Examining the impact of heathland restoration via felling on carabid diversity in the Purbeck Heaths National Nature Reserve

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A thesis submitted as part of a Master's by Research for Bournemouth University

Faculty of Science and Technology

August 2025

Abstract

Lowland heaths have suffered considerable decline across Europe due to factors such as agricultural expansion and afforestation. The internationally significant Purbeck Heaths National Nature Reserve in Dorset has experienced substantial habitat loss, threatening numerous rare and declining species. This study aimed to evaluate how heathland restoration through conifer felling influences the species richness, composition, and functional traits of carabid assemblages. Specifically, it assessed the impact of restorative felling — the removal of planted conifers from former heathland — in the Rempstone and Godlingston areas of Purbeck Heaths. Carabid richness, abundance, and functional traits were assessed using pitfall traps across 35 sites, encompassing forested, established wet and dry heath, and restored wet and dry heath categorised by restoration age: <12 years (new) or >17 years (old). Environmental variables (ground temperature, soil moisture, and relative humidity) and vegetation characteristics were also recorded. Sampling was carried out monthly from May to August 2024, and data were analysed using generalised models (additive and linear) for species richness and abundance, and PERMANOVA to assess differences in carabid species composition, and Kruskal-Wallis tests to evaluate variation in functional traits across habitat types. A total of 354 individuals from 44 species were identified, with *Abax parallelepipedus* being the most abundant. Wet heath restored post-2012 exhibited the highest richness (23 species), while forested and old dry restored heath showed the lowest median richness (2 species each). Richness increased with warmer ground temperatures, highlighting the role of microclimatic conditions. The positive association between warmer ground temperatures and carabid richness suggests that thermally favourable microhabitats enhance carabid activity, underscoring the ecological importance of microclimate in driving community composition. Habitat type strongly influenced species composition, with Old Dry heath assemblages being particularly unique compared to all other habitats. Younger restorations (especially wet) showed high species turnover, while older, more established sites had more predictable communities where species were more consistently shared across sites. Functional trait analysis revealed significant habitat-specific variations: restored wet heaths favoured smaller, spring-breeding, open-habitat specialists, while forests and older dry heaths hosted larger carabids with different trait combinations, reflecting habitat structure and microclimate influences.

These findings support conifer removal as beneficial for carabid diversity, while suggesting a role for retaining some mature conifers to enhance overall diversity. The study highlights the necessity of habitat-specific management, accounting for restoration age and microclimate, to maximise biodiversity conservation in restored heathlands.

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Abbreviations

Abbreviation	Definition
ANOVA	Analysis of Variance
ARC Trust	Amphibian and Reptile Conservation Trust
DEFRA	Department for Environment, Food and Rural Affairs
DNL	Dorset National Landscape
DWT	Dorset Wildlife Trust
FC	Forestry Commission
FE	Forestry England
FSC	Forest Stewardship Council
GAM	Generalised Additive Model
GLM	Generalised Lineal Model
IPCC	International Panel on Climate Change
IQR	Interquartile Range
IUCN	International Union for Conservation of Nature (IUCN)
JNCC	Joint Nature Conservation Committee
NMDS	Non-metric MultiDimensional Scaling
NE	Natural England
NNR	National Nature Reserve
NT	National Trust
PERMANOVA	Permutational Multivariate Analysis of Variance
RSPB	Royal Society for the Protection of Birds
SAC	Special Area of Conservation
SERT	Student Environmental Research Team
SNNR	Super National Nature Reserve
SPA	Special Protection Area
SSSI	Site of Special Scientific Interest
Tukey's HSD	Tukey's Honestly Significant Difference
TSR	Temperature-Size Rule
VIF	Variance Inflation Factor

Acknowledgements

First, I would like to express my gratitude to Forestry England, Natural England, and the Rempstone Estate for granting me permission to survey their heathlands, and to Sophie Clegg for providing invaluable maps — this study would not have been possible without your assistance.

My deepest thanks go to my incredible supervisory team. To Pippa Gillingham, my primary supervisor, for her unwavering belief in my ability to navigate this research and for making every challenge feel surmountable. To Anita Diaz, for her endless wisdom, genuine enthusiasm, and candid advice when I was overthinking far too much. And to Matt Hill, whose patience, guidance, and willingness to lead me through the complexities of using R for the first time were instrumental in my learning process. Their expertise and inspiration made every step of this Master's feel possible.

A special thanks to placement students Emma, Becca, and Tutte, who made the longer days much more enjoyable. Their dedication to sieving insects and identifying beetles was both crucial and greatly appreciated.

Finally, I want to thank my family for their emotional support during what has felt like both a very long and very short year (and for their tolerance of test tubes full of beetles around the house). Your encouragement kept me grounded and motivated throughout this project.

1. Introduction

1.1. Heathland Biodiversity

The importance of ecosystems featuring specialised habitats cannot be overstated. They are critical for maintaining biodiversity, serving as refuges for rare and threatened species (Usher and Thompson, 1993; Buchholz et al., 2013) and supporting essential ecosystem services such as pollination, carbon sequestration, and water regulation (Cordingley et al., 2015; Walmsley et al., 2021). In particular, specialist habitats that support unique species assemblages are often more vulnerable to external pressures such as climate change, pollution, and land-use change (Berry et al., 2003; Piessens et al., 2006). One such ecosystem is heathlands.

Globally, heathlands are recognised by their ability to support a diverse range of faunal groups across multiple continents: they provide habitat for species such as small mammals and carnivores (e.g. mice and foxes in Australia (Nalliah et al., 2022)), prey availability for birds of prey (e.g. raptors and owls in Scotland and Norway (Calladine et al., 2024)), resources for large herbivores (e.g. deer and wild boar in the Netherlands (Kuiters and Slim, 2002)) and bats (e.g. in regions near Poland and Germany (Schmidt, 2008)). In Europe, this biodiversity is found across a range of climatic zones including temperate and Mediterranean regions as well as montane regions (Fagúndez, 2013; Ramil Rego et al., 2013), with both upland and lowland heath communities adapted to different environmental conditions. Upland heaths, typically found at higher altitudes, often above 300m in Great Britain (with a lower limit in the north), are dominated by cooler, damp climates. In contrast, lowland heathlands occur at lower elevations in milder climates (Alonso et al., 2018; Crowle et al., 2024), and are particularly noteworthy for their largely anthropogenic origin (Groves et al., 2012). This distinction is crucial, as the unique history and management of lowland heaths, which form the focus of this study, have profoundly shaped their present-day ecological characteristics.

Lowland heathlands are considered cultural landscapes, having developed over thousands of years through a cycle of human activity. Widespread deforestation beginning in the Neolithic period cleared native woodlands for timber and fuel, particularly on nutrient-poor, acidic and sandy soils that were difficult to cultivate intensively (Webb, 1989; Webb, 1998; Rose et al., 2000; Groves et al., 2012). As a result, these open landscapes became dominated by stress-tolerant dwarf shrubs such as *Calluna vulgaris* (ling heather), and other *Ericacea* species and sclerophyllous vegetation (Webb, 1989, 1998; Fagúndez, 2013; Mitchell et al., 2000a; Mitchell et al., 2000b; Groves et al., 2012). The persistence of this open habitat, however, was not solely due to poor soil conditions. Rather, it was a direct consequence of continued traditional land-use practices such as grazing, cutting, and controlled burning, which prevented natural succession back to woodland and maintained the heathland in a plagioclimax state (Mitchell et al., 2000a; Fagúndez, 2013). This essential role of traditional land use in shaping and maintaining heathlands makes them high-value cultural habitats (Diemont et al., 2013; Walmsley et al., 2021) that provide ecosystem services such as biodiversity, carbon storage and aesthetics (Cordingley et al., 2015).

Britain hosts approximately one fifth of the global coverage of lowland heathland (Newton et al., 2009; Pywell et al., 2011), and evidence suggests that Southern heathlands in England have been managed by humans for millennia, creating their anthropogenic importance (Rose et al., 2000). However, the decline of traditional grazing and conversion to other land uses such as forestry and arable agriculture (Webb, 1998; Newton et al., 2009) has made active management by conservationists essential for preventing natural succession to scrub and forests (Mitchell et al., 2000a; Mitchell et al., 2000b). The primary goal of this management is to create and maintain the structural diversity that supports specialist heathland species Without these disturbances, the nutrient-poor soils alone would not be sufficient to prevent tree colonisation, demonstrating the essential role of traditional land-use in the origin and persistence of lowland heaths (Pywell et al., 2011; Newton et al., 2009; Groves et al., 2012).

A variety of management techniques are employed to achieve this, each with distinct effects on the habitat. Grazing by domestic livestock, for example, is a long-used method that promotes open landscapes and plant diversity by preventing ericaceous species entering their degenerative phase, thus reducing dense woody vegetation (Henning et al., 2017; Kerdoncuff et al. 2023). A growing body of evidence suggests that moderate grazing can positively impact invertebrate assemblages; for example, Waite et al. (2022) found that it benefitted carabid beetle communities by maintaining habitat heterogeneity and preventing dominance by dense vegetation. Historically, heathland management in Britain has also involved burning small patches to maximise grouse production (Webb, 1998) and burning larger areas to manage for grazing by livestock such as sheep, deer, cattle, and ponies (Usher and Thompson, 1993; Bullock and Pakeman, 1996). Meanwhile mechanical management (such as choppering, sod-cutting, and mowing) offers alternative ways to control vegetation, each varying in their intensity and impact on the soil. For instance, sod-cutting is a more intensive method that removes all aboveground biomass and the nutrient-rich topsoil layer down to the sandy layer to encourage pioneer species (Schirmel, 2010; Fartmann et al., 2022). This reduces nutrient load but generates a large amount of waste. Alternatively, choppering is a less disruptive technique that removes vegetation and moss layers without affecting the deeper soil profile; Fartmann et al., 2022). Mowing, which preserves soil structure, controls vegetation height and prevents succession, is a common substitute for grazing where livestock is not an option (Henning et al., 2017). The diversity of these management practices underscores the need for a nuanced approach to heathland conservation, as each method creates a unique microhabitat mosaic, thereby maintaining structural diversity (Webb, 1998; Mitchell et al., 2000b; Hawley et al., 2008; Newton et al., 2009; Rosa García et al., 2013).

1.2 Heathland Decline and Fragmentation

Over recent decades, the synergistic effects of climate change, rapid land management practice changes and excessive agricultural intensification have contributed to the degradation of European heathlands (Webb, 1989; Rose et al., 2000; Newton et al., 2009; Pywell et al., 2011; Fagúndez, 2013; Kalusová et al., 2023). This has resulted in a dramatic reduction in extent, with lowland heath declining by approximately 80% across Europe, including reductions of nearly 70% in Sweden and Denmark since the 1960s, and around 95% in the Netherlands (Newton et al., 2009). The significant decline of this habitat has led to the requirement, at both national and international levels, of designations to protect plant and animal species, highlighting its vulnerability and conservation importance (Webb, 1998; Ombashi and Løvschal, 2022).

This degradation is driven by a combination of pressures, including urban expansion and conversion to cropland or pasture (agricultural intensification), which cause habitat fragmentation and disrupt ecological connectivity (Fagúndez, 2013; Cordingley et al., 2015). A major, and often synergistic threat, is atmospheric nitrogen deposition, which has long-lasting and widespread impacts on these fragile ecosystems. Multiple lines of evidence suggest that nitrogen deposition alters soil chemistry, leading to reduced plant diversity and shifts in species composition. For instance, studies by Southon et al. (2013) on UK heathlands and Maskell et al. (2010) across various British habitats confirm that nitrogen deposition leads to widespread declines in species richness (Maskell et al., 2010) and an increase in grass abundance at the expense of heathland plants (Southon et al. 2013). Southon et al. (2013) further reinforced that these nitrogen-driven changes are accompanied by alterations in soil chemistry and microbial activity such as increased litter nitrogen, changes in soil carbon-nitrogen ratios, and elevated enzyme activity, indicating faster nutrient cycling, which have long-term consequences for ecosystem function. These findings are supported by Fartmann et al. (2015), who examined multiple taxa to compare species responses and found that even 13 years after restoration, the vegetation structure in nitrogen-impacted sites still differed significantly from old-growth heathlands, demonstrating the persistent and irreversible nature of these threats.

1.2.1 Afforestation

The traditional open landscapes of heathlands are increasingly threatened by afforestation for timber production (Cordingley et al., 2015). Historical records spanning several centuries suggest that conifer planting has been widespread for a considerable time (Piessens et al., 2006), largely driven by increasing urbanisation and the demand for productive land use. Initially, afforestation primarily impacted Britain’s native woodlands, with evidence of large-scale clearance dating back to the early Neolithic period (Rackham, 1986; Walmsley et al., 2021). Early settlers replaced these woodlands with conifer plantations, recognising that pines grew quickly on infertile soils and burned more readily than native British tree species (Rackham, 1986, 2008). However, after World War II, afforestation expanded beyond woodlands, increasingly targeting heathlands and other open habitats to improve timber stocks (Champion, 1948; Matsushita, 2015; Neumann et al., 2017; Duchesne et al., 2023). This large-scale afforestation was widely promoted across the UK and extended throughout Europe, including Spain (Ramil Rego et al., 2013), and as far as Japan (Matsushita, 2015) and South Africa (Craib, 1943). Afforestation is recognised as a major driver of heathland and heather moor loss in the United Kingdom, with large areas of heathland converted to conifer plantations (Rosa García et al., 2013). This widespread afforestation has led to significant fragmentation of heathland habitats, disrupting ecological connectivity and profoundly impacting biodiversity and ecosystem function (Andrés and Ojeda, 2002; Pedley et al., 2023).

Afforestation of heathland with conifers initiates a cascade of interconnected negative effects, beginning with significant physical and chemical changes that fundamentally alter the ecosystem. The planting process, which involves creating ridges and furrows for drainage, disrupts natural hydrology and modifies soil structure (Webb, 1989; Campbell et al., 2019). Simultaneously, nutrient inputs from the new conifers increase nutrient leaching into the naturally oligotrophic heathland soils, raising the soil pH and altering its chemical composition (Piessens et al., 2006; Tew et al. 2021). These changes to the soil and hydrology have a direct impact on the ground flora. The establishment of a dense canopy cover limits light availability (Elmarsdottir et al., 2008), while thick needle litter layers inhibit the germination of characteristic heathland plants (Andrés and Ojeda, 2002). This combination of reduced light and physical barriers leads to a decline in plant diversity and a loss of the unique vegetation structure that defines heathlands, which in turn affect ecosystem services (Cordingley et al., 2015).

Ultimately, this chain of events culminates in a profound impact on faunal diversity. The structural and compositional changes, particularly the loss of open heathland habitat and the creation of dense, shaded conditions, are detrimental to specialist species. For example, studies on carabid beetles show that dense canopy cover in conifer plantations negatively affects their functional diversity (Spake et al., 2016). This is further supported by research from Lin et al. (2007), who found that younger forests with more open canopies support a greater diversity of carabid species, while older, more closed-canopy plantations support fewer rare and specialist species. The weight of this evidence highlights that the physical and chemical transformations from afforestation lead to a simplification of the habitat, which directly limits the distribution and diversity of key faunal groups like carabid beetles.

1.3 Impacts of Fragmentation

The effects of habitat fragmentation on biodiversity have been widely studied, showing that impact can vary in degrees of detriment depending on the context (Didham et al., 2012; Püttker et al., 2020; Willmer et al., 2022). A critical aspect of fragmentation is the reduction of habitat connectivity, which limits an organism's ability to move and disperse (Webb, 1990; Lawton et al., 2010). This loss of connectivity, alongside fragmentation itself, intensifies edge effects (Willmer et al., 2022), altering microclimate conditions, increasing vulnerability to invasive species and disrupting species interactions (Hobbs and Atkins, 1988; Saunders et al., 1991; With, 2002). These edge effects impact soil composition and moisture levels, which subsequently affect plant communities and overall ecosystem stability (Harper et al., 2005), and as such these changes correlate with reduced biodiversity (Cordingley et al., 2015).

In priority habitats like heathlands, fragmentation leads to the degradation of environmental conditions, which alters invertebrate trophic interactions, community composition and dispersal dynamics (Dupont and Nielsen, 2006; Didham et al., 2012). These changes directly impact insect population ecology, affecting species identities and relative abundances (de Vries et al., 1996; Worthen, 1996; Didham et al., 2012). While larger habitat patches and increased connectivity generally enhance population survival, the resulting changes in species richness are less predictable, fluctuating according to habitat type and the extent of isolation (Didham et al., 2012). It is crucial to understand that habitat fragmentation does not act in isolation; it interacts with other ecological processes like predation and competition, which significantly shape species responses to habitat change (Didham et al., 2012). Therefore, understanding the complex interplay of these factors is essential for effective heathland restoration, especially in the face of ongoing environmental changes driven by afforestation, climate change and increasing anthropogenic pressures (Didham et al., 2012; Intergovernmental Panel on Climate Change, 2023).

1.4 Conservation and Restoration

While maintenance techniques such as burning, grazing and mowing are crucial for sustaining heathlands, their role in restoration is more nuanced and dependent on the ecological context and the restoration goals (Read and Bealey, 2021; Walmsley et al., 2021). Each restoration project requires an individualised approach based on these specific needs. For example, restoration to control erosion may focus on re-establishing vegetation cover to discourage visitors from taking the most direct route, inadvertently creating informal footpaths (termed ‘desire paths’) through heathland habitats and implementing drainage systems to protect from erosion caused by surface water (Rodway-Dyer and Ellis, 2018). Meanwhile, carbon-focused restoration may emphasise minimising disturbance in wetter habitats, limiting burning (Littlewood et al., 2010), and allowing vegetation succession to enhance peat and organic matter accumulation (Lucchese et al., 2010). In contrast, biodiversity-focused restoration may prioritise selective grazing to promote habitat heterogeneity (Newton et al., 2009).

One example of this complexity is burning, which may not be suitable for restoring afforested heaths, as it primarily removes surface vegetation rather than addressing soil composition and seed banks, and so frequency of burns is a key factor in conserving heathlands (Hawley et al., 2008; Webb and Haskins, 1980). Jofré and Reading (2012) found that burning had positive effects on ground-nesting birds, such as the nightjar and woodlark, however, reptile species like the adder and sand lizard suffered indirectly from the loss of crucial vegetation cover, leading to increased exposure to predators and extreme temperatures – the latter causing direct harm to individuals.

Henning et al. (2017) found that year-round low-intensity grazing with cattle and horses improved vegetation structure and species richness in sandy grasslands and heathlands by reducing competitive grasses like *Calamagrostis*. Despite these benefits, *Calluna* (heather) cover continued to decline, suggesting that grazing alone may not be sufficient for its rejuvenation. The authors recommended combining grazing with additional management measures, for example, temporarily increasing grazing pressure through mowing or manual shrub cutting. Schirmel (2010) conducted a comparative study on the effects of mechanical management, specifically choppering, sod-cutting, and mowing in heathland restoration. The study found that short-term benefits varied across the management techniques: mowing appeared to preserve a typical heathland invertebrate fauna, while sod-cutting promoted conditions for several important and threatened carabid species. Based on the species composition, choppering appeared to have the least effect on carabid beetles.

1.4.1 Restoration by Conifer Removal

Conifer felling serves as a significant restoration technique for afforested heathlands (Walker et al., 2004), effectively reversing the impacts of tree planting by removing the dense canopy and facilitating the return of native heathland vegetation (Eycott et al., 2006). However, the process is not straightforward. Koivula and Niemelä (2003) found that the side effects of logging, such as the accumulation of debris, negatively affected some carabid species while others benefitted from the changes to microhabitat – albeit insignificantly. This highlights the complex interactions within afforested areas compared to heathlands, demonstrating that even seemingly direct intervention can have varied and nuanced outcomes.

Beyond these large-scale restoration strategies, the creation and management of microhabitat features are equally vital. Factors such as vegetation structure and canopy cover play a pivotal role in shaping plant and animal communities in heathland ecosystems. Pedley et al. (2023) highlighted the importance of microhabitat creation during ecological restoration, noting that canopy cover and vegetation structure contribute to habitat heterogeneity, which, in turn, affects the dispersal potential of species that thrive in open habitats. Similarly, Kerdoncuff et al. (2023) highlighted how heathland restoration practices, like burning, influence fine-scale environmental conditions, creating heterogeneity that supports different species.

A literature review carried out by Jones and Schmitz (2009) suggested that the recovery rate of habitats from anthropogenic tree removal is typically faster than recovery from naturally degraded systems. However, the success of heathland restoration varies depending on the initial state of degradation, with recovery differing according to the severity and nature of the damage (Fagúndez, 2013; Walmsley et al., 2021). For example, post-agricultural heathland sites may suffer from nutrient enrichment (Walmsley et al., 2021), slow draining soil (Fagúndez, 2013), and altered vegetation dynamics, while former mining or quarrying sites may experience soil compaction, heavy metal contamination and reduced seedbank availability (Putwain et al., 1982).

Instead of reversing successional changes, restoration efforts may ameliorate negative impacts by facilitating the establishment of alternative communities (Mitchell et al., 1999; de Graaf et al., 2009). This perspective is particularly relevant to understanding how restored heathlands compare to established heathlands and forested areas in terms of species richness, abundance, and composition. Additionally, it raises questions about how environmental factors might influence biodiversity over and above any effect of restoration. Understanding fundamental ecosystem dynamics is essential for addressing both abiotic and biotic changes (Li, 2000; de Graaf et al., 2009).

1.5 Case Study: Dorset Heaths

The Dorset Heaths provide a clear example of the importance of targeted habitat restoration. Over an 18-year period, this area experienced a significant 86% decline in heathland habitat (Forestry Commission, 2013a), with a corresponding increase in number of fragmented patches (Webb and Haskins, 1980; Webb, 1989; Rose et al., 2000). This loss of heathland, largely attributed to afforestation and inadequate management (Rose et al, 2000; Forup et al., 2008; Diemont et al., 2013; Borchard et al., 2014), is consistent with broader ecological theory: larger, less-fragmented patches in Dorset have been shown to support higher invertebrate species richness than smaller, more isolated fragments (Webb, 1989). underscoring the role of connectivity in sustaining ecological communities.

Despite this dramatic habitat degradation, the Dorset Heaths remain a vital refuge for key species. This includes a diverse range of organisms, from rare and native plants such as the yellow centaury and the Marsh gentian (Chapman et al., 1989b; Purbeck Heaths, 2025a; Joint Nature Conservation Committee (JNCC), n.d.); to birds like the Dartford warbler (Moore, 1962; Dorset Council, 2025) and nightjar (Diaz et al., 2011; Purbeck Heaths, 2025a; JNCC, n.d.); all six of the UK's native reptiles (Jofré and Reading, 2012; Purbeck Heaths, 2025a; JNCC, n.d.); and rare invertebrates such as the Purbeck mason wasp (Bagley, 2019; Purbeck Heaths, 2025a; JNCC, n.d.), a threatened species localised to a few Dorset sites for which a Species Action Plan (SAP) was created by JNCC (JNCC, 2007). Other priority species inhabiting the Purbecks include the near threatened Southern damselfly (Boudot, 2020; Purbeck Heaths, 2025a) and the ladybird spider – a species thought to be extinct until it was found in Dorset in 1979 (British Arachnological Society, 2025). Of particular interest, along with rare species such as the Crucifix ground beetle (Telfer, 2016), are those restricted in range such as the heath tiger beetle (Purbeck Heaths, 2025a), which is confined to sites in Dorset, Hampshire, Sussex and Surrey (Dodd and Surrey Wildlife Trust, 2010). This beetle requires bare sandy patches for efficient hunting during larval and adult life stages (Telfer, 2016), which would previously have been created by the cutting of heather turves. While there is a clear consensus on the need for targeted management, the link between specific restoration strategies and species outcomes remains unevenly evaluated across sites and taxa. For example, while studies highlight the correlation between patch size and invertebrate richness (Webb, 1989; Didham et al., 2012; Forestry Commission, 2013a), few assess causality or the specific role of microhabitats. This lack of a generalised, ecosystem-level understanding of restoration success and species response represents a key knowledge gap.

1.6 Carabid Beetles

1.6.1 Carabidae Family

The family Carabidae is large, diverse and occupies a wide range of habitats and almost every environment type (Lawrence and Newton Jr, 1982; Koivula, 2011). Within Britain and Ireland, it is estimated to comprise 350 species belonging to 87 genera (Luff, 2007; Forest Stewardship Council (FSC) Biodiversity, 2025) with Britain sustaining 76 Nationally Rare species, as listed within GB Rarity Status categories (Telfer, 2016). Carabid beetles, like many invertebrates, play a crucial role in maintaining healthy, functioning ecosystems. They are an essential food source for birds, reptiles and mammals (Holland, 2002), while soil-dwelling species facilitate fine-scale soil bioturbation (Gagic et al., 2015). Carabids help regulate predator-prey dynamics due to their diverse diets, with many being polyphagous (Ghannem et al., 2018). They also influence vegetation growth, composition, and distribution through herbivory, pollination and seed dispersal (Forup et al., 2008), and serve as effective biological control agents, particularly via predation on pest species within agricultural ecosystems (UK Carabid Recording Scheme, n.d.b).

Due to their preference for dispersal by walking, rather than flight (Holland, 2002), carabid movement and colonisation patterns are readily observable. These characteristics make carabid communities and their dispersal patterns useful proxies for monitoring environmental conditions and climate change (Lawrence and Newton Jr, 1982). For instance, research in Germany found that flightless beetles were most abundant in older, more stable successional habitats (Schirmel et al., 2012). Additional studies have found carabid assemblages have been significantly correlated with environmental variables such as vegetation cover, bare soil percentage, and soil moisture (Borchard et al., 2014). Given their crucial ecological roles and sensitivity to environmental disturbances (Koivula, 2011), carabid beetles serve as valuable indicators of habitat quality and restoration success.

1.6.2 Ecological Change and Carabid Functional Traits

The rise of functional trait approaches in ecological research began in the late 20th Century and has since gained popularity, developing from Raunkiaer and Grime's work on functional groups (Nock et al., 2016) to the modern distinction between hard traits and soft traits (Gutiérrez-Cánovas et al., 2024). Hard traits are typically quantifiable, morphological characteristics, such as body size and mandible shape, that directly impact an organism's fitness, while soft traits are qualitative and more often used as proxies for ecological roles or behaviours, such as feeding habits or reproductive strategies (Nock et al., 2016; Gutiérrez-Cánovas et al., 2024).

Heathland restoration techniques can significantly influence carabid assemblages and their functional traits. Response traits indicate an organism's reaction to environmental change, reflecting how species adapt to habitat alterations, such as reproductive rates, larval development time and tolerance to disturbance (Pakeman and Stockan, 2014; Gobbi et al., 2015; Nock et al., 2016). In contrast, effect traits directly impact ecosystem functioning, shaping processes such as nutrient cycling and predation dynamics (Pakeman and Stockan, 2014; Nock et al., 2016). Unlike taxonomic approaches that focus on species identity and diversity, such as species richness and abundance, trait-based analyses assess ecological roles, such as seed dispersal and predation, by examining species' morphological, physiological, and behavioural characteristics (Pakeman and Stockan, 2014). By providing better insights into species' adaptations to habitat modifications, especially in a changing climate, functional trait research can help tailor restoration efforts more effectively. The work of Ribera et al. (2001) reinforces the value of trait-based approaches, demonstrating that morphological and life-history traits of ground beetles are strongly aligned with broad environmental gradients, particularly those shaped by land use intensity and elevation

(Ribera et al. 2001). Their multivariate RLQ analysis showed that species' functional traits are not randomly distributed but instead respond predictably to gradients of disturbance and stress, providing a clear link between habitat management and carabid trait composition. This supports the notion that functional traits are not only ecologically meaningful but can be used for predictive purposes in conservation management.

Some carabid functional traits exhibit plasticity (Tseng et al., 2018) and can therefore shift based on environmental conditions, which may complicate interpretation. For instance, Ribera et al. (2001) highlighted that larger-bodied species were associated with less-managed upland sites, aligning with other studies showing that intensive management tends to favour smaller, more dispersive taxa (Siepel, 1990; Blake et al., 1994, 1996). Similarly, Pakeman and Stockan (2014) found that carabid body size and wing morphology were key traits affected by environmental conditions – specifically, smaller body length and wing macroptery were associated with greater disturbance by ploughing, whereas soil type and management had indirect effects by influencing plant traits, which in turn shaped habitat suitability for carabid species. This pattern aligns with findings from Tseng et al. (2018), who observed that larger-bodied carabid beetles decreased in size in response to warming temperatures, supporting the temperature-size rule in ectotherms (Arendt, 2011). However, they also acknowledge that resource availability plays a critical role, as mentioned by Lövei and Sunderland (1996). Additionally, mandible shape may shift in response to changing prey availability, influencing feeding strategies (Forsythe, 1987; Konuma and Chiba, 2007) while wing morphology can indicate a species' ability to recolonise restored sites (Zera and Denno, 1997). Although these complex interactions pose challenges, they also highlight the value of functional trait analysis in understanding species' responses to habitat restoration.

1.6.3 Carabids in Restoration Contexts

Carabid beetles are frequently studied alongside spiders in agricultural and arable landscapes due to their similar responses to environmental changes and their roles as biological control agents (Thomas et al., 2002; Gao et al., 2024; Schirmel et al., 2012; Topping and Luff, 1995; Buchholz et al., 2010, Knapp et al., 2020; Mei et al., 2023). In other ecosystems, particularly rivers and floodplains, a progressing body of research shows that carabids communities generally benefit from restoration activities that increase habitat heterogeneity, though temporary disruptions can occur during restoration phases. For instance, large-scale European studies on river restoration have found that restored sections exhibit higher carabid species richness and diversity compared to degraded sections (Hering et al., 2015; Sprössig et al., 2022). This is supported by research in Germany which demonstrated that the enhanced habitat heterogeneity from floodplain restitution positively influenced carabid diversity and community composition (Günther and Assmann, 2005).

However, the relationship between restoration and diversity is not always straightforward. While habitat heterogeneity may increase, this can lead to a shift in community composition. Some studies have found that as habitat conditions become more variable following restoration, generalist species, with their broader ecological requirements and greater ability to disperse, may outcompete specialists (Januschke et al., 2011; Kotze and O'Hara, 2003; Büchi and Vuilleumier, 2014). This can lead to a temporary or even long-term decrease in overall species richness if the specialist species are not able to re-establish. These findings, along with the recognition that restoration activities can temporarily disrupt existing communities (Dornelas, 2010), highlight the dynamic and sometimes unpredictable nature of these interventions. Similarly, the role of ground disturbance in shaping carabid communities is complex and context-dependent. Studies on agricultural land show that disturbance intensity, from ploughing (Skłodowski, 2014) to burning (Kerdoncuff et al., 2023), can create microhabitats that shape species assemblages (Skłodowski, 2014) and favour certain species. For example, burning can create favourable conditions for xerophilous and sun-loving beetles by altering environmental conditions (Kerdoncuff et al., 2023). However, the effectiveness of a single technique in promoting overall diversity is not always guaranteed. In contrast to the positive results for specific species, Kerdoncuff et al. (2023) observed no increase in the compositional variation of carabid assemblages following burning, a result influenced by the study's focus on a limited set of dry ridges. This finding is in direct contrast to studies in different ecosystems. For example, Sprössig et al. (2022) found a clear positive relationship between carabid diversity and changes to microhabitats following river restoration in Germany. Their study, which compared pre- and post-restoration communities, showed improvements in both the number of specialist species and indicator species of conservation concern.

The weight of evidence from these contrasting studies shows that the success of restoration for carabid beetles is not universal. Instead, it is highly conditional on the specific habitat requirements of the target species and the ecological conditions of the site. Restoration activities can create conditions that favour certain species, particularly generalists, emphasising the dynamic nature of restoration techniques on carabid communities and the need for carefully tailored approaches to restoration strategies.

1.6.4 Carabid Community Responses to Conifer Removal and Habitat Structure

The relationship between vegetation structure and carabid diversity has been explored in various forest habitats (for instance, Januschke et al., 2011; Borchard et al., 2014 and Pakeman and Stockan, 2014), with compelling evidence indicating that conifer removal and the resulting increase in habitat openness have a significant and often positive impact on carabid assemblages. Studies in UK coniferous production forests, for instance, found that increasing canopy cover tended to drive down carabid functional diversity, likely due to the exclusion of open-habitat specialists (Spake et al., 2016). This is reinforced by findings that forest specialist carabid species increase with stand age, while non-woodland species decline, further illustrating how habitat structure influences species composition over time (Spake et al., 2016).

The synthesis of multiple studies confirms this pattern, showing that conifer felling creates conditions that are particularly beneficial for open-habitat species. For example, research on montane heathlands found that restored habitats supported diverse assemblages of arthropods, with early-stage restoration activities improving the number of heathland indicator species (Fartmann et al., 2022). Similarly, Gardiner and Vaughan (2008) found that even small-scale conifer felling increased invertebrate species richness, while Pedley et al. (2023) observed that open-habitat specialist arthropods dominated within the first seven years after felling. This mirrors previous research that found high arthropod richness after clear-felling, as it creates conditions akin to heathland in the earlier successional stages (Magura et al., 2015).

However, the relationship between canopy cover and carabid diversity is not always straightforward, as there can be conflicting findings and regional variability. For instance, while Spake et al. (2016) emphasised the role of canopy gap creation, other research found positive correlations between carabid abundance and canopy cover, suggesting that denser canopies can also influence species distribution (Yu et al., 2007). This is further complicated by habitat fragmentation, where practices like conifer felling can lead to the increased dominance of a few species and a decline in overall species richness (Fujita et al., 2008; Niemelä, 2001).

Despite these complexities, a clear consensus emerges: vegetation structure, especially the presence of open habitats, is a primary driver of carabid community structure, encompassing assemblage, abundance and function. Studies in restored heathlands found that plant traits were the strongest predictor of carabid traits (Pakeman and Stockan, 2014), and that restored sites with greater bare ground and herbaceous cover supported different carabid assemblages than montane heathlands with dense dwarf shrubs (Borchard et al., 2014). This collectively highlights the critical importance of a nuanced, site-specific approach to restoration that prioritises the creation and maintenance of the specific habitat features that target species require.

1.7 Gaps in Knowledge

Previous research has explored the impacts of heathland restoration on beetle communities across various heathland types (such as in montane or coastal heathlands; Schirmel and Buchholz, 2011; Schirmel et al., 2011; Cameron and Leather, 2012; Borchard et al., 2014; Walmsley et al., 2021; Fartmann et al., 2022) and the felling of conifers (Lin et al., 2007; Pedley et al., 2023). While these studies elucidate the effects of management practices on biodiversity, this project introduces several novel dimensions. Firstly, it specifically investigates the impact of conifer felling as a restoration technique within both wet and dry lowland heath, examining its influence on carabid community structure. This dual habitat focus, particularly within a single geographic region, appears to be less common in existing literature. The Dorset Heaths' unusual juxtaposition of wet and dry heaths offers a unique opportunity for direct comparisons across habitat types and restoration ages with a shared climatic and geographic context, providing insights often inaccessible in more homogenous systems. Secondly, this research incorporates a spatial perspective by investigating the microtopographical influences of felling: it compares carabid abundance and richness between ridges and furrows within restored sites, offering a detailed understanding of how these microhabitats contribute to overall diversity. Thirdly, this study assesses functional trait abundance across pre-treatment (forested) and restored heaths (of different ages), providing insights into how restoration affects functional diversity and the ecological roles of carabid beetles following conifer felling. Finally, this research analyses both alpha diversity (within-habitat) and gamma diversity (regional) (Andermann et al., 2022), and examines how carabid richness relates to environmental factors such as soil moisture, relative humidity, ground temperature and vegetation structure.

Together, these analyses provide a comprehensive assessment of carabid community dynamics in response to felling. This integrated approach, combining field data from 2024 with statistical analyses, allows for a deeper understanding of how heathland restoration through conifer removal affects carabid communities and their functional roles within these valuable ecosystems.

1.8 Study Aims and Hypotheses

This study aims to examine the impact of heathland restoration via conifer removal on ground beetle (Carabidae) communities. The research is guided by the following hypotheses, which are grounded in in established ecological understanding of carabid habitat preferences and community dynamics.

1. a) Carabid species richness will be higher with moderate levels of soil moisture, ground temperature, and relative humidity, but lower with extreme values of these variables.

    Reasoning: Ground beetles are highly responsive to microclimatic conditions. Moderate soil moisture and humidity are necessary to avoid desiccation, while temperature influences metabolic and reproductive activity. Extreme conditions such as flooding or overheating can reduce activity and survival, particularly for less mobile or specialist species.

1. b) Carabid species richness will be highest in sites with greater bare ground cover and low-lying vegetation, and will decrease with increasing shrub and tree cover, bracken height and leaf litter depth.

Reasoning: Vegetation structure affects habitat complexity, microclimate, and food availability. Bare ground supports thermophilic species and facilitates movement, while dense vegetation and leaf litter can reduce light penetration, increase humidity and create physical barriers to foraging. These conditions may limit colonisation, particularly for xerophilic or active-hunting beetles.

2. Recently restored heathland sites will support higher carabid species richness and total abundance compared to established heathland and forested sites.

   Reasoning: Restoration through conifer removal is expected to create heterogeneous, early-successional environments that facilitate colonisation by both specialist and generalist species. In contrast, established heathland may be more structurally uniform, and coniferous forest tend to have lower light levels, deeper leaf litter, and limited understorey, all of which are typically associated with reduced carabid diversity.

3. Carabid species composition will differ significantly between restored heathland, established heathland, and forested areas.

   Reasoning: Each habitat type supports distinct carabid assemblages due to differences in microclimate, vegetation structure, soil conditions and historical land use. Restoration is known to increase beta diversity (e.g. turnover and nestedness) by reintroducing environmental gradients and structural complexity. This hypothesis addresses community-level shifts resulting from restoration interventions.

4. Carabid functional traits will differ significantly between habitat types. Specifically, restored heathland sites will support smaller-bodied, macropterous species with open-habitat preferences, traits associated with colonisation and persistence in dynamic, early successional environments. Established heathland sites are predicted to favour species with intermediate traits, such as moderate body length and wing dimorphism, and a preference for drier ground and denser vegetation.

Forested sites are predicted to support larger-bodied, brachypterous species with preferences for densely vegetated and damp habitats.

Reasoning: Functional traits reflect species' ecological roles and habitat preferences. Open, early successional habitats often support smaller, highly mobile species adapted to dynamic and changing environments, whereas forested habitats may favour larger, flightless, litter-dwelling species displaying preferences for cooler, shaded and damp environments in a more stable setting. Trait-based analysis can therefore reveal changes in ecosystem function associated with felling as a form of habitat restoration.

2. Method

2.1 Study Area

The Purbeck Heaths in southern England, recognised for their size and aesthetic value, were designated a National Nature Reserve (NNR) in 2020 by Natural England (Dorset National Landscape, 2025a). The 3,331-hectare area, called the Purbeck Heaths Super National Nature Reserve (PHSNNR) consists of 11 priority habitats (Natural England et al., 2020), including the Rempstone and Godlingston Sites of Special Scientific Interest (SSSI) (Forestry Commission, 2013a; Natural England, 2018), and is recognised as a Special Area of Conservation (SAC) primarily due to its Northern Atlantic wet heaths with *Erica tetralix* and European dry heaths (JNCC, n.d.). The heaths experience a temperate maritime climate characterised by mild winters, cool summers and relatively high annual rainfall (Met Office, 2016; Dorset National Landscape, 2025b), which influences the region's diverse habitats, including lowland heathlands, wetlands, and woodlands, which support a rich variety of flora and fauna (JNCC, n.d.). The PHSNNR is actively managed by seven landowners: the National Trust (NT), Natural England (NE), the Royal Society for the Protection of Birds (RSPB), Forestry England (FE), the Rempstone Estate, Dorset Wildlife Trust (DWT) and Amphibian and Reptile Conservation Trust (ARC Trust) (Dorset National Landscape, 2025a) (Figure 1). Establishment of this multi-party stakeholder approach to conservation follows on from suggestions made in the Lawton report: to optimise spatial planning in restoration of ecological networks (Lawton et al., 2010). This aligns with the principles outlined in the report, which emphasise not only the restoration of ecological networks through spatial planning but also the importance of improving habitat connectivity through targeted land management.

The forest in the NNR, Rempstone Forest, is a conifer woodland planted deliberately in the 20th Century for timber to be used as building materials (Forestry Commission, 2013a). While annual monitoring in the PHSNNR has collated data on heathland birds, footfall, and fire damage extent (Panter and Caals, 2023), data is lacking on invertebrate populations in the restored areas where 120 hectares of conifer plantation have been felled (Forestry Commission, 2013b). The felling and removal of plantation patches in Rempstone, planned by Forestry England since 2013 (Forestry Commission, 2013b) was expected to enhance habitats by restoring open heaths and mires while creating patches of scrub and woodland (Forestry Commission, 2013a). The objective was to better connect the fragmented heathland habitats and to improve resilience of species populations and the landscape (Forestry Commission, 2013b; Purbeck Heaths, 2025a). The work also contributed towards the Open Habitats Policy (Forestry Commission, 2013b) and Natural England's 21st Century National Nature Reserve Strategy, in which the tailored management of nature reserves encourages environmental recovery (Natural England, 2016). The restoration of Rempstone heathlands through conifer clear-felling by the Forestry Commission plantation (Forestry Commission, 2013b) provides an ideal opportunity to investigate conifer removal as a restoration technique.

2.2 Preparation

Prior to data collection, a risk assessment was completed (Appendix 8.1), and an ethics check was conducted (Appendix 8.2). All work was approved by Bournemouth University. Permission was then obtained to conduct carabid and vegetation surveys from the Rempstone and Godlingston Heath landowners, the Rempstone Estate and Forestry England, with permission from Natural England for work taking place on Sites of Special Scientific Interest (SSSIs) within the Purbeck Heaths National Nature Reserve (Natural England, 2018, 2024) (Appendix 8.3).

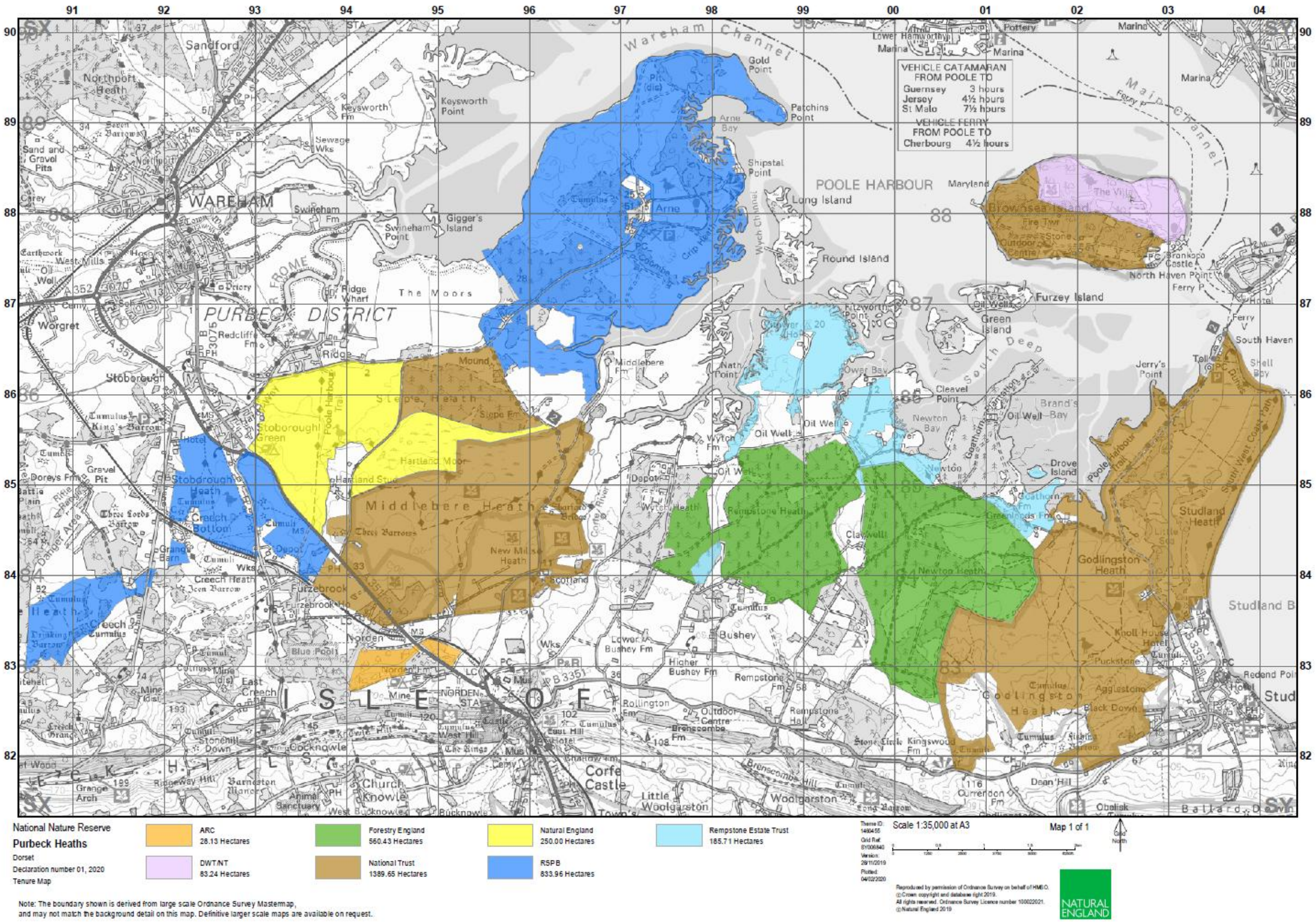


Figure 1. Map of Purbeck Heaths NNR, shaded to display the tenure of the seven landowners: ARC, Forestry England, Natural England, Rempstone Estate Trust, Dorset Wildlife Trust, National Trust and Royal Society for the Protection of Birds. Rempstone and Godlingston heaths are shaded green and brown, respectively. The map is taken from a publication on the Purbeck Heaths website (2025a), and contains Ordnance Survey data © Crown copyright and database rights 2025 Ordnance Survey (AC000085194), and tenure data © Natural England, 2020.

Potential survey locations in Rempstone and Godlingston were identified from an existing list of Student Environmental Research Teams (SERT) squares previously surveyed for vegetation by Bournemouth University students (Appendix 8.4). SERT squares were selected by these teams of placement students in partnership with academic mentors and professional practitioners for previous research (Bournemouth University, n.d.), and these locations were translated onto maps provided by Clegg (2024), to ascertain the management practices applied in each area. Locations subject to multiple forms of management (such as burning, scraping, and/or grazing in addition to felling) were excluded to avoid overlapping of categories, which could complicate analysis. This preliminary filtering resulted in three broad habitat categories across two heathlands: established forest, established heathland and restored heathland in Rempstone and Godlingston Heaths.

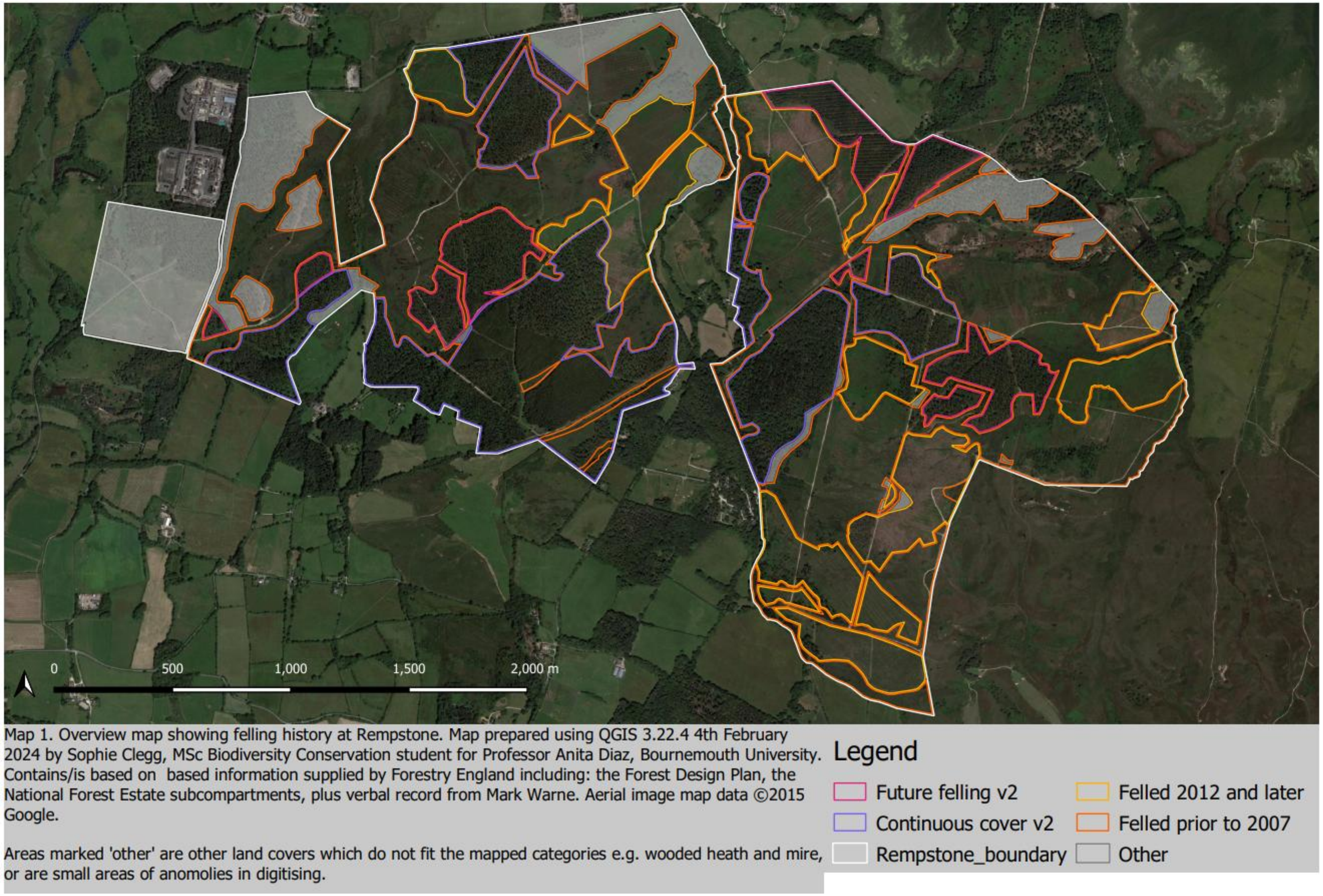


Figure 2. Map created by Clegg (2024) displaying areas in Rempstone that were subject to clear felling both before 2007 (outlined in dark orange) and after 2012 (outlined in light orange), and areas that will be left as continuous cover (outlined in purple) by Forestry England. Forested sites and restored heathland sites were finalised using this map.

Initial walkovers were conducted in January 2024 to classify both established and restored heathlands as either 'wet' or 'dry' based on their vegetation and characteristics. For example, locations with sandy, free-draining soils and dominated by *Calluna vulgaris* and/or *Erica cinerea* with *Ulex* species were classified as dry heaths (Chapman et al., 1989a) while locations lacking in *Calluna* coverage and instead dominated by *Erica tetralix* with *Sphagnum* species, or *Molinia caerulea*, and often *Drosera*, in waterlogged soils were classified as wet (Chapman et al., 1989a). Locations with ambiguous classifications (for example, areas with wet ground but dominated by dry heathland species such as *Erica cinerea*) were excluded from the study to ensure accurate classification and minimise systematic error arising from mixed habitat characteristics. By excluding these transitional sites, the risk of pseudo-replication was reduced, improving reliability of the results (Heffner et al., 1996). Locations within 100 metres of an adjacent site were excluded from the study to reduce spatial autocorrelation (Gillingham et al., 2012) and those within 5 metres of a public footpath were excluded to minimise the chances of trap removal or trampling.

A total of 35 sites were selected across seven habitat types:

1. Conifer canopy cover (henceforth referred to as 'Forest')
2. Established wet heathland (henceforth referred to as 'Wet Heath')
3. Established dry heathland (henceforth referred to as 'Dry Heath')
4. Restored wet heathland where felling occurred between 1990 and 2007 (henceforth referred to as 'Old Wet heath')
5. Restored dry heathland where felling occurred between 1990 and 2007 (henceforth referred to as 'Old Dry heath')
6. Restored wet heathland where felling occurred from 2012 onwards (henceforth referred to as 'New Wet heath')
7. Restored dry heathland where felling occurred from 2012 onwards (henceforth referred to as 'New Dry heath')

Five sites that fitted the above criteria (5 metres from a path, 100 metres from an adjacent site) were selected within each of these seven habitat types (5 sites * 7 habitat types = 35 sample sites). A 120-centimetre bamboo marker was placed at the coordinates with a small section of red tape at the top for easier site location (Figure 3). Final sites were mapped using QGIS (QGIS Developer Team, 2023), with each site being assigned a unique number from one to five, starting from the westernmost point in each habitat category (Table 1, Figure 4).

Figure 3. An example of a closed pitfall trap located 5 metres from the central bamboo marker. This trap was labelled OD1b, indicating it was the trap to the East of site OD1 in the Old Dry heath category, a site restored by conifer felling between 1990 and 2007.

Table 1. Identification codes assigned to the 35 sample sites based on their habitat categorisation.

Habitat Type	**Dry**	**Wet**
‘Old’ restored heath (felled between 1990 and 2007)	OD1	OW1
	OD2	OW2
	OD3	OW3
	OD4	OW4
	OD5	OW5
‘New’ restored heath (felled from 2012 onwards)	ND1	NW1
	ND2	NW2
	ND3	NW3
	ND4	NW4
	ND5	NW5
Permanent Heathland	DH1	WH1
	DH2	WH2
	DH3	WH3
	DH4	WH4
	DH5	WH5
Permanent Forest	F1	
	F2	
	F3	
	F4	
	F5	

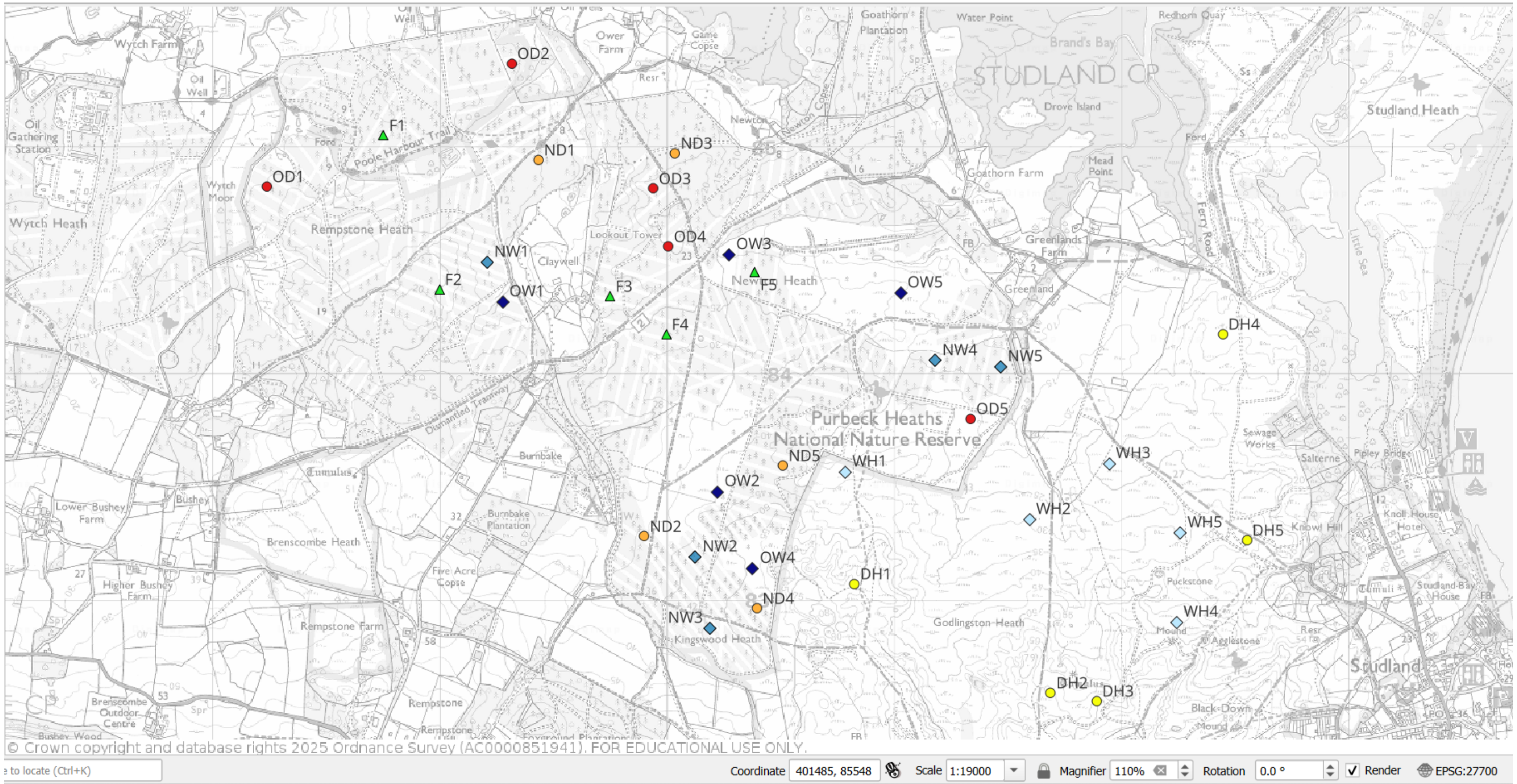


Figure 4. Locations of the 35 sample sites and their codes. Green triangles = Forest, yellow circles = Dry Heath, orange circles = New Dry heath (dry heathland restored after 2012), red circles = Old Dry (dry heathland restored between 1990 and 2007), pale blue diamonds = Wet Heath, sky blue diamonds = New Wet heath (wet heathland restored after 2012), navy blue diamonds = Old Wet (wet heathland restored between 1990 and 2007). © Crown copyright and database rights 2025 Ordnance Survey (AC0000851941). This map may not be copied, reproduced, or distributed without permission.

2.3 Sampling Carabids

The primary method for carabid capture was pitfall trapping. Due to its simplicity and cost-effectiveness, pitfall trapping is preferred over alternative procedures such as panel traps and light traps – both useful for collecting pest species (Liu et al., 2007; Preti et al., 2021) – as well as beat sheets, sweep nets, aspirators, and baits (Grootaert et al., 2010). Moret and Gobbi (2024) compared pitfall trapping and hand searching in alpine grasslands, finding that while both methods are effective and affordable, pitfall trapping is more time-efficient for assessing carabid diversity. Their findings offer guidance on method selection based on research objectives.

The placement of pitfall traps can influence capture rate and sampling accuracy: Kerdoncuff et al. (2023) cored out soil when setting pitfall traps to minimise soil disturbance, whereas various other studies (for instance, Cameron and Leather (2012) and Gillingham et al. (2012)) used hand trowels for excavation. Schirmel et al. (2010) recognised that intense trampling around pitfall traps likely increases carabid capture, supporting earlier work by Topping and Luff (1995), which focused primarily on spiders. These findings align with Woodcock (2005), who reported that carabid capture rates temporarily increase in response to environmental disturbance, a phenomenon known as the ‘digging-in’ effect.

The effectiveness of pitfall trapping for capturing carabid beetles can be influenced by trap design and colour. Schirmel (2010) used white pitfall traps, a colour demonstrated to enhance capture efficiency for both carabids and spiders. This challenges earlier assertions by Luff (1975), who found that glass traps were the most effective among various materials tested, including plastic and metal, both for collecting samples and retaining them. Luff's study indicated that glass traps outperformed others, potentially due to their smooth interior surfaces reducing escape rates. Further research by Buchholz et al. (2010) revealed that the impact of trap colour on arthropod capture is species-dependent, supporting van der Drift's observation (1951) that carabids in the *Notiophilus* genus are visual hunters with large eyes (Morris, 2000) which rely on visual cues during predation. Consequently, brightly coloured traps, such as white or yellow, may attract these visually oriented species more effectively. However, the use of coloured traps can also lead to increased bycatch of non-target species. Pollinators, for instance, might be drawn to traps that mimic common flower colours, resulting in unintended captures. Therefore, while optimising trap colour can enhance target species capture, it is essential to consider the potential for increased bycatch and adjust trapping protocols accordingly. As well as colour, material and size also influence carabid capture: Luff (1975) found smaller traps caught smaller carabids more effectively, and larger traps caught larger carabids. Similarly, Work et al. (2002) reported that although larger traps captured more individuals overall, species richness and composition did not significantly differ. These suggest that larger traps may not necessarily improve biodiversity assessments.

Whilst dry trapping is suitable for short-term capture, best practices recommend using killing agents to reduce in-trap predation and improve sample retention (Grootaert et al., 2010). Studies have used various solutions often mixed with detergent to reduce surface tension, ensuring rapid euthanasia of trapped specimens. Recent examples include Sprössig et al. (2022) who used 10% acetic acid and a small amount of liquid detergent, and Moret and Gobbi (2024) who combined wine vinegar, salt and a drop of soap. Pakeman and Stockan (2014), Skłodowski (2014) and Pedley et al. (2023) used ethylene glycol alone, while Schirmel (2010) combined detergent with ethylene glycol. Lange et al. (2023) used detergent with formalin – a highly toxic killing-preserving agent. However, formalin is known to attract certain arthropod species, potentially biasing results (Topping and Luff, 1995; Skłodowski, 2014). Similarly, ethylene glycol has been suggested as an attractant to carabids by Topping and Luff (1995), although the inclusion of detergent mitigates some of these issues (Schirmel 2010). The primary drawback of using detergent alone is its lack of preservation properties, leading to sample degradation over extended periods. However, in the current study, samples were collected every three days, minimising this concern.

Schirmel et al. (2010) found that longer sampling intervals during pitfall trapping resulted in decreased capture efficiency of ground-dwelling arthropods compared to shorter periods. This may be due to greater opportunities for escape, such as climbing out over other trapped species, plant debris or soil matter. Work by Pedley et al. (2023) was conducted over a two-month sampling period, which may not fully account for seasonal variation. As the data were collected in a limited timeframe, they may not capture the full range of seasonal changes that could influence the study’s findings, such as precipitation, temperature and species activity. As a result, the conclusions drawn from this short-term study might not be fully representative of patterns that occur throughout the entire year. Alternately, Homburg et al. (2019) studied carabid beetles over a 24-year period, providing a much longer-term perspective on population trends and seasonal variations. This extensive timeframe allowed for a more comprehensive analysis of species richness and phylogenetic diversity declines, which were influenced by complex interactions between habitat stability, pesticide use, species traits and climate change. Such long-term studies help distinguish between local and global drivers of insect decline and assess the effectiveness of conservation efforts.

In the present study, pitfall trapping was conducted to assess carabid communities across different heathland sites, and traps were set-up over the course of two weeks during late April 2024 before being opened in May. The delay before opening pitfall traps to survey was to minimise capture bias caused by the digging-in effect (Woodcock, 2005). Additionally, this optimised survey efficiency by ensuring traps were pre-set and ready for data collection. During pitfall trap set-up, four holes were excavated at each sample site (hereby called traps) positioned 5 metres to the North (trap a), East (trap b), South (trap c) and West (trap d) of the central marker. A metre rule was used to measure distances and a hand-trowel for excavation; a pitfall trap was set into each hole to catch carabids. At restored (Old Wet heath, New Wet heath, Old Dry heath and New Dry heath) sites, two traps were set in the elevated ridges and two in the furrows – features created by soil disturbance for drainage during the process of afforestation (Campbell et al., 2019) (Figure 5(a) and 5(b)). In contrast, at Forest, Wet Heath and Dry Heath sites, traps were set without regard to surface type.

While pitfall trapping is effective for sampling active ground-dwelling beetles, it is important to acknowledge certain ecological limitations of this method. Larval stages of some carabid species may be present concurrently with adult stages of others, yet larvae are typically subterranean and are thus underrepresented in surface-active trap samples (Woodcock, 2005). Likewise, adults of several species also exhibit subterranean (hypogean) behaviour or retreat below the surface during dry conditions, making them less susceptible to capture and more susceptible to desiccation (Brandmayr and Pizzolotto, 2016). These factors may introduce sampling biases, particularly in dry microhabitats or during low-moisture periods. These can be overcome by using traps at moderate densities, or by using subterranean traps placed 20-30 centimetres below ground level (Woodcock, 2005).

a)

b)

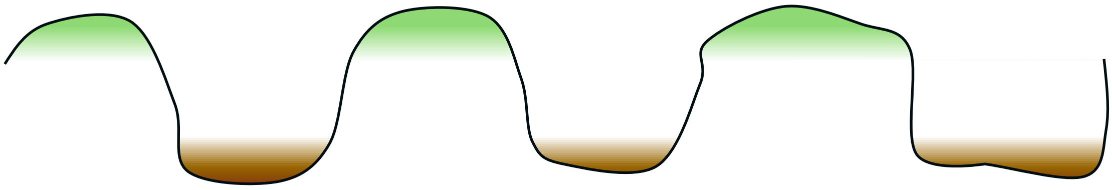


Figure 5. An example of a restored heathland site in the Purbecks. The raised ridges and deeper, flooded furrows created by ploughing during afforestation (Campbell et al., 2019) (a) are visible, and a cross-section of ridges and furrows in restored heathland sites. The ground presents as an undulating series of raised ridges (green) and deeper furrows (brown) (b).

Each pitfall trap consisted of a clear, 295ml plastic cup to hold back the soil and retain hole shape to minimise ground disturbance impacts on samples between survey periods (Brown and Matthews, 2016) without attracting non-target species. An identical cup was nested within this so that, on rainy survey days, the carabid samples would remain in the inner cup as it could float on rainwater collected in the outer cup. The inner cup held 80 millilitres of water with a drop of Ecover detergent to break surface tension of the water, reducing stress time of invertebrates between trapping and euthanisation. Detergent was used instead of ethylene- or propylene-glycol as a killing agent because a few drops alone are efficient in reducing water surface tension, and the substance would cause less harm to the environment if spilled on site (Holland, 2002). Additionally, it was not imperative to use a preservative substance as time between sampling and collection was short. This method was used over dry trapping to reduce in-trap predation of samples (Holland, 2002). In restored sites, care was taken to place the pitfall traps in the shallowest part of the furrows (Figure 5(b), Figure 6), where furrows were least likely to flood as this would greatly reduce the amount of sample capture.

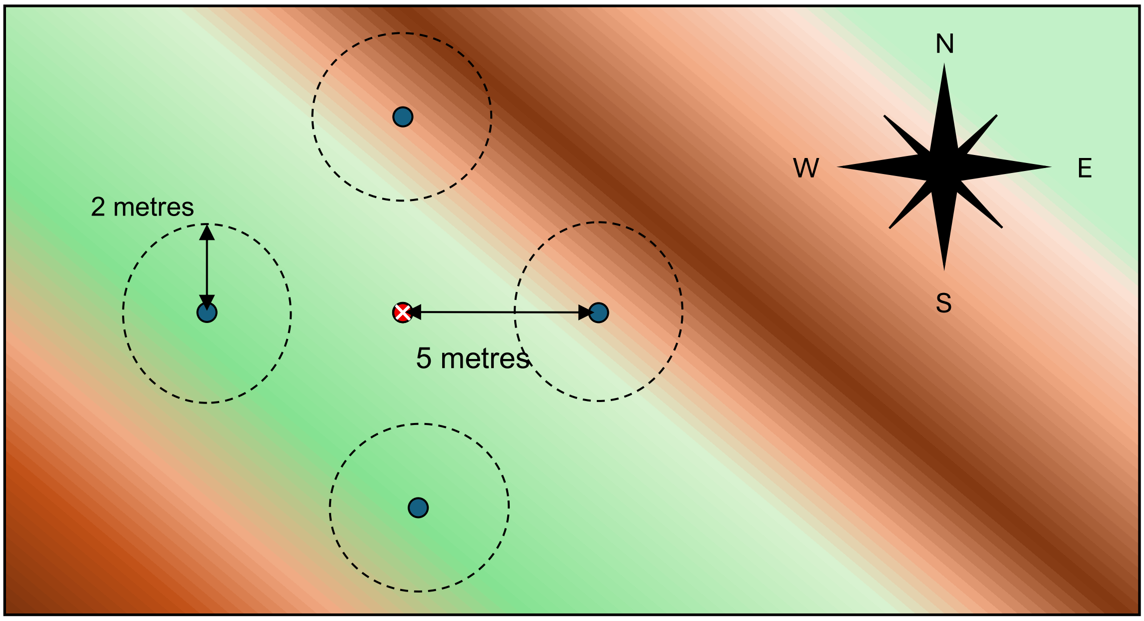


Figure 6. An example of the sample sites in restored heathlands and how they might have been set, where two traps were placed onto ridges (green) and two in furrows (brown) 5 metres from a central marker (x). The deepest part of the furrow is represented by the darkest shade of brown. Vegetation survey radials are represented by the dashed line around each trap.

All 35 sites were surveyed a total of four times: once each in May, June, July, and August 2024. Pitfall traps were opened over the course of three days during each sample period (6th to 8th May; 3rd to 5th June; 8th to 10th July; and 5th to 7th August). Three days was considered to balance likelihood of sample capture whilst ensuring all traps could be opened and closed consecutively within the same sample window. During opening, a 10 square centimetre layer of wire mesh (with hexagonal aperture size of 25 millimetres by 16 millimetres) was placed on top of the trap and secured using bamboo pegs to reduce accidental capture of larger non-target organisms such as amphibians and reptiles. After 72 hours the traps were collected (9th to 11th May; 6th to 8th June; 11th to 13th July; and 8th to 10th August).

Invertebrate samples were rinsed with water over a sieve into a waste container and transferred to 70% Industrial Methylated Spirit (IMS) in 15 millilitre sampling tubes using tweezers. Tubes were secured with a lid, taken to a laboratory and identified using a stereomicroscope. In the laboratory, carabid beetles were separated from other invertebrates and identified to species level where possible, using The Carabidae (ground beetles) of Britain and Ireland (Luff, 2007) and all species names henceforth are as in that book. *Pterostichus nigrita/rhaeticus* was not separated for this study due to the requirement of dissection for confirmation and is referred to as *Pterostichus nigrita/rhaeticus*. *Abax parallelepipedus* was not identified to subspecies level as it was assumed that the species present would be the only one resident in Britain (Luff, 2007), and that this is often not in practice nowadays (Zanella, 2016). Any samples irrelevant to this study, such as other invertebrates, were kept for use in future research but not included in this study. Traps collected from the August period were excluded from analysis due to trampling damage meaning not all sites had pitfall trap data during that period. All survey sites had functioning traps for the May, June, and July sampling periods.

2.4 Environmental Data Collection

Visual vegetation surveying took place once per sample site in May 2024 (Figure 3, Figure 6), prior to invertebrate sampling, as the change in heathland vegetation throughout the survey period was likely to be minimal (Delerue et al., 2018). Presence and absence of bare ground, graminoids, forbs, bryophytes, shrubs, and trees were recorded within a 2-metre radius of each trap within a sample site. For each site, the presence of each vegetation type was assessed across the four traps, resulting in a categorical measure ranging from 0 (absent at all traps) to 4 (present at all traps). Bracken height was measured in centimetres per trap at the end of the survey period using a metre rule.

Due to limited equipment availability, two different brands of data loggers were used across the sites. At 33 sites, an Onset UA-002-64 HOBO Pendant temperature and light data logger (HOBO, n.d.) was secured to the bottom of the bamboo marker using a cable tie and placed into the soil to measure ground temperature. At the remaining two sites, a Tiny Tag TGP-4500 Temperature and Humidity data logger was used, placed in the soil following the same method. Data loggers were buried into the top layer of soil to reduce the impact of high exposure to light on the temperature of the data logger, and thus impacting the temperature data recorded per site (Bramer et al., 2018) – this would have been particularly important in the open heaths.

Each survey period, soil moisture was recorded using a Lutron Soil Moisture meter (PMS-714) placed haphazardly four times per site within the 2-metre vegetation survey radials to a depth of approximately 10 centimetres. Considering flood potential was critical for soil moisture measurements, as the accuracy of the soil moisture probe decreases when the ground is saturated, likely due to the instrument’s maximum moisture content detection limit of 50% (Agricultural Supply Services, 2025). Relative humidity percentage was measured at the central marker using a Kestrel 3000 Weather meter once per survey period. The average of the soil moisture readings and the ground temperatures were calculated for each site to provide a single mean reading per site over the entire survey period.

2.5 Data Analysis

2.5.1 Species-Environmental Variables Relationships

Both Pearson’s correlations and Variance Inflation Factors (VIFs) were used to identify correlated continuous environmental variables (humidity, soil moisture, temperature, leaf litter depth and bracken height) and to minimise multicollinearity within regression models. Pearson’s correlation was applied to assess intercorrelations among these continuous environmental predictors and a correlation matrix was created to identify strong correlations (r > 0.6) (Appendix 8.5). In this analysis, average leaf litter depth and bracken height were highly correlated, so bracken height was removed. Redundant variables were further addressed by removing separate monthly values of relative humidity and soil moisture (May, June, and July), retaining only the mean values across the entire survey period (O'Brien, 2007). After excluding highly correlated variables, VIF was calculated using the *vif* function in the car package (Fox and Weisberg, 2019). The variable with the highest VIF was removed recursively until all VIFs were below 5, the threshold selected to minimise multicollinearity and reduce the risk of poorly estimated regression coefficients (Akinwande et al., 2015). As a result, maximum ground temperature was removed (Appendix 8.6). A Generalised Additive Model (GAM) was then fitted using the remaining continuous variables – total average humidity, total average soil moisture, average ground temperature, minimum ground temperature and average leaf litter depth – to assess the influence of continuous environmental variables on carabid species richness. The model structure for these variables was as follows:

Richness ~ s(Total average humidity) + s(Total average soil moisture) + s(Average ground temperature) + s (Minimum ground temperature) + s(Average leaf litter depth)

The s() terms represent smooth functions applied to variables (Wood and Augustin, 2002). To evaluate the individual importance of each continuous variables and assess the strength and direction of monotonic relationships with carabid species richness, Spearman's rank correlation analysis was also performed. Correlation coefficients (Spearman's ρ) were calculated between richness and each of the variables in the final GAM.

To analyse the categorical environmental variables, the presence of six vegetation categories – bare ground, bryophytes and lichens (hereafter 'lichens'), graminoids, forbs, shrubs and trees – was quantified per site. Each vegetation category was assigned an ordinal score from zero to four, representing the extent of its presence across the traps: 0 (absent in all four traps), 1 (present in one trap), 2 (present in two traps), 3 (present in three traps) and 4 (present in all traps). A correlation matrix was generated to identify any collinearity and, since none of the ordinal categorical variables displayed a correlation above 0.6 in the matrix, all variables were included in the Generalised Linear Model (GLM) with a Poisson distribution and a logistic link function to test the association between carabid richness and categorical environmental variables, using the following code:

```
model <- glm(Richness ~ Bare Ground + Bryophytes + Graminoids + Forbs + Bracken + Shrubs + Trees, family = poisson(link = log), data = VegData
```

Environmental variables were divided into continuous and categorical variables for separate analyses to reduce the risk of overfitting, given the large number of predictors in the GAM (Maloney et al., 2012). Species richness, as the response variable, is count data, which further guided the choice of appropriate modelling techniques (Dobson and Barnett, 2018). A GAM was used because it estimates non-linear relationships between the continuous environmental variables and carabid richness by using smooth functions, offering greater flexibility in modelling these complex effects (Pedersen et al., 2019). For ordinal, categorical environmental variables, a GLM with a Poisson distribution was fitted, as it supports ordinal regression and is suitable for modelling count data (Guisan and Harrell, 2000).

In each sampling period, carabid data from the four pitfall traps at Forest, Wet Heath and Dry Heath sites were pooled to generate a single species list per site. Traps located in ridges and furrows in restored sites (Old Wet heath, Old Dry heath, New Wet heath and New Dry heath) were kept separate, producing distinct species lists for each surface type in restored heaths to examine difference in diversity within these microhabitats for relevant analyses, but when comparing to the established habitats ridge and furrow data were also pooled per site. All statistical analyses were undertaken in the R environment (R Core Team, 2024).

2.5.2 Carabid Richness and Abundance

Preliminary analyses indicated that richness and abundance were not normally distributed (Appendix 8.7) so were subsequently analysed using non-parametric tests (Sanders et al., 2019). To examine the differences in carabid species richness and abundance between the seven habitat types (Forest, Wet Heath, Dry Heath, Old Wet heath, New Wet heath, Old Dry heath, New Dry heath, n= 35), Kruskal-Wallis tests were undertaken. Kruskal-Wallis tests were also used using the *Kruskal.test* function to examine differences in carabid species richness between ridges and furrows in restored sites (Old Wet heath, New Wet heath, Old Dry heath and New Dry heath, n = 40).

Estimated Gamma diversity was calculated among the seven habitat types using the Chao 2 estimator, using the *specpool* function from the vegan package in R (Oksanen et al., 2024). Chao 2 accounts for undetected species that may have been missed during sampling and requires only presence-absence data to estimate true species richness (Colwell and Coddington, 1994). A prevalence plot was created to visualise the accumulative species count from surface types in restored heathlands. The estimated gamma diversity across the seven habitat groups were considered significantly different if there was no overlap in the 95% confidence intervals, as this would suggest estimated species richness for a habitat is statistically different to another (Winner et al., 2018).

Unique species are those that were exclusively found in one of the seven habitats or surface types. These species were absent from all other habitats or surface types in the study and were identified manually from the raw dataset to check for distribution patterns in specialist carabids, which are more susceptible to ecosystem change (Kotze and O’Hara, 2003) and may contribute to turnover (see section 4.5.3).

2.5.3 Carabid Species Composition

Total beta diversity across habitats and within surface types (ridges and furrows) in restored sites was quantified using the *vegdist* function from the vegan package in R (Oksanen et al., 2024), calculating Bray-Curtis dissimilarity based on carabid composition. To visualise the variation in ecological communities, Non-Metric Multidimensional Scaling (NMDS) ordination plots were generated using the *metaMDS* function from the vegan package (Oksanen et al., 2024), based on the Bray-Curtis dissimilarity. Separate NMDS ordinations were conducted for (i) carabid communities within the two surface types in restored habitats (ridge and furrow) and (ii) carabid communities across the seven habitat types. Sites where no carabids were recorded (OW4R, OW4F, NW1R, NW1F, and OD4R) were omitted from the NMDS analysis. To statistically identify differences in carabid composition among (i) the two surface types in restored habitats and (ii) the seven habitat types, a ‘Permutational Analysis of Variance’ (PERMANOVA) was performed using the *adonis2* function in the vegan package (Oksanen et al., 2024). If PERMANOVA detected significant differences, a post-hoc pairwise PERMANOVA was conducted using the *pairwise.adonis* function (installed via GitHub) (Martinez Arbizu, 2020) to determine which habitat types differed significantly from each other.

To assess variation in carabid species composition between (i) the two surface types in restored habitats and (ii) each habitat type, the homogeneity of multivariate dispersions was examined using the *betadisper* function in vegan. One-way ‘Analysis of Variance’ (ANOVA) was performed to determine whether multivariate dispersion differed significantly across groups.

If ANOVA indicated significant differences in multivariate dispersions, a post-hoc Tukey’s Honestly Significant Difference (HSD) was conducted to identify which habitats exhibited greater variability in community structure. To further examine variation in carabid species composition, turnover and nestedness components of beta diversity were calculated using the *beta.div.comp* function from the betapart package in R (Baselga et al., 2023) using the Baselga Jaccard index. Species turnover refers to the replacement of one species by another between sites, indicating changes in species composition. In contrast, nestedness occurs when species poor sites contain only a subset of species found in species rich sites, reflecting patterns of species loss rather than replacement (Baselga, 2010). Results were visualised using stacked bar graphs generated in Excel.

2.5.4 Carabid Functional Traits

Functional traits were collated from the Handbook for the Identification of British Insects (Lindroth, 1974) the Provisional Atlas of the Ground Beetles (Coleoptera, Carabidae) of Britain (Luff, 1998), the Common Ground Beetles identification guide (Forsythe, 1987), The Carabidae (ground beetle) of Britain and Ireland identification guide (Luff, 2007), A Field Guide in Colour to Beetles (Harde, 1998) and Jelaska and Durbešić (2009) (Table 2). Sites where no carabid species were recorded were removed from the functional trait analysis as they provided no relevant data. Unidentified carabid species were also removed. For traits that fell within a range (for instance, body length) the midrange value was selected for categorisation. A Kruskal-Wallis test was performed to compare functional traits across the seven habitats. To determine where significant differences occurred, a post-hoc Dunn’s Test with Benjami-Hochberg (BH) correction was applied to adjust for multiple comparisons.

This method accounts for the non-parametric nature of the data, does not assume equal variances or normal distributions, and helps control for false discovery rate (FDR), reducing the likelihood of Type I errors while being less conservative than Bonferroni correction (Keselman et al., 2002). Stacked bar graphs were generated to illustrate trait prevalence across habitat types. It should be noted that these graphs do not display the Kruskal-Wallis test results, which are provided separately.

Table 2. Functional traits assigned to each species.

Category	Functional Trait	Categories	Value
Morphology		≤ 5mm	1
		> 5 - ≤ 10mm	2
		> 10 - ≤ 15mm	3
		>15 - ≤ 20mm	4
	Body Length	> 20 - ≤ 30mm	5
		Macropterous	1
		Brachypterous	2
	Wing Morphology	Dimorphic	3
Reproduction		Spring	1
		Summer	2
		Autumn	3
		Winter	4
	Breeding Season	Mixed	5
Habitat		Dry	1
Preference	Soil Moisture	Damp	2
	Preference	Wet	3
		Open	1
		Vegetated	2
	Vegetation Cover	Densely vegetated	3
	Preference	Other	4
Activity		Diurnal	1
	Diel Activity	Nocturnal	2
		Crepuscular	3

3. Results

3.1 Species Captured

A total of 354 individuals were identified from across 44 species (Table 3). One carabid remained unidentified but was included in the species richness analysis as a separate species as it was clearly different to all other identified species. All carabid species found were native to the UK, according to the IUCN (Telfer, 2016). Four species (each with a single individual) are categorised as Nationally Scarce: *Bembidion nigricorne*, *Carabus nitens*, *Pterostichus gracilis* and *Syntomus truncatellus*, and one species (13 individuals) categorised as Nationally Rare: *Anisodactylus nemorivagus* (Telfer, 2016). The most abundant and widely distributed species was *Abax parallelepipedus* (n = 71) appearing at 23 out of 35 sites. On average, around eight individuals were captured per species as a result of the sampling effort.

Table 3. List of carabid species found across the 35 survey sites in May, June and July. Nationally scarce species are marked with an asterisk (*) and nationally rare species are marked with a double asterisk (**).

Species	Total	Habitat(s) Most Frequently Found	Site(s) Most Frequently Found
Abax parallelepipedus	71	DH	DH1
Acupalpus dubius	2	NW	NW4R
Acupalpus parvulus	1	NW	NW2R
Amara aenea	5	ND	ND3F
Amara convexior	2	ND	ND5R
Amara lunicollis	2	ND	ND2R, ND4R
Amara tibialis	1	ND	ND4F
*Anisodactylus nemorivagus***	13	NW	NW5R
Bembidion guttula	1	OW	OW3R
Bembidion lampros	16	NW	NW2R
*Bembidion nigricorne**	1	NW	NW5R
Bembidion properans	1	NW	NW4F
Carabus arvensis	31	WH	WH1
*Carabus nitens**	1	WH	WH5
Carabus problematicus	3	NW and ND	NW3R, ND1R, ND4F

Carabus violaceous	2	F and ND	F3, ND3R
Cicindela campestris	2	DH and NW	DH4, NW3F
Dyschirius globosus	9	NW	NW2R
Harpalus affinis	2	ND	ND3F
Harpalus rufipes	1	ND	ND3F
Laemostenus terricola	1	DH	DH2
Leistus fulvibarbis	1	F	F3
Leistus spinibarbis	5	ND	ND2R
Nebria brevicollis	4	F, WH and DH	F3, WH1, WH2, DH4
Nebria salina	27	ND	ND5F
Notiophilus aquaticus	5	WH, NW and DH	WH1, NW3R, NW3F, ND2R, ND4F
Notiophilus biguttatus	4	ND	ND2R
Notiophilus germinyi	4	F	F3, WH1, OW2R, ND2R
Notiophilus palustris	4	F	F3
Notiophilus rufipes	2	F	F2, F3
Notiophilus substriatus	1	WH	WH1
Olisthopus rotundatus	1	OD	OD5R
Oxypselaphus obscurus	46	NW	NW4F
Platynus assimilis	1	NW	NW5R
Poecilus cupreus	2	DH and OW	DH3, OW3R
Poecilus versicolor	8	WH	WH3

Pterostichus diligens	2	NW	NW4F
*Pterostichus gracilis**	1	OW	OW2R
Pterostichus madidus	3	F	F3
Pterostichus minor	14	NW	NW4F
Pterostichus strenuus	5	OW	OW1F
Pterostichus nigrita/rhaeticus	40	NW	NW4F
Syntomus foveatus	4	OW and NW	OW2R, NW2R
*Syntomus truncatellus**	1	NW	NW3R
Unknown	1	ND	ND3F

Of the 26 species caught in restored sites, 11 were recorded only from ridges, 6 were unique to furrows, and 9 occurred in both (Table 4). Notable species such as *Bembidion nigricorne*, *Pterostichus gracilis* and *Syntomus truncatellus* were found unique to ridges, whereas *Anisodactylus nemorivagus* was only found in furrows. These results suggest that both ridges and furrows contribute to carabid diversity, likely providing distinct microhabitats and environmental conditions and hence the conservation significance of these different surface types.

Table 4. Carabid beetles found exclusively in ridges, furrows or shared between the two surface types. Nationally scarce species are marked with an asterisk (*) and nationally rare species are marked with a double asterisk (**).

Species	**Ridges**	**Furrows**	**Both**
Acupalpus dubius	✓		
Acupalpus parvulus	✓		
Amara aenea			✓
Amara convexior	✓		
Amara lunicollis	✓		
Amara tibialis		✓	
*Anisodactylus nemorivagus***			✓
Bembidion guttula	✓		
Bembidion lampros			✓
*Bembidion nigricorne**	✓		
Bembidion properans		✓	
Carabus problematicus			✓
Dyschirius globosus			✓
Harpalus affinis		✓	
Harpalus rufipes		✓	
Olisthopus rotundatus	✓		
Oxypselaphus obscurus			✓

Platynus assimilis	✓		
Pterostichus diligens		✓	
*Pterostichus gracilis**	✓		
Pterostichus minor			✓
Pterostichus strenuus			✓
Pterostichus nigrita/rhaeticus			✓
Syntomus foveatus	✓		
*Syntomus truncatellus**	✓		
Unknown species		✓	

A total of 22 species were unique to one of the seven habitat types (Table 5). All *Amara* species identified in this study *(aenea, convexior, lunicollis* and *tibialis)* were found only on restored heathland sites, as was the Nationally Rare *Anisodactylus nemorivagus* and Nationally scarce *Dyschirius globosus. Olisthopus rotundatus* was the only species unique to Old Dry restored heath. None of the species in the *Pterostichus* genus were found at New Dry heath, Old Dry heath or established Dry Heath or established Wet Heath. Most of these species were unique to restored wet sites (both Old Wet heath and New Wet heath).

Table 5. Carabid beetles found uniquely in each habitat type, and carabids observed in multiple habitats. Nationally scarce species are marked with an asterisk (*) and nationally rare species are marked with a double asterisk (**).

Species	Forest	Wet Heath	Dry Heath	Old Wet heath	Old Dry heath	New Wet heath	New Dry heath
Acupalpus dubius						✓	
Acupalpus parvulus						✓	
Amara convexior							✓
Amara lunicollis							✓
Amara tibialis							✓
Bembidion guttula				✓			
*Bembidion nigricorne**						✓	
Bembidion properans						✓	
*Carabus nitens**		✓					
Harpalus affinis							✓
Harpalus rufipes							✓
Laemostenus terricola			✓				
Leistus fulvibarbis	✓						
Notiophilus rufipes	✓						

Notiophilus substriatus		✓					
Olisthopus rotundatus					✓		
Platynus assimilis						✓	
Pterostichus diligens						✓	
*Pterostichus gracilis**				✓			
Pterostichus strenuus				✓			
*Syntomus truncatellus**						✓	
Abax parallelepipedus	✓	✓	✓	✓	✓	✓	✓
Amara aenea					✓		✓
*Anisodactylus nemorivagus***						✓	✓
Bembidion lampros				✓		✓	✓
Carabus arvensis		✓	✓			✓	✓
Carabus problematicus					✓	✓	✓
Carabus violaceous	✓						✓
Cicindela campestris			✓			✓	
Dyschirius globosus				✓		✓	
Leistus spinibarbis	✓				✓		✓

Nebria brevicollis	✓	✓	✓				
Nebria salina		✓				✓	✓
Notiophilus aquaticus		✓				✓	✓
Notiophilus biguttatus		✓				✓	✓
Notiophilus germinyi	✓	✓		✓			✓
Notiophilus palustris	✓			✓			
Oxypselaphus obscurus				✓	✓	✓	
Poecilus cupreus			✓	✓			
Poecilus versicolor	✓	✓		✓		✓	✓
Pterostichus madidus	✓					✓	
Pterostichus minor				✓		✓	
Pterostichus nigrita/rhaeticus				✓		✓	
Syntomus foveatus				✓		✓	

3.2 Species-Environmental Variables Relationships

After confirming the relatively low Variance Inflation Factors of the final environmental variables to be used in the GAM (Table 6), the correlation matrix generated (Appendix 8.5) showed that end bracken height was highly correlated with average leaf litter depth**.** End bracken height was removed from the final model, and average humidity, average soil moisture, average ground temperature, minimum ground temperature and average leaf litter depth were retained.

Table 6. Final VIF values for continuous environmental variables measured.

Continuous Variable	**VIF Value**
Average humidity	1.15
Average soil moisture	1.05
Average ground temperature	1.22
Minimum ground temperature	1.36
Average leaf litter depth	1.13

The model identified a statistically significant positive association between average ground temperature and carabid richness (Table 7), though it is possible the model may have overfit some aspects of the data. Site-level data broadly reflect this trend: the warmest restored site (ND3, 18.84°C) exhibited relatively high species richness (seven species, 15 individuals), while the coolest site (NW2, 14.39°C) had slightly lower richness (six species) but greater overall abundance (19 individuals). The remaining variables (average humidity, average soil moisture, minimum ground temperature and average leaf litter depth), while some may visually appear to correlate weakly with richness – particularly minimum ground temperature (Figure 7d) –, were not statistically significant in the model (Table 7). These results indicate that while some structural and climatic variables may influence carabid assemblages, average ground temperature is the strongest predictor of taxonomic richness in this dataset.

Table 7. Output from the GAM fitted to the continuous variables. Statistically significant results are highlighted in bold. (*n* = 35: average humidity, average soil moisture, minimum ground temperature average leaf litter depth. *n* = 25: average ground temperature).

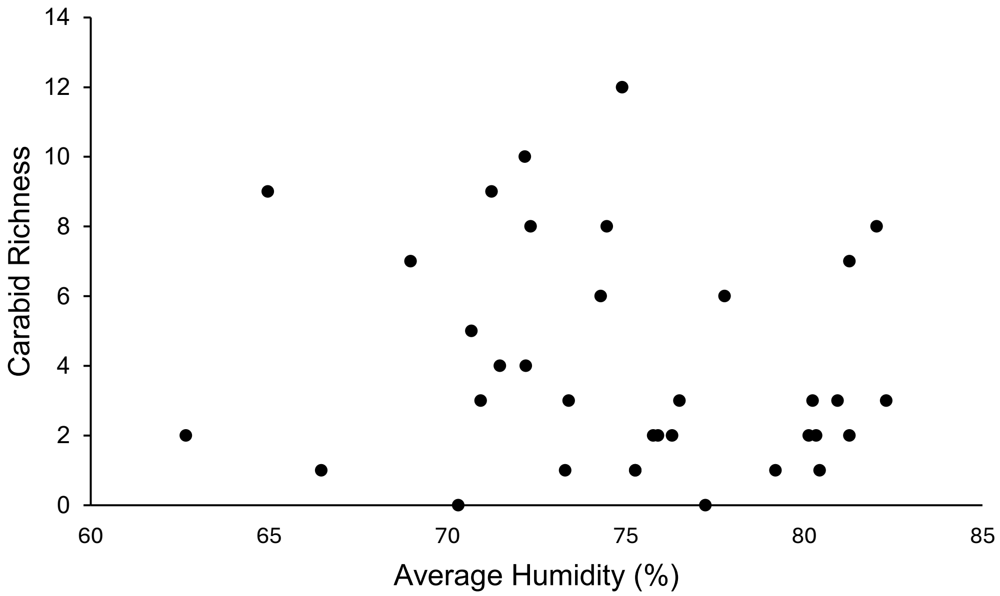
Parametric coefficients:

	Estimate	**Standard Error**	**t value**	**Pr(>|t|)**
(Intercept)	3.48	0.28	12.32	<0.001

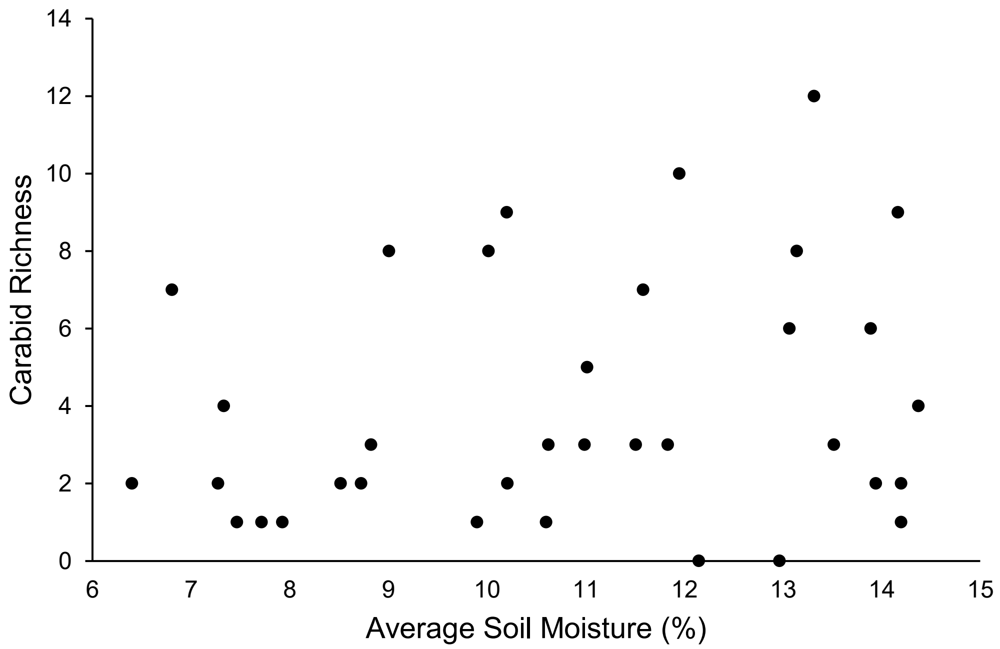
Environmental variable	edf	Ref.df	F	*p*-value
Average humidity	5.13	5.91	3.56	0.054
Average soil moisture	1.97	2.34	2.68	0.120
Average ground temperature	**4.83**	**5.68**	**3.91**	**0.034**
Minimum ground temperature	1.00	1.00	0.33	0.581
Average leaf litter depth	2.40	2.76	0.47	0.586

Visually, there were no strong linear trends between taxonomic richness and the continuous environmental variables assessed in the GAM (Figures 7a to 7e). Spearman's rank correlation revealed no significant relationship between carabid richness and average relative humidity (Spearman's ρ = –0.16, *p* = 0.350, *n* = 35), indicating that higher humidity levels do not strongly promote greater species richness in this system (Table 8). Similarly, no significant positive correlations were found between carabid richness and soil moisture (Spearman's ρ = 0.20, *p* = 0.252, *n* = 35) or minimum ground temperature (Spearman's ρ = 0.14, *p* = 0.506, *n* = 25). A weak, positive correlation approaching significance was observed between carabid richness and average ground temperature (Spearman's ρ = 0.391, *p* = 0.053, *n* = 25). This trend, despite the smaller sample size for temperature data, suggests that warmer microclimates may support greater carabid diversity (Table 8). Average leaf litter depth was significantly positively associated with richness (Spearman's ρ = 0.34, *p* = 0.045, *n* = 35), despite not being a significant predictor in the GAM. This suggests that its influence on richness may be confounded or overshadowed by other environmental factors, such as ground temperature, in the multivariate context (Table 7, 8).

a)



b)



c)

d)

e)

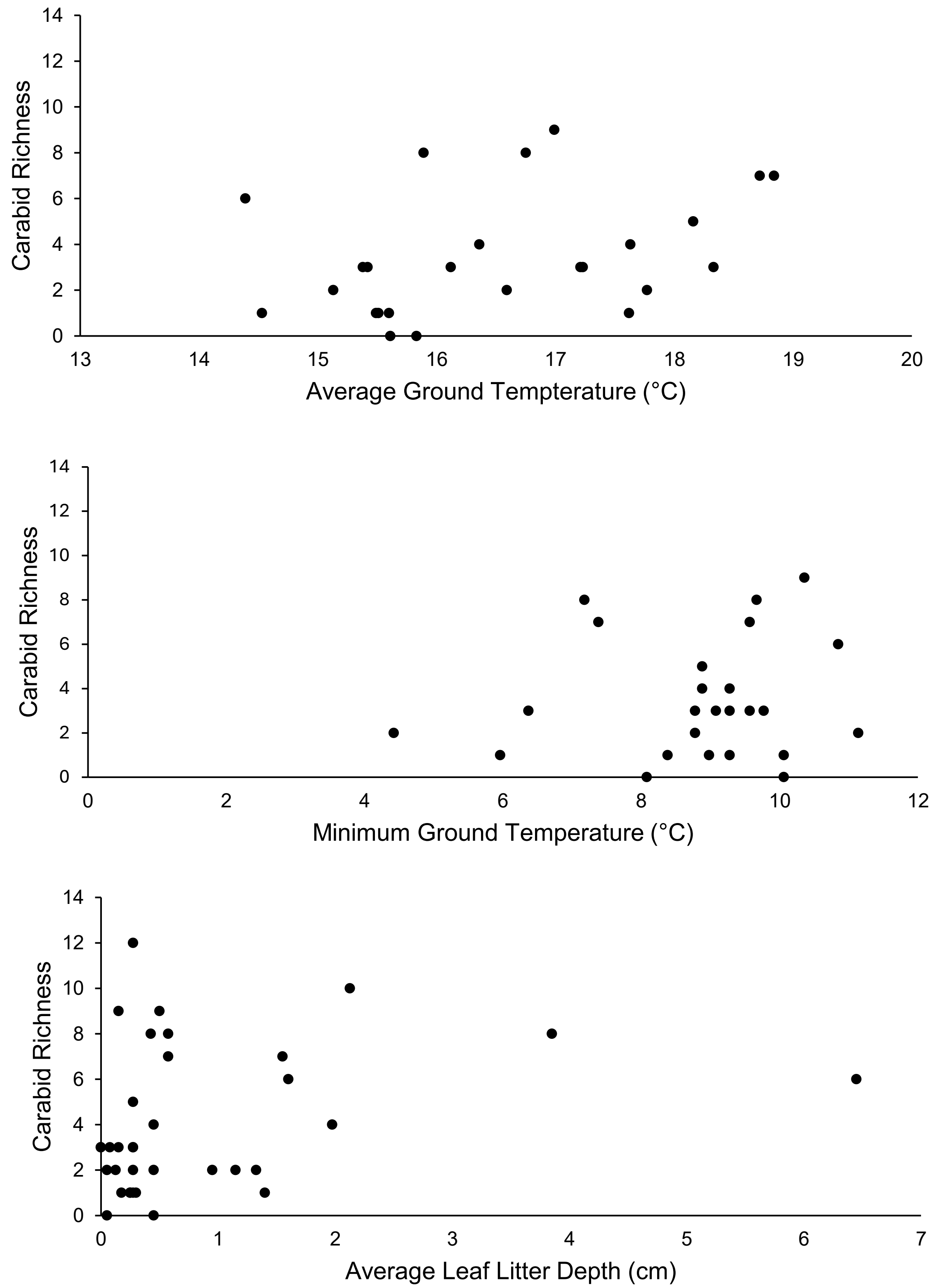


Figure 7. Scatter plots showing the relationship between carabid richness and continuous environmental variables: average humidity (a), average soil moisture (b), average ground temperature (c), minimum ground temperature (d) and average leaf litter depth (e) across all survey sites.

Table 8. Spearman's rank correlation coefficients (ρ) and associated *p*-values for the relationship between carabid beetle taxonomic richness and continuous environmental variables (average humidity, average soil moisture, minimum and average ground temperature, and average leaf litter depth) across all survey sites. Statistically significant results are highlighted in bold.

Continuous Variable	**Correlation Coefficient (ρ)**	***p*-Value**
Average Humidity	-0.163	0.350
Average Soil Moisture	0.199	0.252
Average Ground Temperature	0.391	0.053
Minimum Ground Temperature	0.139	0.506
Average Leaf Litter Depth	**0.341**	**0.045**

The GLM results indicate that tree presence was the only vegetation type significantly associated with carabid species richness, with a positive correlation (estimate = 0.22, $p < 0.01$), suggesting sites with more trees support a greater number of carabid species. In contrast, none of the other vegetation types – bare ground, bryophytes, graminoids, forbs, bracken, or shrubs — show statistically significant relationships with species richness, as all *p*-values exceed 0.05. Among these, graminoids (estimate = 0.15, $p = 0.22$) and bryophytes (estimate = 0.14, $p = 0.26$) have the highest positive estimates, though their effects remain non-significant. Bare ground has a near-zero estimate (-0.03), indicating little to no impact on richness. The variance inflation factor (VIF) values remain below 5, confirming that collinearity between variables is not a concern in the model. (Appendix 8.8), These results highlight a distinct contrast between tree presence and other vegetation types in their relationship with carabid species richness.

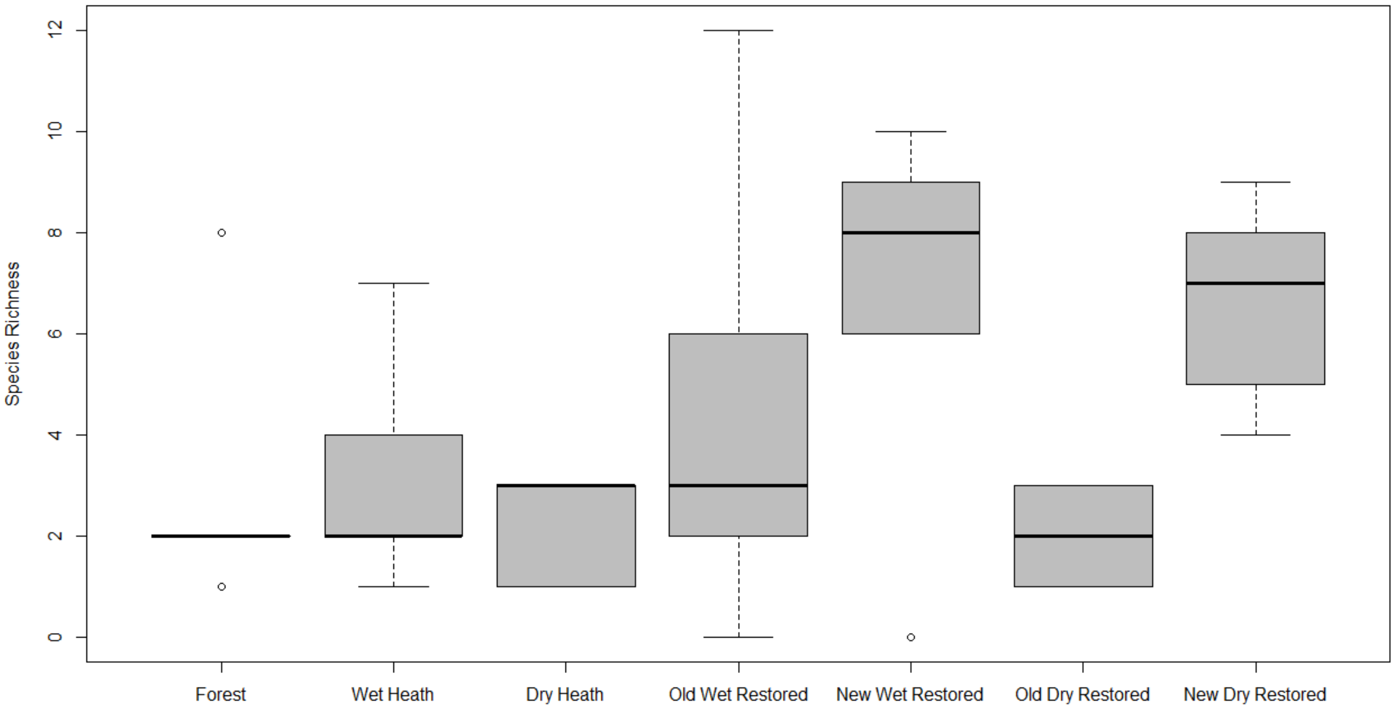
3.3 Carabid Richness and Abundance

Gamma diversity, representing total species richness across all habitats, was 44 species (Table 3). Site-level species richness varied among habitats, with New Wet restored sites supporting the highest richness between them (23 species). In contrast, Dry Heath and Old Dry restored heath exhibited the lowest richness, with only six species each across five sites. The site supporting the greatest carabid abundance (62) was NW4, while DH5 supported the lowest abundance (one), and no carabids were observed at OW4 or NW1 (Table 9).

Estimated gamma diversity for the different habitat types, based on the Chao index, ranged from 10.8 species in Dry Heath (95% CI: 0.35 - 21.95) to 52.4 species in New Wet restored heaths (95% CI: 5.83 - 99.00). The 95% confidence intervals for Forest and Wet Heath habitats overlapped entirely, while those for Forest, Wet Heath, Dry Heath, Old Wet heath and New Dry restored heath overlapped to varying degrees. However, the confidence interval for New Wet restored heath did not overlap with any other habitat, suggesting that its gamma diversity is significantly higher.

No significant differences were found in carabid species richness (Kruskal-Wallis test: Chi-squared = 10.09, p = 0.121, df = 6, n = 35), or abundance (Kruskal-Wallis test: Chi-squared = 11.22, p = 0.081, df = 6, n = 35) across the seven habitats surveyed (Figure 8(a) and 8(b)). The most species rich habitat on average was New Wet restored heath (median = 8.00), while Old Dry restored heath was the least species rich habitat on average (median = 2) (Table 9). On average, the most abundant habitat was New Wet restored heath (median = 19) while the least abundant was Forest (median = 2). Despite the lack of statistically significant differences, abundance patterns suggest that recent wet heath restoration may be particularly effective in enhancing carabid activity or population density.

a)



b)

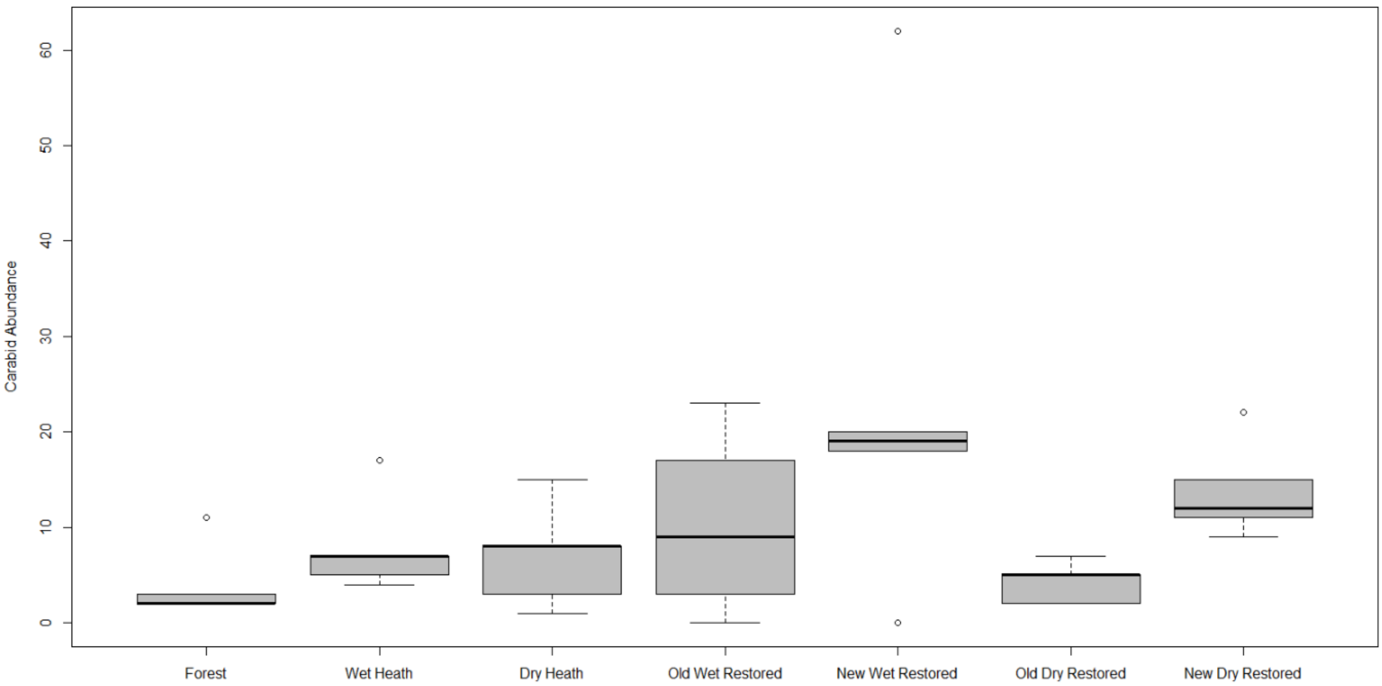


Figure 8. Carabid species richness per habitat type (a) and carabid abundance per habitat type (b). Boxes show 25th, 50th and 75th percentiles. Whiskers extend to the minimum and maximum values within 1.5 times the Interquartile Range (IQR). Centre lines show median values, and outliers are represented as open circles.

Table 9. Species count and most common carabids per survey site. Nationally scarce species are marked with an asterisk (*) and nationally rare species are marked with a double asterisk (**).

Site	Surface	Total species count	Most common species
F1	Other	2	*Abax parallelepipedus*
F2	Other	2	*Notiophilus rufipes, Poecilus versicolor*
F3	Other	11	*Abax parallelepipedus, Notiophilus palustris, Pterostichus madidus*
F4	Other	2	*Abax parallelepipedus, Notiophilus palustris*
F5	Other	3	*Abax parallelepipedus*
WH1	Other	17	*Carabus arvensis*
WH2	Other	7	*Carabus arvensis*
WH3	Other	7	*Carabus arvensis*
WH4	Other	4	*Carabus arvensis*
WH5	Other	5	*Carabus arvensis*
DH1	Other	15	*Abax parallelepipedus*
DH2	Other	8	*Abax parallelepipedus*
DH3	Other	8	*Abax parallelepipedus*
DH4	Other	3	*Carabus arvensis, Cicindela campestris, Nebria brevicollis*
DH5	Other	1	*Abax parallelepipedus*
OW1	Ridge	1	*Pterostichus minor*
OW1	Furrow	16	*Pterostichus nigrita/rhaeticus*

OW2	Ridge	17	*Oxypselaphus obscurus*
OW2	Furrow	6	*Pterostichus nigrita/rhaeticus*
OW3	Ridge	5	*Abax parallelepipedus*
OW3	Furrow	2	*Oxypselaphus obscurus*
OW4	Ridge	0	N/A
OW4	Furrow	0	N/A
OW5	Ridge	1	*Bembidion lampros*
OW5	Furrow	2	*Abax parallelepipedus*
NW1	Ridge	0	N/A
NW1	Furrow	0	N/A
NW2	Ridge	15	*Bembidion lampros*
NW2	Furrow	4	*Dyschirius globosus*
NW3	Ridge	12	*Oxypselaphus obscurus*
NW3	Furrow	6	*Bembidion lampros*
NW4	Ridge	22	*Oxypselaphus obscurus*
NW4	Furrow	40	*Oxypselaphus obscurus*
NW5	Ridge	16	*Oxypselaphus obscurus*
NW5	Furrow	4	*Oxypselaphus obscurus*
OD1	Ridge	2	*Abax parallelepipedus*
OD1	Furrow	3	*Abax parallelepipedus*

OD2	Ridge	1	*Carabus problematicus*
OD2	Furrow	1	*Abax parallelepipedus*
OD3	Ridge	4	*Abax parallelepipedus*
OD3	Furrow	3	*Abax parallelepipedus*
OD4	Ridge	0	N/A
OD4	Furrow	2	*Oxypselaphus obscurus*
OD5	Ridge	3	*Abax parallelepipedus, Olisthopus rotundatus, Oxypselaphus obscurus*
OD5	Furrow	2	*Abax parallelepipedus*
ND1	Ridge	5	*Abax parallelepipedus, Anisodactylus nemorivagus***
ND1	Furrow	4	*Abax parallelepipedus,*
ND2	Ridge	8	*Leistus spinibarbis, Notiophilus biguttatus*
ND2	Furrow	4	*Abax parallelepipedus, Anisodactylus nemorivagus**, Nebria salina, Poecilus versicolor*
ND3	Ridge	7	*Nebria salina*
ND3	Furrow	8	*Amara aenea, Harpalus affinis*
ND4	Ridge	4	*Abax parallelepipedus, Amara lunicollis, Anisodactylus nemorivagus**, Nebria salina*
ND4	Furrow	7	*Abax parallelepipedus*
ND5	Ridge	10	*Nebria salina*
ND5	Furrow	12	*Nebria salina*

At a gamma scale, more individual carabids were recorded in ridges (32) compared to furrows (22). However, at an alpha scale, the Kruskal-Wallis test found no significant differences in species richness between the two surface types on restored heaths, 'ridges' and 'furrows' (Chi-squared = 0.77, p = 0.38, df = 1, n = 40). (Figure 9(a)). Carabids were present in 17 out of 20 traps set in ridges, and 18 out of 20 traps set in furrows. Ridges supported a higher abundance of carabids (median = 4.50) compared to furrows (median = 4.00), but these differences were also not significant (Chi-squared = 0. 12, p = 0.73, df = 1, n = 40). (Figure 9(b)), Figure 9). Prevalence plots showed slightly more stable cumulative numbers for carabids collected from furrows compared to ridges (Figure 10), potentially indicating differences in species turnover.

a)

b)

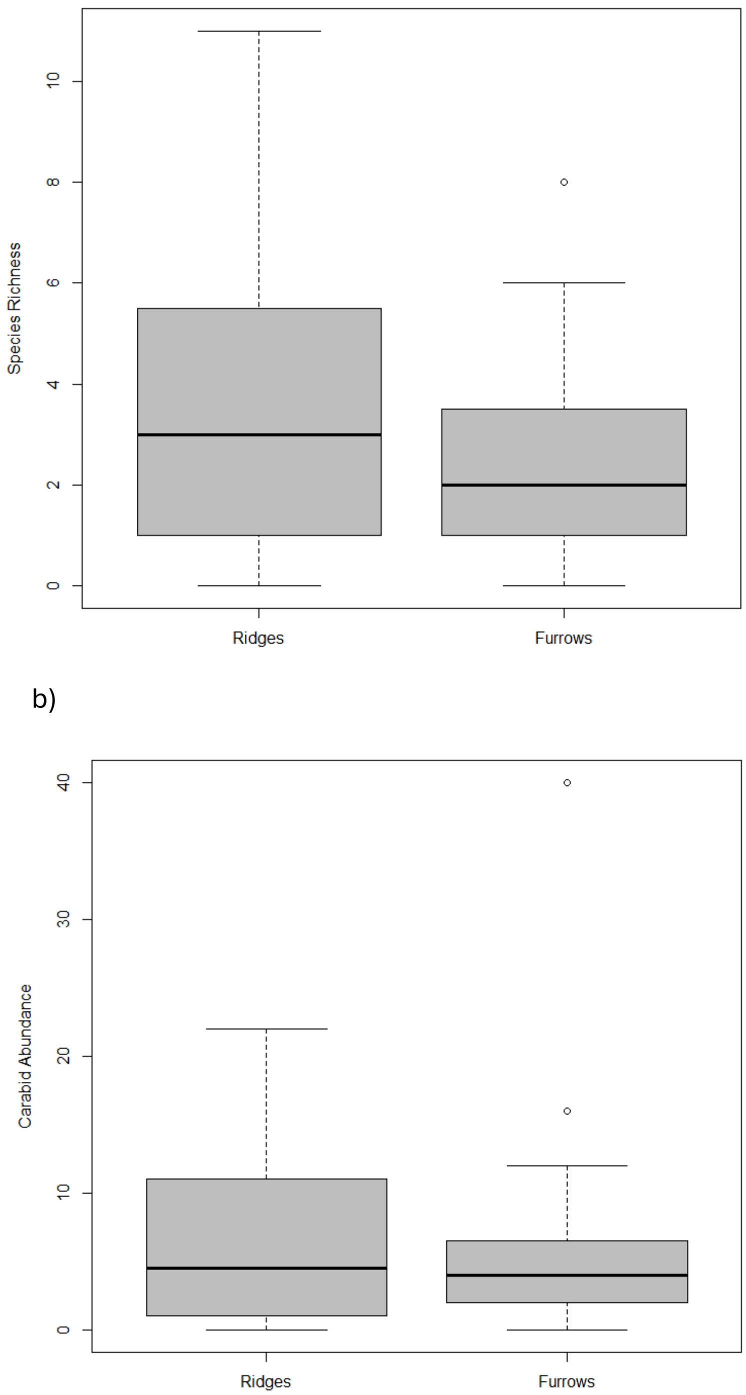


Figure 9. Boxplot displaying the species richness of samples collected from the two surface types (ridges and furrows) from 20 restored heathland sites (a) and carabid abundance per surface type in restored heathland sites. Outliers are represented as white circles. Boxes show 25th, 50th and 75th percentiles. Whiskers extend to the minimum and maximum values within 1.5 times the Interquartile Range (IQR). Centre lines show median values, and outliers are represented as open circles.

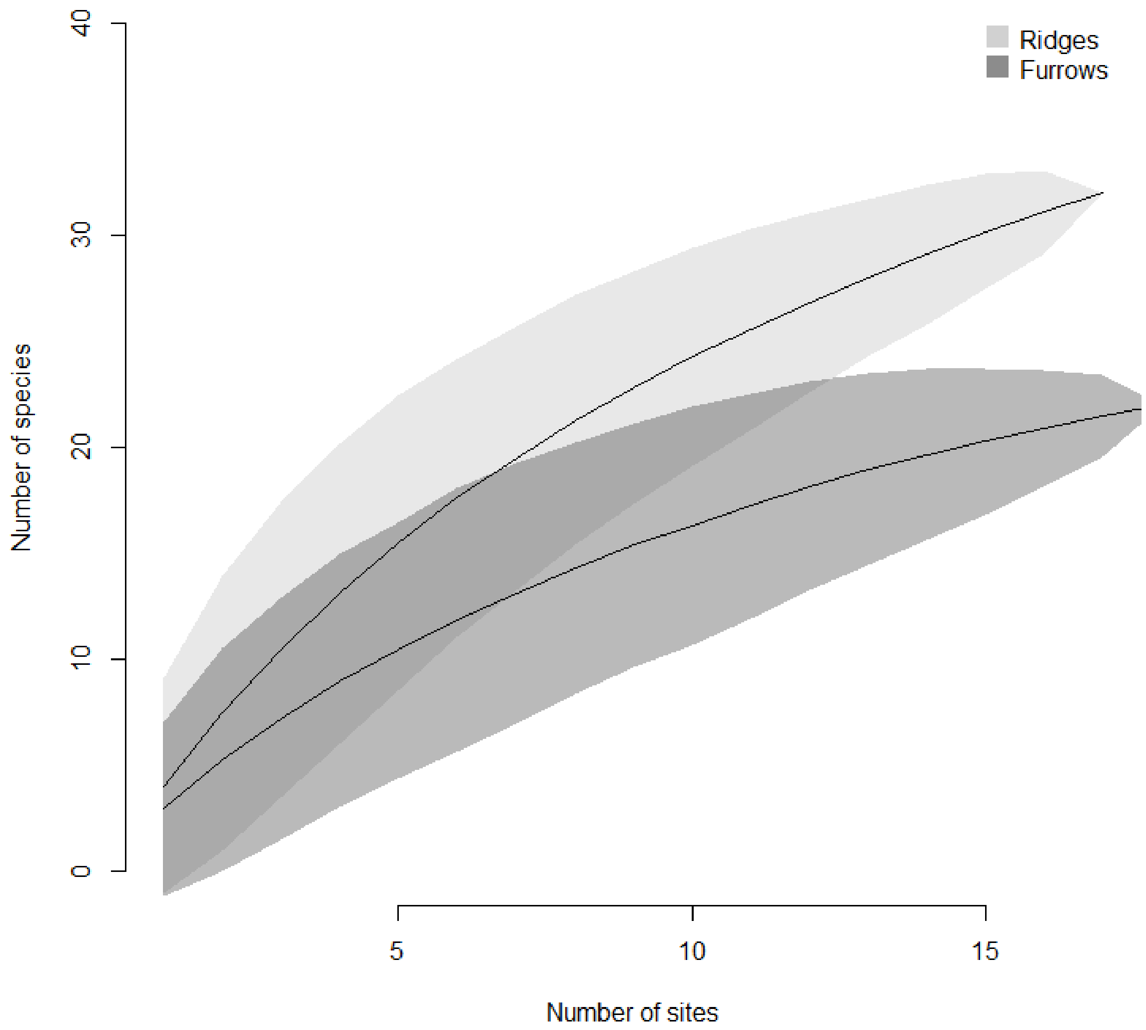


Figure 10. Species accumulation curve for number of carabid species found in ridges and furrows in restored heathlands. Shaded patches (pale grey = ridges, darker grey = furrows) represent 95% CIs.

3.4 Carabid Species Composition

3.4.1 Beta Diversity

The average beta diversity across all sampled habitats was 0.51 (Bray-Curtis dissimilarity). PERMANOVA found no significant difference in carabid species compositions across ridges and furrows in restored heathlands ($F(1,33) = 0.44$, $R^2 = 0.013$, $p = 0.961$), as evidenced by substantial overlap in the NMDS ordination (stress = 0.10) (Figure 12a). However, carabid species composition differed significantly across habitat types ($F(6, 43) = 10.21$, $R^2 = 0.59$, $p = 0.001$) (Figure 12b).

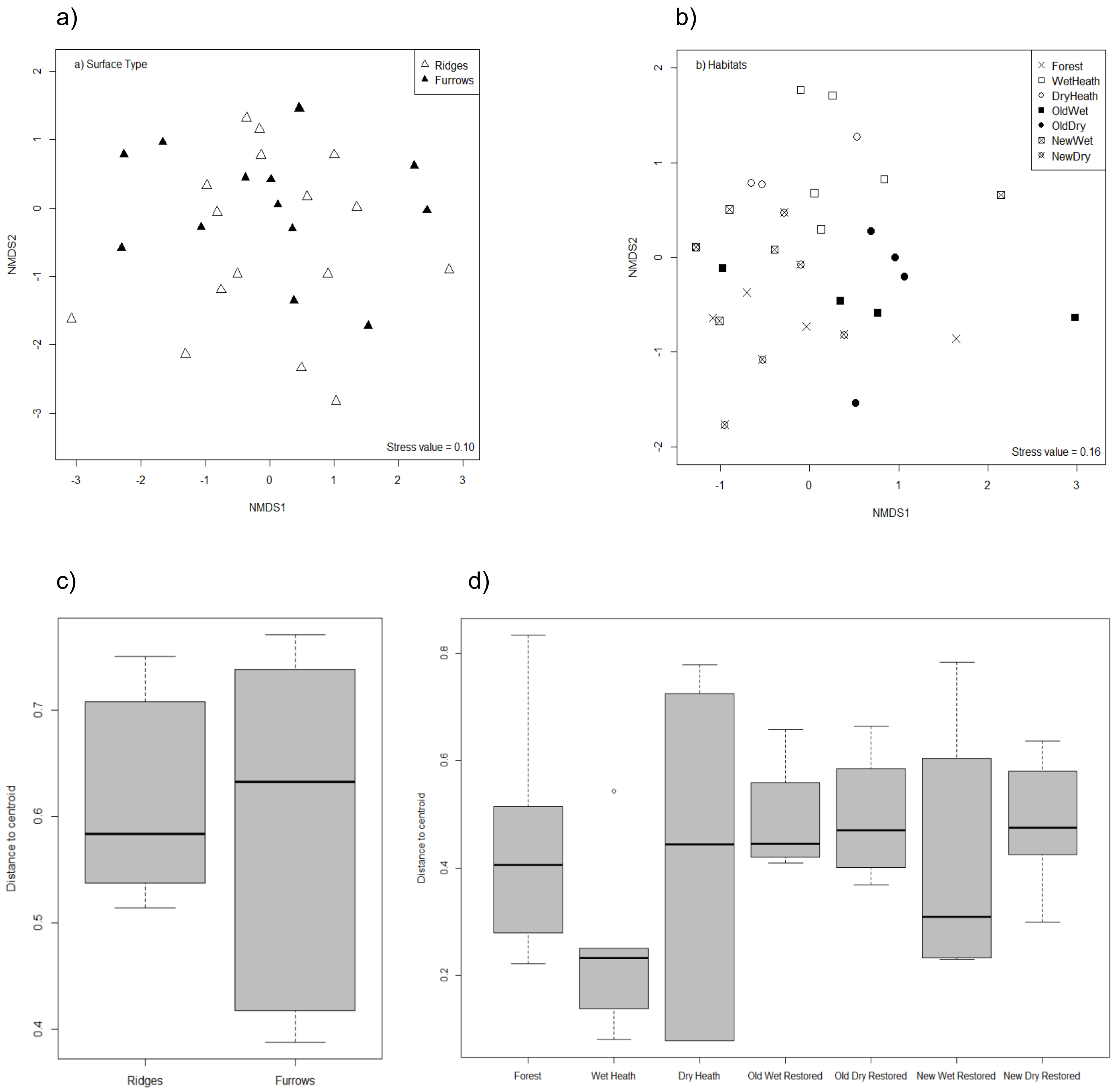


Figure 12. Non-metric Multidimensional Scaling (NMDS) ordination plots of dissimilarity in carabid samples collected from ridges and furrows in restored heathlands (a): white triangles = ridges, black triangles = furrows (stress value = 0.10), and the seven different habitat categories (b): forest = crosses, established wet heath = white squares, established dry heath = white circles, wet heath restored before 2007 ('OldWet') = black squares, dry heath restored before 2007 ('OldDry') = black circles, wet heath restored post-2012 ('NewWet') = white squares with a cross, and dry heath restored post-2012 ('NewDry') = white circle with a cross (stress value = 0.16). Both plots are based on Bray-Curtis dissimilarities. Boxplot of multivariate dispersion distances for carabids collected from the two different surfaces (ridges and furrows in restored heaths (c) and across the seven habitats (d).

A Pairwise PERMANOVA showed significant differences in carabid composition between most habitat types after Bonferroni correction, indicating distinct community structures across the various habitat types (Table 12).

Established Wet Heath and Dry Heath communities did not differ significantly, suggesting similar species composition. Forest sites had significantly different carabid compositions compared to New Wet heath, Old Dry heath and New Dry heath habitats (p adj = 0.021). However, Forest versus established heath habitats (Wet Heath and Dry Heath) were not significantly different after correction, indicating some species overlap.

Restored Wet Heaths did not significantly differ from established Wet Heaths, regardless of when felling occurred. In contrast, restored dry habitats showed greater differentiation: New Dry heath versus Old Dry heath habitats were significantly different (p adj = 0.021). Both New Dry heath and Old Dry heath habitats also differed significantly from established Dry Heath (p adj = 0.021), suggesting distinct communities in restored versus long-established dry heathlands.

Old Dry habitats exhibited significant differences from all six other habitats (p adj = 0.021 for all comparisons), indicating that this habitat type supports a particularly distinct carabid community.

Table 12. Pairwise PERMANOVA. Using adjusted *p*-values, significant results (*p* adj < 0.05) are highlighted in bold.

Comparison	Degrees of Freedom	Sum of Squares	F Model	R^2	*p*-value	Adjusted *p*-value
Forest – Wet Heath	1	0.44	7.25	0.48	0.014	0.294
Forest – Dry Heath	1	0.28	3.42	0.30	0.059	1.000
Forest – Old Wet	1	0.63	5.86	0.35	<0.01	0.084
Forest – New Wet	**1**	**1.02**	**9.09**	**0.45**	**<0.01**	**0.021**
Forest – Old Dry	**1**	**0.69**	**18.22**	**0.60**	**<0.01**	**0.021**
Forest – New Dry	**1**	**0.97**	**15.93**	**0.55**	**<0.01**	**0.021**
Wet Heath – Dry Heath	1	0.25	3.54	0.31	0.044	0.924
Wet Heath – Old Wet	1	0.66	6.74	0.38	<0.01	0.084
Wet Heath – New Wet	1	0.69	6.71	0.38	<0.01	0.084
Wet Heath – Old Dry	**1**	**1.01**	**34.20**	**0.74**	**<0.01**	**0.021**
Wet Heath – New Dry	**1**	**0.71**	**13.43**	**0.51**	**<0.01**	**0.021**
Dry Heath – Old Wet	1	0.35	3.07	0.21	0.035	0.735
Dry Heath – New Wet	**1**	**0.55**	**4.65**	**0.30**	**<0.01**	**0.042**
Dry Heath – Old Dry	**1**	**0.54**	**12.21**	**0.50**	**<0.01**	**0.021**
Dry Heath – New Dry	**1**	**0.53**	**8.03**	**0.38**	**<0.01**	**0.021**

Old Wet – New Wet	1	0.37	2.85	0.17	0.062	1.000
Old Wet – Old Dry	**1**	**0.37**	**5.29**	**0.26**	**<0.01**	**0.021**
Old Wet – New Dry	**1**	**0.54**	**6.28**	**0.28**	**<0.01**	**0.021**
New Wet – Old Dry	**1**	**0.86**	**11.74**	**0.44**	**<0.01**	**0.021**
New Wet – New Dry	**1**	**0.50**	**5.55**	**0.26**	**<0.01**	**0.042**
Old Dry – New Dry	**1**	**0.47**	**12.03**	**0.41**	**<0.01**	**0.021**

Species composition was found to be more variable in ridges (average distance to median = 0.61) than in furrows (average distance to median = 0.59) in restored heathlands based on the homogeneity of multivariate dispersion analysis. However, ANOVA results showed that this difference was not statistically significant (F = 1,33) = 0.34, p = 0.563). There is a relatively even spread of sites within each of these groups throughout the NMDS biplot. Contrastingly, there was variability between habitat groups: the average distances to the median show that New Wet and Old Wet restored habitats have greater within-group variation (average distance to median = 0.33 and 0.32 respectively) than others (Table 13). The least variation was within Old Dry restored heaths and Wet Heaths (average distance to median = 0.12 and 0.16 respectively). A one-way ANOVA found that these multivariate dispersions significantly differed across the seven habitats ($F_{(6,43)} = 3.26$, $p < 0.01$).

Table 13. Results showing how spread out the carabid communities are within each habitat. Higher values indicate greater within-habitat variability in species composition. These results are based on the homogeneity of multivariate dispersions (*permdisp*) analysis, which measures beta dispersion – the variation in species composition within each habitat – and compares it among habitats.

Habitat	**Average Distance to Median**
Forest	0.194
Wet Heath	0.163
Dry Heath	0.227
Old Wet	0.316
New Wet	0.335
Old Dry	0.118
New Dry	0.217

Tukey's HSD test revealed that most habitats did not differ significantly in beta dispersion (Table 14). However, significant differences were found between Old Dry restored heath and New Wet restored heathland habitats (p = 0.011), as well as between Old Wet restored and Old Dry restored habitats (p = 0.026), suggesting that species composition is more variable in New Wet restored heaths compared to older, drier restored sites.

Table 14. Results of Tukey's HSD test comparing beta dispersion (variation in community structure) among habitat types. Using adjusted *p*-values, significant results (*p* adj < 0.05) are highlighted in bold.

Comparisons	**Difference in Means**	**Lower Confidence Interval (95%)**	**Upper Confidence Interval (95%)**	**Adjusted *p*-values**
Forest – Dry Heath	-0.03	-0.27	0.20	0.999
New Dry – Dry Heath	-0.01	-0.22	020	0.999
New Wet – Dry Heath	0.11	-0.11	0.32	0.723
Old Dry – Dry Heath	-0.11	-0.32	0.10	0.674
Old Wet – Dry Heath	0.09	-0.13	0.30	0.857
Wet Heath – Dry Heath	-0.06	-0.30	0.17	0.980
New Dry – Forest	0.02	-0.18	0.23	0.100
New Wet – Forest	0.14	-0.07	0.35	0.415
Old Dry – Forest	-0.08	-0.28	0.13	0.920
Old Wet – Forest	0.12	-0.09	0.34	0.575
Wet Heath – Forest	-0.03	-0.27	0.21	0.100
New Wet – New Dry	0.12	-0.06	0.30	0.414
Old Dry – New Dry	-0.10	-0.27	0.07	0.573
Old Wet – New Dry	0.10	-0.08	0.28	0.607
Wet Heath – New Dry	-0.05	-0.26	0.15	0.983
Old Dry – New Wet	**-0.22**	**-0.40**	**-0.03**	**0.011**
Old Wet – New Wet	-0.02	-0.21	0.17	0.100
Wet Heath – New Wet	-0.17	-0.38	0.04	0.200

Old Wet – Old Dry	**0.20**	**0.02**	**0.38**	**0.026**
Wet Heath – Old Dry	0.05	-0.16	0.25	0.994
Wet Heath – Old Wet	-0.15	-0.37	0.06	0.314

3.4.2 Turnover and Nestedness

Beta diversity, which measures how different carabid communities are between sites, was slightly higher when considering ridges and furrows in restored heaths separately (0.44) than compared to all sites combined (0.43) (Table 15, Figure 13). Within habitat types, beta diversity ranged from 0.34 (in established Dry Heath) to 0.42 (in New Wet restored heath). This variation was primarily driven by species turnover rather than nestedness.

Across all sites, turnover accounted for approximately 78% of beta diversity, meaning different sites had distinct species composition rather than just fewer shared species. This pattern was even stronger when analysing ridges and furrows separately (81.5%). Newly restored sites, especially in wet habitats, had the highest turnover (97.39% in New Wet heath and 90.51% in New Dry heath), suggesting highly variable species compositions in these habitats, reflecting ongoing ecological flux. In contrast, older restorations and more established habitats exhibited lower turnover and higher nestedness, indicating a more predictable species composition. Nestedness was more prominent in wetter habitats, such as Old Wet sites (49.64%) and Wet Heath (48.50%), where differences in carabid species composition were in part due to species loss. This suggests that wetter habitats maintain a core set of species, with some sites losing species rather than gaining entirely new ones.

Overall, wetter heathlands support more similar and predictable carabid communities, meanwhile drier and older sites, whilst still showing relatively high turnover, had a greater contribution of nestedness (for instance, 34-39% in dry heath restored before 2007 and established Dry Heath), indicating a mix of species sharing and localised variation, in contrast to newly restored wet sites, which are dominated almost entirely by turnover.

Table 15. The contribution of nestedness and turnover to total beta diversity when all sites were considered together, and when only ridges and furrows were examined, calculated using Baselga Jaccard index. Percentage contributions are presented in parentheses.

	Total Beta Diversity	Turnover	Nestedness
All sites	0.43	0.34 (77.90%)	0.10 (22.10%)
Surface type	0.44	0.36 (81.50%)	0.08 (18.50%)
Habitat type:			
Forest	0.40	0.25 (61.96%)	0.15 (38.04%)
Wet Heath	0.36	0.19 (51.50%)	0.18 (48.50%)
Dry Heath	0.34	0.21 (60.59%)	0.13 (39.41%)
Old Wet	0.41	0.21 (50.36%)	0.21 (49.64%)
New Wet	0.42	0.41 (97.39%)	0.01 (2.61%)
Old Dry	0.39	0.26 (65.81%)	0.13 (34.19%)
New Dry	0.40	0.37 (90.50%)	0.04 (9.49%)

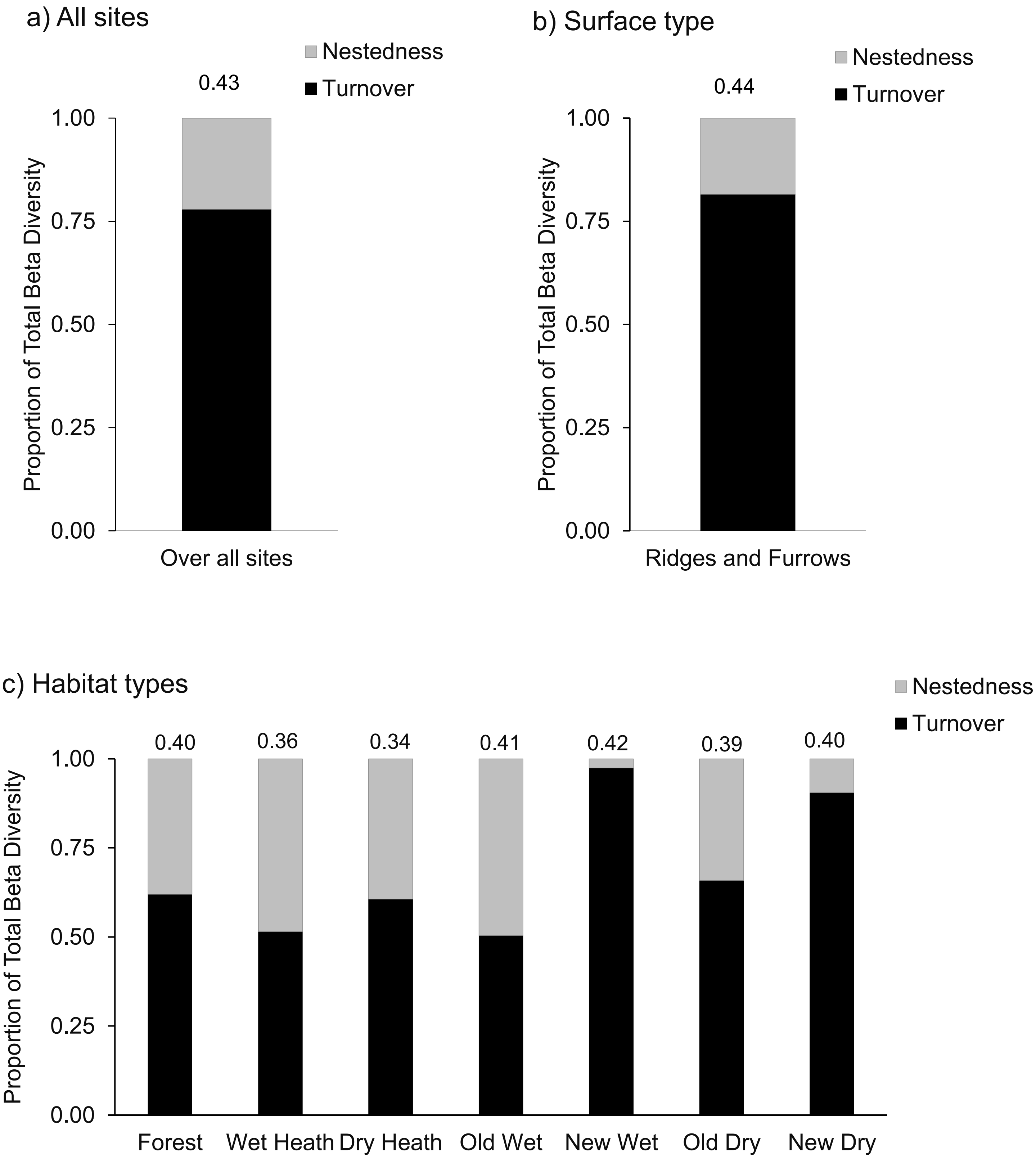


Figure 13. Partitioning of beta diversity into turnover and nestedness components across all survey sites (a), within the surface types (ridges and furrows) in restored heathland sites (b) and within the habitat types (c).

3.5 Carabid Functional Traits

Functional trait analysis revealed that certain characteristics of carabid beetles varied significantly across habitat types (Table 10), particularly, the abundances of carabids exhibiting the two smallest body length categories, wing macroptery and dimorphism, spring breeding, and preferences for dry ground and open vegetation (all of which had *p*-values <0.01). Additionally, carabid body lengths 10-15mm and mixed breeding seasons significantly differed in their abundance over different habitats. Conversely, activity period traits (whether carabids are active during the day or the night) did not show clear habitat-related patterns. However, differences in statistical power across traits, due to varying sample sizes, may have influenced the detection of significant patterns.

Table 10. Results from individual Kruskal-Wallis Rank Sum tests to identify significant differences in functional traits across the seven habitat types. Statistically significant results are highlighted in bold.

Trait	Category	Chi-Squared	Degrees of Freedom	*p*-value
Body Length	**≤ 5mm**	**16.98**	**6**	**0.009**
	> 5 - ≤ 10mm	**20.14**	**6**	**0.002**
	> 10 - ≤ 15mm	**15.37**	**6**	**0.018**
	> 15 - ≤ 20mm	11.23	6	0.082
	> 20 - ≤ 30mm	5.22	6	0.516
Wing Morphology	**Macropterous**	**18.96**	**6**	**0.004**
	Brachypterous	9.02	6	0.173
	Dimorphic	**20.79**	**6**	**0.002**
Breeding Season	**Spring**	**24.33**	**6**	**<0.001**
	Summer	5.6	6	0.470
	Autumn	7.37	6	0.288
	Mixed	**13.31**	**6**	**0.038**
Soil Moisture Preference	**Dry**	**23.39**	**6**	**<0.001**
	Damp	12.16	6	0.058
	Wet	**16.50**	**6**	**0.011**
Vegetation Cover Preference	**Open**	**20.90**	**6**	**0.002**
	Mid	11.01	6	0.088
	Dense	10.91	6	0.091
	Other	11.56	6	0.072
Activity	Diurnal	7.60	6	0.269
	Nocturnal	10.24	6	0.134

Regarding pairwise comparisons (Table 11), wetter sites restored after 2012 (New Wet heath) exhibited distinct trait distributions compared to older habitats, especially dry ones. The abundance of beetles associated with functional traits in New Wet sites frequently differed significantly to other habitats, particularly in:

- Body length (≤ 5mm and > 5 - ≤ 10mm) – differed from Dry Heath, Old Dry heath and Wet Heath.
- Wing morphology (macroptery and dimorphism) – differed from Old Dry heath and established Dry Heath.
- Breeding season (Spring and mixed) – differed from Old Dry heath, established Dry Heath and Forest.
- Soil moisture preference (especially species with a preference for wetter habitats) – differed from New Dry heath and established Dry Heath.

Old Dry heath sites showed no significant difference in abundances of carabids exhibiting traits compared to established Dry Heath, established Wet Heath or Forest. This suggests that heathlands subject to conifer felling before 2007 now resemble more mature habitats, and support more stable communities, with similar abundances of carabid species displaying the same traits. This indicates that species composition has gradually shifted post-restoration. Despite this, Old Dry sites still exhibited significant differences in specific traits compared to newer restoration:

- Body length (≤ 5mm) – differed from New Wet heath.
- Wing morphology (macroptery) – differed from New Dry heath and New Wet heath.
- Spring breeding – differed from Wet Heath.
- Preference for dry ground – differed from Wet Heath and New Dry heath.
- Preference for open vegetation – differed from Wet Heath and New Dry heath.

Established Dry Heath consistently differed from both New Dry heath and New Wet heath sites in the abundances of carabids displaying multiple traits, indicating that habitat age and structure play key roles in shaping carabid communities (Table 11). In contrast, Forest habitats were distinguished from other habitat types by higher abundances of carabids with preference for dry ground (differing from New Wet heath and Wet Heath), preference for open vegetation (differing from New Wet heath and Wet Heath), and mixed breeding seasons (differing from New Wet heath) (Table 11).

Table 11. Results from the Dunn's post-hoc test showing where differences in trait abundances occur between habitat types. All results are significant following significant Kruskal-Wallis test results; hence none are highlighted in bold. After correcting for multiple comparisons, body length 10-15mm was not significantly different between habitats and was removed from this table.

Functional Trait	**Pairwise Comparisons**	**Adjusted *p*-value**
Body Length ≤ 5mm	Dry Heath vs. New Wet	0.009
	New Wet vs. Old Dry	0.019
	New Wet vs. Wet Heath	0.048
Body Length > 5 - ≤ 10mm	Dry Heath vs New Dry	0.024
	Dry Heath vs. New Wet	0.014
	New Dry vs Wet heath	0.033
	New Wet vs. Wet Heath	0.027
Macropterous	Dry Heath vs. New Dry	0.027
	New Dry vs. Old Dry	0.024
	New Wet vs. Old Dry	0.049
Dimorphic	Dry Heath vs. New Wet	0.006
	Forest vs. New Wet	0.011
	New Wet vs. Old Dry	0.036
	Dry Heath vs. Old Wet	0.029
	New Wet vs. Wet Heath	0.014
Spring Breeding	Dry Heath vs. New Wet	0.015
	Forest vs. New Wet	0.013
	New Dry vs. Old Dry	0.048

	New Wet vs. Old Dry	0.004
	Old Dry vs. Old Wet	0.040
	Old Dry vs. Wet Heath	0.017
Mixed Breeding Season	Dry Heath vs. New Wet	0.015
	Forest vs. New Wet	0.013
	New Dry vs. Old Dry	0.048
	New Wet vs. Old Dry	0.004
	Old Dry vs. Old Wet	0.040
	Old Dry vs. Wet Heath	0.017
Preference for Dry Ground	Dry Heath vs. New Dry	0.024
	Forest vs. New Dry	0.018
	Dry Heath vs. New Wet	0.033
	Forest vs. New Wet	0.022
	New Dry vs. Old Dry	0.024
	New Wet vs. Old Dry	0.024
	Old Dry vs. Wet Heath	0.043
Preference for Wet Ground	Dry Heath vs. New Wet	0.040
	New Dry vs. New Wet	0.047
	Dry Heath vs. Old Wet	0.048
Preference for Open Vegetation Cover	Dry Heath vs. New Dry	0.038
	Dry Heath vs. New Wet	0.050
	New Dry vs. Old Dry	0.040
	Dry Heath vs. Wet Heath	0.045
	Forest vs. Wet Heath	0.037
	Old Dry vs Wet Heath	0.038

Older, drier sites did not support small-bodied carabids (≤ 5mm) (Figure 11a), instead 15-20mm was the most prevalent body length in these habitats (Dry Heath and Old Dry heath). Forest and dry heath restored after 2012 (New Dry heath) hosted carabids belonging to all size categories. Carabids with a body length between 15-20mm were mostly prevalent in established Dry Heath, Wet Heath and Old Dry heath, meanwhile carabids below 5mm were more prevalent in Forest habitats and wet restored heaths (Old Wet heath and New Wet heath).

Macroptery was most prevalent in newly restored dry heathlands, while brachyptery was the most prevalent wing morphology in established heathland sites (Wet Heath and Dry Heath). Forest habitats displayed a more even distribution of macropterous and brachypterous species, with macroptery being slightly less common. Older restored wet heaths (Old Wet heath) showed a more even distribution between macroptery and wing dimorphism, with macroptery being slightly more prevalent. There were no wing dimorphic carabids collected from established Dry Heath (Figure 11b).

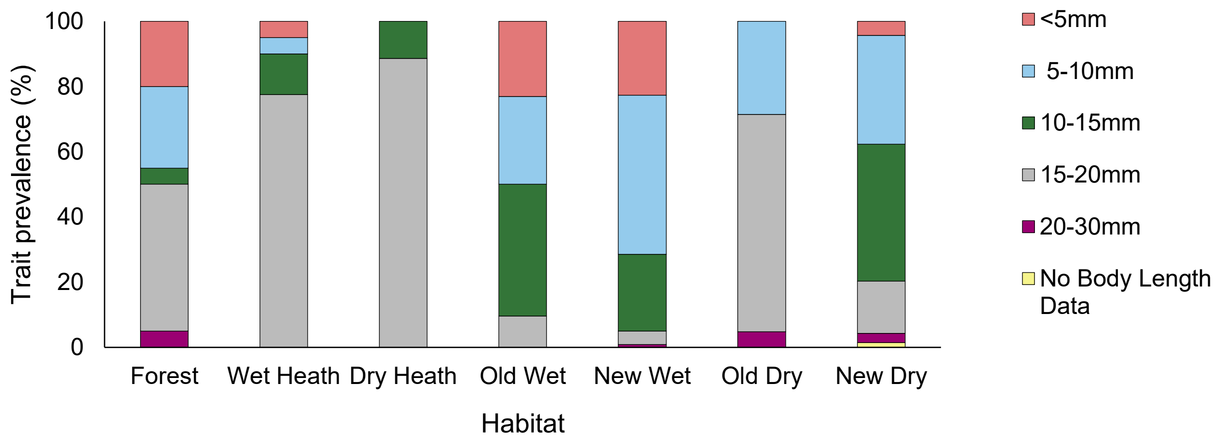
Spring-breeding carabids were more prevalent in established Wet Heaths, and least in established Dry Heaths and Dry Heaths restored before 2007 (Figure 11c), these two habitats displayed a high abundance of carabids exhibiting overlapping breeding seasons. The prevalence of spring, autumn and mixed breeding seasons was slightly more even in dry heathland restored after 2012 (New Dry heath). Among the species collected, only one (*C. nitens*) was a summer breeder, found at a Wet Heath site.

Carabids exhibiting a preference for dry ground were recorded at 26 sites, while those preferring damp ground were present at 30 of the 35 surveyed sites. Although the wet-ground preference trait was found at only nine sites, this trait was the least prevalent in established Wet Heath (Figure 11d), but mostly prominent in restored wet heaths (primarily, wet heath restored before 2007).

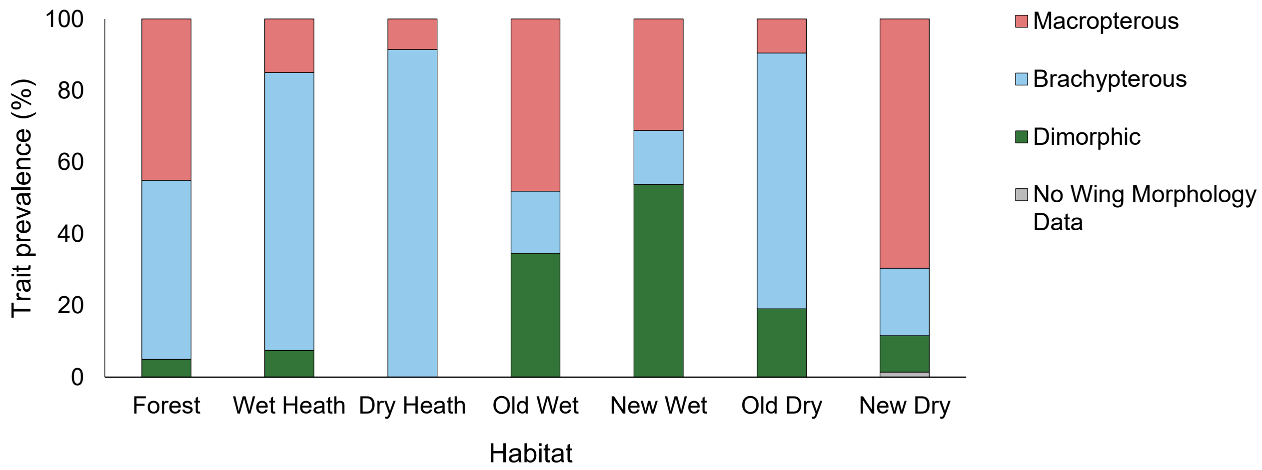
Sites restored before 2007 (Old Wet heath and Old Dry heath) hosted a greater number of carabids with a preference for denser vegetation cover compared to sites restored after 2012 (New Wet heath and New Dry heaths) (Figure 11e), indicating that the conditions provided by mature vegetation in mature habitat types are more favourable for carabids with a preference for dense vegetation.

Dry heathland restored before 2007 was used solely by diurnal species in this study (Figure 11f), however, the proportion of unknown data was high for this trait category, particularly in this habitat, making the findings uncertain.

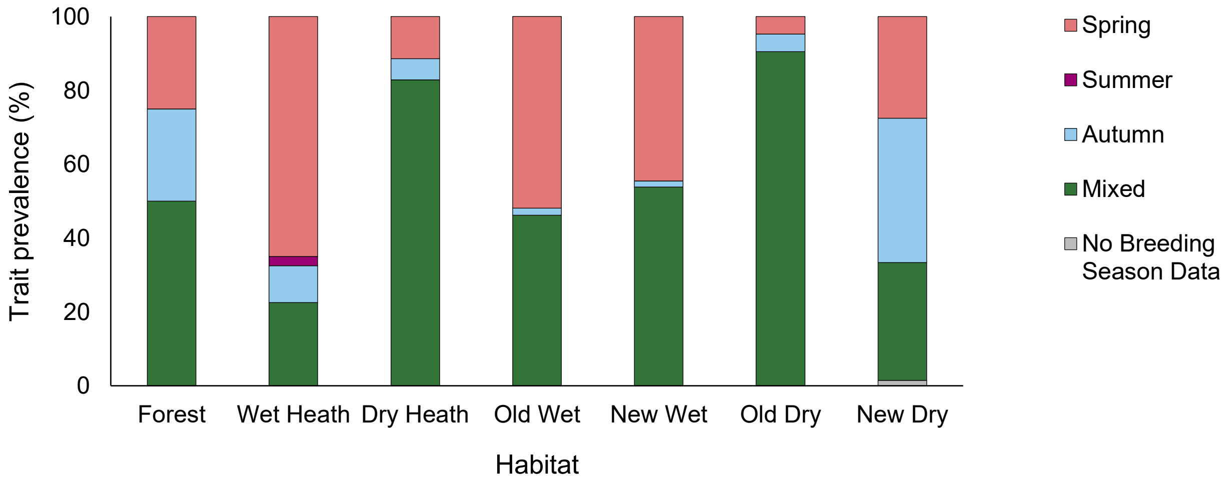
a) Body Length



b) Wing Morphology



c) Breeding Season



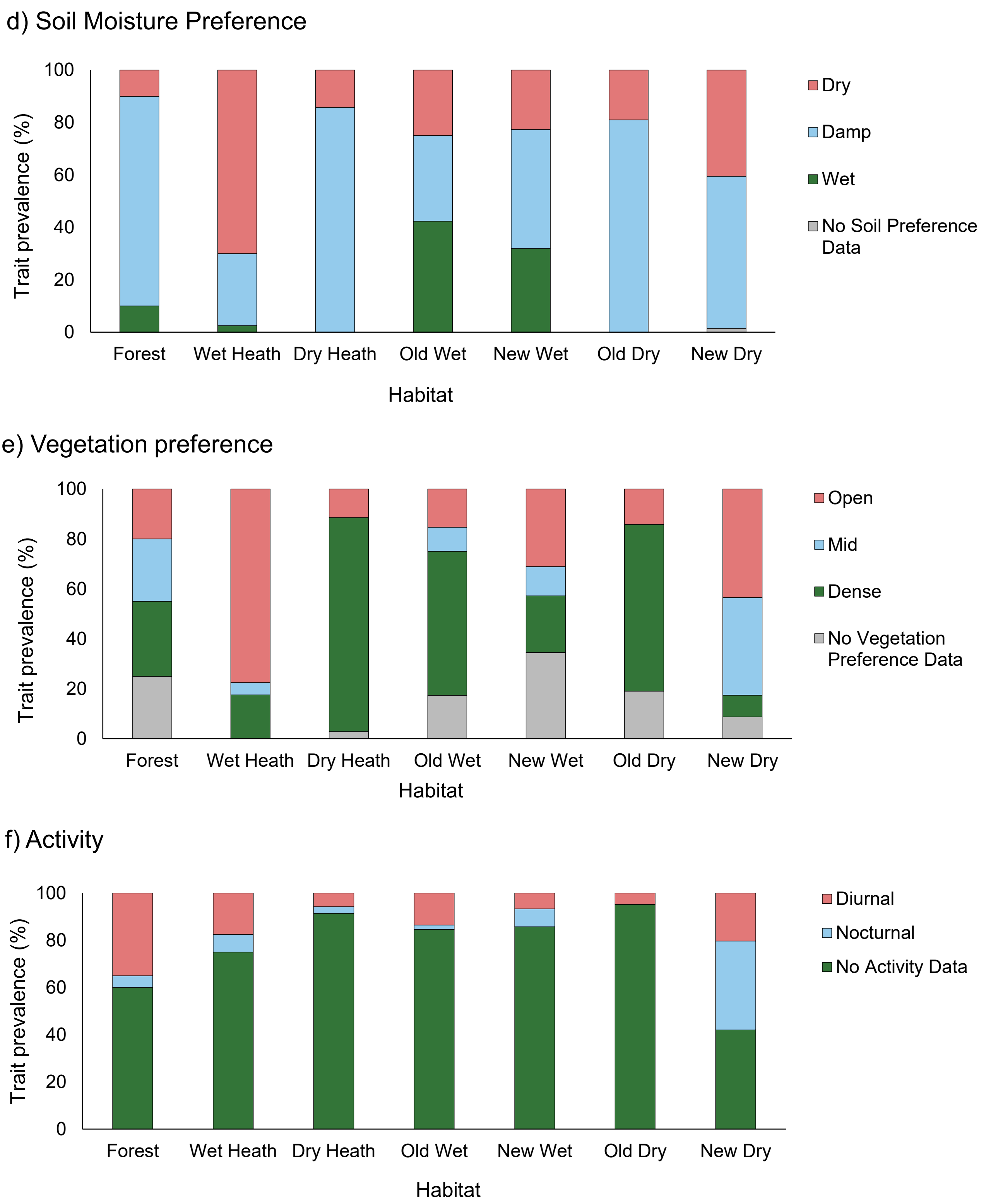


Figure 11. Stacked bar graphs showing prevalence of traits (body length (a), wing morphology (b), breeding season (c), soil moisture preference (d), vegetation cover preference (e) and activity (f)) over the seven habitats. These graphs illustrate trait distribution but do not display the Kruskal-Wallis test results, which are provided separately in Table 9.

4. Discussion

4.1 Species

Overall, the species recorded in this study were consistent with those documented in existing literature (for instance, by Lindroth (1974), Luff (1998 and 2007), Lin et al. (2007), Walters and Telfer (2013) and Telfer (2016)). None of the carabids identified are known to be range-restricted (Telfer, 2016), and many of the species (for instance, *Amara tibialis*, *Notiophilus palustris*, *Carabus problematicus*, *Cicindela campestris*, *Nebria salina*, *Notiophilus aquaticus*, *Notiophilus germinyi*, *Olisthopus rotundatus* and *Syntomus foveatus*) are known heathland associated species (Lin et al., 2007).

Abax parallelepipedus was recorded across all habitat types, suggesting a wider ecological tolerance than typically reported. Although traditionally classified as a forest specialist (in studies across Britan by Jukes et al. (2001) and in Germany by Marcus et al. (2015)), its presence in both wet and dry sites in this study supports more recent evidence of habitat flexibility in southern Britain. Luff (1998, 2007) and the UK Carabid Recording Scheme (n.d.a) note its abundance and southerly distribution in Britain. Additionally, Gillingham et al. (2012) documented its occurrence on moorlands in Glen Finglas (Scotland) and Lake Vyrnwy (Wales) suggesting a broader habitat tolerance than a strict forest association. Despite being flightless (Marcus et al. 2015; Zanella, 2016), *A. parallelepipedus* demonstrated a capacity to utilise diverse habitats within the current study's survey area, including wet and dry habitats, both established and restored over different timescales. This finding supports Hypothesis 3, as it reflects the presence of functionally diverse species across habitat types, highlighting that habitat classifications can be context-dependent and may not fully capture the ecological flexibility of a species across its entire range. Moreover, this apparent adaptability could, in part, reflect broader ecological shifts. Range expansion may be occurring more rapidly in recent years, potentially driven by climate change and habitat restoration efforts, which are altering the availability and quality of suitable habitats. For instance, Homburg et al. (2019), in a two-decade study of carabid communities, documented significant range expansions in certain species, coinciding with increased temperatures and the emergence of new habitat patches. This highlights the influence of climate change in shaping carabid distributions and suggests that even species traditionally viewed as habitat specialists may respond dynamically to changing environmental conditions, meaning that even long-term habitat protection alone may not fully buffer against species declines (Homburg et al., 2019).

Rare occurrences of *Laemostenus terricola* and *Cicindela campestris* in established Dry Heaths suggest that suitable microhabitats, such as dry, sandy soils, persist outside of recently restored areas. *L. terricola* is associated with open biotopes (Putchkov and Aleksandrowicz, 2020; Anderson and McFerran, 2025) and has declined across Europe due to the fragmentation and loss of specific features like rabbit burrows (Putchkov and Aleksandrowicz, 2020). Its occurrence here may indicate remnant habitat quality despite wider regional declines (Gruttke, 1994; Niemelä, 2001). *C. campestris,* commonly found on dry, sandy, free-draining soils (Usher and Thompson, 1993), similarly reflects the underlying edaphic conditions typical of the Purbeck dry heaths.

Conversely, a single *Carabus nitens* individual was recorded in a Wet Heath during June, despite its usual spring activity peak. While unexpected, its known preference for open areas with variable successional stages (Volf et al., 2018) may explain this occurrence, as the surveyed Wet Heaths were treeless and minimally shaded, offering structurally appropriate conditions despite the later timing.

In this study, two species — *Leistus fulvibarbis* and *Notiophilus rufipes* — were found exclusively in forest habitats, consistent with their classification as forest specialists (Jukes et al., 2001; Neumann et al., 2017). However, the forest specialist species identified by Burel in western France (1989) differ from those found in this study, likely reflecting the methodological differences in habitat classification employed, as Burel (1989) distinguished species based on their presence in core forest, peninsula, and corridors, whereas the current study adopted a strict presence/absence criterion within forest sites. Additionally, the geographical separation between western France and the UK, influencing species ranges, may also contribute to this variation. The absence of several species from forest sites in this study, including *Amara lunicollis, Anisodactylus nemorivagus, Carabus arvensis, Carabus nitens, Harpalus rufipes, Nebria salina, Olisthopus rotundatus,* and *Pterostichus diligens* (all primarily found in non-forest habitats) supports their classification as heathland specialists, as suggested by de Vries et al. (1996) and Neumann et al. (2017). Although none of the carabids caught in this study were strictly arboricolous or saproxylic, the presence of shade-adapted species such as *Amara aenea* and *Leistus fulvibarbis* (Fuller et al., 2008) in the forest sites aligns with the understanding that these species may thrive in areas with partial canopy cover or thicker understory (Lindroth, 1974; Nadeau et al., 2015). These species likely benefit from the moderated temperatures and shaded conditions provided by tree cover, utilising leaf litter and potentially tree bark for shelter or foraging. Conversely, the absence of other shade-adapted or closed-canopy specialist species in this study — such as *Carabus nemoralis* (Fuller et al., 2008) — may reflect differences in canopy structure, forest age, or management practices within the surveyed sites compared to those examined in previous research (for instance, by Niemelä et al. (1993) and Koivula (2011)), where practices like conifer felling were shown to influence carabid community composition.

Anisodactylus nemorivagus, though nationally rare, is locally common in parts of southern England, including Dorset and Hampshire (Walters and Telfer, 2013; Telfer, 2016). It is an open-habitat species which typically favours dry, sandy soils (Lindroth, 1974). In this study, individuals were found in both newly restored wet (6 individuals) and dry (7 individuals) sites. Previously unrecorded in the Purbeck Heaths since the 1940s, *A. nemorivagus* was rediscovered during a 2023 survey when a single individual was recorded (Annear, 2024; National Biodiversity Network Atlas, 2023). Its exclusive presence in restored habitats suggests that restoration efforts may be key to its persistence, particularly as it is a Section 41/UKBAP Priority Species (JNCC, 2007). This corroborates findings by Byriel et al. (2023), who indicate that the presence of *A. nemorivagus* in restored sites may be attributed to a mosaic of habitats, including microhabitat diversity, potentially due to environmental condition alterations caused by felling (such as increased light penetration, reduced soil moisture and changes to the understory).

All 17 individual of Nationally Scarce (4 species) or Rare carabids (1 species) were found in restored sites, with none detected in forest habitats, partially supporting Hypothesis 2. This indicates that conifer removal and canopy opening enhance habitat suitability for rarer species, corroborating claims made by Lindroth (1974), Eggers et al. (2010) and Sivell et al. (2025). However, heathland restoration is complex. Byriel et al (2023) challenge the assumption that these species rely exclusively on managed, early successional stages: they found that xerophilic ground beetles could persist in older growth stages. This suggests that while open ground from conifer felling is beneficial, it may not be sufficient on its own. In the current study, the absence of rare species like *A. nemorivagus* from coniferous plantations is more likely due to low microhabitat heterogeneity and dense understory, rather than simply the lack of bare ground.

Nationally Scarce and Rare carabids were present in most restored habitat types (Old Wet heath, New Wet heath, and New Dry heath) but were absent from Old Dry heath, and only occasionally found in established Wet Heath. This indicates that restoration alone does not guarantee habitat suitability, and that other ecological factors influence species persistence and recolonisation, partially supporting Hypotheses 2 and 4.

Several factors may explain this uneven distribution. Firstly, rare species may have persisted in the wider landscape, particularly in adjacent heathland or edge habitats that acted as refugia during afforestation. Yu et al. (2007) found that forest-grassland ecotones, with their transitional zones, exhibited higher carabid diversity than the forest interior, highlighting the importance of edge effect and habitat heterogeneity for carabid communities. Secondly, local environmental factors, such as soil moisture, microclimate, or prey availability, likely play a more critical role than the restoration method itself, especially since some rare species are not strict heathland specialists. For example, *Pterostichus gracilis* is known to occupy wetter habitat near riverbanks, ponds and marshy areas (Lindroth, 1974; Luff, 2007). Finally, these species may possess high dispersal abilities or broader habitat tolerance (eurytopy) than previously recognised. While note classified as Nationally Scarce or Rare, *Carabus problematicus* illustrates this principle: although previously classified as a woodland-associated species in Northwestern Europe by Rijnsdorp (1980), and numerous studies accepting that this species will inhabit dry heaths, lightly-wooded heaths and thin forests, it generally prefer open habitats (Lindroth, 1974; Eggers et al., 2010; Sivell et al., 2025). Gillingham et al. (2012) also recorded *Carabus problematicus* on moorlands, further highlighting its ecological flexibility. This is corroborated by the findings in the current study, as this species was found in dry heaths restored before 2007 and after 2012, and wet heaths restored after 2012, supporting claims that it is more eurytopic.

It is important to note that pitfall trap abundance represents an index of activity-density rather than absolute population density (Thomas et al., 1998). Trap captures are influenced not only by the number of individuals present but also by species-specific activity levels and trapping efficiency, meaning that catch numbers reflect a combination of population size and behavioural factors. Although low capture rates can result from multiple factors, including species rarity, sampling method limitations or temporal and/or spatial factors (Woodcock 2005), they introduce a source of uncertainty when interpreting species-habitat associations. For instance, species such as *Bembidion nigricorne*, *Carabus nitens*, *Pterostichus gracilis* and *Syntomus truncatellus* were represented by only one or two individuals, limiting confidence in any conclusions regarding their habitat preferences, distribution patterns or responses to restoration. While their occurrence may suggest potential habitat suitability or recolonisation, such low numbers mean that observed patterns could equally reflect chance encounters or transient presence, rather than stable populations (Magurran, 2004). Therefore, while suggestive, these findings should not be seen as conclusive evidence of habitat specificity for these species, and it is important to recognise that the strength of evidence varies across the dataset (Cunningham and Lindenmayer 2005).

4.2 Species-Environmental Variables Relationships

The results of this study indicate that carabid species richness in the PHNNR is significantly influenced by environmental variables, particularly temperature and tree cover. Warmer temperatures and more tree cover per site are associated with increased richness overall. These relationships are examined in greater depth in the following sections.

4.2.1 Temperature

Species richness increased significantly with warmer average ground temperatures, supporting Hypothesis 1a, which predicted that carabid diversity would be highest under moderate microclimate conditions. This suggests that cooler ground temperatures in some sites may have limited carabid activity or habitat suitability. As ectotherms, carabids depend on external temperatures to regulate metabolic processes and activity levels (Mellanby, 1939; Ratte, 1984; Lövei and Sunderland, 1996; Holland, 2002). Warmer conditions likely enhanced their foraging and mobility, and may also have increased prey availability through higher invertebrate activity

(Lövei and Sunderland, 1996; Holland, 2002; Kruse et al., 2008; Dee et al., 2020). While temperatures exceeding thermal tolerance can reduce activity, impair function or cause mortality (Huey and Kingsolver, 2019; Jørgensen et al., 2022), the ground temperatures recorded during the field season were well within tolerable limits. Nonetheless, excessive heat can cause dehydration, metabolic inefficiency, or behavioural shifts, such as retreating to cooler microhabitats (Holland, 2002), potentially altering carabid species composition.

Temperature also influences the abundance of soft-bodied invertebrate carabid prey such as caterpillars and springtails through accelerating development, altering survival rates, and affecting movement patterns of prey species (Dee et al., 2020). While higher temperatures may accelerate prey species' development, reducing their vulnerability window to predation, they may also increase prey movement, making them more detectable to foraging carabids (Kruse et al., 2008). Thus, the effects on prey availability are complex and species-dependent (Kruse et al., 2008; Dee et al., 2020).

Carabid dietary preferences are also shaped by thermal conditions. For example, Saska et al. (2010) found that seed consumption in two *Harpalus* species – a hemizoophagous genus (Skłodowski, 2014) – varied with temperature. Specifically, the rate of seed consumption increased with temperature in *Harpalus affinis*, showing a linear trend, whereas *Pseudophonus rufipes* did not exhibit increased consumption above approximately 20°C (Saska et al., 2010). This difference may be linked to their life histories, with *H. affinis* being a day-active spring breeder that benefits from both low early spring temperatures and higher temperatures later in the season, while *P. rufipes*, a nocturnal autumn breeder, is adapted to cooler conditions where night temperatures rarely exceed 20°C (Saska et al., 2010). Additionally, reproductive status influenced feeding rates, as *P. rufipes* individuals were actively reproducing during the study period, whereas *H. affinis* males had likely ceased reproductive activity and were only maintaining basal metabolic functions (Saska et al., 2010). This temperature-driven difference in feeding behaviour highlights the influence of thermal conditions on carabid reproductive strategies.

Thermal dependence is also evident in other reproductive behaviours: ovipositing females may seek out warmer microhabitats that provide optimal conditions for egg development, as higher temperatures have been linked to increased egg production

(Ernsting and Isaaks, 2000; Holland, 2002). Beyond these specific examples, thermal tolerance influences carabid assemblages across diverse spatial scales, particularly in relation to elevational gradients, but interacts with other factors such as morphology and habitat structure (Pearson and Lederhouse, 1987; Schat et al., 2024). While not explicitly tested in this study, this factor warrants further attention. This is because carabid species exhibit varying abilities to withstand temperature extremes, leading to community organisation along thermal gradients. Each species possesses a distinct thermal tolerance range, encompassing both critical thermal limits — the maximum and minimum temperatures beyond which survival is not possible — and preferred temperature ranges where physiological function is optimised. Consequently, at a local scale, species with preferences for cooler microclimates may cluster in shaded areas, while those favouring warmer conditions are found in sun-exposed patches (Wheater et al., 2023). For instance, in the current study, *Dyschirius globosus*, a known sun-loving carabid (Kerdoncuff et al., 2023), was found in restored heathlands where minimal tree cover likely resulted in sunnier microhabitats. Extending this concept to broader regional and global scales, temperature gradients similarly influence species distributions, with species assemblages shifting according to latitudinal and altitudinal temperature variations. More northerly species tend to be found in cooler microsites within landscapes, while southerly species are associated with warmer environments (Gillingham et al., 2012). This organisation along temperature preferences highlights the fundamental role of thermal ecology in shaping carabid diversity and species composition. Consequently, the observed carabid capture rates may have been influenced by ground temperature, as elevated activity increases movement and foraging, and thus a higher chance of capture in pitfall traps (Holland, 2002; Woodcock, 2005; Saska et al., 2010). Future studies should consider this potential temperature-driven bias.

4.2.2 Tree Structure and Vegetation Cover

Tree presence was associated with higher carabid species richness, whereas other vegetation types, including bare ground, bryophytes, graminoids, and shrubs, showed no significant effects. Trees can enhance carabid diversity by increasing structural complexity and moisture retention, while the organic matter input from fallen leaves enriches the soil (Nadeau et al., 2015; Prevedello et al., 2018; Pedley et al., 2023). Studies, including those on restored heaths, demonstrate that this organic matter and deadwood significantly boost beetle diversity, supporting a range of soil organisms and higher trophic levels, including carabid beetles, by providing crucial refuges (Lindroth, 1974; Butterfield, 1987; Nadeau et al., 2015; Vician et al., 2018; Pedley et al., 2023). However, the relationship between habitat structure and beetles is complex, as canopy cover in dense forests likely limits light penetration, reducing understory vegetation, prey availability and microhabitat suitability (Lin et al., 2007).

Early successional heathlands, which develop after disturbance or restoration, are typically characterised by open ground, sparse vegetation, and a higher prevalence of pioneer species (Buchholz and Schirmel, 2011). In contrast, later successional heathlands, which have undergone natural regeneration over longer timescales, tend to have denser vegetation, deeper leaf litter layers, and more established plant communities, including extensive bracken cover, greater cover of graminoids and shrub encroachment (Schirmel and Buchholz, 2011; Buchholz et al., 2013). Multiple arthropods rely on the early successional stages of heathlands (Schirmel and Buchholz, 2011; Buchholz et al., 2013) due to resource availability and dietary preferences – for example, carabids in the *Harpalus* and *Amara* genera climb herbaceous vegetation for food resources (Lindroth, 1974). Dry heathlands in the UK often feature bracken (*Pteridium aquilinum*) as a dominant species (Usher and Thompson, 1993; Bullock and Pakeman, 1996), as observed in some of the Old Dry heathland sites in the current study (Figure 14). Bracken cover can shape microclimates, for instance thicker bracken will increase shade on the ground, which influences temperature and humidity. While the literature highlights the potential influence of bracken and associated leaf litter depth on microclimate and thus carabid communities, the current study found no statistically significant direct relationship between average leaf litter depth and carabid species richness. However, the positive influence of average leaf litter depth on richness, despite being insignificant, suggests that in the Purbecks study system, other factors might be more strongly driving carabid species richness than leaf litter depth alone. Temperature fluctuations caused by physical changes can dry out mosses and reduce ground vegetation cover, affecting carabid habitat suitability (Lindroth, 1974). Conversely, extensive moss carpets may limit the development of low-competitive arthropod species, possibly leading to biodiversity loss (Schirmel et al., 2011). Previous research has demonstrated that areas with denser vegetation (for example, with greater cover of graminoids) can impede carabid movements (Morris, 2000), and leaf litter depth may influence soil moisture and microhabitat availability (Koivula et al., 1999; Lin et al., 2007).

Figure 14. An example of a dry restored heathland site dominated by bracken. The trap observed in the foreground, labelled OD2d, is the westernmost trap at site OD2 (Old Dry), which was restored by conifer felling between 1990 and 2007. The marker flag is visible towards the background in the centreline of the photograph.

Organic matter may also influence carabid fecundity – for example, Ziesche and Roth (2007) found that reproductive rate of *A. parallelepipedus*, which oviposits in leaf litter layers, was greater in mature forest stands compared to younger stands. Similarly, Finnish studies discovered that carabids preferred plots covered with aspen leaf litter due to its effects on soil moisture, humidity, pH balance and soil surface temperatures (Koivula et al., 1999; Lin et al., 2007). These microclimatic changes, driven by leaf litter, enhance habitat complexity by influencing resource availability and creating microhabitats suitable for various species. Additionally, factors such as soil composition and nitrogen content in leaf litter could also influence activity patterns (Vician et al., 2018), further complicating the relationship between habitat conditions and carabid distributions. Structural diversity, including variations in leaf litter depth and composition, has been shown to be essential for beetles in forest ecosystems (Rappa et al., 2022), and similar effects may occur in dry heathlands. However, while these conditions may benefit certain species based on their ecological preferences, the dominance of bracken in heathland could suppress overall vegetation diversity. Pioneer vegetation often associated with restored habitats is inherently less structurally diverse than in mature heathland, translating to fewer available microhabitats for recolonising beetles (Kerdoncuff et al., 2023).

This study found no correlation between species richness and bare ground, despite previous studies emphasising its importance for carabids (Cameron and Leather, 2012). One explanation for this may be that the benefits of bare ground cover are influenced by its interaction with other environmental factors, making its impact site-specific (Cameron and Leather, 2012). For example, substrate type and stone density affect thermal properties and percolation: sandy soils, due to their rapid heat transfer, experience more significant temperature fluctuations in a daily cycle than clay soils, which maintain more stable temperatures (Cameron and Leather, 2012; Wheater et al., 2023). The concept of site-specificity is further supported by Marrec et al. (2021), who found that landscape characteristics only affected eurytopic and open-habitat species richness, with both guilds showing a decrease in species richness as proportion of forest (within a 500m radius) increased.

Plant cover had minimal effects on carabid distribution across habitats, likely due to structural uniformity of vegetation, which limited microhabitat variability. Consequently, carabid communities in this study may have been more strongly influenced by vegetation structure or abiotic conditions than by the presence of specific plant types. This aligns with previous studies emphasising the role of temperature and structural complexity in driving carabid diversity – specifically that warmer, heterogeneous environments often support greater insect diversity due to increased resource availability and habitat niches (Mellanby, 1939; Ratte, 1984; Lövei and Sunderland, 1996; Holland, 2002; Henning et al., 2017; Pedley et al., 2023). Additionally, the presence of generalist species, which can occupy various habitats, may have obscured or weakened the relationship between vegetation and carabid richness (Niemelä, 2001). Equitability, a metric more sensitive to environmental changes than species richness, might have revealed an effect; however, this study did not measure it. Given the lack of significant impacts on both abundance and species richness, it is plausible that equitability would also exhibit minimal variation (Valbuena et al., 2012).

4.2.3 Soil Moisture and Humidity

While soil moisture did not emerge as a significant driver of species richness in this study, moisture availability has been shown to play a crucial role in shaping carabid assemblages (Ludwiczak et al., 2020), often interacting with temperature effects, by influencing habitat selection, movement, site selection for oviposition, and larval development (Holland, 2002; Thomas et al., 2002). Ziesche and Roth (2007) observed that stable moisture conditions in mature coniferous and mixed forests, particularly in comparison to younger stands, supported the reproductive success of *Abax parallelepipedus,* as females in older stands carried significantly more ripe eggs and exhibited extended reproductive periods. This suggests that mature forests provide more favourable microclimatic conditions for this species' reproductive process. However, moisture influences species differently depending on their habitat preference. Species adapted to high-moisture environments would be expected to thrive in more humid conditions. This variation in habitat preference is closely linked to a species' ability to regulate internal water balance, a process directly influenced by humidity through its effect on evaporative water loss (Block, 1996). Xerophilous species, such as *Bembidion lampros,* (Luff, 2007) likely possess physiological adaptations to minimise water loss in dry environments, while species preferring damp conditions, like *Nebria brevicollis* (Forsythe, 1987), may be more vulnerable to the adverse effects of excessively dry environments.

Dry conditions can lead to desiccation, and may be more restrictive than heat alone, particularly for species reliant on stable soil moisture for survival and reproduction (Holland et al., 2007). Within this study, average humidity at the driest site was 62.7% (OW5), and whilst this ought not be considered extremely dry, the low species richness (two species, three individuals) observed there still reinforces the idea that even relatively low humidity or dry conditions can severely limit carabid presence. Too little humidity can hinder larval development and survival due to desiccation, leading to reduced mobility and possibly mortality in carabids (Holland, 2002). If carabids remain close to their oviposition site due to mobility issues, moisture conditions at that location will be more critical than if they travel widely, as immobile species will be dependent on the initial site's moisture conditions (Lövei and Sunderland, 1996; Holland et al., 2007).

Excessive humidity can also act as a limiting factor, favouring moisture-tolerant species while excluding others. Potential mechanisms driving this may include:

- Reduced oxygen availability in waterlogged soils: this can cause hypoxia both in carabid beetles and their prey species (Hoback and Stanley, 2001).
- Changes in prey distribution: larval prey species might drown, or some invertebrates may concentrate in highly humid areas, leading to localised prey availability (Wheater et al., 2023).
- Increased fungal growth: this can negatively impact ground conditions and increase infection risk in carabid species, further influencing survival (Holland, 2002).

Carabid eggs and larvae, which are often soil-dwelling (Lindroth, 1974), can suffer the same issues caused by extreme high and low moisture levels as adult carabids – either desiccation, which can hinder movement, or hypoxia in waterlogged habitats, both potential causes for mortality at all life stages.

4.3 Carabid Richness and Abundance

4.3.1 Richness and Abundance Across Habitats

The results confirmed Hypothesis 2: the highest richness and abundance was recorded in newly restored sites, particularly wet heath, emphasising the role of habitat restoration in maintaining and enhancing carabid diversity at a gamma and alpha scale. Conifer felling likely contributes to this positive effect by increasing habitat heterogeneity through greater sunlight penetration and the creation of open areas, which support favourable conditions for carabid beetles (Fuller et al., 2008; Pedley et al., 2023). The greater species richness recorded in more recently restored heathlands also suggests that retaining scattered wood elements – in this instance, deadwood and short stumps (recorded as 'tree cover' up to stump height) – can enhance biodiversity (Butterfield, 1987; Nadeau et al., 2015; Pedley et al., 2023). This structural complexity, even in the form of low-density woody remnants from felled conifers, may provide valuable microhabitats, refuge, and microclimate variation that supports a wider range of carabid species compared to completely open ground (Pearce et al., 2003; Skłodowski, 2020).

In contrast, the lowest carabid diversity was recorded in forested plots. This finding appears contradictory to the observation that retaining scattered tree stumps in restored areas could be beneficial, but the key difference lies in the nature and density of the woody structures. The forested plots were characterised by dense conifer canopy, resulting in limited ground-level light penetration, dense understorey vegetation and extensive leaf litter – conditions generally less conducive to carabid activity, potentially affecting their foraging, thermoregulation and prey availability (Butterfield, 1987; Lin et al., 2007; Morris, 2000; Magura et al., 2003). On the other hand, the scattered stumps in the newly restored areas – often dry heathlands – create a heterogeneous habitat with patches of sun-exposed ground and varied microtopography (Pearce et al., 2003; Skłodowski, 2020), increasing diversity without the suppressive effects of closed-canopy shade. As these woody remnants decompose, they may offer unique niches and contribute to carabid diversity by providing varied resources and microhabitats, particularly at the advanced stage of wood decay where the moisture content of the debris is higher (Nadeau et al., 2015). While some structural complexity clearly benefits carabids, dense, uniform conifer plantations influence microclimatic conditions, such as cooler temperatures and higher humidity, that are suboptimal for many species, potentially restricting activity, predation opportunities and reproductive success (Butterfield, 1987; Holland, 2002; Magura et al., 2003; Buchholz et al., 2013). This is consistent with studies demonstrating lower carabid abundance in forested sites compared to more open habitats like heathlands and dry grasslands (Buchholz et al., 2013; Spake et al., 2016). However, not all forested environments exert the same influence on carabid diversity. Old-growth or primary forests typically support a more complex structure, with varied canopy gaps, a diverse understory, and a dynamic leaf litter layer (Magura et al., 2003) – structural differences that potentially sustain higher carabid diversity. Natural forests also tend to support richer prey communities and more stable ecological conditions, which may enhance carabid persistence (Ziesche and Roth, 2007). Furthermore, other studies highlight the positive influence of wooded features on biodiversity, including in open habitats and semi-open landscapes, such as heathlands (Cameron and Leather, 2012; Nadeau et al., 2015; Pedley et al., 2023). This discrepancy suggests that the effects of tree cover are context-dependent, likely influenced by factors such as forest density, composition, and structure (Magura et al., 2003). The low diversity observed in this study's wooded sites may therefore be attributed to the relatively uniform structure of conifer plantations, in contrast to the habitat complexity provided by scattered trees in restored areas or the natural heterogeneity of old-growth forests (Magura et al., 2003).

The low richness values observed in Dry Heath and Old Dry restored heath may indicate less suitable habitat conditions or limited resources for carabids in these drier environments. This may be due to limited moisture availability, as the soil moisture levels would typically be lower in dry heaths, which may be unsuitable for many carabid species that prefer more humid conditions for survival and reproduction (Lindroth, 1974). Carabids are often predatory or scavengers, and so drier conditions may result in lower abundances of invertebrate prey, restricting the number of species that can persist (Lindroth, 1974). It is important to note that while these spot measurements of soil moisture and humidity did not show a direct relationship, the distinct habitat types likely reflect longer-term differences in these environmental factors. However, these drier sites hosted more specialist taxa, suggesting that while generalist species may struggle, certain species are better adapted to these conditions. For example, *Laemostenus terricola* was found in established dry heath (DH2), a species associated with dry, rocky environments (McFerran et al., 1996; Putchkov and Aleksandrowicz, 2020). Additionally, *Amara lunicollis*, a species often associated with sandy, open environments (Luff, 2007) was recorded in dry heaths restored after 2012 (ND2 and ND4), supporting the idea that certain species are adapted to drier heathlands, whether established or restored.

The lack of significant differences in species richness and abundance across the habitat types could be due to multiple factors. One possibility is that environmental conditions during the study period were particularly homogeneous – perhaps an especially wet and sunny year resulted in more uniform habitat conditions than usual. In 2024, Southern England was subject to heavy rains in the spring months, a much drier early summer than usual, and heavy thunderstorms in the late summer (Met Office, n.d.a, n.d.b). Additionally, while overall richness and abundance may not have varied significantly, species composition differed significantly across habitats. Since different species were present in different habitats, even where the total number of species or individuals remained similar, this could indicate a process of species turnover, where communities shift in response to environmental or habitat differences without affecting overall richness or abundance. Here, the modest sampling effort in the current study is an important consideration. The mean capture rate of approximately eight individuals per species across all 35 sites is at the lower end of the recommended range (Magurran, 2004). This can reduce confidence in species richness and abundance estimates. The rarefaction effect, for example, describes how sample size can bias richness estimates, as more species are likely to be 'discovered' in samples with a larger number of individuals (Magurran, 2004). To mitigate this, rarefaction analysis should be used to standardise species richness data, enabling comparisons between habitats based on an equal number of individuals. This would confirm if, while some habitats may have a higher observed richness, the differences were not statistically significant after accounting for unequal sample sizes (Magurran, 2004).

The low capture rate also impacts conclusions about rare species. The low capture rates also impact conclusions about rare species. Single-record species, or singletons, such as *Notiophilus substriatus* and *Olisthopus rotundatus*) introduce a degree of randomness into observed distribution patterns (Magurran, 2004). This means that conclusions regarding their habitat use and conservation importance should be viewed as preliminary, as these results may reflect chance encounters rather than stable populations (for example, patterns of species turnover may be exaggerated or obscured due to under-sampling).Despite these limitations, the detection of 4 nationally scarce and 1 nationally rare species, 16 of which occurred in restored habitats, is encouraging, even though further sampling would be required to confirm whether these patterns are consistent or representative of larger community trends.

4.3.2 Richness and Abundance Across Surface Types

While ridges on restored sites exhibited a greater abundance and richness of carabids compared to furrows, these differences were not statistically significant. This result is somewhat counterintuitive, as furrows, with their potentially more sheltered, moist, and cooler conditions (Batori et al., 2022), along with greater organic matter accumulation (Kabala et al., 2013), might be expected to support a more stable and abundant carabid population. This expectation aligns with previous observations by Herzon and Helenius (2008), who reported higher biodiversity in ditches in cropland areas due to factors such as cool, moist conditions, high productivity, complex habitats, and reduced disturbance. However, several factors could explain the observed suggestion of higher carabid abundance on ridges. Firstly, ridges, being more exposed, likely experience greater fluctuations in temperature, particularly higher average ground temperatures on warmer days in the spring and summer. Since carabid activity-density tends to increase with temperature (Holland, 2002), pitfall traps in these areas may have caught more beetles, reflecting increased activity rather than necessarily a larger population size. Secondly, if ridges are more exposed to wind and drying conditions, they may attract more generalist and active predator species with high mobility, such as beetles in the *Carabus* genus (Talarico et al., 2007). These highly mobile species can cover greater distances and therefore may have a higher chance of being captured in pitfall traps. Finally, the proximity of ridges and furrows and their potentially too similar microclimates may have mitigated any substantial differences in carabid abundance and richness. The presence of carabids in most traps across both surface types indicates that both microhabitats are utilised. Therefore, the lack of significant difference may be explained by minimal environmental differences between the ridges and the furrows, and the higher abundance caught on the ridges, may reflect increased activity levels, rather than a larger population size.

4.4 Carabid Species Composition

4.4.1 Species Composition Across Habitats

The results demonstrate that habitat type is a strong determinant of carabid species composition in this heathland system, with significant compositional differences recorded among the different habitats.

Carabid assemblages in Forest sites were moderately distinct, showing significant differences from several restored habitats, particularly New Wet and New Dry heathlands, but were more similar to established Wet and Dry Heaths. This pattern likely reflects structural and microclimatic differences between forested and open heathland systems. For instance, as Rode (1999) suggests, the canopy, understory, and leaf litter in conifer patches create distinct microhabitats and resource distributions that are not replicated in recently restored heathlands.

Differences in carabid assemblages between established Wet and Dry Heaths suggest soil moisture and humidity are critical environmental factors determining species composition, reinforced by the similarity of communities in restored wet heaths (Old Wet heath and New Wet heath) to established Wet Heaths, irrespective of restoration age. This sensitivity of carabid communities to moisture availability is strongly supported by Kirichenko-Babko et al. (2020), who found that even relatively short dry periods led to significant changes in ground beetle assemblages in forest and wetland ecosystems. They further noted that changes in humidity have a significant impact on carabid distribution, with hygrophilous species being particularly responsive – for example, Kirichenko-Babko et al. (2020) found that during the drought season, the number of hygrophilous carabids halved. The more stable moisture conditions in wetter sites likely favour a consistent assemblage of moisture-dependent carabids, contrasting with the potentially more variable and drier conditions in dry heathland sites, which may support a different suite of species better adapted to those conditions.

The influence of moisture as a driver of carabid species compositions is further supported by Fartmann et al. (2021), whose study across a montane heathland successional gradient showed the role of habitat structure in mediating microclimatic conditions, including humidity. The similarity in carabid communities between restored and established wet habitats in the current study likely reflects the rapid development of vegetation structures in these wetter areas that create similar humid microhabitats, irrespective of the time since restoration. Conversely, the distinct communities in Dry Heath habitats, potentially experiencing lower soil moisture and humidity due to differences in vegetation and soil properties, further underscore the importance of these environmental factors, consistent with the microclimatic influences on carabids discussed by Fartmann et al. (2021).

Beyond the differences between wet and dry habitats, the age of restoration also plays a significant role in shaping carabid communities. Old Dry heathlands were significantly different from all other habitats in terms of carabid species composition, with consistently high effect sizes, likely resulting from the gradual establishment of specific environmental conditions and associated resource availability over the long term. For instance, while Mitchell et al. (2000) focused on vegetation and soil, their results underscore the principle that extended periods without major disturbance allow for the accumulation of specific environmental attributes. This temporal aspect likely explains the significantly different carabid assemblage in Old Dry heath sites, as these specific conditions have developed gradually over time. Such conditions may include increased organic matter accumulation through intermediate-stage succession, gradual changes in soil structure, and the stabilisation of vegetation cover, all of which influence local climate conditions and nutrient accessibility (Schirmel and Buchholz, 2011; Lange et al., 2023). While the current study's direct measurements of environmental variables (for example, soil moisture, relative humidity and depth of organic matter) did not always yield strong correlations with carabid composition, this is likely due to these being point-in-time measurements. In contrast, habitat type and restoration age may serve as proxies for long-term environmental development, integrating temporal changes that are not captured in single-time field sampling. As such, these broader categories likely reflect cumulative differences in environmental structure and function, which in turn shape carabid community assembly over time. The extended duration in older sites has likely allowed for both the development of more stable environmental conditions and increased opportunities for colonisation, leading to the formation of more established communities.

The similarity of carabid communities in established habitats (Forested sites, established Wet and established Dry Heathland sites) suggest a shared, long-term development of microhabitats, unlike restored heathlands. This divergence in restored heathlands likely reflects ongoing recolonisation processes and the fact that environmental conditions in these areas remain more transitional or unstable, with factors such as vegetation structure, microclimate, and soil properties still undergoing change (Schirmel and Buchholz, 2011; Lange et al., 2023). The nature of beta diversity differed significantly between wet and dry heathlands. New Dry heathland sites display a pronounced turnover compared to both established Dry Heaths and Old Dry heaths, indicating that, analogous to wet habitats, dry habitat species composition is still in flux post-restoration, reflecting ongoing environmental shifts after conifer felling as communities converge towards established sites, such as soil development or vegetation succession (Vician et al., 2018). This aligns with the expected trajectory of communities converging towards carabid species composition in established sites, a pattern consistent with Borchard et al. (2014) and Lange et al. (2023), who found that carabid turnover was highest immediately following habitat restoration before stabilising in the later years.

The development of characteristic communities in restored dry heaths (Old Dry and New Dry heaths), as evidenced by differences from established Dry Heaths, implies that the recovery of abiotic factors (for instance, ground temperatures, soil pH, organic matter and water-holding capacity) is a more prolonged process in drier environments following conifer removal. This is supported by Harrison (1981), who demonstrated that *Calluna* heathland, characteristic of dry heaths, exhibited slow and delayed recovery following disturbance.

The study highlighted the influence of soil conditions, particularly in acidic, podsolised soils, on recovery rates, indicating that the restoration of these soil properties is a protracted process. Additionally, in older wet heath restorations (pre-2007), species composition has likely already begun to stabilise, converging towards the long-established communities observed on established Wet Heath. This pattern echoes findings in restored grasslands, where plant diversity and habitat complexity accelerate initial species turnover and subsequently promote community stabilisation (Lange et al., 2023). The greater influence of nestedness in dry restored heaths (compared to their wetter counterparts) may reflect stronger environmental filtering effects due to the more extreme and variable conditions in these restored habitats (which have not yet reached the more stable conditions of established heathlands), and ecological gradients such as variations in soil moisture, temperature fluctuations, and the structure and complexity of vegetation cover (Schirmel and Buchholz, 2011;

Lange et al., 2023) Such gradients can act as filters that limit which species are able to establish, contributing to the observed patterns of turnover. Additionally, factors such as ecological resource distribution and dispersal constraints — including body size or wing morphology — may further shape species composition in these habitats (Liu et al., 2015; Neumann et al., 2017). Previous research has observed that, in temperate forests, where environmental filtering dominates, dispersal limitation (where species struggle to reach suitable habitats due to movement barriers) may still influence species distributions (Liu et al., 2015).

In this study, the division of restored heathland sites into “old” (pre-2007) and “new” (post-2012) categories applies a threshold based on the date of conifer felling. While practical, this categorisation inherently simplifies what is likely a continuous successional process. Steel et al. (2013) caution that applying thresholds to continuous ecological data can result in filtered information, which may lead to artifacts or biased inferences. Specifically, they highlight that the choice of threshold can influence scientific conclusions and that researchers must carefully consider whether such thresholds meaningfully capture the ecological processes of interest, or risk masking gradients in the data. Additionally, Steel et al. (2013) discuss the importance of clearly defining what the study is drawing conclusions about (termed the ‘unit of inference’) to avoid issues like pseudo-replication, where multiple data points are incorrectly treated as independent. In the context of restoration timing, treating time since felling as discrete time categories rather than continuous variables may risk oversimplifying underlying ecological dynamics. Therefore, the use of discrete restoration age categories, while necessary for practical reasons within the current study, should be interpreted cautiously. To address these concerns, future analyses might benefit from approaches that treat time since felling as a continuous variable to better capture the complexity of heathland restoration trajectories. This would enhance the ecological relevance of findings and reduce the risk of drawing misleading conclusions based on arbitrary temporal thresholds.

4.4.2 Species Composition Across Surface Types

Surface type in restored heathlands had little influence on carabid composition. The results indicate there may be slightly greater community heterogeneity in ridges compared to furrows, potentially reflecting ongoing colonisation and establishment processes that have not yet stabilised. Alternatively, this variation could be influenced by broader environmental gradients such as differences in moisture availability, soil texture or vegetation, which may subtly shape species distributions. However, these effects are not statistically significant. Almost all species unique to furrows had an affinity with dry ground (*A. tibialis*, *B. properans*, *C. campestris*, *H. affinis* and *H. rufipes* (Holland, 2002)), except for *P. diligens*, a species typically associated with wet habitats (Luff, 2007). This contradicts expectations that furrows, which might be assumed to retain more water, would support more hygrophilic (wet-loving) species, such as *Pterostichus diligens*, *Pterostichus strenuus* (Eyre et al., 2004) and *Bembidion guttula* (Luff, 2007), all of which were unique to Old Wet restored sites in this study. Given the high mobility of carabids, individuals captured exclusively in furrows may not exclusively inhabit that habitat; dry-adapted species could traverse furrows and vice versa, potentially decoupling capture location from long-term habitat use. Supporting this, soil moisture readings from furrows were not dissimilar to those of ridges throughout the study periods. It is possible that, during the spring and summer months when this study took place, the dry summer weather provided a more mesic habitat, better suiting a wider range of carabids (Epstein and Kulman, 1990).

The historical colonisation of the sites may also influence carabid species composition. For example, if dry-adapted species colonised furrows early after restoration, they may have persisted even as conditions continued to change. A similar lag effect has been observed by Neumann et al. (2017), who found that carabid communities were influenced by historical, rather than contemporary, landscape composition. In the current study, the presence of dry-adapted species in furrows may similarly reflect legacy effects, where early colonisers persist despite environmental change. However, the lack of significant differences in carabid communities between surface types suggests that microtopographical variation in restored heathland may not produce sufficiently distinct microhabitats for carabid beetles. Instead, other factors such as subtle variation in microclimate, soil composition, or prey availability may be more influential in shaping carabid assemblages in ridges and furrows. The potential for legacy effects is particularly relevant when considering the differential responses of generalist and specialist species. Generalists, with broader ecological tolerances and higher dispersal capabilities, are typically able to colonise restored habitats more rapidly. In contract, specialist species often have narrower habitat requirements and may take considerably longer to establish, depending on the restoration of specific ecological conditions. As such, the current assemblage may underrepresent these slower-returning species, and full community recovery (particularly of heathland specialists) may not yet be realised. This introduces the question of whether restored habitats are currently providing sufficient structural and ecological complexity to support these species. Furthermore, while conifer clearance is a key component of heathland restoration, rapid and widespread removal may risk reducing the habitat mosaic and structural heterogeneity that supports shade-tolerant or woodland-associated carabids.

Although traps were stratified across ridge and furrow microtopographies to assess the influence of surface structure in restored sites on carabid communities, the effective sampling radius of pitfall traps raises the possibility of spatial spillover. Beetles active in adjacent microhabitats may have been captured by traps set on either surface type, potentially obscuring habitat-driven differences in species composition or activity. Apparent similarities between ridge and furrow samples may therefore reflect the overlapping foraging ranges of mobile carabids rather than true ecological uniformity.

Many traps recorded no individuals of certain species, which can occur either because the species was not present (a ‘structural zero’) or species being present but not detected (a ‘random zero’) (Blasco-Moreno et al., 2019). Martin et al. (2005) stress that ecological datasets with high zero counts often diverge from standard distributional assumptions, such as Poisson, leading to inflated type I or type II errors, loss of statistical power, or misleading interpretations. Zeros were explicitly omitted in certain analyses: gamma and alpha diversity metrics used presence/absence data, thereby omitting zeros as absences. For community composition analyses, the datasets used had all zero values removed, so that functions were applied only to species that were present in at least one of the four traps per site. This helped reduce bias from zero inflation but may have affected the representation of rare species. Turnover and nestedness calculations also used presence/absence data, though rare species were still included, meaning some skew related to zeros may still persist. Trait-based analyses, GLM and GAMs were likely minimally affected, as they relied on richness or environmental variables where zero counts were irrelevant. Blasco-Moreno et al. (2019) recommend using zero-inflated models (ZIMs) to better distinguish between random sampling failures and structural ecological absences

(Blasco-Moreno et al., 2019). Their study found that these models can help account for the effects of zero inflation and overdispersion, improving confidence in ecological interpretations. The sampling effort in this study yielded a mean capture rate of around eight individuals per species, which is below commonly recommended thresholds and likely affected the overall confidence in species richness and diversity estimates, especially at sites with low total captures (Magurran, 2004).

4.5 Carabid Functional Traits

Hypothesis 4 was supported by the findings in this study. Analysis reveals that habitat type and inherent habitat differences caused by conifer felling significantly influence carabid assemblages, primarily by shaping the availability of suitable conditions for species with specific functional traits, including body size, wing morphology, breeding season, and soil moisture preferences.

Many of the functional traits selected for this study were similar to those used by Kerdoncuff et al. (2023), reflecting established methodologies for assessing carabid functional diversity. Although significant differences in individual functional traits were observed across habitat types, restored habitats did not exhibit significantly different functional diversity compared to established heaths. This suggests that while individual trait compositions varied, the overall functional diversity was converging towards that of mature heathlands, indicating successful, albeit ongoing, recovery. This likely reflects the recovery period required for communities following disturbance, where successful recovery is indicated by a functional diversity comparable to that of established heathlands, rather than necessarily a higher level. Across different habitat types, overall diversity may not change substantially in the short-term, but the composition of functional traits will change with the species composition. For instance, while the total number of functional roles may remain similar, the specific species occupying those roles could shift dramatically, reflecting adaptations to the altered environmental conditions (Mayfield et al., 2010). This highlights the need for a more detailed examination of functional trait composition, rather than solely focussing on overall diversity metrics. Additionally, comprehensive activity data are required to allow this analysis of functional richness, evenness, and divergence (Villéger, et al., 2008) across habitat types, which could provide a clearer understanding of how functional trait diversity varies, and whether restored habitats support a broader range of functional traits.

4.5.1 Body Length

Carabids with smaller body sizes, particularly below 15mm, were more abundant in restored heathlands, suggesting that these species may be particularly successful in disturbed sites. *Dyschirius globosus*, the smallest carabid recorded in this study, was primarily found in restored heathlands, where immature vegetation growth and cover were likely less dense. In contrast, larger, more mobile carabid species were more prevalent in mature habitats, indicating their capacity to exploit a wider range of resources. This observation corroborates findings by Blake et al. (1994) who found that larger carabids demonstrated greater adaptability in more structurally complex environments, such as grassland ecosystems. This pattern aligns with previous studies finding similar results in other disturbed environments, including urban areas (Weller and Ganzhorn, 2004), grasslands (Blake et al., 1994) and agricultural landscapes (Langraf et al., 2017). The limited mobility of smaller-bodied species likely impedes their ability to effectively navigate and forage in habitats with dense vegetation cover (Morris, 2000).

4.5.2 Wing Morphology

The current study found that brachypterous (wingless) carabids were more prevalent in more established sites, particularly established heathlands. This significant variation in wing morphology across different habitats shows the importance of dispersal abilities for carabids, especially in fragmented landscapes. Wing morphology is shaped by selective pressures such as habitat stability, resource availability, dispersal requirements, and environmental factors (Zera and Denno, 1997; Ribera et al., 2001; Zalewski et al., 2015). This aligns with the templet theory (the idea that habitat structure and disturbance regimes act as environmental filters, shaping the evolution and persistence of species traits best suited to those conditions). This was demonstrated by Ribera et al. (2001), who found that brachypterous species were more frequent in less intensively managed sites with denser vegetation, while macropterous and dimorphic species dominated more disturbed, open habitats. Their analysis linked wing morphology directly to habitat openness and management intensity, consistent with the patterns observed in the current study. For instance, *Olisthopus rotundatus* is a heathland specialist with limited dispersal capacity (de Vries et al., 1996) and was exclusively found in dry heaths restored prior to 2007 in this study. The results align with the expectation that species with low dispersal power will be restricted to older, more stable habitats. The reduced investment by brachypterous species in dispersal allows for greater allocation of resources towards reproduction and survival (Brandmayr, 1991). Conversely, numerous studies have documented a higher prevalence of macropterous (winged) individuals in unstable or newly disturbed habitats, where dispersal is advantageous for colonising new areas and escaping unfavourable conditions (Brandmayr, 1991; Venn, 2007; Pedley and Dolman, 2014). Over evolutionary timescales, as restored habitats mature and conditions stabilise, the development of wing dimorphism (the presence of both winged and wingless individuals) may occur. Consequently, the successional trajectory of restored heathlands, as plagioclimaxes, involves ongoing management that prevents true ecological equilibrium (Mitchell et al., 1999; Mitchell et al., 2000a). This sustained disturbance in heathland habitats may exert different selective pressures on carabid dispersal traits compared to self-regulating systems. However, such shifts are unlikely to be detectable within the relatively short timeframe of restoration projects, such as in the current study.

4.5.3 Breeding Season

Spring-breeding carabids exhibited strong differences in abundance across habitats, while summer- and autumn-breeding species did not. In particular, spring breeders were more prevalent in wetter and mature heathland sites, indicating that they may require more stable environmental cues for successful reproduction, and that breeding season may influence how carabids respond to habitat characteristics. Given this sensitivity, spring-breeding carabids and those with mixed breeding seasons may be particularly affected by habitat restoration via felling. Seasonal resource availability likely plays a key role. For instance, *N. brevicollis*, undergoes diapause between spring emergence and autumn breeding (Luff, 1998, 2007). Environmental cues such as temperature and moisture, both influenced by habitat restoration, significantly affect diapause timing and subsequent reproductive success (Penney, 1969). Restored sites, with perhaps less dense vegetation, may experience more pronounced temperature fluctuations. For example, the removal of trees is expected to lead to decreased humidity and a greater variation between minimum and maximum temperatures (Suggitt et al., 2011).

The apparent resilience of summer- and autumn-breeding species to habitat differences likely stem from their differing life cycle timing and resource requirements, which may be less sensitive to the immediate effects of restoration. In addition, these species – particularly autumn breeders – may not have been present in the most suitable habitats for reproduction during the sampling period, potentially contributing to the less pronounced impacts observed. Autumn breeders may be less affected by habitat restoration due to differences in seasonal food availability than spring breeders. For instance, studies by Šerić Jelaska et al. (2014) have shown that autumn-active carabids consume a higher proportion of slugs and Lepidoptera than those in spring, suggesting that dietary flexibility in autumn may help buffer these species from habitat-induced changes in microclimate and prey abundance.

4.5.4 Soil Moisture Preference

Significant differences in abundance of carabids displaying a preference for dry or wet soil conditions suggests that species adapted to these extremes are more sensitive to habitat changes following conifer felling than those with a more flexible moisture tolerance. Damp ground specialists were most abundant in forest sites, indicating a dominance of shade-tolerant and litter-dwelling species. This supports research carried out by Wiezik et al. (2007), who found that litter-dwelling beetle communities in undisturbed forest reserves, characterised by high moisture and complex litter layers, were dominated by stenotopic species, while managed conifer stands showed a decline in these specialists.

The low abundance of wet-ground specialists in established Wet Heath – a habitat where they would be expected to thrive – was unusual. This discrepancy may stem from several factors. Despite its classification, established Wet Heath likely exhibits microtopographical variation (for example, in elevation, vegetation cover and soil texture) that influences local soil moisture levels (Gurnell, 1981). Some areas may be drier or structurally distinct from newly restored wet sites, possibly due to denser vegetation or compacted soils, rendering them less suitable for species requiring persistently wet conditions. Additionally, established Wet Heath may support a more mature and complex carabid community, including predators that regulate the abundance of wet-ground specialists. In contrast, restored sites, with potentially fewer competitors or predators, might allow these specialists to thrive. The sparse vegetation in these restored habitats could lead to altered water table and drainage conditions compared to established wet sites. Consequently, increased sun exposure might result in greater susceptibility to drying.

Clear-felling alters the hydrology of an area, such as increasing soil moisture and humidity (Suggitt et al., 2012), potentially benefitting carabid species that prefer wetter conditions, such as *Agonum* and *Bembidion* species (Buglife, 2020). In the current study, there was a notable difference in *Bembidion* species abundance between restored wet and dry heaths. Specifically, restored wet heaths supported a higher abundance of moisture-loving species, with 17 individuals of *B. guttula*, *B. nigricorne*, and *B. properans* recorded, compared to only two individuals of *B. lampros* in restored dry heaths. Established heaths may have developed more efficient drainage pathways over time, or be more exposed to drying and sunlight, leading to seasonal drying or fluctuating water levels. This contrasts with newly restored areas, which may initially retain more moisture due to temporary furrows from felling, or a thicker layer of decomposing organic matter. However, soil moisture data revealed a seasonal shift between established Wet Heath and newly restored wet heath: site WH2 exhibited the greatest average soil moisture in May, NW2 in June and WH5 in July. This suggests that even in established heathlands, moisture levels will vary throughout the season. Therefore, if established Wet Heath is indeed prone to seasonal drying, fluctuating water levels, or less consistent standing water, it is likely to be less attractive to carabids that require consistently wet conditions, potentially explaining why slightly more wet and damp specialists were found in restored wet sites.

4.5.5 Vegetation Preference

The prevalence of carabids displaying a preference for densely vegetated habitats was greatest in established Dry Heath. Conversely, carabids exhibiting a preference for open habitats were most abundant in established Wet Heath, a habitat which, despite being more established, remained open and sparsely vegetated, lacking both trees and tree stumps. This observation supports the notion that the maintenance – or creation – of open conditions, such as those resulting from conifer felling, benefits species associated with heathland, including specialists such as *Bradycellus ruficollis* and *Cicindela campestris* (de Vries et al., 1996; Pawson et al., 2006; Schirmel and

Buchholz, 2011). Previous studies also recognise that conifer felling leads to an increase of open-habitat species, while closed-canopy specialists decrease (Niemelä et al., 1993; Koivula, 2011). The reduced barriers to movement in these open environments, including shorter vegetation and a thinner litter layer, are particularly beneficial to smaller-bodied carabids with limited dispersal (Greenslade, 1964; Kerdoncuff et al., 2023). In contrast, the increased litter accumulation and vegetation density in forested areas may create conditions unfavourable to these open-habitat specialists. This supports findings from Lin et al. (2007), who suggest that the ameliorating effects of tree and bracken litter in reforested areas may not favour carabids with specific habitat needs, which prefer open, less vegetated environments. As vegetation density increases post-restoration, species preferring denser vegetation are likely to become more abundant, as observed in dry and wet sites restored before 2007.

4.5.6 Activity Patterns

The distribution of diel activity across habitats showed that nocturnal and diurnal activity patterns did not exhibit a discernible pattern. This contrasts with Pravia et al. (2019), who demonstrated a significant association between diel activity and habitat type in bog restoration, with nocturnal species dominating in open bog and diurnal species in restored areas. The discrepancy between these findings suggests that, in the current study system, the ecological roles of carabids with different activity patterns are not as closely related to habitat disturbance via clear-felling. It is likely that other factors, such as water table depth, vegetation structure or temperature, exert stronger influence on distributions of carabids with specific activity patterns than heathland restoration alone (for example, diurnal species in particular are generally more active in warmer environments than nocturnal species (Holland, 2002)). It is important to note that the current study examined restored and established heathland habitats, whereas Pravia et al. (2019) focused on bog restoration, and this difference in habitat type could contribute to the observed discrepancy. Pravia et al. (2019) also found that even 18 years post-felling, carabid communities did not fully converge to original bog conditions, indicating that habitat restoration is a complex and long-term process. This complexity, involving persistent environmental changes, could explain why diel activity patterns in our study were not strongly linked to restoration status. Pravia et al., (2019) acknowledge that the chosen traits may not fully capture the nuances of community assembly, leaving room for unmeasured traits or environmental factors to be at play. The unknown activity patterns for some species, and the resulting incomplete dataset for this trait, may be masking subtle variations that remain undetectable, reinforcing the need for cautious interpretation of this particular trait analysis, and limiting ability to draw definitive conclusions.

However, the results in the current study are more consistent with those of Ribera et al. (2001), who also found that diel activity patterns showed weak or no correlation with environmental gradients, based on RLQ analysis of multiple traits. In their study, variables such as wing development and breeding season showed strong links to environmental disturbance, while diel activity had correlation ratios close to zero, suggesting it may be a less ecologically informative trait in relation to habitat disturbance, particularly in structurally complex or transitional environments.

Research by Luff (1978), Lövei and Sunderland (1996) and Tuf et al. (2012) suggest that forest species tend to be nocturnal; however, the current study did not support this. This discrepancy may be explained by seasonal shifts in activity patterns observed in some carabid species (Lövei and Sunderland, 1996; Tuf et al., 2012), such as *Pterostichus melanarius*, a carabid that is nocturnal until August, where it switches to a diurnal activity pattern (Lövei and Sunderland, 1996). Similarly, Luff (1978) found that between May and the end of August, *Harpalus rufipes* was most active just after midnight, whereas after September this species exhibited peak behaviour progressively earlier in the night.

5. Limitations

While this study provides valuable insights, several limitations should be considered if it is to be repeated.

5.1 Study Design

One of the main challenges in ecological research is maintaining long-term monitoring (Pywell et al., 2011). Ecosystem changes often occur gradually, varying by habitat type — for example, heathlands develop relatively slowly (Read and Bealey, 2021). As a result, short-term studies may not provide an accurate picture of restoration outcomes, making multi-year research essential for informing conservation strategies. Some studies have addressed this challenge; for instance, Pedley et al. (2023) examined arthropod communities at various time points (1, 3, 5, 7, 9, 13, and 21 years) after clear-felling in Thetford Forest. Instead of tracking changes prospectively, they utilised forests at different successional stages to infer long-term trends. However, distinguishing the effects of different restoration techniques remains difficult unless research is conducted under controlled conditions. Extended monitoring is crucial to capturing meaningful ecological responses to restoration efforts.

While the research was conducted over several months, it does not account for long-term ecological changes, which may influence certain species more than others. For example, beetles in the *Carabus* genus display notable temporal and spatial variation (Holland, 2002). As a result, the findings represent a snapshot in time rather than a progression of restoration outcomes. Additionally, this study was relatively small in terms of sample sizes, and it is likely to carry many type II errors due to low statistical power. While pseudo-replication was avoided by combining data obtained from ridges and furrows to ensure equal replicates per habitat, separate analyses comparing samples from ridges and furrows in restored heathland sites were still undertaken. To strengthen the robustness of this analysis and improve reliability of results, future research could incorporate more survey sites or additional replication, which would capture a wider range of topographical features, helping confirm whether any patterns observed between ridges and furrows are specific to the Rempstone and Godlingston survey sites or follow general trends. Incorporating additional survey sites and increased replication would reduce uncertainty and help clarify whether observed patterns reflect broader ecological processes or are stie-specific anomalies.

Considering ground-dwelling beetles and their environmental sensitivity, this study would benefit from the collection of extra environmental variables such as soil pH and precipitation, which are both influential factors on invertebrate distribution (Liu et al., 2007; Diaz et al., 2011). Additionally, larvae were not collected or analysed, and as larval development is key to understating carabid ecology, this should be prioritised if the study is to be repeated. This study focused on carabids as a model group, while the integration of other taxa would yield a more holistic understanding of ecosystem recovery post-felling. Following this, a repeat of the experiment, and thus long-term monitoring, would elucidate the long-term trajectory of carabid communities following conifer felling in restored heathlands.

5.2 Equipment

Over the course of the study, three pendant data loggers were lost and, despite batteries being changed prior to sampling, seven data loggers were defective or ran out of battery during the study. This resulted in an incomplete dataset for ground temperature.

5.3 Sample Collection

As previously mentioned, the estimate of species richness is likely unrealistic due to the small sample size, which limits the strength of conclusions drawn from the study. This is evident from the species accumulation curves for carabids collected from different surface types, which did not reach an asymptote. Furthermore, the sampling effort was compromised by the loss of data from the August sample period due to trap damage, potentially omitting key seasonal variation in carabid species presence. Therefore, additional and more consistent sampling — spanning all habitat and surface types across the full active season — is likely necessary to more accurately capture the true species diversity, both in established and restored habitats. Creating rarefaction curves would help to account for biases caused by unequal sample sizes (Magurran, 2004).

Regarding environmental variables, the relatively small sample size (n = 35 for most environmental variables, n = 25 for ground temperature) may have limited the statistical power to detect relationships, particularly for variables with p-values approaching significance. Future studies with larger datasets could provide more conclusive evidence regarding the role of environmental variables in shaping carabid diversity. Increasing sampling frequency, for instance, weekly, instead of monthly, would also help overcome this limitation, particularly for capturing temporal variations.

One particular drawback of this study was the one-time collection of ground temperature data at the end of the survey season, rather than periodically throughout the season (i.e. after each survey window). This resulted in a substantial amount of lost data, which could have influenced the interpretation of how ground temperature correlates with carabid richness. Future studies should aim for continuous or periodic data collection to provide more accurate insights into microclimatic conditions. Additionally, measuring more environmental factors, such as soil pH, soil type, and prey availability would provide a more holistic view of the drivers of carabid species composition across these habitats.

While species richness provides valuable information, future analyses should incorporate equitability and Shannon diversity indices. These measures, crucial for understanding the evenness of species distributions, are often more sensitive to environmental variation (Magurran, 2004; Graham et al., 2009) and would allow for a more comprehensive exploration of how environmental factors influence the ecological dynamics within these habitats, particularly concerning habitat complexity and environmental gradients.

This study's findings regarding humidity-related trends in carabid diversity are limited by the potential influence of random variation and unmeasured environmental factors, underscoring the necessity for further research with larger sample sizes or *in situ* equipment. The bryophytes category in this study encompassed mosses, liverworts, hornworts and lichens, which may themselves have varied impacts on microhabitats, for example, shade and ground temperature, depending on the species structure and growth form (Lakatos, 2011). It would be good practice to record to genus level where possible.

Beetle dispersal is influenced by hunger levels (Mols, 1987; Holland, 2002), which may have impacted the samples collected in the pitfall traps. In-trap predation of, for example, smaller carabids, cannot be dismissed as diet was not confirmed, thus data would have been skewed. Dietary analysis would provide a more accurate profile of carabid activity. The carabid surveying encountered an underrepresentation of smaller carabid species, such as *Syntomus* and *Bembidion*, which could be due to their reduced dispersal capacity associated with smaller body size (Gutiérrez and Menéndez, 1997). Additionally, pitfall trapping is a measure of activity-density rather than species richness (Thomas et al., 1998). Future research could combine multiple carabid sampling techniques, such as sweep-netting or camera trapping to more accurately monitor temporal dynamics of invertebrate density (Gao et al., 2024).

During the summer periods, the study was subject to interference from cows, foxes, and possibly other fauna, resulting in traps being upturned, trampled and removed. Such disturbance led to data loss in the August sampling period, and as a result this data was not included in the analysis. Upon repetition, it would be of good practice to ensure pitfall traps were placed in areas of minimal ungulate disturbance and were covered with a 'roof' (Woodcock, 2005), although this may influence the number of forest species displaying high mobility, potentially attracted by the cooler, shaded patches (Buchholz and Hannig, 2009). Additionally, fitting the pitfall traps with a funnel would reduce bycatch of small mammals and reptiles (Brown and Matthews, 2016) and reduce risk of carabid escape. Inclement weather during trap deployment likely impacted sample capture. Very heavy rain was recorded on several of the sampling days, causing some traps to float or become displaced above ground level, rendering them ineffective for capturing ground-dwelling carabids. This issue has been recognised in previous research, for example, Pakeman and Stockan (2014).

5.4 Data Analysis

Due to time and resource limitations, invertebrates such as gastropods, arachnids, annelids and non-carabid coleoptera were not identified to species level.

Estimating functional diversity proved challenging due to the limited availability of comprehensive trait data. Building a robust trait database requires extensive literature review and expert consultation. Future studies should prioritise expanding this database, incorporating key traits like mandible morphology (for instance, shape and size), which significantly influences carabid dietary habits (Konuma and Chiba, 2007). Trait selection inherently presents challenges, as trait relevance can vary across ecological context, while inconsistent categorisation across studies can hinder data standardisation and interpretation. For example, wing morphology might be classified as macropterous, brachypterous, or include intermediate forms. Similarly, assigning species to functional trait categories can be ambiguous. Knapp et al. (2020) categorised carabid coloration as ‘dark’ (black or brown) or ‘metallic/colourful’ (multi-coloured). However, this classification overlooks species exhibiting both dark and metallic characteristics (such as *Carabus granulatus*), species with contrasting body regions (such as *Acupalpus dubius*) (Luff, 2007), and species with patterned dark colouration. While Knapp et al. (2020) reported data at the tribal level, potentially mitigating this issue, it underscores the difficulty of using broad colour classifications. Consequently, body coloration was initially considered in the current study but ultimately excluded from functional trait analysis due to these overlapping and ambiguous categories.

6. Conclusion

This study examined how conifer felling for heathland restoration influences carabid beetle communities, with particular attention to diversity, species assemblages, and functional trait distribution across habitats of differing restoration ages and vegetation covers.

The prediction that carabid richness would increase with moderate microclimates (Hypothesis 1.a) was partially confirmed, with results showing that sites with warmer ground temperatures, likely influenced by canopy removal, exhibited higher carabid diversity. However, Hypothesis 1.b, which anticipated greater carabid richness in sites with more bare ground and low-lying vegetation, was not supported. Instead, structural heterogeneity (specifically the presence of woody vegetation and deeper leaf litter) was associated with higher carabid richness across the studied habitats, encompassing established forest and heathlands of varying restoration ages. Furthermore, there was no significant impact of microtopography (ridges and furrows) on carabid richness or abundance in the restored heathland sites.

The results confirmed that recently restored sites host the highest carabid richness and abundance, particularly newly restored wet heathlands, validating Hypothesis 2. These sites outperformed both older restored dry heathlands and, in general, established forested sites. This indicates a positive initial response to conifer removal in lowland heaths under wetter conditions.

The research found a strong association between carabid species composition and habitat type, supporting Hypothesis 3: carabid communities differed significantly between restored heathland, established heathland, and forested areas. Beta diversity was primarily driven by species turnover rather than nestedness, indicating that differences in species composition were mostly due to species replacement. This pattern was especially pronounced in newly restored sites, particularly in wet heathlands, reflecting highly variable and dynamic species communities. In contrast, older and more established habitats, while still dominated by turnover, showed a higher contribution of nestedness, suggesting that some communities differed mainly through species loss. Of the 44 recorded species, 16 were unique to newly restored habitats, while only 5 were exclusive to established forests and heaths, and 23 occurred across multiple habitat types. This highlights the importance of habitat heterogeneity in supporting diverse carabid assemblages.

Functional trait analysis provided strong evidence that carabid traits, such as body length, dispersal ability, breeding season, and soil moisture preferences, varied considerably across habitat types, as predicted in Hypothesis 4. Newly restored sites (post-2012) were found to support a higher abundance of smaller, macropterous, spring-breeding carabids typically of early-successional environments. In contrast, established sites and habitats restored before 2007 were home to larger, less dispersive species better adapted to dry soils and dense vegetation, reflecting more stable, mature conditions.

The findings from this investigation are largely consistent with existing literature. Positive initial carabid responses to conifer felling corroborates research by Fartmann et al. (2022) and Pedley et al. (2023), who also reported increased species richness and the promotion of open-habitat specialists in the early years following canopy removal. Likewise, shifts in species composition and functional traits align with studies by Spake et al. (2016) and Borchard et al. (2014), linking changes in vegetation structure to carabid assemblages. However, the analysis revealed that structural heterogeneity was associated with higher diversity, challenging the conventional assumption that only open habitat is beneficial. Given that sites with greater structural heterogeneity higher carabid richness, the current study supports a more comprehensive restoration strategy than clear-felling alone. Results also indicate potential lag effects in the recolonisation of habitat specialists, and the possibility that rapid, large-scale clearance could inadvertently disadvantage shade-tolerant species while temporarily favouring generalists. This aligns with concerns raised in the literature regarding habitat homogenisation and its impact on landscape-level (gamma) diversity.

This research demonstrated that conifer felling, and the subsequent creation of open, early-successional habitat, can successfully increase carabid diversity. However, the successful and sustainable recovery of these communities requires a more holistic approach. Therefore, future heathland restoration and conservation strategies should prioritise: the creation and maintenance of habitat (and microhabitat) heterogeneity, including small forest patches and areas of varying ground cover; the implementation of thorough long-term monitoring that incorporates detailed environmental data and functional trait analysis; and using a rotational management system that ensures a range of forest stands at different ages. Implementing these recommendations will be crucial for the long-term success of heathland restoration and for enriching carabid diversity within these valuable habitats.

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8. Appendices

8.1 Risk Assessment

Bournemouth University

Risk Assessment Form

About You & Your Assessment	
Name	Jenny Manley
Email	jmanley@bournemouth.ac.uk
Your Faculty/Professional Service	Faculty of Science and Technology
Is Your Risk Assessment in relation to Travel or Fieldwork?	Yes
Status	Approved
Date of Assessment	06/02/2024
Date of the Activity/Event/Travel that you are Assessing	

What, Who & Where	
Describe the activity/area/process to be assessed	Surveying invertebrates in the Purbecks National Nature Reserve
Locations for which the assessment is applicable	Rempstone Heath, Godlingston Heath
Persons who may be harmed	Student

Hazard & Risk	
Hazard	Harmful substances
Severity of the hazard	Low
How Likely the hazard could cause harm	Low
Risk Rating	Low
Control Measure(s) for Harmful substances: Ensure students understand the substances they will be handling (e.g. alcohol solution, distilled water) Ensure students wear a lab coat and goggles in the lab Ensure students know where the eye wash stations are located, and where to wash hands of any harmful substances Ensure spillages are cleared up immediately, and notified to a member of staff	
With your control measure(s) in place - if the hazard were to cause harm, how severe would it be? Low	
With your control measure(s) in place - how likely is it that the hazard could cause harm? Low	
The residual risk rating is calculated as: Low	
Hazard	Fire or explosion
Severity of the hazard	Medium
How Likely the hazard could cause harm	Medium
Risk Rating	Medium
Control Measure(s) for Fire or explosion: Ensure students and staff know where to find fire alarms and extinguishers in the laboratory Ensure exit routes on the heathland are clearly communicated to all students working on site Ensure flammable items (such as alcohol solution) are kept away from open flame Ensure students know where the nearest fire exit is Ensure all students check in and check out with the project leader at the start and end of the day	
With your control measure(s) in place - if the hazard were to cause harm, how severe would it be? Low	
With your control measure(s) in place - how likely is it that the hazard could cause harm? Low	
The residual risk rating is calculated as: Low	

Hazard	Slips/trips
Severity of the hazard	Low
How Likely the hazard could cause harm	Medium
Risk Rating	Low

Control Measure(s) for Slips/trips:

Notify students of survey sites (and access to them) prior to undertaking fieldwork

Ensure the laboratory floor is clear of all trip hazards (e.g. lock bags in lockers before entering the lab, hang coats up at the door, keep equipment on desk surfaces)

Ensure any spillages in the laboratory are cleared up immediately, notify others in the lab of the spillage

Suggest appropriate footwear for the fieldwork (e.g. walking boots for uneven terrain, wellies for boggy areas, no heels or open-toed sandals)

With your control measure(s) in place - if the hazard were to cause harm, how severe would it be? Low

With your control measure(s) in place - how likely is it that the hazard could cause harm? Low

The residual risk rating is calculated as: Low

Hazard	High/Low temps & weather factors
Severity of the hazard	Low
How Likely the hazard could cause harm	Medium
Risk Rating	Low

Control Measure(s) for High/Low temps & weather factors:

Consider the consequences of the weather factors (e.g. dry mud can be very uneven, so wear shoes with good ankle support; more rain can make wet areas even deeper, so suggest wellies)

Warn students of risks when fieldwork commences - may need to take extra care if the landscape has changed from risk assessment

Check the weather prior to carrying out field work, suggest ways to minimise harm (e.g. on hot weather days apply suncream, wear a sunhat and light clothing that covers shoulders; on cold wet days suggest breathable raincoats, woolly hats, scarves and gloves, spare thermal layers).

With your control measure(s) in place - if the hazard were to cause harm, how severe would it be? Low

With your control measure(s) in place - how likely is it that the hazard could cause harm? Low

The residual risk rating is calculated as: Low

Hazard	Water/Drowning
Severity of the hazard	Medium
How Likely the hazard could cause harm	Low
Risk Rating	Low

Control Measure(s) for Water/Drowning:

Warn students about water bodies prior to surveying

Discourage students from swimming in any waterbodies on the survey site

Identify and avoid surveying near large or unnecessary waterbodies if possible

Ensure a 'buddy system' on site so that at least one person knows where a person is at any given time

Ensure students work in teams of 2 (minimum)

With your control measure(s) in place - if the hazard were to cause harm, how severe would it be? Low

With your control measure(s) in place - how likely is it that the hazard could cause harm? Low

Hazard	COVID-19
Severity of the hazard	High
How Likely the hazard could cause harm	Low
Risk Rating	Medium

Control Measure(s) for COVID-19:

Ensure hand sanitiser is available on site, where soap and water is not

Ensure students are equipped with face masks before sharing transport or carrying out any lab work

Ensure there is good airflow in indoor envionments, such as the lab or shared transport (e.g. open the windows)

Encourage hand washing with soap and water at regular intervals. If none is availalble encourage hand sanitisation with an alcohol rub

With your control measure(s) in place - if the hazard were to cause harm, how severe would it be? Medium

With your control measure(s) in place - how likely is it that the hazard could cause harm? Low

The residual risk rating is calculated as: Low

Hazard	Contracting a disease
Severity of the hazard	Medium
How Likely the hazard could cause harm	Medium
Risk Rating	Medium

Control Measure(s) for Contracting a disease:

Notify students of the risks of fieldwork and diseases that can be contracted (e.g. Lyme disease, Leptospirosis), and ways to mitigate the spread (e.g. do not touch face after handling samples, sanitise after handling samples, use tweezers and containers to transfer samples to pots)

Ensure students undertaking site work wear long sleeves and trousers that cover bare legs

Ensure students wash their hands with soap and water (where possible) after handling samples in the field. If no soap and water is availalble ensure hand sanitiser is available

Ensure students know how to check for ticks (for example), and the signs of Lyme disease (e.g. 'the target', fever and chills, headache, fatigue, muscle aches)

With your control measure(s) in place - if the hazard were to cause harm, how severe would it be? Low

With your control measure(s) in place - how likely is it that the hazard could cause harm? Low

The residual risk rating is calculated as: Low

Review & Approval

Any notes or further information you wish to add about the assessment	
Names of persons who have contributed	Jenny Manley
Approver Name	Pippa Gillingham
Approver Job Title	Staff
Approver Email	pgillingham@bournemouth.ac.uk
Review Date	

Uploaded documents

No document uploaded

Hazard	Lone Working
Severity of the hazard	Medium
How Likely the hazard could cause harm	Low
Risk Rating	Low

Control Measure(s) for Lone Working:

Ensure the student is confident in their work and understands what they are asked to do before carrying out lone work

Ensure the student has access to a working phone, a first aid kit and a map (or GPS) when on site

Ensure any student working alone keeps in regular contact with the project manager. If the student is the project manager, ensure they keep in regular contact with a pre-agreed supervisor

Ensure the lone worker knows who to contact in case of an emergency in the field (e.g. 999 for fire services, police and ambulance services, a personal contact number for advice or to voice any concerns on the project)

With your control measure(s) in place - if the hazard were to cause harm, how severe would it be? Low

With your control measure(s) in place - how likely is it that the hazard could cause harm? Low

The residual risk rating is calculated as: Low

8.2 Ethics Checklist

Bournemouth University

Research Ethics Checklist

About Your Checklist	
Ethics ID	55234
Date Created	15/02/2024 13:15:08
Status	Approved
Date Approved	22/02/2024 16:33:09
Risk	High

Researcher Details	
Name	Jenny Manley
Faculty	Faculty of Science & Technology
Status	Postgraduate Research (MRes, MPhil, PhD, DProf, EngD, EdD)
Course	Postgraduate Research - FST
Have you received funding to support this research project?	No

Project Details	
Title	Examining the effectiveness of heathland restoration on Coleoptera community compositions in Rempstone Forest and the Purbeck Heath National Nature Reserve
Start Date of Project	22/01/2024
End Date of Project	30/09/2024
Proposed Start Date of Data Collection	05/05/2024
Original Supervisor	Phillipa Gillingham
Approver	Research Ethics Panel

Summary - no more than 600 words (including detail on background methodology, sample, outcomes, etc.)

Beetles are one of the oldest orders on the planet and, due to their inhabiting a vast range of environments, can be used as proxies for the environment. The Purbecks National Nature Reserve is a large area of heathland, where felling of conifer plantations is hoped to increase diversity of native species. However, invertebrate diversity and abundance has not been measured on Rempstone Heath and Godlingston Heath, where conifer plantation felling has commenced and will be in the future. 35 sites will be selected to represent permanent forest, permanent heathland, and restored heathland (where forest has been felled) over two time periods – between 1990 - 2007 and from 2012 onwards. Beetle species presence, diversity and abundance will be measured from each category using the pitfall trapping method.

This study aims to identify the effectiveness of heath restoration on beetle communities in these two areas of Purbeck Heaths. The objectives are to:

- Determine the most relatively abundant species of Coleoptera in restored forest compared to wet and dry heathlands.
- Identify the habitat associated with the most diverse beetle community, out of forest plantation, permanent heathland and restored

heathland.

- Analyse differences in beetle communities found in newly and previously restored heaths compared to long-established wet and dry heaths and permanent forest plantations.

At each site, 4 holes will be dug to lay pitfall traps 5m to the North, East, South and West of the site coordinates. Traps will be opened over 3 days and collected after 72 hours, to increase likelihood of sample capture, and ensure all traps can be opened and closed consecutively within the same sample window. Invertebrate samples will be pooled per site. Each trap will consist of two 10oz plastic cups (the outer cup will hold the soil back) flush to the ground. The inner cup will contain water with a drop of non-toxic detergent. The traps will be tightly secured between sampling windows to avoid capture outside of survey windows. When opened, traps will be covered by a wire mesh with holes of 25mm. Bamboo sticks will be marked with red tape at the top, for easier site location, and a sign will inform members of the public of the nature of the work to be carried out. Vegetation structure will be measured, via visual surveying, in a 2m radius around each trap.

Samples will be transferred (using tweezers) to sampling tubes containing an alcohol solution for preservation - the tubes will be waterproof. The samples will be taken into a laboratory and identified under a microscope. The process will be repeated monthly, from May to August 2024. Beetle community compositions will be analysed.

Ethical issues have been considered. Permission to survey will be sought prior to sampling. Reduced water tension (via use of detergent in the traps) will hasten euthanisation of invertebrates, reducing stress time as efficiently as possible. The use of non-toxic detergent and alcohol on site will be strictly monitored by the project leader: waste liquids will be contained and removed from the Nature Reserve each day in a tightly sealed container, to be appropriately discarded of in a laboratory setting. A small funnel will be used to rinse the samples before they are transferred to the sample tubes to minimise risk of spillage. Sample tubes will contain alcohol solution prior to being taken on site, to minimise risk of spillage from a large container when on the heathland. Wire mesh will minimise risk of amphibian, reptile and small mammal capture as bycatch. Any samples irrelevant to this study will be retained and used for other research where possible (for example, spiders).

Filter Question: Does your study involve experimentation on any of the following: animals, animal tissue, genetically modified organisms?

Additional Details	
Please describe the animal, animal tissue or genetically modified organisms	Invertebrates. The project is designed around Coleoptera (beetle) capture, but there is chance of bycatch of non-target species, such as spiders, slugs, snails, small reptiles, small mammals and small amphibians.
Please describe the methodology of the experiment	Prior to data collection, a risk assessment will be completed and permission will be sought from the Rempstone and Godlingston Heath landowners to survey the areas. Four pitfall traps will be set at each of the 35 survey sites. For each trap, a hole will be dug and a plastic cup will be placed in the ground, with an identical cup inside. Both cups will sit flush with the ground. The inner cup will hold water with a drop of non-toxic detergent, to catch and euthanise invertebrates that fall in. The cups will have a wire mesh placed over the top to reduce bycatch of larger, non-target organisms. Each pitfall trap will be secured with a lid ('closed') during non-sample windows, to prevent capture of organisms outside of survey periods. During survey periods, the pitfall traps will be 'opened' for 3 days and 'closed' 72 hours later. Once collected, the invertebrate samples will be rinsed on site and transported to a laboratory to be sorted and identified. Vegetation structure will be visually surveyed at each pitfall trap, as will environmental variables such as light, temperature and soil moisture, and bamboo markers will be placed at each site for easy site location. This process will be repeated monthly from May to August 2024. Upon survey completion, traps and markers will be collected and taken off site, and soil will be replaced into the excavated holes.

Dissemination Plans	
How do you intend to report and disseminate the results of the study?	
Peer reviewed journals,Internal Report,Publication on website	
Will you inform participants of the results?	Yes
If Yes or No, please give details of how you will inform participants or justify if not doing so	
Summary of the results of the study (i.e. the thesis) will be sent to stakeholders who granted permission to survey on Rempstone Heath and Godlingston Heath.	

Final Review	
Are there any other ethical considerations relating to your project which have not been covered above?	No

Risk Assessment	
Have you undertaken an appropriate Risk Assessment?	Yes

Filter Question: Does your study require external permission/licences?

Additional Details	
What permission/licence do you need and from whom?	Permission to survey from stakeholders: Natural England, the Rempstone Estate and the Forestry Commission
Please state the licence reference/number under which your research activities are permitted to proceed (if applicable)	NOT KNOWN

Attached documents
9.1. Risk Assessment.pdf - attached on 16/02/2024 16:59:46

8.3 Notices of Permission to Survey

Notice Of Permission

Proposed Title: Examining the effectiveness of heathland restoration on Coleoptera community compositions in Rempstone Forest and the Purbeck Heaths National Nature Reserve

Student: Jenny Manley
jmanley@bournemouth.ac.uk

Life & Environmental Sciences Department,
Bournemouth University

The purpose of this study is to identify the effectiveness of heathland restoration on invertebrate communities as part of a Master's by Research with Bournemouth University. It will consider the effects of felling of conifer plantations on vegetation structure, ground moisture, humidity, and ultimately carabid beetle community compositions, including species' abundance and diversity.

Background

Beetle community compositions, colonisation patterns and species' adaptability can be used as proxies for environmental conditions and to measure climate evolution, due to their inhabiting almost every environment type (Lawrence and Newton 1982). Whilst invertebrate populations in the Purbeck Heaths have been monitored in the east of the Single Grazing Unit (SGU), data is lacking from the West, including in Rempstone forest, where restoration is soon to commence via the felling of 120 hectares of conifer plantation (Forestry Commission 2013). The Purbeck heathlands play host to a range of key species, including rare species and those restricted in range, such as the heath tiger beetle, which is confined to sites in Dorset, Hampshire, Sussex and Surrey (Dodd and Surrey Wildlife Trust 2010). Notably, findings around this area include the heath short spur observed in the SGU in recent surveys, a ground beetle native to the UK but rediscovered after decades of no records (Personal Communication by Gillingham 2023; National Biodiversity Network Atlas 2023).

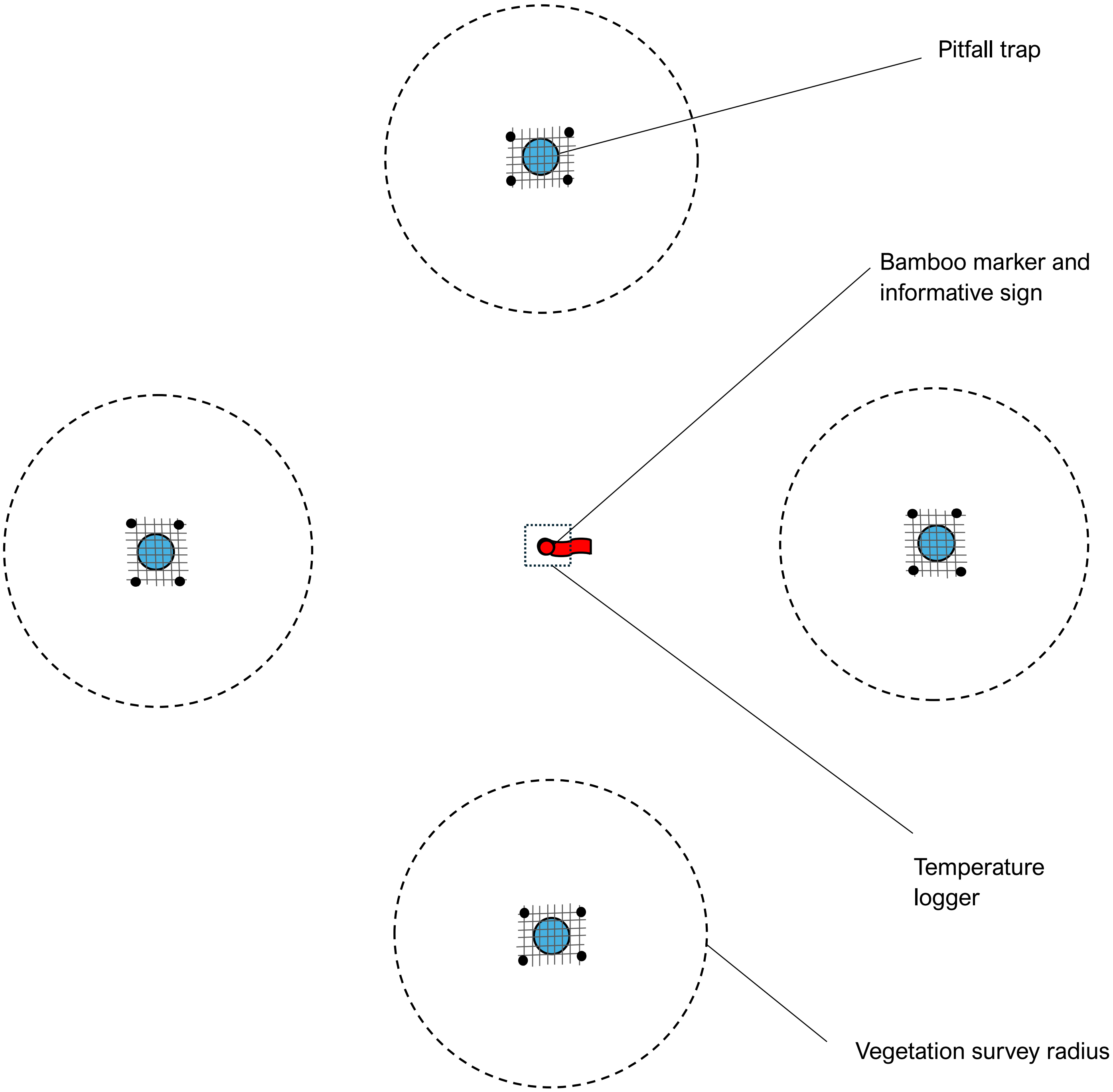
The implications of the reversal of past heathland fragmentation on beetle communities is unknown thus far, particularly over the separate habitat types. This study will determine whether the proposed restoration is likely to affect any rare beetle species, and how ground beetle populations differ over the different habitat types on the Purbeck NNR, including the restored wet and dry heaths (restored during more and less recent times), wet and dry heaths, and the site to be restored (plantation).

Method

35 sites will be chosen within Rempstone Heath and Godlingston Heath to represent habitats where felling of conifer plantations has occurred over wet and dry habitats over different time periods. Within these categories, beetle community composition will be measured by using the pitfall trapping method. The categories are as follows:

- 5 restored wet heathland sites where felling occurred between 1990 and 2007 (‘old’ and ‘wet’)
- 5 restored dry heathland sites where felling occurred between 1990 and 2007 (‘old’ and ‘dry’
- 5 restored wet heathland sites where felling occurred from 2012 onwards (‘new’ and wet’)
- 5 restored dry heathland sites where felling occurred from 2012 onwards (‘new’ and ‘dry’)
- 5 sites representing permanent wet heathland
- 5 sites representing permanent dry heathland
- 5 sites representing continuous canopy (as a pre-treatment category).

Each survey site will be at least 100m distance from any others and set away from public footpaths to reduce disturbance. A trowel will be used to excavate soil from four holes and four pitfall traps will be set per site (each one 5m from the site coordinates). Each trap will consist of a 295ml cup set into the ground, with an identical cup inside that sits flush with the surface of the ground. Within this, water mixed with a few drops of non-toxic Ecover detergent will be used to capture carabid beetles – the detergent will reduce water surface tension for both quick euthanisation and to reduce in-trap predation. A square of 25mm-hexagonal aperture mesh will be placed over every pitfall trap and pegged down with bamboo pegs to minimise change of by-catch of larger, non-target organisms. A 1m tall bamboo stick marked with red tape at the top will be placed at each site to help locate traps, and a sign will inform members of the public of the work to be carried out.



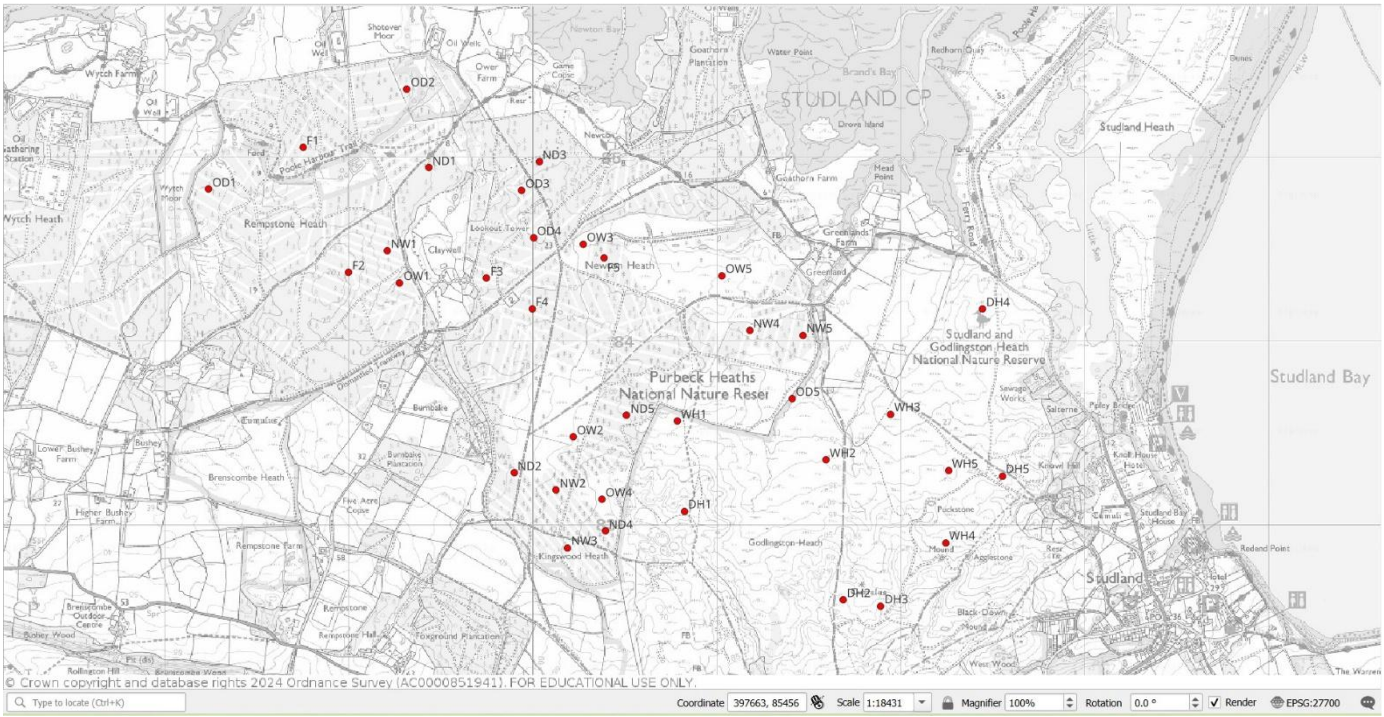
The pitfall traps will be set out in mid to late April in preparation for surveying.

Once the surveys begin, the traps will be opened over the course of three days and collected 72 hours later. Upon sample collection, the cups will then be closed with tight-fitting lids between survey periods. At each site, a temperature logger will be fastened with a cable tie to the bamboo stick to measure ground temperature. Vegetation structure will be recorded in a 2m survey around each pitfall trap, and soil moisture taken as an average percentage per site using a Lutron soil moisture probe.

The pitfall trapping process will be repeated once a month from May to August 2024. Upon completion of the surveys, the traps will be collected and removed, as will the bamboo markers, data loggers and signs, and the soil replaced into the holes.

The samples will be rinsed on site with water and transferred to 70% IMS in sample tubes. Waste liquid will be contained and removed from site in a large plastic bottle. An ethics check will be approved prior to any field work commencement.

Locations of Survey Sites



Site ID	What 3 Words	Easting	Northing	Habitat	Type
F1	dote.idea.tags	398752	085050	Forest	
F2	bench.dwarf.estimated	398998	084372	Forest	
F3	sonic.nappy.drum	399749	084342	Forest	
F4	tastier.lizard.exam	399996	084174	Forest	
F5	announce.epic.necklaces	400386	084450	Forest	
DH1	nuptials.dean.recitals	400825	083075	Heath	Dry
DH2	tripling.puzzle.doted	401688	082595	Heath	Dry
DH3	candle.mega.couriers	401890	082559	Heath	Dry
DH4	trombone.jaunts.rewarding	402445	084175	Heath	Dry
DH5	riverboat.supplied.blotches	402551	083267	Heath	Dry
WH1	limits.drape.paintings	400786	083566	Heath	Wet
WH2	hedge.countries.lemons	401595	083356	Heath	Wet
WH3	remodel.shrug.hydration	401946	083602	Heath	Wet
WH4	dumpy.shock.dumplings	402244	082904	Heath	Wet
WH5	resold.fury.unpacked	402259	083297	Heath	Wet
ND1	hesitate.remark.wonderful	399434	084942	Felled after 2012	Dry
ND2	mend.code.flannel	399899	083284	Felled after 2012	Dry
ND3	typical.instance.soups	400035	084972	Felled after 2012	Dry
ND4	scripted.vanilla.smashes	400395	082967	Felled after 2012	Dry
ND5	pressing.treaties.eyelashes	400510	083596	Felled after 2012	Dry
NW1	agreeable.coasters.bride	399208	084489	Felled after 2012	Wet
NW2	scrapping.campus.sprays	400125	083191	Felled after 2012	Wet
NW3	stripped.scoping.choppers	400188	082877	Felled after 2012	Wet
NW4	broth.possible.confining	401180	084058	Felled after 2012	Wet
NW5	vision.astounded.hips	401468	084031	Felled after 2012	Wet
OD1	corrects.navy.loves	398238	084825	Felled before 2007	Dry
OD2	neck.snow.until	399316	085367	Felled before 2007	Dry
OD3	acrobat.mixes.twins	399939	084816	Felled before 2007	Dry
OD4	spenders.dairy.darkens	400005	084561	Felled before 2007	Dry
OD5	reservoir.spines.educated	401408	083686	Felled before 2007	Dry
OW1	period.handle.gravitate	399277	084315	Felled before 2007	Wet

OW2	younger.wash.contemplate	400221	083479	Felled before 2007	Wet
OW3	breakaway.score.motivates	400275	084525	Felled before 2007	Wet
OW4	publish.bead.disprove	400377	083141	Felled before 2007	Wet
OW5	alpha.syndicate.tinkle	401029	084354	Felled before 2007	Wet

South England Forest District
The King's House, Lyndhurst
Hampshire, SO43 7NH

Tel: 0300 067 4601

Anita Diaz
Department of Life & Environmental Sciences
Faculty of Science & Technology
Christchurch House, Talbot Campus, Fern Barrow
Poole
Dorset BH12 5BB

Date: 21 March 2024

PERMIT NUMBER **025466/2024** FILE REF Rec. **12/28**

THIRD PARTY ECOLOGY SURVEY PERMISSION

The Permit Holder **Anita Diaz, Bournemouth University, Department of Life & Environmental Sciences, Faculty of Science & Technology, Christchurch House, Talbot Campus, Fern Barrow, Poole, Dorset, BH12 5BB** hereinafter referred to as the **Permit Holder**

2. THE RIGHTS GRANTED

Permission is given to the Permit Holder to undertake an **Ecological survey of ground beetles and vegetation** on Forestry England land, subject to the following conditions:

Please contact Mark Warn (Wildlife Ranger & Landscape Recovery Manager) Mark.Warn@forestryengland.uk or on 07881 502221 in advance before arriving on site.

Student included in this permission: Jenny Manley

3. THE SITE

The area over which the rights are granted is shown below:-

Rempstone Heath and co-ordinates as per application and as agreed with Mark Warn.

4. THE DURATION

From **08/04/2024 (proposed setting up time)** To **15/08/2024 (planned take down time) with survey dates as agreed in between.**

The permission will subsist at the discretion of the Forest Management Director who may withdraw it at any time.

5. THE CHARGE

There will be no charge for this permission.

6. CONDITIONS

(a) The activity will be staged as per Section 3 above. Any deviation from the area must be authorised in writing by the Forest Management Director.

(b) The responsibility for ensuring that the area and/or the route(s) are safe and suitable for the activity will rest with the Permit Holder. Survey equipment may not be routed over public rights of way and the Permit Holder will ensure that public rights of way are not impeded. Ensure your route and activity are planned using the constraint map provided.

(c) The Permit Holder will be responsible for obtaining any licences or other necessary consents

(d) The Permit Holder will pay compensation or make good to the Forest Management Director's satisfaction all damage to Forestry England property caused by the exercise of this permission. The Permit Holder will clear all equipment and litter brought onto Forestry England land by the Permit Holder, participants and spectators, to the satisfaction of the Forest Management Director.

(e) The Permit Holder will indemnify Forestry England against all claims arising from any loss or damage, or injury or death to participants, spectators, Forestry England employees and any third parties arising from the exercise of this permission and will during the period of this permission maintain an insurance policy with a reputable insurance company to an amount of not less than £10 million in respect of any one claim. The amount of such insurance shall not limit the liability of the Permit Holder to Forestry England. The Permit Holder will produce the said insurance certificate and on request a receipt for the premium paid not less than 14 days in advance of the activity.

(f) The Permit Holder will ensure that adequate and proper arrangements are made to the satisfaction of the Forest Management Director to protect the safety of participants, members of the public and all others likely to be within the vicinity of an activity and protect the forest environment. The minimum you agree to comply with is outlined in Appendix 1. However there may be additional requirements depending on the activity in order to comply with current best practice, guidance and relevant legislation.

(g) The Permit Holder will advise Forestry England within 24 hours of the end of the activity of any accident or near miss to a participant, spectator, or third party which arises as a result of the exercise of this permission.

(h) If Forestry England's tenants and/or landlords or other persons having an interest in the land are likely to be affected by this permission, then the Permit Holder will notify all those persons of the activity not less than 14 days before the activity. If their permission is required the Permit Holder will obtain permission. Forestry England will support the Permit Holder to contact those persons likely to be affected.

(i) The Forest Management Director will ensure that all holders of a contract to provide services to, or purchase goods from, Forestry England on the land affected by this permission are notified of the permission, and the approved route or area to be used, and will require them to notify any sub-contractors and their employees.

(j) The Forest Management Director will ensure that all forest district staff are notified of the permission and the approved route or area to be used.

(k) The Permit Holder will ensure that no vehicles owned by the Permit Holder, his representatives, participants and spectators may enter Forestry England land unless with the prior written authority of the Forest Management Director who will specify to the Permit Holder which access routes or areas may be used.

(l) You must ensure that you have sufficient and appropriate insurance in place in respect of the use of your vehicle on Forestry England property. If in doubt please check with your insurers as your normal motor insurance policy may not provide appropriate cover in these circumstances.

(m) Forestry England accepts no responsibility for loss or damage to your property unless the loss or damage is due to acts or omissions by Forestry England or its agents.

(n) The Permit Holder will ensure that Forestry Commission Byelaws are observed, except as expressly authorised by this Agreement. A copy of the Byelaws will be supplied on request by the Forest Management Director. In particular the Permit Holder will ensure:

- a speed limit of 15 miles per hour is observed at all times
- there is no smoking or the lighting of fires or stoves
- all gates are left in the position as found

- reasonable care is taken to prevent disturbance to wild fauna and flora and to agricultural livestock
- compliance with any instructions issued by the Forest Management Director or his authorised representative
- forest roads are not obstructed

(o) Forestry England reserves the right to revoke this permission at any time by notice given to the Permit Holder in writing. If the revocation is to meet Forestry England requirements a refund of the charge will be made unless a suitable alternative location can be provided. If the revocation is required as a result of default by the Permit Holder or any representative no refund will be made.

(p) Forestry England may share the personal and contact information of the lead permit holder with other permit holders or businesses operating in the forest. This will only ever be shared to ensure that you are notified of activity happening in the forest which may impact upon the permissions you have, and will be done to ensure public safety on Forestry England land. This is an essential element of safely managing permits in the forest.

The personal information you supply will be held securely by Forestry England in line with the Data Protection Act 1998. Forestry England is a data controller under the Data Protection Act 1998 and is registered with the Information Commissioners Office for this purpose. Our Registration Number is Z6542658.

(q) All research data to be submitted to Forestry England – The minimum you agree to comply with is outlined in Appendix 1

By signing this document you agree to such disclosure by Forestry England to other users.

In the interests of safety Forestry England strongly recommends that you carry a mobile phone and first aid kit and leave details of the mobile number, route and expected return time with a friend, relative or responsible person.

6. ACCEPTANCE

I accept the foregoing conditions;

Signed ..

.... Date ......21 March 2024.......................
(Permit Holder)

8.4 Site Selection from SERT Squares

Sert Code	Grid ref	w3w	place	Habitat Ty
1	SZ0233784982	universally.inert.themes	Studland	Wet
2	SZ0248385010	driving.greet.mimic	Studland	Dry
3	SZ0325686039	forgot.repay.deflection	Studland	Wet
4	SZ0249385152	amps.certainty.wells	Studland	Dry
5	SZ0285485777	treat.video.album	Studland	Wet
6	SZ0296285800	lame.wonderfully.rocky	Studland	Wet
7	SZ0266085466	until.slave.move	Studland	Wet
8	SZ0283185653	cowboy.pokers.probe	Studland	Wet
9	SZ0277185356	digs.island.closer	Studland	Wet
10	SZ0289585729	traded.cares.echo	Studland	Wet
11	SZ0256184429	sulked.caressing.happy	Studland	Dry
12	SZ0255084484	brownish.lofts.dressy	Studland	Dry
13	SZ0241384561	towels.apricot.entertainer	Studland	Dry
14	SZ0238184673	mammoths.joins.venues	Studland	Dry
15	SZ0237384768	scuba.headings.products	Studland	Dry
16	SZ0266085233	drift.forces.invite	Studland	Wet
17	SZ0239685195	elevated.downsize.homelands	Studland	Dry
18	SZ0247085511	focus.hosts.liked	Studland	Dry
19	SZ0254085636	entry.guides.glass	Studland	Dry
20	SZ0247585578	behind.chip.elaborate	Studland	Dry
21	SZ0290182775	trees.reissued.drags	Godlinston	Acid grassland
22	SZ0269282585	willpower.nibbles.owned	Godlinston	Mire
23	SZ0214982179	jammy.easygoing.firewall	Godlinston	Dry
24	SZ0212682625	magpie.blip.gobbles	Godlinston	Wet
25	SZ0238882714	targeted.working.linguists	Godlinston	Mire
26	SZ0255883275	flank.quilting.spirit	Godlinston	Dry
27	SZ0224883291	squeaking.rotate.regulate	Godlinston	Wet
28	SZ0176683121	subtitle.cavalier.empires	Godlinston	Mire
29	SZ0158883355	underline.napkins.nipping	Godlinston	Wet
30	SZ0167282594	inform.minivans.powerful	Godlinston	Dry
31	SZ0212681987	celebrate.devotion.sourced	Godlinston	Acid grassland
32	SZ0224582139	middle.chops.booklets	Godlinston	Acid grassland
33	SZ0055482449	dolls.outhouse.drum	Godlinston	Mire
34	SZ0244884180	droplet.pegs.skidding	Godlinston	Dry
35	SZ0242583656	cringes.piles.approvals	Godlinston	Mire
36	SZ0194583618	switch.norms.sweetened	Godlinston	Wet
37	SZ0117083848	desktops.alas.partners	Godlinston	Restored wet
38	SZ0146583988	influencing.chap.cleanser	Godlinston	Restored wet
39	SZ0129983657	slice.compress.rewriting	Godlinston	Restored wet
40	SZ0075483430	condensed.cliff.ejects	Godlinston	Mire
41	SZ0082283098	scores.blesses.hires	Godlinston	Dry
42	SZ0189982564	rounds.drawn.thanks	Godlinston	Dry
43	SZ0191284391	exposes.collapsed.homework	Godlinston	Acid grassland
44	SZ0212284267	stumble.menu.kickbacks	Godlinston	Acid grassland
45	SZ0174884127	happily.alpha.package	Godlinston	Acid grassland
46	SZ0164383825	limbs.tables.community	Godlinston	Acid grassland
47	SZ0198383264	fruits.communal.overcomes	Godlinston	Wet
48	SZ0170083645	freezers.lakeside.daunted	Godlinston	Wet
49	SZ0145983528	important.marmalade.topical	Godlinston	Wet
50	SZ0079583564	tiny.appealing.tested	Godlinston	Wet

8.5 Correlation Matrix for Continuous Environmental Variables

Correlation matrix generated to assess collinearity between continuous environmental variables prior to modelling.

Continuous Variable	**Average Humidity**	**Average Soil Moisture**	**Min. Ground Temperature**	**Avg. Ground Temperature**	**Average Leaf Litter Depth**	**End Bracken Height**
Average Humidity	1.00					
Average Soil Moisture	0.020508	1.00				
Min. Ground Temp	-0.31056	0.105605	1.00			
Avg. Ground Temp	0.008528	0.091472	-0.35669	1.00		
Avg. Leaf Litter Depth	0.098161	-0.06274	0.280428	-0.27789	1.00	
End Bracken Height	0.345884	-0.38435	0.297284	-0.21092	**0.691244**	1.00

8.6 VIF Values for Continuous Environmental Variables

VIF (Variance Inflation Factor) values for continuous environmental variables measured. Variables highly correlated with carabid taxonomic richness (>5) are highlighted in bold.

Continuous Variable	VIF Value
Average humidity	1.243788
Average soil moisture	1.083966
Minimum ground temperature	**5.263284**
Maximum ground temperature	**8.566457**
Average ground temperature	2.798710
Average leaf litter depth	1.140776
End bracken height	3.279859

8.7 Shapiro-Wilks Test

Results from the Shapiro-Wilks test showing non-normal distribution of carabid species across all sites. Nationally scarce species are marked with an asterisk (*) and nationally rare species are marked with a double asterisk (**).

Species	**W statistic**	***p*-value**
Abax parallelepipedus	0.66784792	<0.001
Acupalpus dubius	0.2499621	<0.001
Acupalpus parvulus	0.1614563	<0.001
Amara aenea	0.3162820	<0.001
Amara convexior	0.1614563	<0.001
Amara lunicollis	0.2499621	<0.001
Amara tibialis	0.1614563	<0.001
*Anisodactylus nemorivagus***	0.4770036	<0.001
Bembidion lampros	0.3394550	<0.001
*Bembidion nigricorne**	0.1614563	<0.001
Bembidion properans	0.1614563	<0.001
Carabus arvensis	0.5527796	<0.001
Carabus nitens *	0.1614563	<0.001
Carabus problematicus	0.3168756	<0.001
Carabus violaceous	0.2499621	<0.001
Cicindela campestris	0.2499621	<0.001
Dyschirius globosus	0.2935301	<0.001
Harpalus affinis	0.1614563	<0.001
Harpalus rufipes	0.1614563	<0.001
Laemostenus terricola	0.1614563	<0.001
Leistus fulvibarbis	0.1614563	<0.001
Leistus spinibarbis	0.3791527	<0.001
Nebria brevicollis	0.3718218	<0.001
Nebria salina	0.2931900	<0.001
Notiophilus aquaticus	0.3791527	<0.001

Notiophilus biguttatus	0.3183227	<0.001
Notiophilus germinyi	0.3718218	<0.001
Notiophilus palustris	0.3183227	<0.001
Notiophilus rufipes	0.2499621	<0.001
Notiophilus substriatus	0. 1614563	<0.001
Olisthopus rotundatus	0.1614563	<0.001
Oxypselaphus obscurus	0.3624835	<0.001
Platynus assimilis	0.2471082	<0.001
Poecilus cupreus	0.1614563	<0.001
Poecilus versicolor	0.5148186	<0.001
Pterostichus diligens	0.1614563	<0.001
*Pterostichus gracilis**	0.1614563	<0.001
Pterostichus madidus	0.2471082	<0.001
Pterostichus minor	0.2231311	<0.001
Pterostichus strenuus	0.2157929	<0.001
Pterostichus nigrita/rhaeticus	0.3312763	<0.001
Syntomus foveatus	0.3162820	<0.001
*Syntomus truncatellus**	0.1614563	<0.001
Unknown species	0.1614563	<0.001

8.8 VIF Values for Categorical Environmental Variables

Generalised Linear Model results for the ordinal data of the seven vegetation types and their correlation with carabid species richness. Significant variables ($p < 0.05$) are highlighted in bold.

Coefficients:	**Estimate**	**Std. Error**	**Z value**	**Pr(>|z|)**
(Intercept)	-0.39	1.06	-0.37	0.71
Bare Ground	-0.03	0.14	-0.25	0.80
Bryophytes	0.14	0.13	1.13	0.26
Graminoids	0.15	0.13	1.22	0.22
Forbs	0.04	0.07	0.58	0.57
Bracken	0.03	0.06	0.52	0.60
Shrubs	0.11	0.13	0.87	0.39
Trees	**0.22**	**0.08**	**2.70**	**<0.01**