ORIGINAL RESEARCH

Traditional prescribed burning of coastal heathland provides niches for xerophilous and sun-loving beetles

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Abstract

In Western Norway, farmers have traditionally used fire as a management tool in coastal heathlands to enhance the fodder quality for livestock. Rotational prescribed burning increases landscape heterogeneity by creating a mosaic of different regeneration stages of heather. Ground beetle (Coleoptera: Carabidae) responses to fire in traditionally managed coastal heathland have already been studied, but less is known about other beetle groups in this system. We compared the beetle activity between patches of mature and recently burnt heath, by looking at diversity indices, species composition and ecological preferences and traits. Contrary to previous studies, we did not find an increase in beta diversity after disturbance, but we found that prescribed burning offers micro-environmental conditions which enhanced the activity of sun-loving and xerophilous species. We also identified new indicator species for both mature and pioneer heath in five beetle families: Carabidae, Staphylinidae, Curculionidae, Leiodidae, and Scirtidae. Rotational prescribed burning was confirmed to be an efficient conservation tool for specialists without affecting the overall diversity of the site. We recommend the use of several taxa, ecological preferences and traits to assess the impact of prescribed burning and to monitor the condition of traditionally managed coastal heathlands.

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Introduction

Atlantic heathlands are the outcome of a long history of traditional land use (Gimingham 1975; Webb 1998) and belong to the now highly valued cultural landscapes of Europe (Diemont et al. 2013; Hernández-Morcillo et al. 2017; Vos and Meekes 1999). In Western Norway, coastal heathland vegetation appeared about 6000 years ago (Hjelle et al. 2018) and expanded through increased pastoral agriculture (Prøsch-Danielsen and Simonsen 2000) and the extensive use of fire (Kaland 1986). Today, Norwegian coastal heathlands are classified as endangered (Fremstad and Moen 2001; Hovstad et al. 2018) as only 10% of the original area remains (Hjeltnes 1997). At least half of the habitat has seen its ecological state degraded by 50% over the past 50 years, mainly due to land abandonment (Hovstad et al. 2018). Northern and temperate Atlantic wet heathlands are particularly dependent on active management to control succession and prevent tree growth (Halada et al. 2011), including livestock grazing, mowing and prescribed burning (Måren et al. 2018; Måren and Vandvik 2009; Neumann et al. 2021; Vandvik et al. 2005).

Fire has been shown as a key architect of ecosystems (Bond and Keeley 2005) to the same extent as grazing or flooding, and has driven the natural successional dynamics of several habitats such as savannahs (Bond 2019) or heathlands (Keeley 1986; Vandvik et al. 2014), even before human influence. Fire is also an effective tool for restoration (Aarrestad and Vandvik 2000; Hulme et al. 2002): in regularly burnt habitats, the plant community quickly renews itself from vegetative re-sprouting (Hobbs and Gimingham 1984a; Mallik and Gimingham 1985) and from the seedbank (Hobbs and Gimingham 1984b; Keeley et al. 2011; Måren and Vandvik 2009; Vandvik et al. 2014). The combination of low-intensity sheep or goat grazing with small-scale rotational burning on traditionally managed coastal heathland enhances landscape heterogeneity and the complexity of successional dynamics (Måren et al. 2018; Vandvik et al. 2005; Velle et al. 2014).

Postfire vegetation successional dynamics of European heathland vegetation have been well-documented (e.g., Letten et al. 2014; Mallik and Gimingham 1983; Prentice et al. 1987), especially in Western Norway (e.g., Måren et al. 2010; Velle et al. 2012; Velle and Vandvik 2014), but fewer studies have explored the recolonisation of burnt patches by other organisms, such as arthropods (see however Bargmann et al. 2015; Krause and Assmann 2016; Pryke and Samways 2012). Yet, arthropods in particular have great potential for monitoring changes in land management (Alvarado et al. 2019; Kelly et al. 2015), restoration programs (Borchard et al. 2014; Watts et al. 2008) or habitat recovery after disturbance (Gerisch et al. 2012; Moretti et al. 2006), complementing the use of vegetation surveys (Hacala et al. 2020). Ground-dwelling invertebrate assemblages are mainly driven by the structural diversity of the soil surface and of the standing vegetation (Brose 2003), so they will show high sensitivity to small-scale disturbances (Perry et al. 2018). Factors which are likely to influence recolonisation patterns can be fitted into three categories: fire characteristics, such as intensity, frequency and spatial extent (Buckingham et al. 2019; Moretti et al. 2006; Wikars and Schimmel 2001); environmental parameters, such as type and structure of the vegetation, type and thickness of litter layer, and soil moisture (Brose 2003; Gardner et al. 1997; Šustek 2004); and species traits such as mobility or diet (Bargmann et al. 2016; Buckingham et al. 2015; Driscoll et al. 2020).

The response of ground beetles (Coleoptera: Carabidae) to prescribed heathland burning in Western Norway has been investigated by Bargmann et al. (2015, 2016). Carabidae provide optimal candidates for bioindication: it is one of the most taxonomically well-known beetle families (Kotze et al. 2011; Rainio and Niemelä 2003) and the ecological features

and traits of the different species are well-documented (Lövei and Sunderland 1996). Carabid assemblages also show great diversity and specialisation according to habitat (Blake et al. 1994) and are sensitive to environmental disturbance (Cajaiba et al. 2018; Koivula et al. 2002). It would, however, be ill-advised to assume that carabids show an exhaustive picture of beetle (Coleoptera) assemblage patterns following prescribed burning when the correlation between the different families has not been clearly established (Koivula 2011; Lange et al. 2014; Mladenović et al. 2018). For example, Pryke and Samways (2012) found different responses to fire between Scarabaeidae and Carabidae in Mediterranean systems. Morphological, behavioural and ecological traits being key drivers of postburn beetle activity (Wikars and Schimmel 2001), families with a high proportion of specialists such as Staphylinidae (Lange et al. 2014) are relevant to include in fire disturbance research.

In this study, we investigated the effect of small-scale burning on the activity of the beetle assemblage of traditionally managed coastal heathland in Western Norway. Traditional management involves rotational burning to promote winter forage for the low-productivity Old Norwegian Sheep breed. The heath regeneration cycle was originally described by Barclay-Estrup and Gimingham (1969): the pioneer phase, generally up to 5 years after the fire, where fresh buds of *Calluna vulgaris* are resprouting and grasses and sedges dominate the living vegetation; the building phase, between 5 and 15 years after fire, where *Calluna* shrubs grow to their adult stage and become dominant over the other life forms; the mature phase, from 15 up to 25–30 years after the fire, where the assemblage dynamics stabilize; and finally the degenerative phase, from 30 years after burn onwards, where dying *Calluna* shrubs leave open gaps in the canopy and allow local regeneration of pioneer vegetation. In managed heathlands, moderate grazing pressure can prevent *Calluna* from entering a degenerative phase. As the pioneer phase is the most palatable for the sheep (Thorvaldsen et al. 2017), it is in the farmer's interest to ensure some heath in the pioneer phase is always available for the livestock. Thus the optimal heathland system for farming is be a mosaic of regeneration stages created by uninterrupted small-scale rotational burning over at least 20 years, as illustrated by the study site from Bargmann et al. (2015, 2016). We decided to focus on a heathland system which had been left unmanaged for several decades before the farmer started burning again in 2018 on small areas. At this early stage of restoration, the complexly intertwined mosaic has not yet become established and recently burnt patches represent isolated stands of pioneer vegetation within the mature heath matrix. Thus, we can question whether at this scale prescribed burns disturb the system enough to provide alternative environmental conditions for some beetle specialists.

We therefore decided to compare beetle activity on pioneer patches following recent burns with activity observed on size-equivalent patches of mature heath. We tested hypotheses related to diversity (H1), composition (H2) and distribution of selected ecological preferences and morphological traits (H3). H1: alpha diversity is expected to be lower in the short-term after the fire disturbance, due to the partial destruction of the aboveground layer and the disruption of habitat continuity. Pioneer vegetation is also less structurally diverse, thus offers fewer micro-habitats for recolonising beetles compared with mature heath (Murdoch et al. 1972). On the other hand, the regeneration dynamic of the vegetation layer is heavily influenced by stochastic drivers (Måren et al. 2018): we can therefore expect a higher variability between pioneer stands, which would increase the beta diversity of the collected assemblages compared to mature stands (Battisti et al. 2016). H2: we predict that fire will be the main driver of divergence in species distribution between patch types. We expect pioneer and mature stands to share a common species pool due to the spatial limitation of the disturbance, but also to be respectively characterised by exclusive or distinctly more active species, which we should be able to identify with an indicator

analysis. H3: the differences in species activity between pioneer and mature patches should be primarily driven by ecological preferences such as moisture and vegetation cover (Schirmel and Buchholz 2011). The shrub-dominated vegetation and thick bryophyte layer of mature stands should provide better conditions for shade-loving and hygrophilous species, while sun-loving and xerophilic species are expected to be more active on pioneer stands which offer very short vegetation cover, more bare ground and drier soil (Lamotte 1975). We also expect dispersal ability to influence species activity on the different patch types, but to a lesser extent as the burns are isolated and spatially limited (Bargmann et al. 2016). Pioneer heath patches should be recolonised more easily by full-winged and bigger species, while brachypterous and smaller species should be more frequent in mature patches. Finally, as most ecological traits should be phylogenetically conserved (Barton et al. 2011) and as mean size is likely to be heavily influenced by the large genus *Carabus*, we expect the family distribution to differ according to patch type.

Materials and methods

Study area

The study area is located on Hopøyna island, at 60° 38′ N and 4° 49′ E, in Øygarden municipality, Vestland county, Norway (Fig. 1). This area is part of the outer region of the

Fig. 1 Locations of the replicates on Hopøyna, Øygarden (Norway). Dark grey circles and triangles represent replicates burnt in 2018 and 2019 respectively. Light grey squares represent mature replicates. Figure created in QGIS (QGIS Association, http://www.qgis.org). Digital orthophotograph from the Norwegian Mapping Authority (Kartverket, CC BY 3.0). Norway outline from Wikimedia Commons (CC BY 3.0)
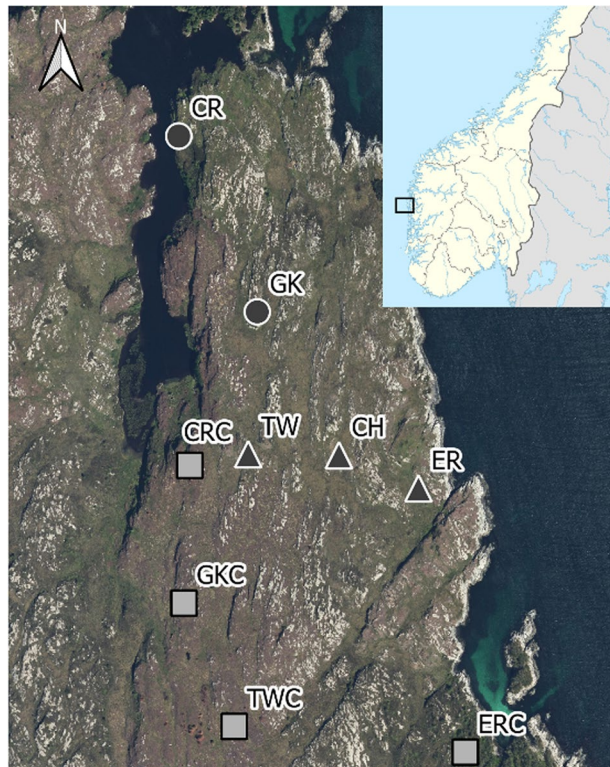
Nordhordland UNESCO Biosphere Reserve, which was designated in 2019. The climatic conditions are oceanic, with a mean January temperature of 3.8 °C, a mean June temperature of 13.1 °C and an average yearly precipitation of 1500 mm, with November the wettest month and June the driest (www.seklima.met.no). The eastern side of the island, where our study area is located, has consistent geological and localised climate conditions. The irregular topography of the island creates a pattern of two alternating edaphic conditions, both of which are nutrient-poor. Ridges with visible acidic bedrock make "islands" of drier shrub-dominated plant communities (*Calluna vulgaris*, *Erica tetralix*, *Juniperus communis*), separated by poorly drained depressions with *Molinia caerulea* and *Sphagnum* spp. dominated mires. The entire 115-hectares island is grazed at low density (0.4 sheep per ha) by the Old Norwegian sheep breed (*Ovis aries*, gammelnorsk sau). With such low density, the grazing pressure is expected to be spatially and temporally heterogeneous according to the daily and seasonal movements of the sheep. To provide better quality fodder for the animals, the farmer has been rejuvenating the heath by burning patches of vegetation (approx. 0.05–0.1 ha) in new locations every year since 2018, progressively moving southwards on the island. Due to the traditional burning technique, these burns are mostly restricted to the dry ridges: the farmer ignites the fire at the top of the hump, and the flames move down the slope before quicky dying on lower wet areas. Burnt patches are therefore rather narrow (up to 40 m across), mostly restricted to higher stands, and surrounded by an undisturbed matrix of mires mixed with remnants of mature heath.

Data collection

In 2019, we selected five replicates on the northern end of the island, in two areas burnt in early spring 2018 (CR and GK) and 2019 (TW, CH and ER), respectively (Fig. 1), and five replicates on the southern end of the island still covered with mature heathland. For the pioneer replicates, the sampling areas were defined as the burnt patches themselves, of approximately 500 m^2. For the mature replicates, we selected sampling areas of similar sizes that were suitable for prescribed burning and defined them according to the route of a hypothetical fire. In each replicate, a 40 m transect was set along the south-facing slope of a ridge to follow the actual (pioneer) or hypothetical (mature) pathway of the fire. Four octagonal sets of transparent plastic cups (Ø 6.5 cm, 250 mL) were placed along each transect, for a total of 32 pitfall traps per replicate. Cups were set approx. 1 m apart from each other (the shallow soil was a substantial constraint) and there was a minimum distance of 10 m between octagon centres (Fig. 2).

The pitfall traps were set for 2 weeks from mid-June to early July (early summer) and 2 more weeks from mid-July to early August (mid-summer). The soil was removed with a metal core of the same diameter as the plastic cups to avoid substantial soil disturbance. The immediate surrounding litter (about 5 cm radius around the traps) was cleared to prevent debris from falling into or across the cups. Traps were filled about one-third with a salt-saturated solution and a drop of neutral detergent, and in the burnt area they were covered by metal roofs (10×10 cm) elevated at approx. 4–5 cm above ground to protect them from the sheep and the rain. Roof presence should not affect capturability efficiency (Buchholz and Hannig 2009; Phillips and Cobb 2005). Traps were emptied every week and all adult beetles were collected and stored in 70% ethanol for identification. For most families, specimens were identified to the species level using the series Beetles of Britain and Ireland (Duff and Schmidt 2012a, b, 2020). For Carabidae, we favoured more local references from Fauna Entomologica Scandinavica (Lindroth 1985, 1986). Staphylinidae
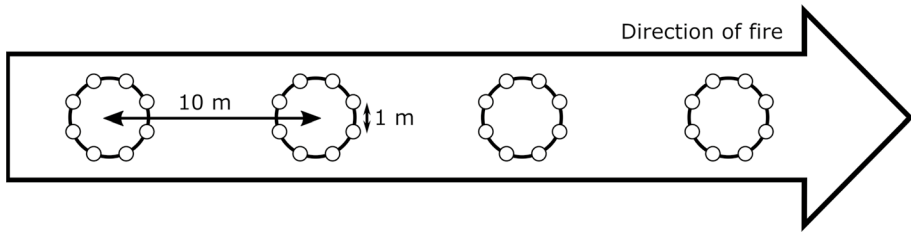
Fig. 2 Beetle sampling design at the replicate level. Small white circles are pitfall traps grouped by eight. Each 40 m transect, comprised of four octagons, was set along the fire direction

were identified using Palm (1961, 1963, 1966, 1968, 1970, 1972). Only specimens from the genus *Atheta* were not identified at the species level due to missing genital parts. All identifications were validated by a taxonomic expert.

Morphological traits and ecological preferences were collected from the same references as for the species identification. We selected moisture and vegetation cover preferences to characterise species' ecological affinities, and we selected body size and wing morphology as proxies of mobility. Moisture preferences were divided into five categories: Hygrophilous ++; Hygrophilous +; Eurytopic; Xerophilous +; Xerophilous ++, with "++" defining a limiting factor and "+" a preference. Vegetation cover preferences were divided into three categories: "Forest cover" for species associated with woody habitats and trees; "Open systems" for species indifferently colonising a variety of open or semi-open habitats; "Exposed ground" for species bound to the absence of vegetation. Wing characteristics were defined into four categories: "Full-winged", "Short-winged", "Wing-dimorphic" (both short-wing and full-wing morphologies found in the populations) and "Wingless".

Data analysis

Statistical and ordination analyses were based on species count data, spatially and temporally pooled at the replicate level (n = 10). All analyses were performed in R (v. 4.1.3) with R-Studio (v. 1.4.1717) (R Core Team 2022). The package vegan (v. 2.6-2) (Oksanen et al. 2022) was used to calculate diversity indexes and for the ordination analysis. The coefficients of association and indicator values were calculated with the package indicspecies (v. 1.7.12) (De Cáceres et al. 2022). All plots were produced with the package ggplot2 (v. 3.3.5) (Wickham et al. 2022).

We estimated beetle alpha diversity at patch level (H1) by calculating species richness (S), Shannon diversity index (H) and Simpson's evenness index ($E_{1/D}$). The evaluation of evenness is not consensual throughout the literature: one of the biggest biases of some indices, including the most popular Pielou's evenness, is the dependency on species richness. We therefore decided to follow Smith and Wilson (1996)'s recommendation and relied on Simpson's evenness $E_{1/D}$, calculated from the inverse of dominance D divided by species richness S. This index performs poorly on symmetry between abundant and rare species, but whether this criterion is desirable or not is at the discretion of the user. To our opinion, it is meaningful that an even distribution of common species within an assemblage has more weight than an even distribution of rare species. Because of the low replication level, differences in diversity

and abundance between the pioneer and the mature heaths were tested with the nonparametric Wilcoxon test. Beta diversity was estimated with the *betadisper* function in vegan, which compares the dispersion of groups of samples. We used Bray–Curtis dissimilarity, which showed robustness to beta diversity assessments (Schroeder and Jenkins 2018), and abundance data were log-transformed (log $(x + 1)$) to limit the influence of extreme values. The difference between group dispersions was tested with ANOVA.

We used Constrained Correspondence Analysis (CCA) to display how beetle species would fit along the fire gradient and to compare the composition of active assemblages at both ends (H2). CCA was chosen over Redundancy Analysis (RDA) because of the high axis length (over 2 units) showed in a preliminary Detrended Correspondence Analysis (DCA). We limited the influence of rare species which occurrences could be biased because of our clumped sampling design by log-transforming our abundance data (Ter Braak and Šmilauer 2015) and removing singletons (Legendre and Gallagher 2001). We tested two models, one with the constraining factor divided into two categories (mature and pioneer heath) and one with three categories (unburnt, 2-years postburn, 1-year postburn), and kept the one which fitted the data better. Significances of the two main constrained axes were tested with an ANOVA permutation test (function *anova.cca* on vegan). The phi association and IndVal indicator analyses were run with the *multipatt* function of the indicspecies package on the raw abundance data (De Cáceres 2022). Phi's coefficient of correlation (Sokal and Rohlf 2010), which was originally developed for phytosociological surveys, aims to measure the affinity of species to different vegetation types or groups. This coefficient compares observed against expected occurrences. It is independent from the size of the dataset and can also provide negative correlation values (Chytrý et al. 2002). On the other hand, the IndVal index (Dufrêne and Legendre 1997), which has been widely used to predict species bio-indication potential, evaluates how similar is the target group to the sites where the species is collected (De Cáceres and Legendre 2009). It is made of two components: the specificity (A), which is the probability that a site belongs to a target group based on the presence of the indicator species, and the fidelity (B), which is the probability to find the indicator species in sites belonging to the target group. IndVal is less context-dependent than association coefficients as it does not consider species absence in other groups as a strengthening factor of indication. It should be noted that both phi and IndVal calculate indicator values independently for each species: any individual species coefficient does not affect the values for others. The significances of association and indication were tested with permutations.

We tested the mean difference of relative proportions of ecological traits in species active on recent burns compared with assemblages on mature patches with Fisher t-tests (H3). We calculated community weighted means (CWMs) for body size so that the trait repartition was representative of the assemblage structure and was not influenced by rare species. The genus *Atheta* (Staphylinidae) was excluded from the trait analysis as most individuals could not be identified at the species level.

Results

Over the whole sampling period, we collected 1580 individuals of 68 species from 13 different families. The main families recorded were Carabidae (1039 individuals), Staphylinidae (308), Elateridae (86) and Curculionidae (69). Of the red-listed species, we found one specimen each of *Enalodroma hepatica* (NT) and *Cymindis vaporariorum* (EN) (Artsdatabanken 2021) in mature heath.

Alpha and beta diversity (H1)

On average, more species were recorded on mature heath replicates (S = 31.8; H = 2.91) compared with recently burnt patches (S = 23; H = 2.56) (Table 1). We observed however no significant difference for evenness and beta-diversity.

Assemblage composition and indicator species (H2)

The CCA was performed on 1562 specimens belonging to 44 species. The first axis, which explains 25% of variance, is driven by fire ($\chi^2 = 0.36$; $F_{1,7} = 2.98$; p-value = 0.001) (Fig. 3). The second constrained axis separates the replicates according to the year of the burns and explains 17% of the variance ($\chi^2 = 0.25$; $F_{1,7} = 2.03$; p-value 0.021). The mature heath replicates are grouped on the right side, with a pool of 14 species dominated by *Micrelus ericae* (total abundance n = 60, recorded on 5 out of 5 replicates), *Drusilla canaliculata* (n = 73, 5/5) and *Dalopius marginatus* (n = 61, 5/5) (Fig. 4). *Carabus nemoralis* (n = 24, 5/5), *Contacyphon hilaris* (n = 13, 5/5) and *Calathus micropterus* (n = 4, 2/5) were found exclusively on mature stands (Fig. 4). The three patches burned in 2019 (ER, CH, TW) are grouped in the bottom-left corner of the ordination. They were characterized by exclusive occurrences of *Geostiba circellaris* (n = 7, recorded on 3 out of 3 replicates) and *Bembidion lampros* (n = 8, 2/3) and almost exclusive occurrence of *Dyschirius globosus* (n = 32, 3/3) and *Cicindela campestris* (n = 16, 2/3). For the patches burnt in 2018 (GK, CR), the only exclusive species was *Leiodes obesa* (n = 3, recorded on 2 out of 2 replicates). The other noticeable feature was a higher activity of *Dalopius marginatus* (n = 17, 2/2), also common on mature patches (n = 61, recorded on 5 out of 5 replicates), compared with 2019

Table 1 Comparison of abundance, species richness S, Shannon Index H, Evenness $E_{1/D}$ and beta-diversity between active beetle assemblages of pioneer (P) and mature (M) heath patches

Indexes	Pioneer	Mature	Direction	Test results	p-value	95% conf. interval
Abundance	135.6	180.4	P < M	$W_4 = 8$	0.17	[− 102; 18]
Species richness S	23	31.8	P < M*	$W_4 = 0$	0.011	[− 13; − 4]
Shannon H	2.56	2.91	P < M**	$W_4 = 0$	0.0079	[− 0.63; − 0.04]
Evenness $E_{1/D}$	0.40	0.43	P ≈ M	$W_4 = 10$	0.69	[− 0.22; 0.16]
Distance to group median	0.293	0.213	P > M	$F_{1,8} = 3.00$ Sum sq = 0.016 Mean sq = 0016	0.12	–

Values represent averages between replicates. 95% confidence intervals of abundance and species richness S are estimations of lower coverage due to low sample size. Significance: NS for non-significant; * for p-value < 0.05; ** for p-value < 0.01
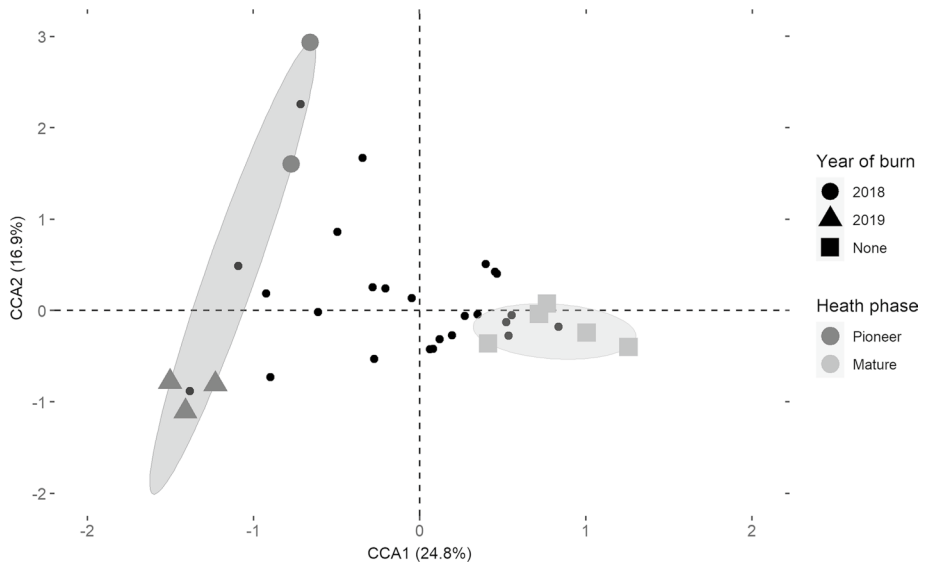
Fig. 3 Constrained ordination (CCA) on beetle species activity across replicates, according to the year of burn (3 categories: no burn, 1 year after burn, 2 years after burn). Displayed axes are the two first constrained dimensions, which explain 25% and 17% of the variance, respectively

burns (n = 1). Some species were more active on pioneer patches compared with mature ones (Fig. 4), as for instance *Poecilus versicolor* (n = 112, 5/5 in pioneer; n = 7, 4/5 in mature) and *Pterostichus strenuus* (n = 118, 5/5 in pioneer; n = 23, 4/5 in mature). Finally, some species were common indifferently of the heath phase, such as *Staphylinus erythropterus* (n = 28, 4/5 in pioneer; n = 30, 5/5 in mature), *Notiophilus aquaticus* (n = 86, 5/5 in pioneer; n = 50, 5/5 in mature) and *Nebria salina* (n = 30, 5/5 in pioneer; n = 20, 4/5 in mature).

Overall, the IndVal analysis featured fewer species than the phi correlation analysis, and all species with significant IndVal values also had significant phi values (p < 0.05), except *Agathidium atrum* and *Cychrus caraboides* (Table 2). *Poecilus versicolor* (IndVal = 0.97; phi = 0.669) and *Dyschirius globosus* (IndVal = 0.894; phi = 0.531) were identified as potential indicator species of pioneer heath patches. *Pterostichus strenuus* was more strongly correlated with recent burns (phi = 0.651) compared with *Dyschirius globosus*, but this result was not emphasized by the IndVal analysis. Eight species showed positive correlation with mature patches, and among them *Carabus nemoralis* (IndVal = 1; phi = 0.892), *Contacyphon hilaris* (IndVal = 1; phi = 0.805), *Micrelus ericae* (Indval = 0.992; phi = 0.795) and *Drusilla canaliculata* (IndVal = 0.949; phi = 0.592) also had significant IndVal values. Despite strong phi values, *Carabus granulatus* (phi = 0.84), *Pterostichus niger* (phi = 0.824), *Ischnosoma splendidum* (phi = 0.739) and *Carabus violaceus* (phi = 0.699) were not highlighted by the IndVal analysis. On the other hand, *Agathidium atrum* (IndVal = 0.92; phi = 0.635) and *Cychrus caraboides* (IndVal = 0.918; phi = 0.614) were indicative of mature patches according to IndVal results, but their phi correlation coefficients were only marginally significant. Specificity was the most variable component of the IndVal indicator, while fidelity was maximum for all species except *Dyschirius globosus*. This means that most indicator species were found across all replicates of their corresponding group, but only three of them were exclusive, namely *Dyschirius globosus*
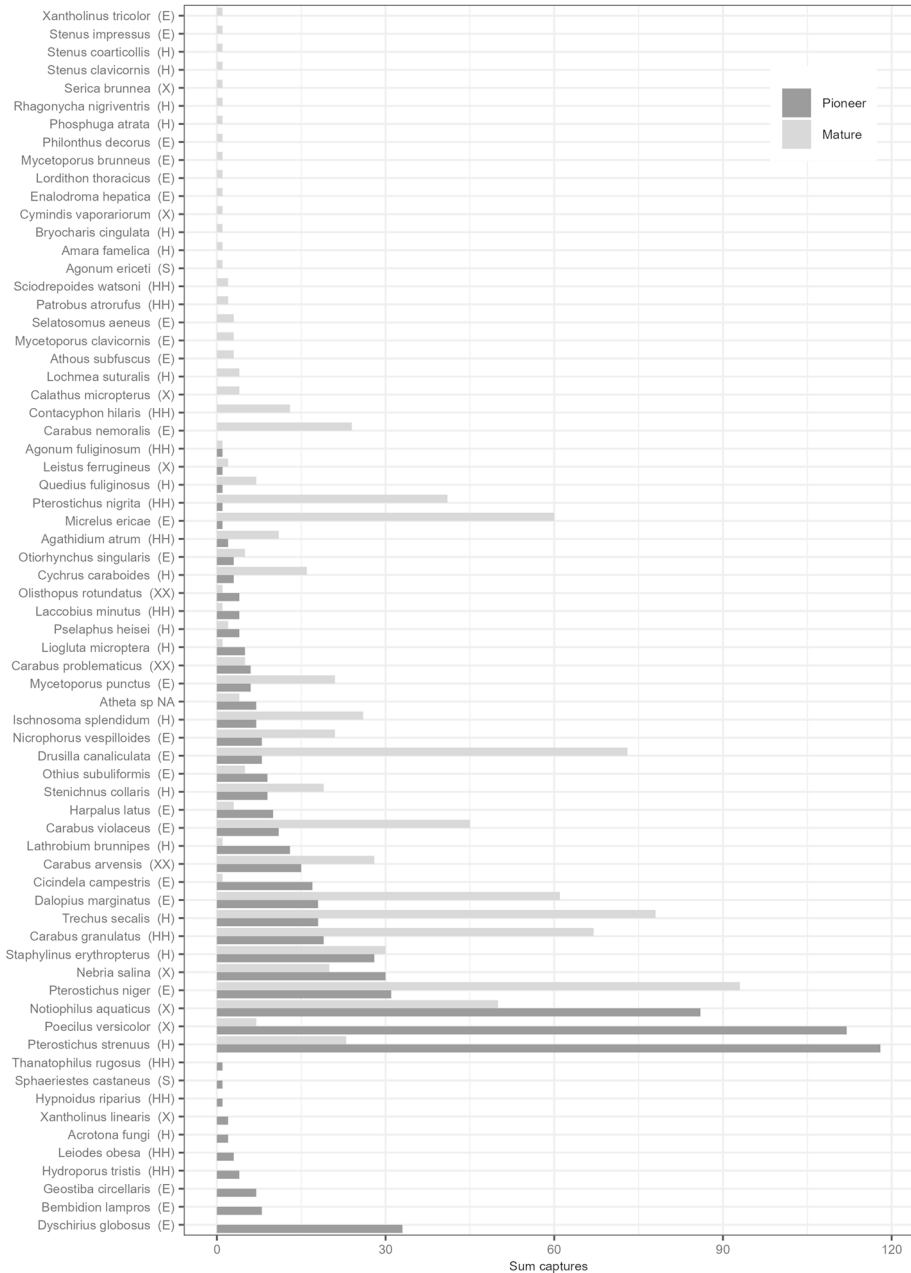
Fig. 4 Total abundances of beetle species collected in pioneer (dark grey) and mature (light grey) heath, sorted after occurrence in only mature heath (top), both mature and pioneer heath (middle) and only pioneer heath (bottom). Capital letters in brackets are for moisture preference: "HH" for strict hygrophilous, "H" for tolerant hygrophilous, "E" for eurytopic, "X" for tolerant xerophilous, "XX" for strict xerophilous, "S" for stenotopic. As Atheta specimens were only identified to genus level, they were not attributed any moisture trait

Table 2 Correlation indices from Pearson's phi coefficient of association and indicator values from IndVal on beetle species for the pioneer and mature heath groups

Species	Phi value	IndVal value	IndVal A	IndVal B
Group pioneer				
Poecilus versicolor	0.669**	0.97*	0.9412	1
Pterostichus strenuus	0.651*	–	–	–
Dyschirius globosus	0.531	0.894*	1	0.8
Group mature				
Carabus nemoralis	0.892**	1*	1	1
Carabus granulatus	0.84**	–	–	–
Pterostichus niger	0.824*	–	–	–
Contacyphon hilaris	0.805**	1*	1	1
Micrelus ericae	0.795**	0.992*	0.9836	1
Ischnosoma splendidum	0.739**	–	–	–
Carabus violaceus	0.699**	–	–	–
Agathidium atrum	0.635	0.92*	0.8462	1
Cychrus caraboides	0.614	0.918*	0.8421	1
Drusilla canaliculata	0.592*	0.949*	0.9012	1
Dalopius marginatus	0.55	–	–	–

Components A and B from IndVal represent specificity (probability that a site belongs to a group based on the presence of the indicator species) and fidelity (probability to find the indicator species in sites belonging to the group) respectively. Significance: all values shown with p-value < 0.1; * for p-value < 0.05; ** for p-value < 0.01

for pioneer patches and *Carabus nemoralis* and *Contacyphon hilaris* for mature patches respectively.

Ecological preferences and dispersal traits (H3)

Fisher t-test results for ecological preferences and dispersal traits are summarised in Table 3. Strict hygrophilous species, such as *Pterostichus nigrita*, *Agathidium atrum* and *Contacyphon hilaris* (Fig. 4), were more active on mature heath patches ($15.6 \pm 4.9\%$ of captures) compared with pioneer patches ($5.7 \pm 2.7\%$ of captures) (Fig. 5A). Almost half of the specimens collected on mature stands were eurytopic ($46.9 \pm 10\%$ of captures), while they comprised only one quarter ($24.4 \pm 6.0\%$) of the activity on pioneer stands. Surprisingly, tolerant hygrophilous species represented a higher proportion of captures on pioneer patches ($32.3 \pm 9.7\%$) compared with mature patches ($23.4 \pm 6.8\%$), but the difference was not significant. Tolerant xerophilous species, but not strict xerophilous species, were more active on pioneer patches ($34.1 \pm 9.7\%$ of captures) compared with mature patches ($9.8 \pm 4.7\%$ of captures). The difference was particularly driven by *Poecilus versicolor*, which was recorded more than 100 times across all pioneer replicates against less than 10 times in mature replicates (Fig. 4). Pioneer stands were also characterised by a higher activity of species associated with exposed ground ($22.4 \pm 15\%$), such as *Bembidion lampros, Dyschirius globosus, Cicindela campestris, Olisthopus rotundatus* and *Poecilus versicolor*, while these were almost absent from mature stands (Fig. 5B). Woodland beetles were indifferent to patch type, while a higher
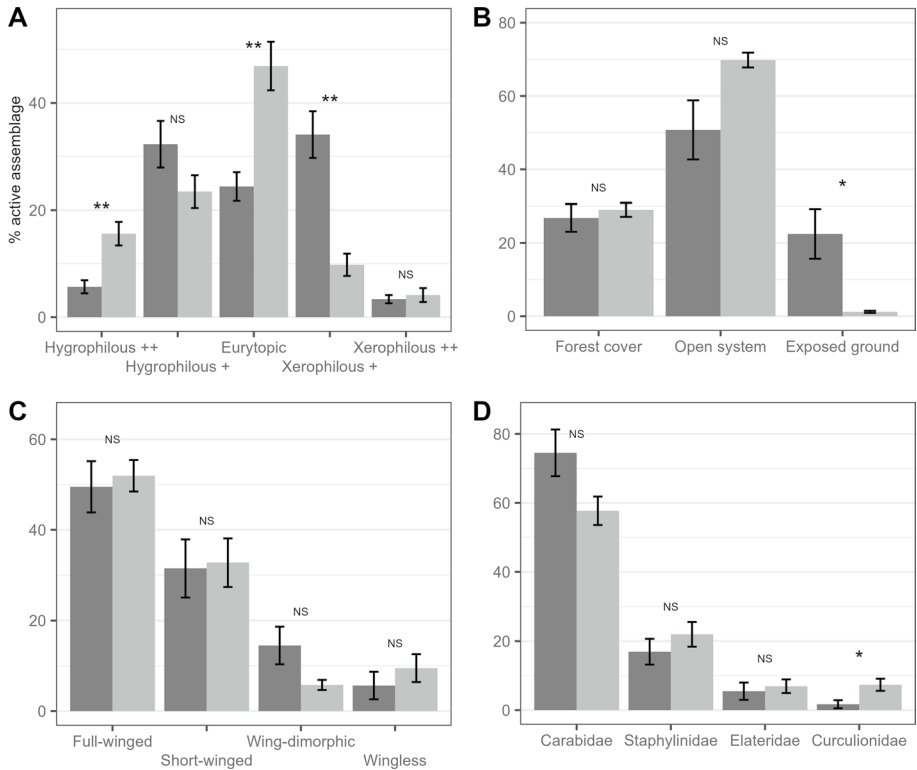
Fig. 5 Distribution of beetle captures between pioneer and mature patches according to moisture preferences (**A**), vegetation cover preferences (**B**), wing morphology (**C**), and main family (**D**). Average proportions with standard error SE are shown in dark grey for pioneer patches and light grey for mature patches. Significance: NS for p-value > 0.05; * for p-value < 0.05; ** for p-value < 0.01

proportion of species associated with open habitats was collected on mature patches (69.8 ± 4.5%) compared with pioneer patches (50.8 ± 2.7%), even if the difference was only marginally significant (Table 3).

Regarding mobility traits, species collected on mature stands were on average larger (CWL = 10.7 ± 1.0 cm) than species collected on pioneer stands (CWL = 8.9 ± 1.1 cm) (Table 3). We could not detect any significant difference related to wing morphology, but we could observe a higher rate of wing-dimorphic species in pioneer patches (14.5 ± 9.3%) compared with mature patches (5.8 ± 2.5%) (Fig. 5C). The distribution between full-winged and short-winged morphology was on the other hand consistent across the study site: for both patch types, half of the active assemblages were made of full-winged species and one-third of short-winged species.

Collected assemblages had similar community structure regardless of patch type, with a clear dominance of Carabidae over the other families (Fig. 5D). Carabids represented a higher proportion of captures in pioneer stands (74.5 ± 15.1%) compared with mature stands (57.7 ± 9.2%), but the difference was only marginally significant (Table 3). Staphylinidae and Elateridae did not show any clear pattern, but we found more Curculionidae in mature patches (7.4 ± 3.9%) than in pioneer patches (1.7 ± 1.7%). This difference seemed to be driven by the activity of *Micrelus ericae* in older heath patches (Fig. 4).

Table 3 Summary of Fisher t-tests on beetle ecological preference and trait distributions between pioneer (P) and mature (M) heath patches according to moisture preferences, vegetation cover preferences, community weighted length, wing morphology and main family

	Pioneer average ± sd	Mature average ± sd	Direction	Fisher t-test result t	Degree of freedom df	p-value	95% conf. interval
Moisture (%)							
Hygrophilous ++	5.7 ± 2.7	15.6 ± 4.9	P < M**	− 3.93	6.26	0.0071	[− 0.16; − 0.04]
Hygrophilous +	32.3 ± 9.7	23.4 ± 6.8	P > M	1.67	7.15	0.14	[− 0.04; 0.21]
Eurytopic	24.4 ± 6.0	46.9 ± 10.2	P < M**	− 4.27	6.47	0.0044	[− 0.35; − 0.1]
Xerophilous +	34.1 ± 9.7	9.8 ± 4.7	P > M**	5.03	5.73	0.0027	[0.12; 0.36]
Xerophilous ++	3.4 ± 1.7	4.1 ± 2.9	P ≈ M	− 0.51	6.49	0.63	[− 0.04; 0.03]
Vegetation cover (%)							
Forest cover	26.8 ± 8.4	29 ± 4.2	P ≈ M	− 0.52	5.9	0.62	[− 0.13; 0.08]
Open system	50.8 ± 18.0	69.8 ± 4.5	P < M	− 2.29	4.5	0.076	[− 0.; 0.12]
Exposed ground	22.4 ± 15.1	1.2 ± 0.7	P > M*	3.14	4.01	0.035	[0.02; 0.4]
Size (mm)							
Com. weighted length	8.9 ± 1.1	10.7 ± 1.0	P < M*	− 2.68	7.88	0.028	[− 3.35; − 0.25]
Wing morphology (%)							
Full-winged	49.5 ± 12.7	51.9 ± 7.8	P ≈ M	− 0.37	6.64	0.72	[− 0.18; 0.13]
Wing-dimorphic	14.5 ± 9.3	5.8 ± 2.5	P > M	2.02	4.57	0.1	[− 0.03; 0.2]
Short-winged	31.5 ± 14.3	32.8 ± 11.9	P ≈ M	− 0.15	7.75	0.88	[− 0.21; 0.18]
Wingless	5.6 ± 6.1	9.5 ± 6.9	P ≈ M	− 0.89	6.88	0.4	[− 0.14; 0.06]
Main families (%)							
Carabidae	74.5 ± 15.1	57.7 ± 9.2	P > M	2.12	6.61	0.074	[− 0.02; 0.36]
Staphylinidae	16.9 ± 8.4	22.0 ± 8.0	P ≈ M	− 0.97	7.98	0.36	[− 0.17; 0.07]
Elateridae	5.5 ± 4.3	6.9 ± 4.4	P ≈ M	− 0.45	4.41	0.67	[− 0.1; 0.07]
Curculionidae	1.7 ± 1.7	7.4 ± 3.9	P < M*	− 2.67	4.65	0.048	[− 0.11; 0]

Discussion

One to 2 years after fire, small-scale burning locally reduced alpha diversity without significantly increasing beta diversity between patches (H1). Fire was the main driver of divergence in species composition between pioneer and mature stands, for which we could identify new indicator species (H2). Beetle activity was driven by moisture and the absence of vegetation cover but was not affected by species dispersal ability (H3).

Beetle activity partially driven by ecological preferences

Beetle responses to small-scale burning followed ecological preferences according to moisture gradients and vegetation structure (Moretti et al. 2010; Schirmel and Buchholz 2011; Šustek 2004): xerophilous and sun-loving species were more active if not exclusive to pioneer patches, while strict hygrophilous species were more frequent on mature patches. It should be underlined that it is difficult to distinguish purely pyrophilous species, which are fire-dependent, from species which are only favoured by the environmental conditions following the burns (Wikars and Schimmel 2001). As none of the species we collected being defined as fire-loving in the literature, we hereafter consider species preferentially active on burnt patches as fire-favoured.

These trends were mostly reflected in our correlation and indication analyses: for example, xerophilous *Poecilus versicolor* and sun-loving *Dyschirius globosus* were indicative of pioneer stands, while strict hygrophilous *Contacyphon hilaris* and *Carabus granulatus* were associated with mature stands. However, three out of eight species which correlated with mature patches were associated with forest cover (*Carabus violaceus*, *Agathidium atrum*, *Pterostichus niger*), while the frequency of this trait was surprisingly even across patch types. The paradox is mostly due to *Pterostichus strenuus*: despite being classified as shade-loving, it was five times as abundant in recent burns compared with mature stands. For ecological preference characterisation of Carabidae we relied on the Nordic Fauna (Lindroth 1986), which describes this species as typical of "litter layer of damp deciduous forests" and "shaded sites in open country". However, more recent references contradict these habitat preferences: British and Irish faunas (Anderson et al. 2000; Duff and Schmidt 2012b) characterise *Pterostichus strenuus* as eurytopic, while Šustek (2004) described it as true hygrophilous but indifferent to vegetation cover. This species also showed contrasting responses to plant height in ecological studies, as it was for example more abundant on heavily grazed pastures (Dennis et al. 1997) but clearly avoided cutting management on silage fields (Haysom et al. 2004). Like Hatteland et al. (2005, we observed other seemingly divergent patterns between assumed ecological preferences and species activity. For example, both *Quedius fuliginosus* and *Lathrobium brunnipes* should have moderate demand for humidity (50%), particularly in open habitats (Irmler and Lipkow 2018), but the former was mostly found in mature patches while the latter was almost exclusive to a 2018 burn (GK). Likewise, litter-dweller *Geostiba circellaris* (Betz et al. 2018) was collected on pioneer patches only, while it could have been expected to thrive in well-preserved litter of mature heath.

These contradictions mostly highlight the need to consider several ecological preferences and traits when assessing arthropod responses to disturbance (Buckingham et al. 2019; De Bello et al. 2010; Driscoll et al. 2020; Giménez Gómez et al. 2022): even if moisture and vegetation structure are important drivers of beetle activity (Schirmel and

Buchholz 2011; Šustek 2004), these two factors alone cannot provide a comprehensive understanding of observed species distribution (Cadotte and Tucker 2017). For example, we collected on average bigger beetles in mature stands than in pioneer stands, and while community weighted size was considered as a mobility trait, the difference we observed could be explained by a change in trophic dynamics (Buckingham et al. 2019; Driscoll et al. 2020; Harvey et al. 2008; Kwon et al. 2013). Litter destruction by fire mostly affects small detritivores whose diet depends on micro fragments of dead leaves, while bigger species can feed on more coarse matter (Buckingham et al. 2015). In undisturbed systems with preserved soil biota and complex vegetation structure, generalist predators would not only be protected from predation (Brose 2003) but would also find more prey (Murdoch et al. 1972). This could explain why our largest specimens, from the predatory genus *Carabus*, were three times as abundant in mature replicates than in recent burns. Drawing this reasoning further, the limitation of competition and predation on pioneer patches could favour more specialised predators. For example, the rapid recovery of the collembola community after a light fire could attract collembolan feeders such as *Notiophilus aquaticus* (Bargmann et al. 2016; Malmström et al. 2008), whose morphological adaption for diurnal collembolan hunting means that they would benefit from vegetation clearance (Baulechner et al. 2022). For fungivorous species, we observed contrasting responses: on the one hand, *Acrotona fungi* and *Leiodes obesa*, despite both being hygrophilous species (Duff and Schmidt 2012b; Palm 1970), could potentially favour pioneer patches as low-intensity burning can be followed by the establishment of a diverse fungal community (Fox et al. 2022; Hjältén et al. 2010; Wikars 2002); on the other hand, *Agathidium atrum* may be indicative of mature patches because it feeds on myxomycetes growing on decaying plant tissue (Duff and Schmidt 2012b).

Ecological preferences and trait-based approaches featuring life-history, morphology and behaviour have shown to be very useful and pertinent to assess beetle responses to disturbance (Bettacchioli et al. 2012; Mouillot et al. 2013) or management (Giménez Gómez et al. 2022; Larsen et al. 2008; Ribera et al. 2001). However, there is clear scarcity and inconsistency of knowledge for non-carabid species (Cardoso et al. 2011; Salnitska et al. 2022). For example, due to substantial gaps for Staphylinidae which comprised 20% of our captures, we had to discard diet preferences from our analysis even though this trait has shown to be an effective response indicator to fire management (Bargmann et al. 2016; Bulan and Barrett 1971; Driscoll et al. 2020). As ecological interpretation of collection data is influenced by the initial choice of traits (Zhu et al. 2017), bridging these knowledge gaps through open databases would be essential. Currently, only Carabidae are covered by a widescale, open and collaborative trait database (Homburg et al. 2014). On the other hand, databases including other families target specific trophic groups, such as saproxylic beetles (Hagge et al. 2021) or dung beetles (Buse et al. 2018), and rely on regional scale studies for which applicability is likely to be limited beyond their ranges (Brose et al. 2006). A generalist Coleoptera database would undoubtedly revolutionise the field, but it needs primary data of good quality as the foremost prerequisite (Wong et al. 2019), which requires not only considerable time and resources but also well-defined methodological standards (Moretti et al. 2017; Schneider et al. 2019).

A matter of scales

The disturbance induced by traditional prescribed burning has low intensity and is spatially limited (Hobbs and Gimingham 1984b). Thus, unlike severe wildfires in forest or shrubland

in flat landscapes (Buckingham et al. 2019; Driscoll et al. 2020; Kwon et al. 2013; Pippin and Nichols 1996), there is no major disruption of connectivity which would require high dispersal abilities to recolonise recently burnt areas (Bargmann et al. 2016). Yet, despite the isolation and the limited size of the burnt patches, the beetle activity still diverged from the mature stands even 2 years after the fire. In Bargmann et al. (2015, 2016), the study site had been under rotational prescribed burning for 20 years: it can be argued that this controlled recurring disturbance, which maintains the system into a continuously renewed habitat mosaic by combining rejuvenation and regeneration, would be a factor of stability of the beetle assemblage at the site scale (Battisti et al. 2016; Beckage et al. 2011; Bond 2019). In our study, fire was not part of the system dynamic as prescribed burning was not used for at least the past 50 years (Hjelle et al. 2018). A remaining question is if small-scale burning stimulated already present species by expanding existing conditions, or if it created an exclusive micro-habitat which allowed exogenous species to colonise the area.

We cannot address how this disturbance affected the original beetle assemblage per se, firstly because of the scope and limitations of our study. Our focus at the patch level resulted in a heavily clumped trapping design, which should not be affected by spatial auto-correlation (Baker and Barmuta 2006; Ward et al. 2001) but is not suited for density assessment and could lead to the underestimation of rare species (Ward et al. 2001). This latter issue can be particularly visible in our mature patches, in which 20 out of 24 exclusive species were only collected three times or fewer over the whole sampling period. We therefore advise strong caution when interpreting these species' responses to fire. Furthermore, it should always be emphasized that pitfall catches are estimations of species "activity-trappability-density" (Jansen and Metz 1979; Sunderland et al. 1995), and that accurate density measures are only possible under specific design requirements which were not met in our study (Baars 1979; Perner and Schueler 2004; Zhao et al. 2013).

The pitfall trapping method has been criticised for many potential biases related for instance to species behaviour and body mass (Hancock and Legg 2012; Mommertz et al. 1996; Wallin and Ekbom 1988), trap setting and design (Brown and Matthews 2016; Hohbein and Conway 2018; Lange et al. 2011; Schirmel et al. 2010; Schmidt et al. 2006), and surrounding environment (Greenslade 1964; Koivula et al. 2003; Melbourne 2009; Phillips and Cobb 2005), this latter point being particularly sensitive when comparing different micro-habitats and vegetation structures. Walking behaviour can differ not only between species from the same genus (Mommertz et al. 1996), but also according to their habitat preferences: beetles are more likely to walk randomly in their preferred habitats, while they will follow directed patterns in unfavourable environments (Wallin and Ekbom 1988). These different behaviours would affect the time spent in the capture zone and could lead to overestimation of favoured species against underestimation of unfavoured species (Baars 1979). Short vegetation and a thin litter layer would also facilitate beetle movement and thus increase capture efficiency (Greenslade 1964), but this effect does not seem consistent according to species (Melbourne 2009) or vegetation layer (Koivula et al. 2003; Phillips and Cobb 2005), and was only observed when a substantial area of vegetation was clipped around the traps (from 30 to 250 cm radius). We assumed that clearing this amount of vegetation around each trap would have been detrimental considering our study scale, our limited period of sampling and our clumped sampling design, and therefore we only cleared the immediate surrounding of our traps (about 5 cm radius) to prevent debris from falling into or across the cups.

Methodological considerations aside, how informative could be our captures from mature patches of the original community before the prescribed burns? Our choice of replicates was limited by the farmer's burning strategy from north to south and by the site

topography which made neighbouring vegetation unrepresentative of the stands before fire, leading to a grouped spatial arrangement of the different heath stages. However we argue that north-south geographical bias was unlikely regarding the size of the sampling area (less than 25 ha) (Irmler et al. 2010), the absence of prominent relief which would disrupt population exchanges and affect local climate, the homogeneity of geological conditions and the continuity of management history. Our results seemed to confirm our assumption as mature replicates displayed similar composition despite being further apart compared with burnt stands. We can therefore consider that the assemblages we collected on the mature patches were quite representative of the beetle community over the whole sampling area before the fire management, even if the list of inventoried species could not be exhaustive due to our choices of study scale and design (Ward et al. 2001).

As the closest fire-managed heathland is located at 15 km away from our study area, with a 5 km wide stretch of open fjord in between, the colonisation of fire-favoured species from exogenous sources would be quite unlikely. Conversely, our site topography with exposed bedrock on ridges already created a vegetation mosaic which could, even to a lesser extent, offer suitable conditions for xerophilous and sun-loving species. The most realistic interpretation of our results would be that species exclusive to pioneer stands were already present in the area prior to fire but were missed from mature patches due to lower activity. Thus, in these circumstances, small-scale prescribed burning would enhance specialist beetle activity by increasing the area and number of dry and exposed micro-habitats.

Implications for heathland conservation and monitoring

Up to 2 years after the burn, alpha diversity was still lower on pioneer heath stands compared with mature stands, as expected with the niche simplification effect (Bulan and Barrett 1971). However, despite adding selection pressure to already existing micro-scale environmental factors (Jentsch and White 2019), fire did not significantly increase beta-diversity even if divergence between patches was seemingly higher on recent burns. The vegetation composition of early successional stages of heathland after prescribed burning was shown to be mainly driven by stochasticity, deterministic factors becoming increasingly important with time since fire (Måren et al. 2018). Several studies have observed a postfire increase of beta-diversity in plant communities (Vandvik et al. 2005; Velle et al. 2014) and arthropod assemblages (Bargmann et al. 2015; Brunbjerg et al. 2015). Beta-diversity measurements can however be affected by random sampling effect due to smaller community size and by strong micro-environmental conditions unrelated to fire (Myers et al. 2015). Our study site not only shows distinctive topographical features with a mosaic of ridges and depressions, but it is also an island subjected to salt-spray and sheep grazing all year round. This combination of factors is likely to influence the dynamics of the beetle assemblages independently from the fire effect (Finch et al. 2007; Kelly et al. 2015; Moranz et al. 2012).

Likewise, species richness responses to burning are not straightforward in the literature, as several studies reported increased alpha diversity after fire for plants (Velle et al. 2014), arthropods (Brunbjerg et al. 2015), and more specifically beetles (Bargmann et al. 2015). In Mediterranean heathlands, if overall beetle species richness did not change with time since fire (Yekwayo et al. 2018) trends at the family level diverged, with for example Scarabaeidae showing negative response while Carabidae remained unaffected (Pryke and Samways 2012). In forested systems, Carabidae and Staphylinidae also showed different postburn trends in diversity (Gandhi et al. 2001), but not always in abundance (Kwon et al.

2013), while overall ground-dwelling arthropod richness would not change (Coleman and Rieske 2006). Thus our work highlights the importance of including several taxa to assess the effect of fire on biodiversity (Kwon et al. 2013; Moretti et al. 2006; Pryke and Samways 2012), especially in the context of monitoring habitat resilience which could require the identification of suitable indicator species.

Comparing with Bargmann et al. (2016), we confirmed *Poecilus versicolor* and *Carabus violaceus* to be correlated with pioneer and mature heath patches respectively, the former being a sun-loving eurytopic (Lindroth 1985) and the latter being a forest species found locally common in wet heathland (Hatteland et al. 2005). However, our findings were only partially consistent with those of Bargmann et al. (2016): if we could support the association of *Bembidion lampros* and *Cicindela campestris* with pioneer stands, even if these two species were not emphasized in our own indicator analysis, we detected no significant trend for *Nebria salina* and *Notiophilus aquaticus*. Most importantly, our results diverge concerning *Dyschirius globosus*, which we found indicative of pioneer patches while it showed as characteristic of building phase in Bargmann et al. (2016). We identified new potential indicator species among Carabidae, such as *Pterostichus strenuus* for pioneer stands, or *Carabus granulatus* and *Cychrus caraboides* for mature stands, but more interestingly our analysis highlighted the importance to investigate all Coleoptera families for the determination of potential indicators (Yekwayo et al. 2018), as only five out of ten species associated with mature patches were Carabidae. Thus, we also recorded two Staphylinidae (*Ischnosoma splendidum*, *Drusilla canaliculata*), one Curculionidae (*Micrelus ericae*), one Leiodidae (*Agathidium atrum*) and one Scirtidae (*Contacyphon hilaris*), while these two later families made for less than 2% of total captures respectively.

It must however be emphasized that the choice of analytical approach does influence the results, as the phi coefficient and the IndVal value did not highlight identical species. Overall, IndVal was more restrictive than the phi correlation analysis, as it detected fewer species (8 against 11 in total) and excluded some which had surprisingly high correlation values (e.g. *Carabus granulatus*, *Pterostichus niger*). On the other hand, both *Agathidium atrum* and *Cychrus caraboides* had significant IndVal scores but were not significantly correlated to mature stands according to Pearson's phi. For an extensive comparison of these two indexes, with suggested improving transformations, we recommend Tichy and Chytry (2006) and De Cáceres and Legendre (2009). As both indices offer some complementarity without requiring many additional analytical steps, it may be valuable to include both to enhance comparability between ecological studies.

Selecting indicator species for management perspectives should be done in the scope of a well-defined monitoring program with a good knowledge of species' ecology (Landres et al. 1988). For example, we mentioned earlier that Staphylinidae, due to their diversity and sensitivity to fine-scale disturbances would make, in theory, optimal candidates. However, this family is particularly challenging for both collection and identification (Duelli and Obrist 1998; Levesque and Levesque 1995; Salnitska et al. 2022; Schmidt et al. 2006), and we can assume that we probably underestimated the activity and richness of Staphylinidae in our study, due to our sampling method and the deterioration of *Atheta* specimens.

As the biodiversity benefits of small-scale rotational burning relies on the resulting mosaic of heath regeneration stages, it could be valuable for the biosphere reserve managers to use indicator species of the different phases to monitor the condition of heathlands in Western Norway (Bal et al. 2018). Indeed, creating new micro-habitat conditions for xerophilous and sun-loving species should not threaten species associated with mature heath. *Poecilus versicolor* could be a suitable indicator for pioneer phase as it was identified in both Bargmann et al. (2016) and our study, but it should be underlined that as an

eurytopic and generalist species it may not be representative of a more rare and special-ised assemblage. For the mature phase, a good candidate could be the Ericaceae specialist *Micrelus ericae* (Duff and Schmidt 2012a): this Curculionidae is well-distributed in Europe and has distinct morphological features which makes its identification easy for non-experts. Furthermore, *Micrelus ericae* could be a good indicator of the heath condition in general, regarding for instance the droughts which are likely to occur more frequently in Northern areas (Haugum et al. 2021).

Conclusion

Rotational prescribed burning as traditionally applied in coastal heathland management increases the abundance and richness of specialists by creating a fine mosaic of new eco-logical conditions (Brunbjerg et al. 2015; Pedley et al. 2013; Schirmel and Buchholz 2011; Velle et al. 2014). Even if we could not demonstrate an increase of beta diversity after disturbance (H1), controlled burning facilitated the activity of xerothermic species inde-pendently of their dispersal abilities (H3). We highlighted the importance of using a com-bination of several traits and ecological preferences to assess the responses of arthropod assemblages to disturbance, as their relevance will differ according to local environmental conditions and fire characteristics (Driscoll et al. 2020). There is therefore the need for a more thorough investigation of life traits and ecological preferences in less-studied taxo-nomic groups, especially those offering a high potential of specialisation. We were able to identify new indicator species for both the pioneer and the mature heath (H2), including five non-carabid beetles, but our results showed substantial differences between the two indices used (IndVal and Phi), as well as with the related literature (Bargmann et al. 2016; Brunbjerg et al. 2015). We therefore encourage future studies to investigate different taxa, not only among ground-dwelling arthropods (e.g., spiders in Bell et al. (2001) but also to include soil invertebrates (Yekwayo et al. 2018), in order to provide a more comprehensive overview of the effects of prescribed burning which is currently used as an essential tool for Atlantic heathland conservation and management.

Data availability The abundance and trait data presented in this study are available in the supplementary material.

Declarations

Competing interests The authors declare no competing interests.

Consent to publish All authors have given consent to publish.

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