Species trait selection along a prescribed fire chronosequence

TESSA BARGMANN,[1,2] EINAR HEEGAARD,[3] BJØRN ARILD HATTELAND,[1,4] JOSEPH DANIEL CHIPPERFIELD[1] and JOHN-ARVID GRYTNES[1]　[1]Department of Biology, University of Bergen, Bergen, Norway, [2]Department of Geography, University of Bergen, Bergen, Norway, [3]Forestry and Forest Resources, Norwegian Institute of Bioeconomy Research, Ås, Norway and [4]Division for Biotechnology and Plant Health, Norwegian Institute of Bioeconomy Research, Lofthus, Norway

Abstract. 1. Fire is a widespread management practice used in the maintenance of European heathland. Frequent prescribed burns in small patches have been shown to benefit carabid communities; however, how fire favours specific life-history traits is poorly understood.

2. In this study, we identify characteristic species of the successional stages within heathlands, and find the traits which are characteristic of species in burnt areas versus areas dominated by older heath stands.

3. We identify 10 species as indicator species for heathland in the pioneer stage (0–5 years old); *Amara lunicollis, Bembidion lampros, Calathus fuscipes, Carabus problematicus, Cicindela campestris, Nebria salina, Notiophilus aquaticus, Poecilus cupreus, P. lepidus* and *P. versicolor*. *Dyschirius globosus* is identified as an indicator for the building stage (6–14 years old), and *Carabus violaceus* as an indicator for the mature stage (15–25 years old).

4. Moisture preference and diet are identified as traits that determine species response to prescribed fire. Collembolan specialists and species with no moisture preference are shown to be most abundant in burnt patches, whereas generalist predators and species with a high moisture preference are less tolerant of fire.

5. Knowledge of species sorting along a prescribed fire gradient can provide valuable information for heathland conservation.

Key words. Carabidae, coastal heathland, community assembly via trait selection, conservation management, ground beetle, indicator value, prescribed burning, Succession.

Introduction

The use of fire has a long history as a management tool in European heathlands (Mallik & Gimingham, 1983; Kaland, 1986; Webb, 1998). Primarily it has been used to burn away older stands of heather, giving way to new, more nutritious vegetation for grazers. Fire also causes changes in floristic and faunistic compositions by temporarily reducing the occurrence of dominant species (Mallik & 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 (Vandvik *et al.*, 2005; Bargmann *et al.*, 2015). Due to its widespread usage and important role in determining plant and animal assemblages, the effects of prescribed burning are of considerable interest to heathland managers and scientists alike.

There is extensive literature that focuses on the response of heathland plants to prescribed burning (e.g. Clément & Touffet, 1981; Mallik & Gimingham, 1983; Måren & Vandvik, 2009; Velle & Vandvik, 2014), and a number of studies have focussed on insect responses

Correspondence: Tessa Bargmann, Department of Geography, University of Bergen, Postbox 7802, 5020 Bergen, Norway. E-mail: tessa.bargmann@uib.no

(e.g. Gardner & Usher, 1989; McFerran *et al.*, 1995; Bargmann *et al.*, 2015; Brunbjerg *et al.*, 2015). These studies primarily focus on species diversity and abundance, as well as the successional dynamics after burning. Nevertheless, to be able to aid predictions for how species traits are selected for by different environmental factors, there has been an increased interest in trait-based approaches, so that findings can be extended to areas outside the studied community (Lavorel & Garnier, 2002; Violle *et al.*, 2007). These approaches have, for example been used to identify species traits in a wide range of species, that are indicative of fragmentation (Driscoll & Weir, 2005), land use change (Vandewalle *et al.*, 2010), flooding (Lambeets *et al.*, 2008) and other types of anthropogenic disturbance (Carignan & Villard, 2002). Disturbance is an important determinant of life-history traits in disturbance prone environments (Southwood, 1977; Lytle, 2001; Ribera *et al.*, 2001; Lambeets *et al.*, 2008). Indicator species analyses and trait-based approaches can therefore have many practical applications in conservation, in the management of natural reserves (De Cáceres *et al.*, 2010), and in the monitoring of environmental disturbance (Carignan & Villard, 2002), by providing information about how species assemblages may change as a result of management or natural and anthropogenic perturbations.

Insects in particular have been considered good indicators of ecosystem integrity (Dufrêne & Legendre, 1997), because they tend to be more closely associated with abiotic factors such as soil characteristics and moisture levels (Usher, 1992; De Bruyn *et al.*, 2001) than with biotic factors (Schoener, 1986; Carignan & Villard, 2002). This study focuses on carabid beetles, which are often used as indicator species, in part due to their well-known taxonomy, habitat requirements and life-history characteristics (Lövei & Sunderland, 1996; Rainio & Niemelä, 2003; Koivula, 2011; Kotze *et al.*, 2011). Moreover, previous studies have shown that carabid beetle distributions are driven strongly by small-scale habitat and microclimate effects (Gillingham *et al.*, 2012). Although prescribed burns have been shown to benefit carabid communities in general (Gardner & Usher, 1989; Usher, 1992; Bargmann *et al.*, 2015; Brunbjerg *et al.*, 2015), it has been suggested that further research should focus on the indicator potential of both rare and common species and specialist groups (see Kotze *et al.*, 2011), as well as how successional stages favour specific life-history traits (Schirmel *et al.*, 2012). A number of studies have used carabids as model organisms to measure trait-environment interactions and trait sorting between habitats (e.g. Ribera *et al.*, 2001; Schirmel *et al.*, 2012, 2015; Duflot *et al.*, 2014; Pakeman & Stockan, 2014). They have demonstrated that carabid traits are linked to land use change (Ribera *et al.*, 2001), habitat disturbance and hydrology (Gerisch, 2011), as well as plant traits (Pakeman & Stockan, 2014). Nevertheless, while there are studies that have investigated carabid traits and their indicator value for heathlands in general (e.g. Ribera *et al.*, 2001; Schirmel *et al.*, 2012; Borchard *et al.*, 2014), they most often compare two or three study areas (i.e. different heath types) rather than investigate the effect of fire or successional stages within the same heath type.

As heathlands are of high conservation importance in Europe (Usher & Thompson, 1993; Lindgaard & Henriksen, 2011; Kaland & Kvamme, 2013), and fire is a common management measure used for their conservation, it is important to obtain more detailed knowledge about how prescribed burning selects for individual species and species traits. This knowledge can have many practical applications. For example it can be used to inform optimal fire intervals, and to be able to quantify and predict how species assemblages may change with fire regime. Knowledge of how species sorting of carabids occurs in each successional stage could therefore provide valuable information for heathland conservation. In this study, we ask whether there are carabid species that are characteristic of each successional stage across a 23-year fire chronosequence, and investigate whether there are patterns in occurrence of certain species traits along this fire gradient.

Methods

Study area

The study area is on the islands Lygra and Lurekalven (60°42′N and 5°5′E), about 40 km north of Bergen in western Norway (Fig. 1). The area has an oceanic climate with a mean June temperature of 12 °C, a mean January temperature of 2 °C and a mean annual precipitation of c. 1600 mm (www.met.no). Both islands have acidic, nutrient-poor soil, and are dominated by *Calluna* heath, mires and mixed grass heaths, with some smaller patches of forest (mainly *Betula pubescens* and *Pinus sylvestris*). Moist heath tends to occur on deep soils in poorly drained depressions or north-facing slopes, whereas dry heath occurs on shallow soils on ridges or south-facing slopes (Fremstad, 1997; Aarrestad & Vandvik, 2000). This heathland is a cultural landscape that has been managed by different traditional heathland farming methods such as grazing, burning and turf cutting. Without such a management regime, the area is expected to undergo secondary succession to forest, as is exemplified by neighbouring islands. Prescribed burning, and grazing by sheep were reintroduced to both islands in 1992. The grazing pressure on the islands of Lygra and Lurekalven is approximately one sheep per hectare (Velle, 2012), and is relatively equal on both islands. Grazing was constant over the study years. Burns are carried out in late winter when the ground is frozen to avoid burning the soil.

Data collection

In 2012, we set a total of 180 250 ml plastic pitfall traps in 60 groups of three near the centre of burn patches from
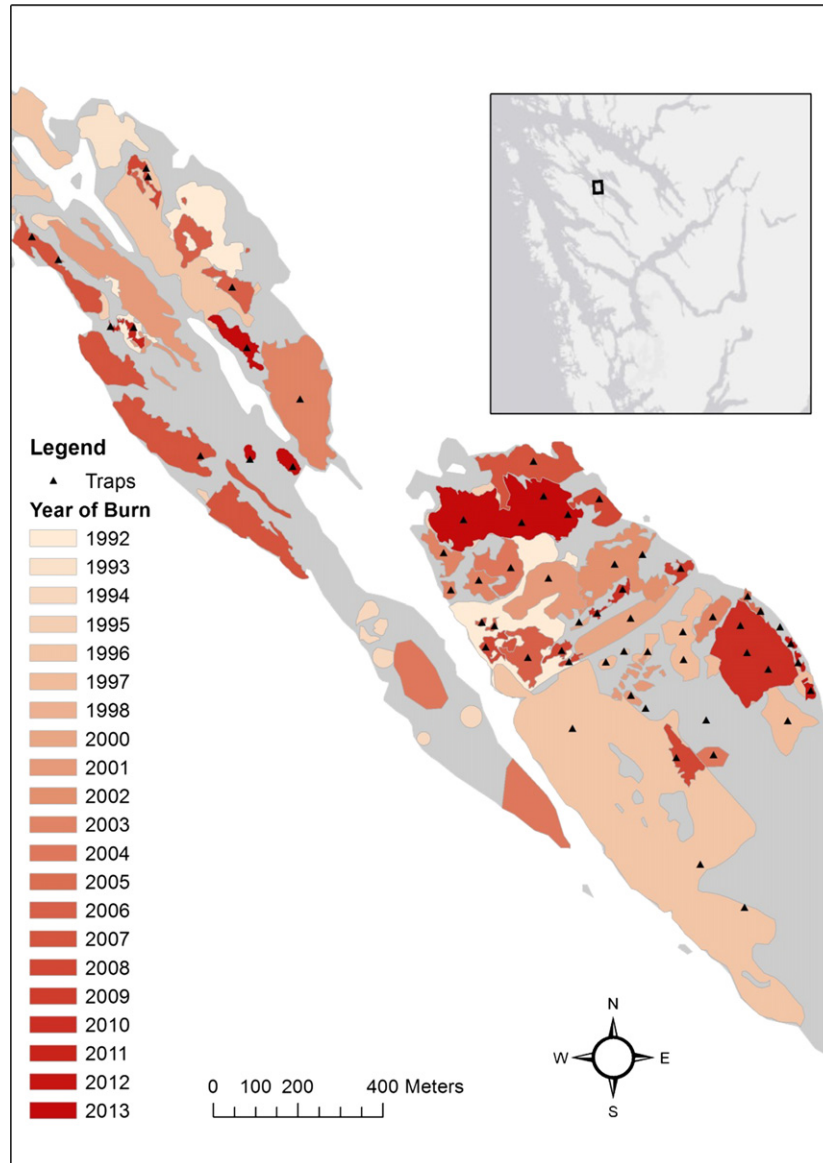
Fig. 1. Map of the study area in western Norway showing the location of the pitfall traps along with the burn mosaic resulting in prescribed burns between 1992 and 2013. Basemap sources: Esri, DeLorme, HERE, MapmyIndia.

1992 to 2012. The pitfall traps in each group were placed in a triangle formation about 30 cm apart from each other, and the samples from these were pooled to make one sample. Burn sizes were variable, with patch size ranging between 0.02 and 20 hectares. Due to prescribed burns in February 2013 the locations of eight groups of traps were burnt before the 2013 trapping season. The trap locations were chosen in advance by placing GPS points in the centre of the patches from different burn years. Traps were set as close to these points as possible in the field. All traps were set in dry heath, preferably on top of ridges, as this is where this heath type is usually found. The localities were chosen so that there was a good

spread over the stages of *Calluna* development. Stages were defined based on age ranges of *Calluna* outlined in Barclay-Estrup and Gimingham (1969) and were divided into the following phases; pioneer (0–5 years), building (6–14 years) and mature (15–23 years). In the pioneer and early building stage, plant species diversity is higher relative to the later stages, but decreases towards the end of the building- and the mature stage as the density of *Calluna* increases (Barclay-Estrup & Gimingham, 1969), and out-competes most herbs and grasses (Hobbs *et al.*, 1984). Due to burning done in 2013, and data being collected in 2 years, the number of localities per stage varied in 2012 and 2013; pioneer (22/25 localities), building (20/22

localities) and mature (18/13 localities). Data for the 2 years were pooled in the analyses.

Pitfall traps were filled about one-third with saturated salt solution and a drop of dishwashing detergent, and were covered by a metal lid to keep the trapping solution from becoming diluted by rain or disturbed by sheep. Traps were emptied every month between 10 April to 22 September in 2012 and 9 May to 19 September in 2013. The 1 month delay in trapping in 2013 was due to a cold spring, when the soil was still frozen in April. There was very limited sample loss due to sheep disturbance (9 out of 1620 traps over the two sample years). Samples were filtered and material was stored in 70% ethanol until identification.

Adult carabids were identified using both Lindroth (1985, 1986) and Luff and Turner (2007), while nomenclature follows Luff and Turner (2007). The wing morphology of all dimorphic species was noted. Other species trait information (see Table 1) was taken from a variety of sources; body size, dietary, life history and activity pattern traits were taken from Ribera *et al.* (1999) and Lindroth (1985, 1986). Where these sources disagreed, Lindroth was used because it describes the carabids of Fennoscandia. Missing trait data for *Notiophilus aquaticus, Poecilus lepidus* and *Trechus secalis* was taken from Ribera *et al.* (2001), Kegel (1990) and Wallin (1989) respectively. Moisture preferences are from Luff and Turner (2007). Information for the locomotion trait was taken from Forsythe (1983), where 'runners' are species whose leg measurements make them fast runners but weak horizontal pushers, and 'pushers' are stronger horizontal pushers and slower runners. 'Digger' refers to burrowing species.

Data selection

The data set contained a number of rare species; four species were recorded only once (*Agonum fuliginosum, Leistus terminatus, Nebria brevicollis* and *Olisthopus rotundatus*), five were recorded twice (*Bradycellus caucasicus, Notiophilus biguttatus, N. germinyii, Patrobus assimilis* and *Pterostichus vernalis*) and four were recorded between three and five times over the 2-year sampling period (*Amara communis, Bradycellus ruficollis, Carabus coriaceus* and *Cymindis vaporariorum*) (See Bargmann *et al.* (2015) for a full species list). As most analyses employed in community ecology can be biased in the presence of rare species, we retained only the 23 remaining species with more than five records (see Table 1).

Table 1. Species traits of the species included in the trait and indicator value analyses.

Species	wing	size	ows	lcd	day	breed	mpe	mpa	diet	loc	moist
Amara lunicollis	M	2	1	1	1	1	2	2	4	2	2
Bembidion lampros	D	1	1	1	1	1	2	1	1	2	3
Calathus fuscipes	B	3	2	2	3	3	2	2	2	2	2
Carabus nemoralis	B	4	1	1	3	1	2	2	2	2	3
Carabus problematicus	B	4	2	2	3	2	1	2	2	2	2
Carabus violaceus	B	4	2	1	3	3	2	2	2	2	2
Cicindela campestris	M	3	2	1	1	1	2	1	2	1	2
Cychrus caraboides	B	3	2	2	3	3	2	2	2	2	2
Dyschirius globosus	D	1	1	1	1	1	2	4	2	3	1
Harpalus latus	M	2	1	1	3	2	2	4	4	2	3
Loricera pilicornis	M	2	1	1	2	2	3	2	1	1	1
Nebria salina	M	3	2	1	3	3	1	2	2	1	2
Notiophilus aquaticus	D	2	1	1	1	1	2	2	1	1	1
Poecilus cupreus	M	3	1	1	1	1	3	1	3	2	3
Poecilus lepidus	B	3	2	2	1	2	3	2	2	2	3
Poecilus versicolor	M	3	1	1	1	2	3	1	2	2	1
Pterostichus diligens	B	2	2	1	3	1	3	1	2	2	1
Pterostichus melanarius	B	3	2	2	2	3	1	2	2	2	2
Pterostichus nigrita	M	3	2	1	3	1	2	2	2	2	1
Pterostichus niger	M	3	2	1	3	3	1	2	2	2	1
Pterostichus strenuus	M	2	1	1	3	1	2	1	2	2	2
Synuchus vivalis	M	2	2	1	3	3	2	2	4	2	2
Trechus secalis	B	1	2	1	3	3	2	2	1	2	1

Trait codes; wing (M = macropterous, B = brachypterous, D = dimorphic), size = body length in mm (1 = <4.5, 2 = 4.5–10, 3 = 10–20, 4 = 20+), ows = overwintering strategy (1 = adult, 2 = larva), lcd = life cycle (1 = 1 year, 2 = 2 years), day = activity period (1 = diurnal, 2 = both, 3 = nocturnal), breed = breeding season (1 = spring, 2 = summer, 3 = autumn), mpe = main period of emergence (1 = spring, 2 = summer, 3 = autumn), mpa = main period of activity (1 = spring, 2 = summer, 3 = autumn, 4 = whole year), diet (1 = collembola, 2 = generalist predator, 3 = mixed/omnivore, 4 = mostly plant matter), loc = locomotion (1 = runner, 2 = pusher, 3 = digger), moist = moisture preference (1 = wet, 2 = no preference, 3 = dry).

Statistical analysis

Characteristic species for each phase of *Calluna* regeneration after fire were determined by calculating Dufrêne-Legendre indicator values using the indval function in the labdsv package (and see Dufrêne & Legendre, 1997; Roberts, 2013) in R version 2.15.3 (R Core Team, 2013). These values are calculated from the relative abundance and the relative frequency of occurrence of a species within different groups, in this case, stages, of sites. The value is maximal when all individuals of a species occur in only one stage and in all sites of that stage. The analysis was run with 999 iterations to calculate probabilities.

In the past, species traits have been largely neglected in analyses of species diversity and environmental gradients, because statistical methods to relate the two were relatively limited (Ribera *et al.*, 2001). This is due to the so-called 'fourth-corner' problem (Legendre *et al.*, 1997), which refers to the difficulty in relating species traits to habitat characteristics, given species presence or abundance. There have, however, been various attempts at trying to solve this issue, such as with RLQ analysis (Dolédec *et al.*, 1996), the fourth-corner method (Legendre *et al.*, 1997) and community assembly via traits selection, or CATS (Shipley *et al.*, 2006), which is equivalent to generalised linear regression using species traits as predictor variables (Warton *et al.*, 2015).

To determine trait responses to prescribed fire, we extended the procedure in Warton *et al.* (2015) by applying a hierarchical Bayesian log-linear model that includes the random contributions associated with the organisation of the sampling regime (i.e. random effects associated with sampling year, locality and species). The response variable is the number of individuals of each species within a locality. A negative binomial error distribution was assumed as there proved to be an element of over-dispersion in the data. The need for random contributions (sampling year, locality and species) presents itself as the traps are each sampled over 2 years, with each locality containing several replicates of the response. Moreover, the expected number of individuals sampled varies from species to species and is related to the rarity/commonness of that species. In addition to these random contributions, a species-specific offset set to the logarithm of the relative proportion of each species was included. This was done to account for differences in the selection probabilities of the species, in accordance with CATS in Warton *et al.* (2015). Fixed effects in the full model were time since the last prescribed burn and all 11 trait variables, as well as their interactions with time since burn. Models were parameterised using Integrated nested Laplace approximation (INLA) (Rue *et al.*, 2009; Fong *et al.*, 2010) as implemented in the INLA package for R (Rue *et al.*, 2013). We used uninformative priors for the coefficients for each of the fixed effects as well as for the parameters controlling the random effects (the hyperparameters). To select the minimally sufficient model, we performed a forward selection of the fixed effects using the Deviance Information Criterion (DIC) as the model performance criterion. Like other information criteria, DIC is a measure of the model's ability to predict the observed data with a penalty applied for the model's complexity, and can be interpreted as the Bayesian equivalent of AIC (Spiegelhalter *et al.*, 2002). Although we have chosen forward selection, and aim for the simplest model, there may be alternative models with biologically sound relationships that are hidden by covariations with other factors. Nevertheless, we have chosen this method because we did not want to bias the selection procedure in favour of specific traits. The trait variables are categorical and we apply the default contrast in R (treatment contrast). Analyses were done in R version 2.15.3 (R Core Team, 2013).

Results

Over the two sampling years, 3384 adult carabids belonging to 36 species were identified. *Pterostichus niger* was the most common species found, followed by *Poecilus cupreus*, *Pterostichus melanarius*, *Nebria salina*, *Carabus problematicus* and *C. violaceus*.

The indicator species analysis identified ten species as characteristic of patches that had been burnt 0–5 years ago (i.e. the pioneer phase of *Calluna* development; Table 2). These species included the very commonly recorded *N. salina* (IndVal = 57.4) and *P. cupreus* (IndVal = 52.5), as well as more rarely trapped species such as *Amara lunicollis* (IndVal = 12.6) and *Bembidion lampros* (IndVal = 17.0). *Dyschirius globosus* (IndVal = 21.1) and

Table 2. Indicator values for species with values of more than 10 in each *Calluna* stage (pioneer = 0–5 years, building = 6–14 years and mature = 15–23 years).

Species	Pioneer	Building	Mature	*P*-value
Amara lunicollis	**12.6**	–	–	0.031
Bembidion lampros	**17.0**	–	–	0.004
Calathus fuscipes	**21.1**	–	–	0.007
Carabus problematicus	**36.6**	15.9	14.8	0.019
Cicindela campestris	**18.0**	–	–	0.015
Nebria salina	**57.4**	–	–	0.001
Notiophilus aquaticus	**16.2**	–	–	0.024
Poecilus cupreus	**52.5**	20.6	–	0.001
Poecilus lepidus	**16.7**	–	–	0.036
Poecilus versicolor	**24.3**	–	–	0.002
Dyschirius globosus	–	**21.1**	–	0.003
Carabus violaceus	–	26.0	**33.8**	0.026
Carabus nemoralis	–	17.2	11.7	–
Harpalus latus	17.8	–	–	–
Pterostichus melanarius	20.6	30.4	27.0	–
Pterostichus niger	16.9	40.4	38.5	–

The indicator value is 100 when all individuals of the species in question are observed in all the sites of only one group. Bold numbers indicate where the indicator value is significant for that stage. Dashes show where the indicator value <10 and the *P* > 0.05 respectively.

C. violaceus (IndVal = 33.8) came up as characteristic of the building (6–14 years since fire) and mature stages (15–23 years since fire) respectively.

The minimally sufficient model for trait response based on DIC scores was one that included the traits moisture preference and diet with their time since burning interactions. The time since the last management burn did not significantly affect the predicted species occurrence of collembolan specialists with a preference for wet habitats (i.e. the intercept traits; Fig. 2b). Beetles with no moisture preference significantly reduce their abundance along the time since burning gradient when compared to species with a high moisture preference (Fig. 2a), whereas species with a preference for dry habitats do not appear to differ from moisture-loving species along the gradient. According to the model, generalist predators have a lower abundance than collembolan specialists directly after burn (see Appendix 1). Nevertheless, as the time since burning increases, the abundance of generalist predators will catch up and pass the abundance of the collembolan specialists.

Discussion

Our study identified diet and moisture preference as significant traits determining carabid abundance after fire, where collembolan specialists and species with no moisture preference were predicted to be relatively more abundant in recently burnt heathland. On the other hand, generalist predators and moisture-loving species were predicted to increase in occurrence as time since the prescribed fire increased.

We found 12 of the 23 species in the indicator analysis to be indicative of one of the three different stages after fire. Ten carabid species were indicative of heath burnt

between zero and 5 years ago, and two species were associated with longer times since prescribed burning. Six of the ten species we have identified as characteristic for recently burnt heathland are heathland or open habitat specialists; *A. lunicollis, C. campestris, N. salina, N. aquaticus, P. lepidus* and *P. versicolor. Carabus problematicus* is also considered a heathland species in Fennoscandia (Lindroth, 1985), and both *A. lunicollis* and *C. problematicus* have been found to be common in heathlands in other Norwegian studies (Hatteland *et al.*, 2005, 2008). *Pterostichus nigrita* was the only heathland specialist in the analysis not to be identified as characteristic for recently burnt heath. This indicates that typical heathland species have a particular affinity for heath burnt less than 5 years ago, and suggests that heathland-specific carabid assemblages generally tolerate relatively short fire return cycles. We found very few species to be characteristic of building and mature heathland (6–14 and 15–24 years since fire respectively). This suggests that while recently burnt patches attract a particular assemblage of species that prefer these habitats over neighbouring patches which are in later stages of succession, most other species found in this landscape have no preferences for a particular stage. It is also important to note that the two species indicative of the building and mature phases, *D. globosus* and *C. violaceus*, respectively, are generalists both in terms of their diets and their habitat preferences.

In accordance with this study, *N. aquaticus* and *C. problematicus* have previously been identified as indicative of fire (Brunbjerg *et al.*, 2015). While McFerran *et al.* (1995) also trapped more individuals of *N. salina* in burnt areas, they found more individuals of *C. problematicus* in unburnt patches. Nevertheless, there are three subspecies of *C. problematicus* in Scandinavia (Lindroth, 1985), and it is possible that the subspecies found at our study site
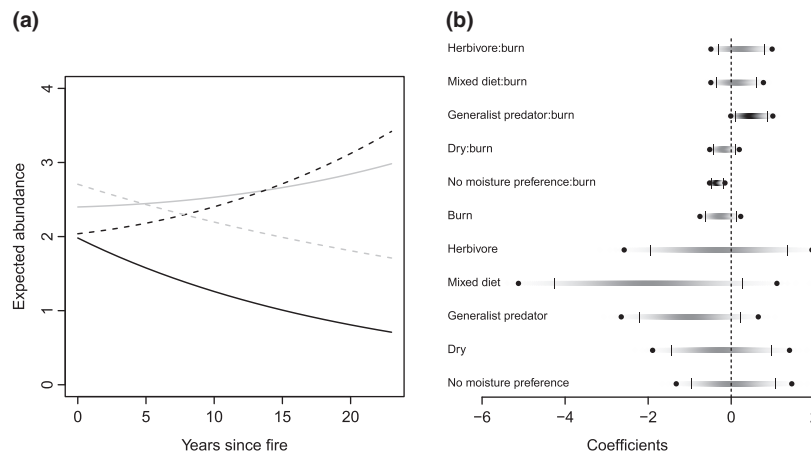

Fig. 2. Expected species abundances over the fire gradient (a). Solid lines show diet traits and dashed lines show moisture traits. Black lines are the traits in the intercept (collembolan specialist and wet moisture preference), and grey lines are the traits which are significantly different from the intercept traits (generalist predator and no moisture preference). Posterior densities of the effects in the minimally sufficient model (b). Dots and vertical lines show the 99% and 95% highest posterior density (HPD) respectively. The burn variable is centred and scaled to zero mean and unit variance. We use treatment contrast to define the model matrix.

has different habitat preferences. *Calathus fuscipes* is another species found to be indicative of fire in this study. But it has also been identified as an indicator of trampling (Brunbjerg *et al.*, 2015), which indicates that this species may prefer disturbed habitats in general. Furthermore, sheep generally prefer younger stages of heath because the vegetation there is more nutritious, making it more difficult to separate the potential effects of trampling and burning in this study area.

Two of the four collembolan specialists in our trait analysis, *B. lampros* and *N. aquaticus,* were identified as species preferring recently burnt patches. Although it did not come up as an indicator species, another collembolan specialist, *Loricera pilicornis*, was also only caught in the pioneer stage. Since collembolans are known to appear very early on in succession (Hågvar, 2010), this explains the preference of collembolan specialists to recently burnt heath over heathland in later successional stages. The remaining indicators of newly burnt heath were generalist predators, apart from *A. lunicollis*, which feeds mostly on plant matter. If fire selects for diet traits in the same way for all species, and since we have shown a general trend for generalist predators to increase in abundance with time since fire, prey availability is probably not a factor that determines the occurrence of these species in recently burnt heath. Apart from *P. versicolor*, these species all either have a preference for dry habitats or no moisture preference at all, which in this study is shown to be a predictor for high abundance in recently burnt patches. On the other hand, *D. globosus,* a generalist predator which has a preference for wet habitats, is characteristic of the building phase of *Calluna* (6–14 years after fire). This suggests that moisture preference may be a more important trait than diet in determining abundance in post-fire heathland, if the species in question is a generalist predator. Nevertheless, *C. violaceus* is a generalist predator with no moisture preference, but characteristic of the mature phase (15–23 years since fire), highlighting that this is not a pattern that is applicable for all species. Although this is a large species, it is possible that it is limited by its dispersal ability, as large, brachypterous species have been suggested to have a low power of dispersal in mosaic landscapes (Den Boer, 1970). This may be due to their preference for unmanaged, upland habitats (Blake *et al.*, 1996; Ribera *et al.*, 2001). Furthermore, species in the *Carabus* genus are known to have a preference for larger prey such as earthworms and gastropods (Evans & Forsyth, 1985; Hatteland, 2010), which may be more abundant in unburnt heathland.

Another important point to keep in mind with respect to the response of species with wet moisture preferences is that since this study was restricted to dry heath, the negative effects of burning on species living mostly in wet heath are likely to be more pronounced. On the other hand, wet heaths are much less flammable, and fires set in them are also less likely to burn away vegetation. This may mean that although species that prefer wet habitats are more likely to be negatively affected by fire in general,

their moisture preference may exclude them from particularly flammable habitats. Nevertheless, it would be of interest to investigate trait responses within wet heath as well.

None of the dispersal-related traits (locomotion, body size and wing morphology) came up as significant in our analysis, however, prey type has previously been strongly linked to morphology traits, where leg measurements were highly correlated with diet (Ribera *et al.*, 1999). It is also important to note that, in our study, the diet traits often co-occurred with particular body sizes. Specifically, collembolan specialists were small or very small, whereas generalist predators tended to be larger. Thus, although our minimally sufficient model did not include body size, it may well be an important trait to consider. No other traits co-occurred significantly with particular diet or moisture preferences. On the other hand, wing morphology, while it did not end up in our minimally sufficient model, was dependent on size, overwintering strategy, life cycle duration and leg morphology. Unsurprisingly, breeding season also coincided more often with particular overwintering strategies and the main period of emergence.

Wing morphology has been linked to disturbance, where brachypterous individuals are more frequent in undisturbed sites, and macropterous individuals are more abundant in fragmented and heterogeneous landscapes (De Vries *et al.*, 1996; Ribera *et al.*, 2001). Nevertheless, as dispersal power has been shown to be an important determinant of carabid presence in fragmented habitats (Wamser *et al.*, 2012), and because many of the species we found within recently burnt patches are considered poor dispersers (*A. lunicollis, N. aquaticus, P. lepidus, P. versicolor* (Den Boer, 1990)), the fact that these traits do not seem to affect species occurrence over the fire gradient indicates that our fire patches are small enough to be unproblematic for poorly dispersing species. Likewise, there were no patterns in life-history traits; overwintering strategies and activity periods were all more or less equally distributed between stages. In other words, in the given range of patch sizes, species habitat preferences, rather than any other life-history traits or morphology, determine species abundance. It is important to keep in mind, however, that larger patch sizes may select for species traits differently, and dispersal traits may become more important as individuals must travel farther to reach preferred habitats.

With pitfall trap data, it is important to keep in mind that the species caught represent activity density in addition to actual abundance, and that this means that more active species are overrepresented (Greenslade, 1964; Baars, 1979). Approximately one-third of the species trapped in this study occurred five times or less, and four of these are considered heathland specialists (*C. vaporariorum, B. caucasicus, B. ruficollis* and *O. rotundatus*). It is problematic that we are not able to determine the response to fire of species that are characteristic of heathlands, but our trait analysis may give some indication as

to how these species can be expected to respond. Based on our findings, there is probably no reason for concern in the case of *O. rotundatus*, as it is a good disperser (Den Boer, 1990), and a generalist predator with a preference for dry habitat. The two *Bradycellus* species prefer dry habits and preferentially consume plant matter, however, both species are rather small and brachypterous, and thus probably have limited dispersal abilities (Den Boer, 1990). These species may therefore be sensitive to fire if prescribed burns are too large. *Cymindis vaporariorum* is a generalist predator that prefers moist habitats. Thus, according to our findings, this is a species that may be sensitive to burning. In fact, the three times that *C. vaporariorum* was caught, it was trapped in patches where burning had occurred at least 5 years previously, giving some support for the fire sensitivity of this species.

This study has found that diet and moisture preference are the two carabid traits that most affect species sorting after prescribed burning, indicating that habitat preferences are more important than life history and morphology traits in determining carabid species presence, at least at the scale of this study. The burn patches in this study area were relatively small, as is typical for prescribed fire in Norwegian heathlands, but it is important to consider that larger burns may be more limiting to dispersal and other potentially fire-sensitive life-history traits. We find that diet is an important determinant for species abundance of collembolan specialists in recently burnt heathland, but that the occurrence of generalist predators is probably determined by moisture preference. In general, heathland specialists are indicative of recently burnt patches (0–5 years since fire). When determining fire intervals for the optimal management of characteristic heathland species, however, it should be kept in mind that not all species of carabids or even other taxa may be as tolerant of fire. There is a need to study less mobile species that may be more fire sensitive, or respond to disturbance at different spatial scales (Carignan & Villard, 2002; Cameron & Leather, 2012).

Acknowledgements

References

Aarrestad, P.A. & Vandvik, V. (2000). *Vegetasjonsendringer i vestnorsk kystlynghei: effekter av skjøtelsesformene brann og sauebeite ved rehabilitering av gammel lynghei på Lurekalven i Hordaland.* NINA, Trondheim, Norway.

Baars, M.A. (1979) Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia*, **41**, 25–46.

Barclay-Estrup, P. & Gimingham, C.H. (1969) The description and interpretation of cyclical processes in a heath community: I. Vegetational change in relation to the *Calluna* cycle. *Journal of Ecology*, **57**, 737–758.

Bargmann, T., Hatteland, B.A. & Grytnes, J.A. (2015) Effects of prescribed burning on carabid beetle diversity in coastal anthropogenic heathlands. *Biodiversity and Conservation*, **24**, 2565–2581.

Blake, S., Foster, G.N., Fisher, G.E. & Ligertwood, G.L. (1996) Effects of management practices on the carabid faunas of newly established wildflower meadows in southern Scotland. *Annales Zoologici Fennici*, **33**, 139–147.

Borchard, F., Buchholz, S., Helbing, F. & Fartmann, T. (2014) Carabid beetles and spiders as bioindicators for the evaluation of montane heathland restoration on former spruce forests. *Biological Conservation*, **178**, 185–192.

Brunbjerg, A.K., Jørgensen, G.P., Nielsen, K.M., Pedersen, M.L., Svenning, J.C. & Ejrnaes, R. (2015) Disturbance in dry coastal dunes in Denmark promotes diversity of plants and arthropods. *Biological Conservation*, **182**, 243–253.

Cameron, K.H. & Leather, S.R. (2012) How good are carabid beetles (Coleoptera, Carabidae) as indicators of invertebrate abundance and order richness? *Biodiversity and Conservation*, **21**, 763–779.

Carignan, V. & Villard, M.-A. (2002) Selecting indicator species to monitor ecological integrity: a review. *Environmental Monitoring and Assessment*, **78**, 45–61.

Clément, B. & Touffet, J. (1981) Vegetation dynamics in Brittany heathlands after fire. *Plant Ecology*, **46**, 157–166.

De Bruyn, L., Thys, S., Scheirs, J. & Verhagen, R. (2001) Effects of vegetation and soil on species diversity of soil dwelling Diptera in a heathland ecosystem. *Journal of Insect Conservation*, **5**, 87–97.

De Cáceres, M., Legendre, P. & Moretti, M. (2010) Improving indicator species analysis by combining groups of sites. *Oikos*, **119**, 1674–1684.

De Vries, H.H., Den Boer, P.J. & Van Dijk, T.S. (1996) Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference. *Oecologia*, **107**, 332–342.

Den Boer, P.J. (1970) On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). *Oecologia*, **4**, 1–28.

Den Boer, P.J. (1990) Density limits and survival of local populations in 64 carabid species with different powers of dispersal. *Journal of Evolutionary Biology*, **3**, 19–48.

Dolédec, S., Chessel, D., Ter Braak, C.J.F. & Champely, S. (1996) Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics*, **3**, 143–166.

Driscoll, D.A. & Weir, T. (2005) Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. *Conservation Biology*, **19**, 182–194.

Duflot, R., Georges, R., Ernoult, A., Aviron, S. & Burel, F. (2014) Landscape heterogeneity as an ecological filter of species traits. *Acta Oecologica*, **56**, 19–26.

Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.

Evans, M.E.G. & Forsyth, T.G. (1985) Feeding mechanisms and their variation in form of some adult ground-beetles (Coleoptera: Caraboidea). *Journal of Zoology*, **206**, 113–143.

Fong, Y., Rue, H. & Wakefield, J. (2010) Bayesian inference for generalized linear mixed models. *Biostatistics*, **11**, 397–412.

Forsythe, T.G. (1983) Locomotion in ground beetles (Coleoptera Carabidae): an interpretation of leg structure in functional terms. *Journal of Zoology*, **200**, 493–507.

Fremstad, E. (1997) *Vegetasjonstyper i Norge*. NINA, Trondheim, Norway.

Gardner, S.M. & Usher, M.B. (1989) Insect abundance on burned and cut upland *Calluna* heath. *The Entomologist*, **108**, 147–157.

Gerisch, M. (2011) Habitat disturbance and hydrological parameters determine the body size and reproductive strategy of alluvial ground beetles. *ZooKeys*, **100**, 353–370.

Gillingham, P.K., Palmer, S.C.F., Huntley, B., Kunin, W.E., Chipperfield, J.D. & Thomas, C.D. (2012) The relative importance of climate and habitat in determining the distributions of species at different spatial scales: a case study with ground beetles in Great Britain. *Ecography*, **35**, 831–838.

Greenslade, P.J.M. (1964) Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology*, **33**, 301–310.

Hågvar, S. (2010) Primary succession of springtails (Collembola) in a Norwegian glacier foreland. *Arctic, Antarctic, and Alpine Research*, **42**, 422–429.

Hatteland, B.A. (2010) *Predation by carabid beetles (Coleoptera, Carabidae) on the invasive Iberian slug Arion lusitanicus*. PhD thesis, University of Bergen, Bergen, Norway.

Hatteland, B.A., Hauge, E., Kirkendall, L.R. & Solhøy, T. (2005) *Diversity and habitat preferences of ground beetles (Coleoptera, Carabidae) in a coastal area of North Trøndelag, Central Norway*. Proceedings of the 11th European Carabidologist Meeting, DIAS Report No 114, pp. 125–135, Århus, Denmark.

Hatteland, B.A., Pedersen, T.N., Mortensen, F. & Solhøy, T. (2008) Species-area relations and island distribution of carabid beetles (Coleoptera, Carabidae) on small islands off the coast of western Norway. *Norwegian Journal of Entomology*, **55**, 73–80.

Hobbs, R.J., Mallik, A.U. & Gimingham, C.H. (1984) Studies on fire in Scottish heathland communities: III. Vital attributes of the species. *The Journal of Ecology*, **72**, 963–976.

Kaland, P.E. (1986) The origin and management of Norwegian coastal heaths as reflected by pollen analysis. *Anthropogenic Indicators in Pollen Analysis* (ed. by K.E. Behre), pp. 19–36. Balkema, Rotterdam/Boston, Netherlands/Massachusetts.

Kaland, P.E. & Kvamme, M. (2013) *Coastal Heathlands in Norway – Descriptions of 23 Reference Areas*. Miljødirektoratet, Trondheim, Norway.

Kegel, B. (1990) Diurnal activity of carabid beetles living on arable land. *The Role of Ground Beetles in Ecological and Environmental Studies* (ed. by N.E. Stork), pp. 65–76. Intercept, Andover, UK.

Koivula, M.J. (2011) Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. *ZooKeys*, **100**, 287–317.

Kotze, D.J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M.J., Lövei, G.L., Mossakowski, D., Noordijk, J., Paarmann, W., Pizzolotto, R., Saska, P., Schwerk, A., Serrano, J., Szyszko, J., Taboada, A., Turin, H., Venn, S., Vermeulen, R. & Zetto, T. (2011) Forty years of carabid beetle research in Europe–from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. *ZooKeys*, **100**, 55–148.

Lambeets, K., Vandegehuchte, M.L., Maelfait, J.P. & Bonte, D. (2008) Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. *Journal of Animal Ecology*, **77**, 1162–1174.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

Legendre, P., Galzin, R. & Harmelin-Vivien, M.L. (1997) Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology*, **78**, 547–562.

Lindgaard, A. & Henriksen, S. (2011) *Norsk rødliste for naturtyper 2011*. Artsdatabanken, Trondheim, Norway.

Lindroth, C.H. (1985) *The Carabidae (Coleoptera) of Fennoscandia and Denmark*. Fauna Entomologica Scandinavica E.J. Brill/Scandinavian Science Press Ltd., Copenhagen, Denmark.

Lindroth, C.H. (1986) *The Carabidae (Coleoptera) of Fennoscandia and Denmark*. Fauna Entomologica Scandinavica E.J. Brill/Scandinavian Science Press Ltd., Copenhagen, Denmark.

Lövei, G.L. & Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, **41**, 231–256.

Luff, M.L. & Turner, J. (2007) *The Carabidae (Ground Beetles) of Britain and Ireland*. Royal Entomological Society, St Albans, UK.

Lytle, D.A. (2001) Disturbance regimes and life-history evolution. *The American Naturalist*, **157**, 525–536.

Mallik, A.U. & Gimingham, C.H. (1983) Regeneration of heathland plants following burning. *Plant Ecology*, **53**, 45–58.

Måren, I.E. & Vandvik, V. (2009) Fire and regeneration: the role of seed banks in the dynamics of northern heathlands. *Journal of Vegetation Science*, **20**, 871–888.

McFerran, D.M., McAdam, J.H. & Montgomery, W.I. (1995) The impact of burning and grazing on heathland plants and invertebrates in County Antrim. *Biology and Environment: Proceedings of the Royal Irish Academy*, **95B**, 1–17.

Pakeman, R.J. & Stockan, J.A. (2014) Drivers of carabid functional diversity: abiotic environment, plant functional traits, or plant functional diversity? *Ecology*, **95**, 1213–1224.

R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rainio, J. & Niemelä, J. (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*, **12**, 487–506.

Ribera, I., Dolédec, S., Downie, I.S. & Foster, G.N. (2001) Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology*, **82**, 1112–1129.

Ribera, I., Foster, G.N., Downie, I.S., McCracken, D.I. & Abernethy, V.J. (1999) A comparative study of the morphology and life traits of Scottish ground beetles (Coleoptera, Carabidae). *Annales Zoologici Fennici*, **36**, 21–37.

Roberts, D.W. (2013) labdsv: Ordination and Multivariate Analysis for Ecology. R package version 1.6-1. <http://cran.r-project.org/> Accessed 7th April 2015.

Rue, H., Martino, S. & Chopin, N. (2009) Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the royal statistical society: Series b (statistical methodology)*, **71**, 319–392.

Rue, H., Martino, S., Lindgren, F., Simpson, D. & Riebler, A. (2013) INLA: Functions which allow to perform full Bayesian analysis of latent Gaussian models using Integrated Nested Laplace Approximation. R package version 0.0-1383402327.

Schirmel, J., Blindow, I. & Buchholz, S. (2012) Life-history trait and functional diversity patterns of ground beetles and spiders along a coastal heathland successional gradient. *Basic and Applied Ecology*, **13**, 606–614.

Schirmel, J., Mantilla-Contreras, J., Gauger, D. & Blindow, I. (2015) Carabid beetles as indicators for shrub encroachment in dry grasslands. *Ecological Indicators*, **49**, 76–82.

Schoener, T.W. (1986) Patterns in terrestrial vertebrate versus arthropod communities: do systematic differences in regularity exist? *Ecology* (ed. by J. Diamond and T.J. Case), pp. 556–586. Harper & Row, New York City, New York.

Shipley, B., Vile, D. & Garnier, É. (2006) From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science*, **314**, 812–814.

Southwood, T.R.E. (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, **46**, 336–365.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & Van Der Linde, A. (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **64**, 583–639.

Usher, M.B. (1992) Management and diversity of arthropods in *Calluna* heathland. *Biodiversity and Conservation*, **1**, 63–79.

Usher, M.B. & Thompson, D.B.A. (1993) Variation in the upland heathlands of Great Britain: conservation importance. *Biological Conservation*, **66**, 69–81.

Vandewalle, M., De Bello, F., Berg, M.P., Bolger, T., Doledec, S., Dubs, F., Feld, C.K., Harrington, R., Harrison, P.A. & Lavorel, S. (2010) Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation*, **19**, 2921–2947.

Vandvik, V., Heegaard, E., Måren, I.E. & Aarrestad, P.A. (2005) Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. *Journal of Applied Ecology*, **42**, 139–149.

Velle, L.G. (2012) *Fire as a Management Tool in Coastal Heathlands: A Regional Perspective*. PhD thesis, University of Bergen, Bergen, Norway.

Velle, L.G. & Vandvik, V. (2014) Succession after prescribed burning in coastal *Calluna* heathlands along a 340-km latitudinal gradient. *Journal of Vegetation Science*, **25**, 546–558.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional!. *Oikos*, **116**, 882–892.

Wallin, H. (1989) Habitat selection, reproduction and survival of two small carabid species on arable land: a comparison between *Trechus secalis* and *Bembidion lampros*. *Ecography*, **12**, 193–200.

Wamser, S., Diekoetter, T., Boldt, L., Wolters, V. & Dauber, J. (2012) Trait-specific effects of habitat isolation on carabid species richness and community composition in managed grasslands. *Insect Conservation and Diversity*, **5**, 9–18.

Warton, D.I., Shipley, B. & Hastie, T. (2015) CATS regression-a model-based approach to studying trait-based community assembly. *Methods in Ecology and Evolution*, **6**, 389–398.

Webb, N.R. (1998) The traditional management of European heathlands. *Journal of Applied Ecology*, **35**, 987–990.
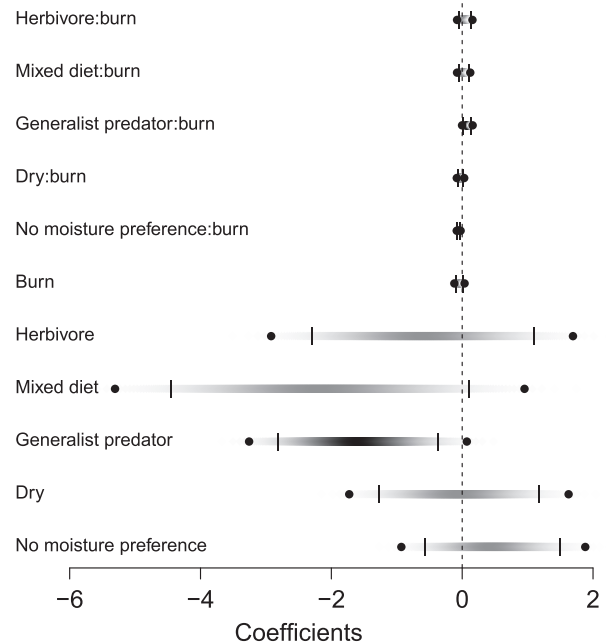
Appendix 1. Posterior densities of the effects in the minimally sufficient model, with unscaled burn. Dots and vertical lines show the 99% and 95% highest posterior density respectively.