Effects of Management on Heathland Vegetation in Western Norway

Inger Elisabeth Måren

Dissertation for the Degree of Philosophiea Doctor (PhD)
University of Bergen, Norway
2009

UNIVERSITETET I BERGEN

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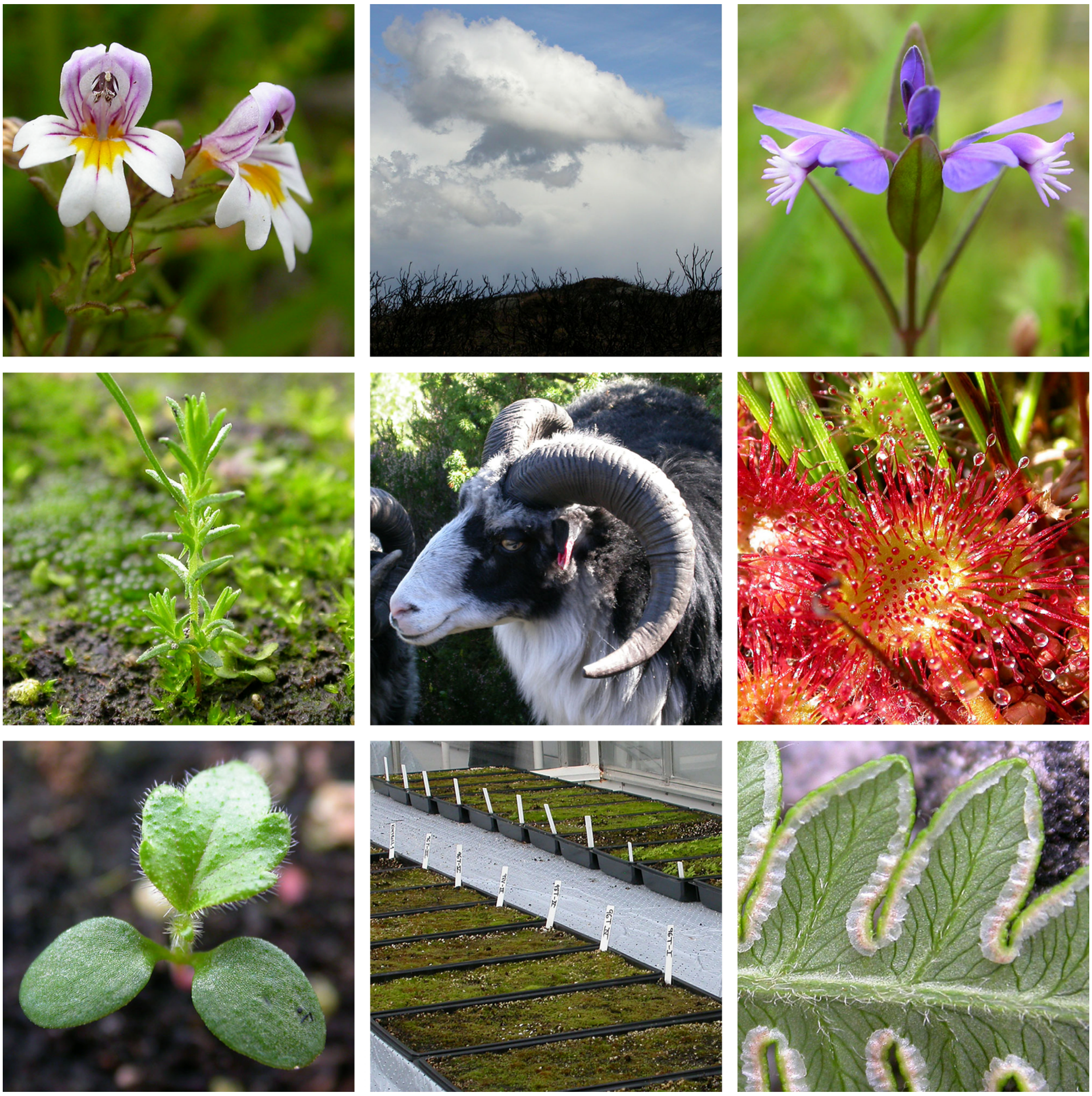

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In memory of my grandfather,
Johan Måren; 12.01.1918 – 02.12.2008

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for the Degree of Philosophiea Doctor (PhD)
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Abstract

Måren, I.E. 2009. Effects of Management on Heathland Vegetation in Western Norway. PhD Thesis, Faculty of Science, University of Bergen, Norway.

Aims: This synthesis of studies examines the effects of anthropogenic disturbance regimes; the traditional management practices of livestock grazing and prescribed burning, on vegetation and seed banks in coastal heathlands of Western Norway. Effects of germination cues on the key species *Calluna vulgaris* are also discussed. Threats and conservation aspects in relation to different mechanical and chemical bracken control measures are investigated. The concept of heathland conservation is integrated into a wider frame-work, discussing biodiversity, ecosystem services and the global context.

Methods: I combine long-term (> 10 years) experiments and chronosequence data (0-30 years) with germination trials on seed banks and seeds to investigate patterns and processes of heathland vegetation, seed bank dynamics, role of seed bank, effects of fire-related germination cues on *Calluna vulgaris*, and the effects of bracken control measures in response to the land-use practices of grazing and burning. The project is based on field data, seed bank samples and seed samples collected at Lygra, North Hordaland, western Norway. The greenhouse seedling emergence trials were carried out at the Norwegian Arboretum at Milde, Bergen, while the seed germination experiments were performed at Wakehurst Place, Royal Botanic Gardens Kew, UK.

Major results: (i) Fire induced strong successional trends in the species composition, while grazing added complexity to the post-fire successional dynamics, increased variability among habitats, and created ecological opportunities for additional species. (ii) Vegetation species richness showed a unimodal pattern over the post-fire succession, while the seed bank species richness showed no trend, suggesting that the seed bank acts as a refuge, providing a constant source of recruits for species to colonize newly-burnt areas. Fire also produces germination cues such as ash and smoke, enhancing seed germination in the key species *Calluna vulgaris*. (iii) Bracken control by means of cutting twice yearly is nearly as effective as spraying with the herbicide asulam combined with yearly follow-up cutting.

Conclusions: Traditional management regimes do not have simple additive effects within the heathland system but interact to create heterogeneity. The traditional management has not depleted or destroyed the seed banks; indeed, continued management is needed to ensure the sustainability of northern heathlands.

Implications for conservation: Sustainable management strategies are needed to preserve diversity and heathland conservation should aim to replicate the complexity that traditional management regimes create, both in terms of the actual disturbances as well as the spatial scales at which they are applied. Organic farming and nature conservation may call for alternative approaches to herbicide application for bracken control; results presented here show this to be feasible. Open landscapes such as heathlands are of importance for people's well-being through their recreational and therapeutic values as ecosystem services. Consequently, they should be managed in a sustainable manner for the future.

Keywords: Bracken control, *Calluna vulgaris*, disturbance regimes, ecosystem services, evidence-based conservation, germination cues, heathland ecology, landscape history, land-use, plant interactions, *Pteridium aquilinum*, regeneration ecology, scale, seeds, seed banks, semi-natural habitats, smoke, spatial variation, species composition, species diversity, statistical analyses of time-series data, succession, temporal variation, vegetation dynamics.

Acknowledgements

This thesis could not have reached completion without significant guidance, advice, encouragement and practical assistance. Consequently, I have a number of people I would like to acknowledge. The project was initiated in May of 2003, after receiving a PhD grant at the former Botanical Institute at the University of Bergen. Vigdis Vandvik, Department of Biology, has been my main supervisor. She has supervised me brilliantly through the whole PhD track of ups and downs. Her stern vision and relentless ambitions have guided me through every step. Engaging in this process she has taught me much more about the world of science and beyond, than how to write scientific papers. In sum, I consider myself incredibly lucky to have her as my mentor. Co-supervisors John B. Birks and Peter Emil Kaland at the Department of Biology and Ole Reidar Vetaas at UNIFOB have given helpful advices as well. I thank Beate Helle, Brooke Wilkerson and Fride Høistad for help with illustrations, John-Arvid Grytnes with R, Oddvar Pedersen with distribution maps, and all my colleagues at FBI and EECRG for company and coffee breaks. I thank the staff at Bergen Museum and the Department of Biology for administrative support. I would also like to thank Robin Pakeman at the Macaulay Institute, Aberdeen, for his hospitality and for sharing his extensive knowledge on *Pteridium aquilinum* during my stay in the autumn of 2004.

My work is based on field research carried out at The Heathland Centre, Lygra, Hordaland, during the spring and summers of 2003, 2004, 2005 and 2007. Some of the data used have also been collected prior to my PhD period, as far back as 1994. Several people helped with field work and I want to thank all my field assistants: Fride Høistad, Rakel Blaalid, Håvard Laukland, Janne Wilhelmsen, Per Arild Aarrestad, Liv Guri Velle, Kristine Ekelund, Sigrunn Dommarsnes, Vibeke Dahl, Mons Kvamme and Peter Emil Kaland for very enthusiastic and carefully done work. Even in 6 ^{o}C and horizontal rain in the middle of June they amazingly kept their spirits up. Some of the most efficient field assistants have been recruited from my family; Keith McInturff, Sebastian and Johan McInturff Måren, in descending order of efficiency (and age). The staff at the Heathland Centre at Lygra has also been most helpful with everything from providing boats, sharp scythes, to warm coffee, in addition to all sorts of practical and sometimes essential information. Arne Frisvoll, Bjørn Moe and Einar Heegaard helped identify lichens and bryophytes.

The greenhouse trials were carried out at The Norwegian Arboretum at Milde where Christian Mong, Mari Jokerud and Hana Pánková helped with the time-consuming set up of the two seed bank trials. Thanks also to the staff at the Arboretum, especially to Ella Blomsø Ødegård and Else Jorunn Melstokkå, for technical support and great help with keeping it all going in a very professional manner.

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Last, but not least; thanks to all my friends and family for patience and support. Sebastian and Johan are the joy of my life, and Keith, he is my man! What should I have done with out *all* of you? Special thanks to Santa this year for doing the Christmas-thing while I was writing up the synthesis and the last paper.

Declaration

This thesis consists of an introduction, three published papers and two submitted papers for publication. All papers are co-authored. The nature of the contributions by the different authors is outlined below.

PAPER I:
Måren, I.E. & Vandvik, V. In Press. Fire and regeneration: The role of seed banks in the dynamics of northern heathlands. Accepted for publication in *Journal of Vegetation Science*.
Inger Elisabeth Måren – Experimental design, field work, soil analyses, greenhouse trials, data processing, statistical analyses, writing, editing
Vigdis Vandvik - Experimental design, statistical analyses, writing, editing

PAPER II:
Måren I.E., Janovský Z., Spindelböck J.P., Daws M.I., Kaland, P.E. &Vandvik, V. Submitted. Prescribed burning of northern heathlands: *Calluna vulgaris* and germination. Submitted to *Plant Ecology*.
Inger Elisabeth Måren – Experimental design, field work, greenhouse trials, data analysis, writing, editing
Zdeněk Janovský – Field work, data analysis, writing
Joachim P. Spindelböck – Laboratory work, data analysis, writing
Matthew I. Daws - Laboratory work, editing
Peter Emil Kaland – Compiling of palaeoecological data, writing
Vigdis Vandvik - Experimental design, editing

PAPER III:
Vandvik, V., Heegaard E., Måren, I.E. & Aarrestad P.A. 2005. Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. *Journal of Applied Ecology*, 42, 139-149
Vigdis Vandvik- Field work, data processing, statistical analyses, writing, editing
Einar Heegaard - Statistical analyses
Inger Elisabeth Måren – Field work, writing, editing
Per Arild Aarrestad - Experimental design, field work, data processing, editing

PAPER IV:
Måren, I.E., Vandvik, V. & Ekelund, K. 2008. Restoration of Bracken-invaded *Calluna vulgaris* heathlands: Effects on vegetation dynamics and non-target species. *Biological Conservation*, 141, 1034-1044.
Inger Elisabeth Måren - Field work, data processing, statistical analyses, writing, editing
Vigdis Vandvik - Statistical analyses, writing, editing
Kristine Ekelund - Experimental design, field work, data processing, editing

PAPER V:
Måren, I.E., Vandvik, V. & Ekelund, K. 2008. Effectiveness of chemical and mechanical bracken *Pteridium aquilinum* control treatments in northern coastal heathlands on the island of Lygra, Hordaland, Norway. *Conservation Evidence*, 5, 12-17.
Inger Elisabeth Måren - Field work, data processing, statistical analyses, writing, editing
Vigdis Vandvik - Statistical analyses, editing
Kristine Ekelund - Experimental design, field work

List of papers

The dissertation is based on the following five papers, referred to by their Roman numbers in the Synthesis.

I Måren, I.E. & Vandvik, V. In Press. Fire and regeneration: The role of seed banks in the dynamics of northern heathlands. Accepted for publication in *Journal of Vegetation Science*.

II Måren I.E., Janovský Z., Spindelböck J.P., Daws M.I., Kaland, P.E. & Vandvik, V. Submitted. Prescribed burning of northern heathlands: *Calluna vulgaris* and germination cues. Submitted to *Plant Ecology*.

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IV Måren, I.E., Vandvik, V. & Ekelund, K. 2008. Restoration of bracken-invaded *Calluna vulgaris* heathlands: Effects on vegetation dynamics and non-target species. *Biological Conservation*, 141, 1034-1044.

V Måren, I.E., Vandvik, V. & Ekelund, K. 2008. Effectiveness of chemical and mechanical bracken *Pteridium aquilinum* control treatments in northern coastal heathlands on the island of Lygra, Hordaland, Norway. *Conservation Evidence*, 5, 12-17.

Synthesis

Effects of Management on Heathland Vegetation in Western Norway

Inger Elisabeth Måren

Introduction

One of the central ideas in contemporary ecology is that disturbance plays an important role in natural communities, influencing population persistence, community composition, and maintenance of diversity (Pickett & White 1985). Disturbances are ubiquitous, inherent and unavoidable, affecting all levels of biological organization, from ecosystems to individuals, with differing consequences and mechanisms at each hierarchical level (Rykiel 1985). The definitions of disturbance have developed over the last decades, from the view of disturbance as a process of removing or damaging biomass (Grime 1979) to relatively discrete events in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment (White & Pickett 1985). Processes that alter the birth and death rates of individuals present in a certain area have also been defined as disturbances (Petraitis *et al.* 1989). In this sense it is necessary to discuss both direct disturbances affecting the survivorship of individuals directly, and indirect disturbances affecting conditions which in turn influence individuals of a certain area.

Disturbances are primary causes of patchiness and heterogeneity in ecosystems (Turner *et al.* 2003) and act as evolutionary forces causing adaptation in the biota exposed to them (Darwin 1859, van Langevelde *et al.* 2003, Hughes *et al.* 2008). Disturbances affect diversity at different scales; alpha diversity within habitat, beta diversity between habitats, and gamma diversity at the landscape level (Huston 1994). Small-scale disturbances create patches of different successional stages of varying age and thereby affect habitat diversity (turnover) as well as overall species diversity. The effects of disturbances are often contingent on the frequency, intensity and timing of their interactions, on the present and past states of the system and their interaction with future events (White & Pickett 1985). Generally, following disturbances some species may decrease or retreat while others may increase or invade (Gibson & Brown 1991).

The intermediate disturbance hypothesis (Grime 1973, Horn 1975, Connell 1978) predicts the greatest species richness when disturbances occur at intermediate frequencies or with intermediate intensities. Individual disturbances may be seen as ecological 'reset' mechanisms, creating a link to the concept of succession; the idea that the recovery from disturbance over time is, at least to some extent, predictable (Underwood & Anderson 1994). Successional trajectories after disturbance may be considerably modified by, for example, local effects, stochastic factors, and the non-equilibrium status of most communities (McCune & Allen 1985, Glenn-Levin *et al.* 1992, Samuels & Drake 1997). Consequently, some factors contribute to predictability of successional dynamics while others add more uncertainty. The key question is therefore not if but rather to what extent different patches, when subjected to a disturbance, will respond in similar ways. The recovery after disturbances may be considerably moderated by interactions with local environmental variation (Swanson *et al.* 1988, Menges & Hawkes 1998, Stohlgren *et al.* 1999, Harrison *et al.* 2003), or by interactions or synergisms with other disturbances (Paine *et al.* 1998, Wolfe-Bellin & Moloney 2000, Kulakowski *et al.* 2003).

Disturbance may be natural or anthropogenic in origin (Turner *et al.* 2003) and may lead to gradual or sudden, subtle or dramatic changes in ecosystems (White & Jentsch 2001). Disturbance is an important and integral part of many ecosystems and hence many habitat types and species are even dependent on disturbance, especially for regeneration (Pickett & White 1985). Species respond directly to environmental variations generating opportunities for coexistence and increasing diversity (Chesson *et al.* 2004). One of the mechanisms that may promote species coexistence is the "storage effect", which involves species that exploit temporal niches through seed banking (Chesson 2000).

Disturbance is also the key process shaping and characterizing semi-natural environments. Human-induced disturbances repeated throughout centuries have shaped the semi-natural habitats surrounding us today. The spatial and temporal distribution of disturbance, in the form of locally adapted management regimes, has given rise to regionally distinct semi-natural landscapes such as species-rich summer-farm systems (Sernander 1920, Vandvik 2004), calcareous grasslands (Watt 1947, Grubb 1977, Eriksson 1993) and coastal heathlands (Gimingham 1972, Webb 1986), or more globally distributed semi-natural landscapes such as open forests managed by agro forestry (Måren & Vetaas 2007, Bhagwat *et al.* 2008), semi-dry grasslands managed by fire (Cole 1986, van Langevelde *et al.* 2003, Bond 2005) or marginal lands managed by livestock grazing (Meiners 1991, Omer *et al.* 2006). Human-use of marginal lands and forests has throughout history created many types of open semi-natural landscapes. In particular, the land-use practices of keeping livestock, prescribed burning and fodder collection are widely practiced on a global scale. Domestic livestock utilise *ca*. 50% of the earth's ice-free areas (Gaia 1985), providing large quantities of high-grade protein for the benefit of people, by consuming plants that have little nutritional value to man on marginal lands unsuitable for agriculture (Vetaas & Kolding 1991). The coastal heathlands of northern Europe is a very good example of such a low-intensity farming system where marginal lands are grazed by large herbivores.

Disturbance, however, plays a dual role in these systems; it is the underlying factor for their existence, shaped by the local farming practice, but it may also act as a destructive force by, for instance, increasing the likelihood of invasions of undesirable species of both non-native and native origin.

The understanding of relationships between disturbance, heterogeneity and succession are crucial for our ability to conserve and manage semi-natural habitats. These systems have emerged and have been maintained over millennia of extensive and often very complex human disturbance regimes (Fægri 1988, Lawton 1999). However, many of the traditional land-use practices in developed countries are no longer economically viable and there is a general trend of either discontinuation or intensification of management practices (Edelmann 1997, Mannion 2002, WallisDeVries *et al.* 2002). The successional changes that follow abandonment have been identified as major factors adversely affecting the flora and fauna of Europe (Stanners & Bordeau 1995, Bernes 1993, Fremstad & Moen 2001), and today different management practices are being re-introduced as conservation and restoration tools. Therefore improving our understanding of the effects of disturbances in semi-natural habitats will facilitate ecologically informed management decisions (Turner *et al.* 2003). The conceptual framework of the major disturbances, i.e. management regimes, of coastal heathlands is presented in the following, and their effects are reviewed.

Low-intensity farming systems – coastal heathlands

The coastal heathlands of north-western Europe are anthropogenic in origin and developed *ca.*. 6-1000 years ago as a result of forest clearance in areas with a mild winter climate that could support grazing year-round (e.g. Gimingham 1972, Kaland 1979, 1986, de Smidt 1979, Prösch-Danielsen & Simonsen 2000). In Western Norway only on the outermost islands, in the hyper-oceanic zone, the heathland vegetation may be natural in origin (Kaland 1986). The human-induced deforestation, followed by the establishment of open heath vegetation in the south-western part of Norway, seems to have been metachronous taking place over a period of *ca.* 4000 years between 6000-2200 BP (Prøsch-Danielsen & Simonsen 2000), likewise in Jutland of Denmark (Odgaard 1992) and on the Shetland Islands (Bennet *et al.* 1992). However, some areas remained wooded for much longer (Fremstad *et al.* 1991), and within the same region there are great differences in the timing of the deforestation. The expansion of heathlands occurred mainly at the expense of pine- and birch forests (Haaland 2002). Norwegian heathlands are found in the highly oceanic section (O3, Moen 1999); a narrow zone along the Atlantic coastline, dominated climatically by mild winters and humid, cool summers; the coastline from Lindesnes to Lofoten has monthly winter means above 0 °C (Moen 1999). Norwegian heathland vegetation types are described in detail in surveys of Norwegian vegetation types by Fremstad (1997).

The coastal heathlands of north-western Europe constitute a more or less continuous 3600 km belt along the Atlantic coast from Portugal in the south to northern Norway in the north. The European heathlands share many characteristics; they are open landscapes, dominated by *Calluna vulgaris* (L.) Hull (hereafter called *Calluna*) (Fig. 1), but they also differ due to differences in climate, geology and local management regimes. Cold-sensitive species, such as *Erica cinerea* are restricted to southern and western regions (northern limit is at Sunnmøre, Fig. 1), while more moisture demanding species, and alpine and arctic species such as *Betula nana*, *Arctostaphylos alpinus* and *Loiseleuria procumbens* are components in the northernmost heathlands. *Empetrum nigrum* coll. also increases in abundance northwards (Fægri 1960). In contrast to heathland areas in Scotland and Ireland, Norwegian heaths harbour wooded areas, either as single standing trees or as small groves and due to the rugged topography of the coastline there is a heterogeneous distribution of heathland habitats. Today, the coastal heathlands of Norway constitute one third of the European coastal heathland belt.

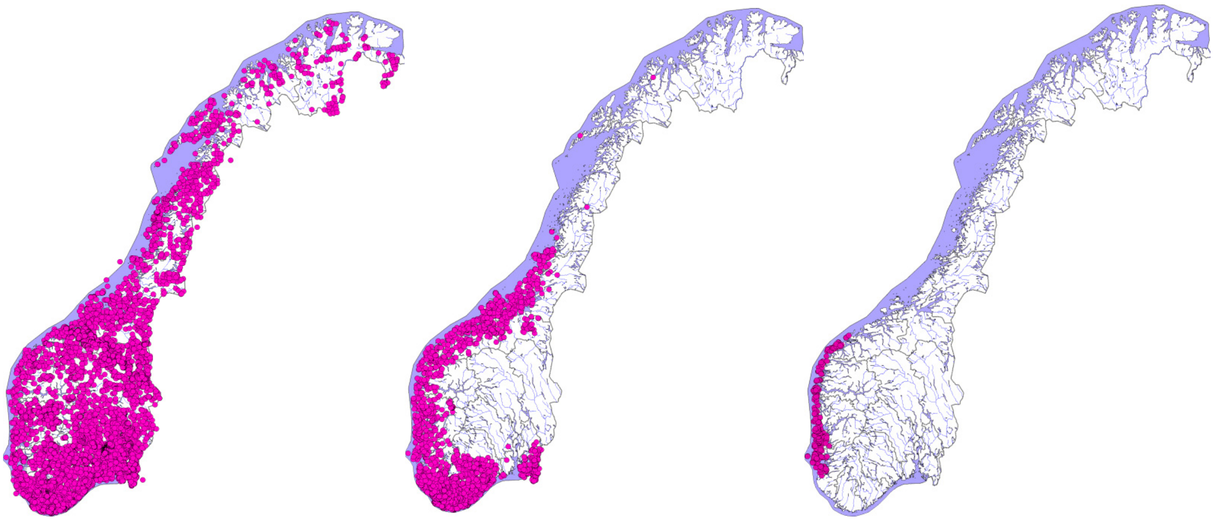

Figure 1. Distribution maps of *Calluna vulgaris, Erica tetralix* and *E. cinera* (left to right) in Norway.

Coastal heathlands are generally dominated by *Calluna vulgaris* in association with other ericaceous shrubs such as *Erica tetralix* and *E. cinera*. *Calluna* is widely distributed in Europe, Eurasia and at the tip of north western Africa. *Calluna* is a monotypic genus; a low, much branched shrub, normally hemi-spherical and evergreen with minute leaves (Gimingham 1960). *Calluna's* duration of life is generally limited to *ca.* 30 years. However, a plant aged 58 years has been recorded from an alpine forest in Norway (Mork 1946). Watt (1947, 1955) applied the terms pioneer, building, mature and degenerate to describe the succeeding life history phases of *Calluna.* This cyclical pattern of general *Calluna* development has been accepted and used in most heathland studies since then, however, in later years it has been realized as one of a greater number of possible developmental pathways (Hobbs & Gimingham 1987, Gimingham 1988).

Characteristically, *Calluna* has a wide ecological amplitude (Gimingham 1972), and it is an important component of both natural and semi-natural heath vegetation. *Calluna* is known as an oligotrophic calcifuge species. Approximate limits of pH at the surface are 3.2-7.0, but it is usually found within the range of 3.5-6.5. *Calluna* is known to produce copious seeds (Nordhagen 1937, Legg *et al.* 1992, Barclay-Estrup & Gimingham 1994) which accumulate in the soil to form long-lived seed banks (Miller & Cummins 1987). Seeds are minute; about 0.6 by 0.35 mm. The longevity of seeds in the soil is now well established and a life span of 150 years in blanket peat has been estimated (Cumming & Legg 1995). Well over 90% of the population of buried *Calluna* seeds lies within the top 50 mm of podzolic soils (Putwain *et al.* 1982, Miller & Cummins 1987, 2001). The seedlings develop a tap root directed vertically and root hairs are absent (Gimingham 1992). After fire *Calluna* normally regenerates both vegetatively from surviving stem bases and from seeds, depending on the age of the burnt individual (Gimingham 1992). Curiously, in coastal areas of Central Norway, north of 62°N, *Calluna* is reported to only regenerate from seed (Nilsen *et al.* 2005) after fire, regardless of the *Calluna's* age at the time of burning.

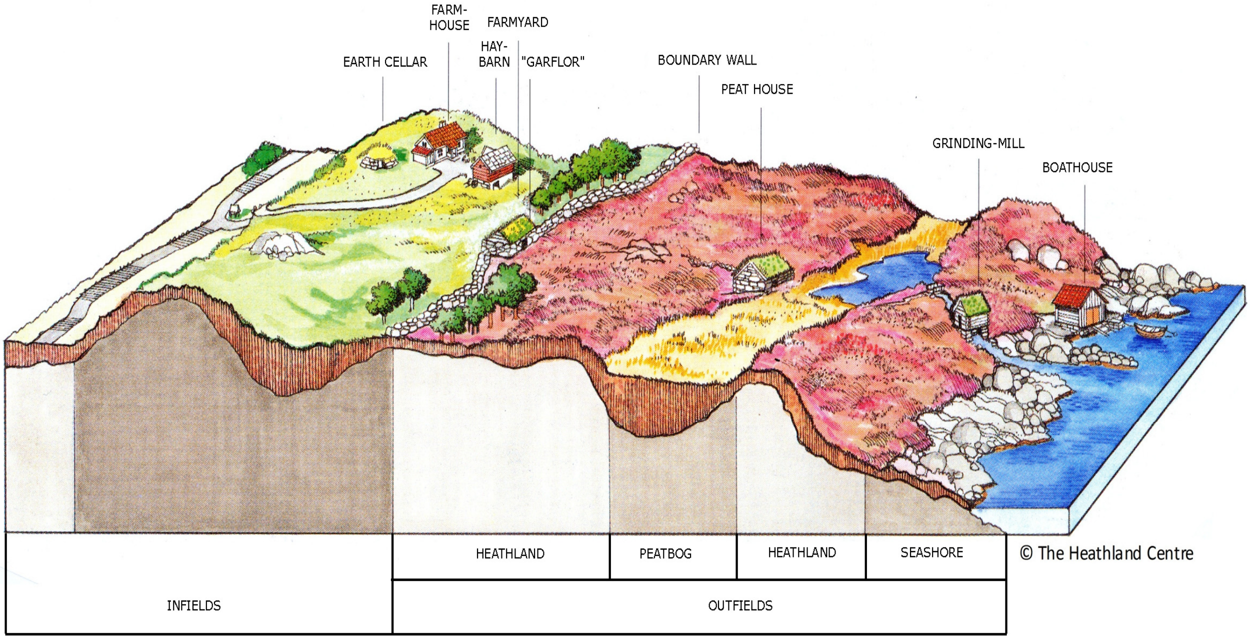

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Figure 2. Schematic presentation of the west Norwegian heathland farm characterized by small infields and large outfields. The outfields served a dual function; (i) livestock grazing grounds, winter fodder and peat for fuel, and (ii) a fertilizer source for the infields; animal manure was collected in the summer by keeping the animals in the "garflor" overnight and in winter pulverised peat litter in the barn collected manure and urine, which was spread on the infields in spring. Redrawn after Ingvaldsen (1976).

Figure 3. The Old Norse breed of sheep (*Ovis brachyura borealis*) at Lygra, North Hordaland, Norway.

Calluna has been vital to the survival of the Norwegian coastal farmer (Fig. 2). The grazing of livestock on this plant in winter has, in combination with seasonal fishing, made a sustainable livelihood for the farmer and his family. In order to maintain the best fodder quality certain areas of the heathland was regularly burnt during winter or early spring (Kaland 1999). Prescribed burning combined with moderate grazing was the appropriate way to keep the heath pastures in optimal condition, indeed burning was an integral part of the farming practise all along the west coast. The frequency of burning depended on the grazing pressure; the lower the grazing pressure, the more often it was burnt in order to maintain good fodder quality (Kaland 1999). Cattle were fed in byres in the winter, while sheep mostly grazed outside year around.

Historically, the common breed of sheep was Old Norse breed (*Ovis brachyura borealis*); light weight, long legged and short tailed (Fig. 3). This breed, and similar kinds, were once widespread along coastal northern Europe, but were replaced by modern breeds *ca.* 100 years ago. However, in the small island community of Austevoll south-west of Bergen, the local breed of the ancient breed avoided extinction and the local farmers also preserved the traditional knowledge of how to manage this breed. During the last 40 years, it has been reintroduced along most of the coast (Løne 1976, 1991). The increased interest in keeping this breed is the combined results of conservation efforts and the growing market for organic products, such as meat form this breed. My project has been affiliated to the Norwegian Research Council Project "VILLSAU; developing a sustainable local industry in vulnerable cultural landscapes", specifically investigating this old breed's impact on coastal vegetation.

Coastal heathlands have been maintained by spatially and temporally heterogeneous land-use practices, i.e. anthropogenic disturbance regimes (Fig. 4), including grazing by domestic and wild animals, prescribed burning, turf-cutting and harvesting of heather and bracken (see e.g. Gimingham 1972, 1992, Kaland 1986, Webb 1986, 1998). In the past 50-100 years, these traditional management regimes have gradually ceased, resulting, in Norway, mainly in wood encroachment by native species, but also by introduced species such as *Picea sitchensis* (Skogen 1987, Granström 1988, Fremstad *et al.* 1991, Webb 1998, Mitchell *et al.* 1999). Bracken invasion in heathland areas is also an increasing problem along the west coast. Many invasives show resilience to management. Other present threats are eutrophication, fragmentation, invasion and intensification (Fig. 4), in addition to climate change (Aarrestad 2007, Millennium Ecosystem Assessment 2005, www.maweb.org). Successional trajectories may vary among areas with different environmental conditions and management histories (Hobbs & Gimingham 1984b, Britton *et al.* 2000). The extent to which the response to, and the relationship between, different land-use practices are affected by the environmental heterogeneity of the landscape also varies.

Different modern management regimes, including grazing at different stocking rates (Bokdam & Gleichman 2000, Pakeman *et al.* 2003), burning (Hobbs & Gimingham 1984a, 1984b, Mallik & Gimingham 1985, Øvstedal & Heegaard 2000, Britton *et al.* 2001), mechanical cutting (Calvo *et al.* 2002), litter stripping (Mitchell *et al.* 1999) and turf stripping (Bokdam & Gleichman 2000, Diaz *et al.* 2008), have been applied to halt the loss of this habitat, with varying degrees of success. The number of successful restorations are rather low. The European heathland ecosystem has recently been classified as greatly endangered (EC Habitats Directive 92/43/EEC, Aarrestad *et al.* 2001).

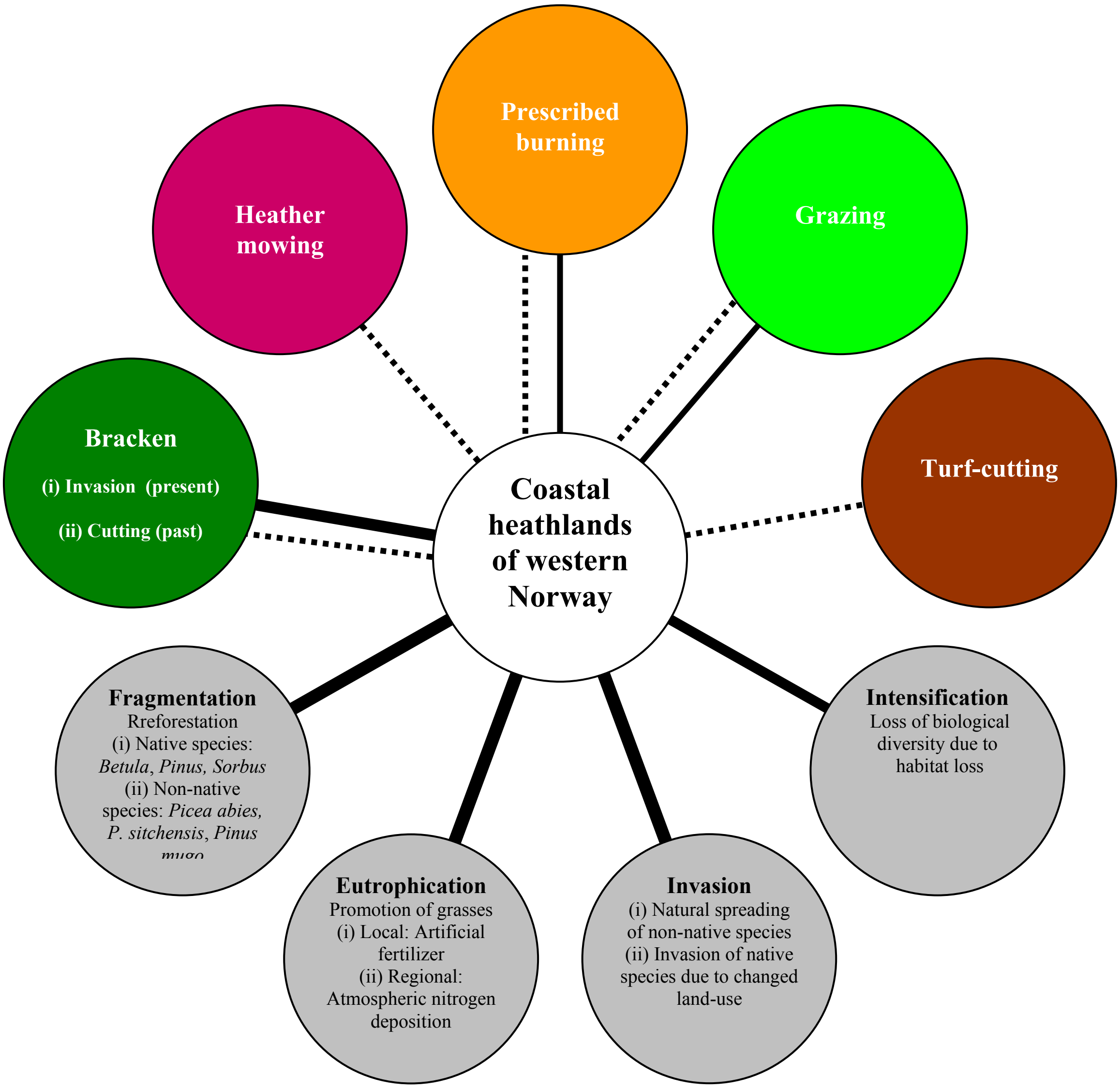


Figure 4. A simplified overview of anthropogenic disturbance regimes affecting the structure and function of the west Norwegian coastal heathland system in the past (broken lines) and at present (solid lines). Thick lines indicate overriding factors. Coloured circles represent traditional management regimes where as grey circles represent present day disturbances/threats – leading to the loss of heathland habitat.

Objectives

This thesis aims to contribute to our understanding of the effects of past and present human land-use on coastal heathlands; the dominating low-intensity farming system in the coastal areas of western Norway. These heathlands have been shaped and maintained over centuries and millennia by two main anthropogenic disturbances, namely fire and grazing. Today, these semi-natural landscapes are highly threatened, in some areas due to decreased use or abandonment, in other areas due to intensified use, fragmentation and/or destruction.

The main objective is broken down into two general themes, which again are broken down into a series of specific aims or objectives that form the basis for the five papers included in this thesis:

(i) *Disturbances as drivers of the "everyday dynamics" of traditionally managed heathlands*

Fire as the main ecological reset mechanism in managed heathlands:
* Revegetation dynamics after fire – early phase and long-term (0-30 years) - *Paper I and III*
* The role of seed banks in the successional dynamics of the heathland system - *Paper I*
* Germination cues and fire responses in *Calluna vulgaris* - *Papers I and II*
* Can chronosequence data be used as substitutes for experimental data in this system? – *Paper I*

Effects of grazing and habitat variability on the post-fire succession:
* Post-fire revegetation dynamics along local environmental gradients - *Paper III*
* Grazing as a fine-scale disturbance interacting with post-fire successional dynamics and environment - *Paper III*

(ii) *Threats, restoration and conservation*

Effects of different bracken control measures in northern coastal heathlands:
* Best treatment for bracken reduction - *Papers IV and V*
* Restoration of heathland structure and community composition - *Papers IV and V*
* Do herbicides affect structure, diversity, or composition of the non-target community? – *Paper IV*

Contributions to evidence-based management, conservation and restoration strategies:
* Implications for conservation - *Papers I to V*
* Communication of research to different target groups; scientists, managers and decision makers requires different publication strategies, focus and channels - *Papers IV and V*

I approach the outlined objectives from various angles, using a range of different data-sets and analytical techniques, using the heathlands at the Heathland Centre at Lygra, western Norway, as the study system. In the following sections I present the outlined objectives. Results on vegetation and seed bank dynamics are presented mainly in the first section and in Papers I to III. Results on bracken control are presented in the latter sections under "Threats" and "Conservation" and in Papers IV and V.

Study area – Lygra, North Hordaland, western Norway

The coastal heathlands of the North Hordaland region are distributed on many islands of varying size and proximity from the mainland. Heathland development took place at different times, hence creating heathlands of different ages (Fig. 5). Earliest development took place around 4000-5000 BP, with a marked increase of charcoal and *Calluna* pollen, in combination with a decline in arboreal tree-pollen, demarking the start of the transition from forest cover towards an open coastal heathland system (Kaland 1986). However, in some areas this process took place considerably later, up to around 1000 BP. *Calluna* has been present in western parts of Norway throughout the Holocene, which started at *ca.* 11500 cal. BP (Bondevik & Mangerud 2002) in this region, but its abundance increased considerably during the establishment of coastal heath vegetation in the period between 1000-5000 BP.

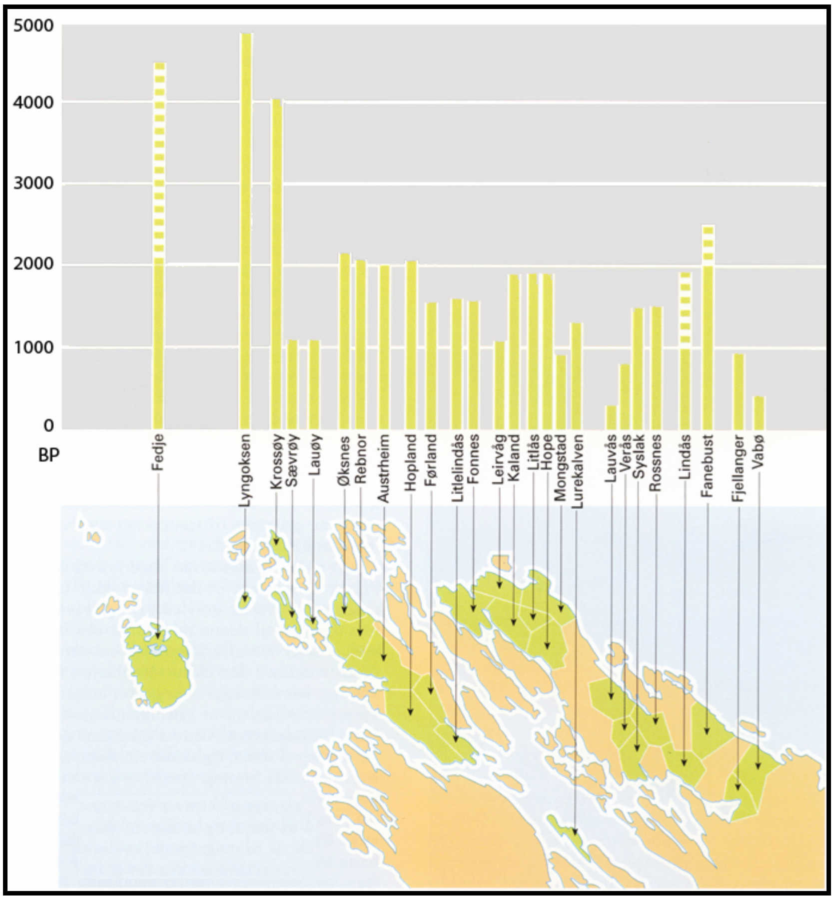


Figure 5. Heathland development in the North Hordaland region. The time line to the left indicates years before present (BP). Arrows with corresponding names are farm-names where palaeoecological investigations have enabled dating of the main deforestation and establishment of a dominant *Calluna* cover. Striped sections of columns indicate "uncertain" heathland creation (After Kaland 1986).

Outer Lygra is now part of The Heathland Centre (www.lyngheisenteret.no), established in 1995. It consists of a landscape of international value, protected through active estate management to maintain traditional methods of farming and ancient breeds of livestock. The Centre is organised in four parts; farming, ecology, cultural history, and information centre. The Centre's objectives are to (i) manage the coastal heathlands with a management regime as close to the traditional land-use practice as possible, supporting its conservation in a national and a European context, (ii) provide an infrastructure for research and teaching, and (iii) disseminate knowledge about the coastal heathlands to the public.

The islands of Lygra and Lurekalven are situated at 60°42’ N and 5°60’ E, in the Lurefjorden fjord basin, approximately 20 km inland from the Norwegian west coast, 40 km north-west of Bergen (Fig. 6). The topography of Lygra is relatively flat, with low ridges and narrow valleys following the strike direction (NW-SE) of the Bergen Arc System (Kolderup & Kolderup 1940). The island is divided into heath-dominated Utluro to the north and the forested and intensively cleared and farmed Innluro to the south. The study sites included in this thesis are located at the outer parts of the island; Utluro. Here, hard and slowly erosive bedrock gives rise to a nutrient-poor soil type (Austrheim 1978). Lurekalven and Lygra islands are separated by a narrow strait; Lurekalven being the northernmost of the two islands. Lurekalven is narrow, the highest point is 54 m asl, and the topography is relatively rugged, also following the strike direction of the Bergen Arc System.

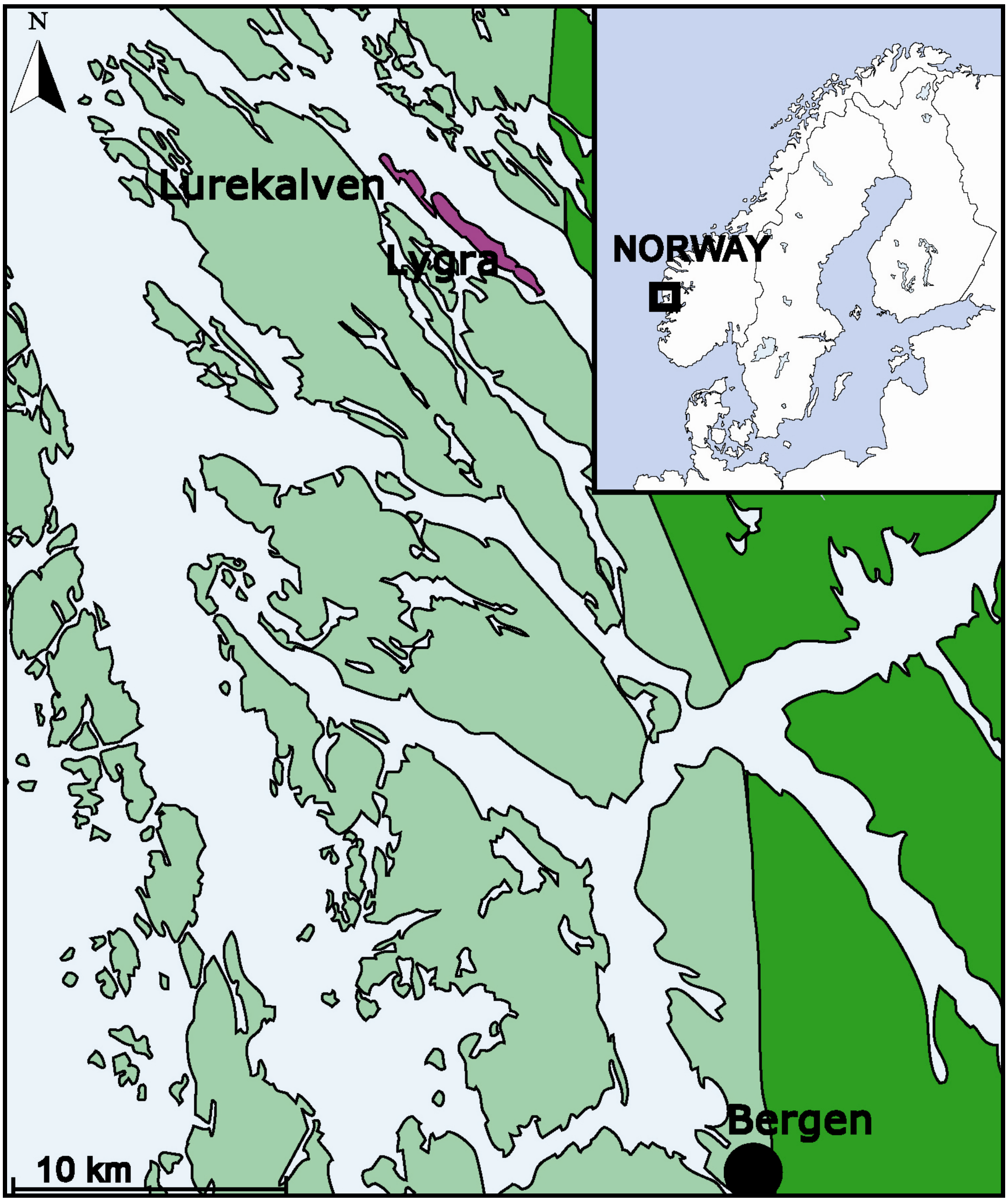


Figure 6. The study area is situated at the Heathland Centre, Lindås municipality, Hordaland County, western Norway. The islands of Lygra and Lurekalven are situated in the Lurefjorden fjord basin, approximately 20 km inland from the Norwegian west coast and 40 km north of Bergen. Light-green depicts the extent of the heathland distribution at *ca*. 1900 AC.

The climate is characteristically oceanic with relatively small differences between June and January mean temperatures; 12°C and 2°C, respectively (Aune 1993), a long growing season of *ca.* 220 days above 5°C, abundant precipitation at 1800 mm (Førland 1993) relatively evenly distributed throughout the year, and strong winds. The area seldom experiences snow cover or long periods of frost. However, hyper-oceanic species such as *Erica cinera, Scilla verna* and *Vicia orobus* are missing from Lygra. Moisture is a major source of local environmental variability; dry heath on shallow soils often occurs on ridges or on south-facing areas, whereas moist heath on deeper soils often occurs on north-facing slopes or in convex, poorly drained areas (Aarrestad & Vandvik 2000). Sheep of Old Norse breed (*Ovis brachyura borealis*) graze year-round on both islands. Today, in sharp contrast to the outfields of Lurekalven and Lygra, neighbouring islands are mainly reforested by dense plantations of *Picea sitchensis* and *Pinus mugo*, or by natural woodland encroachment both by native and introduced species. The recent history of prescribed burning is recorded in detail in Figure 7.

Due to early settlement and extensive turf cutting at Lygra, finding suitable sites for palaeoecological sampling has not been possible; consequently the main deforestation has not been documented in detail. However, written documentation reveals that parts of the outfields have been under continuous management by burning, grazing, and turf and heather cutting for centuries up until today, creating a mosaic heathland of different successional stages (Paper III). The vegetation at present is dominated by *Calluna* heaths, grass heaths and mires and *Salix* shrubs in wetter areas. Ericoid shrub species such as *Calluna vulgaris*, *Erica tetralix*, *Vaccinium myrtillus V. vitis-idaea, V. uliginosum*, *V. oxycoccus, Arctostaphylos uva-ursi* and *Empetrum nigrum* coll. occur throughout, in combination with common graminoids, forbs and mosses. The area is grazed by *ca.* 0.1 cows ha^{-1} in summer and by 1.0-1.2 sheep ha^{-1} year^{-1}(Samson Øpstad; *unpublished data*), which is comparable to advised stocking levels in other heathland areas, see Hulme *et al.* (2002) and Pakeman *et al.* (2003), describing moderate stocking levels at < 1 sheep ha^{-1} year^{-1}. *Pteridium aquilinum,* bracken, is proving a formidable management challenge for the Heathland Centre. It has been present at Lygra for a long time, but the species has increased substantially over the recent years and by 2004 it had invaded *ca.* 30% of the vegetated outfield areas (excluding bare rock and coastal slabs).

The island of Lurekalven was covered by a mixed deciduous forest until it was cleared *ca.* 700 AD by a local farm (Kaland 1979). The larger part of the island then developed into *Calluna* heath while smaller areas were used for hay meadows or cultivated infields. The farm was abandoned *ca.* 1350 AD, after the plague, and the island has not been inhabited since. However, it has been managed for grazing for a variety of livestock (Kvamme 1982). From 1950 onwards the island gradually fell out of use, leading to rapid woodland encroachment, mainly by *Betula pubescens*, but also by *Salix caprea*, *Populus tremula* and *Sorbus aucuparia* (Kaland & Vandvik 1998). In 1992 trees and shrubs were clear felled and burning and grazing was re-introduced (Fig. 6). The overall grazing pressure has been *ca.* 0.8 sheep ha^{-1} year^{-1} (Samson Øpstad; *unpublished data*). Today, the island is largely covered by *Calluna* heath, with mires and *Salix* shrubs in wetter areas and mixed grass-heaths on more nutrient-rich soils along beaches and on former infields. Woodland stands of *Betula, Salix, Sorbus, Pinus* and *Populus* are situated on southern slopes or in sheltered valleys. Also here bracken is locally present (on former infields), but to a lesser degree than on Lygra.

Nomenclature follows Lid and Lid (2005) for vascular plants, Smith (1978, 1990) for mosses and Krog *et al.* (1994) for lichens.

Figure 7. The recent history of prescribed burning on the islands of Lygra and Lurekalven, Lindås, Hordaland County. Colour coding indicates where and when different areas were burnt. The map is compiled by B. Wilkerson using a variety of data sources; GPS-polygons, aerial photos and sketches; consequently, some are very accurate while others are rougher depictions.

Ecological effects of heathland land-use

The papers included in this thesis investigate the effects of anthropogenic disturbances, repeated over centuries and even millennia, on the vegetation and the soil stored seed bank at a range of temporal and spatial scales. In the coastal heathland system prescribed burning and grazing are the two main components constituting the anthropogenic disturbance regime. Here, I have mainly focused on the effects of fire (Papers I, II & III), and to a lesser degree on the specific effects of grazing (Papers III & IV). Previous studies have shown successional trajectories to vary among areas with different environmental conditions and management histories (Hobbs & Gimingham 1984b, Britton *et al.* 2000). However, little research effort has been directed at investigating to what extent the response to, and relationship between, different management practices are affected by the environmental heterogeneity of the landscape. Regarding conservation and restoration efforts in heathlands, the focus has been on the target species and a few other keystone species (Pakeman & Hay 1996, Marrs *et al.* 1998a,b, Mitchell *et al.* 1998, Pakeman *et al.* 1998, 2000, Marrs *et al.* 2000, Britton *et al.* 2001). In addition to this focus, it is important to assess and evaluate the responses of the non-target species (Cadbury 1976, Pakeman *et al.* 1997), the rate and direction of revegetation (Pakeman *et al.* 2007), biodiversity dynamics, species composition and other ecosystem characteristics in assessing the conservation and restoration success (Papers IV & V).

Fire

Fire is a disturbance influencing plant communities in many parts of the world. However, fire differs from many other disturbances in the way that it "consumes" complex organic molecules and it has been argued that fire is more analogous to herbivory than to other abiotic disturbances (Bond & Keeley 2005). After fire, an open habitat is created with a flush of nutrients released (Evans & Allen 1971), creating, from a plant's perspective, a unique opportunity for colonization and growth. Fire plays a significant role in the succession of heathland flora. The effects of fire on vegetation and soil depend on intensity and frequency, which in turn is influenced by a wide range of variables such as vegetation structure and age, the season of burning, weather conditions, fuel characteristics and topography (Pyne *et al.* 1996). Public opinion to the use of fire as a management tool may range from pyromania to pyrophobia due to the nature of the constraints on its practical use in vegetation management (Bond & van Wilgen 1996). Indeed, knowledge of the effects of fire on vegetation dynamics and structure is essential for judicious use of fire as a management tool.

Under the patchy fire regimes characteristic of traditional heathland management of western Norway (Webb 1998), fire increased heathland diversity (Papers I & III), first by allowing a new assemblage of species in the newly burnt patches, and secondly by increasing fine-scale species density within sites. The newly burnt, pioneer phase (0-5 years) (*sensu* Watt 1955, Gimingham 1972) was characterized by bare soil, abundant litter layer and by low abundances of all species except a few geophytes such as *Trientalis europaea, Anemone nemorosa, Potentilla erecta, Lotus corniculatus* and *Campanula rotundifolia,* all of which have the capacity to regenerate vegetatively after fire (Paper I). Several of the graminoids regenerate from rhizomes; *Avenella flexuosa* and *Agrostis capillaris*. *Avenella* may germinate from seeds, depending on local seed rain as it has a transient seed bank (Hester *et al.* 1991). The rapid spread and increase after fire of a number of grasses and herbs included *Carex pilulifera*, *Festuca vivipara*, *Hypericum pulchrum*, *Lotus corniculatus* and *Potentilla erecta* (Paper III). The building phase (6-15 years) was dominated by species-rich graminoid and herb-dominated vegetation and high soil pH. The mature phase (16-25 years) was characterised by an increasing dwarf shrub layer, height and cover of *Calluna*, lichen cover and organic content of the soil, and decreasing herb abundance and soil pH. *Calluna* regenerated profusely after fire (Papers I & III); while it was only found in 37% of the subplots the first year after fire, 87% were colonized after three years (Paper III). Recruits originated both from seed and vegetative resprouting. We found that fire induced strong successional trends in the species composition paralleled by changes in species richness. At all scales investigated (0.0625 m^2 subplots, 1 m^2 plots, 100 m^2 sites), richness decreased in the first year after fire, then increased to well above pre-fire levels in the following three years (Paper III). The same trend of increasing diversity after fire was seen in the seed bank study of Paper I.

Seed bank and vegetation dynamics in post-fire succession

Soil seed banks are a highly important functional element of a wide range of ecosystems. The existence and potential importance of soil seed banks have been recognized by ecologists and evolutionary biologists since Darwin (1859). Thompson *et al.* (1997) distinguished three types of seed banks; transient, short-term and long-term persistent. Long-term persistence is thought to be advantageous in highly variable environments, while transient persistence should be expected with environmental stability and a high probability of successful reproduction and germination. Several authors have pointed out that the species composition of seed banks changes over the course of succession (e.g. Miles & Young 1980, Pakeman & Hay 1996). Seed banks are dynamic, determined by inputs and outputs through time and space, seed density, species composition and genetic variation (Fig. 8, Simpson *et al.* 1989) varying within and among species, creating temporal and spatial dispersal patterns (van der Valk 1992). Input is dominated by local supply through seed rain (Hobbs & Gimingham 1984b), although distant seed sources may be important contributors in some systems (Fenner 1985). Further, input depends upon factors such as seed production, age/size of plants, environmental conditions and pollinator availability. Output is dependent upon germination success which is influenced by factors such as predation, pathogens, senescence, environmental constraints, germination cues and mortality (Simpson *et al.* 1989, Baskin & Baskin 1998, van Staden *et al.* 2000). The long-term persistence of any species at a site requires that, at least occasionally, seeds germinate; plants grow to maturity, flower and produce seeds.

The traits allowing the formation and long-term survival of seed banks are well studied, and seed banks have been documented across a range of evolutionary lineages, ecological situations and biogeographic regions (Fenner 1985, Thompson *et al.* 1997, Baskin & Baskin 1998, Hopfensperger 2007). Accordingly, it has been suggested that the combination of fire and nutrient-poor soils leads to a dominance of seeders in the landscape, explaining, for example, the high diversity of the South African fynbos and the Australian kwongan (Wisheu *et al.* 2000). The soil seed reservoir is of great significance for the regeneration of vegetation following disturbance (Grubb 1988, Thompson 1992, Pakeman & Hay 1996, Mitchell *et al.* 1998). Consequently, seed banks may strongly influence the path of vegetation succession following fire. However, species vary in their capacity to persist as seeds in the soil over time, leading to differences in seed bank composition and propagule availability for post-fire colonisation. Seed bank density and diversity usually decrease or remain relatively unchanged as time since disturbance increases (Milberg 1995). Seed banking could act to mediate the genetic consequences of rarity, increasing the likelihood of persistence and maintaining the evolutionary potential of a species (Levin 1990, McCue & Holtsford 1998).

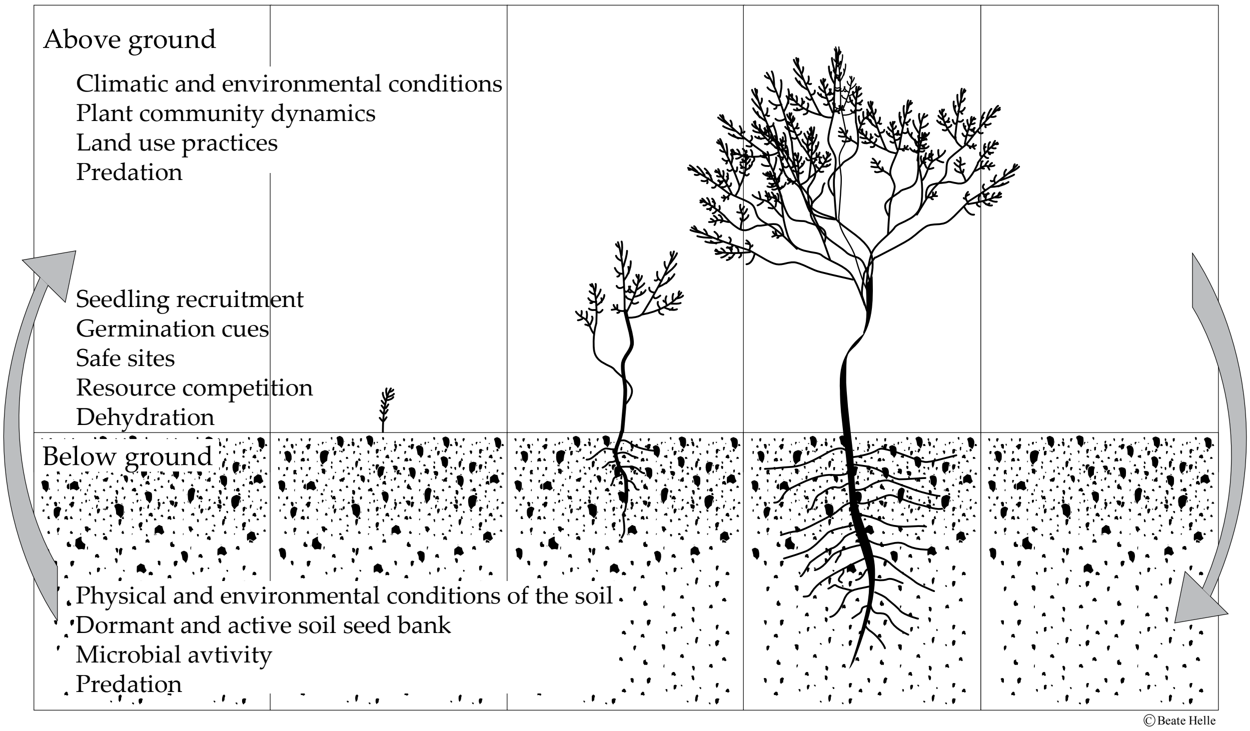


Figure 8. Schematic presentation of above- and below-ground processes in heathland vegetation dynamics.

The ability to form a long-term persistent seed bank is particularly important in systems subjected to temporally unpredictable large-scale environmental variability (Grubb 1977, Chesson & Warner 1981) such as in drought-prone environments (Henderson *et al.* 1988, Phillippi 1993a,b, Osem *et al.* 2006) where seed banks can act as “refuges” for local plant populations, allowing them to escape adverse conditions by "dispersing through time". Strong selective pressures operate on the mechanisms regulating dormancy and germination under such conditions, exemplified by bet-hedging germination strategies where dormancy fractions of local populations are tightly linked to the probability of bad years (Venable & Brown 1988, Phillippi 1993a,b). At the community scale, seed banks can play a role in local diversity maintenance through temporal storage effects (Chesson & Warner 1981, Hoopes *et al.* 2005). Because of their implications for population persistence and community resilience, seed banks have also been of interest for management, conservation and restoration research. However, these studies typically reach the opposite conclusions, namely that seed banks very often have little potential for the conservation and restoration of natural ecosystems (e.g. Mitchell *et al.* 2008). Many studies find lower species richness and higher proportions of weeds and early-successional species in the seed bank relative to the standing vegetation (Milberg 1995, Bekker *et al.* 2000), and conclude that seed banks should be seen as a “spillover” of ungerminated seeds rather than as an independent driver of population and community dynamics (Bekker *et al.* 2000). In Paper I we investigate how these contrasting views relate to the heathland system by analysing vegetation and seed bank along a 24-year post-fire replicated chronosequence.

Succession theory generally predicts a unimodal relationship (asymmetric) between species richness and time after large-scale disturbance (Vetaas 1994, del Moral 2007). We predicted (Paper I) that if seed banks represent a spillover in this system, this unimodal trend will be seen in the soil seed bank as well as in standing vegetation, possibly, with a slight delay in the seed bank as it tracks the successional trajectory of the standing vegetation. Further, relatively few species would be represented in the seed bank. On the other hand, if the seed bank acted as a refuge we predicted that a broad spectre of heathland species should be represented in the seed banks, and that the diversity will not be tracking the unimodal diversity trend of the vegetation. On the basis of our results (Paper I) we propose that in this managed heathland system, seed banks act as refuges, and not as spillover, for many of the common heathland species, based on; (i) The high correspondence between the vegetation and the seed bank, which is consistent with a system where a high fraction of the species relies on persistent seed banks (refuges, "dispersal through time") for colonization of newly available habitat rather than on colonization by dispersal through space (Thompson & Grime 1979, Bossuyt & Honnay 2008). (ii) The diverse flora of the seed banks, including many target heathland species. (iii) The refuge or "dispersal through time" model of heathland seed banks is also supported by the species richness patterns over the course of the secondary succession. Twenty four years of succession is not associated with drastic changes in the soil seed bank, the predicted hump back diversity pattern is found in the standing vegetation but it is not tracked by the seed bank. (iv) The seed bank – vegetation similarity is highest in mid-succession, suggesting that the seed bank flora contributes significantly to the humped diversity pattern seen in the vegetation.

Figure 9. Seedling of *Betula pubescens*, newly burnt heath at Lygra, seedling of *Calluna vulgaris* to the left and *Erica tetralix* to the right, and seed bank trial set up at the greenhouses at the Norwegian Arboretum, Milde.

Paper I highlights the importance of sampling intensively and of carefully designed germination trials to capture the variation in species composition inherent to these heathland soil seed banks (Fig. 9). It is feasible to study a range of stand ages in a small environmentally uniform area and to infer a developmental sequence from these, exemplified by the chronosequence study of Paper I. However, different stands may not always represent a developmental sequence, but rather a collage of different successional pathways (Hobbs & Gimingham 1984b). Soil-stored seeds represent part of the vegetation's response to disturbances, including management and restoration efforts. While it is often overlooked in descriptions of vegetation dynamics, such descriptions of plant communities are incomplete without an understanding of the soil seed bank's role, as pointed out by Major and Pyott (1966). Accordingly, knowledge of seed bank dynamics, and its germination responses, is essential to the understanding of heathland vegetation responses to disturbance.

Fire-related germination cues and Calluna vulgaris

Following fire, a subsequent wave of germination from soil-stored seed banks is a well known phenomenon where seed germination is stimulated indirectly through responses to micro-environmental changes or directly through responses to high temperatures or chemical cues derived from smoke, charcoal or ash (Zackrisson *et al.* 1996; Reyes & Casal 1998, van Staden *et al.* 2000). The ecophysiological responses to such fire-related germination cues have been studied extensively on species in ecosystems with naturally occurring frequent fires (van Staden *et al.* 2000, Brown *et al.* 2003, Read *et al.* 2000, Keeley 1987, Keeley & Fotheringham 1988, 1997, 1998, Crosti *et al.* 2006). A major active compound in the smoke response has recently been identified as butenolide (3-methyl-2*H*-furo[2,3-*c*]pyran-2-one), a derivate from the combustion of cellulose. This represents a universal and reliable cue signalling the combustion of plant material (Flematti *et al.* 2004a,b, Van Staden *et al.* 2004, Light *et al.* 2008), and it has been shown to stimulate germination and seedling growth in a number of species of different biogeographic and ecological affinities in natural fire-prone ecosystems (Light *et al.* 2008). Many studies have also found ash-beds to favour seedling growth (Keeley 1987). However, the response of seed germination to ash is less well understood (Reyes & Castal 1998). In comparison to in natural fire-prone systems, there is a limited understanding of the germination responses of species to fire-related cues in “anthropogenic fire-prone" semi-natural systems such as the coastal heathlands of northern Europe. European heathland species accumulate substantial soil seed banks, which contribute to post-fire recruitment (Paper I), and yet there has been little evidence that they are directly stimulated by heat or fire-related chemicals (Hobbs *et al.* 1984a, Mallik *et al.* 1984, Mallik & Gimingham 1985). Here, prescribed fires are still part of the recommended management protocol for heathland management and conservation; consequently the effects of fire on the germination dynamics require investigation.

In Paper II we investigated the effects of fire on *Calluna* regeneration and seed bank dynamics by (i) studying germination from the soil seed bank over the course of a post-fire chronosequence to quantify the patterns of seed accumulation and "withdrawal" from the soil seed bank during post-fire succession, (ii) performing experiments on fresh *Calluna* seeds (Fig. 10) to test whether the seed bank behaviour of *Calluna* can be accounted for by ecophysiological responses to fire-related germination cues, and (iii) conducting experiments on soil seed banks to test whether the patterns observed under (i) can be recreated experimentally. In particular, we predict that if the seed bank dynamics of these heathlands are regulated by fire-related germination cues (smoke and ash), then we should observe increased germination under experimental treatments with smoke and/or ash in soil seed bank samples collected from mature heath but not in samples collected from newly-burnt heath which have already been exposed to these cues *in situ*.

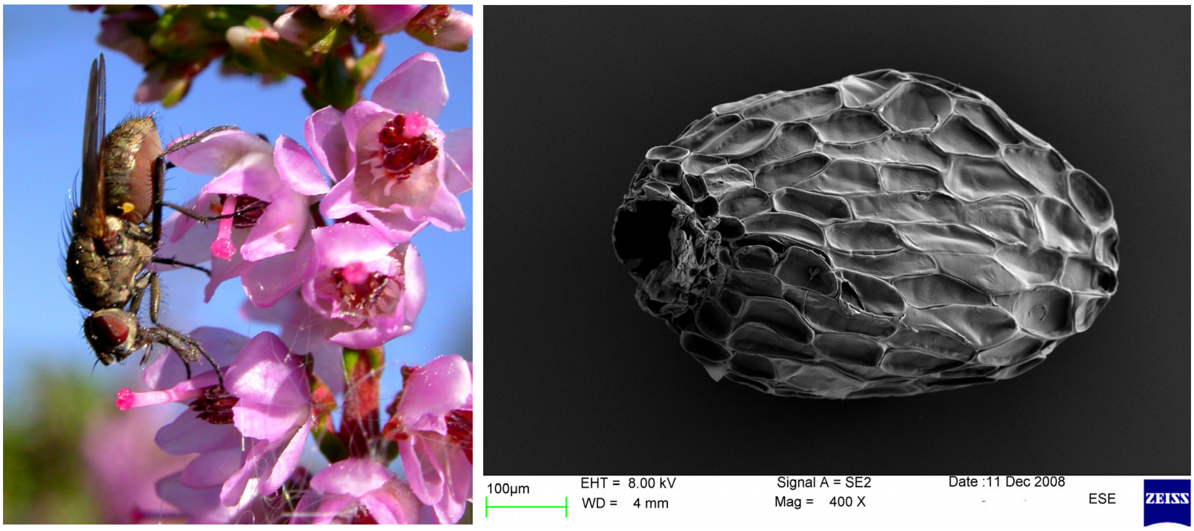


Figure 10. Left: *Calluna vulgaris* flowers and a potential pollinator. Right: *Calluna vulgaris* seed photographed with a scanning electron microscope, 400 x magnification, by Jan Berge.

The germination response of *Calluna* seeds to the fire-related cue of plant-derived aqueous smoke solution was positive, providing indirect evidence that fire stimulates *Calluna* seed germination. While we observed increased germination under experimental treatments with smoke and/or ash in the soil seed bank samples collected from the mature heath, we did not observe the same trend in the samples collected from the newly-burnt heath, in line with our prediction. These sites have most likely already been exposed to these cues *in situ*. While the ecophysiological response to smoke (data-set ii) parallels what is already known from other studies (Thomas & Davies 2002) our study is the first to combine this response with observational and experimental studies on the seed bank (data-sets i and iii). Combined, these data yield insights into the ecological effects of the anthropogenic disturbance of prescribed burning on the dominant species of the heathland system, namely *Calluna*. These results demonstrate that assessing the germination response of a species to fire can best be achieved through experimental studies that complement seed bank species descriptions (Paper I). It also demonstrates the added value and importance of comparing results across methodology. Requiring specific cues for seed germination is a major adaptive response that allows seeds to 'sense' prevailing environmental conditions, thereby providing a means of habitat selection (Harper 1994, Baskin & Baskin 1998). Interestingly, in a heathland context, smoke treatment has, for example, also been shown to stimulate germination responses in a range of Ericaceae species from the Cape Floral Region in South Africa (Brown *et al.* 1993, van Staden *et al.* 2000). As plant-derived smoke constitutes an important cue for seed germination it has major implications for our understanding of conservation and restoration biology (Brown & van Staden 1997).

Grazing

In grazed ecosystems the main biotic factor affecting vegetation structure and dynamics is the obvious effects of biomass removal by herbivores by browsing and grazing (Bakker *et al.* 2006). Herbivores may also play an important role in long distance dispersal of propagules, enhancing local colonisation processes and plant diversity (Pakeman 2001). In heathland terms, overgrazing may damage the heather canopy and cause disappearance of *Calluna* as a dominant and lead to the invasion of grasses (Tansley 1939, Ratcliffe 1959, Gimingham 1992, Hester & Baillie 1998). Overgrazing is also linked to the concept of carrying capacity; the maximum possible stocking of herbivores that the grazing grounds can support on a sustainable basis (Mysterud 2006). Undergrazing, on the other hand, may lead to heather degradation, shrub and tree encroachment and grass invasion (Miles 1981, Diemont 1996).

By a replicated series of post-fire successions, subjected to two grazing regimes, we investigated the interactive effects of fire and grazing along the local moisture gradient (Paper III). At Lurekalven we found that the effects of sheep grazing on the successional dynamics differed among moisture habitats. However, species diversity was not affected by local environment or grazing. Diversity decreased in the first year after fire but increased beyond the pre-fire levels over the course of the post-fire succession. In these heathlands grazing acts as a heterogenizing factor. This can be explained by several factors; First, animals do not graze landscapes evenly (Senft *et al.* 1987, Hester *et al.* 1999, Rao *et al.* 2003, Fuhlendorf & Engle 2004), and this is especially true in systems where free-ranging grazers have access to large and topographically diverse areas at relatively low stocking rates (Coughenour 1991, Palmer & Hester 2000). At Lurekalven, as observed elsewhere, the sheep prefer; burnt to unburnt heath, ridges with a good overview of the landscape to steeper or lower-lying areas, and dry to moist grounds (S. Øpstad, *personal communication*). The local grazing pressure can consequently be summarized as a response to the interactive effects of topography, moisture and fire. This was reflected in the compositional patterns as the response to fire in ungrazed heath was strongest in the dry sites. However, the response was stronger in the intermediate moist grazed heath (i.e. the preferred flat hilltops and ridges). Second, the grazing responses of species depended on their distributions along the moisture gradient and post-fire successional gradients. Although grazing may decrease local species richness in the preferred sites, the fine-scale variation of grazing intensity may result in increased floristic heterogeneity at the landscape scale (Paper III, Introduction).

As outlined in the previous sections, the coastal heathland vegetation responds at different spatial and temporal scales to the interactive effects of the management regimes imposed by heathland farming. Generally, the co-occurrence of the anthropogenic disturbances of prescribed burning and livestock grazing has a synergistic effect on plant communities both in time and space (Coughenour 1991). Many grazers, in this case the Old Norse sheep, are attracted to recently burnt ground to feed on post-fire regrowth of grasses and herbs. Grazing, in turn, reduces the fuel load by consumption and trampling, hence lowering the intensity of the fires. The two management practices of grazing and prescribed burning do not have simple additive effects within the heathland system studied, as demonstrated by our results in Paper III. We show that grazing created ecological opportunities for additional sets of species, increased variability among habitats, and added complexity to the post-fire successional dynamics.

Bracken control can also be described as a disturbance to facilitate conservation or restoration (see page 19 for details on bracken control). In the UK, restoring *Calluna* heathlands by bracken control have occasionally resulted in grass-dominated communities and simply controlling bracken by herbicides may not result in conservation or restoration of *Calluna* heathlands (Pakeman *et al.* 1997). This seemed not to be the case in our study area (Papers IV and V). The grazing regime at the site, with local breeds of sheep and cattle (Fig. 11), is one plausible explanation, as trampling by cattle can be an important factor in bracken control, at least in areas where bracken stands are not too dense; Williams (1980) found bracken regrowth after asulam application to be considerably slowed by grazing sheep and cattle compared to sites grazed by sheep alone. In addition, our use of follow-up annual cutting treatments may also have increased the rate of success in re-establishing desirable heathland vegetation (see also Lowday & Marrs 1992a,b).

Figure 11. Left: local breed of horse "fjording", right: local breed of cattle "vest-norsk fjordfe" grazing at Lygra.

Threats

Abandonment in conjunction with drastically changed land-use practices is a major threat to the conservation value of Europe's semi-natural landscapes today (Gimingham 1972, Webb 1998). Over the past 50 to 100 years the traditional management regimes in the coastal region of western Norway have gradually fallen out of use, resulting in large-scale woodland encroachment (Skogen 1987, Fremstad *et al.* 1991, Aarrestad *et al.* 2001, Paper III). This successional trajectory, however, is influenced by, for example, management history, distance to the nearest woodlands, climatic conditions and topography (Moen *et al.* 2006).

Excessive burning (Maltby *et al.* 1990), overgrazing (Hester & Ballie 1998, Hulme *et al.* 2002, Pakeman *et al.* 2003), the use of artificial fertilizers (Aerts & Heil 1993) and enhanced nitrogen deposition in the form of atmospheric eutrophication (Diemont 1996, Marrs *et al.* 2004) change the successional trajectories of heathlands towards grasslands. Invasions of native or alien species may also follow changed management regimes or the cessation of such, consequently causing a shift in the vegetation dynamics.

In spite of recent changes for the worse in the coastal heathlands of Norway, they are some of the best preserved heathland areas in Europe. This is, however, not due to deliberate conservation or restoration efforts, but rather to fortunate natural conditions such as low levels of atmospheric eutrophication; Lygra has a nitrogen deposition rate of *ca.* 8 kg N/ha/yr (Hole & Tørseth 2002), which is comparatively low. The empirical critical load of nitrogen (NL) for wet and dry heathlands has been set at 10-20 kg N/ha/yr (Aarrestad 2007). Outbreaks of the heather beetle (*Lochmaea suturalis*) do occur in Norwegian heathlands, but to a lesser extent than further south. Increased nitrogen levels influence the frequency and severity of these beetle attacks (Power *et al.* 1998). Regional changes in climate are expected to affect the distribution of habitats and species, but little knowledge of how this will affect semi-natural landscapes exists (Kålås *et al.* 2006). One can argue that increased winter temperatures and precipitation will increase the rate of woodland encroachment and bracken invasion in heathlands. Soil chemical properties change over the course of succession, especially when *Betula pubescens* invades, resulting in increased pH, exchangeable calcium and extractable phosphorus (Miles 1981, Mitchell *et al.* 1997). Thermophilous species may also eventually out-compete alpine and arctic species along the coast northwards. There is also little understanding of how climatic conditions affect the development of seed banks and consequently even less knowledge of how changing climate will affect seed bank dynamics. *Pteridium aquilinum*, bracken (Fig. 12), reaches its northern limit in the European heathland habitat in western Norway. This may explain why it seems less vigorous and invasive compared to in continental Europe and in the UK. Traditionally, we assume heathlands are relatively stable assemblages maintained by management; however, we have to consider the influences of climate change and enhanced atmospheric eutrophication for their future management. Accordingly, the assumption of the heathland community as a fixed management target may have to be reconsidered.

Bracken invasion and bracken control

Bracken is the most widely distributed Pteridophyte on earth and the only terrestrial fern to dominate large areas outside woodlands in temperate climates (Marrs *et al.* 2000). Its clones can occupy several hectares, expanding quickly in areas where there is good oxygen supply in the soil. Its extensive rhizome network works as a store for carbohydrates and contains

Figure 12. *Pteridium aquilinum*, bracken, invasion of the heathlands at Lygra.

large numbers of dormant buds (Lowday 1984, Marrs & Watt 2006). It is one of a diverse group of species that are able to expand under grazing by combining the ability to maintain dominance at high density with the avoidance of grazing (Tryon 1941, Page 1976, 1994, Marrs & Watt 2006). Changes in climate and land-use may favour the spread of bracken (Marrs *et al.* 2000). For example, bracken may benefit from reductions of extensive livestock grazing (cattle effectively trample and also eat some bracken; Williams 1980, Page 1982, Pakeman *et al.* 2005), as well as from recent increases in airborne nitrogen deposition and the use of artificial fertilizers (bracken occurs on relatively fertile soils; Miles 1985). Once bracken is established, slowly-decaying litter (Ghorbani *et al.* 2006) and potentially toxic compounds (Dolling *et al.* 1994, Dolling 1996) may inhibit seed germination, establishment and growth of many characteristic heathland species, including *Calluna*.

One of the keys to bracken control lies in exhausting the rhizome reserves of the buds and their carbohydrates (Braid 1937, Williams & Foley 1976, Lowday & Marrs 1992a, Pakeman & Marrs 1994) and traditionally, bracken was kept in check by grazing and cutting, as fronds were used as livestock beddings. Most evaluations of different control measures focus on reducing bracken cover and restoring heather and a few other key species (Pakeman & Hay 1996, Marrs *et al.* 1998a, Mitchell *et al.* 1998, Pakeman *et al.* 1998, 2000, Marrs *et al.* 2000, Britton *et al.* 2001). Nature conservation and organic farming may have more demanding criteria for restoration success (Paper IV), particularly with regards to non-target species (Cadbury 1976, Pakeman *et al.* 1997, Stewart *et al.* 2005), the use of herbicides, the rate and direction of revegetation (Pakeman *et al.* 2007), biodiversity and species composition.

We compared the efficiency of different mechanical and herbicide bracken control practices (Papers IV & V), focusing on restoration of the heathland community and potential impacts of herbicides on species composition and diversity. We found biannual cuttings or spraying with asulam (followed up by annual cutting) were the most effective means of reducing bracken cover long-term. We found more species benefiting from the removal of bracken than suffering from the treatments such as *Juniperus communis, Vaccinium vitis-idaea, Hypericum pulchrum, Veronica officinalis, Conopodium majus, Lotus corniculatus, Carex pilulifera, Festuca vivipara, Ceratodon purpureus, Mnium hornum* and *Cladonia* spp. The species affected negatively specifically by asulam belonged to different taxonomic and functional groups; *Vaccinium myrtillus*, *Galium saxatile, Veronica officinalis, Lotus corniculatus, Viola palustris, Trientalis europaea*, *Potentilla erecta*, *Agrostis capillaris, Anthoxanthum odoratum, Hylocomium splendens* and *Pseudoscleropodium purum* (Paper IV). As asulam is not legal in Norway, Gratil was included in the experimental protocol (in Norway, Gratil has been recommended as an alternative to asulam based on a two-year experiment; Skuterud 1998). Contrastingly, our results showed bracken to regain dense cover the third year after Gratil treatment (Paper IV). This result highlights the importance of long-term monitoring in researching vegetation dynamics in relation to conservation and restoration efforts (Stewart *et al.* 2005).

Conservation

Conservation efforts are often advocated on the grounds of two main motivations; nature's intrinsic values and nature's utilitarian values. Heathland conservation may be driven by both motivations. Because heathlands are anthropogenic in origin they are in need of management in order to maintain their present state. In contrast to their European Union counterparts, which are protected under the Habitats Directive, the northern heathland habitats of Norway still lack national legislative instruments to ensure their conservation.

In order to preserve diversity in the studied heathland systems, conservation management should aim to preserve the level of complexity of the traditional management regimes, both in terms of the actual disturbances, in this case fire and grazing, as well as the spatial and temporal scales at which they are applied (Papers I & III). Further, the considerable change in effects along the local environmental gradient (Paper III) brings into question the efficiency of general management plans. Consequently, local environmental variability needs to be considered in the conservation of semi-natural habitats. The higher levels of floristic and compositional heterogeneity under the combined management regime (Paper III) may, in turn, allow for a higher diversity of other organisms, such as hemipterans (Hartley *et al.* 2003) and other invertebrates. It may also affect functional aspects such as patterns of interaction between species; for example, plant-pollinator networks (Forup *et al.* 2008).

In northern areas, where temperature is the main limiting factor for bracken growth, future increases in temperature and duration of the growing season could imply range expansion, increasing rates of bracken invasions and denser bracken stands in already-invaded areas (Marrs *et al.* 2000, IPCC 2007). Bracken is today absent from the northernmost heathlands, but south of *ca.* 62°N it is expanding in coastal heathland areas. Future climate change could therefore result in a greater need for bracken control measures in the management of northern heathlands.

While much is known about the effects of herbicides on the target species, there is less information regarding their effects on non-target vegetation dynamics and on endangered or vulnerable non-target species likely to be found in heathlands (Marrs 1985). For successful conservation management these effects should be of most important consideration (Critchley *et al.* 2003, Bremner & Park 2007, Paper IV). For organic farming, which preclude the use of chemical control, alternative control methods need to be formulated. Our work (Papers IV & V) shows that biannual cutting retards regrowth sufficiently for effective control. Annual cutting was nearly as efficient as biannual cutting after five years and hence a more economic option long-term. By including the 'double control-method' (spraying of adjacent areas without bracken cover) in our experimental setup (Paper IV), we were able to identify a group of bracken-suppressed, yet herbicide-sensitive species, exemplified here by *Veronica officinalis* and *Lotus corniculatus*. Such herbicide-sensitive species may be particularly difficult to restore by chemical control, especially if repeated spraying is part of the protocol. Chemically-based bracken control also creates an ethical dilemma for nature conservation, as well as for farmers aiming to produce, for example, meats, dairy products and honey for the increasing organic market (Paper IV). Consequently, for northern areas we recommend mechanical control and/or combined with mixed livestock grazing wherever feasible.

The use of paleoecological records (Paper II & Study area) can provide a longer temporal perspective in addressing conservation issues. In this study it shows that anthropogenic deforestation and subsequent heathland formation in the North Hordaland region go far back in time. The use of such records can reduce the uncertainty of what is "natural" (Willis & Birks 2006) and additionally bring certainty to what can be considered as evolutionary adaptations to a certain management regime such as prescribed burning (Paper II).

The combined findings of my studies highlight the importance of basing management prescriptions on ecological theory that incorporates the role of spatial and temporal heterogeneity (Leibold *et al.* 2004). Such considerations are particularly important because low-intensity land-use involving disturbances may present a dilemma for the conservation of semi-natural systems. Disturbances are integral parts of the very systems that we want to conserve, yet at the same time disturbances may facilitate unintended change, for example by opening up regeneration niches for alien species or for native species that become invasive under the new environmental pressures (Hobbs & Hunneke 1992, Thompson *et al.* 1995, Harrison *et al.* 2003).

Evidence-based conservation

Conservation today aims at unravelling the factors, anthropogenic or natural in origin, which drives change in species, ecosystems and landscapes. Once we pinpoint these factors we can develop management prescriptions to aid conservation at different levels. Evidence-based conservation has the goal of supporting decision making in conservation and environmental management through the production and dissemination of systematic reviews on the effectiveness of management and policy interventions (CEBC, Sutherland *et al.* 2004). Sutherland *et al.* states that "much of current conservation practices are based upon anecdote and myth rather than upon the systematic appraisal of the evidence". The concept is borrowed from the field of medicine (Stevens & Milne 1997), and the medical model clearly demonstrates the potential value of an evidence-based approach. The facilitation of the dissemination of applied results is of the utmost importance for the sustainable development of management protocols. I have emphasised dissemination via several avenues. Paper V is an example of such a contribution. In addition I have disseminated my results in several popular science articles (Måren & Ekelund 2005, Måren *et al.* 2005, Måren & Ekelund 2006, Måren & Nilsen 2007, Måren & Vetaas 2008, Vetaas & Måren 2008, Måren & Nilsen 2008), read by farmers, managers, teachers and decision makers. Policy measures should be based on evidence and explicit use of evidence. Hence, the documenting of practices and evaluating of their effectiveness should be an integral part of all conservation projects. It is important to support decision making in nature management by sharing knowledge as to which management interventions work and which do not.

Biological diversity versus Ecosystem Services

Human induced land-use changes pose one of the major threats to biodiversity worldwide (Sala *et al.* 2000). Policy-makers increasingly accept that preserving biodiversity is important for the functioning and stability of ecosystems and for the provision of ecosystem services (ES), as well as being justifiable on moral, ethical and aesthetic grounds (Loreau *et al.* 2001, Kremen 2005, Billeter *et al.* 2008). The UN-commissioned Millennium Ecosystem Assessment (MA 2005, www.maweb.org) emphasises the central role of biodiversity, arguing that it is "an ecosystem service in its own right [and also] a necessary condition underpinning the long-term provision of other services, such as food and clean fresh water"

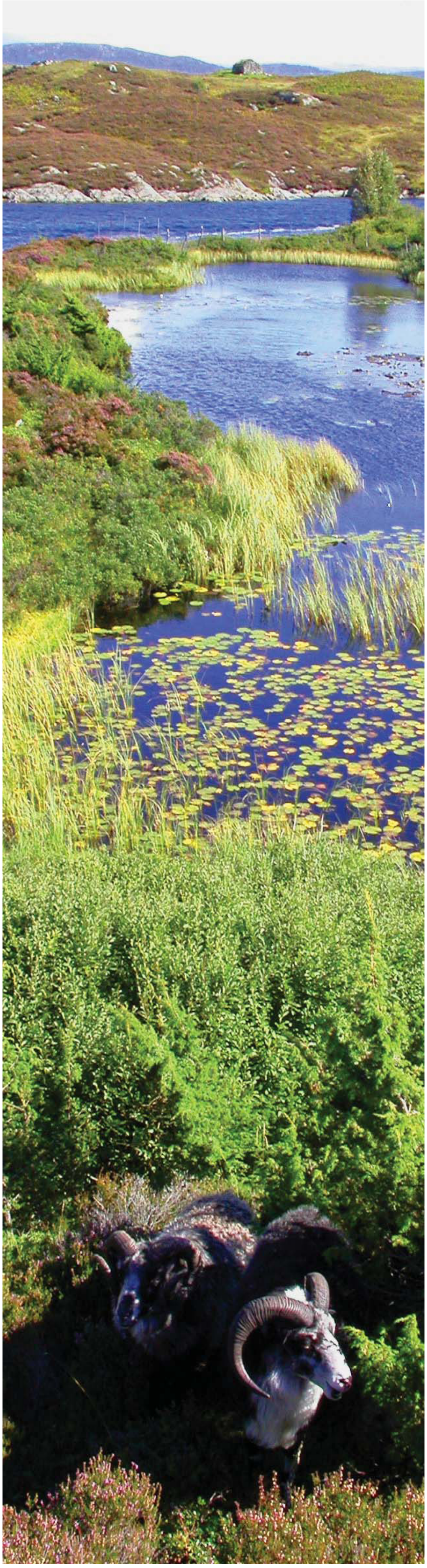
(MA Summary for decision-makers). The increasing demands on ecosystem services over the past 50 years have been fulfilled at the cost of ecosystem degradation and diversity loss, today one of the key issues in global conservation. Immediate action is needed to enhance the conservation and sustainable use of ecosystems to maintain their contribution to human well-being. It has long been recognised that livestock management and prescribed burning are important in manipulating the mosaics of heath and grass vegetation. Heterogeneity, in abundance and special arrangement of habitats, have significant impact on the out-come of grazing practices for biodiversity (Paper III).

Major drivers of these practices are government-support mechanisms and the availability of alternative income sources. For the conservation of heathland habitats there is a need to integrate ecology and economics in the evaluation of biodiversity and ES. The role of economics is an important driver of management decisions in ecosystems where the production of certain products (livestock, honey, fodder) must be included in the ES assessment. Market mechanisms and international agreements, plus agricultural policies and government support mechanisms are now driving agricultural systems, and, consequently are shaping the future of semi-natural landscapes. This also holds true for the northern heathlands. The role of specific economic drivers in relation to influencing management decisions needs to be incorporated when assessing ES and biodiversity. Today, a great deal of the management policy is based upon faith and political agendas rather than on the benefits to biodiversity and ES.

Global context

Many of the management practices characterizing semi-natural landscapes of high conservation value in the northern and western developed world are still very much in use in developing countries further south. Here, expanding populations exert ever increasing pressures on natural resources. This, in turn, causes real problems in the conservation of biological diversity while trying to maintain ES for the local communities. There seems to be a dichotomous approach to conservation, mainly on the basis of "north" and "south", where land-use practices and corresponding semi-natural habitats in the north receive relatively more acceptance and value than the corresponding practices and habitats in the south. This is a serious dilemma which should be considered by researchers in the field of conservation and general ecology of semi-natural habitats, since researchers from the developed countries very often are involved in designing both research projects and conservation outlines for developing countries in the south.

Another aspect of heathland ecology in a global context is their similarity to biogeographic affinities in other parts of the world. In many natural fire-prone Mediterranean-type plant communities, species have developed adaptive responses to recurrent fire (Bond & Van Wilgen 1996). These species also constitute a large fraction of the flora in landscapes managed by fire, such as the European heathlands. Consequently, there are several other ecosystems that resemble the Mediterranean heathlands of Europe such as the South African fynbos (Bond *et al.* 1990, Keeley 1992, van Staden *et al.* 2000), the Australian kwongan (Dixon *et al.* 1995, Roche *et al.* 1997, Tieu *et al.* 2001, Read *et al.* 2000), the North American chaparral (Keeley & Keeley 1987, Brown 1993, Keeley and Fotheringham 1997, 1998, Baskin & Baskin 1998) and the Chilean mattoral (Fuentes *et al.* 1994). This poses exiting and challenging possibilities for comparative studies and a greater basis of sound, robust ecological knowledge.



Conclusions

The objectives of this synthesis focus on the effects of anthropogenic disturbance in the dynamic heathland vegetation. Responses to the land-use practices of burning and grazing were evaluated from several angles and elucidated in detail by the five included papers.

Major findings emerging from this synthesis of studies are that; (i) disturbances of fire and grazing exert considerable influences on revegetation dynamics and species richness, both at temporal and spatial scales (Papers I & III), (ii) fire induces successional change where the seed bank acts as a refuge, providing a constant resource of recruits for species that colonize newly-burnt sites (Paper I). Fire also produces germination cues such as ash and smoke, enhancing seed germination in the key species *Calluna vulgaris* (Paper II), and (iii) bracken control by means of cutting twice yearly is practically as effective as spraying with the herbicide asulam (with follow-up cuttings; Papers IV & V).

Continued management is needed in order to conserve the characteristic vegetation dynamics of heathlands, and to conserve biodiversity at the species level as well as at the landscape level. The preservation of biodiversity can only be achieved through a mosaic of habitats, created by the described traditional land-use practices.

Organic farming and nature conservation may call for alternative approaches to herbicide application for bracken control. Our results show that this is feasible. Open landscapes such as heathlands are of importance for people's well-being through their recreational and therapeutic values. Consequently, they should be sustainably managed for the future.

This thesis contributes to enhance our knowledge of coastal heathlands by investigating the consequences of anthropogenic disturbance on vegetation. It is imperative that the conservation of heathlands gains attention as heathland areas are being rapidly reduced and existing fragmented heathlands have been shown to exhibit extinction debts.

Further perspectives

For this PhD project I mainly used Lygra as the study area. This was done in order to approach the research questions from different angles, taking advantage of the well documented management history at Lygra. For the future it is important to conduct comparative studies, primarily along the west coast, but also in the southern and northern heathland areas in Norway.

Woodland encroachment and afforestation are occurring on a large scale in all but the most westerly region of western Norway. Future heathland research should include studies of patterns and processes connected both to natural and to anthropogenic induced successional trajectories following these events.

The phenomenon of changing species diversity in such a short span of time, as a result of burning, provides an interesting topic for research. The seed bank research initiated here should be continued and expanded, for example, by looking at the composition and similarity of seed bank and vegetation of former heathlands, now afforested by introduced or natural species, and recently cleared forested plantations. Are there differences in composition and density between the two? Is the seed bank a reliable source for revegetation in the course of heathland restoration? The role of seed banks in ecosystem dynamics needs further investigation as semi-natural habitats in general have received much less attention than agricultural habitats.

The concept of bracken control is relatively new in the conservation of heathlands in Norway. Consequently, there are many aspects in need of investigation. As we can expect the distribution of bracken to expand in the face of a) changing climate, increased temperatures/precipitation, and b) further discontinued management in existing heathlands, it is important to look ahead and invest in management strategies for the future. First, one needs to quantify the scale of bracken invasion on a national level. Second, a management-protocol for handling bracken invasions in heathlands should be compiled in congruence with national natural resource management aims.

Phenology, pollination ecology and plant ecophysiology of heathland species have received relatively little attention in the research of heathlands in general, and in northern heathlands in particular. In heathland research there is a great potential for cross-disciplinary collaborative work with zoology, as heathlands possess a relatively rich invertebrate fauna, and also a relatively rich bird fauna, which should be explored further in the future.

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