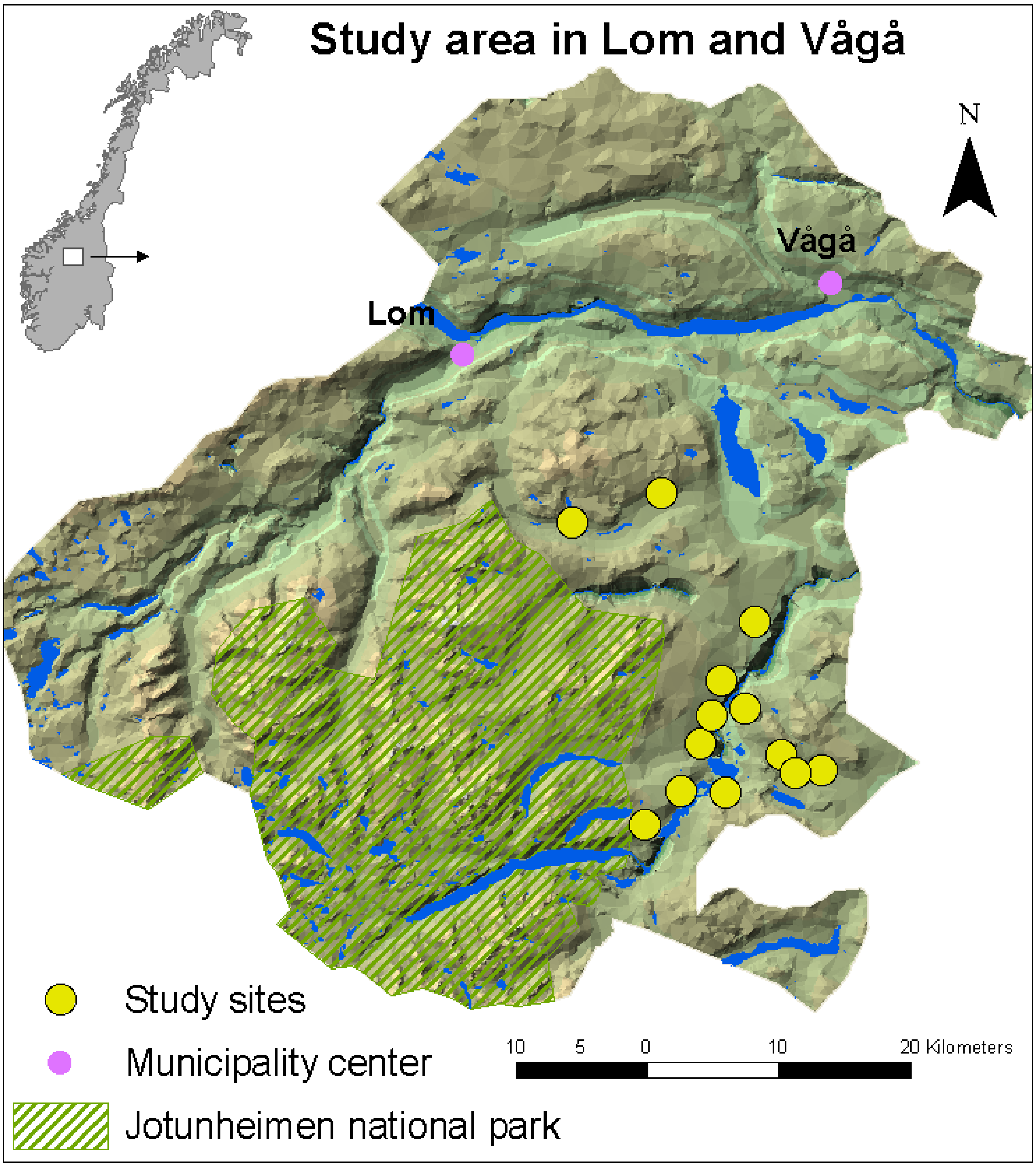

Figure 1

A map of the studied area in the Eastern Jotunheimen (map: S.K. Hanssen).

Seasonal farming declined during the last century. The practice of "mountain winter farming" ended during the 1930s (Asak 1981) and after the 1960s abandonment of summer-farming activities have escalated (Asak 1975, Grenne 1998). Milk production on the summer-farms came to an end and the earlier free-range grazing of goats and cattle were abandoned in most areas. Two joint farms of goat keeping were, however, established, in 1965 and the goats at these farms were still allowed to free-range grazing. But as the goats have to return to the barns for milking the area grazed is limited. A few cattle herds are still brought to the summer-farms but most of the cattle graze only in enclosures. However, semi-domestic reindeer and sheep have generally increased in numbers in the mountain area as cooperatives were established in the 1940s and 1970s respectively.

Today there are 180 summer farms in the eastern part of Jotunheimen registered in the local council of Vågå, but only 35 of these produce milk (Karlstad pers com). In the local council of Lom 190 summer farms are registered, of which 17 are in use (Dalseng pers com).

The climate is continental. Sediment analyses indicate that climatic conditions have been varying during the Holocene but that summer temperatures during the last 100 years have been higher compared with the rest of the period (Nesje et al. 2004). During the last 30 years, however, the mean annual temperature was -0,2^{o}C and mean annual precipitation 490 mm (data provided by Norwegian Meteorological Institute). The bedrock is mostly basic (gabbro, amphibolite, phyllite, and limestone), but gneiss and quartzite is also present. Most of the study area were covered with till, mostly as a continuous layer (data provided by Norwegian Geological Survey).

Human impact has decreased forest distribution the last 2000 years as it had been observed a decline in arboreal pollen and increase in pollen types related to grazing and fodder production (Bjune 2005). After the 1960s, however, forest is establishing in the open semi-natural vegetation types. However, the cultural landscapes still include species rich open, semi-natural habitats (Olsson et al. 2000). Open heathland communities are present and dominated by *Ericacae* species such as *Calluna vulgaris* and *Vaccinium* species, but with high abundance of grasses, sedges, and herbs. Close to summer-farms, mostly in enclosures, semi-natural grasslands are found. Most of these are only moderately fertilised and include a high number of grasses, sedges and herb species (Olsson et al. 2004). Willow (*Salix* sp.), juniper (*Juniperus communis*), birch, and pine are establishing in open habitats below the forest line (Olsson et al. 2000.). The forest line (940-1260 m a.s.l) is composed of mountain birch (*Betula pubescens* ssp. *tortuosa*) and in some parts pine (*Pinus sylvestris*).

Changes in vegetation of the semi-natural cultural landscape 1960s - 2002

Changes in sub-alpine vegetation

The semi-natural cultural landscapes have changed in the study area the last 40 years. A series of vegetation maps (1960s – 2002) digitized from aerial photos (I, III) shows that a considerable part of open vegetation types such as grasslands and even more heathlands are transformed to scrub and forest (Figure 2). Also transitions from forest and scrubland to open vegetation had occurred (Figure 2). Establishment of forest in open habitats have been observed in most studies of summer-farm landscapes in Norway (Olsson et al. 2000) and is considered a threat to biodiversity and cultural heritage in the cultural landscapes. The transitions from forested areas to open vegetation types have, however not, been dealt much with when discussing cultural landscapes in mountains in south central Norway. Although they have been considered in studies from the northern part of Norway (Tømmervik et al. 2004) and the British Islands (Thomson et al. 1995).

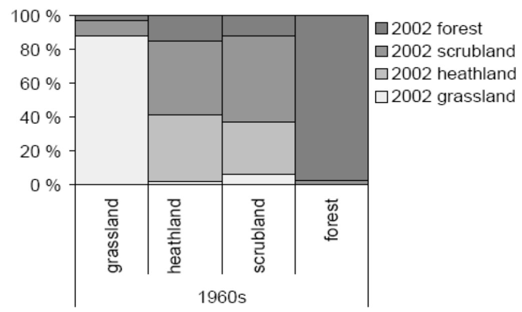

Figure 2
Vegetation transitions in the sub-alpine study sites in Eastern Jotunheimen.

The transitions in the study area were significantly related to changes in grazing pressure by domestic animals. Heathland and scrubland were the vegetation classes that had changed most (Figure 2). They were found in the sub-alpine commons outside the enclosed pastures. Here the most frequent change in grazing pressure was a small decrease in the amount of fodder eaten per area annually (Figure 3a). Free-range grazing by cattle and goats had before the 1960s maintained open semi-natural vegetation in summer-farm surroundings. In the 1960s this practice was largely abandoned and partly replaced by grazing by sheeps. Sheep is, however, not as effective to suppress forest and scrub establishment as cattle and goats (III). Therefore a high percentage of heathland was transformed to forest and scrubland (Figure 2; I, III).

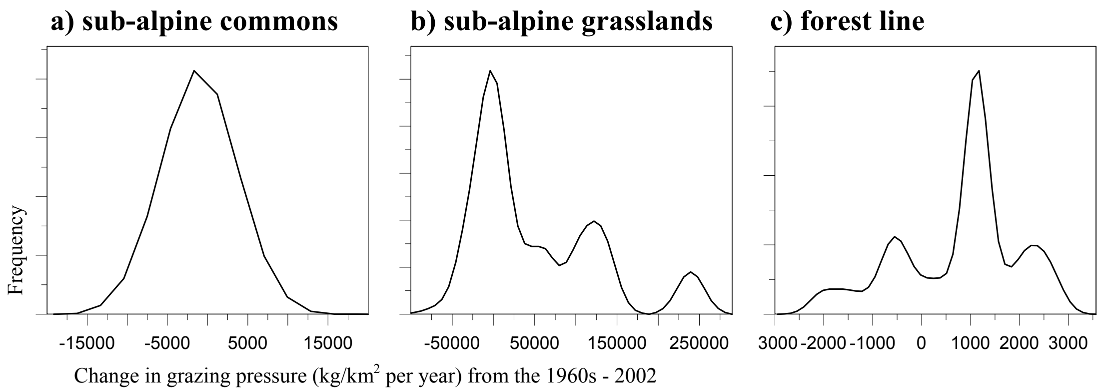

Figure 3
The change in the total grazing pressure indices (kg/km^2 per year) from the 1960s – 2002 in a) the sub-alpine commons, b) the enclosures, and c) the forest line in Eastern Jotunheimen.

Grasslands (today mostly enclosed by fences) had also changed, but less so compared with the commons outside the fences. Most of the grasslands had during 1960s – 2002 been influenced by the same grazing pressure as before the 1960s (Figure 3b). Cattle were still grazing in some of the grasslands. Where cattle grazing were abandoned sheep had replaced them. Some of the enclosed grasslands had experienced an increase of grazing pressure which can be attributed to the new breed (NRF) that is larger compared with the cattle breeds used earlier in the area. In addition, the cattle were not let out to free-range grazing but kept within the smaller enclosures, which contribute to the higher grazing pressure. The grazing pressures in the enclosures were high enough to suppress most tree establishment although scrub had to some extent established.

As studies from heavily grazed areas have shown, the transitions from scrubland and forest as well as heathland to more open vegetation observed in this study area can be due to high grazing pressures. In this study area these transitions were attributed to the very high increase in number of goats in three summer-farm sites (Figure 2; III).

Changes in the altitudinal position of the forest line

In the study area a shift in altitudinal positions of the forest line was observed, although the overall shift was small (+4.3 m altitudinally; Figure 4). There were, however, large variations between different areas with a mean change in one area of +17.14 m compared with another area with a mean change of -0.15 m (II).

These shifts were significantly related to changes in grazing pressure from domestic animals (II, III). The study by (Hofgaard 1997) also showed that domestic animals have a high impact on the altitudinal position of forest lines. The highest upward displacements from 1960s to 2002 had occurred where the decrease of grazing pressure was large (II). In this area cattle and goat had lowered the forest line before the 1960s (III). When their free-range grazing was abandoned, the pressure on the forest line was released. Sheep range-grazing had, however, increased during the period from 1960s to 2002. Sheep had no effect on neither scrub and forest expansion in the sub-alpine zone, nor the altitudinal shifts of the forest line (III). This may be due to a combination of the sheep inability to graze larger plant species (Staalenad et al. 1995). Semi-natural reindeer, however, were able to maintain the pressure on the forest line after cattle grazing had ended (III).

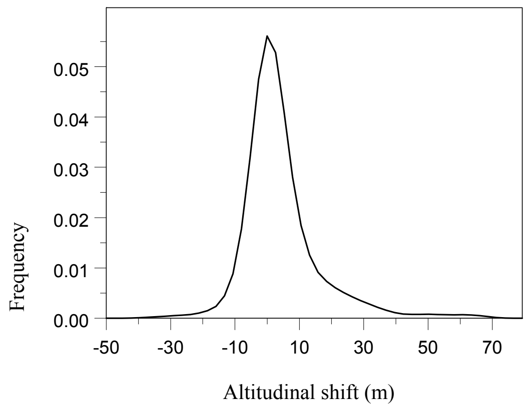

Figure 4
The frequency distribution of shift in altitudinal positions observed in the study area of Eastern Jotunheimen

The future of the semi-natural cultural landscapes

Development of the semi-natural cultural landscapes in the future is dependent upon the land-users and their activities. Three scenarios describing possible future land use were used in this study. Even if the policy makers define schemes for protection of landscapes or threatened species, the protection will only be effective if the land-users follow the legislations, regulations and management plans that are decided; the policies have to be legitimized (Kull 2002). Local stakeholders were therefore included in a sustainability appraisal of future agri-environmental policies (V). In the fist scenario (business as usual, BAU) trends of agricultural practices continued. This resulted in continued livestock husbandry, but at lower intensities.

In the second scenario (liberalization, LIB) all subsidies stopped. No land-user saw the possibility to maintain summer-farming under such conditions. The semi-domestic reindeer and sheep cooperatives, however would remain, but with reduced herds.

In the third scenario (managed change for biodiversity, MCB) agri-environmental considerations should be taken and green-payments given. The land-users would achieve support for livestock husbandry in prioritized areas such as species rich semi-natural grasslands.

Comparisons of the scenarios can be used as tools to integrate landscape ecology with landscape planning (Opdam et al. 2002). There is a close relationship between landscape and rural development (V). People using the semi-natural landscapes of Eastern Jotunheimen are aware of and will, if economically feasible, manage both the cultural heritage and the rare species that are linked to the cultural landscape. The different agricultural activities in the three scenarios would result in different levels of forest and scrub establishment in the cultural landscape (V) due to different number of domestic animals (I, IV). In all scenarios, however, forested areas would increase. Under none of the agri-environmental policies defined it was economic feasible to go back to the pre-1960 practices of husbandry, so the trend of forest expansion would continue. However, if agri-environmental subsidies were given, areas of semi-natural grasslands would increase as a consequence of the demand from the authorities that high intensive fodder production had to be abandoned. Arable land would be used as pastures to fulfil the environmental objectives of the schemes.

Future for rare species in semi-natural cultural habitats

There are many rare species in the semi-natural cultural landscape and many of them are red listed due to the decline in habitats (Kålås et al. 2006). What will happen with them in the future? One of the rare species in the semi-natural grasslands is the endemic *Primula scandinavica*. To be able to evaluate the future survival for such a species, one needs to know the key requirements. *Primula scandinavica* requires open areas in order not to be outcompeted and some disturbance to be able to establish (V). In the investigated areas, it was most frequent in grasslands (both open and scrub-dominated) and had the highest density in human disturbed habitats (V). The existence of those open vegetation types are dependent upon grazing by domestic animals (III).

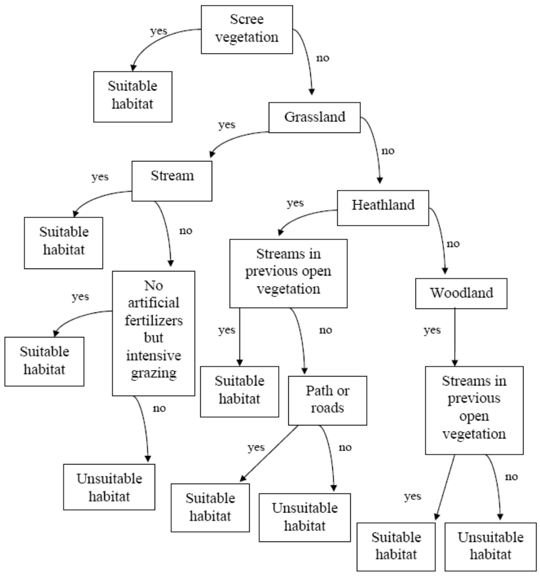

Figure 5
A classification tree describing a suitable habitat of *Primula scandinavica* using generalizations of the results in V.

Scenario procedures have been used to investigate the impact of changed environment on species distribution (Bomhard et al. 2005, Bolliger et al. 2007). Future vegetation mosaics in the region has been estimated for three scenarios described above (IV). It is therefore possible to estimate the potential distribution of suitable habitats for *P. scandinavica* under each scenario. A classification tree (Figure 5) constructed using generalizations of the habitat requirements (V) can be used to indicate the future distribution of suitable habitats by defining vegetation using the landscape scenarios produced in IV and changing the human disturbance variables defined in V pursuant to the policy scenarios. The results following such a procedure indicate that future distribution of suitable habitats for *P. scandinavica* will depend on agri-environmental policy makers. If continued trends of agricultural practices continue (BAU), number and size of suitable habitat patches decrease compared with present distribution (Table 1). More dramatic results will, however, be present if all subsidies are stopped (LIB) and lot of suitable habitats will be lost. If agri-environmental considerations are taken (MCB), on the other hand, area of suitable habitats will increase.

Populations found in natural habitats were small, but seed-production was not different between semi-natural habitats and natural habitats. This result indicates self-supporting populations even if grazing by livestock would end. The species survival in such a case depends therefore on the ability for small and isolated populations to form viable metapopulations.

Table 1
Suitable patches in 2002 and the three scenarios.

Scenario	Number of suitable patches	Total area of suitable patches (hectare)	Mean area of the suitable patches (hectare)	SD of the area of the suitable patches (hectare)
2002	415	125.55	0.299	1.333
BAU	336	87.43	0.256	1.2.58
LIB	115	9.58	0.077	0.141
MCB	341	151.53	0.438	1.642

Conclusions and future prospects

The semi-natural cultural landscape has changes considerably in south central Norwegian mountain the last 40 years. The earlier open sub-alpine landscape has to a large extent become scrubland or even forest. This corresponds to a change in livestock husbandry during the same period. Changes in goat and cattle grazing pressure and grazing patterns have stopped the earlier suppression of scrubland and forest. Increased semi-domestic reindeer numbers have, above the forest line, partly continued to suppress upward expansion of forest.

It is expected that changes will occur also in the future. Agri-environmental policies will influence agricultural practice and the semi-natural cultural landscape will be formed with respect to the practice used. The changes also have an effect on the biodiversity. Rare species such as *Primula scandinavica* occurring in vegetation types that are decreasing will lose suitable habitat patches.

This study leads to some recommendations to further research:

In Paper III it is shown that goat husbandry is the practice that best maintain an "open" landscape. More information about the goat's influence on semi-natural cultural landscapes has to be obtained. In depth investigations dealing with the influence of goat grazing pressure on plant species composition have been started near one of the joint goat husbandry summer-farms. To analyze the changes over time an experiment has been started where changes in plant species compositions in an enclosure (no goats allowed to graze) is compared with changes in plant species compositions where goats are allowed to graze,. Further studies investigating whether goat husbandry is economic feasible and could be used as a management measurement should be performed.

Many have claimed sheep to have had large influence on landscape dynamics. This study suggests the opposite. Studies should, however, be performed to investigate if sheep have an effect and if so at which grazing pressures. It should also be studied if the most ecologically beneficial grazing pressures and grazing patterns is economic feasible. This study included changes in and below the forest line only. Above the forest line the numbers of domestic animals have increased (II, III). Studies investigating the role of sheep and semi-domestic reindeer in alpine areas have also high relevance when investigating semi-natural cultural landscapes. In the study area it exist a study dealing with the influence of sheep and reindeer grazing pressure in alpine areas (Størseth 2002). No differences in the influence on plant composition between these two species were observed. It would, however, be useful to use the species composition data from this study to investigate whether there have been any changes over time, and further, relate this to changes in numbers of domestic animals over time. Climate has changed during the last decade in this region (data provided by the Norwegian meteorological institute). The combined effects of climate and grazing pressure by domestic animals, or even all herbivores in the area should be studied. As natural forest lines define the climatic border between the boreal and the alpine zone, the upward shifts of the forest line have been attributed to change in climate. This study indicated that the shifts observed in the cultural landscape of Eastern Jotunheimen, were highly correlated to changes in grazing pressure (II, II).

Primula scandinavica is a species endemic to Norway and Sweden (V). This means that Norway have a responsibility for this species survival. This study showed that it is common in semi-natural grasslands, but that it is also present and viable in natural habitats (V). More investigation on the species metapopulation dynamics have to be performed in order to assess how threatened the species is. Scenarios of the distribution of suitable habitats for *P. scandinavica* can be used to gain more knowledge. In this synopsis the results from a static scenario modelling procedure are shown. Developing this study to also include more dynamic modelling procedures as well as including more species would be very useful.

Errata list

In the Synopsis Objectives:

Paper II = Paper V

Paper III = Paper II

Paper IV = Paper III

Paper V = Paper IV

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Paper I

A map-based method for exploring responses to different levels of grazing pressure at the landscape scale

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Abstract

At the beginning of the last century European cultural landscapes were a mosaic of open and forested habitats. During the 20th century however this mosaic were altered. Changes in grazing pressure from domestic animals have been suggested as one of the drivers of these alterations. This short communication presents a methodology developed to calculate an index of potential grazing pressure change at the landscape level. Information about location, type and number of grazing animals is used to produce detailed Geographical Information System (GIS) maps of potential grazing pressure change. Spatial information from these maps can then be geographically linked to vegetation maps such that the effect of grazing pressure changes on vegetation can be statistically analyzed. The methodology described in this short communication might be a useful tool in planning strategies both for conservation efforts and sustainable resource use.

Keywords: Grazing pressure; Landscape change; GIS; BioScene

Introduction

A cultural landscape is a land area shaped by human use (Framestad et al. 1998). European cultural landscapes have experienced substantial change in recent decades (Fjellstad and Dramstad, 1999; Partel et al., 1999; Olsson et al., 2000; Taillefumier and Piegay, 2003; Bender et al., 2005a, b; Bjune, 2005). Changes in land use, including abandonment of traditional agricultural practices that involve the grazing of domestic animals, has been suggested as one of the driving forces behind these alterations. Regeneration of woodland in open habitats has been attributed to decreased grazing by livestock (Staaland et al., 1998; Carmel and Kadmon, 1999; Partel et al., 1999; Humphrey and Patterson, 2000; Olsson et al., 2000; Bender et al., 2005a); however, few studies have tested this claim. Such studies require that vegetation changes be spatially linked to changes in grazing pressure, an approach that has rarely been undertaken. The aim of this article is to present a rapid and practical method for calculating an index of potential grazing pressure from large herbivores that can be spatially linked to vegetation changes.

Landscape changes can be assessed by remote sensing methods using aerial photographs or satellite images from different times (Staaland et al., 1998; Carmel and Kadmon, 1999; Partel et al., 1999; Jensen, 2000; Olsson et al., 2000; Tommervik et al., 2004). The photographs and images enable construction of time series of vegetation maps over a specified time interval, which then can be compared to obtain information about landscape and vegetation changes. If the goal is to link changes in grazing pressure from domestic animals to the landscape alterations observed in these maps, grazing pressures need to be quantified at the same resolution and scale (both in time and space) as the vegetation maps. The grazing pressure is not homogenous in the entire area of a selected landscape (Hunter, 1962: Sowell et al., 1999), and the composition of the livestock present is often not uniform. Historical data about livestock numbers and grazing regimes have to be collected and this has been performed in many of the studies referred to above. Nevertheless, the heterogeneous nature of grazing pressure has not been adequately addressed and linked to the spatial distribution of the vegetation changes. The method presented here, uses spatial grids of potential grazing pressure that reflect both spatial and temporal heterogeneity based on available information about grazing animals and grazing regimes. Such grids would provide more detailed information than general descriptions of grazing pressure changes.

Geographical locations of each cell in both spatial grids of potential grazing pressure and grid-based vegetation maps can be attributed. Vegetation changes can therefore be spatially linked to the potential grazing pressure grids. This paper includes an application of the method to assessing whether changes in livestock grazing pressure have been a driver of vegetation changes observed in a Norwegian mountain landscape.

Method description

To produce an index of potential grazing pressure change, first information about factors that influence grazing pressure must be obtained. These factors vary most often in space, and this have to be considered. Thereafter information about these factors must be collected from two or more points in time to assess the temporal changes.

Grazing pressure in year *y* in a site *c* by species *i* (g_{icy}) is determined by 1) the size of the total area (a_{icy}) grazed by species *i* in site *c* in year *y*, 2) the number of individuals (n_{icy}) of species *i* in site *c* in year *y*, 3) the number of days (t_{icy}) species *i* in site *c* grazed in year *y*, and 4) the uptake (u_{icy}) of plant biomass species *i* in site *c* grazed in year *y*. These factors vary in a mountain landscape with the different species of grazers, and therefore each factor must be evaluated separately for each species, but the potential grazing pressure of species *i* in site *c* in year *y* (g_{icy}) (kg km^{-2} year^{-1}) can be calculated as:

$$g_{icy} = n_{icy} \cdot t_{icy} \cdot u_{icy} / a_{icy} \qquad a_{icy} > 0 \qquad (1a)$$

$$g_{icy} = 0 \qquad a_{icy} = 0 \qquad (1b)$$

for range grazers and domestic animals grazing in enclosures. Dairy animals are assumed to graze the most near barns because they return regularly each day for milking. The grazing pressure of dairy animals in a site would thus also be affected by 5) the distance from the barn used in year *y* by the dairy animal *i* grazing in site *c* (d_{icy}), and also 6) the number of daily returns to the barn for species *i* in site *c* in year *y* (b_{icy}). The length of the daily walking distances for species *i* (l_{icy}) can be used to define the area that species i can reach in a site c in year y. I have assumed that the area that dairy animals of species i in a site c in year y can reach is contained within a circle around the barn with a radius (r_{icy}), calculated as $r_{icy} = l_{icy} / 2\ b_{icy.}$ The total area grazed by dairy species i in site c in year y (a_{icy}) will thus be $\pi\ r_{icy}{}^{2}$. Using the above mentioned assumptions, the potential grazing pressure of dairy animal i in site c in year y (g_{icy}) can be calculated as gradually decreasing with distance from the barn (d_{icy}) where species i is milked in year y:

$$g_{icy} = (n_{icy} \cdot t_{icy} \cdot u_{icy} / a_{icy})\ (1 - d_{icy}/r_{icy}) \qquad d_{icy} < r_{icy} \qquad (2a)$$

$$g_{icy} = 0 \qquad d_{icy} > r_{icy} \qquad (2b)$$

Information on the area, numbers and grazing periods of domestic animals can be obtained from local stakeholders such as livestock owners/herders, or can be found in written documents such as in local government archives. Uptake of plant biomass is assumed to correlate with body size of the animal species. Cordova *et al.* (1978), Allison (1985) and Illius and Gordon (1987) have stated that energy demands of grazers are proportional to 0.75 power of the weight (w) in kg of an animal scaled by 60 g per day ($0.06 w_{kg}{}^{0.75}$). This estimate of an animals's mean metabolic bodyweight is therefore used to calculate fodder uptake for this study and within each species sex and age of the animals must be considered.

Geographical Information Systems (GIS) allow information about grazing for each animal species to be included in map layers that have spatial attributes. The areas grazed by one animal species can be drawn as polygons to illustrate where grazing takes place. This polygon layer can then be converted to a grid-based layer and assigned attributes for factors that determine grazing pressure, allowing the computation of a layer describing an animal's potential grazing pressure in a specific area at a specific time.

The total potential grazing pressure at year y is then the sum of all the potential grazing pressures of all species. By comparing time series of potential grazing pressure maps, changes in grazing pressure can be calculated and used as explanatory variables to analyse the effect on vegetation.

Method application

A case study from a mountain area in south-central Norway

This method was applied to an area in eastern Jotunheimen, a mountain region in south-central Norway, in the time period from 1960s to 2002. Summer farming has taken place here since medieval times, where range grazing of sheep, goat, cattle, and semi-domestic reindeer has been a major land use. As in other European mountains, summer farm practices have changed during the last century with the latest major changes occurring in the 1960s (pers com.). Olsson et al. (2000) quantified vegetation changes in this area and found that 70% of the heathland vegetation (defined as species-rich vegetation dominated by heaths, graminoids, and herbs) in the 1964 had been succeeded by woodland (defined as vegetation dominated by shrubs and/or trees) 25 years later. This change was interpreted as being related to decreased and/or ceased livestock grazing (Olsson et al. 2000). To test the assumption that decreased grazing pressure leads to the establishment of woodland in mountain heathlands located below the forest line, 13 circular study plots with a diameter of at least 1 km were selected. The location of each plot was selected such that one/several summer farm(s) surrounded by mountain pastures was included in the circles. The number of grazing livestock in the plots had increased in some plots and decreased in others.

Maps of potential grazing pressure within the plots were produced following the procedure described above. Information about grazing pressure factors for sheep, goats, cattle, and semi-domestic reindeer were based on interviews of stakeholders (summer-farm users, members of the semi-domestic reindeer cooperative and the sheep owners' cooperative), along with agricultural plans from the municipalities, the Norwegian Mapping Authority and Norwegian Institute of Land Inventory, and published data (Selsjord, 1958a, 1958b, 1960, 1964, 1966, Skjenneberg and Slagvold, 1979, Volden and Anderssen, 2002, Graffer, 1963; Huston, 1978; Saether et al., 2006). These factors were then transferred to the Geographical Information System ArcGIS and its extension ArcMap version 9.1 (ESRI) to calculate potential grazing pressure maps for the 1960s and 2002 and the mean change of potential grazing pressure (grid resolution: 10 x 10 meter) (Figure 1). The mean change in grazing pressure within the 13 plots ranged from -1530 kg km^{-2} $year^{-1}$ to 2020 kg km^{-2} $year^{-1}$.

Within each plot vegetation for both the 1960s and 2002 was digitized from aerial photos to map where heathland had been succeeded by woodland (1960s-2002) (Figure 1). Logit models were fitted by partial canonical correspondence analyses (CCA) (ter Braak and Smilauer, 2002) to analyze whether changes in grazing pressure from domestic animals had had an effect on the regeneration of woodland in heathlands. Using the procedures described in ter Braak and Smilauer (2002, pp: 58-62) the probability that scrub and/or trees establishment in open heathland could be calculated from the equation:

$$p(w) = N_w\ (Score_w(exp(\sum \beta_i X_i)/N_{total}(\sum Score_a(exp(\sum \beta_i X_i)), \qquad (3)$$

where N is number of cells. w is cells were woodland had succeeded heathland and X_i is the explanatory variable i. *Score* and β_i is the results of the CCA were the first is the canonical score of the vegetation types (species) a and the second the canonical coefficient of X_i.

It was assumed that previous grazing pressure did matter and that the grazing behavior of the domestic animals could be influenced by slope (Ganskopp et al 2000), grazing pressure in the 1960s and slope was thus included as possible covariables in the analyses. A map of the slope within the study area was calculated from a digital terrain model using ArcMap. Extended spatial autocorrelation was revealed, permutations were therefore always among the study plots with no permutation within plots. The Canoco 4,5 software was used to perform the statistical analyses.

The statistical analyses showed that grazing pressure change had a significant effect on the probability of change from heathland to woodland from the 1960s to 2002 ($p = 0.016$, % explained variance = 13.9). Where grazing pressure had decreased, there were a high probability of woodland establishment in heathlands. The vegetation changes were however also significantly influenced by the grazing pressure change's interactions between both grazing pressure 40 years ago and slope and including these parameters the model explained the data better ($p = 0.028$, % explained variance = 27.6) (Table 1).

Where previous grazing pressure had been high, there was higher probability of woodland establishment compared to where previous grazing pressure had been lower, but in plains where the grazing pressure had increased the most, the probability of woodland establishment was however highest at low previous grazing pressures. A switchover between low and high previous grazing pressure seemed to happen were change in grazing pressure exceeded 1500 kg/km^2 per year (Figure 2). At steeper slopes and where grazing pressure had decreased, there was higher probability of woodland establishment compared to less steep areas. On the other hand, where grazing pressure had increased the probability of woodland establishment was highest in less steep areas (Figure 2).

Discussion

In vegetation change studies performed at relatively small scales (both in time and area), such as experiments on species and species composition dynamics, grazing pressures have either been manipulated or clearly defined by observations (Hulme et al., 1999; Humphrey and Patterson, 2000, Austrheim et al., 2007). Such methods give exact estimations about small-scale dynamics, but some aspects of these experiments are problematic. The response of events that influence the vegetation dynamics such as succession in former open habitats towards woodland as a response of change in grazing pressure, is time delayed. Therefore long time studies do have to be performed to capture the response. Experiments with longer time frames have been conducted (Bokdam and Gleichman, 2000; Welch and Scott, 2000), but research money today is rarely awarded for such studies, so a more common approach is to use a space for time substitution design, in which grazing and abandonment are treatments (Peco et al., 2005; Peco et al., 2006). Another problem is that the spatial scale of an ecological system is larger than those being studied, which can make it problematic to predict the dynamics of the system (Freckleton, 2004). Grazing pressure at a landscape scale is difficult to estimate and/or to observe. A method that is often used in studies of vegetation changes and livestock grazing over time is to relate rough information about domestic animal numbers from the municipal, county or country level to vegetation changes (Tommervik et al., 2004), or just to assess whether there has been grazing or not (Pykala, 2004, 2005,). Including the impact of several animal species in these assessments has rarely been attempted. The method described here can facilitate an estimation of grazing pressures at the landscape level but at the spatial scale of single grid cells and thereby makes possible the spatial linkage of grazing pressure and vegetation change.

This method might have shortcomings because it assumes uniform foraging within the area a_{icy} assumed to be available for species i at site c in year y. However, as mentioned, animals do not graze uniformly; they graze preferentially, and different vegetation types have different productivity. Additionally, topographical or other features might act as barriers or hindrances which would influence the spatial distribution of grazing pressure. These challenges were minimized in the present study by limiting the analysis to one vegetation type, by including slope as a covariable, and by excluding areas unaccessible due to physical barriers (streams) for the grazing animals.

Another application of this method of constructing maps of potential grazing pressure is using it for scenario work. It was recently used to visualize future scenarios of landscapes given different agri-environmental policies (Olsson et al., 2008). The results from these analyses could further be used as tools in conservation planning along with rural development planning. In planning for sustainable resource use, such as meat production from range grazing animals as well as maintaining sustainable populations of game animals, this method could also be applied because information on sustainable grazing pressures in relation to vegetation dynamics can be assessed. The construction of maps on potential grazing pressure, as has been illustrated in the case study presented here, allows the visualization of grazing pressure levels at which one vegetation type is succeeded by another (Fig. 1).

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Table 1

The explanatory variables that best explained the dynamics in heathland vegetation in South-eastern Jotunheimen. The results are based upon canonical correspondence analyses (CCA).

	Axis 1	*Axis 2*
Eigenvalue	0.2757	0.7243
Score woodland (N = 1495)	-0.5305	-1.3934
Score heathland (N = 1105)	0.7177	1.8851
β grazing pressure change	$3.65e^{-4}$	0
β grazing pressure change : slope	$3.66e^{-5}$	0
β grazing pressure change : previous grazing pressure	$2.73e^{-7}$	0

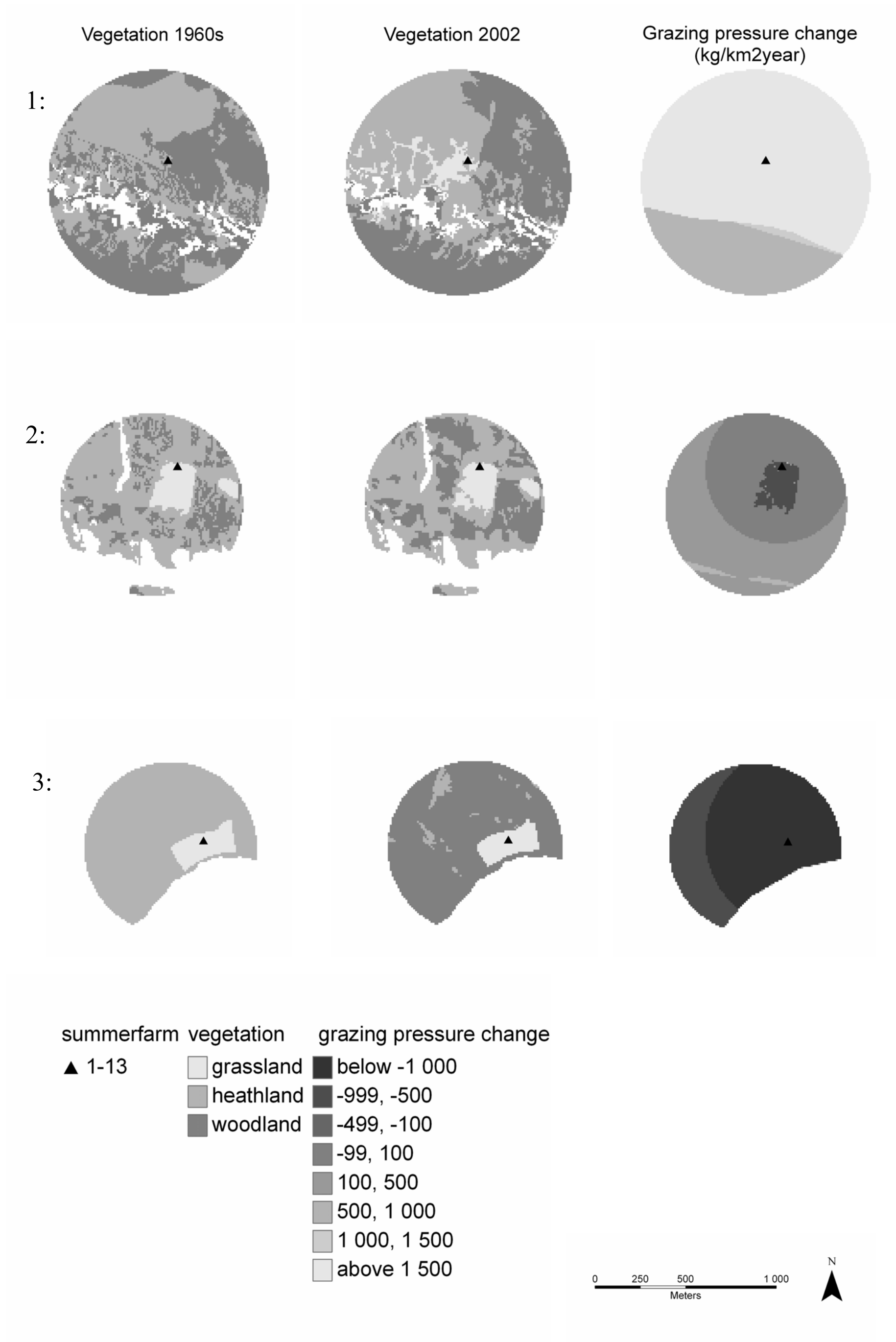

Figure 1

Maps of vegetation in the 1960s and 2002 and grazing pressure changes from 1960s to 2002 in three of the 13 study plots.

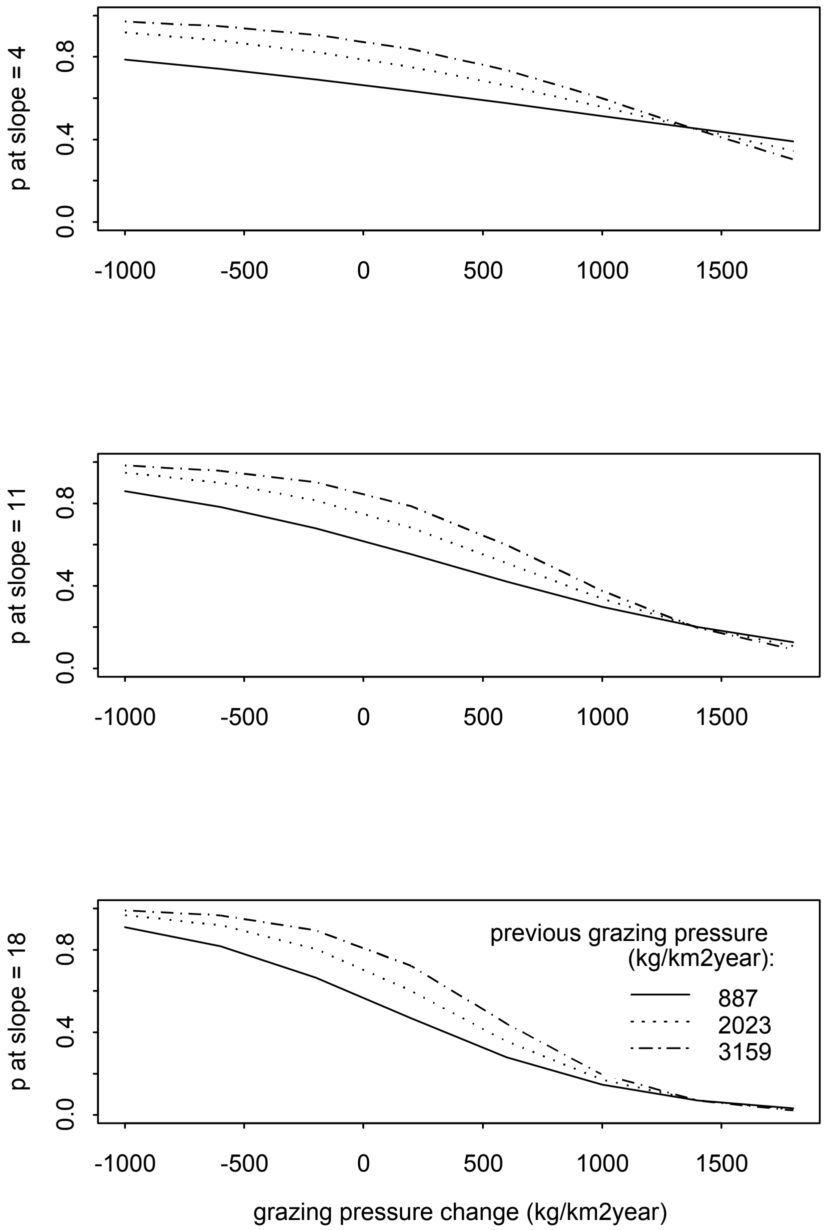

Figure 2

The probability (p) of woodland establishment in former heathlands as a function of changes in grazing pressure by domestic animals from the 1960s to 2002 for three different grazing pressures 40 years ago in three different slopes. The values selected for grazing pressure and slope were: 1) mean of the variables – SD of the variables, 2) mean of the variables, and 3) mean of the variables + SD of the variables.

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Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook *Corvus frugilegus.*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.
1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.

1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit *Parus montanus*.
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988	Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
1988	Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
1988	Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
1988	Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.).
1989	John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989	Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
1989	Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990	Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
1990	Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990	Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
1991	Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway.

1991	Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient. Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos. Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
1991	Nina Jonsson	Dr. philos.	Aspects of migration and spawning in salmonids.
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992	Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2

1994	Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek.
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient. Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*.
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)
1994	Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*.
1994	Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cockoo.
1994	Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.
1995	Hanne Christensen	Dr. scient. Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*.
1995	Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition.
1995	Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
1995	Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations.
1995	Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden.
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae.
1996	Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient. Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines.

1996	Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996	Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.
1996	Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region.
1997	Gunvor Øie	Dr. scient Bothany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae.
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spurce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997	Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
1997	Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher.
1997	Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997	Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
1997	Arild Magne Landa	Dr. scient. Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation.
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*.
1997	Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins.

1998	Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity.
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro.
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998	Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway.
1999	Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999	Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.
1999	Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.
1999	Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease

1999	Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999	Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material

2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and
2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo Salar* L.) parr and smolt
2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).

2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations.
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates

2006	Nils Egil Tokle	Phd Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	phD Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	phD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, */Mamestra Brassicae/* L. (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania

2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, */Taeniopygia guttata/*