Heathlands

A Lost World?

GÖTEBORGS
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Heathlands – A Lost World?

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Till Valle och Arvid

Figure 1. *Arnica montana*. Illustration by Kerstin Hagstrand-Velicu.

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Keywords Heathland, *Calluna*, Conservation, Coleoptera, Carabidae, Lycosidae, Management, Restoration, Conservation strategy

Abstract Heathland is a familiar landscape type in southwest Sweden. It is open with few trees, and the vegetation is dominated by dwarf-shrubs growing on nutrient-poor soils. Dry heaths with Heather *Calluna vulgaris* and wet heaths with Bell Heather *Erica tetralix* are common vegetation communities in the heathland, and they often form mosaics. The heathland landscape is highly threatened, with large substantial areal losses of 95% in Sweden since the 1800s. Heathland supports around 200 red-listed species, including plants, insects, birds and reptiles. In this thesis, I have studied some of the last remaining heathlands in Sweden, and I have investigated how different successional stages and vegetation communities differ in species composition and diversity of beetles (Coleoptera), wolf spiders (Araneae: Lycosidae) and vascular plants (Tracheophyta). I have also studied different methods to restore grass-dominated heaths.

In Papers I-II, I showed that old and degenerated heaths have rather low diversity of plants, ground beetles and wolf spiders. The ground beetle and wolf spider fauna in the old heaths included species that are shade-tolerant generalists that are also found in forests. However, a few heathland specialists seem to be associated with old stands of heaths. Young successional heaths had a higher diversity, and restoration of old *Calluna vulgaris* stands to pioneer vegetation resulted in higher species richness of plants and ground beetles. The ground beetles that were most favoured by the treatments were mainly generalists that are found in open habitats, not only in heathlands. The lack of heathland specialists in the restored plots may be a result of fragmentation. The studied heathland sites were isolated with long distances to the nearest well-managed heathland.

In Paper III, I could show that the different vegetation communities in the heathland contained different assemblages of beetles. The rich variation of habitats contributed to a high species diversity with a total of 367 species of beetles identified in the study. Fifty-two of these were classified as species with high conservation value. Many environmental variables, e.g. wetness, salinity, nutrients and sandy soils, were responsible for the differences in species composition of beetles. Vegetation communities that had clearly different environmental conditions also had a more specialised fauna of beetles.

In Paper IV, I studied the effects of different restoration methods on heaths that have become dominated by grasses. The methods I tested were: high-intensity burning, low-intensity burning and top-soil removal. Both burning treatments resulted in low regeneration of *Calluna vulgaris* and high grass cover. However, the treatment with top-soil removal resulted in a high number of *Calluna vulgaris* seedlings, low grass cover and a rich pioneer heathland flora.

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Sammanfattning

Så sent som för hundra år sedan bestod stora delar av sydvästra Sverige av vidsträckta, öppna landskap med ljunghedar. Vegetationen präglades av ljung och andra vedartade växter som växte i de näringsfattiga jordarna. Markerna betades av får, kor och getter. Det milda kustklimatet bidrog till att man kunde ha djuren ute på ljungheden året runt. På vintern vissnade gräset ned och då var ljungen den viktigaste födan för djuren. Men när ljungplantorna blev gamla så blev de inte lika välsmakande och djuren undvek att beta av dem. Då brände man ljunghedarna, så att man hela tiden hade tillgång till bra bete. Den här skötseln med betesdjur, ljunghedsbränningar och övrig aktivitet i markerna skapade ett variationsrikt landskap som gynnade många växter och djur. Det fanns hela tiden nybrända ytor med spirande vegetation där många marklevande insekter, spindlar och andra småkryp kunde gräva sina bon och hitta föda. I något äldre vegetation blommade istället fibblor, blåklockor och andra örter som lockade till sig bin och fjärilar som tog för sig av nektar och pollen. Gamla, överåriga bestånd med ljung slöt sig tätt samman och skapade en skuggig miljö där sandödlor och andra djur fann skydd. Den här stora variationen i ljungheden har bidragit till att över tvåhundra rödlistade arter fortfarande har den som sin livsmiljö.

I slutet av 1800-talet startades stora skogsplanteringsprojekt i Sverige, där man gick man ur huse för att plantera träd på ljungheden. Miljontals plantor sattes, och den tidigare så vidsträckta ljungheden ersattes av skog. På bara drygt hundra år förändrades landskapet, och idag återstår bara några få procent av den ursprungliga arealen av ljunghed. Det mesta av den kvarvarande ljungheden hävdas inte, utan består nästan uteslutande av gammal ljung och enbuskar.

I den här avhandlingen har jag studerat växter, marklevande skalbaggar och spindlar på ljungheden. Jag har jämfört olika successionsstadier och vegetationssamhällen på ljungheden samt undersökt vilka växter och djur som finns i respektive miljö. Jag har även undersökt hur mångfalden skiljer sig åt mellan olika miljöer. Mina resultat visar att yngre successioner har en tydligt högre mångfald och hyser många arter som inte finns i äldre successioner. I den äldre ljunghedsvegetation finns istället många arter som även återfinns i skogsmark. Men ett fåtal speciella arter verkar föredra gamla bestånd med ljung. Ljunghedar som har en rik variation av miljöer har också en hög artrikedom, vilket vi visade med en undersökning av skalbaggsfaunan på en ö i Göteborgs skärgård. Där noterade vi hundratals arter skalbaggar och drygt femtio naturvårdsintressanta arter.

Ljunghedarna är numera utsatta för en ökad kvävebelastning, och det leder till att ljung och andra ris ersätts av gräs; ljunghedsvegetation övergår i gräshedsvegetation. I en av mina studier jämförde jag tre olika metoder för att restaurera ljunghedar som har blivit gräsdominerade. Metoderna jag testade var: högintensiv bränning, lågintensiv bränning och borttagning av det övre jordlagret. Borttagning av jordlagret gav bäst effekt och ledde till ökad föryngring av ljung och andra ljunghedsväxter, och en lägre andel gräs.

Sammanfattningsvis föreslår jag att ljunghedarna bör skötas mer frekvent och intensivt, så att alla de livsmiljöer som gör ljungheden så artrik och speciell existerar samtidigt. Skötselplanerna för ljunghedarna i skyddade områden bör utformas utifrån ett mer biologiskt perspektiv än vad tidigare har skett. Skötselåtgärderna i ljunghedarna bör utföras utifrån en detaljerad kunskap om de nuvarande och de potentiella biologiska värdena i skötselområdena.

LIST OF PAPERS

This thesis is based on the following papers which will be referred to in the text by their Roman numerals:

I Lindholm, M., Gunnarsson, B. & Appelqvist, T. Are power-line corridors an alternative habitat for carabid beetle (Coleoptera: Carabidae) and wolf spider (Araneae: Lycosidae) heathland specialists? Journal of Insect Conservation (2019). https://doi.org/10.1007/s10841-019-00141-1

II Lindholm, M., Gunnarsson, B. & Appelqvist, T. Restoration of late successional *Calluna* heathlands – effects on carabid fauna and vegetation. Manuscript

III Lindholm, M., Appelqvist, T & Gran, O. Ground living beetles (Coleoptera) in coastal heaths and grasslands and their association with vegetation communities. Manuscript

IV Lindholm, M., Appelqvist, T. & Gunnarsson, B. Restoration of Calluna heathland – effect of late seasonal burning and soil removal on regeneration of *Calluna vulgaris* and heathland vegetation. Submitted manuscript

My contributions to the four papers:

(I) I came up with the research idea, conducted all the field work, made all the analyses and I wrote the manuscript with assistance of BG and TA.

(II) I came up with the research idea together with TA and BG, conducted all the field work, made all the analyses and I wrote the manuscript with assistance of BG and TA.

(III) I came up with the research idea together with TA and OG, conducted part of the field work, made all the analyses and I wrote the manuscript with assistance of BG.

(IV) I came up with the research idea, conducted all the field work, made all the analyses and I wrote the manuscript with assistance of BG and TA.

INTRODUCTION

Many people associate heathlands to an open landscape, with few trees and sparse vegetation. And at times, heathland give an impression of harsh conditions and windswept monotony, but in late summer when the Heather is in bloom and the heaths are all purple, the landscape is truly beautiful. The area of heathland in Sweden reached its peak around 1860, but is now much reduced in both area and quality through loss of traditional management and afforestation. Although it is one of our most threatened environments and it constitutes key habitats for biodiversity, heathland in Sweden has been forgotten for a long time, with little or no attention from nature conservation authorities and scientists.

For ecological purposes, the characteristics of heathland vegetation need to be defined. I have confined the studies to heathlands of southwest Sweden – areas of ericaceous dwarf-shrub growing on nutrient-poor acidic soils. Other common names of this landscape are coastal heathland, *Calluna* heathland or lowland heathland. In my thesis, the shorter term heathland is used for this landscape type, and Heather *Calluna vulgaris* is referred to as *Calluna*. Dry heaths and wet heaths are common vegetation communities in the heathland and they often form mosaics. The concept of structure of *Calluna* stands is important in heathland ecology. Gimingham (1972) defined four ecological meaningful phases of *Calluna* structure that I use in my thesis: (i) the pioneer-phase: establishment and early development (0–5 years old), (ii) the building-phase: plant is vigorously growing and dome-shaped (5–15 years). (iii) the mature-phase: reduction in vigour with a more open canopy (15–25 years), (iv) the degenerate-phase: gap in the centre with dead branches, the outer branches lying flat on the ground (25–30 years old).

Distribution and history of European heathlands

The main distribution of heathlands is in Atlantic Europe, a region with oceanic climate with high precipitation and mild winters. They occur along the Atlantic seaboard from Portugal, through northern Spain, western and northern France, the Netherlands, Belgium, the British Isles, Denmark, southern Sweden and western Norway, with some extensions into the sandy plains of northern Germany and Poland.

Heathland development in Scandinavia took place over a long temporal scale (6000–100 years BP), creating heathlands of different ages, and they developed and extended as a result of human activity. Forest clearances followed by burnings, and the use of the land for grazing prevented the regeneration of the forest. In Sweden, the oldest heathlands have been dated by pollen analyses to the Viking Age (800 AD), with main expansions around 1600 and 1800 AD (Atlestam 1942). However, recent studies in Norway have dated the oldest heathlands to the Neolithic (6000 years BP) and the time of the first human settlements (Hjelle et al. 2018). It is reasonable to believe that the heathlands in Sweden are from the same period, since the first inhabitants in western Norway came from southwest Sweden, and shortly after they arrived they started utilizing the heathland (Kaland 1979). Over time, heathlands started to expand as a result of forest clearances followed by the use of land for grazing, cutting vegetation for fuel and harvesting the vegetation for fodder. In Sweden, heathlands used to be a significant part of the landscape in the provinces of Bohuslän, Västergötand and Halland, reaching a peak in the 1860s (Schotte 1921), when the rural population was relatively high and needed grazing land and sources of fuel for the herring fisheries. To a lesser extent, there were also heathlands in the provinces of Skåne, Blekinge, Dalsland and Småland. There is no information on how much area of heathland there was in Sweden at this time, but in 1890 there were around 500,000 ha (Schotte 1921), and 30,000 ha in the 1950s (Damman 1957). Today, there are around 10,000 ha of heathlands in the provinces of Bohuslän, Västergötland and Halland (Figure 2), and probably less than 1,000 ha in the rest of Sweden.

Presumably, heathlands existed prior to human activity in exposed coastal areas, on thin soils on rocky ground and after forest wildfires. Natural occurring wildfires are believed to be evolutionary important in boreal forests, with a recurrence interval of 50–100 year (Zackrisson et al. 1996). Måren et al. (2010) claim that the burning regimes with a recurring occurrence of 10–30 years in the heathlands of northern Europe is of importance in habitat and biodiversity maintenance. Species have probably not evolved in this anthropogenic system, but they have greatly increased in distribution and abundance due to these particular management regimes.

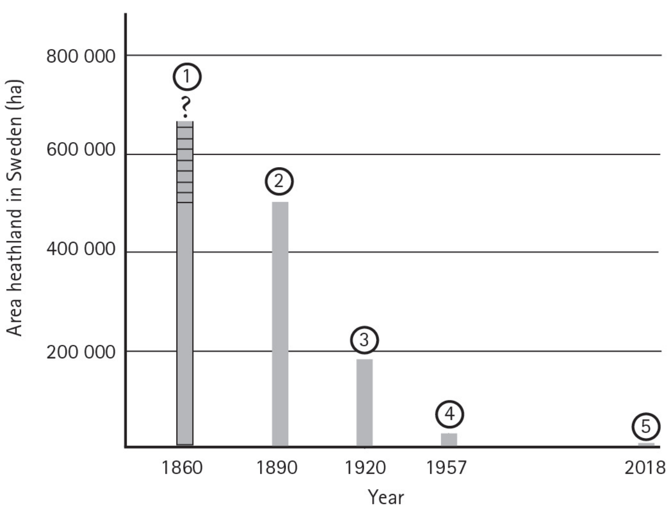
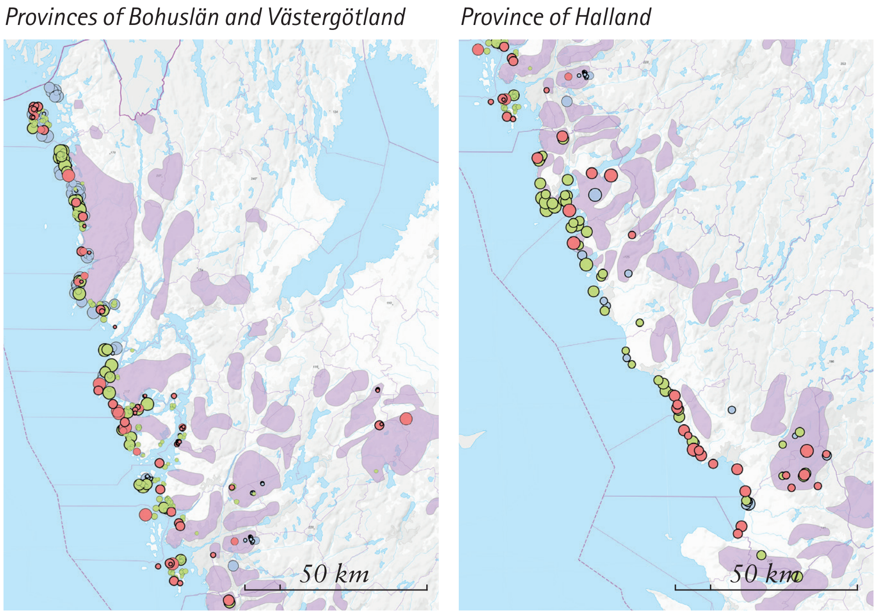


Figure 2. Area heathland in Sweden at different times. 1. Afforestation projects in Sweden starts (Holmberg 2005). No information of heathland area during this time has been found. 2. 500,000 ha of heathland in Sweden (Schotte 1921) 3. 180,000 hain Sweden (Schotte 1921). 4. 30,000 ha in Sweden (Damman 1957). 5. 10,000 ha in the provinces of Bohuslän, Västergötland and Halland (Larsson and Lindholm 2018).



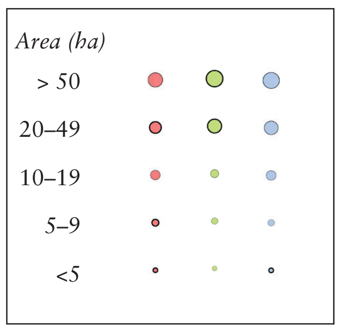


Figure 3. Past and present distribution of heathlands. The purple areas are the distribution of heathlands in the early 1900s (Nilsson 1990). The colored dots are present distribution of heathlands (Larsson and Lindholm 2018). Red dots are regularly managed heathlands containing red-listed heathland species (Artdatabanken 2015). Green dots are heathlands that have typical heathland structures and species, but are not regularly managed. Blue dots are abandoned heathlands in a degenerated phase that have good potential for restoration.

Figure 4. *Pedicularis sylvatica* is an oceanic heathland species that can be found in wet *Erica tetralix* heaths. It is classified as Near Threatened (Artdatabanken 2015). Illustration by Kerstin Hagstrand-Velicu.

Nature conservation importance of heathlands

The European heathlands reached their peak around 1860 (Specht 1983). Since then, they have had very large historical losses in extent and widespread decline in quality, with substantial areal losses of 60-90% in many countries. They are now in threat category Vulnerable (VU) in the European Red List of Habitats (European Union 2016). In Sweden, the area of heathland was reduced by about 95% between 1920 and 2018 (Figure 2 and 3). The remaining heathlands have become fragmented, and they are remnant patches in a matrix of conifer forests, farmland and urban land. Most of the remaining heathlands have not been managed for decades, and they are dominated by old, degenerated stands of heather with low quality offering poor conditions for heathland specialist species (European Union 2016, Larsson and Stenström 2019). Habitat fragmentation is recognised as a major cause of diversity loss (Fahrig 2003, Krauss et al 2010), and this has also been observed in heathlands (Moore 1962).

Calluna support about sixty insect species, and this is more than any other dwarf shrub in Sweden (Sundberg et al. 2019), and heathland management benefits the conservation of more than 200 red-listed species (Table 1, Appendix). Eighteen of these species have their entire Swedish population on heathlands, and forty-eight species have their main distributions on heathlands (Larsson and Stenström 2019). Five of these are Critically Endangered species (CR) and 24 are Endangered species (EN). A few heathland species are classified as Extinct from Sweden (RE), for example the plant *Euphrasia scottica* and the weevil *Coniocleonus nebulosus*, but since the habitat loss is about 95% in 100 years, the true number of extinct species in Sweden is probably far higher. Some heathland species are not threatened in Sweden but have been declining in Europe and are on the Red List in other countries. For example, the ground beetle *Carabus nitens* (Figure 8a) is one of the most endangered ground beetles in Europe (Assman and Janssen 1999), but it can still be found in several locations in Sweden, and not only heathlands. However, when this species occurs in heathlands in southwest Sweden, it is always a well-managed heathland with a species rich invertebrate fauna with many rare species.

a b

Figure 5. Two mining bees that use bare sand for nesting. (a) *Andrena marginata* forage for nectar and pollen on mainly *Knautia arvensis* and *Succisa pratensis*. It is classified as Near Threatened (Artdatabanken 2015). (b) *Andrena hattorfiana* forage for nectar and pollen on mainly *Knautia arvensis*. Illustrations by Kerstin Hagstrand-Velicu.

Table 1. Species in heathlands that are categorized as red-listed in the 2015 Swedish Red list (Artdatabanken 2015). Data from Larsson and Stenström (2019) and Larsson et al. (n.d.). Abbreviations: NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered, RE = Regionally Extinct, DD = Data Deficient.

	NT	VU	EN	CR	RE	DD
Butterflies *Lepidoptera*	31	10	11	3		
Birds *Aves*	6	2	2			
Ants, wasps etc. *Hymenoptera*	14	7	6			
Reptiles *Reptilia*		2				
Vacular plants *Tracheophyta*	10	18	12	1	1	
Lichens *Lichenes*			1			
Beetles *Coleoptera*	23	6	1	1	1	
True bugs *Hemiptera*	1					
Fungi *Fungi*	22	11	4			1
Flies *Diptera*	1	3				
In total:	**108**	**59**	**36**	**5**	**2**	**1**

Heathland management

Heathland requires management intervention to sustain it. Prehistoric and historic management of heathland involved prescribed burnings, grazing and to some extent fuel gathering (Webb 1998). *Calluna* was important winter fodder for domestic animals, and the heathland ecosystem was maintained through regular burning. The agricultural use of heathland has become less economic, and now the management motives have changed from exploitation to conservation of a highly valued cultural landscape type and habitats of very high nature conservation value. However, many heathlands in Sweden were protected mainly for their high recreational and cultural values and not for their biological values. This has resulted in vaguely written action plans for the nature reserves, with focus on scenery rather than specified management goals that would provide better conditions for the heathland flora and fauna. I discuss this further in Discussion and conclusions. The aims of managing heathland for conservation involve:

(i) maintain heath vegetation of different successional stages,

(ii) prevent expansion of unwanted plants such as bracken *Ptiridium aquilinium*, birch *Betula spp*., blackberry *Rubus spp*., and grasses Poaceae,

(iii) maintain valuable elements such as disturbed and bare ground.

Grazing

Traditionally, heathland provided grazing for sheep, cattle and other grazing stock which were put out on the heaths in extensive grazing systems (Webb 1998). *Calluna* was an important forage plant since it could provide forage of reasonable quality on poor soils. Furthermore, *Calluna* is an evergreen plant which also offered food during the winter when this is lacking on grass pastures (Gimingham 1972, Specht 1983). The impacts of grazing on heath vegetation are quite complex and include many factors, e.g. animal type, livestock behaviour, body size, seasonal variation in foraging behaviour, learning behaviour, plant quality, availability of water and shelter (Lake et al. 2001). Cattle prefer grassy patches of heathland habitats (Pratt et al. 1986), and they move onto dry heaths when forage became short (Putnam et al. 1986), or when they are resting. Cattle cause damage to old *Calluna* by trampling and uprooting, and can in a few years kill out *Calluna* and lead to its replacement by grass (Gimingham 1972). Cattle are heavy and create bare ground, especially on sandy and wet ground. Sheep are more selective grazers than cattle and they have a more variable diet (Grant et al. 1987). However, they mainly eat *Calluna* outside the growing season and prefer grasses during the summer (Grant et al. 1987). They are predominantly grazers and can create a short grass sward due to their ability to eat close to the ground (Lake et al. 2001). They are considered to preferentially graze forbs and flower heads and should be avoided in flower-rich heaths. Sheep are light and do not contribute to bare ground creation, but the light weight makes them less likely to damage *Calluna* by trampling.

Burning

In Sweden, prescribed burnings have been used to stimulate fresh forage for grazing animals in the past. Today, prescribed burnings are a part of the recommendations for heathland management and conservation (Bernes 2011). The burnings have two important ecological effects: (i) it modifies the structure of the vegetation; and (ii) it ensures that the nutrient status remains low. Burning prevent *Calluna* from reaching its degenerate phase and it stimulates vegetative regeneration and germination of *Calluna* seed.

With time, *Calluna* declines in its ability to regenerate vegetatively with age, and this is of great importance for burning management. For twelve-year-old plants, up to 58% of the stems will regenerate, but for a 25-year-old plant, only about 10% will regenerate (Mohamed and Gimingham 1970), and regrowth from old stands after prescribed burnings are mainly from seeds (Hobbs and Gimingham 1984). The best vegetative regeneration is from 6-10-year-old plants (Miller and Miles 1970). The effects also vary according to the intensity of the fire, and temperatures above 500°C will kill the *Calluna* plants (Whittaker 1961). The intensity of the fire is affected by moisture content of the vegetation (Whittaker 1961), stand structure (Gimingham 1972) and wind direction (Whittaker 1961). Prescribed burnings are often carried out in late winter or early spring, when the ground is still wet and cold, and the *Calluna* stems are dry and combustible. After a burning, shoots from the stem base of *Calluna* starts to grow, and after two to four growing seasons, *Calluna* has recovered dominance again (Mallik and Gimingham 1983, Vandvik et al. 2005, Måren and Vandvik 2009).

Mallik and Gimingham (1983) studied the post-fire succession on a *Calluna* heathland in Scotland, and they recognized three regeneration strategies after the fire. First group, woody plants with buds on persistent shoots near the soil surface (chamaeophytes). Second group, grasses and rosette plants that have their dormant buds in the upper crust of the soil, protected by covering of old leaf bases (hemicryptophytes). Third group, plants where the sprouting occurs on underground parts, e.g. buds in the rhizomes (geophytes). Mallik and Gimingham (1983) observed that the first plants to appear after fire were certain grasses and perennials of group two and three that produced their vegetative shoots immediately after fire, e.g. *Carex pilulifera, Festuca ovina, Agrostis canina, Potentilla erecta* and *Lotus corniculatus*. This was an effect of several factors, including the removal of ericaceous dominance by the fire, the well protected buds of the plants, increased light availability and nutrient release. A few months after the fire started, *Calluna* expanded rapidly and after the second growing season, *Calluna* was dominant and its canopy overtopped the other plants in group one and two. Plants in group two and three survived in the community in a suppressed condition or were eliminated under complete *Calluna* cover.

Many heathland plants produce large and long-term persistent seed banks that are important for the regeneration after a fire (Mallik et al. 1984). Måren and Vandvik (2009) studied the role of seed banks in a coastal *Calluna* heathland in western Norway. They found similar post-fire successional trends as Mallik and Gimingham (1983). The first species to colonize were geophytes such as *Potentilla erecta, Lotus corniculatus, Campanula rotundifolia*, all of which could reproduce vegetatively after fire, followed by graminoids and herbs. *Calluna* regained cover in the vegetation quite rapidly, and around the fifth year it covered about 40%. They could also show that the heathland seed bank is long-lived, and that the traditional management with prescribed burnings did not destroy it. They concluded that the seed bank acts as a refuge for many common heathland species. Granström (1988) showed a high longevity for many heathland species, e.g. a considerable amount of seeds from *Calluna* and other ericaceous plants in a conifer plantation (former heathland) germinated after 85 years. This showed that it was possible to restore a heathland to some extent, even after a long period of afforestation. However, many species did not have long-lived seeds, and they need to be reintroduced. Vandvik et al. (2005) demonstrated that the successional trends after a fire differed along a local environmental gradient. The effects of the fire were most severe in the upper parts of south-facing slopes with very dry vegetation. Based on the results of this and other studies (e.g. Britton et al. 2000, Hartley et al. 2003), they questioned the efficiency of general management prescriptions, and they argued for site-specific conservation management.

Figure 6. *Plebejus optilete.* Illustration by Kerstin Hagstrand-Velicu.

Top-soil removal

The removal of top-soil or turf is an ancient heathland management practice. Throughout the heathlands of Norway, northern Flanders, the Netherlands, Britain and North Germany, turf cutting was a widespread practice as it provided a source of fuel and bedding for livestock (Webb 1998). Recently, signs of similar activity have been found in heaths in Tjurpannan, southwest Sweden (Riksantikvarieämbetet 2019), and it is easy to believe that it has occurred in more locations in Sweden. Nowadays, the need of heather turfs as fuel and bedding has ceased, and top-soil removal is mainly used as a restoration method. Removing the top-soil reduces nutrients and contributes significantly to maintaining impoverished soil conditions (Aerts et al. 1995, Smith et al. 1991, Verhagen 2001, Symes and Day 2003, Allison and Ausden 2004). However, it can take a long time for the heathland flora to recover after the top-soil has been removed. The establishment of species from individuals in the surroundings depends on the dispersal capacity of the species. Verhagen et al. (2001) studied the vegetation after top-soil removal, and a large number of the heathland species from the surrounding areas were still lacking from the experimental plots after nine years. Seed dispersal seems to be a major limiting factor.

Species that are neither present in the vegetation nor in the seed bank need to be established from the surrounding landscape. Many species have low dispersal power, and birch *Betula spp.* is one of few plants that can disperse long distances by the wind (Mallik et al. 1984). They have light, winged seeds that get scattered by the wind ready to colonize open ground after a fire. Even *Calluna* that have relatively small seeds, disperse no more than 6 meters from their plants at wind speeds of about 4 m s^{-1} (Soons and Bullock 2008). The dispersal capability may therefore be a limitation in the present fragmented heathland landscape (Bakker and Berendse 1999). For example, the red-listed and rare heathland plant species *Arnica montana* (Figure 1), disperse the most vital seeds no more than a few meters, despite its plumed achenes. Lighter achenes disperse over larger distances, but they have considerably lower viability (Strykstra et al. 1998).

Instead of waiting for passive dispersal, active introduction can be used as a tool to speed up the establishment of the target species. Allison and Ausden (2004) performed an experiment with top-soil removal and addition of heathland clipping, and this resulted in an established heathland vegetation after five years. The vegetation consisted of a species-rich mix of both ericaceous dwarf-shrubs together with a wide range of heathland herbs and grasses.

Verhagen et al. (2001) showed that the depth of the soil that is removed is crucial for the duration of its effects. A complete removal of the organic layer (the O-horizon) resulted in nutrient-poor conditions for at least a decade whereas partial removal led to more fertile conditions and a faster increase in the availability of nitrogen and other nutrients.

Restoration of heaths currently dominated by grass

In many areas of Europe, lowland heathland dominated by *Calluna* is being degraded and replaced by grass-dominated vegetation (Welch and Scott 1995, Aerts and Heil 1993, Marrs 1993, Heil and Diemont 1983). Heathlands are oligotrophic habitats and very sensitive to nutrient increase from aerial deposition (Bobbink et al. 1998, Verhagen and van Diggelen 2006). Expansion of grasses on *Calluna* heathland may occur as a result of deposition of atmospheric nitrogen (N) compounds (Heill and Diemont 1983, Alonso et al. 2001, Bobbink et al. 1998, Marrs 1993, Heil and Diemont 1983, Stevens et al. 2004, Stevens et al. 2006). Atmospheric N contributes to an increased productivity and accelerated nutrient cycle (Schmidt et al. 2004, Calvo et al. 2005). The majority of atmospheric-deposited nitrogen accumulates within the soil, and even intensive burning and mowing management of *Calluna* has little effect on reducing it (Power et al. 1998). Reducing levels of nitrogen through removal of soil should help maintain the dominance of *Calluna* in areas of high nitrogen deposition (Verhagen et al. 2001, Allison and Ausden 2004, Terry et al. 2004). Aerts (1989) showed that *Calluna* is able to outcompete grasses even at fairly high levels of nitrogen availability as long as it maintains an intact canopy. However, since prescribed burnings effectively open up the canopy, it might be expected that the combination of reduced shading and enhanced nitrogen availability would give grasses the competitive edge over *Calluna*.

AIMS

My thesis is based on empirical studies performed in southwest Sweden during the years 2012 to 2016. I address three main questions:

(i) How do different successional stages of heaths differ in species composition and diversity of plants, carabid beetles and wolf spiders? (Papers I-II)

(ii) How do different heathland vegetation communities differ in species composition and diversity of beetles (Coleoptera)? (Paper III)

(iii) How does the heathland vegetation respond to high-intensive fires and top-soil removal and can these methods be used in restoration of grass-dominated heaths? (Paper IV)

The results are discussed with respect to future conservation strategies of heathlands in Sweden, and how they can be used as recommendations and advice in practical nature conservation.

METHODS

Study sites

All studies were carried out in southwest Sweden, in the provinces of Bohuslän, Västergötland and Halland, and in total 13 different heathlands were used as study sites (Figure 7). The sites have a long history as heathlands, even if some sites have been abandoned and the heaths were in a degenerate phase or later. Remmene is a military training field, and the other sites have been designated as nature reserves or Natura 2000 protected areas. The mean precipitation in the region is between 800 and 1000 mm per year, and the mean temperature is between -0.5 and -2°C in winter and between 15 and 16°C in summer.

The studied habitats were predominantly dry heaths of *Calluna vulgaris*-type (Påhlsson 1998). This is comparable with Böcher's (1943) vegetation community *Empetrum-Vaccinium vitis-idaea*-group and *Vaccinium myrtillus*-group, and Gimingham's (1972) *Calluna-Vaccinium* heaths and *Calluna-Empetrum nigrum* dry heaths. *Calluna vulgaris* was the most abundant species of the plant communities with V*accinium vitis-idea* and *V. myrtillus* as associated species. These dwarf-shrubs provided the dominant layer, and below there were often a variety of other plants – other dwarf-shrubs, grasses, sedged, herbs etc. and a ground layer of lichens and mosses. In Paper III, I also studied wet heaths of *Erica tetralix*-type (Påhlsson 1998), and a few non-heath vegetation communities. In the wet heaths, *Erica tetralix* and *Calluna vulgaris* were the most abundant species and they were accompanied by *Carex panicea, Trichophorum cexpitosum, Pedicularis sylvatica* and *Narthecium ossifragum*. In Paper I, sites with dry heaths of *Genista spp.– Calluna vulgaris*-type (Påhlsson 1998) were also studied.

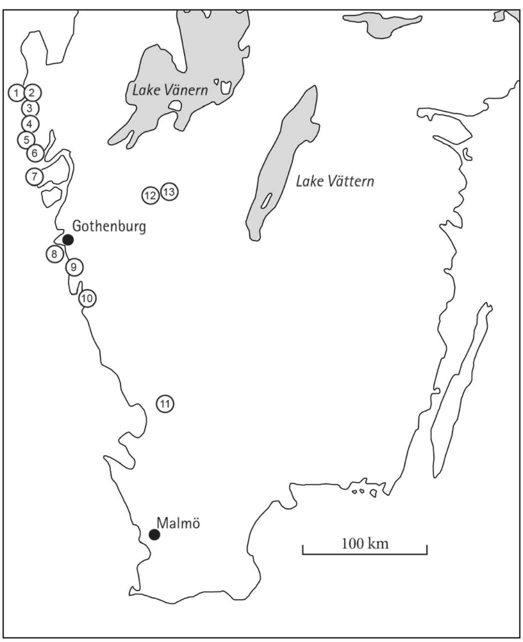


Figure 7. Map of southern Sweden and the study sites:

1. Hälsö
2. Gullbringa
3. Tjurpannan
4. Veddö
5. Valön
6. Bua hed
7. Härmanö
8. Galterö
9. Sandsjöbacka
10. Näsbokrok
11. Mästocka hed
12. Tånga hed
13. Remmene hed

Study sites 1-7 were used in Paper II, study site 8 was used in Paper III, study site 9 was used in Paper I and IV, study sites 10-13 were used in Paper I.

Vegetation and environmental variables

Vegetation measurements were performed in all studies. In Paper I, II and IV, a quadrat (0.5 x 0.5 m in Paper I and IV, 1 x 1 m in Paper II) frame with grid squares was used to measure the vegetation and the species frequency. In Paper III, a circle (radius of 1 m) was used and all vascular plants within the circle were recorded.

In Paper I an II, data of species frequencies was used to get environmental factors using the Ellenberg indicator values of plants adapted from Ellenberg et al. (1992). Ellenberg indicator values are widely used by plant ecologists in both central and northern Europe (e.g. Persson 1980, Diekmann 1994, Thompson et al. 1993, Hill et al. 1999). They are based on ecological observations, and were originally derived for use in Central Europe, but they are also suitable for use in northern Europe (Thompson et al. 1993). Previous studies have shown that Ellenberg indicator values correlated significantly with the results of empirical experiments (Thompson et al. 1993, Shaffers and Sýkora 2000). The variables in this study follow the coding system: nitrogen (N), moisture (F), light (L) and reaction (R). Reaction (R) stands for the acidity of the soil and can be comparable with pH. The Ellenberg indicator values temperature (T) and continentality (K) have been omitted since they dont correspond well in this region (Hill et al. 1999). A more detailed explanation of the variables can be found in Ellenberg et al. (1992). To estimate the composite value of an environmental variable for each sampling unit, the weighted average was calculated according to the equation in Diekmann (2003):

$$WA_j = \frac{\sum_{i=1}^{n} (r_{ij} \times x_i)}{\sum_{i=1}^{n} r_{ij}}$$

WA_j was the weighted average for sampling unit j, r_{ij} was the response of species i in sample unit j, and x_i the indicator value of species i. Absent species and those lacking Ellenberg indicator values were disregarded.

In Paper III, a different equation was used to estimate the environmental variables:

$$WA_j = \frac{\sum_{i=1}^{n} (s_{ij} \times x_i)}{\sum_{i=1}^{n} s_{ij}}$$

WA_j was the weighted average for sampling unit j, s_{ij} are presence of species *i* in sample unit *j*, and x_i the indicator value of species *i*. Absent species and those lacking indicator values were disregarded.

The vegetation height was measured by the drop disc method (Holmes 1974). In this method, a disc dropped down slowly at a vertically held ruler, and the height was measured where the disc stopped. The disc was 0.30 m in diameter and weighed 0.2 kg.

Scientific names of taxon followed Dyntaxa (2018). Vegetation communities followed Påhlsson (1998).

Study groups – Beetles and wolf spiders

Ground beetles (Coleoptera: Carabidae) were studied in Paper I and II, and all families of beetles (Coleoptera) were studied in Paper III. Ground beetles in heathlands have been extensively studied (Hopkins and Webb 1984, Usher 1992, Schirmel and Buchholz 2011, Rainio and Niemelä 2003, Cuesta et al. 2006, Gardner et al. 1997, Assmann and Janssen 1999, Borchard et al. 2014, Garcia et al. 2011, Cameron and Leather 2012, Garcia et al. 2010). The results from these studies show that there are characteristic ground beetle communities associated with the different phases of vegetation. However, more species have a preference to younger vegetation stages, and these habitats have a higher species richness of ground beetles (Gardner 1991, Schirmel and Bucholz 2011, Bargmann et al. 2015), and a higher proportion of rare and endangered ground beetles are connected to the pioneer growth-phase (Buchholz et al. 2013, Schirmel and Bucholz 2011). However, few species live entirely in very young vegetation stages and most species require bare ground in which to nest and older vegetation communities to obtain food (Webb 1986). In a study of heathlands in Scotland, very high grazing pressure reduced both the cover of

Figure 8. (a) *Carabus nitens* is a sun-loving ground beetle that is mainly found in wet heaths. It has declined severely in Netherlands, Belgium, Denmark and Germany (Assman and Janssen 1998), but it can still be found in many locations in Sweden. (b) *Onthophagus nuchicornis* is a dung beetle of the scarab beetle family. It digs tunnels underneath the dung piles of cows and sheep, and it drags the dung down to feed larvae in an underground brood chamber. It is classified as Near Threatened (Artdatabanken 2015). Illustrations by Kerstin Hagstrand Velicu.

Calluna and the ground beetle species richness (Gardner et al. 1997). Several ground beetle species have also been shown to have a distinct preference with respect to moisture (Thiele 1977, Lindroth 1985, Lindroth 1986), and the community compositions of ground beetles are influenced by the wetness of a site (Luff et al. 1989, Gardner 1991, Usher 1992, Gardner 1997, Borchard et al. 2014, Yanahan and Taylor 2014). For example, different species in the genera *Harpalus* have different ecological requirements (Thiele 1977, Lindroth 1985, Lindroth 1986); some species prefer high temperatures and others prefer dry conditions. Even the size of the sand particles has an effect of the ground beetle fauna, especially among the sand-loving species from the genera *Amara* and *Harpalus* (Thiele 1977).

Wolf spiders (Arachneae: Lycosidae) were studied in Paper I. Spiders have also been shown to have preferences for different successions. In a study in Dorset, the succession of spiders was investigated in stands of different ages for ten years after a heathland burning (Merett 1976). One group of species had their peak during the first few years after burning but was gone by the end of ten years. Furthermore, there was a clear relationship between bare ground and abundances of several species. For example, the wolf spider *Arctosa perita* which is more common in sand dunes where it lives in burrows in the sand. It was colonizing sandy areas on recently burned heathland. Another group of spiders was most abundant during the first years, but did not disappear quite as fast and was not dependent on bare ground. This group could persist in small numbers in older vegetation but they were always most numerous during the pioneer phases. The last group were web-spinning spiders and spiders that live in litter. The species in this group did not appear in large numbers until the vegetation had a closed canopy, and the peak densities were in mature heathland of 20 years or more. Schirmel and Bucholz (2011) also showed that the younger stages of vegetation contained many specialists that preferred high temperatures, as well as more threatened species.

For my studies, beetles and spiders were sampled using pitfall traps. The traps consisted of plastic cups (80 mm diameter, 120 mm deep) filled up to one third, with monopropylene glycol and a few drops of detergent. Each trap was covered with a roof that was fixed to the soil by four iron pegs to protect it from rain and to prevent animals from pulling out the traps. The specimens were stored in 70% ethanol. Adult individuals were identified to species level.

Scientific names of beetles and spiders followed Dyntaxa (2018).

Diversity indices

Three indices were used to estimate diversity of arthropods: Species richness (Paper I-III), Shannon diversity index (*H*')(Paper I-III) and Sørensen quantitative index (C_N) (Paper III).

Species richness was defined as number of species of a taxon in an area or habitat. This is the simplest and most intuitive measure of diversity (Magurran 2004). However, the sampling of beetles and spiders had some complications. Some sites collected more individuals which resulted in more species for these sites. Therefore, we calculated the estimated species richness by doing an individual-based extrapolation from the raw data following Colwell et al. (2012).

Shannon diversity index (*H'*) has a long tradition of use, and the index can be used in comparisons with other studies. The index uses the abundancy and number of species when it calculates the diversity. By transforming the index to exponential Shannon diversity index ($e^{H'}$) it can give an intuitively meaningful measure as the number of species in the sample if all species had been equally common (Jost 2006). Shannon diversity index (*H´*) was calculated as:

$$H' = -\sum (p_i \times \ln p_i)$$

where p is relative frequency of species i (Magurran 2004).

Sørensen quantitative index (C_N) is a measure of similarity that it is simple, easy to interpret and widely used. It uses the number of shared species in two sites based on quantitative data (individuals). Sørensen quantitative index was calculated as:

$$C_N = \frac{2jN}{(N_a + N_b)}$$

where Na is the total number of individuals in site A, N_b is the number of individuals on site B, and jN is the sum of the lesser values (number of individuals) for those species found at both sites (Magurran (2004).

Species richness of plants was measured at different scales following Gray (2000). Point species richness is the number of species from a single sample unit, i.e. number of species in a quadrat frame, and site species richness is the species richness of a number of sampling units from a site, i.e. number of species in all quadrat frames in a site. This scale dependent species richness is useful in habitats with disturbances, such as heathlands. Low disturbance favours a few competitive plants, at the expense of stress-tolerant species and ruderals (Grime 2002). However, a certain amount of disturbance would create higher plot diversity, since it decreases the competition from dominant species.

Statistical analyses

Statistical analyses were carried out using several software programs:

(i) R, version 3.5.2, and labdsv package, version 1.8, for calculating indicator species.

(ii) IBM SPSS Statistics, version 24, for non-parametric and parametric univariate analyses.

(iii) PAST, version 3.0, for non-parametric multivariate analyses of community structures.

(iv) EstimateS, 9.1.0, for calculating estimated species richness.

(v) Canoco, version 5, for multivariate analyses e.g. species composition.

RESULTS

Biodiversity in different successional stages of heaths (Paper I–II)

The natural processes of disturbances no longer operate at an appropriate scale or frequency to maintain natural populations of species (Ausden 2010). The goal of managing habitats for conservation is often to mimic natural disturbances to provide suitable habitats for many species. Heaths, however, can persist for 20-30 years in a late successional phase without any habitat management. Management of heaths with a long rotation of 20 years can therefore be rather cheap compared to continuous management of grazing and cutting in grasslands. But, *Calluna* stands in these heaths are often uniformly even-aged with few other plants, and important habitats for diversity, such as bare soil and flowering herbs, are missing. The biological value of these heaths is therefore questionable.

To investigate the value of these degenerated heaths, we studied power-line corridors (PLC) in Paper I. PLCs are only managed by regular clearings of trees and shrubs every 6-9 years, and the heath vegetation is kept continuously at a late successional phase. The PLCs are covering an area of 300,000 ha in Sweden (Grusell and Miliander 2004), and have therefore gained a lot of conservation interest in recent years (Berg et al. 2013, 2016). Some studies have suggested that PLCs serve as habitats for a variety of species, e.g. reptiles, birds and flower-visiting insects (Sheridan et al. 1997, Yahner et al. 2001, Russel et al. 2005, Sjödin et al. 2008, Berg et al. 2013, 2016). However, we suspected that many ground-living heathland arthropods, e.g. carabid beetles and wolf spiders, need more intensive management and that PLCs are suboptimal habitat for these taxa.

In this study, we compared the diversity of plants, ground beetles and wolf spiders in PLCs with traditionally managed heathland. The results showed that the heath vegetation and the diversity of ground beetles and plants in the PLCs were clearly different from traditionally managed heathlands. They also contained different assemblages of ground beetles and wolf spiders. The PLCs contained more shade-tolerant species and less open-ground species, and they were more similar to a forest habitat than a well-managed heathland habitat with respect to species composition. The vegetation in the corridors were in a late successional phase with low abundances of herbs and relatively much shrub. The characteristic and valuable heathland structures of pioneer flora were also absent. Based on the results of our study, PLCs are not a suitable replacement heathland habitat for the study groups, and we recommend more intensive management of the corridors to make them more valuable.

In Paper II, we studied the effects of *Calluna* heath restoration (cutting and burning) on vegetation and ground beetle fauna. Vegetation, different diversity indices and species composition of ground beetles, were compared before and after treatment, and with control plots. The results showed that the restored plots had a more diverse flora and fauna compared to before treatment and control plots. The site diversity of plants was almost twice as high after the restoration. This rather quick colonization of several species indicates that many of the plants regenerated from a pre-existing seed bank. There was also an increase of point diversity of plants, and this was expected since disturbance from management actions (cutting and burning) disfavour many competitive plants, e.g. many dwarf shrubs, in favour of smaller herbs. This was also consistent with the results in Paper I; the degenerate phase of *Calluna* heaths has lower point diversity than early phases. Mean species richness of ground beetles increased with only three species in the restored plots. The rather small increase of species richness of ground beetles could be an effect of the fragmentation. Many ground beetles in the heathlands, e.g. *Carabus arcensis, C. cancellatus, C. nitens, C. convexus, Cymindis angularis,* are flightless and therefore limited in their powers of dispersal. This makes them very vulnerable to environmental changes and it will take a long time to build up a diverse ground beetle fauna if the habitats are isolated. Plants and invertebrates, like ground beetles, have different strategies and this has importance for conservation. Many plants are long-lived or have seeds or vegetative states that make them persistent to environmental changes. Invertebrates have generally no long-term resting stage, and they can soon be extinct from an area if the conditions changes.

Species richness is a measure of quantity rather than quality and it says nothing about which species have been found. The analyses of individual species and the multivariate analyses answered this question. The multivariate analyses showed a significant change of species composition after the restoration. Moreover, the individual species analyses showed that many open-habitat species increased or colonized the areas, e.g. *Calathus fuscipes, C. erratus, Pterostichus versicolor, Harpalus latus, Nothiophilus aquaticus*, while shade-tolerant species decreased, e.g. *Pterostichus niger, P. oblongopunctatus, Trechus secalis*.

Biodiversity of beetles in different vegetation communities (Paper III)

Heathland contains many different habitats, and in order to set up a management plan it is essential to have the adequate knowledge of species in the different habitats. In Paper I and II, we compared different successional stages of *Calluna* heaths and could show that they were different with respect to species composition and biodiversity. In Paper III, we studied beetles in different vegetation communities in a heathland, and identified the variables

Figure 9. *Erica tetralix* is an oceanic ericaceous dwarf shrub that has named a group of species and the eastern limit of a biogeographical region (Malmer 1965). The *Erica* group comprises the oceanic species *Erica tetralix, Narthecium ossifragum, Pedicularis sylvatica, Galium saxatile* and *Juncus squarrosus. Gentiana pneumonanthe* also belong to this group, although it is not an oceanic species. The limit runs from northeast Skåne to the southern part of Lake Vättern and further to Lake Vänern and Dalsland. Illustration by Kerstin Hagstrand-Velicu.

that influenced their distribution. We could identify six vegetation communities in the study area: (i) Dry heaths with vegetation of *Calluna vulgaris*-type, (ii) wet heaths with vegetation of *Erica tetralix*-type, (iii) damp meadows with vegetation of *Agrostis capillaris-Alchemilla* spp.-type, (iv) wet meadows with vegetation of *Deschampsia cespitosa* type, (v) salt marshes with vegetation of *Juncus gerardi-Festuca rubra* type, and (vi) sand dunes with vegetation of *Ammophila arenaria-Leymus arenarius*-type.

The result showed an overall high diversity with a total of 367 identified species of beetles, and over 50 species were classified as species with high conservation value. Many environmental variables were responsible for the differences in species composition of the beetles.

The sand dunes and salt marshes had a more specialised fauna than the other habitats. This was expected, since the environmental conditions of these habitats were quite different. For example, they had more salt-tolerant plants, higher nitrogen value, higher pH value and more of sandy soils. All vegetation communities contained exclusive species, i.e. species that were mainly found in one vegetation community. However, wet heaths and wet meadows had a similar beetle fauna, and wetness is probably an important variable for species composition. This has also been confirmed by other studies (Luff et al. 1989, Gardner 1991, Usher 1992, Gardner 1997, Borchard et al. 2014, Yanahan and Taylor 2014). Fifty-two species that were classified as species with high conservation value were found in the study. This high number of species can probably be explained by the rich variation of habitats in the site and the long habitat continuity. Rove beetles (Staphynolidae) were also an important group for the diversity in the area, and we suggest more studies of life history strategies and habitat preferences in heathlands of this group.

Restoration of grass dominated heaths (Paper IV)

In many areas in Europe, *Calluna* heathlands are being degraded and replaced by grass-dominated vegetation (Welch and Scott 1995, Aerts and Heil 1993, Marrs 1993, Heill and Diemont 1983), and this has also been observed in Sweden (Figure 10). Expansion of grasses on *Calluna* heathland may occur as a result of deposition of atmospheric nitrogen compounds (Alonso, Hartley & Thurlow, 2001). Most of the nitrogen in the heathlands is stored in the top-layer of the soil (Allen 1964), and by removing the top-soil, the nitrogen levels will be reduced to favour *Calluna* and other dwarf shrubs at the expense of competitive grasses (Britton et al. 2000, Härdtle et al. 2006). However, mechanical top-soil removal is expensive and labour intensive (van Diggelen et al. 2017). Prescribed burnings on the other hand, can be made with a relatively low amount of labour and a low cost (Symes and Day 2003). Traditional prescribed burnings are performed in winter or early spring, when the litter on the ground is wet and the burnings contribute to only a small amount of nutrient loss (Allen 1964, Evans and Allen 1971, Härdtle et al. 2006).

In this study, we have performed an experiment to test if a late seasonal burning in spring with high-intensity fire, will have similar effect as top-soil removal, i.e. reduce the grass dominance and increase the regeneration of *Calluna*. Our results showed that grass cover in the late seasonal burning plots after treatments were lower (25%) than the traditional burning plots (50%), Hulegården, Stenunga. 58° 4' 16''N, 13° 4' 37''E.

1984-08-25

2011-08-06

Månsholmen. 58° 13' 43''N, 13° 16' 3''E.

1985-08-21

2012-08-21

Figure 10. Twenty-seven years between the pictures at two locations in the province of Västergötland. *Calluna* is almost lost and grasses have clearly increased. These and more pictures can be seen at http://www.mulensmarker.se, and in the book Åter till mulens marker by Carlsson and Hagman (2015). Published by permission from the photographer Tore Hagman.

but it was still high compared to the top-soil removal plots (5%). The number of *Calluna* seedlings after treatments was very low in both types of burning plots, only 14 seedlings per square meter. This can be compared with the top-soil removal plots with about 100 seedlings per square meter. We conclude that late seasonal burnings are not an effective method to restore a grass dominated heaths. Notably, the treatment with top-soil removal gave high number of *Calluna* seedlings, low grass cover and surprisingly rich pioneer heathland flora. The effect of top-soil removal on *Calluna* seedlings and grass cover is consistent with many studies (e.g. Diemont and Linthorst Homan 1989, Britton et al. 2000, Härdtle et al. 2006). However, the quick recovery of the heathland flora in our plots is contradictory to studies by Verhagen et al. (2001), that showed that a large number of heathland species were still lacking in the top-soil removal plots after nine years. The results are probably depending on the size of the treated plots; our rather small plots would probably be recolonised faster than larger plots. Based on the results of our study, we considered the top-soil removal to be the best method to restore grass-dominated *Calluna* heathland in the area.

DISCUSSION AND CONCLUSIONS

The importance of young successional heaths

In the *Calluna* heaths, we observed a more diverse heathland flora and fauna in the early successional stages compared to the late stages. Well-managed heaths provide a range of important habitat and physical conditions, such as bare ground and sandy soils for burrowers, sunny and hot areas for many open-ground species. The old stands of *Calluna* had more shade-tolerant species that were also common in the forests. However, older *Calluna* heaths seem to support a few heathland specialists, e.g. *Carabus cancellatus* and *C. arcensis*, but these species were also observed in younger *Calluna* heaths. The habitat preferences for these species are not yet known, and they might have a complex life cycle and different habitat requirements during different times of the year.

The study of wolf spiders in Paper I did not show as many habitat specialists compared to the beetles. This is probably due to less species of wolf spiders compared to ground beetles. However, there are indications of young-successional specialists: *Alopecosa pulverulenta, Pardosa agricola, P. monticola, P, nigriceps, P. palustris, P. pullata*. And a few species that are more shade-tolerant: *Pardosa alacris, P. lugubris and Pirata uligunosus*. Spiders are known for having good dispersal abilities and the instars are using ballooning to move long distances, and they are probably less affected by fragmentation than ground beetles. In this respect, they might be better as indicator species for young-successional stages than ground beetles.

It is important to point out that that we used beetles and spiders that are mainly ground living as study groups. Many species in these groups prefer warm and sunny conditions, e.g. south-facing slopes and sparse vegetation with a hot microclimate. Other taxonomic groups may have different preferences. For example, vegetation in late successional stages have been shown to be important habitats for butterflies (Berg et al. 2013, 2016), bees (Russel et al.

2005) and birds (Kroodsma 1982, Marshall and VanDruff 2002). Old stands of *Calluna* has also a complex vegetation and more niches for web-spinning spiders and climbing spiders (Merett 1976). Sites with too high-intensity management can have less diversity than sites with low intensity management (Bell et al. 2001).

The importance of variation in the heathland

Even if the young successional stages are important, we should not forget the importance of variation. The rich variation of habitats and environmental conditions in the heathlands contributes to their high diversity (Paper III). It is important that all structural variation and successional stages are present every year, and habitat continuity is also one of the most important factors needed for the conservation of invertebrates (Kirby 2001). The aim of management should be a full range of successional stages and a varied structure, from bare ground to tall mature heath.

Fragmentation

We had only a small increase of species richness of ground beetles in the restored sites of old and degenerated heaths (Paper II). This small increase could be an effect of habitat fragmentation. Fragmentation is probably an important factor in heathland conservation. It might be more efficient to restore old heaths that are close to sites with a diverse heathland flora and fauna, than small and isolated islands that will not be colonised by heathland species for a long time. Hundreds of hectares of heathlands have recently been restored in Sweden (Sahlén 2016), and some of these sites were also studied in Paper II. The restored sites are isolated, and it will take a long time for species colonise the sites. Therefore, it is worth considering active dispersal of threatened species to these newly restored heathland sites.

Heathland management for biological values or cultural values?

Heathland has not only high biological values, it has also high cultural values and a long history that goes back thousands of years to the first settlements. Many well-preserved features from this period still remain, including relics of the first settlements in Sweden. Throughout history, these heathland areas survived because they were used and had a real value to people. Furthermore, the wild, open desolate landscape of heathlands is highly appreciated for human recreations (Webb 1986). The first heathland to be protected in Sweden was Bollaltebygget in the province of Halland in 1934 (Holmberg 2005), and it was protected for its high cultural and recreational values. Similarly, since then, many of the protected heathland areas in Sweden have been protected mainly for their high cultural and recreational values. We argue that not only cultural and recreational values should be considered. It is important to include biological values, including species diversity, when deciding which heathland to protect, and which management actions to inforce. All too often the aims of management actions are vaguely specified; the aims are mainly “to preserve an open landscape with its high cultural values and typical vegetation”. Many of the important heathland habitats require more intensive management actions, and they should be specified and the management aims should be clearly defined. Other studies (e.g. Britton et al. 2000, Hartley et al. 2003, Vandvik et al. 2005) have also questioned the efficiency of general management prescriptions and argued for a site-specific conservation management.

Unconventional management methods

Heathland has been grazed throughout its history, and cattle and sheep have been a significant part in developing the landscape, and grazing has several important benefits for the diversity. Therefore, the livestock contributes both to a higher biological value and a cultural value. However, livestock grazing is not a requirement to achieve high biological diversity of a heathland. Some of the most valuable heathland areas in Sweden are not grazed, such as Remmene hed, Tönnersjöfältet and Skillingaryd. They are military training fields that are burned, but the military activities, e.g. pit-digging and disturbance by heavy vehicles, also create large soil disturbance that are positive for many species. These sites contain large populations of many rare and threatened heathland species. For example, in Remmene hed there were 200,000 individuals of *Arnica montana* in 2015 (Figure 1) (Sundberg 2017). This shows that some species respond well to these alternative management methods. Top-soil removal is another management method that is rather unconventional in Sweden. However, we could show in Paper IV, that removal of top-soil was an efficient method to restore the *Calluna* heaths and lower the dominance of grasses, and we suggest that this method should be evaluated at a larger scale.

Figure 11. *Caprimulgus europeus* is distributed in southern Sweden in a variety of habitats, from dry heathland to forest clearings and open woodland. It prefers heathland with some trees and small shrubs. It is listed on Annex 1 of the EU Birds Directive because of population decline due to habitat degradation. It was on the Swedish Red List 2000-2010, but since 2015 it is classified as Least Concern 2015 (Artdatbanken 2015). Illustration by Kerstin Hagstrand-Velicu.

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Figure 12. *Antennaria dioica* is a dioecious perennial with pale-pink flower. It is associated with low fertility soils and can be found in heaths and grasslands. Illustration by Kerstin Hagstrand-Velicu.

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APPENDIX

Red-listed heathland species (ArtDatabanken 2015). Data from Larsson and Stenström (2019) and Larsson et al. (n.d.)

LICHENES

Cladonia peziziformis EN

FUNGI

Agaricus cupreobrunneus DD
Agaricus litoralis NT
Camarophyllopsis foetens NT
Camarophyllopsis hymenocephala VU
Camarophyllopsis schulzeri NT
Clavaria amoenoides NT
Clavaria flavipes VU
Clavaria fumosa NT
Clavaria zollingeri VU
Clavulinopsis cinereoides VU
Cuphophyllus canescens EN
Cuphophyllus flavipes NT
Cuphophyllus lacmus VU
Cuphophyllus russocoriaceus NT
Entoloma atrocoeruleum NT
Entoloma griseocyaneum NT
Entoloma lividocyaneum NT
Entoloma prunuloides NT
Geastrum minimum VU
Geastrum schmidelii NT
Hygrocybe aurantiosplendens NT
Hygrocybe intermedia VU
Hygrocybe punicea NT
Hygrocybe splendidissima NT
Laccaria maritima NT
Lycoperdon ericaeum NT
Microglossum atropurpureum VU
Neohygrocybe nitrata NT
Neohygrocybe ovina VU
Phallus hadriani VU
Poronia erici VU
Porpoloma metapodium EN
Psatyrella ammophila NT
Ramariopsis subtilis NT
Scleroderma septentrionale NT
Tulostoma brumale NT
Tulostoma fimbriatum EN
Tulostoma kotlabae EN

TRACHEOPHYTA

Arnica montana VU
Botrychium lunaria NT
Botrychium matricariifolium VU
Botrychium multifidum NT
Botrychium simplex EN
Carex hostiana NT
Carex pulicaris VU
Catabrosa aquatica VU
Dianthus superbus EN
Eryngium maritimum EN
Euphrasia micrantha VU
Euphrasia scottica RE
Genista anglica EN
Genista pilosa NT
Gentiana pneumonanthe VU
Gentianella campestris ssp. baltica EN
Glyceria declinata VU
Helichrysum arenarium VU
Helosciadium inundatum EN
Hypochaeris maculata VU
Hypochoeris glabra VU
Isolepis setacea EN
Juncus capitatus EN
Juncus squarrosus NT
Lycopodiella inundata NT
Lycopodium tristachyum VU
Lycopodium zeilleri VU
Lysimachia minima VU
Mertensia maritima CR
Pedicularis sylvatica NT
Phleum arenarium EN
Platanthera bifolia subsp. bifolia NT
Pulsatilla vernalis EN
Pulsatilla vulgaris VU
Radiola linoides VU
Rosa inodora EN
Rubus sordirosanthus NT
Taraxacum maculigerum VU
Thymus pulegioides VU
Thymus serpyllum NT
Viola tricolor subsp. curtisii VU

LEPIDOPTERA
Adscita statices NT
Agonopterix atomella EN
Amphipoea crinanensis NT
Apamaea anceps NT
Aplocera efformata NT
Archips betulana VU
Archips betulans NT
Argynnis niobe NT
Bembecua ichneumoniformis NT
Calamia tridens NT
Catoptria lythargyrella VU
Chesias rufata EN
Clepsis pallidana VU
Coleophora genistae EN
Coleophora lixella NT
Coleophora parthenogenella NT
Cupido minimus NT
Delplanqueia dilutella NT
Digitivalva arnicella VU
Dyscia fagaria EN
Epirrhoe galiata NT
Eupithicea subumbrata NT
Eupithicea venosata NT
Euxoa recussa NT
Hadena bicruris NT
Hadena confusa NT
Hadena perplexa NT
Heliothelia wulfeniana NT
Hesperia comma NT
Hyphoraia aulica EN
Levipalpus hepatariella VU
Lythria cruentaria NT
Mesogona oxalina NT
Mirificarma lentiginosella EN
Nemophora cupriacella VU
Orgyia antiquoides VU
Pachycnemia hippocastanaria EN
Pempeliella ornatella NT
Phengaris alcon EN
Phibalapteryx virgata NT
Phyllonorycter staintoniella CR
Platyptilia tesseradactyla VU
Prolita solutella EN
Pseodoterpna pruinata CR
Pyrausta ostrinalis NT
Scotopteryx luridata VU
Scotopteryx mucronata EN
Scythris crypta EN
Selidosoma brunnearia NT
Sideridis turbida VU
Synanthedon flaviventris NT
Syncopacma suecicella CR
Trifurcula subnitidella NT
Zygaena filipendulae NT
Zygaena lonicaerae NT

DIPTERA
Asilus crabroniformis VU
Cyrtopogon luteicornis NT
Machimus arthriticus VU
Paragus constrictus VU

HEMIPTERA
Stagonomus bipunctatus NT

HYMENOPTERA
Andrena apicata NT
Andrena argentata NT
Andrena batava VU
Andrena marginata NT
Andrena nigrospina NT
Andrena nitida VU
Andrena similis EN
Arachnospila wesmaeili NT
Biastes truncatus VU
Colletes fodiens NT
Crossoserus exiguus NT
Diodontus tristis VU
Dufourea halictula VU
Dufourea inermis EN
Halictus leucaheneus EN
Lasioglossum sabulosum NT
Lasioglossum sexmaculatum NT
Lasioglossum tarsatum NT
Megachile dorsalis NT
Mutilla europaea NT
Myrmica specioides NT
Nomada armata VU
Nomada baccata EN
Nomada fuscicornis VU
Osmia maritima EN
Priocnemis confusor EN
Sphecodes puncticeps NT

COLEOPTERA
Acalles ptinoides NT
Amara infima NT
Amara littorea VU
Anthicus bimaculatus NT
Aphodius porcus NT
Aphodius sordidus NT
Bembidion nigricorne NT
Carabus convexus VU
Cardiophorus asellus NT
Coniocleonus nebulosus RE
Cymindis macularis NT
Dicronychus equisetioides VU
Galeruca pomonae VU
Harpalus anxius NT
Harpalus griseus NT
Harpalus neglectus NT
Harpalus servus NT
Ischnopterapium modestum NT
Lepyrus capucinus NT
Lycoperdina succincta NT
Margarinotus neglectus VU
Margarinotus obscurus NT
Margarinotus purpurascens NT
Meligethes corvinus NT
Onthophagus fracticornis NT
Onthophagus nuchicornis NT
Philonthus lepidus NT
Poecilus punctulatus EN
Sibinia pyrrhodactyla NT
Strophosoma faber VU
Strophosoma fulvicorne NT

REPTILIA
Coronella austriaca VU
Lacerta agilis VU

AVES
Alauda arvensis NT
Anthus campestris EN
Anthus pratensis NT
Carpodacys erythrinus VU
Emberiza citrinella VU
Numenius arquata NT
Perdix perdix NT
Riparia riparia NT
Saxicola rubetra NT
Saxicola rubicola EN