Life after fire: the impact of fire on species composition and diversity in coastal heathlands

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Contents

Abstract

Fire prone coastal heathlands are widespread, and range from naturally fire prone Mediterranean-type heathlands, to the anthropogenic heathlands of north-west Europe. Regardless of its source, fire is an important disturbance factor in these systems. This thesis investigates the effects of fire on the species diversity and composition of two heathland systems; one in south-eastern Tasmania and one in western Norway. I ask whether two important species groups in heathland, plants and carabids depend upon, and to what extent they exhibit adaptations to, recurrent fire. The results suggest that heathlands and their species clearly respond to fire. In the absence of fire, south-east Tasmanian heathlands have seen a 32% reduction in area and an overall reduction in plant species richness since c. 1970. The species composition has transitioned from a dominance of small shrubs and non-woody species, to taller species, thus altering the vegetation structure. In Norwegian heathland, rotational burning was found to increase species richness and turnover of carabids, and lead to the formation of distinct species assemblages associated with different phases of the *Calluna* life cycle. Heathland specialists were found more often in recently burnt heath, while generalists occurred across all post-fire successional stages. Plants in both study areas exhibited germination responses that imply sensitivity to fire-cues. Typical Tasmanian heathland species were found more often in heat-treated soil seed bank samples, while more invasive species germinated from unheated samples. The Norwegian germination experiment showed that many heathland plants respond positively to smoke and ash cues, although responses varied among functional groups. There were also indications of a trait-driven response to fire in carabids. Moisture-loving and generalist predator species were identified as more fire-sensitive, while collembolan specialists without moisture preferences were more common in recently burnt patches. These findings have implications for the management of these study sites, but also for coastal heathlands in Tasmania and north-western Europe in general. In these areas, burning is generally necessary to maintain vegetation, promote germination in a range of heathland species, and keep plant and carabid diversity high. Fire needs to increase in frequency relative to present-day fire regimes if Tasmanian coastal heathlands are to persist. Burning should also continue in Norwegian coastal heathlands, to create a fire mosaic with a bias to younger phases, thereby maximizing carabid diversity.

Acknowledgements

Six years ago I was at a guest lecture, listening to an extremely enthusiastic professor talk about anthropogenic heathlands in Norway. Thank you, Peter Emil Kaland, for inspiring me to come to Bergen and showing me that heathlands are worth getting excited about.

I am very lucky to have had four supervisors to help me along the way; John-Arvid Grytnes, Bjørn Arild Hatteland, Inger Elisabeth Måren and Vigdis Vandvik. You have given me a lot of freedom, and have always been there to help and encourage me. Thank you so much for all the work you have put into my thesis! I am also very grateful to Jamie Kirkpatrick, for letting me work with him, and for introducing me to Tasmanian heathlands.

Thank you to all the lovely people who kept me company in the field, helped me carry beetles, and the occasional slug, toad or shrew; Amy Eycott, Keno Ferter, Vivian A. Felde, Lise Tingstad, Clara P. Martínez and Joanne Inchbald. Special thanks to Amy, who was almost always with me for adventures on Lurekalven. I thank Torhild Kvingedal and the staff at Lyngheisenteret for ferrying me around, and for letting me dig holes everywhere. Thank you to Einar Heegaard and Joseph Chipperfield for their help on my final manuscript, and to Frode Ødegaard, John Skartveit and the late Torstein Solhøy for their help with literature, field equipment, and species identification.

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List of Papers

This thesis is based on the following papers which will be referred to by their roman numerals hereinafter.

Paper I: Bargmann, T & Kirkpatrick, JB (2015) Transition from heathland to scrub in south-eastern Tasmania: extent of change since the 1970s, floristic depletion and management implications. *Biodiversity and Conservation,* 24(2): 213-228

Paper II: Bargmann, T, Måren, IE & Vandvik, V (2014) Life after fire: smoke and ash as germination cues in ericads, herbs and graminoids of northern heathlands. *Applied Vegetation Science,* 17(4): 670-679

Paper III: Bargmann, T, Hatteland, BA & Grytnes, JA (*under review*) Effects of prescribed burning on carabid beetle diversity in coastal anthropogenic heathlands. *Biodiversity and Conservation*

Paper IV: Bargmann, T, Heegaard, E, Hatteland, BA, Chipperfield, JD & Grytnes, JA (*manuscript*) Indicator value and species traits of carabid beetles across a prescribed fire chronosequence in anthropogenic coastal heathland

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Declaration

This thesis consists of a synthesis, two published papers, one submitted paper and one manuscript. All papers are co-authored. The nature of author contributions is outlined below.

Paper I:

Tessa Bargmann: experimental design, field and lab work, data analysis, writing and editing
Jamie B. Kirkpatrick: experimental design, field and lab work, co-writing and editing

Paper II:

Tessa Bargmann: data analysis and writing
Inger E. Måren: experimental design, field and lab work and editing
Vigdis Vandvik: experimental design and editing

Paper III:

Tessa Bargmann: experimental design, field and lab work, data analysis and writing
Bjørn Arild Hatteland: experimental design, help with species identification and editing
John-Arvid Grytnes: experimental design, help with field set up, data analysis and editing

Paper IV:

Tessa Bargmann: experimental design, field and lab work, data analysis and writing
Einar Heegaard: data analysis, editing
Bjørn Arild Hatteland: experimental design, help with species identification and editing
Joseph D. Chipperfield: data analysis, editing
John-Arvid Grytnes: experimental design, help with field set up and editing

Synthesis

Introduction

Heathland is a wide-spread vegetation type characterised by a dominance of evergreen sclerophyllous shrubs, generally on nutrient poor soils with low productivity (Specht and Moll 1983; Webb 1986). It occurs on almost every continent, primarily in the Mediterranean climate regions; as Australian kwongan or mallee, Californian chaparral, Chilean matorral, South African fynbos and Mediterranean garrigue or maquis (Cowling et al. 1996; Joffre and Rambal 2002). Various studies have compared flora and fauna in the different Mediterranean-type heathlands (Cody and Mooney 1978; Cowling et al. 1996), and despite their large geographical range, a number of parallels have been drawn between them in terms of biodiversity patterns (Ojeda et al. 2001), patterns of endemism (Cowling et al. 1994), and life history traits (e.g. Keeley and Bond 1997). Although these landscapes share very few species, they are each dominated by structurally similar assemblages, notably of species in Asteraceae, Ericaceae/ Epacridaceae and Fabaceae, as well as Proteaceae in the fynbos and kwongan.

In addition to the heathlands occurring in Mediterranean climate regions, heathlands also occur in other parts of the world, such as in non-arid areas of Australia (Kirkpatrick 1977), and in considerably wetter climates in north-west Europe (Webb 1986). While Australian heathlands are comparable to those in Mediterranean climates in terms of their species diversity (Kirkpatrick and Harris 1999), north-west European heathlands are much more species poor, and are largely dominated by *Calluna vulgaris* and other Ericaceous species. Nevertheless, all of these landscapes are structurally similar, and are formed and maintained by similar processes (see Figure 1). There are many different natural factors that can lead to heathland formation, such as water balance (too much or too little water), nutrient-poor soils, exposure, salt spray and wildfire, all of which help to keep vegetation low and prevent succession to forest (Specht and Moll 1983; Webb 1986; Kirkpatrick and Harris 1999). Not all heathlands require the same set of factors to persist; there are montane heathlands that are not exposed to salt spray, and California chaparral, for example, is generally not replaced by other vegetation types in the absence of fire (e.g.

Hanes 1971). However, despite the fact that different heathlands have different requirements for persistence, there is a general consensus that fire plays a pivotal role in heathland formation in many areas, and that it mediates species richness, dominance and structural patterns (Mallik and Gimingham 1983; Kirkpatrick and Harris 1999). It has even been suggested that comparable fire regimes in heathlands may have been an equally important driver of ecosystem convergence as climatological and geographical factors (Keeley et al. 2011). This is demonstrated in the parallels in plant traits found in these systems, such as resprouting ability after fire (Keeley 2012). In general, the literature agrees that a proneness to fire is characteristic of most heathland landscapes, and that fire regimes represent one of the most important disturbance factors maintaining vegetation composition in heathland vegetation all over the world (Gimingham 1972; Kaland 1986; Schwilk et al. 1997).

Figure 1: Coastal heathland on Bruny Island, Tasmania (left) and Lygra, western Norway (right).

Although many heathlands are probably formed and maintained by natural processes, many are also likely to have been created and maintained by human disturbance regimes (Specht and Moll 1983), and many heathlands may not exist or have the extent that they have today without human interference. This is particularly well documented for heathlands in north-western Europe, which have resulted from early farming and clearing of forests by humans centuries ago (Kaland 1986; Webb 1998). There are a number of human activities, such as turf cutting, grazing and mowing, that have led to the formation and maintenance of north-west European heathlands in particular (Gimingham 1972; Webb 1986; Kvamme et al. 2004), but fire is perhaps the one that has been used most extensively in other heathlands of the world. There is strong evidence that anthropogenic fire has been widespread in Australia, where Aborigines have used so called "fire-stick farming” to clear scrub in order to hunt small prey (Jones 1969; Bliege Bird et al. 2008). Although the extent to which humans employed fire in Australia is uncertain (Bowman 1998), there is a consensus that they have in some way contributed to maintaining these landscapes by burning (Clark 1983). This is also true in Tasmania, Australia (Kirkpatrick and Harris 1999; Jackson 1999).

Since both natural and anthropogenic fires have been shaping heathland ecosystems worldwide for a long time (Mallik and Gimingham 1983; Kvamme et al. 2004; Keeley et al. 2011), fire is an important disturbance factor within heathlands in general, and makes them a perfect system for various ecological questions pertaining to post-fire disturbance and succession. In heathlands that have been maintained to a large extent by humans, fire may be a particularly important disturbance factor to study, especially in the light of changing fire regimes and climate change (Enright et al. 2014). Although heathlands in Tasmania and Norway are dissimilar both in terms of species and management, both are heathland types that are currently facing reductions due to a change in fire regimes (Kirkpatrick and Harris 1999; Kvamme et al. 2004). As a result, it is vital that fire and its effect on heathland diversity are studied, in order to prevent further loss of this vegetation type and its associated species in both regions. Even though these systems are in opposite hemispheres, and much dissimilarity exists, many of the effects of fire on successional dynamics and biodiversity in one system will also be of ecological interest to the other. This thesis will therefore focus on patterns and mechanisms of species composition and diversity in fire prone coastal lowland heathlands in south-eastern Tasmania and south-western Norway.

Tasmanian heathlands

Tasmanian coastal heathland is located primarily in the north, east and south-east of the state, on nutrient poor soils (Kirkpatrick 1977). Although these heathlands are not quite as species rich as Western Australian kwongan, they are one of the most species rich vegetation types in Tasmania, with up to 60 vascular plant species being found in 100 m^2 (Kirkpatrick and Harris 1999). In fact, nearly half of Tasmanian vascular plants are recorded within heathlands. Many of the plant families common in Australian heathlands are also dominant in Tasmanian heathlands, and include the Asteraceae, Cyperaceae, Fabaceae, Epacridaceae, Myrtaceae, Orchidaceae, Proteaceae and Restionaceae. Of the plant species found in Tasmanian heathlands, 50 are considered rare or threatened in the state (Kirkpatrick and Harris 1999).

Coastal heathland was the first vegetation type to be formally described for Tasmania (Kirkpatrick 1977), and by 1995 about one quarter of Tasmanian lowland heath was found in designated reserves (Kirkpatrick and Harris 1999). However, despite the fact that this vegetation type currently has a high reservation status, Tasmanian coastal heathlands are still threatened by weed invasion, land clearing, the pathogenic fungus *Phytophthora cinnamomi,* and shifting fire regimes. Fire regimes in Tasmania have been changed extensively over the last two centuries, and there has been a shift from the small more frequent burns of the Aborigines, to the large high-intensity fires of early European settlers, and finally to the current large and less frequent fires (Marsden-Smedley 1998). These current fires are so large and infrequent that since the 1930s, one percent of the fire seasons was responsible for over 40% of the burnt area within the Tasmanian Wilderness World Heritage Area (UTAS Innovation Ltd. 2007). What is more, it is areas near the coast in particular that have experienced an even more reduced frequency of burning since the 1970s (Gilfedder et al. 2003; Hayes and Kirkpatrick 2012). As a result, many of the fire prone coastal heathlands of Tasmania have been markedly reduced.

North-west European heathlands

The coastal heathlands of Europe span 3600 kilometres, from the north of Portugal to Lofoten in northern Norway, and Norway alone is home to roughly one third of this latitudinal range (Kaland and Kvamme 2010). Although European heathland is not as species rich as Australian heathland, it has a long history as a cultural landscape (Gimingham 1970; Kvamme et al. 2004). It has been shown that it is a man-made landscape, which has its origin approximately 5000 years ago, when people began to settle and convert woodlands into heathlands by burning and grazing (Gimingham 1970; Kaland 1986). The clearing of forests that gave way to anthropogenic heathlands in western Norway occurred mostly during the Bronze and Iron ages, between 6000-3300 BP (Prøsch-

Danielsen and Simonsen 2000). However, the process of forest clearance occurred in small patches and took more than 4000 years, with the youngest dated deforestation occurring 800-900 years ago (Kvamme et al. 2004). Due to their ancient beginnings, a high valuation of heathland landscapes has persisted, and they continue to be of great cultural and aesthetic value to many Europeans.

The heathlands of Europe are currently under threat. Their decline has been widely attributed to the cessation of traditional farming practises such as burning, grazing, turf stripping, mowing and periodic cultivation, which results in a transition to other successional stages (Gimingham 1994 and see Figure 2). Because of this, heathlands are now a priority for conservation in Europe (Council of the European Union 1992), not only because of their biodiversity value, but also because they are a rapidly declining cultural landscape (Gimingham 1994; Webb 1998). The Norwegian red list for nature types lists coastal heathlands as endangered, based on the fact that their area has declined by 50-80% over the last 50 years (Lindgaard and Henriksen 2011). Furthermore, a large proportion of species that are associated with cultural landscapes are also listed as threatened (Kålås 2010).

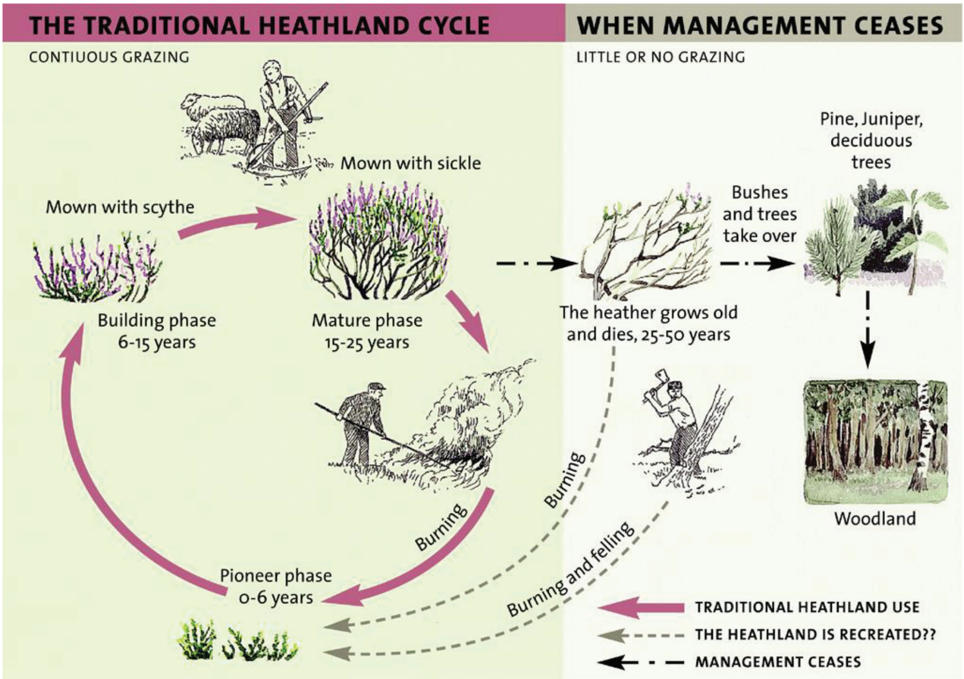

Figure 2: Illustration by P.E. Kaland and E. Hazebroek (taken from Kvamme et al. 2004).

There is a long history of fire usage as a management tool for heathlands in Europe (Mallik and Gimingham 1983). Primarily, fire is useful for grazers in that it burns away older and therefore less nutritious heather, and allows new, more nutritious heather to grow. It also allows for changes in floristic and faunistic compositions, as it can temporarily reduce the presence of otherwise dominant species (Mallik and Gimingham 1983). This can result in a more bio-diverse landscape, if fires are controlled in such a way that they create a mosaic of heath of different ages. As a result, there has been much interest in the use of traditional management practises as means to preserve heathlands in the literature, the efficacy of which has been shown to increase both animal (Usher 1992; Usher and Thompson 1993) and plant diversity (Vandvik et al. 2005), promote regeneration of heath (Sedláková and Chytrý 1999; Calvo et al. 2002; Nilsen et al. 2005) and keep nutrient budgets in heathlands in check (Fottner et al. 2007). Fire in particular is often a favoured management strategy with many farmers and landowners, because it is a relatively cost- and time-efficient measure (see Figure 3).

Figure 3: A typical management fire on a western Norwegian heathland (Lurekalven).

Plants and fire

In any landscape that is subjected to recurrent fire, organisms must adapt. Fire can drive the evolution of adaptations in heathland species, and it can be a significant factor in determining community assemblages, species richness, and structural and dominance patterns (Kirkpatrick and Harris 1999; Vandvik et al. 2005; Keeley et al. 2011; Enright et al. 2012).

Many plants in naturally fire-prone heathlands have been shown to respond favourably in their germination to fire-cues (Keeley et al. 1985; Brown 1993; Dixon et al. 1995; Keeley 1995; Gilmour et al. 2000). The same has also been shown for *Calluna vulgaris* in anthropogenic heathlands (Måren et al. 2010; Vandvik et al. 2014) . A number of heathland species are known to survive fire by vegetative resprouting, and about 67% of Australian heathland species are estimated to regenerate in this way (Pausas et al. 2004). In Europe, various studies have also confirmed that vegetative resprouting is an important strategy for *Calluna* (Mallik and Gimingham 1983; Aarrestad and Vandvik 2000; Calvo et al. 2002). However, adaptations to fire are not limited to vegetative regeneration; it is also possible for plants to regenerate from seed after burning, and some species are enhanced by fire. Fire cues are very complex, and while the exact mechanisms for germination responses are not completely understood, there are many specific underlying cues that have been documented. Some examples of specific mechanisms are dry heat (Jeffery et al. 1988), chemical substances such as ethylene and various nitrogenous substances (Van de Venter and Esterhuizen 1988; Keeley and Fotheringham 1997), as well as ash (Reyes and Casal 1998) and smoke (De Lange and Boucher 1990; van Staden et al. 2006; Light et al. 2010; Måren et al. 2010; Flematti et al. 2013).

While responses to fire specific germination cues have been relatively well investigated for Tasmanian species (e.g. Keith 1997; Bell 1999; Gilmour et al. 2000), they have been less studied in Norway. However, one study has shown that smoke and ash can promote seedling germination in *Calluna* (Måren et al. 2010; Vandvik et al. 2014), and there are similar positive responses to fire cues in a few plants in other European heathlands (Mallik and Gimingham 1985; González-Rabanal and Casal 1995). As fire is an important but also contested part of the recommended management regime for northern heathlands, it is important to investigate the fire responses of a wider range of plants characteristic of the heathland habitat.

Although species diversity is apparently reduced as heath turns to scrub, many species may be able to survive in the soil seed bank (Russell and Parsons 1978; Molnar et al. 1989) and re-establish after fire. However, the similarity between soil seed bank and above ground vegetation can be very low (Wills and Read 2002, 2007; but see Måren and Vandvik 2009). In addition, the mode of regeneration is often the most important factor determining species absence in the seed bank, and species found in the above ground vegetation but not the soil seed bank are also more likely to have the capacity to resprout after fire (Wills and Read 2007). However, although this trait may be useful given appropriate fire intervals, it may make it difficult for such heathland species to persist once they have been lost from the above ground vegetation. This is especially problematic as species typical of Australian lowland coastal heathland appear to have a limited capacity for long distance dispersal, due to their tendency to have large, heavy seeds (Keith et al. 2002). Therefore, although seed banks may be valuable in preserving heathland species in a period without fire, their capacity for regeneration may be relatively low. As a result, heaths that have been lost to scrub as a result of a reduced fire frequency should be studied for their capacity to regenerate if fire were to be re-introduced into the system.

Despite the fact that fire can promote plant diversity and germination response, the ideal fire interval needed to maintain species rich heath is not always easy to determine. For example, the fire frequencies required to maintain heathland have been shown to vary with environment and biota (Kirkpatrick and Harris 1999; Britton et al. 2000; Keith et al. 2002). In Australia, long times between fire intervals have been shown to reduce regenerative capacity, increase senescence and result in overall population decline and diversity (Enright et al. 2012; Gosper et al. 2012). However, very frequent fires have also been shown to be deleterious to heathland communities (Bradstock et al. 1997; Kirkpatrick and Harris 1999; Keith et al. 2002; Enright et al. 2012). Although regeneration times of heath in north-western Europe can also be highly variable (Britton et al. 2000; Velle et al. 2012; Velle and Vandvik 2014), burning is usually done to coincide with *Calluna* dominance, which has a relatively well defined succession cycle divided into the pioneer, building, mature and degenerate phases (Barclay-Estrup and Gimingham 1969; Figure 2).

Furthermore, the fire regimes in Europe have a more solid historical basis (Gimingham 1970; Kaland 1986; Webb 1986; Kvamme et al. 2004), particularly in north-west European heathlands, where the landscape is entirely anthropogenic. In fact, it is probably for this very reason that Norwegian fire regimes are easier to determine than those of the naturally fire prone heathlands of Tasmania; because the coastal heathlands of Norway and their species have been exposed to the same types of regimes for centuries. In fact, *Calluna* populations in anthropogenic heathlands appear to be so well adapted to prescribed burning, that they have developed fire-cued germination responses, while their naturally occurring populations have not (Vandvik et al. 2014). However, although Tasmanian heathlands are affected by wildfires, anthropogenic fire has also been a part of their history, and lessons learned from prescribed burning in Europe may still be of interest. Furthermore, general successional and species diversity patterns as a result of fire should be transferable from either system to the other.

Carabids and fire

Heathland flora has most often been the focus in studies of response to prescribed burning (e.g. Clément and Touffet 1981; Mallik and Gimingham 1983). However, the response of insects to fire (Andersen and Müller 2000; Clarke 2008), as well as their possible adaptations along environmental gradients in general (Gerisch et al. 2012) are still relatively unknown. This can be a problem, because heathland reserves are most often selected based on their flora (Gardner 1991; Telfer and Eversham 1996), and because plant diversity is not necessarily a good predictor of insect diversity (Usher 1992; Faith and Walker 1996). As a result, it is difficult for heathland managers to make adequate management plans that take the needs of all species living in heathlands into account, and makes it difficult to assess how well the diversity of such habitats is preserved. Acquiring knowledge of insect responses is therefore a necessary part in providing a more comprehensive understanding of heathland biodiversity. It is particularly important considering that insects represent a large proportion of diversity in general, and because they are generally not that easy to observe, making them difficult to assess on a superficial level.

Carabid beetles are a relatively well studied species group, and therefore a lot is known about their taxonomy, life history strategies, diets and habitat preferences. As a result they are sometimes considered “indicator species” of ecosystem functioning (Lövei and Sunderland 1996; Rainio and Niemelä 2003; Koivula 2011; Kotze et al. 2011). The detailed knowledge of their preferences and life cycle characteristics makes them ideal model organisms in the assessment of responses to environmental disturbances. Since disturbance is such an important element in the determination of species traits in disturbance-prone habitats (Southwood 1977; Lytle 2001; Ribera et al. 2001; Lambeets et al. 2008), trait-based approaches and indicator species analyses using carabids can therefore be very informative, and help to inform the monitoring (Carignan and Villard 2002) and management of natural reserves (De Cáceres et al. 2010).

In forests, carabid beetles have been shown to thrive as a result of fire and other disturbances (Gongalsky et al. 2006; Martikainen et al. 2006), where a difference in carabid species assemblage with phase of secondary succession has been documented (Niemelä et al. 1993). The same is true in the different stages of heathland succession (Schirmel et al. 2012). In fact, some studies have advocated for more disturbance for better conservation of the unique species assemblages of carabids found in this vegetation type (Bertoncelj and Dolman 2013). Furthermore, there are a number of studies that indicate that the best management strategy for heathland carabids is to create a mosaic of different successional patches, with a preference for earlier stages (Schirmel and Buchholz 2011; Buchholz et al. 2013; Borchard et al. 2014; Brunbjerg et al. 2015). Overall, it appears that early successional stages and recently burnt areas are more suitable for many rare and xerophilic species (Usher 1992; Schirmel and Buchholz 2011; Buchholz et al. 2013), as well as typical heathland carabids (Borchard et al. 2014). While there are various studies that assess carabid assemblage and species richness patterns in heathland, most studies do not look specifically at prescribed burning, rather separating their study regions into two or three categories (e.g. overgrown versus restored or burn versus unburnt). However, a greater resolution in time since prescribed fire may be better in representing diversity changes with time, and more accurately reflect the nature of management burns currently employed in anthropogenic heathlands.

In addition to the knowledge that is lacking about carabid responses to fire in general, very little is known about species level responses and shifts in functional diversity along environmental gradients (Gerisch et al. 2012). Thus, although relatively frequent management burns in small patches may benefit carabid communities in general, further research should focus on how successional stages favour specific life history traits (Schirmel et al. 2012). Knowledge of how species sorting of carabids occurs in each stage could provide valuable information for heathland conservation if they are to be used as indicator species of the different stages of succession after fire. Information about possible carabid adaptations to fire may help to inform managers about how species assemblages may change after burning even for species that are not observed.

Objectives

Fire can be both a threat and a necessity in heathlands. I therefore hypothesised that the species present in heathland systems are adapted in some way to fire. Thus, we need to know how organisms in heathlands respond to prescribed burning to be able to optimally manage them. To achieve optimal management, it is necessary to 1) understand the effects of fire, or lack thereof, on species composition and diversity and 2) to investigate whether heathland species and communities depend upon, and to what extent they have adaptations to, recurrent fire. To address these main objectives, the aims of this thesis were:

1. Determine the extent to which heathlands and their plant and carabid species depend upon recurrent fire and fire cues
    a. Is heathland being lost due to the absence of fire, and what spatial attributes of heathland are likely to be the most instrumental in heathland loss? **(Paper I)**
    b. What is the impact of the fire cues smoke, ash and heat on germination of important plant functional groups? **(Paper I & II)**
    c. Are there carabids that are associated with any particular habitat along a time-since-burning gradient? **(Paper IV)**
2. Investigate how burning/ lack of burning affects species diversity
    a. How does burning affect local species richness and composition? **(Paper I & III)**
    b. How does burning affect local species turnover? **(Paper III)**
3. Investigate the adaptations to burning of plants and carabid beetles
    a. To what extent do plants survive and germinate after fire? **(Paper I & II)**
    b. Which carabid traits make them particularly suited/ sensitive to prescribed fire? **(Paper IV)**
4. Determine the composite implications of these findings for heathland management **(Paper I-IV)**.

Methods and Study Systems

South-eastern Tasmania, Australia

The study region of Paper I is in south-eastern Tasmania, extending from Tasman Head on Bruny Island in the south to the Friendly Beaches in the north, and includes all lowland heaths mapped in this area by Kirkpatrick in 1977 (Figure 4). These heathlands have a mild temperate oceanic climate with a mean annual rainfall ranging from 609 mm on northern Bruny Island, to 830 mm on the south-eastern tip of the Tasman Peninsula (www.bom.gov.au). The mean maximum temperature of the warmest month ranges from 18 to 23°C, while the mean minimum temperature of the coldest month ranges from 5 to 7°C, with generally warmer temperatures in the north.

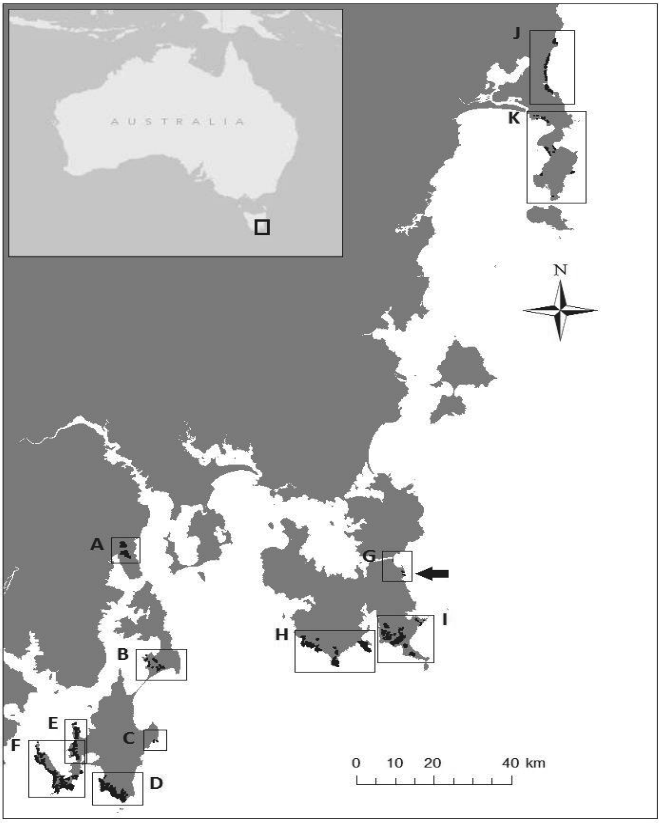

Figure 4: Map of south-eastern Tasmania (taken from Paper I). Black areas show the locations of coastal heathlands in this study: A Blackmans Bay, B Bruny North Island, C-F Bruny South Island, G Tasman Arch, H Tasman Peninsula (East), I Tasman Peninsula (West), J Friendly Beaches, K Freycinet. The arrow indicates where soil seed bank samples were taken.

These heathlands represent 11 of the 13 described lowland heath community types of Tasmania (Kirkpatrick and Harris 1999) which are; rock pavement heath, six dry heath communities dominated by *Allocasuarina monilifera, Banksia marginata*, *Eucalyptus amygdalina* and *E. nitida*, *Leptospermum scoparium*, *L. glaucescens,* and *Melaleuca ericifolia*, respectively, and four wet heath community types dominated by *Leptospermum scoparium, Melaleuca squarrosa*, *M. gibbosa*, and *M. squamea*, respectively.

Paper I aimed to map the extent of transition from heathland to scrub due to a prolonged period without fire in the study region between c1976 and 2013. We also wanted to determine whether the transition to scrub resulted in the loss of local species richness and changed species composition. Finally, we wanted to know to what extent the soil seed bank may be able to aid in recolonization of species no longer present above ground, if they were subjected to management fire. We compared aerial photographs from 1966 and 1978 to remote sensing imagery from 2010, as well as checked for changes on the ground. Maps showing the extent of heathland in both time periods were then made using ArcGIS. A generalised linear model was constructed to assess which characteristics (e.g. patch size, distance to the next heath, and distance to the sea) of heathland were most associated with heathland area loss. In order to be able to determine species loss and composition, we also recorded above ground vegetation at one site at Tasman Arch that had transitioned to scrub, and took soil seed bank samples to check which species may be preserved there. This heathland was classified as dry *Allocasuarina monilifera* heath in the 1970s (see arrow on Figure 4). Soil seed banks were germinated under a heat treatment as well as a control in a greenhouse trial (Figure 5). Fisher's exact tests were used to determine

Figure 5: Germination experiment at the University of Tasmania. Soil seed banks have been subjected to heat treatment.

if there were differences between species composition in the seed bank and the above ground vegetation of both years. The Sørensen similarity index of species composition was calculated for the above ground vegetation between time periods. Finally, the species composition of germinates from the seed bank in the heated and un-heated treatment was compared using constrained analysis of principal coordinates. ANOVA was used to determine if the scores on the constrained axis differed between heated and unheated trays.

Lygra, Norway

The Norwegian study area of Papers II-IV is located on the islands of Lygra and Lurekalven at $60^{o}42'$N and $5^{o}5'$E, about 40 km north of Bergen in western Norway (Figure 6). The islands are separated by a narrow strait, where Lurekalven is situated parallel to and directly north-west of Lygra. While the topography of Lygra is relatively flat, Lurekalven is more rugged, with its highest point at 54 meters above sea level. The area has an oceanic climate with a mean June temperature of 12^{o}C and a mean January temperature of 2^{o}C. Mean annual precipitation is c. 1600 mm a year (www.met.no).

Both islands have acidic, nutrient-poor soil, and are dominated by *Calluna*, mires and mixed grass heaths, with some smaller patches of forest (mainly *Betula pubescens* and *Pinus sylvestris*). Four main heathland types can be found here, as defined by Fremstad (1997); dry *Calluna* dominated heath (H1a), which is found primarily on well drained shallow soils on ridges or south- and west-facing slopes, dry grass and herb dominated heath (H2b), found in areas with a high grazing pressure, wet heath (H3), which tends to occur on deeper soil in poorly drained valleys or north-facing slopes, and *Calluna* and fern dominated heath (H4), which is found in moist north-facing slopes (Fremstad 1997; Aarrestad and Vandvik 2000).

Complete deforestation and establishment of *Calluna* heath has been dated to approximately 1300 BP on the nearby island of Lurekalven, where the landscape has also been kept open ever since (Kaland 1986). The exact date of forest clearance could not be determined at Lygra specifically, due to the common practise of peat collection in the bogs of the area. Nevertheless, as archaeological findings have dated farming practises back to the late Neolithic (~3500 BP) in this particular area, it is likely that Lygra has been at least partly deforested since then (Kvamme et al. 2004). Prescribed burning and year round grazing by an Old Norse breed of sheep was reintroduced onto both islands in 1992. Recent fire history is therefore well documented, with patches having been subjected to prescribed burning almost every year. In accordance with traditional management methods in Norway, burning is always done in winter or early spring to ensure that the ground is still frozen, so that the fire does not burn away the soil and soil seed bank.

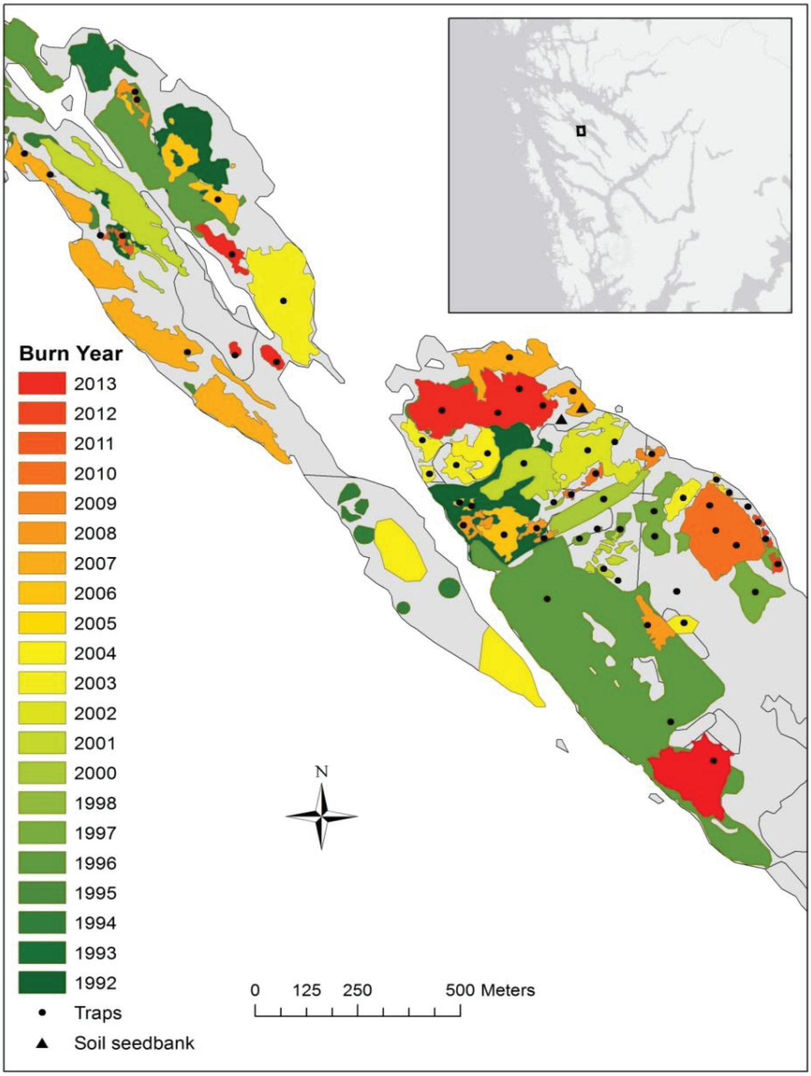

Figure 6: Map of the study area in western Norway, showing the burn mosaic and the location of pitfall traps and soil seed bank samples (modified from Paper III). The island of Lygra is in the south-east, and Lurekalven is in the north-west.

Paper II investigates the effects of fire by examining plant germination response to fire cues. As the response of *Calluna vulgaris* to fire cues had already been assessed, we focussed on the germination response of important functional groups within European heathlands, namely ericads, herbs and graminoids. We chose to study the effect of fire on these functional groups experimentally by testing the effects of aqueous smoke solution, ash and a combination of the two treatments. To accomplish this we carried out a greenhouse germination trial that compared seed banks from old heath (28 years since the last fire) with seed banks from newly burnt heath (burnt the previous year), where we expected that fire-cued germination had already occurred (see locations of seed bank samples on Figure 6). The seedling count data were analysed using linear mixed effects regressions including ash and smoke treatments, an interaction between the two, and a random effect term for sample.

The final two papers also use Lygra as a study site, and aim to investigate how time since management fire affects carabid beetle richness, composition and species turnover (Paper III). We also wanted to assess whether species life history traits are selected for by time since the last burn, thereby determining whether there is a shift in species traits along the burn gradient (Paper IV). In order to answer these questions we identified all carabids caught in 60 sets of three traps (see Figure 7) which were placed in the centre of different burn patches in a fire mosaic. Carabids were trapped in pitfall traps over 4-5 months in their most active period in two consecutive years.

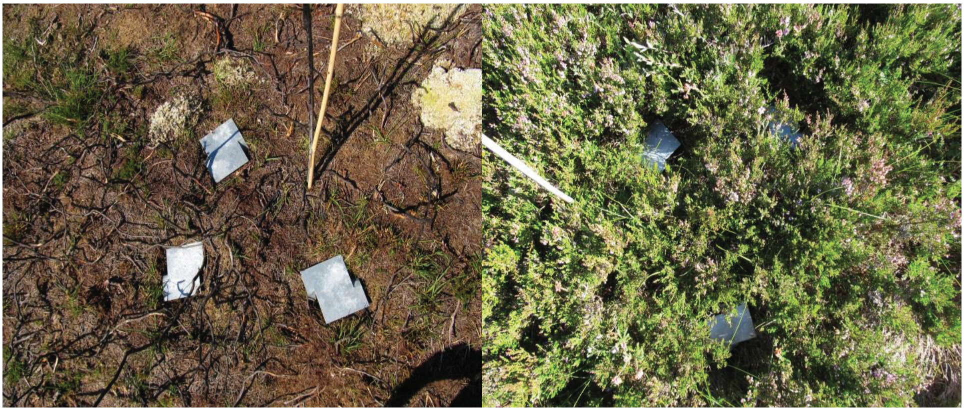

Figure 7: Pitfall traps with metal roofs in a recently burnt patch (left) and a patch burnt 10 years ago (right).

In Paper III, the species richness and turnover of each plot was estimated using individual-based rarefied data. This was done to account for differences in the numbers of individuals collected due to the fact that pitfall trap data represents both abundance and activity density of the species caught (Greenslade 1964; Baars 1979). Linear regressions were fitted for each diversity measure over the time-since-burn gradient. De-trended correspondence analyses (DCA) were run to summarise variation in species assemblages, and the sample scores of the DCA were subsequently related to the time since fire.

Paper IV determined indicator species and traits (e.g. diet and life-history) that are characteristic for different stages along the time-since-burning chronosequence. Indicator species were calculated using Dufrêne-Legendre indicator values (Dufrêne and Legendre 1997). To investigate trait responses, a hierarchical Bayesian log-linear model was constructed (see the Methods section of Paper IV for details). The full model included 11 carabid traits and time since the last prescribed fire as fixed effects, sampling year, trap number and species as random effects, and an offset for the relative proportion of species in the analysis, in accordance with Warton et al. (2015). Model selection was done by forward selection using the Deviance Information Criterion (DIC), and the model was parameterised using Integrated nested Laplace approximation (INLA) (Rue et al. 2009; Fong et al. 2010).

Results and Discussion

Heathland in the absence of fire

This thesis shows that the extent of the studied heathlands and the species in them are dependent on recurrent fire. In Tasmania, a reduced fire frequency has caused a one-third reduction in the overall landscape over the last four decades (Paper I, Table 1), with much of what used to be heathland having been converted to scrub more than 2 meters tall (Figure 8). Paper I also showed that fragmentation, the size of heathland patches, and their distance from the next patch are the strongest predictors for heathland area loss. This is additional support for the need to maintain continuous heathlands, rather than isolated patches.

Figure 8: An example of heathland (left) and heathland that has transitioned to scrub (right) on Bruny Island in April 2013.

Importantly, the succession from heathland to scrub in south-eastern Tasmania has not been caused by species invasions from adjacent landscapes, but rather by a shift in dominance to woody heathland plants such as species of *Allocasuarina, Banksia, Eucalyptus, Hakea, Leptospermum* and *Melaleuca.* A similar pattern is true of European heathlands, where woody species begin to dominate and replace herbaceous species as the time since fire increases (Barclay-Estrup and Gimingham 1969; Calvo et al. 2002). However, while it has been hypothesised that succession from heathland to forest may be a cyclical process, and that forests can be converted back to heathland given an appropriate management regime (Webb 1986), heathland restoration is often difficult and time consuming. Likewise, it is unclear how easily Tasmanian heathlands can be restored once they have undergone succession.

In addition to fire being an essential part of maintaining the landscape, this thesis provides further evidence that burning promotes the presence of heathland plants. Paper II showed that the fire cues ash and smoke stimulate germination of ericads and graminoids in Norwegian coastal heathland (Paper II, Table 1 & Figure 1). Specifically, we have shown that this effect is stronger in seed banks that have not been burnt in a long time, supporting the role of fire in the successional dynamics of heathlands. This is a finding that has also been supported by a number of previous studies that have investigated the effects of fire and fire-related cues on germination in European heathlands (Mallik and Gimingham 1985; González-Rabanal and Casal 1995; Valbuena et al. 2000; Måren et al. 2010; Vandvik et al. 2014). Our germination study of south-eastern Tasmania also showed that scleromorphic heathland species respond favourably in their germination to heat treatment, whereas unheated treatments were dominated by species that are known to colonise mechanically disturbed areas (e.g. *Juncus*).

Despite the evidence for fire-cued stimulation of germination in heathland plants both in Europe (Valbuena et al. 2000; Måren et al. 2010; Paper II) and Australia (Dixon et al. 1995; Keith 1997; Bell 1999; Crosti et al. 2006; Paper I), it is important to keep in mind that it is only useful for restoration of heathland to have a fire stimulated seed bank if the species represented in the seed bank are in fact representative of above ground heathland vegetation. Seed bank versus above ground species similarity has been shown to be relatively high on Lygra, suggesting that these seed banks can be very effective in providing potential recruits for recolonization after fire (Måren and Vandvik 2009). In contrast, we found that there is a low similarity between the seed bank and the standing vegetation at our study site in south-eastern Tasmania. This suggests a weak capacity to aid the regeneration of heathland species after fire, when heathland has already been converted to scrub. In fact, the germination experiment from our study area in Tasmania revealed that the seed bank seems to favour invasive over heathland species, and that no rare or endemic species that were lost above ground were preserved in the seed bank. One explanation for this is the fact that the majority of the species in our study regenerate after fire by resprouting rather than from seed (65%; See Paper I, Figure 3). This finding is in accordance with a previous study that estimated 67% of Australian heathland species to be capable of resprouting (Pausas et al. 2004). Thus, although many heathland species are tolerant of or even enhanced by fire, it is important to consider seed bank species composition when estimating its capacity for heathland restoration by fire. Our findings from Paper I emphasise the need for recurrent fire before a succession to scrub has taken place. Furthermore, while a low above ground versus seed bank similarity is not an issue in our Norwegian study site, taking the seed bank into account is also relevant in the study of European heathlands, especially if a long time has passed since the last fire.

Species diversity after burning

In both study systems, species richness was reduced and species composition was altered when fire ceased or the interval between prescribed burning was long. This was the case for both plants and carabid beetles in Paper I and Paper III, respectively. Paper I showed a drop in plant species richness from 54 species in 1976 to 33 species in 2013 where what was previously a heathland had become scrub (Paper I, Appendix Table 2). The Sørensen similarity of species composition between the years was 66%. Thus, although some Australian heathlands have been shown to not significantly alter their floristic composition when the time since the last fire is long (Hanes 1971; Jarman et al. 1988), this is not the case in the heathland studied here. Even more worryingly, the area studied in south-eastern Tasmania lost many common Tasmanian heathland species, including the endemics *Eucalyptus tenuiramis* and *Lomatia tinctoria,* and the rare *Lepidosperma tortuousum.* All the species that were lost between sampling times were small shrubs or non-woody species. Thus, heathlands that transition to scrub are not only more species poor, but they also move toward a species composition that is dominated by generally taller species, changing the structure of the vegetation. This is the same pattern that is also found in European anthropogenic heathlands, where heathland specialists establish more readily after prescribed fire (Velle et al. 2014).

Plants are not the only heathland species that are promoted by the use of fire; Papers III and IV have shown that recently burnt patches are also particularly attractive to carabid beetles that are specialists of heathlands or other open habitats. Over the 23-year fire chronosequence, carabid species richness decreased steadily as time since the last fire increased (Paper III, Figure 2). In addition to higher species richness after fire in general, we also found more characteristic heathland and open habitat species in heath burnt less than twelve years ago (e.g. *Amara lunicollis, Cicindela campestris, Nebria salina, Poecilus lepidus*; see Paper III, Appendix A1). Generalist species were more likely to be found across the entire chronosequence. Furthermore, the species compositions of different patches were significantly correlated with the time since the last prescribed fire (Paper III, Figure 3). This suggests that creating a mosaic of patches in different successional stages is important to conserve the different species assemblages that inhabit the landscape. These findings are in accordance with previous studies that have found similar patterns in carabid (Schirmel and Buchholz 2011; Buchholz et al. 2013; Brunbjerg et al. 2015) and plant assemblages (Vandvik et al. 2005; Velle and Vandvik 2014) across successional gradients.

Many beetles experience large intergenerational fluctuations in species abundance form one year to the next (Den Boer 1990; Muona and Rutanen 1994). Therefore, temporal species turnover can be informative to determine the effect of fire on species diversity, and to explore whether changes in species richness across successional stages are consistent over time. The results of Paper III show that species richness is not only consistently higher in recently burnt plots over the two sampled years, but also that species turnover is higher in these early years after fire (Paper II; Figure 4). While species turnover decreased linearly with time since the last burn, the combined species richness of the two sampled years began to level off at around 15 years since fire. This suggests that patches in the pioneer and building stages of the *Calluna* cycle (ca. 0-14 years of age), are the most valuable in maintaining high levels of carabid diversity. These results indicate that dispersal of carabids from neighbouring patches to recently burnt patches is occurring to a large degree, and that heathland carabids in general have a preference for these stages.

Species response to fire

The results of Papers I, II and IV suggest that heathland plants and carabids have adaptations to or preferences for fire or fire-related cues. In accordance with previous studies on the favourable germination response to fire of Australian heathland plants, Paper I showed that a number of common heathland species, such as *Acacia genistifolia, Astroloma humifusum, Boronia parviflora/pilosa, Dillwynia glaberrima* and *Pimelea linifolia,* occurred more frequently in the heat treatment than in the unheated treatment of our germination trial. The graminoids in this study showed contrasting germination responses depending on whether they were found above ground or not. Species that were only recorded in the seed bank germinated more readily in unheated treatments, while those species that were found above ground were more common in the heated treatment. These findings indicate that there is some level of fire adaptation in typical heathland species, and that mechanical disturbance would thus create vastly different species assemblages which are unfavourable for the conservation of heathland.

Paper II has shown that favourable germination responses to the fire cues smoke and ash also exist in heathland species in addition to *Calluna* in Norwegian heathlands. In particular, we found that graminoids and ericads are promoted in their germination by fire, while herbs are not affected to the same extent. These responses vary within species groups and are dependent on the time since fire. For example, *Erica tetralix* responded positively to both the smoke and the ash treatments regardless of whether the seeds were from old heath (i.e. 28 years old) or recently burnt heath. *Calluna* germination on the other hand, was only promoted by these fire cues in the samples that were taken from old heath. This difference in responses may be reflective of the different habitat niches of these species, where *Calluna* is predominantly found in dry heath, and *Erica* in wet heath (Bannister 1966; Aarrestad and Vandvik 2000). Wet heath is usually not as easily burnt as dry heath, meaning that *Erica* may not have had the same exposure to fire cues in the past.

The graminoids in this study had a germination response similar to that of *Calluna*, that is, they responded negatively in their germination to smoke in the newly burnt heath samples, but positively in response to both ash and smoke treatments in the unburnt heath sample. Interestingly, this was the case despite overall higher germination counts in the newly burnt samples. This indicates that graminoids that are persistent in the seed bank are also more likely to have fire-cued germination. However, it is important to note that in Paper II, we did not distinguish between species of the functional groups, so we are not able to determine whether we are recording a response of certain species that may have fire adaptations, or whether, like with *Calluna,* the germination response to fire varies with the time from the last exposure.

In Paper IV, we have shown that a number of carabids, especially heathland specialists, have a preference for recently burnt habitats (Paper IV, Table 2). While plants have a number of adaptations that help them to persist or recover after fire, the ability of animals to survive fire is largely linked to their mobility. In fact, it is likely that the spatial attributes of fires are generally more important to animals than they are to plants, because animals rely more heavily on patch sizes being small enough, and habitat connectivity being good enough for them to disperse into suitable areas directly after fire (Clarke 2008). Carabid dispersal abilities vary considerably from species to species due to differences in body size and wing and leg morphologies (Den Boer 1990), therefore, it would have been reasonable to expect traits linked to dispersal to be linked with fire response. However, Paper IV did not reveal any dispersal traits to be significantly linked to time since burning. Instead, we showed that diet and moisture preference determine species abundance along the fire chronosequence (Paper IV, Figure 2). This may be attributed to the small patch sizes at our study site, meaning that carabid presence in a particular patch is determined by habitat preferences rather than the speed at which they are able to return to a patch. It is therefore important to note that larger patch sizes may have negative effects. Nevertheless, provided that patches are small enough to facilitate dispersal from neighbouring patches after prescribed fire, and that beetles do not have to traverse patches of unsuitable habitat, Paper IV suggests that recently burnt heathland is attractive to a number of heathland and open habitat specialists. This is particularly the case for species specializing on collembolan prey, and species that do not have a preference for moist habitats. The presence of collembolan specialists can be explained by the presence of collembolans, which are known to appear very early on in succession (Hågvar 2010). The negative response of moisture-loving species to fire can probably be explained by the drying effect that fire has on the heath.

Implications for management and conclusions

The different components of this thesis have shown that in general, burning is needed to maintain heathland vegetation, promote germination in a range of heathland species, and keep both plant and carabid diversity high. Paper I demonstrates that prescribed fire needs to be more frequent in Tasmania, in order to prevent species loss and overall extent of the heathland landscape. In Norwegian heathland, rotational burning is a necessity for carabid beetles, where fire improves species richness, turnover, and leads to the formation of distinct species assemblages that are associated with different phases of the *Calluna* life cycle. Finally, the results of Papers I-IV have shown that heathland species in particular respond favourably to fire or fire-related cues. These findings have implications for the management not only of these particular study sites, but also of coastal heathlands in Tasmania and north-western Europe in general.

Based on the results presented in Papers II-IV, burning should continue on Lygra and Lurekalven as it is currently done, to create a habitat mosaic of different burn ages, with a bias to the pioneer and building phases (i.e. ca. 0-14 years since fire). This burning regime could also likely be extended to other heathlands of a similar type. However, it is important to keep in mind that Paper III and IV focus on dry heath, and that species found within wet heath may not respond in the same way to burning. This is particularly important to point out keeping in mind that the carabids with wet moisture preference were the least likely to be found in recently burnt patches. In addition, not all heathlands will have had the same exposure to prescribed fire, and since coastal European heathlands are not naturally fire prone, this means that species inhabiting them may not be as well adapted to burning as those that have been managed by fire. This has already been shown for *Calluna* in Norwegian heathlands, where fire history determines the fire-cued germination response (Vandvik et al. 2014). Fire history is not the only factor that can determine fire response, however, as post-fire successional trends have also been shown to vary geographically (Velle and Vandvik 2014). Thus, geographical and climatological factors should also be taken into account when adopting a fire management regime.

Optimal fire regimes can be difficult to determine, due to various factors; frequency, intensity and timing, which need to be optimised. As north-west European heathland fires are largely prescribed, and there is a considerable amount of knowledge about fire histories, these fire regimes are not as hard to define as they are in Tasmania (New 2014). Here, heathland fires may be either natural or anthropogenic, and fire histories are not as well understood. What is known, however, is that both too short and too long fire intervals can be problematic for heathland communities (Kirkpatrick and Harris 1999; Keith et al. 2002; Enright et al. 2012). Nevertheless, there is evidence from Western Australia that anthropogenic fires prevent both local habitat and biodiversity loss, as well as create a higher diversity of successional stages than created by wildfire (Bird et al. 2005; Bliege Bird et al. 2008). Thus, historical fire regimes should be studied to develop appropriate fire intervals (Tucker and Cadotte 2013). In addition to the issue of optimal fire interval, it is also very important to determine the ideal intensity and the seasonality of prescribed fire (Gill 1999; New 2014). In Norway, heathlands are almost always burnt in winter to make "cool burns", that is, relatively low intensity fires, to avoid burning the soil. In contrast, it has been suggested that Australian heathlands would fare better under a fire regime that includes a mosaic of fire intensities (Gill 1999). This may be reflective of the fact that Australian heathlands are naturally fire prone, and have been exposed to a much wider range of fire intervals and intensities in the past.

Although fire appears to improve species richness and turnover, as well as maintain characteristic species compositions in general, it is important to keep in mind that not all species may be as tolerant of fire. Fire return times must therefore be considered carefully, not only with respect to species diversity, but also the successional dynamics of other taxa. For example, many groups of insects, such as Lepidoptera (e.g. Swengel 1996; Swengel et al. 2011) and Hemiptera (e.g. Morris 1975) have species that cope very poorly with fire, and the survival of small vertebrates after burning seems to depend largely on their shelter, diet and foraging patterns (Friend 1993). Furthermore, in this thesis, I have only investigated the fire response of plant species in the seed banks of both study systems. This excludes the possible responses of species that regenerate by resprouting which, at least in Australia, is a considerable proportion of heathland species. Another difficulty is that resprouting ability, like fire-cued germination, can differ in the same species in different populations (Nilsen et al. 2005; Kattge et al. 2011). Thus, although there is considerable evidence to show that fire is essential in the management of both Norwegian and Tasmanian coastal heathlands, its specific usage in terms of intensity, seasonality and fire return time should always be considered.

Future perspectives

There is a wide range of ways in which the findings from the different components of this thesis can be built upon. On the landscape level, future studies in Tasmania in particular should focus on the optimal fire regimes; fire intensity, interval and seasonality, needed to maintain heathlands. They should try to incorporate historical fire regimes in conjunction with ecological data. In both systems, the effect of patch size on different species groups should be also investigated, in order to account for the dispersal capacities of both plants and animals after burning.

More studies should also focus on the species level responses to fire. The results of Paper II suggest that a wide range of plants respond positively in their germination to fire cues, but similar, more detailed studies would aid the understanding of the distribution of fire-related cues among plants within heathland ecosystems. It would also be of great interest to investigate whether fire response patterns are similar in other populations of the same species, as there is some indication that fire-history and geographical location affects fire responses. The same is true for further study of carabid beetles, which should also include investigations of dispersal ability and the effects of patch size on their ability to survive and colonise heathland after prescribed burning. For example, it is possible that a particular species has a general preference for burnt heathland, but is not found in burnt patches due to its poor dispersal ability. In future studies, it would also be interesting to compare the effects of different heathland management regimes on carabid diversity and trait selection, to identify the relative importance of fire in comparison to or in combination with other management measures.

The effects of fire on other taxa should also be studied, to investigate to what extent other species typical of heathland landscapes depend upon or survive prescribed fire. It is likely that less mobile species will have different fire requirements, and even an extensive knowledge of plant and carabid trait responses will be limited in predicting the responses of other organisms.

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