



Spiders on lowland heath: Functional diversity and abundance in relation to heathland structure

A dissertation submitted in partial fulfilment of the requirements of the degree
Master by Research (MRes)

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Abstract

Habitat loss and fragmentation has had negative effects on biodiversity worldwide. The Dorset Heathlands, despite historical changes and drastic losses, are home to some of the rarest species in the UK. The dominant plants, ericaceous shrubs, vary in structure according to age, creating a heterogeneous landscape of different habitats. Conservation and restoration management can influence patterns of growth stages which can alter species composition and diversity. The diversity of different functional traits of species can be defined by their activity, which is related to their use of resources. The overall aim of this study examines the influence of heathland vegetation structure and habitat type on the abundance and functional diversity of spiders.

Sampling was conducted within the Purbeck Heaths National Nature Reserve (PHNNR) over 30 sites (10 dry heath, 10 restored dry heath and 10 wet heath); each sample site measured 20m x 20m. A combination of pitfall traps, sweep netting and vacuum methods were undertaken fortnightly over two months (May and June 2023). Vegetation structure data were also gathered by estimating cover and using a drop disc to measure the vegetation height within sites. Including juveniles, a total of 1,661 individual spiders were collected across all three methods representing 66 species from 18 different families. A total of 835 mature individuals from 16 families were used in the analyses. The abundance of individual spider species with different functional traits, and diversity, were compared across the different habitat types and related to vegetation structure, using contingency tables and chi-square tests, ANOVA with post hoc Tukey, generalised linear models, and Multimodal inference analysis in R.

Results indicated that the wet heaths were significantly different from the dry and restored heaths. Wet heaths had a higher percentage cover of pioneer heather, whilst restored dry heaths contained a higher percentage cover of building heather as well as all shrub species. The dry heath had a higher percentage cover of bare ground, mature heather, litter layer and moss lichen layer. The wet heaths had a higher abundance and species richness of spiders and were more functionally diverse. The restored heaths had a significantly higher abundance of the traits ground dwellers, nocturnal species and those with a preference for living on the ground than the dry habitat. In addition, the wet heaths had significantly more of the orb-web weavers and those that build an orb-web trait than the dry heaths. The most significant variables influencing the abundance of spider functional traits and species were moss layer, pioneer heather, vegetation height and the habitat type of wet heath. The functional traits ground hunter, capture of prey through pursuit, no use of a web, nocturnal and ground dwellers had highest abundance in the study and the most significant inverse relationship with moss layer, pioneer heather and vegetation height. The wet heath had significantly more frequent traits of the tangled cribellate web builders, cathemeral species and those that preferred to live in vegetation than were in the restored dry heath. The most abundant spiders were *Pardosa pullata*, predominantly recorded on the wet heath, and *P. nigriceps* on the dry. The wet habitat type was significantly different from the restored dry habitat for the species *Dysdera erythrina* and *Dictyna arundinacea*.

Overall, the results suggest that the current heathland structure, particularly the moss layer, pioneer heather and vegetation height, influences the diversity and abundance of spider functional traits, generating additional evidence to support the importance of heterogeneity and the mosaic theory of heathland management. Further research is required across the wider

PHNNR and over a longer sampling period to include additional sampling methods to further the understanding of how conservation and restoration efforts affect biodiversity.

KEYWORDS: Lowland Heathland, Vegetation Structure, Spider Abundance, Functional Diversity, Habitat Types, Conservation

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1: Introduction

1.1 Spiders and heathland

On a global scale, habitats and biodiversity are being lost at such an alarming rate, it is culminating into the sixth mass extinction event (Thomas *et al.* 2004, Sánchez-Bayo and Wyckhuys 2019). These losses are linked to different drivers, with land use change being the most dominant (Jaureguiberry *et al.* 2022). The loss and fragmentation of habitats can have effects on species diversity (Rybicki *et al.* 2020), and the importance of clearly defining species interactions in terms of their diversity, the communities, and ecosystems they are present in, has been previously highlighted in several publications (Wilson 1999, Díaz and Cabido 2001, Violle *et al.* 2007, and Tilman 2001).

The diversity of species can be defined by the abundance, range of different species, where they occur in the stratum and where they are present in any given space (Tilman and Downing 1994, Whittaker *et al.* 2001). Integrating the way in which species interact with a given habitat and between each other is regarded as defining functional diversity (Cadotte *et al.* 2011). Functional diversity can then be used to infer that a species characteristic or function (defined as a trait), can be scaled up to be representative of the properties of an ecological community and even ecosystem (Petchey *et al.* 2009). A change in species community can shift the species traits present, which in turn can affect ecological interactions on different levels (Pichon *et al.* 2022). Therefore, understanding the drivers of species richness and functional traits can contribute to conservation management in terms of diversity and ecosystem services (Díaz and Cabido 2001).

The diversity of different functional traits of species can be defined by their activity, which is related to their use of resources. This is the essence of functional diversity, where the kind of resources a species utilises as well as where and when they use these resources are considered traits (Swenson *et al.* 2020). A review of functional diversity suggests it is a powerful predictor of how organisms can impact a habitat and ecosystem, providing evidence to link them together, if there are strong validation measures (Petchey and Gaston 2006). Additionally, the choice of functional traits is as important as which measures are used to analyse the data (Swenson *et al.* 2020). Examples of functional traits include phenology, daily activity, spatial preference or occurrence, and prey capture strategy (Cardoso *et al.* 2011).

Spiders remain an understudied group within the arthropods (Milano *et al.* 2021), despite their diversity, with a total of 50,936 species described across the globe across 132 families and 4310 genera (World Spider Catalog 2023). Their contribution to overall biodiversity and ecosystem function is valuable due to their sensitivity to environmental change (Buchholz and Schröder 2013, Dippenaar-Schoeman *et al.* 2015) and position as both prey and predator within an ecosystem (Wise 1993). In the UK, a total of 666 species from 34 families have been recorded and included in the 2019 checklist (Lavery 2019). Conservation of this taxa should be of high importance since around 20% of UK spider species are considered at risk by the IUCN (Harvey *et al.* 2017) with 323 UK spider species designated Nationally Scarce (present in 16-100 10km squares) or Nationally Rare (15 or fewer squares) (Bee *et al.* 2020).

Land use change (in the tropics) has been suggested to decrease spider species richness and functional diversity as spider diversity is related to habitat structure (Potapov *et al.* 2020). It has been suggested that spider diversity, the communities present, and their corresponding functional traits, can be influenced by habitat type and its structure (Hamřík *et al.* 2023). In

addition, and more specifically, the heterogeneity of microhabitats on heathland influences the composition of spider communities (Urák *et al.* 2023). Some studies have concluded that structural characteristics of vegetation and habitat can be important predictors of the spider functional groups present and their diversity (Buchholz 2010, Cardoso *et al.* 2011, Delgado de la flor *et al.* 2020). Recording functional traits of spiders can also add to the understanding of how communities respond to changes in a specific habitat (Podgaiski *et al.* 2013), management intensity (Bell *et al.* 2001) at both a landscape and local scale (Schirmel *et al.* 2016, Pedley and Dolman 2020). Using an approach that is based on traits can assist in understanding the interactions of populations in terms of variation in space and time and the effect on their dynamics (Lowe *et al.* 2020).

In Britain, more than 80% of Lowland Heathland has been lost since the 1800's, alongside associated ecosystem assemblages (Rose *et al.* 2000). It is included in the EU Habitats Directive and consists of the Annex I (and sub habitats) of both 4010 Northern Atlantic wet heaths with *Erica tetralix* and 4030 European dry heaths (McLeod *et al.* 2005). The UK contains 20% of the lowland heath present in Europe and the heathlands of Dorset have been classified by Natural England as a National Character Area (NCA 135). The entire NCA is a total of 61,662 ha, of which 6% is lowland heath, estimated at around 3,952 ha (Natural England 2013). The Dorset heathlands are considered a plagioclimax landscape, composed of different types (including; dry, humid, wet heath and peatland (mires)) that are related to each other in terms of topography (Webb and Vermaat 1990). Each type can be characterised by the plant community it contains, namely ericaceous shrubs (Webb and Hopkins 1984) and their structure can be defined in growth stages of pioneer, building, mature and degenerate (Gimingham 1972). The lowland heathland typical of Dorset contains the following different components; acid grassland, dry sandy areas dominated with *Erica cinerea* (including bare areas), humid patches with both *Calluna vulgaris* and *Erica tetralix*, wet areas dominated with *Erica tetralix* and mire bogs composed of sphagnum mosses. For a heathland mosaic to be considered in 'good' or 'favourable condition', it should contain heather with variation in structure as well as height (i.e., a variety of different heather stages) and include some early successional habitat, other areas that have bare ground, lichen, scrub like gorse and a few groups of trees (Alonso *et al.* 2018). In good condition dry sites, you would expect there to be 80% *Erica* species and the remainder a mix of bare ground and lichen and in wet sites you would expect low cover of shrub species with the pioneer stage being the most dominant, and generally low vegetation height overall with few patches of bare ground (Natural England 2013).

Heathland loss and fragmentation is the result of a range of anthropogenic causes, including urbanisation and afforestation with conifers (Moore 1962, Webb and Haskins 1980). Conifer plantations have been previously described as biological deserts (Brockerhoff *et al.* 2008) with known negative impact on the hydrology (Buytaert *et al.* 2007) and soil nutrients (Bremer and Farley 2010) of heathlands. In addition, canopy cover and levels of leaf litter within plantations can have negative effects on arthropod and plant community structure (Oxbrough *et al.* 2012 and Oxbrough *et al.* 2005). In Purbeck, former conifer plantations on both dry, humid and wet heathland are in the process of being returned to heathland (Hawley *et al.* 2008). Restoration of heathland from former conifer plantation has proven to be a challenge as it can depend on heathland plants remaining in the seedbank (Pywell *et al.* 2002, Pywell *et al.* 2011). Despite the challenge for heathland plant regeneration, in Thetford Forest, UK, clear fells of conifer plantation on former heathland patches can be species rich and host beetle and spider species that are associated with dry open habitats similar to heathland communities (Pedley *et al.* 2023). There is evidence that open areas in conifer plantations, like fire breaks, can be

important habitats for invertebrates associated with heathlands and for beetles and spiders, open areas that were previously clear-felled are rich in rarer species (Pedley *et al.* 2023). Another study, although based in Ireland and focused on the structural heterogeneity of plantations, suggests a mosaic of different aged stands can sustain specialist spiders as well as their overall diversity (Oxbrough *et al.* 2005).

Webb and Hopkins (1984) examined heathland fragmentation on the Poole basin heathlands and its effect on diversity, suggesting a higher diversity of spiders on larger fragments with more complex structure. Other historical studies on lowland heathland in Dorset inferred that certain spider species demonstrate preferences for specific habitats (Snazell 1982), and their activity was affected as a heathland matured following a fire event (Merrett 1976). In a subsequent study, the fragmentation of heaths and the presence of plagioclimax vegetation communities was found to be the important factor for conservation due to its representativeness in terms of vegetation diversity (Webb and Vermaat 1990). In Denmark, research suggests that the management of heathland needs to include practices that encourage structural heterogeneity, not solely focussing on the bare and early successional stages (Byriel *et al.* 2023).

The loss of heathland affects the related ecosystem function (Fagúndez 2013) and the loss of any one species and its functional type can affect management decisions (Díaz and Cabido 2001). Different management methods can influence a change in the structure and growth phase of a heathland (Gimingham 1970), which can alter the species composition (Gardner *et al.* 1997). The microhabitats created by different heather stages in different habitat types can provide opportunities for an increase in spider diversity and the presence of specialist (indicator) species (Urák *et al.* 2023). The negative effect of grazing on spider richness and abundance has been documented (Řezáč and Heneberg 2019) and Dennis *et al.* (2001) concluded that the height of plants is more important than their composition for spider communities. It has been suggested that the effect of different management practices on heathland can be determined by monitoring spider communities present (Maelfait *et al.* 1990, Buchholz 2010). For example, a grazing regime incorporating different livestock types at low density can affect spider species abundance and richness (Dennis *et al.* 2015) with ungrazed patches supporting a higher diversity of spiders than grazed (Dennis *et al.* 2001). A study from northern England suggests that the differences in spider species recorded between upland calcareous grassland, acid grassland and limestone heath habitat types were due to structural differences in vegetation present (Lyons *et al.* 2018). However, spiders recorded on different heathland sites in southern England showed similarity in terms of species present on different growth stages, although the proportions of species caught were different (Merrett 1983).

Spiders can be considered indicators of habitat quality due to their sensitivity to changes in the environment and local disturbance (Marc *et al.* 1999, Pearce and Venier 2006, Cardoso *et al.* 2004). In the UK, Moore (1962) describes in detail the loss of lowland heathland and how this has impacted on the presence of known indicator species across a range of taxa. Webb (1994) examined the differences in presence of eight heathland indicator species across twelve heathland sites between two time periods, 1960 and 1980-87. He concluded that developing lists of indicator species would be of use to assess heathland habitat quality and presented lists of species that could be used as indicators for Aranea, Lepidoptera, Carabids, Hemiptera and plants. More recently it was suggested, for peatland habitats, that the total number of spider species present that are considered indicators in peat bogs, could be a suitable substitute for the conservation value of the total invertebrate fauna (Scott *et al.* 2006).

Ultimately, it is known that the different habitat types on lowland heathland contain different spider species of which some are habitat type specific (Merrett 1976, Pedley *et al.* 2013, Scott *et al.* 2006, Snazell 1982). There has been research documenting the changes and responses of both the flora and fauna, including spiders, of the Dorset heaths to different management practices however, this is now over 20 years old. Studies from Europe, centred around peat bogs, have examined the microhabitats within a heather plant and investigated if there were any relationships with specific spider traits (Urák *et al.* 2023). In the UK, Scottish upland wetland habitat structures (namely ponds) and spider diversity have been assessed for relationships (Ávila *et al.* 2017). To the best of my knowledge, there has not been any research with a focus on the potential influence and relationship of vegetation structure to the spider assemblages undertaken on the Dorset lowland heathlands since the early 2000's. More specifically, there has not been research into spider abundance, functional traits and the relationship or influence of vegetation structure, the result of ongoing conservation management, on lowland heathland.

To determine if the ideal plagioclimax heathland communities are present on the Purbeck heathlands, information on the current heathland structure of the different habitat types of dry, restored dry and wet heath and their relationship to and potential influence on spider functional traits needs to be investigated. Restored dry heath habitat type will be on an area that was a former conifer plantation. These habitats have been selected for their relative homogeneity and consistency in the associated environmental variables and processes. The exclusion of peatland (mire) was deliberate to exclude potential confounding variables within the study.

1.2 Research Aim, Objectives and Hypotheses

This MRes aimed to investigate the relationships between and influence of heathland vegetation structure and habitat type on the abundance and functional diversity of spiders. It will address the current lack of information available on this subject for the Purbeck lowland heathlands hence, it will extend and enhance the knowledge of spider functional diversity in relation to lowland heath structural diversity. Additionally, this study will address the lack of information available for spider species currently present on lowland heathland in Dorset, UK.

This study will address the aim by:

- Collating information on vegetation characteristics that affect vegetation structure.
- Monitoring spider communities across three heathland habitats (including restored).
- Relating spider abundance, frequency of occurrence and their functional diversity to the variables collated and the heathland habitat types.
- Disseminating results to the key stakeholders to inform future site management.

This study uses an area of lowland heathland in Dorset to examine the structural diversity of sample sites within Purbeck Heaths National Nature Reserve (PHNNR), Dorset. The PHNNR covers 3,331 hectares located around the Poole Harbour, adjacent to the Bournemouth, Poole and Christchurch area. The PHNNR encompasses several Sites of Special Scientific Interest (SSSIs), Special Areas of Conservation (SAC), Special Protected Areas (SPA) and Ramsar sites, within its boundaries. These heathlands are home to some of the rarest species in the UK and some of the species within the spider assemblages can be considered specialist (Smith *et al.* 2023) and distinct (Way *et al.* 1986, Pedley *et al.* 2013). This study focuses on the vegetation characteristics of heathland structure, the spider fauna recorded and their associated functional traits across dry, wet and restored dry heath.

Within the PHNNR there is now an area with no internal fencing to create the Purbeck Heaths Grazing Unit (PHGU). The study sites are within this PHGU and comprise of three habitat types and a total of 30 sample sites which were selected for the study. The sites measured 20m x 20m and were comprised of 10 dry heath, 10 restored dry heath and 10 wet heaths. The habitat types were selected to exclude peatland (mire) and did not include wet restored sites as there were none present within the PHGU.

This study will address the following questions with the null and alternative hypotheses:

1. Is the vegetation structure variable across the sample sites and habitat types?

H₀ Heathland vegetation structure is not significantly variable across the sample sites and habitat types.

H₁ Heathland vegetation structure is significantly variable across the sample sites and habitat types.

2. Is there a relationship between spider functional traits and heathland vegetation structure and habitat type?

H₀ there is no relationship between the spider functional traits (from the groups of spider guilds, web type, daily activity, spatial preference) and either vegetation structure or habitat type.

H₁ there is a relationship between the spider functional traits (from the groups of spider guilds, web type, daily activity, spatial preference) and either vegetation structure or habitat type.

3. Does heathland vegetation structure or habitat type influence spider abundance or functional diversity?

H₀ heathland vegetation structure and habitat type does not influence spider abundance and functional diversity

H₁ heathland vegetation structure and habitat type influences spider abundance and functional diversity

4. Does heathland vegetation structure or habitat type influence the occurrence of specific spiders?

H₀ heathland vegetation structure and habitat type does not influence the occurrence of specific spider species

H₁ heathland vegetation structure and habitat type does influence the occurrence of specific spider species

2: Methods

2.1 Study area - Purbeck Heathland

All the research sites were within the PHGU, PHNNR, Dorset, England, in-between 50.704431° N, -2.035700° W and 50.662814° N, -2.090426° W (see Figure 1 and 2). The PHNNR site area is a total of 3,331 hectares (8,231 acres) and claims to be the largest area of lowland heath managed as a single nature reserve in England (Purbeck Heaths webpage). Within the boundary of the PHNNR, there is a large area, approximately 30% of the entire PHNNR (1370 ha), that is managed through grazing with cattle, horses, pigs and donkeys. This is referred to as the Purbeck Heaths Grazing Unit (PHGU). The PHNNR surrounds Poole harbour to the southwest and to the north is the densely populated area of Bournemouth, Christchurch and Poole. Geologically, they are on the Tertiary sands of the London and Hampshire Basins (Moore 1962). The soils are acidic with sand and gravels laid down from Bagshot beds and include pockets of clay. The area is low lying with a mosaic of open dry and wet heathland, acid grassland and birch, pine and areas of scrub. In the past, it supported the local community through the traditional practices of grazing, gathering fuel and fodder (Partnership 1994). Through the 18th Century, heathland was lost from being turned into urban conurbations, agricultural land, to the mineral extraction industry and substantial areas of conifer plantations were planted by large estates (Partnership 1984). This continued from the early 20th century when Forestry England, after the war, added large plantation blocks of conifer species like Corsican pine (*Pinus nigra*), Pinus contorta (*Pinus contorta*), Sitka spruce (*Picea sitchensis*) and Douglas fir (*Pseudotsuga menziesii*) on former heathland, some of which was drained for this purpose (Forestry England: Purbeck Forest Design Plan 2013).

2.2 Study sites

Study sites were from a selection of Bournemouth University Student Environment Research Team (SERT 2013) squares within the PHNNR. The BU Purbeck Wildlife SERT was established in 2015 and is a collaborative project that aimed to trial the use of Priority Habitat Assessment Monitoring for heathlands to enable evidence led management plans to be developed through the National Trust (NT) and other PHNNR partners. Continued annual monitoring provides the basis for the long-term vegetation structure and composition monitoring across the PHNNR.

There are currently 140 squares, each measuring 20m x 20m, that are monitored across the PHNNR, of which 36 are monitored by the NT for their set of priority invertebrates which occurs every three years. Sites for my study within the PHNNR were selected from the 140 according to location, habitat type and in alignment with other priority surveys being conducted in 2023 to avoid increased disturbance or duplication. Initial site selection was ground-truthed and a few replacements were chosen to avoid proximity issues to ensure sites were least 50m apart, to minimise spatial autocorrelation (Gillingham 2011). A total of 30 sites were selected based on their current habitat type: 10 dry heath, 10 restored dry heath and 10 wet heaths (see Figure 2). Dry, restored dry and wet heath habitat types have relatively homogenous environmental variables and processes. Mires are hydrologically and ecologically different therefore their exclusion was to reduce the potential confounding variables of data collected from them within the study.

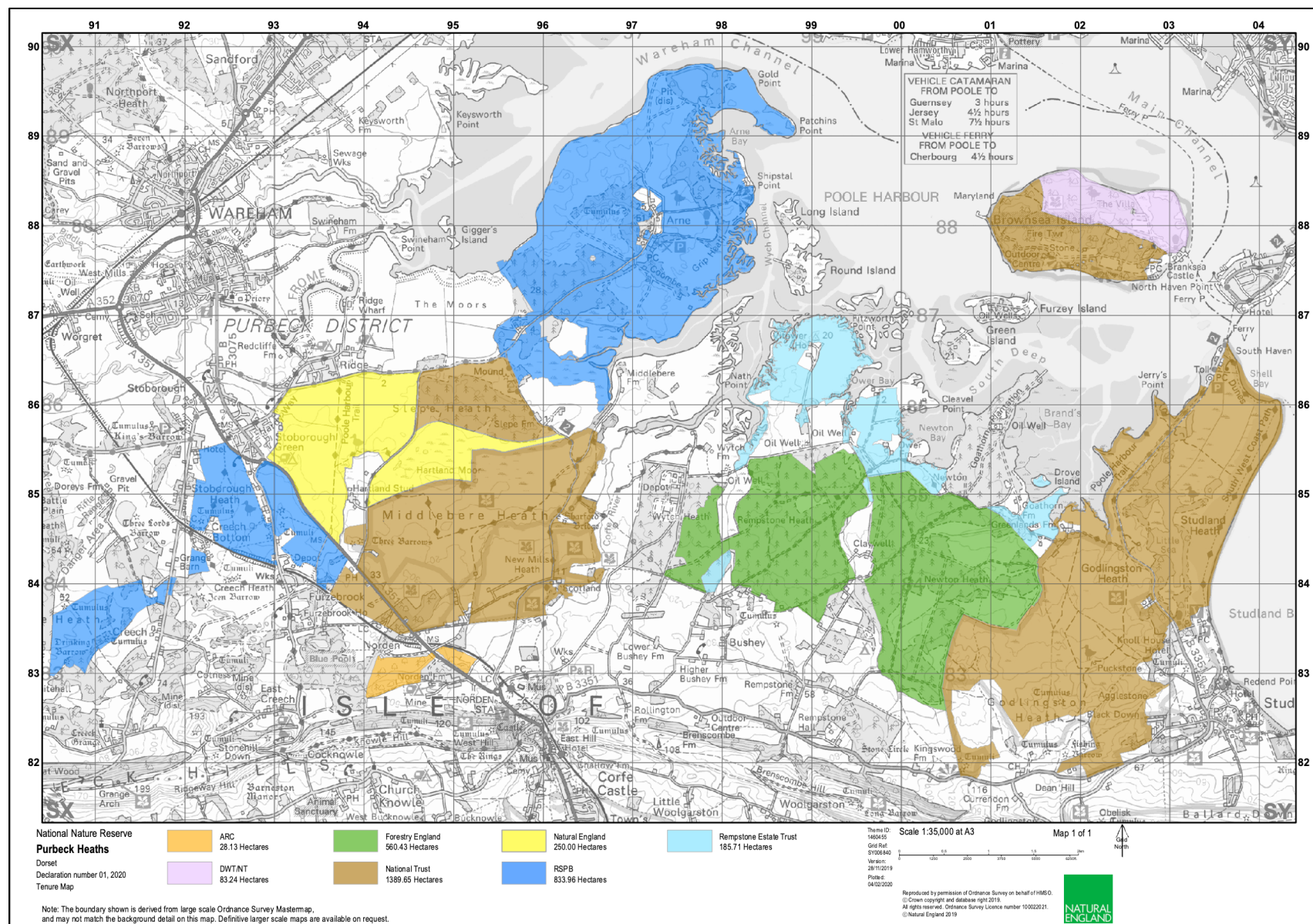
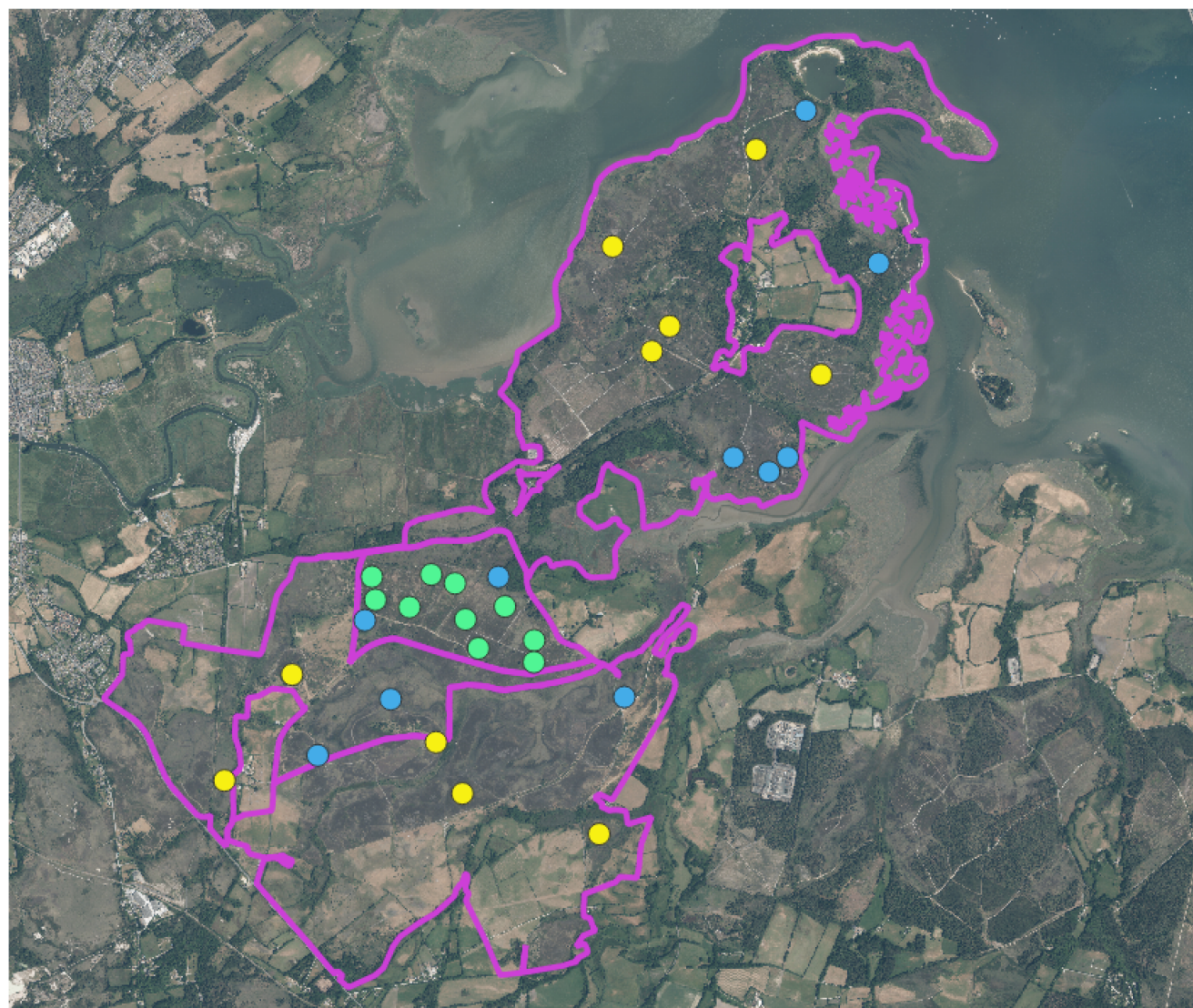


Figure 1. Map of Purbeck Heaths NNR (Contains, or is derived from, information supplied by Ordnance Survey. © Crown copyright and database rights 2019. Ordnance Survey 100022021, source: <https://www.gov.uk/government/publications/purbeck-heaths-national-nature-reserve>)



MRes Spiders on lowland heath Purbeck Heath NNR landscape

Legend

MRes Sites Habitat Type:

- Dry
- Restored Dry
- Wet
- Purbeck Heaths SGU

OpenStreetMap

Ariel Tiles:
SY 90-99 & SZ 00-03

Map created by Caroline Kelly 25/04/2025
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Ordnance Survey (AC0000851941)

0 750 1,500 m



Figure 2. Map of sample site locations and habitat type

2.3 Vegetation structure data

The existing SERT vegetation structure data was available for use, there was full permission from BU and PHGU partners for it to be utilised and this study was deemed to be an opportunity to trial its wider use. The vegetation structure characteristics were measured in 2022 by the Purbeck Wildlife SERT students using standardised methodology to maintain consistency of data collection between plots. Students sampled each square (pre-selected) by randomly placing five 2m x 2m quadrats within the 20m x 20m square. Within each quadrat, the percentage cover of a total of 48 vegetation characteristics was estimated and the presence or absence of signs of grazing animals recorded (see Supplementary Information Table S1.1). For this study, the mean of the five quadrats from my 30 sample sites has been used for nine of these vegetation characteristics (see Table 1), selected for their ability to infer the overall composition of the vegetation. It should be noted that only three out of the four heather stages were recorded. The focus was on the structure of developing and growing heather, and degenerate heather, considered senescent or decaying, was not included to avoid any confounding effect.

2.3.1 Vegetation height data

In addition to the existing SERT data, I conducted vegetation height surveys as the dataset did not include this variable, which has been shown to affect spider species composition (Dennis *et al.* 2001, Lyons *et al.* 2018, Urák *et al.* 2023). Vegetation height was measured using the drop disc method detailed in Stewart *et al.* (2001), replacing the ruler with a marked 1.25m long piece of doweling. Each sample site was surveyed by using two belt transect lines at right angles from the south to east side of the square (see Figure 3). Using a random number generator, the two start points along the 20m side of the square and 10 stopping points along each of the two belt transect lines in metres were determined. The drop disc stick was placed on either side of the belt transect line, the disc ‘dropped’ from 1m high, and measurements taken reading the marked centimetres off the stick. Vegetation height at all the sites were surveyed following the end of the sample collection in July.

Table 1. Environmental variables used to explain the vegetation and site characteristics

Vegetation Characteristic (Abbreviation)	Classification	Measurement
Bare Ground (BG)	Continuous	mean % cover
Building Heather (Bd)	Continuous	mean % cover
All Forb Species (Fb)	Continuous	mean % cover
All Graminoid Species (Gd)	Continuous	mean % cover
Litter Layer (LL)	Continuous	mean % cover
Mature Heather (Mt)	Continuous	mean % cover
Moss Lichen Layer (ML)	Continuous	mean % cover
Pioneer Heather (Pr)	Continuous	mean % cover
All Shrub Species (Sh)	Continuous	mean % cover
Vegetation Height (Vh)	Continuous	centimetre
Habitat Type (Hab Type)	Categorical	dry, restored dry, wet
Heather Stage (Hstage)	Categorical	pioneer, building, mature
SSSI Condition (SSSICond)	Categorical	favourable, unfavourable, improving

2.4 Spider Sampling methods

Prior to any sampling being conducted, I proposed my methodology to my supervisors and subsequently obtained ethical approval from BU. As soon as my methodology was approved, I was then able to request permission from all the landowners and formally apply for SSSI consent from Natural England. The sampling commenced on 1st May 2023 and took place fortnightly, to coincide with the first peak of spider activity (Merrett 1967 and 1968).

To ensure that the study incorporated a representative sample of the heathland spider fauna three methods were used to collect samples, namely pitfall traps, sweep netting and vacuum sampling. Using a combination of different sampling methods will capture different species, with different functional traits, that will contribute to a better understanding of how and where these communities are responding to conservation and restoration efforts (Merrett 1983, Churchill and Arthur 1999, Bali *et al.* 2018). Duffey (1972) described in detail how various techniques can be used across three height zones for any habitat.

Sites were visited using a route that minimised disturbance of wildlife (e.g., using existing paths where possible). Use of a transect method within each sample site was preferred to minimise the disturbance of other taxa so sampling occurrences used the south corner as the entry point and the north as the exit point.

2.4.1 Sample design

Pitfall and sweep net methods of sample collection were conducted on four separate occasions. These occurred fortnightly, from May to June 2023 to coincide with the peak spider phenology (DeKeer and Maelfait 1987, Bee *et al.* 2020). A stopping rule was employed when high numbers of individual families were being recorded as recommended by Scott *et al.* (2006).

2.4.2 Pitfall sampling

Each site was sampled using 4 pitfall traps, placed 5m apart (6.64m/11.64m/16.64m/21.64m) along a southwest to northeast diagonal transect line of 28.284m (see Figure 3). Soil was excavated using a bulb planter and hand trowel and the soil retained to ensure the disturbance was rectified at the end of the study. Each pitfall contained two 70mm diameter plastic glasses (double walled to prevent pitfall collapse when collecting) with overflow holes 1cm from the rim. Each pitfall was filled to 1/3 depth (60ml which was reduced to 50ml) with water and a small drop of detergent. After the first collection and several sand lizards captured the amount of water was reduced to 50ml to prevent further fatalities which proved successful. The pitfall trap was placed into the ground at or just below the surface. Each pitfall was open for 2 days before collection as there was no preservative used (Schmidt *et al.* 2006) to avoid the use of the potentially toxic chemicals propylene glycol or ethylene glycol due to SSSI site designation, livestock, and public presence on the sites. To prevent small reptiles and mammal casualties, a 2x2cm wire mesh was secured over the top of each pitfall at ground level. The contents from all pitfalls per site were emptied, pooled, rinsed and then placed in 70% ethanol. Once the samples were collected the pitfall traps were 'closed' using sturdy lids until the next collection date.

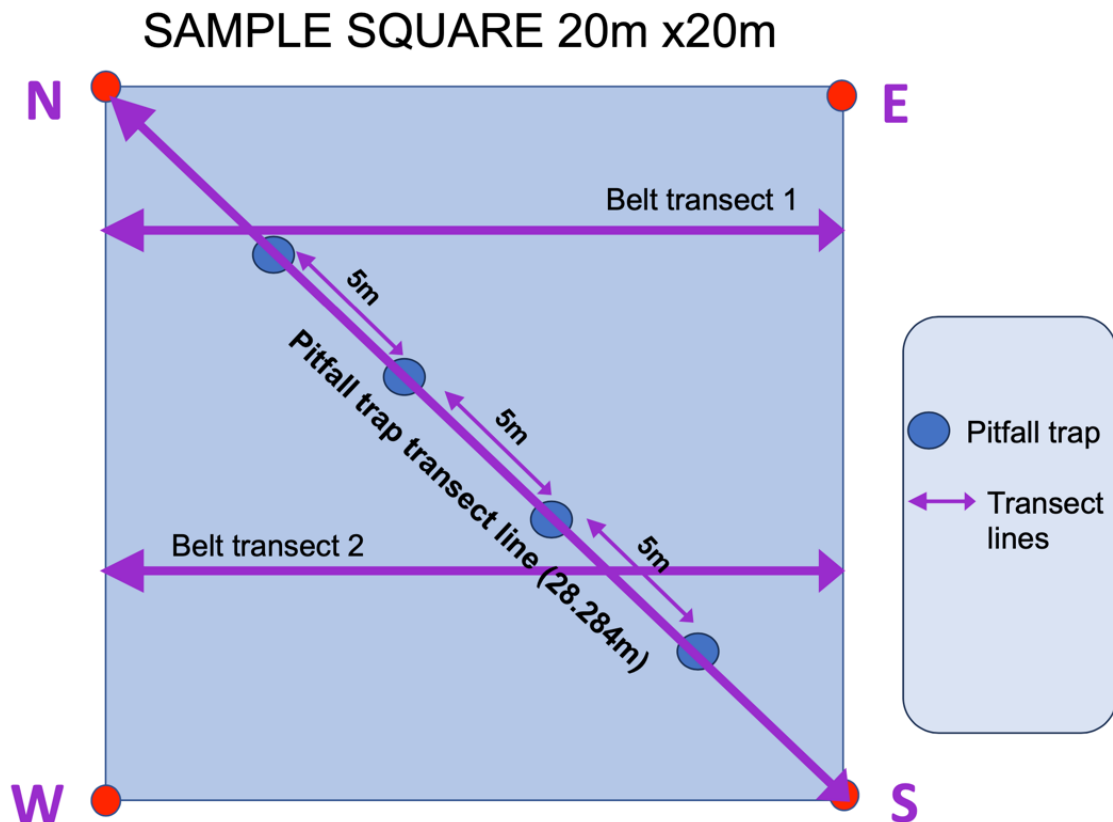


Figure 3. Sample square, dimensions, belt transect lines and pit fall trap locations (vegetation height measured x10 locations along each belt transect line)

2.4.3 Sweep Net sampling

Sweep netting was undertaken at each sample site immediately prior to opening the pitfall traps to limit any 'fallout' of vegetation associated species ending up in the pitfall traps. The NHBS Standard sweep net was used. Working south to north along the diagonal transect (see Figure 3), a total of 10 sweeps were made at random intervals on either side of the transect line. The contents of the sweep net were then placed in a bucket and a timer set for 5 minutes. Any beetles, bugs and spiders that emerged during that time were pooted out and placed directly into a container containing 70/30 ethanol and water.

2.4.4 Vacuum sampling

Vacuum samples were taken at a selection of 6 sites, chosen according to the proximity to the road due to the weight of the machine. This was hoped to enable the comparison between sampling methods. Samples were taken by walking along the south to north central transect, and collecting on alternate sides every 5 paces, maximum suction time 20 seconds each, collecting a total of 4 suction samples/site and maximum time of one minute. The maximum vacuum area was $1 \times 1 \text{m}^2$, calculated according to the diameter of the nozzle. The vacuum sampler was a modified garden leaf blower with a collecting bag securely attached. Samples collected were placed into a white tray and Aranea and Coleoptera were pooted or spooned into sample vials containing 70% ethanol. The vacuum samples taken from each site were pooled together. The timing of sample collections occurred following the collection periods 3 & 4 only, this was due to unforeseen circumstances that delayed this sampling.

2.5 Study species

2.5.1 Species identification

The spiders from the samples at each site were sorted and identified using family keys (Jones-Walters 1989), Roberts Volumes I, II & III 1985, Locket & Millidge 1951, Locket *et al.* 1974 as well as the Great Britain and Ireland checklist (Lavery 2019), to both family and species level. Samples were sorted and identified to species where possible, or recognisable taxonomic units within families where not (e.g., the money spiders). BU students on placement assisted with fieldwork, sample sorting, microscope identification and imaging (for verification) but all identifications were verified first by me, then Chris Spilling and contractor (yet TBC) as expert arachnologists for specimens I was not confident to identify.

2.5.2 Functional traits

Functional traits, based on prior knowledge, (Cardoso *et al.* 2011, Bee *et al.* 2020, Locket & Millidge 1951, Locket *et al.* 1974, Roberts 1985) from each individual were recorded (see Table 2). These comprised of spider family level guild (ambush hunter, ground hunter, other hunter, orb-web weaver, sensing web, sheet web weaver, space web, specialist), prey capture method (ambush, capture, pursuit), web type (funnel, none, orb, sheet, tangled cribellate, tangled sticky), daily activity (cathemeral, diurnal, nocturnal) and spatial preference (ground, vertical). Spider species were assigned a rarity score based on the recent checklist (Lavery 2019) and the conservation status definition of Great Britain (Harvey *et al.* 2017).

Table 2. Spider traits used to explain the functional diversity in the sample (1. Bee *et al.* 2020, 2. Cardoso *et al.* 2011, 3. Locket *et al.* 1974, 4. Roberts 1985, 5. Roberts 1995)

Spider Trait Group	Classification	Trait level (abbreviation)	Reference
Daily Activity	Categorical	x3 - cathemeral (C), diurnal (D), nocturnal (N)	1,5
Guild	Categorical	x8 - ambush hunter (Amb), ground hunter (Grd), other hunter (Other), orb web weaver (OrbWW), sheet web weaver (ShWW), space web (SpWW), specialist (Spec)	1,2,4,5
Prey Capture Method	Categorical	x3 - ambush (A), capture (C), pursuit (P)	1, 3, 4, 5
Spatial Preference	Categorical	x2 - ground (G), vertical (V)	1
Web Type	Categorical	x7 -funnel (Funnel), none (None), orb, sheet (Orb), tangled cribellate (TangledCrib), tangled sticky (TangledStk)	2

2.6 Data analysis

All data were collated using Microsoft Excel and key data extracted using pivot tables for mean values, frequency and calculated proportions. These created the data frames for use in R Studio (Posit Software, RStudio, version 2023.03.0, build 386) (R Core Team, 2023). All data associated with this study can be found in [BORDar](#).

2.6.1 Is the vegetation structure variable across the sample sites and habitat types?

For these analyses, each quadrat measurement of the percentage cover vegetation characteristics (see Table 1) bare ground, pioneer heather, building heather, mature heather, all shrub species, all forbs, all graminoids, litter layer, moss layer was considered an independent datapoint (SERT 2020 data, N=150). In a separate analysis, each measurement taken of the vegetation height were considered as independent data points (N=600). The habitat type data were then attached to each vegetation characteristic or height data point for each sample site location they occurred at.

To investigate if there were any significant differences or relationships with the vegetation structure between the different sample sites, the vegetation characteristic data (Table 1) was used. The R package ggplotly and tidyverse were used for these analyses. The initial exploratory statistics suggested that there may be significant differences, so boxplots with confidence intervals were plotted, then ANOVA tests were run in R to examine the strength of significance. A significant result was then further tested using a post hoc Tukey to identify the difference between each site.

The vegetation characteristic data (Table 1) was then used to examine the relationship to the site's habitat type (Fixed Factor). This was to investigate if there were any significant differences in the vegetation characteristics between the three habitat types; wet heath, restored dry heath and dry heath. Initial exploratory statistics suggested that there may be significant differences, so boxplots with confidence intervals were generated, potential differences determined, and data examined using ANOVA tests in R to analyse the strength of significance. Any significant result was then further tested using a post hoc Tukey to identify the difference between the habitat types. Results are presented in section 3.1.

2.6.2 Is there a relationship between spider functional traits and heathland vegetation structure or habitat type?

For these analyses, each spider species in the pooled site samples was considered an independent data point (N=445) and allocated the relevant functional traits from within each of the functional trait groups; guilds, prey capture method, web type, daily activity, and spatial preference. The vegetation structure variables were then attached to each individual for each location they occurred at.

To examine the relationship between the differences in means of the vegetation structure across the levels of the functional trait groups (Table 2), ANOVA in R was used. The spider trait groups were treated as the independent variable with the vegetation characteristics as dependant. This was to determine if there were any significant differences between the mean vegetation characteristics data across the functional trait groups. An ANOVA was performed separately for each of the functional trait groups; guilds, prey capture method, web type, daily activity, and spatial preference. Any significant result was then further tested using a post hoc Tukey to identify the difference between each trait.

To examine if there are any significant associations between the categorical data of spider functional group and heather stages and the habitat types, R was used to perform a chi-square test for independence. This was to determine whether the association between the categorical variables was statistically significant. These tests were performed separately for each functional trait group; guilds, prey capture method, web type, daily activity, and spatial preference. For both tests, the observed and expected frequencies of the functional traits were

calculated forming a contingency table. The observed frequencies are the actual counts of each trait and the expected are calculated using the contingency table totals with an assumption of independence between the functional traits and habitat type. Results are presented in section 3.2.

2.6.3 Does heathland vegetation structure or habitat type influence spider abundance or functional diversity?

Total abundance per site, across all four sampling periods, was calculated (N=30) and an ANOVA run in R to determine if there was a difference in abundance between the three habitat types. A significant result was then further tested using a post hoc Tukey to identify the difference between each of the habitat types.

For the functional diversity analyses, each spider species in the pooled site samples was allocated the relevant functional traits within each of the functional trait groups; guilds, prey capture method, web type, daily activity, and spatial preference. The vegetation variables and habitat type were then attached to each species for each location they occurred at. The abundance of each trait at each location was considered an independent data point (N=30). To investigate if the presence/absence or abundance of individual spider traits is influenced by the vegetation structure or habitat types, all the associated variables needed to be analysed with each other simultaneously. Therefore, all variables were included in a generalised linear model (GLM) and a Multimodal inference analysis using the 'dredge' tool (MuMIn package in R (Barton 2012)), using Akaike's information criteria, was performed. MuMIn 'dredge' tool works by fitting every possible combination of independent variables from the defined 'full' model to explain either the presence/absence or abundance of individuals with each trait (the dependent variable) across the study site. It produces a ranked list of models based on Akaike's Information Criterion (Akaike 1974) and AICc (used instead of AIC when sample sizes are small, as they are here with 30 locations). AIC is regarded to be a measure of the 'goodness of fit' of a model (Akaike 1974). As suggested in Burnham and Anderson (2004), using the best models, predictor values and summing Akaike weight, the importance of each independent variable in terms of the probability of influence on the dependant variable (spider traits) can be suggested. Each functional trait variable was used in the analysis as a separate response to the vegetation characteristics and habitat factors (total of thirteen see Table 1) using Base R to run a GLM analysis.

The Binomial presence or absence data frame was assessed using the following R code to generate the full GLM output : `"mod1 <- glm (data=d, = Other ~ Vh + BG + Pr + Bd + Mt + Sh + LL + ML+ Gd + Fb + HabType + HStage, + SSSICond, family = "binomial", data = d, na.action = "na.fail")"`.

The Poisson abundance data frame was assessed using the following R code to generate the full GLM output : `"mod1 <- glm (data=d, = Other ~ Vh + BG + Pr + Bd + Mt + Sh + LL + ML+ Gd + Fb + HabType + HStage, + SSSICond, family = "poisson", data = d, na.action = "na.fail")"`.

The results of the GLM Binomial (for the presence and absence) and GLM Poisson (for the trait abundance) analyses were then used as the foundation to run a "dredge" analysis using the MuMIn package in R using the following code, with one dredge per dependent variable:

```
Dredge1 <- dredge (mod1, beta = c("none"), evaluate = T, rank = AICc)
subset (dredge1, delta <2)
```

From the output of the analysis, I extracted a table of the best models (within $<2\Delta\text{AICc}$'s) which are a combination of the variables that have the 'best fit'. Similarly to Astorga *et al.* (2014), these competing models were used to explore and confirm which variable or combination of variables were the best predictors of either probability of the presence or abundance of spiders within each functional trait group. The relative importance of each predictor was examined by summing the Akaike weights for each model where that variable appeared, giving a percentage of inclusion in all possible models.

To assess the significance of the best models and which habitat type was exerting the most significant difference in specific traits, the best model for each trait where habitat type was included was tested using ANCOVA in R ($n=16$). If that model included other vegetation characteristics they were included in the analysis. This was to determine if there was a relationship between trait abundance and vegetation characteristics as well as whether there were differences in abundance between the habitat types. A significant result was then further tested using a post hoc Tukey to identify the difference between each of the habitat types to determine which habitat type had the highest value for each trait. Results are presented in section 3.3.

For the presence/absence analysis some specific functional traits were not analysed if they were either present (1) or absent (0) in all sites. This occurred for a total of nine variables (out of the full total 21); guild (ground hunter), prey capture method (pursuit), web type (funnel, none), daily activity (catheymeral, diurnal, nocturnal) and spatial preference (ground, vertical). As these presence/absence analyses are therefore limited, they have not been included in the results and discussion, although the results can be seen in the Supplementary Information 2 Table 1 document for completeness.

2.6.4 Does heathland vegetation structure or habitat type influence the occurrence of specific spiders?

From the pooled samples, the spider species selected for modelling as a dependent variable were based on their overall abundance, rarity status and presence at 5 or more sample sites ($N=15$, see SI1 Table S4.1 & Tables 14 & 15). For the analyses to test what influences the occurrence of the selected spider species, the abundance of each spider species at each sample site location was considered an independent data point ($N=30$).

To investigate if the abundance of a spider species is influenced by the vegetation structure or habitat types, all the associated variables needed to be analysed with each other simultaneously. Abundance of each selected species in turn was the dependent variable, with the vegetation structure characteristics and habitat types as independent variables in a generalised linear model (GLM) and a Multimodal inference analysis (MuMIn package in R (Barton 2012)), using Akaike's Information Criteria, was performed for each species.

Using the jumping spider *Aelurillus v-insignitus* as an example, the Poisson abundance data frame was assessed using the following R code to generate the full GLM output : `"mod1 <- glm(data=d, = AeVin ~ Vh + BG + Pr + Bd + Mt + Sh + LL + ML + Gd + Fb + HabType + HStage, + SSSICond, family = "poisson", data = d, na.action = "na.fail")"`.

The results of the GLM Poisson analyses were then used as the foundation to run a "dredge" analysis using the MUMIn package in R using the following code:

```
dredge1 <- dredge(mod1, beta = c("none"), evaluate = T, rank = AICc)
subset(dredge1, delta < 2)
```


From the output of the MuMIn analysis, I extracted a table of the best models (within $<2\Delta\text{AICc}$'s) which are a combination of the variables that have the 'best fit'. Similarly to Astorga *et al.* (2014), these competing models were used to explore and confirm which variable or combination of variables were the best predictors of the probability of the presence of an individual spider species. The relative importance of each predictor was examined by summing the Akaike weights for each model where that variable appeared, giving a percentage of inclusion in all possible models.

Out of the fifteen species used in the analysis, the predictor variable of habitat type was in the best models for only seven species. To assess the significance of the best models and which habitat type was exerting the most significant difference in specific spider species, the best model for each of the seven species where habitat type was included was tested using ANCOVA in R. If that model included other vegetation characteristics they were included in the analysis. This was to determine if there was a relationship between species abundance and vegetation characteristics as well as differences in abundance between the habitat types. A significant result was then further tested using a post hoc Tukey to identify the difference between each of the habitat types to determine which type had the highest influence. Results are presented in section 3.4.

3: Results

In total, there were 1,661 individuals collected across all three methods (Pitfalls 77.5%, Sweeping 15.4%, G-Vac 7.2%). Only individuals that could be identified to species level were included in the analyses (50.99%), the remaining 49% were either of the family Linyphiidae (16.79%) or juveniles (32.22%). Therefore, data used in the analyses comprised of 61 species from 16 families with a total of 835 individuals, which when combined, generated 445 records. The vacuum samples were not included due to the small sample size (only collected at 6 sites due to difficulty transporting the sampler around the site) and high component of juveniles.

Of the 240 samples taken from the 30 sites, from pitfall and sweep net methods only, over the 4 sample periods, 100% of the pitfall samples contained one or more individual spiders. In contrast, only 50% of the sweep net samples contained one or more individual spiders. The pitfall traps contained most of the individuals captured (87.78%) compared to the sweep net method (12.21%) (see Supplementary Information (SI)1 Table S3.1). In terms of the habitat type, both the pitfall traps and sweep net samples had highest abundance in the wet habitat (X-squared = 14.42, df = 2, $p < 0.001$), see Figures 10 a & b and SI1 Table S3.1 & S3.2 for the full results. The most abundant and dominant spider family (50.18% of all samples combined) were the Lycosidae (Figure 12), comprising of *Pardosa pullata* (256 individuals, 30.66% of the sample) and *Pardosa nigriceps* (163 individuals, 19.52% of the sample) which were found on all three habitat types (see Table 14 & 15 & SI1 Table S4.1).

3.1 Is the vegetation structure variable across the sample sites and habitat types?

Overall, there was a low mean percentage cover of bare ground, litter layer, all forbs and all graminoids. More than half of the sites had high percentage cover of pioneer, building and mature heather, moss lichen layer and all shrubs. The mean vegetation height across the sites was generally within the building heather range of 11-30cm. Please see the SI1 Table S1.2 for the full set of results.

Table 3 Summary ANOVA results for vegetation characteristics between sample sites

Vegetation Characteristic	Df	Fvalue	P
Bare Ground	29	5.11	<0.001
Pioneer Heather	29	5.59	<0.001
Building Heather	29	5.34	<0.001
Mature Heather	29	9.12	<0.001
Litter Layer	29	7.58	<0.001
Moss & Lichen Layer	29	9.22	<0.001
All Shrub Species	29	13.31	<0.001
All Forb Species	29	1.56	0.050
All Graminoid Species	29	17.34	<0.001
Vegetation Height	29	10.44	<0.001

There was statistically significant variability in the vegetation structure between the sample sites (see Table 3 & 4 and SI1 Table S1.2 – S1.6 for the full results from the analysis). All the environmental vegetation characteristics, except for all forb species, tested using ANOVA, generated $p < 0.001$. Post hoc Tukey tests revealed several significant differences between sites. These suggest rejecting the null hypotheses in favour of the alternative H_1 Heathland vegetation structure is significantly variable across the sample sites and habitat types.

Overall, the wet habitat was significantly different from the other two habitats (Table 4). It contained a higher percentage cover of pioneer heather, all shrub, all forb and all graminoid species (mean % 8.71, 65.88, 0.4 and 27.75 respectively). The restored dry habitat contained a higher percentage cover of building heather (mean % 32.92), and all shrub species (mean % 83.04). The dry habitat had higher percentage cover of bare ground, mature heather, litter layer and moss lichen layer (mean % 5.16, 41.41, 16.90 and 42.18 respectively).

The ANOVA test suggested statistically significant differences in mean vegetation height across the three habitat types. The largest significant difference was between the wet (mean 13.15) and restored dry, (mean 25.26) (see Figure 4 & Table 4 and S11 Tables S1.2 – S1.6 for the full results from the analysis.).

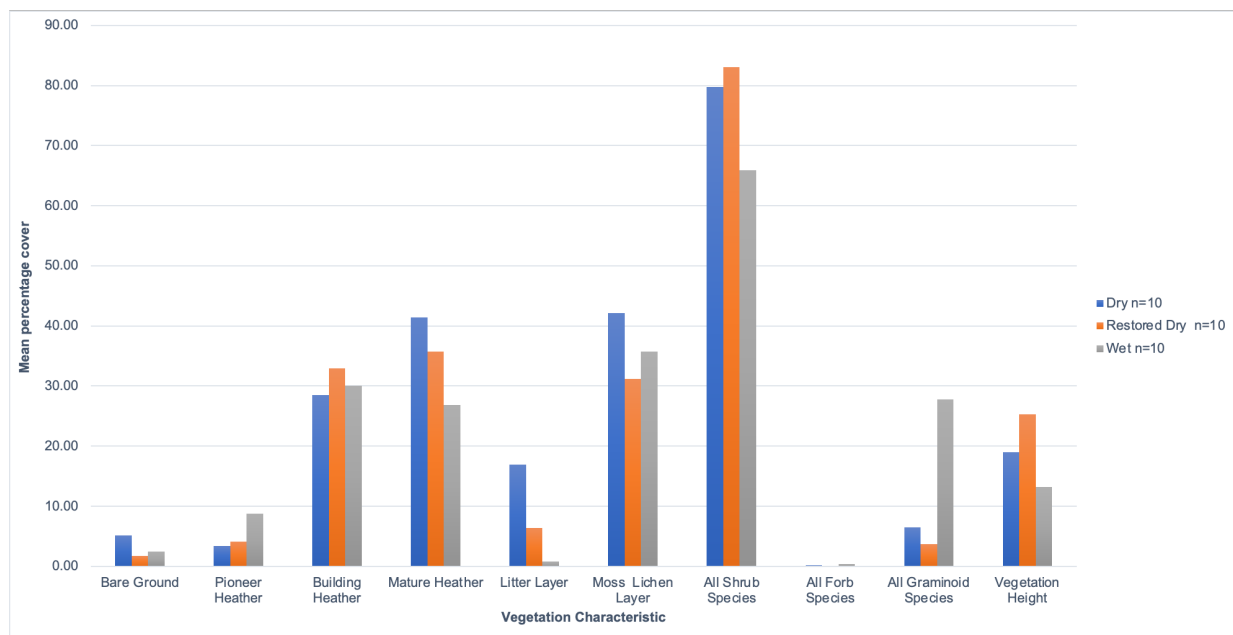


Figure 4 The mean percentage cover of the vegetation characteristics grouped by habitat type

Table 4 Summary of the means for each vegetation characteristic, ANOVA and Tukey results in relation to the habitat types recorded, significant results in bold

Vegetation characteristic	Dry n=10		Restored Dry n=10		Wet n=10		ANOVA			Tukey
	Mean	SD	Mean	SD	Mean	SD	Df	Fvalue	P	
Bare Ground	5.16	11.24	1.76	3.05	2.48	5.07	2	2.97	0.054	
Pioneer Heather	3.39	4.73	4.13	6.70	8.71	13.14	2	5.20	0.007	W > RDry
Building Heather	28.54	24.56	32.92	27.32	30.00	21.77	2	0.41	0.665	
Mature Heather	41.41	33.47	35.70	28.53	26.80	30.63	2	2.83	0.062	
Litter Layer	16.90	26.42	6.35	10.18	0.84	2.23	2	12.38	<0.001	W > Dry
Moss Lichen Layer	42.18	31.21	31.14	29.70	35.72	29.65	2	1.69	0.189	
All Shrub Species	79.77	18.89	83.04	18.81	65.88	30.03	2	7.72	<0.001	W > Rdry
All Forb Species	0.17	0.77	0.00	0.00	0.40	1.73	2	1.73	0.182	
All Graminoid Specie	6.49	15.89	3.71	8.57	27.75	31.97	2	19.24	<0.001	W > Rdry
Vegetation Height	19.03	11.41	25.26	15.37	13.15	6.18	2	54.36	<0.001	W > Rdry

3.2 Is there a relationship between spider functional traits and heathland vegetation structure or habitat type?

3.2.1 Is there a relationship between spider functional traits and heathland vegetation structure?

In terms of the spider functional traits and vegetation structure the ANOVA and subsequent Tukey tests suggested a statistically significant difference in vegetation characteristics between three out of the five functional trait groups and related significant pairwise differences between their traits (see Table 5). However, when Bonferroni corrections are applied, none of the results would be considered significant. A summary of the main results follows but please see Table 5 & 6 for the pairwise results and SI1 Table 2.1 & 2.2.

There were significant differences in the dependent variable, mean percentage cover of mature heather (30-49cm) across the different traits of the independent variable, spider web types (ANOVA $F(5, 439) = 2.25$, $p = 0.049$), with Tukey tests showing differences between the traits tangled sticky and 'None' ($p = 0.012$ Table 5). The mean percentage cover of mature heather was 31.45 for spiders with no web ('none') and 52.10 for spiders with tangled sticky webs (SI1 Table 2.1).

There were also significant differences in the dependent variable, mean percentage cover of the moss lichen layer across the groups of Daily Activity (ANOVA $F(4, 442) = 3.15$, $p = 0.044$) with Tukey tests showing differences between diurnal and cathemeral spiders ($p = 0.033$ Table 5). The mean percentage cover value of moss lichen layer for diurnal spiders was 32.72 and for cathemeral spiders was 40.29 (SI1 Table 2.1).

There were significant differences in the dependent variable, mean percentage cover of all Forbs across the groups of spiders with different web types (ANOVA $F(5, 439) = 2.27$, $p = 0.046$) with Tukey tests showing differences between spiders with tangled cribellate webs and none ($p = 0.0429$), as well as tangled sticky webs ($p = 0.033$ Table 5). The mean percentage cover value of all forbs for spiders with no webs was 0.22, 'tangled sticky' webs 0.05, and 'tangled cribellate' webs 0.68 (SI1 Table 2.1). Additionally, mean percentage cover of all graminoids also was also different for spiders with different web types (ANOVA $F(5, 439) = 2.45$, $p = 0.033$) with Tukey tests showing differences between the traits tangled sticky and tangled cribellate ($p = 0.013$ Table 5). The mean percentage cover value of all graminoids for spiders with 'tangled sticky' webs was 3.95 and 'tangled cribellate' webs was 29.10 (SI1 Table 2.1). The other vegetation characteristics did not have any significant differences in relation to the web types present ($p > 0.05$ Table 5 & SI1 Table 2.1).

Finally, there were significant differences in the dependent variable, mean vegetation height, across the different traits of the independent variable, spider guilds (ANOVA $F(6, 438) = 2.17$, $p = 0.044$) although Tukey tests showed only a small difference between the specialist and orb weaver traits ($p = 0.087$ Table 5). The mean vegetation height for the 'specialists' was 23.58 and for the 'orb-web weavers' was 17.13 (SI1 Table 2.1).

There were no significant differences across any functional trait group with any of the following mean percentage cover vegetation characteristics of; bare ground, pioneer heather (0-10cm), building heather (11-29cm) and all shrub species. Please see SI1 Table S2.1 & S2.2 for the full results of the ANOVA.

Table 5 Summary of the functional trait groups ANOVA and pairwise Tukey results of their traits in relation to the vegetation characteristics, significant results in bold

Vegetation characteristic	Spider Guilds			Capture Method			Web Type			Daily Activity			Spatial Preference			Significant Pairwise Tukey results
	Df	Fvalue	P	Df	Fvalue	P	Df	Fvalue	P	Df	Fvalue	P	Df	Fvalue	P	
Bare Ground	6	0.66	0.683	2	0.42	0.659	5	0.62	0.684	2	1.18	0.308	1	0.02	0.886	
Pioneer Heather	6	1.14	0.340	2	0.36	0.700	5	1.16	0.327	2	0.02	0.979	1	0.68	0.409	
Building Heather	6	1.05	0.395	2	1.50	0.225	5	1.40	0.222	2	1.51	0.223	1	0.26	0.608	
Mature Heather	6	1.12	0.347	2	0.98	0.378	5	2.25	0.049	2	1.72	0.180	1	0.75	0.386	Tangled Sticky - None
Litter Layer	6	0.98	0.437	2	2.37	0.095	5	1.34	0.245	2	2.72	0.067	1	0.81	0.370	
Moss & Lichen Layer	6	1.68	0.125	2	2.84	0.060	5	2.19	0.055	2	3.15	0.044	1	0.23	0.636	Diurnal - Cathemeral
All Shrub Species	6	0.52	0.791	2	0.84	0.433	5	1.45	0.204	2	0.96	0.384	1	0.03	0.860	
All Forb Species	6	0.88	0.511	2	0.55	0.580	5	2.27	0.046	2	0.91	0.405	1	1.52	0.218	Tangled Cribellette - None
All Graminoid Species	6	0.40	0.878	2	0.54	0.585	5	2.45	0.033	2	1.07	0.343	1	0.89	0.347	Tangled Sticky - Tangled Cribellette
Vegetation Height	6	2.17	0.044	2	0.43	0.649	5	1.95	0.085	2	2.10	0.124	1	0.10	0.756	Specialists - Orb Web Weavers

3.2.2 Is there a relationship between spider functional traits and habitat type (or heather stages)?

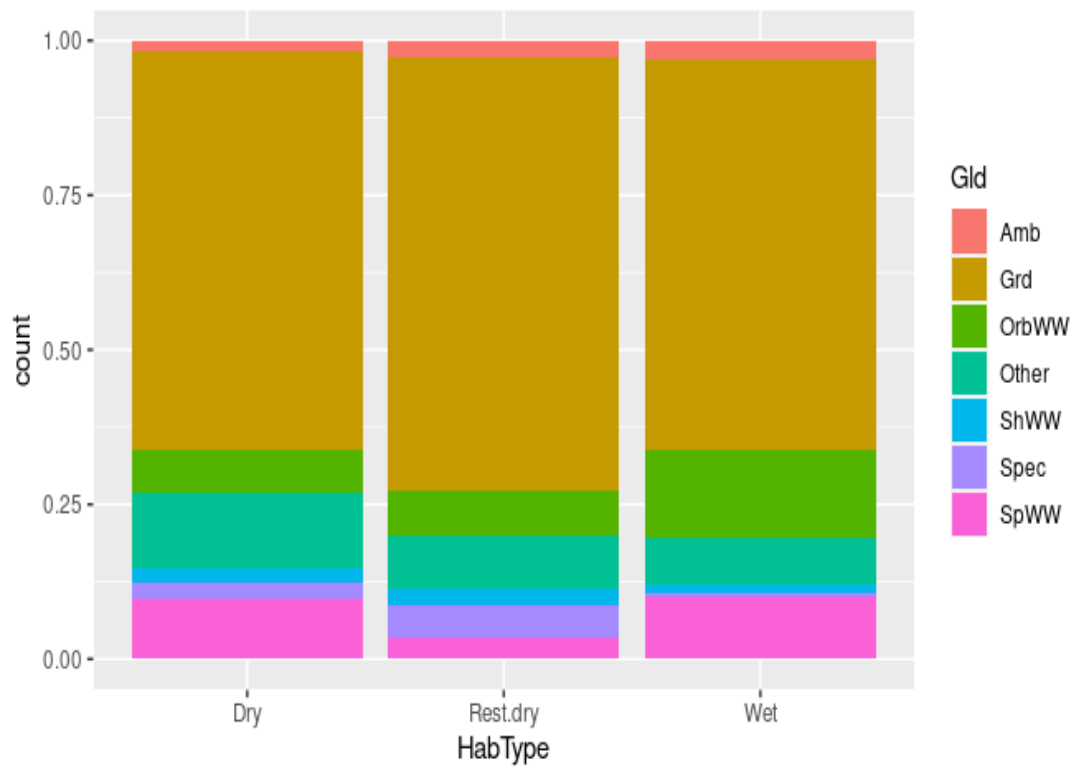
In terms of the spider functional traits and habitat type, the chi-squared tests suggested there was evidence to reject the null hypotheses in favour of the alternative H_1 , there are associations between the spider functional traits and habitat types. Three out of the five functional trait groups; Web Type - none, Daily Activity - diurnal and Spatial Preference - ground showed a significant association with the wet habitat. A summary of the main results follows but please see Table 6 and SI1 Table S2.3 & 2.4 for the full results.

However, there was no significant association between any of the three Heather Stages and Functional Trait Group, please refer to Table 6 for the full results.

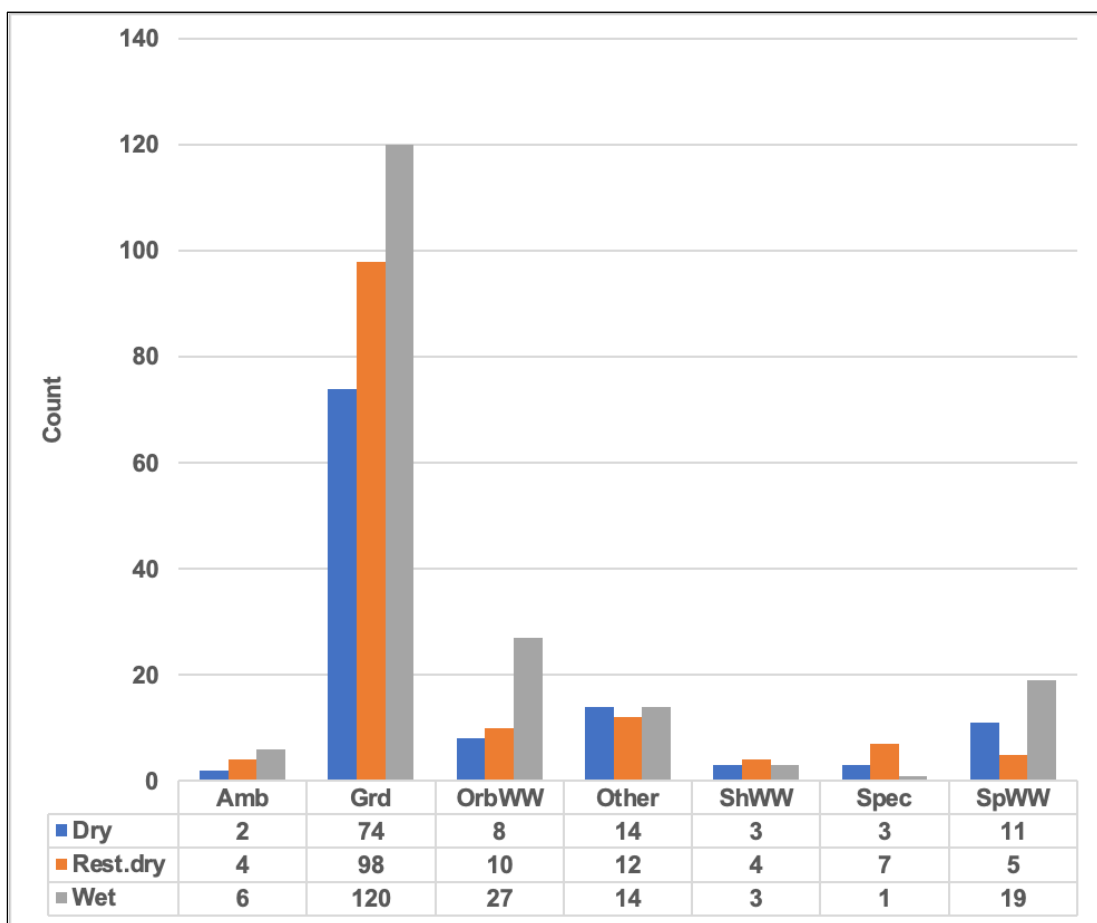
Table 6 Chi-squared results table of the functional trait groups

Functional Trait Group	Habitat Types			Heather Stage		
	Pearson's Chi-squared test			Pearson's Chi-squared test		
	X-squared	df	p-value	X-squared	df	p-value
Spider Guilds	20.576	12	0.057	12.53	12	0.404
Prey Capture Method	9.0827	4	0.059	3.1963	4	0.526
Web Type	29.564	10	0.001	13.839	10	0.181
Daily Activity	14.634	4	0.006	5.6407	4	0.228
Spatial Preference	8.0297	2	0.018	2.1939	2	0.334

The association between the traits and the three habitat types is presented as proportion and frequency bar charts (see Figures 5-9 a and b). The ground hunter guild (consisting of the following spider families; *Gnaphosidae*, *Liocranidae*, *Lycosidae*) was the most frequently recorded in all three habitats (Restored Dry 70%, Dry 64%, Wet 63%, SI Table S2.3) and the most abundant in the overall sample (77% of all individuals recorded). The observed values for the ground trait in both the dry and wet habitats were lower than the expected values, suggesting there may be an association between them (SI1 Table 2.4). The chi-square test revealed no significant association between spider guilds or prey capture method and the habitat types ($X^2 = 20.576$, $df = 12$, $p = 0.057$ and $X^2 = 9.082$, $df = 4$, $p = 0.059$). Please see Figure 5 a& b, Table 6 and SI1 Table S2.3 & S2.4 for the full results.



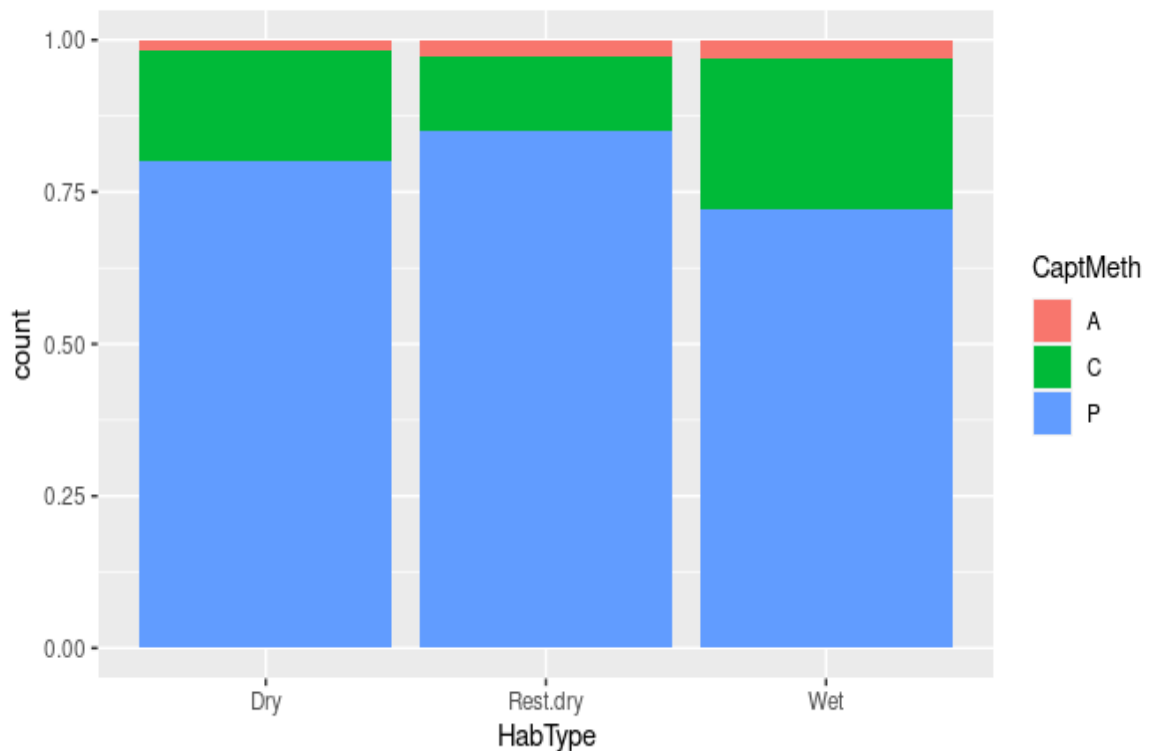
a.



b.

Figure 5a Proportion and 5b frequency of the functional traits in the functional group Guild in relation to the three habitat types (Ambush (Amb), Ground (Grd), Orb Web Weaver (OrbWW), Sheet Web Weaver (ShWW), Specialist (Spec), Space Web Weaver (SpWW))

Within the functional trait group prey capture method, the most frequently recorded (SI1 Table S2.4), and highest proportionally (SI Table S2.3), was the pursuit trait (consisting of species from the following spider families; *Clubionidae*, *Dysderidae*, *Gnaphosidae*, *Liocranidae*, *Lycosidae*, *Miturgidae*, *Philodromidae*, *Phrurolithidae*, *Pisauridae*, *Salticidae*, *Tetragnathidae*). The observed values of the traits capture web and active hunters were both higher in the Wet habitat type than expected, suggesting there may be an association between them (SI1 Table S2.4). The observed value of the pursuit trait in the wet habitat type was lower than the expected suggesting there may be a relationship there. However, the chi-square test revealed no significant association between the functional group prey capture method, and the habitat types ($X^2 = 9.0827$ df = 4, $p = 0.059$) (please see Figure 6a & b, Table 6 and SI1 Table S2.3 & S2.4 for the full results).



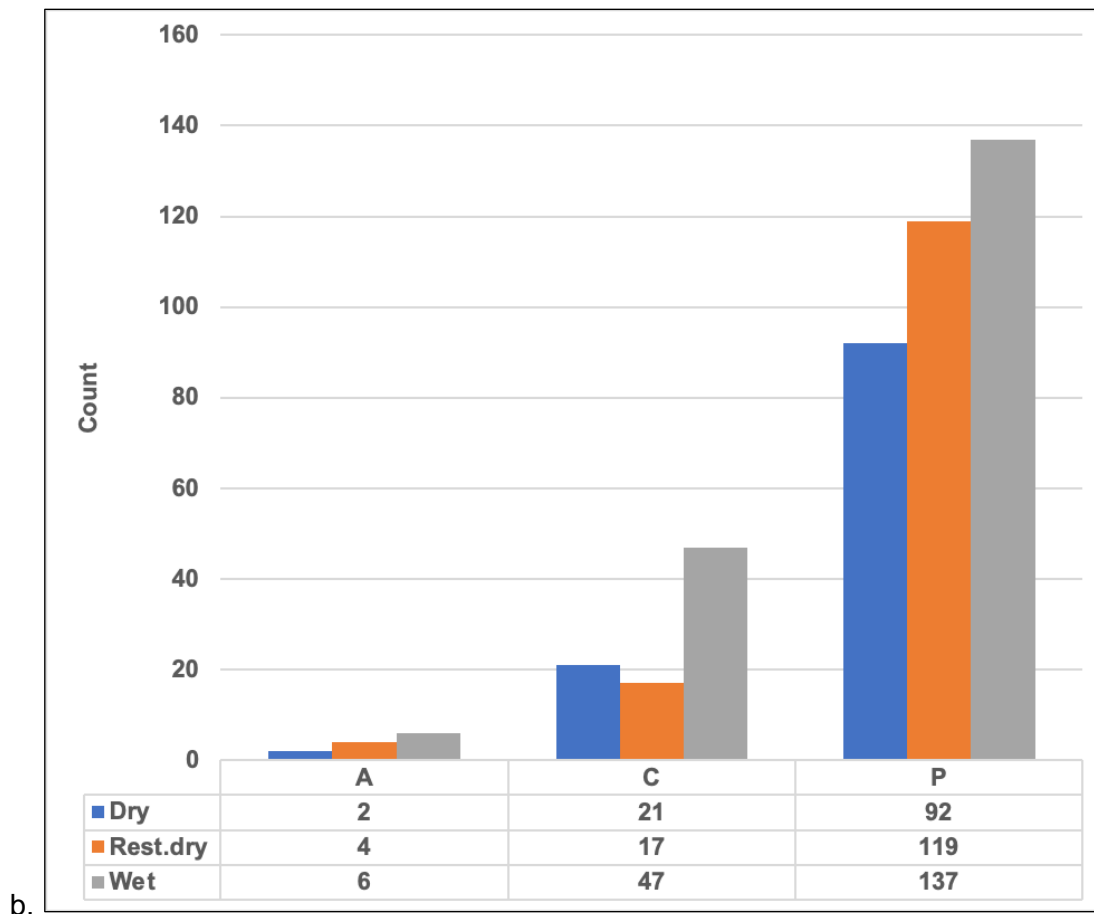
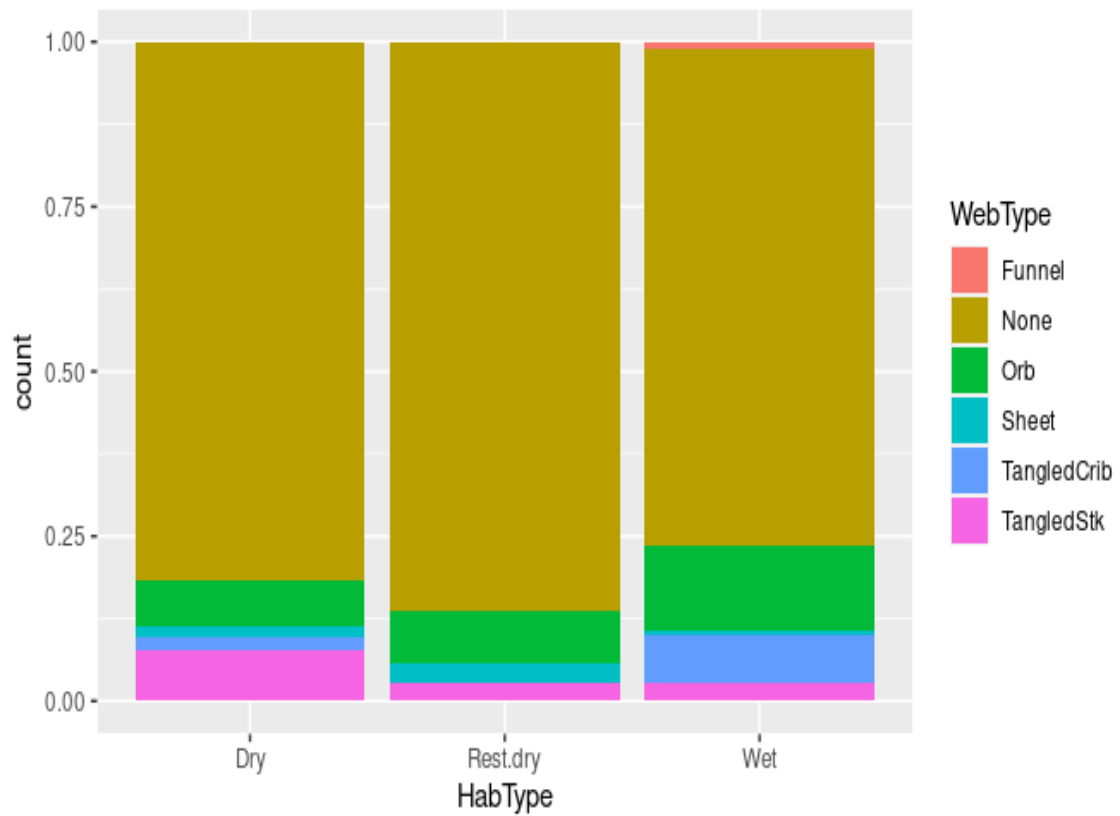
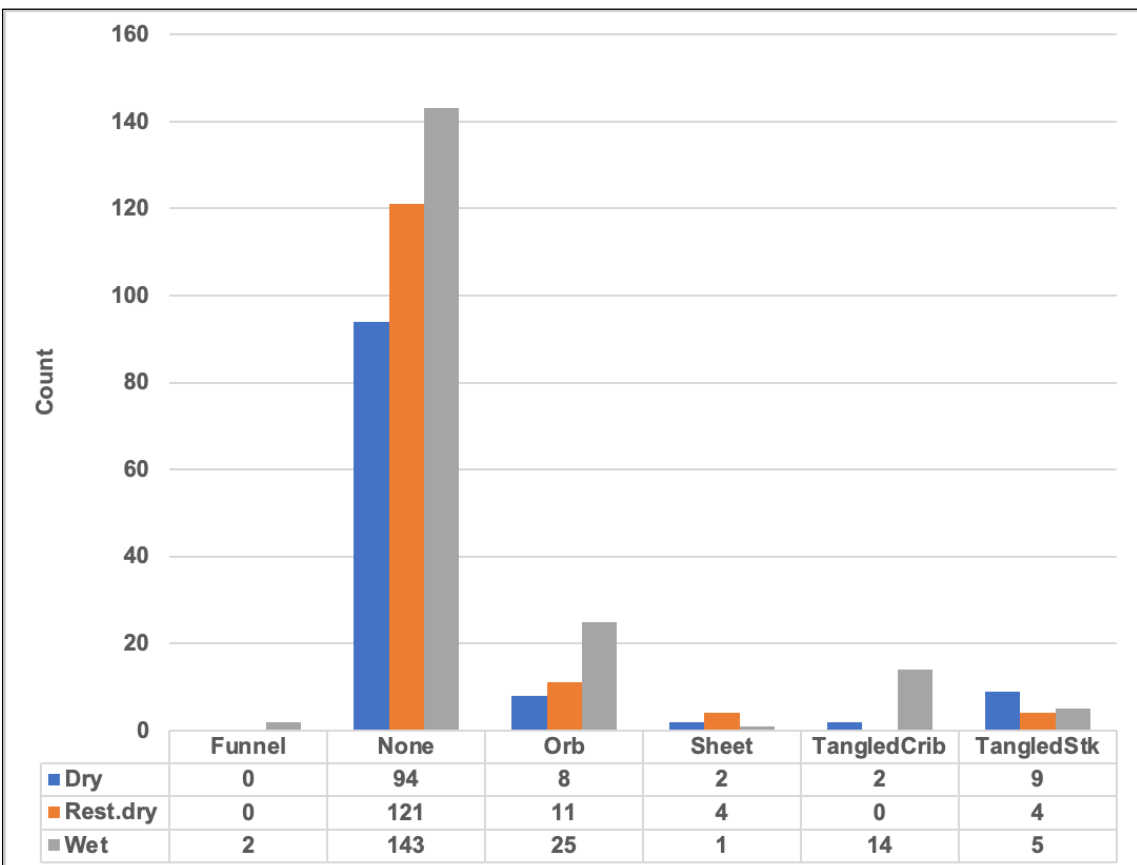


Figure 6a Proportion and 6b frequency of the functional traits in the functional group Prey Capture Method (Active, Capture by web, Pursuit) in relation to the three habitat types

In all the habitat types, within the functional trait group ‘web type’, the most frequently recorded (SI1 Table S2.4), and highest proportionally (SI Table S2.3), was the trait ‘none’. This particular trait is represented by the ground, ambush, other and specialist spider families. Its observed values were higher in the dry and restored dry habitat types than expected, however the value was lower than the expected in the wet habitat type (SI1 Table S2.4). The web type trait ‘funnel’ was not recorded in either the dry or restored dry habitats, similarly to the ‘tangled cribellate’ trait in the restored dry habitat type (SI1 Table S2.4). The chi-square test for independence revealed significant associations between the functional group web type and the habitat types ($X^2 = 29.564$, $df = 10$, $p = 0.001$), (please see Figure 7a & b, Table 6 and SI1 Table S2.3 & S2.4 for the full results).



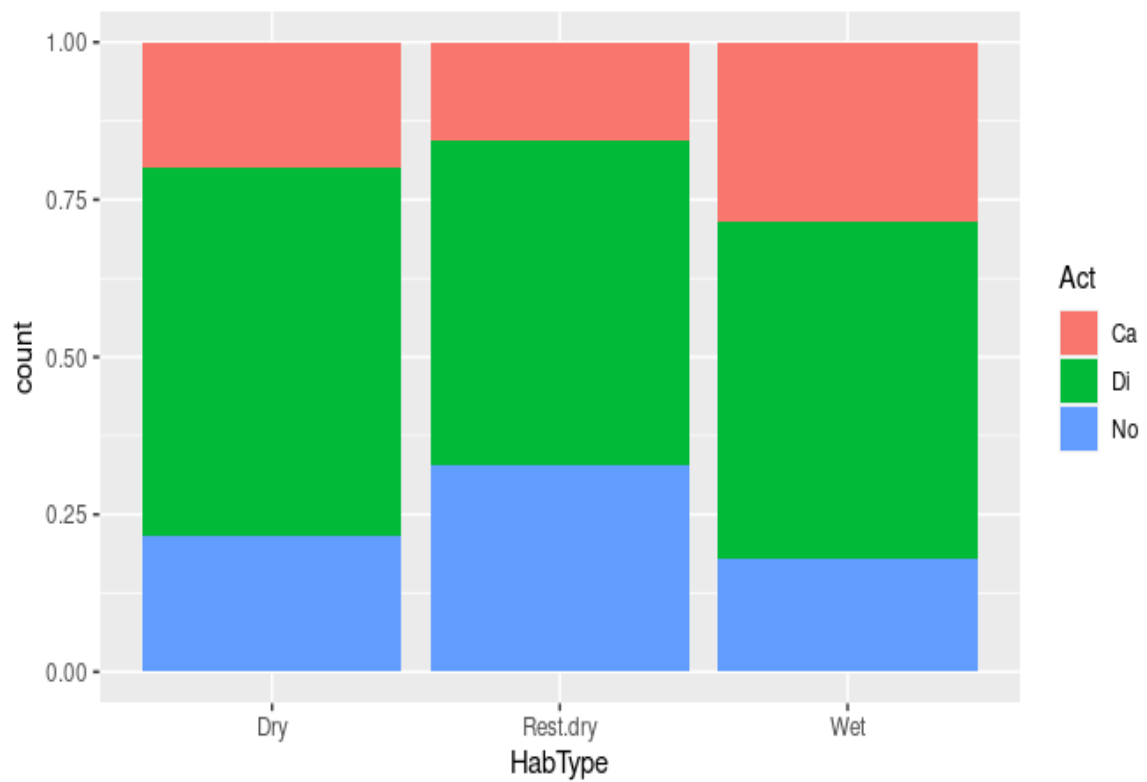
a.



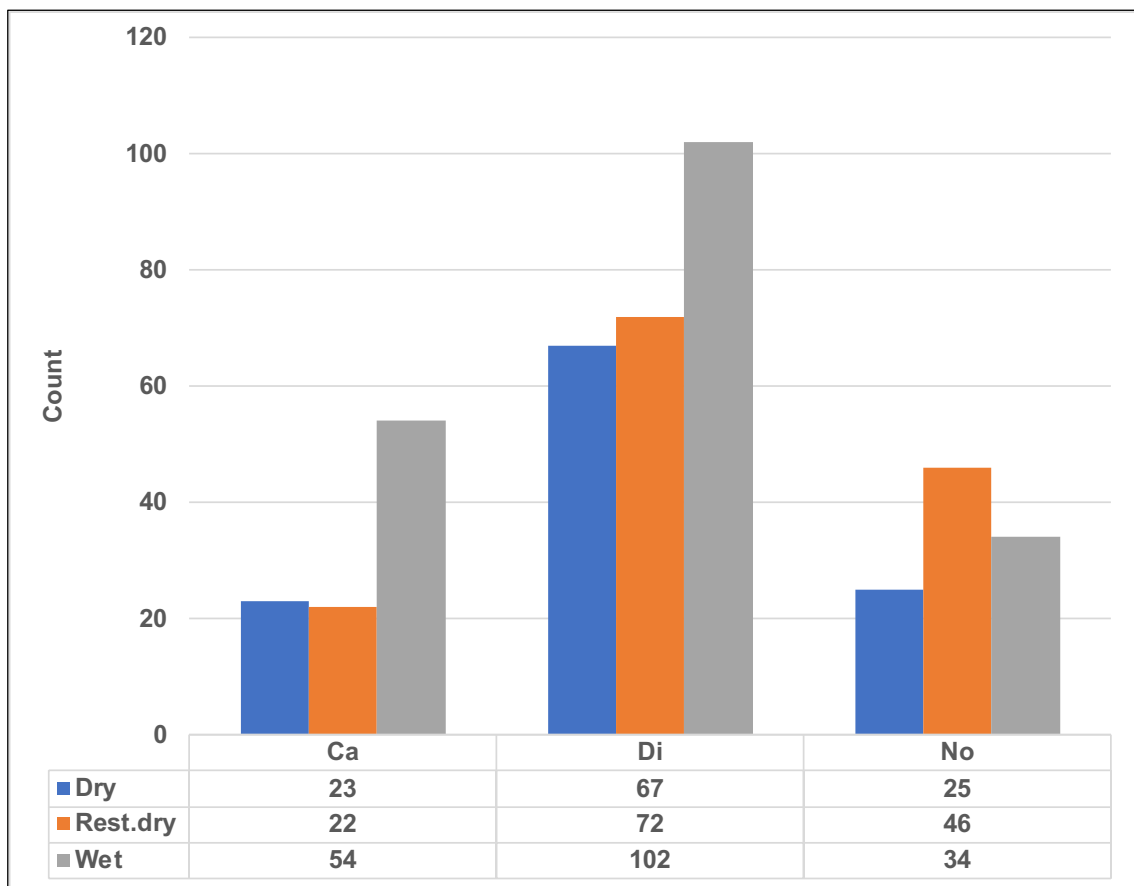
b.

Figure 7a Proportion and 7b frequency of the functional traits in the functional group Web Type in relation to the three habitat types

In all the habitat types, within the functional trait group daily activity, the most frequent trait (SI1 Table S2.4), and highest proportionally (SI1 Table S2.3), was diurnal (consisting of the following spider families; certain *Gnaphosidae* and *Lycosidae* species, *Miturgidae*, *Pisauridae*, *Salticidae*). Its observed values were lower than expected in the wet and restored dry habitat types suggesting a significant association, and the observed value was higher than expected in the dry habitat (SI1 Table S2.4). This suggests that there is a significant association between the trait diurnal and the dry habitat. The cathemeral trait was lower in the dry and restored dry habitats but higher in the wet. For the nocturnal trait, the observed values in the dry and wet were lower than expected suggesting a significant association. The chi-square test for independence revealed significant associations between the daily activity functional trait group and the habitat types ($X^2 = 14.634$, $df = 14$, $p = 0.006$). Please see Figure 8a and b, Table 6 and SI1 Table S2.3 & S2.4 for the full results.



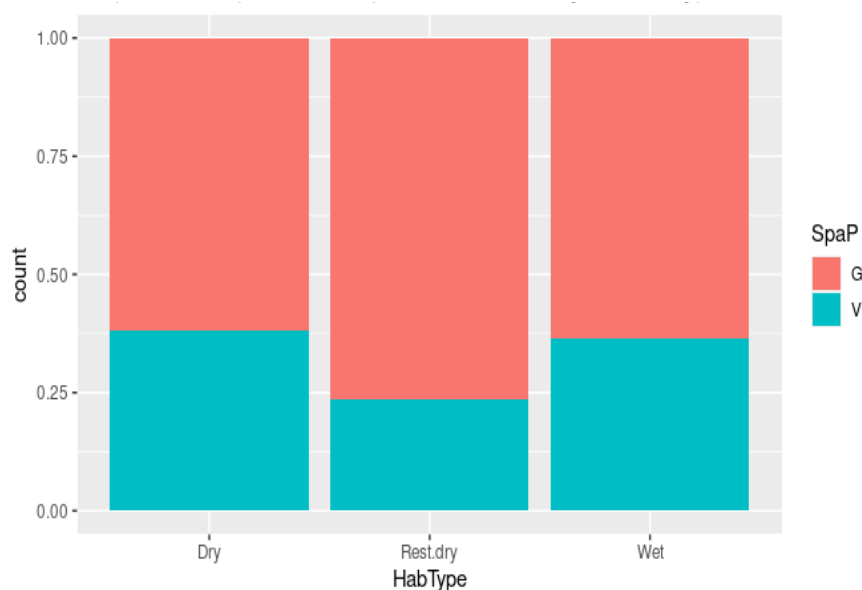
a.



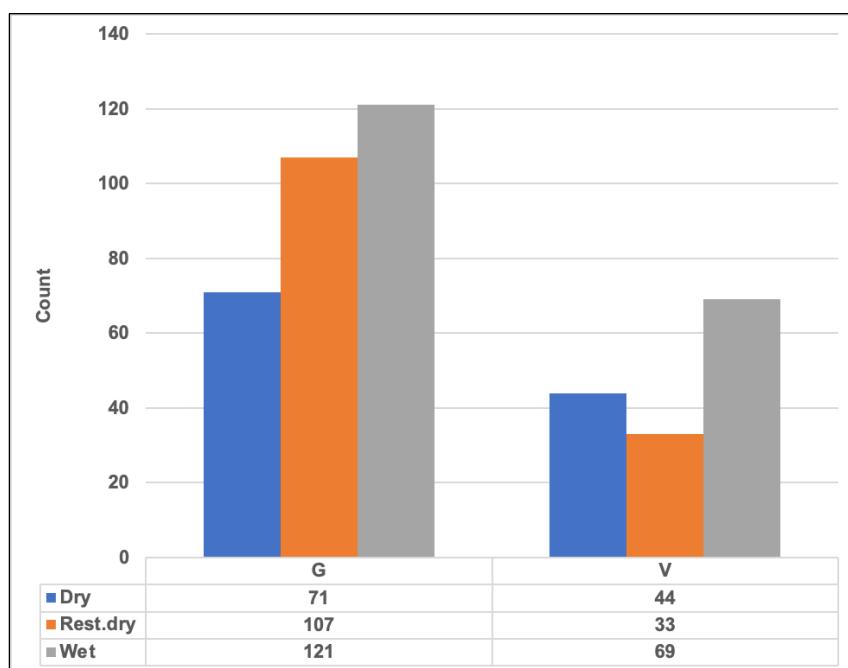
b.

Figure 8a Proportion and 8b frequency of the functional traits (Cathemeral, Diurnal, Nocturnal) in the functional group Daily Activity in relation to the three habitat types

In all the habitat types, within the functional trait group spatial preferences the most frequent trait (SI1 Table S2.4) and highest proportionally (SI Table S2.3), was the preference to be lower near the ground (consisting of the following spider families; *Araneidae*, *Dysderidae*, *Gnaphosidae*, *Hahiniidae*, *Liocranidae*, *Lycosidae*, *Miturgidae*, *Phrurolithidae*, *Salticidae*, *Tetragnathidae*, *Theridiidae*, *Thomisidae*). The observed values for these spiders in the dry and wet habitat types were lower than expected suggesting an association. Spiders found on vegetation had a lower observed than expected value in restored dry habitat again suggesting that spatial preference has a significant association to a particular habitat type (SI1 Table S2.4). The chi-square test for independence revealed significant associations between the Spatial Preference trait and the Habitat Types ($X^2 = 8.0297$, $df = 2$, $p = 0.018$), please see Figure 9a a & b, Table 6 and SI1 Table S2.3 & S2.4 for the full results.



a.



b.

Figure 9a Proportion and 9b frequency of the functional traits in the functional group Spatial Preference (Ground or Vegetation) in relation to the three habitat types

3.3 Does heathland vegetation structure or habitat type influence spider abundance or functional diversity?

3.3.1 Does heathland habitat type influence spider abundance?

The pitfall samples contained most of the individuals recorded, with total abundance highest in the wet habitat (see Figure 10b & S11 Table S3.1). The most abundant family was Lycosidae, which mainly comprised of the species *Pardosa pullata* and *P. nigriceps* (Figure 12 and Table 10 & S11 Table S4.1). The results demonstrated some influence of habitat type with the wet habitat type having the highest abundance, species richness and functional diversity (see Figures 10-14). The result of the ANOVA suggested there was no evidence to reject the null hypotheses in favour of the alternative H_1 habitat type influences spider abundance. A summary of the main results follows but please see S11 Tables S3.1-3.5 for the full results.

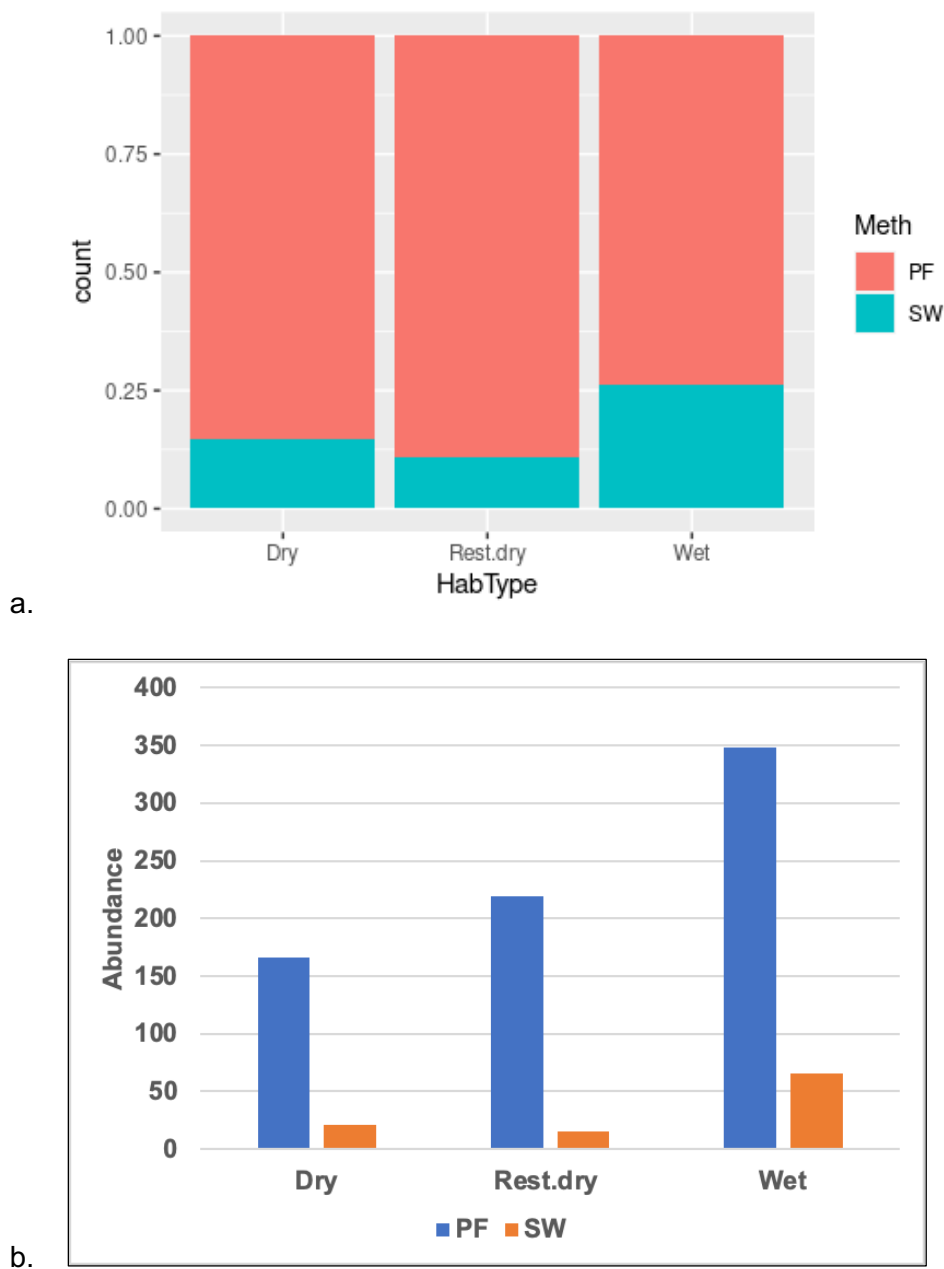


Figure 10a. Proportions of records (n=445) and 10b. abundance of individuals (N=835) for the pitfall and sweep net methods in the three habitat types

In terms of abundance, the most dominant spider family (50.18% of all samples combined) were the Lycosidae (Figure 12), which were found on all three habitat types (Figure 11). The Wet habitat had higher total abundance (mean 41) than the Restored Dry (mean 23) or Dry sites (mean 19) (ANOVA $F(2, 442) = 3.01$, $p = 0.050$) although not considered significant. See Figures 11-13 and the full results in SI1 Table S3.1 - S3.5.

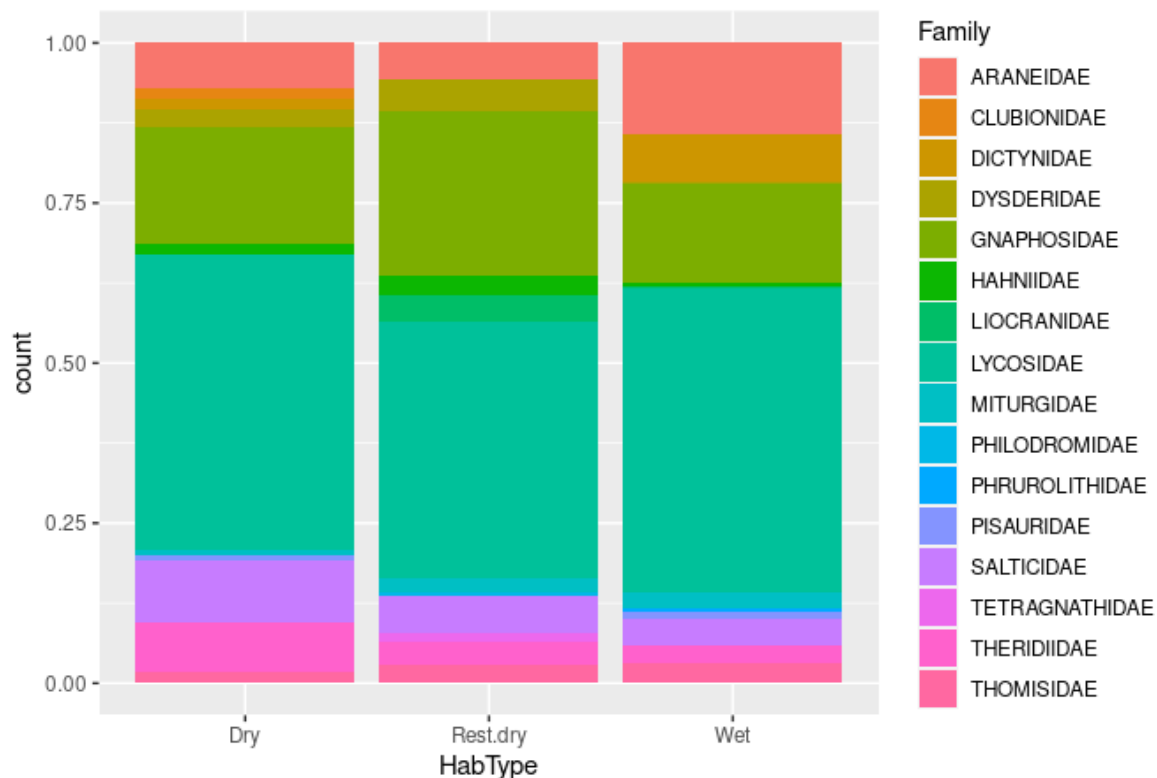


Figure 11 Proportions of the spider families recorded (n=445)

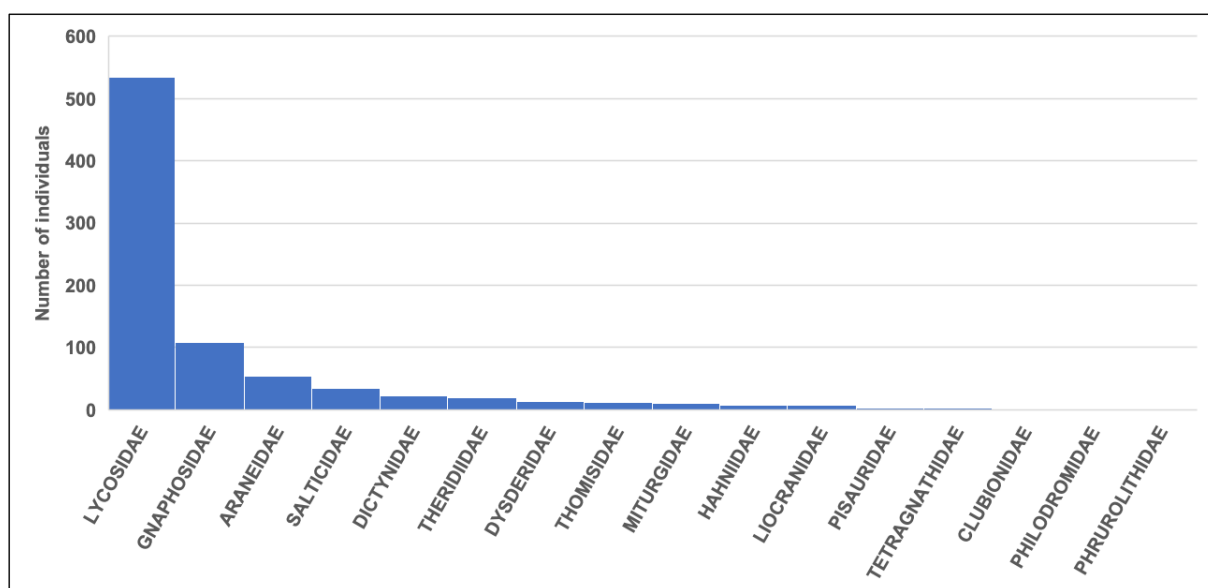


Figure 12 Abundance of the spider families in the sample (n=835)

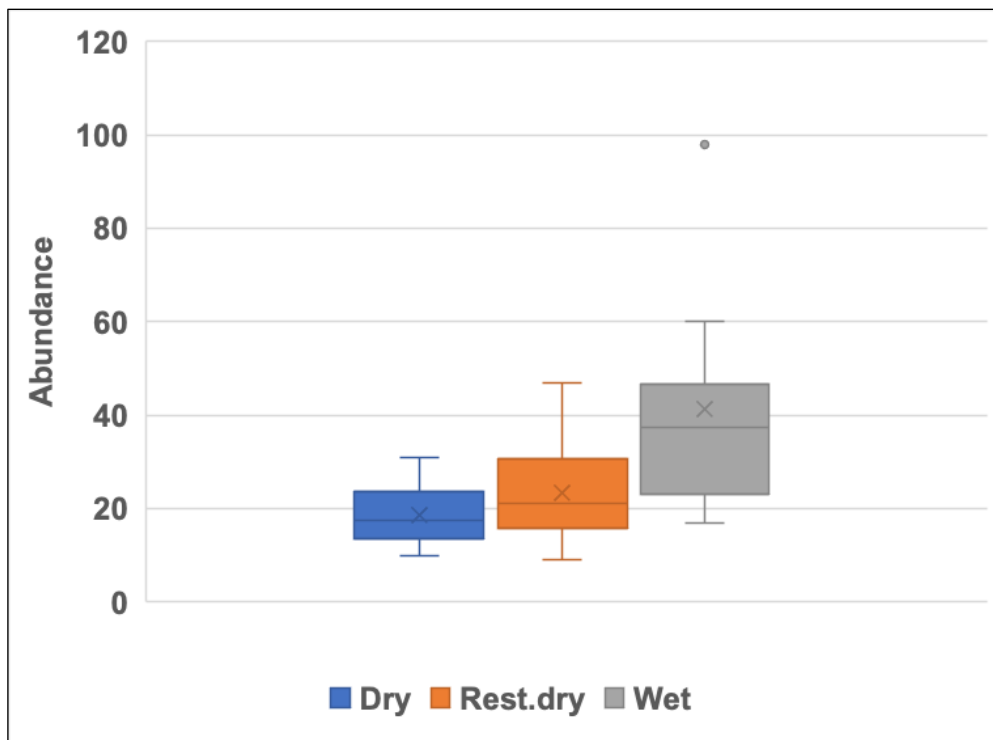


Figure 13 Abundance of spiders recorded across the three habitat types (N=30, total individuals =835)

In terms of species richness, the Wet habitat was significantly more species rich (mean 12.8) than the Restored Dry (mean 10.7) or Dry sites (mean of 8) (ANOVA, $F(2, 27) = 7.00$, $p = 0.004$) with Tukey tests showing significant differences between the Wet and Dry habitat types ($p = 0.002$). Please see Figure 14 and the full analysis in SI1 Table S3.1 – S3.5.

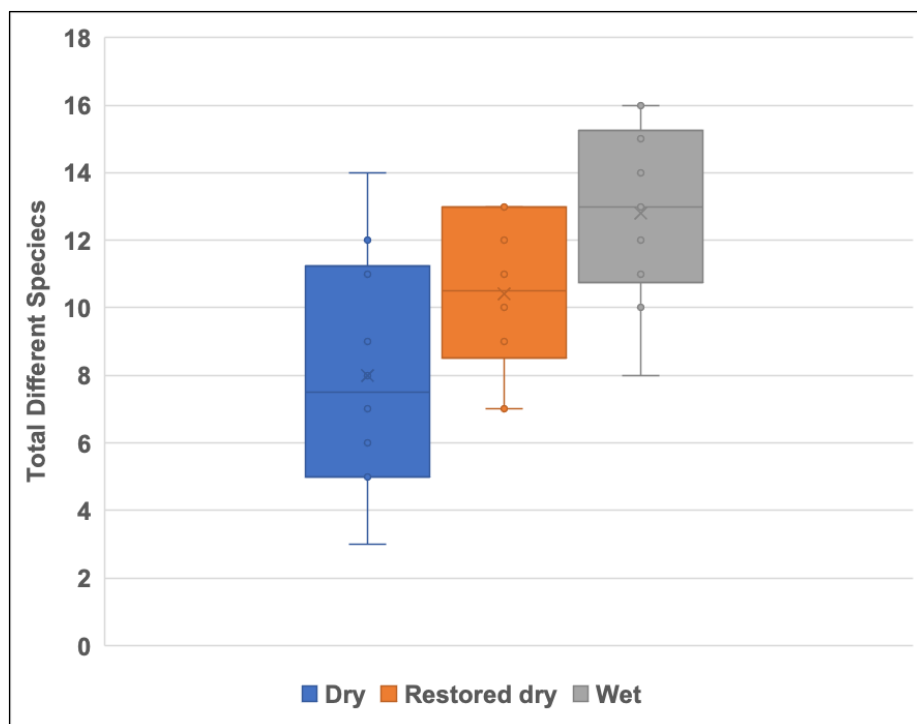


Figure 14 Total different spider species recorded across the three habitat types (N=30)

In terms of the total number of different functional traits recorded (functional diversity), the Wet habitat was more diverse (mean 15.3) than the Restored Dry (mean 13.5) or Dry sites (mean of 12.8) although not considered significant (ANOVA, $F(2, 27) = 2.99$, $p = 0.06$). Please see Figure 15 and the full analysis in SI1 Table S3.1 – S3.5.

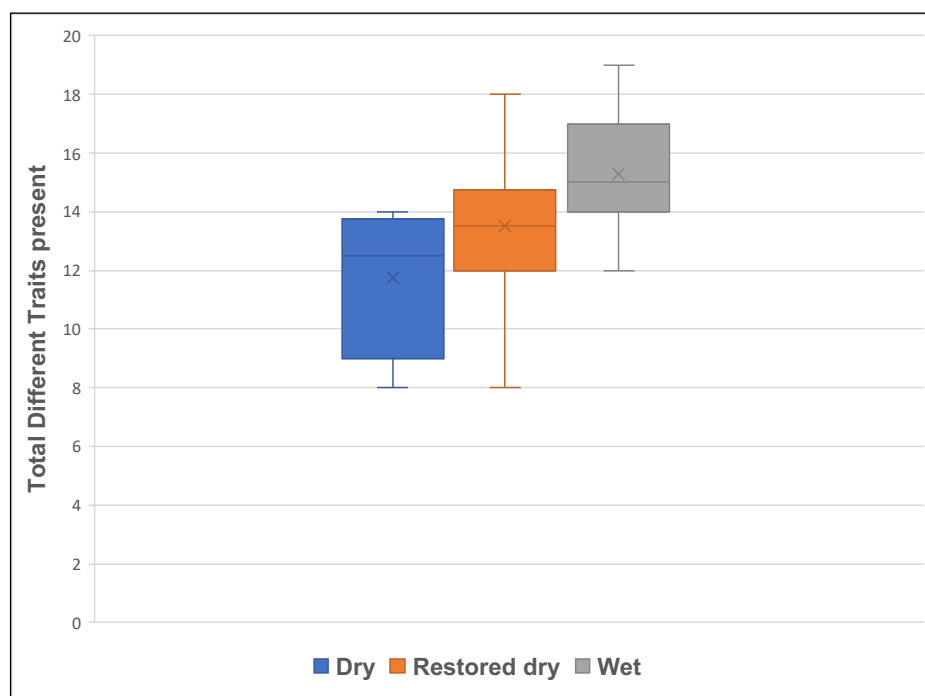


Figure 15 Total Different Traits recorded across the three habitat types (N=30)

3.3.2 Does heathland vegetation structure or habitat type influence spider functional traits?

The GLMs for each functional trait with MuMIn dredge and subsequent ANCOVA with Tukey tests on the top models that included habitat type, suggested there was enough evidence to reject the null hypotheses in favour of the alternative H_1 heathland vegetation structure and habitat type influences spider functional diversity. The results demonstrate statistically significant ($p < 0.001$) influence of vegetation structure and habitat type (Table 7 & 8) on specific functional traits.

The MuMIn dredge results indicated that all thirteen vegetation characteristics were the best predictors of the probability of their influence on one or more of the seventeen functional traits as they appeared in the top models. However, these differed in terms of the number of traits they had a high probability to influence. Six vegetation characteristics influenced five or more traits, namely moss layer, pioneer heather, all forbs, all graminoids, habitat type and SSSI condition. The remaining seven vegetation characteristics influenced four or fewer functional traits. The traits that were influenced, by the vegetation characteristics of all forbs, all graminoids, moss and lichen layer, pioneer heather and SSSI condition with probability of more than 60% were; ground hunter, use of pursuit, no web, diurnal and preference for near ground layer.

The moss and lichen layer influenced eight functional traits where the predictor weight was high (i.e. 1.00) suggesting its importance, for traits ground hunter, sheet web weaver, use of

capture web, pursuit, no web, cathemeral, diurnal, and in vegetation layer. Pioneer heather influenced seven functional traits, where the predictor weight was high (i.e. 1.00) suggesting its importance, on traits ground hunter, orb-web weaver, use of pursuit, use of no web, orb-web, diurnal and prefer being near ground layer. There were four other vegetation characteristics where the predictor weight was high (i.e. 1.00) suggesting their importance of influence. These were; all forbs, and all graminoids, both important for traits ground hunter, use of pursuit, no web, diurnal, and prefer being near ground layer. Habitat type also had high predictor weights (i.e. 1.00) for five traits, use of capture, tangled cribellate web, cathemeral, prefer being near ground layer and in vegetation. SSSI condition also had high predictor weights (i.e. 1.00) for five different traits, ground hunters, use of pursuit, no web, diurnal and in the vegetation layer.

For the remaining seven vegetation characteristics, the predictor weight was high (i.e. 1.00, suggesting importance) for only one, two, three or four traits. These were; bare ground (funnel web type and prefer near ground layer), building heather (for sheet web and funnel web type) and all shrubs (for sheet web type), litter layer (for the traits funnel and sheet web plus preference of being in the vegetation), mature heather (for the tangled sticky web trait), vegetation height (for both prefer being near ground and in vegetation) and heather stage (on space web weavers, use of capture web, cathemeral and prefer being near ground layer).

Subsequently, examining the influence of habitat type using ANCOVA on the best models where this variable was included, highlighted its significant influence on five out of the twenty-one functional traits. These included; orb-web weaver and specialist's guilds; prey capture web method; tangled cribellate web type and cathemeral activity trait group. The wet habitat type was significantly different from the restored dry habitat for the trait's specialists, use of capture web and tangled cribellate web builders. Finally, the wet habitat type was significantly different from the dry habitat type for the traits orb-web weavers and cathemeral species.

A summary of the main results follows but please see Table 7 & 8 and SI2 Tables S2-S6 for the full results.

3.3.2i Analysis and subsequent ANCOVA results for the functional trait group of Guilds

From the analysis of the functional trait group guild, for the ambush trait, the best model included the SSSI Condition only, which was included in 12 of the 15 models. The second-best model was the intercept which is indistinguishable from the other top models. The third model included SSSI Condition and mean percentage cover of pioneer heather and did not differ appreciably from the best model (delta AICc: 0.93). Pioneer heather appeared in five of the 15 top-ranking models and was positively correlated with this trait (delta AICc < 2.0; see Table 7 & 8). When the relative importance of each predictor was examined by summing the Akaike weights for each model where that variable appeared, SSSI Condition had a weight of 0.8 and pioneer heather had a weight of 0.32, i.e. they are included in 80% and 32% of all possible models. All shrubs had a weight of 0.3, both vegetation height and mature heather had weight of 0.18 and all other variables had a weight of less than 0.18 (SI2 Table S2). There were no significant relationships between the dependent variable, ambush trait in relation to the independent variables, mean percentage cover of all shrubs (ANCOVA $F(1, 26) = 0.34$, $p = 0.564$) and no differences with habitat types (ANCOVA $F(2, 26) = 1.20$, $p = 0.316$), so a Tukey test was not conducted (see Table 7 & 8).

For the trait ground hunters, the best model included SSSI condition, habitat type, mean percentage cover of pioneer heather and all graminoids, which were positively correlated with this trait as well as mean percentage cover of all forbs and moss layer which were negatively correlated with this trait. The second-best model, which did not differ appreciably from the best model (delta AICc: 266.6) did not include habitat type but did also include mean percentage cover of litter layer which was negatively correlated with this trait (SI2 Table S2). Mean percentage cover of pioneer heather, all graminoids, all forbs and moss layer appeared in all three top-ranking models (delta AICc < 2.0; see Table 7 & 8). They all had a weight of 1, i.e. it is included in 100% of all possible models. Habitat type had a weight of 0.41 and litter layer had a weight of 0.34. There was a significant relationship between the dependent variable, ground hunter trait in relation to the independent variables, mean percentage cover of pioneer heather (ANCOVA $F(1, 23) = 5.83$, $p = 0.024$) and all graminoids (ANCOVA $F(1, 23) = 23.68$, $p = <0.001$.) There were no significant differences with habitat type (ANCOVA $F(2, 23) = 0.04$, $p = 0.673$), see Table 7 & 8.

For the trait orb-web weavers, there were eight competing best models (within 2 AICc) of which the best model included habitat type with Akaike weight of 0.69 and mean percentage cover of pioneer heather with Akaike weight of 1.0 which was positively correlated with this trait. The second-best model did not differ appreciably from the best model (delta AICc: 0.99), and it included mean percentage cover of building heather, which was negatively correlated with this trait (see SI2 Table S2). Pioneer heather appeared in all the eight top-ranking models and had a weight of 1, i.e. it is included in 100% of all possible models. Habitat type appeared in five out of the eight top-ranking models and had a weight of 0.69, i.e. it is included in 69% of all possible models. All the other variables had a weight of less than 0.45. There was a significant relationship between the dependent variable, ground trait in relation to the independent variables, mean percentage cover of pioneer heather (ANCOVA $F(1, 21) = 26.68$, $p = <0.001$), mature heather (ANCOVA $F(1, 21) = 7.89$, $p = 0.011$) and all shrubs (ANCOVA $F(1, 21) = 6.41$, $p = 0.019$). There were also significant differences in the dependent variable, orb-web weaver trait between habitat types (ANCOVA $F(2, 21) = 6.12$, $p = 0.008$, with Tukey tests showing differences between the wet and restored dry habitat types ($p = <0.044$, see Table 7 & 8).

For the trait other hunter, there were 10 competing best models (within 2 AICc) of which the best model included SSSI condition and the mean percentage cover of all forbs and building heather, positively correlated with this trait with Akaike weight of 0.181. The second-best model included mean percentage cover of all forbs, as well as SSSI condition and did not differ appreciably from the best model (delta AICc: 104.6, see SI2 Table S2). All forbs appeared in all the 10 models, had a weight of 1, i.e. it is included in 100% of all possible models and was positively correlated with this trait (delta AICc < 2.0; see Table 7 & 8). Mean percentage cover of building heather had a weight of 0.52 and all other variables had a weight of less than 0.35. There was a significant relationship between the dependent variable, ground trait in relation to the independent variables, mean percentage cover of all forbs (ANCOVA $F(1, 26) = 5.64$, $p = 0.025$). Habitat type did not appear in the top models therefore no ANCOVA was conducted.

For the trait sheet web weavers, the best model included the heather stage, with mean percentage cover of building heather, mature heather, moss layer and pioneer heather which were positively correlated plus all forbs and all shrubs which were negatively correlated with this trait with Akaike weight of 0.146. The second-best model included as above with SSSI condition and mean percentage cover of litter layer but not pioneer heather (delta AICc: 47.6). Building heather and moss layer both appeared in all the 11 top-ranking models

(delta AICc < 2.0; see SI2 Table S2). and they both had a weight of 1, i.e. included in 100% of all possible models. All forbs had a weight of 0.94 and all shrubs had a weight of 0.93, heather stage had a weight of 0.78, mature heather had a weight of 0.68, pioneer heather had a weight of 0.59 and all other variables had a weight of less than 0.45. Habitat type did not appear in the top models therefore no ANCOVA was conducted, see Table 7 & 8.

For trait space web weavers the best model included habitat type and heather stage with mean percentage cover of all shrubs and weight of 0.157. The second-best model included habitat type, heather stage and SSSI condition and did not differ appreciably from the best model (delta AICc: 0.9). Heather stage appeared in all 12 of the top-ranking models with an Akaike weight of 1 and habitat type appeared in seven (delta AICc < 2.0; see Table 7 & 8) with a weight of 0.48. All other variables had a weight of less than 0.45 (see Table 7). There were no significant relationships between the dependent variable, space web weaver trait in relation to the independent variables, mean percentage cover of building heather, moss layer, all shrubs and vegetation height (ANCOVA $F(1, 23) = 2.88/0.08/0.62/3.18$, $p = 0.103/0.785/0.439/0.088$) or differences across habitat type (ANCOVA $F(2, 23) = 1.58$, $p = 0.228$), see Table 7 & 8.

For specialists the best model included the vegetation height, which was positively correlated with this trait with weight of 0.193. The second-best model included vegetation height and bare ground and did not differ appreciably from the best model (delta AICc: 0.9). Vegetation height appeared in eight of the nine top-ranking models and was positively correlated with this trait (delta AICc < 2.0; see Table 7 & 8). Vegetation height had an Akaike weight of 0.89, i.e. it is included in 89% of all possible models. Bare ground had a weight of 0.21 and all other variables had a weight of less than 0.2 (see Table 7). There was a significant relationship between the dependent variable, specialists in relation to the differences across habitat types (ANCOVA $F(2, 26) = 4.81$, $p = 0.017$, with Tukey tests showing differences between the wet and restored dry habitat types ($p = 0.033$, see Table 7 & 8).

3.2ii Analysis and subsequent ANCOVA results for the functional trait group of Prey Capture Method

From the analysis of the functional trait group of prey capture method, the trait ambush best model included SSSI condition with a weight of 0.13. The second-best model was the intercept model which is indistinguishable from the other top models. The third model included pioneer heather and SSSI condition. SSSI condition appeared in 13 of the 15 top-ranking models and pioneer heather appeared in five ($\Delta AICc < 2.0$; see Table 7). SSSI condition had a weight of 0.8, i.e. it is included in 80% of all possible models. Pioneer heather had an Akaike weight of 0.32 and all other variables had a weight of less than 0.30 (see SI2 Table S3). There were no significant relationships between the dependent variable, ambush trait in relation to the independent variables, mean percentage cover of all shrubs (ANCOVA $F(1, 26) = 0.34$, $p = 0.564$) or differences across habitat type (ANCOVA $F(2, 26) = 1.20$, $p = 0.316$), therefore no Tukey tests were conducted ($p > 0.050$, see Table 7 & 8).

For the trait capture web the best model included the habitat type, heather stage and moss layer which was positively associated with this trait. The second-best model included all shrubs and did not differ appreciably from the best model ($\Delta AICc: 0.07$). Habitat type and moss layer appeared in all four top-ranking models with an Akaike weight of 1 ($\Delta AICc < 2.0$; see Table 7). Heather stage had a weight of 1, all shrubs had a weight of 0.32 and all other variables had a weight of less than 0.30, (see SI2 Table S3). There was a significant relationship between the dependent variable, capture web trait in relation to all graminoids (ANCOVA $F(1, 23) = 9.83$, $p = 0.005$), litter layer (ANCOVA $F(1, 23) = 5.17$, $p = 0.033$), and difference between habitat types (ANCOVA $F(2, 23) = 5.76$, $p = 0.009$), with Tukey tests showing significant differences between the habitat types wet and restored dry $p = 0.032$ (see Table 7 & 8).

For the trait pursuit the best model included all forbs, litter layer, moss layer which were negatively correlated with this trait, all graminoids and pioneer heather which were positively correlated with this trait and SSSI condition with Akaike weight of 0.601. The second-best model was the same as the first but with litter layer excluded and did not differ appreciably from the best model ($\Delta AICc: 0.82$) (see SI2 Table S3). SSSI condition, all forbs, all graminoids, moss layer and pioneer heather appeared in both top-ranking models ($\Delta AICc < 2.0$; see table 7) and had a weight of 1, i.e. were included in 100% of all possible models. Litter layer had a weight of less than 0.60. There were significant relationships between the dependent variable, pursuit in relation to the independent variables, mean percentage cover of all graminoids (ANCOVA $F(1, 23) = 14.41$, $p = 0.001$), all forbs (ANCOVA $F(1, 23) = 10.36$, $p = 0.004$) and pioneer heather (ANCOVA $F(1, 23) = 5.61$, $p = 0.027$), (see Table 7 & 8). Habitat type did not appear in the top models therefore no ANCOVA was conducted for this variable.

3.3.2iii Analysis and subsequent ANCOVA results for the functional trait group of Web Type

From the analysis of the functional trait group web type, the trait funnel webs best model included the bare ground and mature heather which were positively correlated with this trait as well as litter layer, which was negatively correlated, with Akaike weight of 0.5. The second-best model excluded mature heather but included all graminoids with bare ground and litter layer and did not differ appreciably from the best model (delta AICc: 0.0. Bare ground and litter layer appeared in both top-ranking models (delta AICc < 2.0; see Table 7) with a weight of 1, i.e. they are included in 100% of all possible models. Mature heather and all graminoids had a weight of 0.5. None of the above variables included in the top models had a significant relationship when ANCOVA was conducted. Habitat type did not appear in the top models therefore no ANCOVA was conducted on this variable.

For the trait none (i.e.no web) the best model included all forbs, all graminoids, litter layer, moss layer, pioneer heather and SSSI condition with Akaike weight of 0.648. The second-best model included all these variables except litter layer and did not differ appreciably from the best model (delta AICc: 1.22). All forbs and moss layer appeared in both the top-ranking models, were negatively correlated with this trait and had a weight of 1 (delta AICc < 2.0; see Table 7). All graminoids and pioneer heather appeared in both the top-ranking models, were positively correlated with this trait and had a weight of 1 (delta AICc < 2.0; see Table 7). SSSI condition had a weight of 1 and litter layer had a weight of 0.65 (see SI2 Table 4). There were significant relationships between the dependent variable, 'none' (i.e.no web) trait in relation to the independent variables, mean percentage cover of all graminoids (ANCOVA $F(1, 23) = 24.51$, $p = <0.005$) and pioneer heather (ANCOVA $F(1, 23) = 5.73$, $p = 0.025$). Habitat type did not appear in the top models therefore no ANCOVA was conducted on this variable.

For the orb-web trait, the best model included moss layer, pioneer heather and all shrubs with an Akaike weight of 0.164. The second-best model included mature heather, pioneer heather and habitat type and did not differ appreciably from the best model (delta AICc: 0.34). Habitat type appeared in four of the 11 top-ranking models and pioneer heather appeared in all 11 which was positively correlated with this trait (delta AICc < 2.0; see Table 7). Habitat type had a weight of 0.36, i.e. it is included in 36% of all possible models. Pioneer heather had a weight of 1, mature heather had a weight of 0.52 and all other variables had a weight of less than 0.50. There was a significant relationship between the dependent variable, orb-web trait in relation to the mean percentage cover of all graminoids (ANCOVA $F(1, 23) = 14.18$, $p = 0.001$), moss layer (ANCOVA $F(1, 23) = 9.03$, $p = <0.006$) and pioneer heather (ANCOVA $F(1, 23) = 22.49$, $p = <0.05$) although there were no significant differences between habitat types $p = >0.05$ (see Table 7 & 8).

For the sheet web trait, the best model included building heather and mature heather which were positively correlated with this trait, as well as all forbs, litter layer and all shrubs which were negatively correlated with this trait, with Akaike weight of 0.105. The second-best model included the same variables as the top model with the addition of all graminoids and vegetation height which did not differ appreciably from the best model (delta AICc: 0). Building heather, litter layer and all shrubs appeared in all the 10 top-ranking models (delta AICc < 2.0; see Table 7) and all shrubs had a weight of 1, i.e. they are included in 100% of all possible models. All forbs had a weight of 0.74, all graminoids and vegetation height both had a weight of 0.53,

and all other variables had a weight of less than 0.48 (SI2 Table S4). There were no significant relationships between the dependent variable, sheet web trait in relation to the independent variables, mean percentage cover of all forbs, litter layer, moss layer, mature heather and all shrubs or habitat type (see Table 7 & 8).

For the tangled cribellate web the best model included all shrubs, which was negatively correlated with this trait, with habitat type and heather stage with Akaike weight of 0.377. The second-best model included building heather with habitat type and heather stage and did not differ appreciably from the best model (delta AICc: 0.97). Habitat type appeared in all the four top-ranking models (delta AICc < 2.0; see Table 7) with a weight of 1, i.e. it is included in 100% of all possible models. Heather stage had a weight of 0.81, all shrubs had a weight of 0.57, building heather had a weight of 0.43 and all other variables had a weight of less than 0.35 (SI2 Table S4). There were significant relationships between the dependent variable, tangled cribellate trait and the independent variables, mean percentage cover of litter layer (ANCOVA $F(1, 23) = 4.71$, $p = 0.041$), all shrubs (ANCOVA $F(1, 23) = 5.46$, $p = 0.029$) and differences between habitat type (ANCOVA $F(2, 23) = 5.92$, $p = 0.008$), with Tukey tests showing significant differences between the wet and restored dry habitat ($p = 0.016$, see Table 7 & 8).

For the trait of tangled sticky web, the best model included mature heather with Akaike weight of 0.384. The second-best model included mature heather with SSSI condition and did not differ appreciably from the best model (delta AICc: 1.5). Mature heather appeared in all the five top-ranking models and was positively correlated with this trait (delta AICc < 2.0; see Table 7). and a weight of 1 i.e. it is included in 100% of all possible models. All other variables had a weight of less than 0.35 (SI2 Table S4). Habitat type did not appear in the top models therefore no ANCOVA was conducted for this variable.

3.3.2iv Analysis and subsequent ANCOVA results for the functional trait group of Daily Activity

From the analysis of the functional trait group Daily Activity, for the trait cathemeral the best model included the moss layer, which was positively correlated with this trait, with habitat type and heather stage and an Akaike weight of 0.336. The second-best model included SSSI condition with moss layer, habitat type and heather stage and did not differ appreciably from the best model (delta AICc: 0.5). Habitat type and moss layer appeared in all the four top-ranking models with a weight of 1, with moss layer positively correlated with this trait (delta AICc < 2.0; see Table 7 and SI2 Table S5). All other variables had a weight of less than 0.40 (SI2 Table S5). There was a significant relationship between the dependent variable, cathemeral trait and the independent variables, mean percentage cover of all graminoids (ANCOVA $F(1, 24) = 8.28$, $p = 0.008$), moss layer (ANCOVA $F(1, 24) = 4.72$, $p = 0.040$) and differences between habitat types (ANCOVA $F(2, 24) = 6.62$, $p = 0.005$). Tukey tests showed differences between the wet and dry heath habitats ($p = 0.023$) as well as between the wet and restored dry heath habitat types ($p = 0.044$, see Table 7 & 8).

For the trait diurnal the best model included all forbs and moss layer which were both negatively correlated with this trait and also all graminoids and pioneer heather, which were both positively correlated, as were habitat type and SSSI condition with Akaike weight of 0.446. The second-best model included all the same variables as the first model except habitat type and did not differ appreciably from the best model (delta AICc: 0.76). All forbs, all graminoids, moss layer, pioneer heather and SSSI condition appeared in all the three top-ranking models (delta AICc < 2.0; see Table 7 and SI2 Table S5) so all had a weight of 1. All other variables had a weight of less than 0.45 (SI2 Table S5). Habitat type appeared in only one of the top models. There were significant differences in the dependent variable, diurnal trait in relation to the independent variable all graminoids (ANCOVA $F(1, 24) = 18.53$, $p < 0.05$) though no significant difference in habitat type (ANCOVA $F(2, 24) = 0.94$, $p = 0.405$).

For the nocturnal trait, the best model included habitat type only with Akaike weight of 0.206. The second-best model was the intercept, and the third best model included bare ground and did not differ appreciably from the best model (delta AICc: 0.61). Habitat type appeared in four of the eight top-ranking models (delta AICc < 2.0; see SI2 Table S5 and Table 7 & 8) and had a weight of 0.60, all other variables had a weight of less than 0.22 (SI2 Table S5). There was no significant difference in the dependent variable, nocturnal trait in relation to the independent variable, habitat type (ANCOVA $F(2, 27) = 2.64$, $p = 0.090$ see Table 7 & 8).

3.3.2v Analysis and subsequent ANCOVA results for the functional trait group of Spatial Preference

From the analysis of the functional trait group spatial preference, for the trait of occurring on the ground, the best model included all forbs and vegetation height which were negatively correlated with this trait, as well as bare ground, all graminoids and pioneer heather which were positively correlated, as were habitat type and heather stage with Akaike weight of 1. As there was only one top-ranking model all the variables above had a weight of 1, i.e. they were included in 100% of all possible models (see Table 7 & 8 and SI2 Table S6). There were significant relationships between the dependent variable, ground trait and the independent variables, mean percentage cover of all graminoids (ANCOVA $F(1, 22) = 30.36$, $p = <0.05$) and pioneer heather (ANCOVA $F(1, 22) = 9.82$, $p = 0.005$) although no significant differences between habitat types (ANCOVA $F(2, 22) = 1.27$, $p = 0.301$) (see Table 7 & 8).

For the trait of occurring in the vegetation the best model included litter layer and moss layer that were negatively correlated and vegetation height, which was positively correlated, as well as habitat type and SSSI condition with Akaike weight of 0.44. The second-best model included the same variables as the first model with the addition of mature heather and did not differ appreciably from the best model (delta AICc: 1.65). Litter layer, moss layer, vegetation height, habitat type and SSSI condition appeared in all the four top-ranking models (delta AICc < 2.0 ; see Table 7) and all other variables had a weight of less than 0.45 (SI2 Table S6). There was an overall significant difference between the habitat types (ANCOVA $F(2, 21) = 3.76$, $p = 0.040$), however Tukey tests showed no individual differences between them ($p \geq 0.05$, see Table 7 & 8).

Table 7 Subset of the best models (within <2AICc's) for the different functional traits present and the relative importance of each predictor (vegetation characteristic, habitat type) examined by summing the Akaike weights for each model where that variable appeared (more than 50% in bold)

		Bd	BG	Fb	Gd	LL	Mt	ML	Pr	Sh	Vh	HbTyp	HStag	SSSICon
Guild	Ambush	0.17		0.10		0.06	0.18		0.32	0.30	0.18	0.05	0.05	0.80
	Ground Hunters			1.00	1.00	0.34		1.00	1.00			0.41		1.00
	Orb Web Weavers	0.17	0.00			0.07	0.41	0.14	1.00	0.41	0.09	0.69		0.10
	Other Hunter	0.52	0.33	1.00	0.07				0.07	0.15				0.72
	Sheet Web Weavers	1.00		0.94	0.19	0.27	0.68	1.00	0.59	0.93	0.25		0.78	0.29
	Space Web Weaver	0.42				0.06	0.08	0.15		0.46	0.36	0.48	1.00	0.23
	Specialists		0.21	0.08	0.10	0.11	0.13				0.89	0.11		0.16
Prey Capture Method	Ambush	0.17		0.11		0.06	0.18		0.32	0.30	0.18	0.05	0.05	0.80
	Capture				0.21	0.13		1.00		0.32		1.00	1.00	
	Pursuit			1.00	1.00	0.60		1.00	1.00					1.00
Web Type	Funnel		1.00		0.50	1.00	0.50							
	None			1.00	1.00	0.65		1.00	1.00					1.00
	Orb	0.08			0.31	0.07	0.52	0.45	1.00	0.39		0.36		0.16
	Sheet	1.00	0.21	0.74	0.53	1.00	0.48	0.11	0.21	1.00	0.53	0.48		0.21
	Tangled Cribellette	0.43				0.19		0.20		0.57		1.00	0.81	
	Tangled Sticky		0.15		0.14		1.00				0.15			0.17
Daily Activity	Cathemeral				0.18			1.00		-0.01		1.00	1.00	0.26
	Diurnal			1.00	1.00	0.25		1.00	1.00			0.45		1.00
	Nocturnal		0.22			0.22			0.11		0.10	0.60		
Spatial preference	Ground		1.00	1.00	1.00				1.00		1.00	1.00	1.00	
	Vegetation		0.18			1.00	0.19	1.00		0.19	1.00	1.00		1.00
	Total number in best models	9	9	11	14	17	11	13	13	12	11	15	8	16
	Total number in best models >50%	3	2	8	7	4	4	8	8	3	4	7	6	8

Table 8 ANCOVA and Tukey results from the extracted best models of the MuMIn dredge for the functional traits in relation to the habitat type (significant influences in bold)

Functional Trait group	Functional Trait	Mean Abundance for each Habitat Type			ANCOVA for Habitat Type			Tukey Pairwise	
		Dry	Restored Dry	Wet	D	F	P	Pairwise	P
Guild	Amb	2.20	0.50	0.67	2	1.20	0.316		
	Grd	13.80	18.40	32.90	2	0.40	0.673		
	OrbWW	1.00	1.10	3.60	2	6.12	0.008	Wet-Dry	0.044
	Other	1.90	1.40	1.30	2				
	ShWW	0.30	0.50	0.30	2				
	Spec	0.30	1.00	0.10	2	4.81	0.017	Wet-Rest.dry	0.033
	SpWW	1.20	0.60	2.50	2				
Prey Capture Method	A	0.20	0.40	0.50	2	1.20	0.316		
	C	2.67	1.80	6.20	2	5.76	0.009	Wet-Rest.dry	0.032
	P	16.00	21.20	34.30	2				
Web Type	Funnel	0.00	0.00	0.20	2	1.96	0.162		
	None	16.30	21.00	35.00	2				
	Orb	1.00	1.20	3.40	2	3.17	0.061		
	Sheet	0.20	0.50	0.10	2	1.02	0.377		
	TangledCrib	0.20	0.00	2.00	2	5.92	0.008	Wet-Rest.dry	0.016
	TangledStk	1.00	0.40	0.50	2				
Daily Activity	Ca	2.60	2.30	6.70	2	6.62	0.005	Wet-Dry	0.023
	Di	11.80	15.70	30.70	2	0.94	0.405		
	No	4.30	5.40	3.80	2	2.64	0.090		
Spatial Preference	G	10.40	16.40	30.00	2	1.27	0.301		
	V	8.30	6.60	10.60	2	3.76	0.040		

3.4 Does heathland vegetation structure or habitat type influence the occurrence of specific spiders?

3.4.1 Does heathland habitat type influence the occurrence of specific spiders?

The most abundant spiders were *Pardosa pullata* (256 individuals, 30.66% of the sample) and *Pardosa nigriceps* (163 individuals, 19.52% of the sample) which were found on all three habitat types (see Table 9 & SI1 Table S4.1). *P. pullata* was predominantly recorded on the wet habitat and *P. nigriceps* on the dry, both are common ubiquitous species, and the latter is more commonly associated with, and found, in low vegetation (Bee *et al.* 2020). Twelve out of the fifteen most abundant individuals recorded, used in the analyses, had the following functional traits: ground hunter, capture of prey through pursuit, nocturnal, and/or ground dwellers (see Table 11). The preferred and cited habitat preference of all the most abundant species would be considered dry (see references 1-6 listed on Table 9).

In relation to habitat type, there were only three of the most abundant species in this study where the cited habitat preference is exclusively heathland namely; *Aelurillus v-insignitus* (NS), *Zelotes latreillei* and *Dysdera erythrina*. Seven species recorded as preferring mixed heathland and other habitats, included; *Mangora acalypha*, *Alopecosa barbipes*, *Alopecosa pulverulenta*, *Asagena phalerata* and *Haplodrassus signifer*. The species *Drassyllus praeficus* (Nationally Scarce) was mainly recorded on wet sites in this study yet is associated with chalk grassland and occasionally with dry heathland (Bee *et al.* 2020). In addition, *Drassodes cupreus*, cited as recorded on heathland and old grassland, was more abundant on dry (7) or restored dry (8) habitat types (see Table 9).

Finally, three out of the fifteen most abundant species are considered widespread (Bee *et al.* 2020) with no preferred habitat; *Dictyna arundinacea* was mainly recorded on the wet habitat (12 and only 1 individual on dry), *Zora spinimana*, which is considered a grassland species, was found on all habitats but mainly recorded in wet and restored dry habitat and finally, *Trochosa terricola* is cited as preferring dry habitats but was more abundant in the wet (5) than in the dry or restored dry habitats (2,3). Please see Table 9 and SI1 Table S4.1.

In relation to indicator species, two thirds of the most abundant species recorded across all the sites and habitat types have been cited in historical research papers on heathlands (SI1 Table S4.1 and Table 9 & 10). In addition to this, a third (five out of fifteen) of the most abundant species recorded have been previously suggested as heathland indicator species (Table 9, SI1 Table S4.1, Webb 1994). Finally, the sample contained two bog indicator species (*Arctosa leopardus* and *Pirata latitans* SI1 Table S4.1) and nine out of the fifteen most abundant species would be considered appropriate for peat bogs by Scott *et al.* 2006 (Table 9).

Table 9 List of the most abundant species, their functional traits, abundance and rarity score (Rarity score 0=none, 1=Nationally Scarce, 2=Nationally Rare), used for the species-level analysis (species in bold included in a Webb 1994 suggested indicators list)

Species	Family	Functional trait					Preferred habitat	Rarity Score	Number of sites Recorded on	Abundance					References
		Guild	Capture Method	Web Type	Daily Activity	Spatial Preference				Dry	Restored dry	Wet	Grand Total	%of abundance	
<i>Pardosa pullata</i> *	LYCOSIDAE	Grd	P	None	Di	G	Dry	0	23	19	36	201	256	30.66	1, 2, 5, 6, 7
<i>Pardosa nigriceps</i> *	LYCOSIDAE	Grd	P	None	Di	V	Dry	0	22	65	53	45	163	19.52	1, 2, 3, 5, 6, 7
<i>Mangora acalypha</i>	ARANEIDAE	OrbWW	C	Orb	Ca	V	Dry	0	19	8	7	26	41	4.91	4, 6
<i>Alopecosa pulverulenta</i> *	LYCOSIDAE	Grd	P	None	Di	G	Dry	0	18	6	20	14	40	4.79	7
<i>Alopecosa barbipes</i>	LYCOSIDAE	Grd	P	None	Di	G	Dry	0	16	13	17	7	37	4.43	1, 2, 4, 6
<i>Haplodrassus signifer</i>*	GNAPHOSIDAE	Grd	P	None	No	G	Dry	0	15	11	12	5	28	3.35	1, 2, 4, 6, 7
<i>Drassyllus praeficus</i>	GNAPHOSIDAE	Grd	P	None	No	G	Dry	1	15	4	7	10	21	2.51	6
<i>Drassodes cupreus</i>*	GNAPHOSIDAE	Grd	P	None	No	G	Dry	0	12	7	8	3	18	2.16	1, 2, 3, 4, 5, 6, 7
<i>Aelurillus v-insignitus</i>	SALTICIDAE	Other	P	None	Di	G	Dry	1	5	13	2	0	15	1.80	1, 6
<i>Dysdera erythrina</i>	DYSDERIDAE	Spec	P	None	No	G	Dry	0	10	3	10	1	14	1.68	1, 4, 6
<i>Dictyna arundinacea</i> *	DICTYNIDAE	SpWW	C	Tangled Crib	Ca	V	Dry	0	8	1	0	12	13	1.56	5, 6, 7
<i>Zelotes latreillei</i> *	GNAPHOSIDAE	Grd	P	None	No	G	Dry	0	9	3	4	5	12	1.44	1, 2, 3, 6, 7
<i>Zora spinimana</i> *	MITURGIDAE	Other	P	None	Di	G	Dry	0	7	1	5	5	11	1.32	2, 3, 5, 6, 7
<i>Asagena phalerata</i>	THERIDIIDAE	SpWW	C	Tangled Stk	Ca	G	Dry	0	8	5	2	3	10	1.20	
<i>Trochosa terricola</i> *	LYCOSIDAE	Grd	P	None	No	G	Dry	0	8	2	3	5	10	1.20	1, 2, 3, 5, 6, 7

References: 1. Merrett 1976, 2. Snazell 1982, 3. Merrett 1983, 4. Webb 1984, 5. BugLife 2010, 6. BugLife 2014, 7. Scott *et al.* 2006 (*Bog appropriate sp.)

Table 10 List of species with a rarity score (1=Nationally Scarce, 2=Nationally Rare) including their functional traits, abundance (species in bold included in a Webb 1994 suggested indicators list)

Species	Family	Functional trait						Rarity Score	Number of sites Recorded on	Abundance					References
		Guild	Capture Method	Web Type	Daily Activity	Spatial Preference	Preferred habitat			Dry	Restored dry	Wet	Grand Total	% of abundance	
Haplodrassus umbratilis	GNAPHOSIDAE	Grd	P	None	No	G	Dry	2	1	0	1	0	1	0.12	4
Micaria silesiaca	GNAPHOSIDAE	Grd	P	None	Di	G	Dry & Wet	2	4	2	2	1	5	0.60	1, 4
<i>Phaeocedus braccatus</i>	GNAPHOSIDAE	Grd	P	None	Di	G	Dry	2	1	0	2	0	2	0.24	
<i>Zelotes longipes</i>	GNAPHOSIDAE	Grd	P	None	No	G	Dry	2	3	1	1	1	3	0.36	1
<i>Aelurillus v-insignitus</i>	SALTICIDAE	Other	P	None	Di	G	Dry	1	5	13	2	0	15	1.80	1, 6
Cercidia prominens	ARANEIDAE	OrbWW	C	Orb	Ca	G	Dry	1	2	0	0	2	2	0.24	4, 5
<i>Drassyllus praeficus</i>	GNAPHOSIDAE	Grd	P	None	No	G	Dry	1	15	4	7	10	21	2.51	6
Gnaphosa leporina	GNAPHOSIDAE	Grd	P	None	No	G	Wet	1	3	1	0	4	5	0.60	1, 2, 3, 4
<i>Hypsosinga sanguinea</i>	ARANEIDAE	OrbWW	C	Orb	Ca	V	Wet	1	1	0	1	0	1	0.12	
<i>Kochiura aulica</i>	THERIDIIDAE	SpWW	C	TangledStk	Ca	V	Dry	1	1	0	1	0	1	0.12	5
Ozyptila scabricula	THOMISIDAE	Amb	A	None	Ca	G	Dry	1	2	0	2	0	2	0.24	4, 6
Pardosa tenuipes	LYCOSIDAE	Grd	P	None	Di	G	Wet	1	2	0	1	1	2	0.24	4
<i>Scotina celans</i>	LIOCRANIDAE	Grd	P	None	No	G	Wet	1	5	0	6	1	7	0.84	2, 3, 6
Xerolycosa nemoralis	LYCOSIDAE	Grd	P	None	Di	G	Dry	1	3	1	1	2	4	0.48	4, 6

References: 1. Merrett 1976, 2. Snazell 1982, 3. Merrett 1983, 4. Webb 1994, 5. BugLife 2010, 6. BugLife 2014

3.4.2 Does heathland vegetation structure or habitat type influence the occurrence of specific spiders?

The results for each of the most abundant species (n=15) from GLMs with MuMIn dredge and subsequent ANCOVA with Tukey tests suggested there was evidence to reject the null hypotheses in favour of the alternative H_1 heathland vegetation structure and habitat type influences the occurrence of specific spider species. This was true for eight out of the fifteen species where the top models included habitat type, The results demonstrate statistically significant influence of habitat structure on ten of the fifteen species analysed and the wet habitat type was significantly different than the other types in two out of the eight species where ANCOVA was performed as habitat type was included in the top models (see Table 11 & 12).

The MuMIn dredge results indicated that all thirteen of the vegetation characteristics were predictors of the probability of abundance of one or more of the species included in the analysis as they appeared in the top models. There were nine vegetation characteristics that appeared in the top models for more than half of the species analysed. These were (in order of frequency); all graminoids, all forbs, building heather, bare ground, litter layer, all shrubs, vegetation height, habitat type and SSSI condition. Out of these nine, there were three characteristics where the predictor weight was high (i.e. 0.50 to 1.00 suggesting their importance) occurring in the best models for five different species. These were; all graminoids (for *Aelurillus v-insignitus*, *Haplodrassus signifer*, *Pardosa nigriceps*, *Pardosa pullata* and *Trochosa terricola*), all shrubs (for *Alopecosa barbipes*, *Alopecosa pulverulenta*, *Mangora acalypha*, *Pardosa nigriceps* and *Zelotes latreillei*) and vegetation height (for *Alopecosa pulverulenta*, *Drassyllus praeficus*, *Dysdera erythrina*, *Pardosa pullata* and *Zora spinimana*).

From the remaining six (out of nine vegetation characteristics), there was one vegetation characteristic where the predictor weight was high (i.e. 0.50 to 1.00 suggesting its importance) occurring in the best models for four different species. This was; building heather (for *Alopecosa barbipes*, *Alopecosa pulverulenta*, *Drassodes cupreus* and *Zora spinimana*). Additionally, there were four characteristics where the predictor weight was high (i.e. 0.50 to 1.00 suggesting their importance) occurring in the best models for eight different species. These were; building heather (for *Aelurillus v-insignitus*, *Drassyllus praeficus* and *Pardosa pullata*), all forbs (for *Drassodes cupreus*, *Pardosa pullata* and *Zora spinimana*), habitat type (for *Aelurillus v-insignitus*, *Haplodrassus signifer* and *Pardosa pullata*) and SSSI condition (for *Drassodes cupreus*, *Pardosa nigriceps* and *Zelotes latreillei*). Finally, there was one characteristic where the predictor weight was high (i.e. 0.50 to 1.00 suggesting its importance) occurring in the best models for two different species. This was litter layer (for *Dictyna arundinacea* and *Haplodrassus signifer*).

There were ten species with one or more vegetation characteristics with a summed weight of 1 i.e. 100% probability of influence, as follows: *Aelurillus v-insignitus* (x1 = habitat type), *Alopecosa barbipes* (x2 = building heather and all shrubs), *Dictyna arundinacea* (x1 = litter layer), *Drassodes cupreus* (x3 building heather, all forbs and moss layer), *Haplodrassus signifer* (x3 = all graminoids, litter layer and habitat type), *Mangora acalypha* (x3 = mature heather, pioneer heather and all shrubs), *Pardosa nigriceps* (x5 = all graminoids, moss layer, pioneer heather, all shrubs and SSSI condition), *Pardosa pullata* (x6 = building heather, all forbs, all graminoids, vegetation height, habitat type and heather stage). *Zelotes latreillei* (x1 = SSSI condition) and *Zora spinimana* (x3 = building heather, all forbs and vegetation height).

The remaining species with one or more vegetation characteristics over 50% (but less than 100%) probability of influence were; *Alopecosa pulverulenta*, *Drassyllus praeficus*, *Dysdera erythrina* and *Trochosa terricola*. For *Asagena phalerata*, despite having vegetation characteristics included in the best models, the occurrence and probability of influence of those vegetation characteristics was less than 50% (predictor summed weight of 0.5) in the best models.

Subsequently, following the MuMIn dredge the examination of habitat type using ANCOVA on the best models that included habitat type, highlighted its significant influence on two out of the eight species analysed. These were *Dysdera erythrina* and *Dictyna arundinacea*. The wet habitat type was significantly different from the restored dry habitat for the species *Dysdera erythrina* (most abundant in the restored dry) and *Dictyna arundinacea* (most abundant in the wet).

A summary of the main results follows but please see Tables 9-12 and SI1 Table S4.1 as well as SI2 Tables S7-10, for the full results.

3.4.2i Analysis and subsequent ANCOVA results of the four most abundant species

For the abundance of *Pardosa pullata* the best model was the only model and included bare ground, all forbs, all graminoids, vegetation height, habitat type and heather stage (delta AICc < 2.0; see SI2 Table S7). All the variables in the top model had a weight of 1. *Pardosa pullata* in relation to the independent variables, mean percentage cover of all graminoids (ANCOVA $F(1, 23) = 16.12$, $p = <0.005$), mean vegetation height (ANCOVA $F(1, 23) = 12.60$, $p = 0.002$) and differences between habitat type (ANCOVA $F(2, 23) = 4.77$, $p = 0.018$), with Tukey tests showing differences between the wet and dry habitat types ($p = 0.040$, see Table 11 & 12) as expected as related to the higher abundance in the wet habitat type.

For *Pardosa nigriceps*, the best model included all graminoids, moss layer, pioneer heather, all shrubs and SSSI condition with Akaike weight of 0.53. The second-best model included all the same variables but with the addition of litter layer and did not differ appreciably from the best model (delta AICc: 0.253). Both all graminoids and all shrubs were positively correlated although moss layer and pioneer heather were negatively correlated with this species (delta AICc < 2.0; see SI2 Table S7). When the relative importance of each predictor was examined by summing the Akaike weights for each model where that variable appeared, all graminoids, moss layer pioneer heather, all shrubs and SSSI condition had a weight of 1, i.e. they are included in 100% of all possible models. Building heather and litter layer both had a weight of less than 0.25. Habitat type did not appear in the top models therefore no ANCOVA was conducted.

For *Mangora acalypha* the best model included mature heather, pioneer heather, all shrubs and habitat stage with Akaike weight of 0.499. The second-best model included the same variables, but without habitat stage, and did not differ appreciably from the best model (delta AICc: 0.305). Mature heather and pioneer heather were positively correlated, and all shrubs were negatively correlated with this species (delta AICc < 2.0; see SI2 Table S7). Akaike weight for mature heather, pioneer heather and all shrubs was 1.0, i.e. they are included in 100% of all possible models, see Table 11 & 12. Habitat type did not appear in the top models therefore no ANCOVA was conducted.

For *Alopecosa pulverulenta* the best model included building heather, moss layer, mature heather, pioneer heater, all shrubs and vegetation height with an Akaike weight of 0.159. The second-best model included all variables from the top model excluding mature heather and did not differ appreciably from the best model (delta AICc: 1.146). Moss layer was negatively correlated with this species with both building heather and pioneer heather positively correlated and all three appeared in six out of the nine top-ranking models. All shrubs and vegetation height appeared in eight out of the nine top-ranking models and were negatively and positively correlated with this species (delta AICc < 2.0; see SI2 Table S7). The Akaike weight for all shrubs and vegetation height was 0.92, i.e. they were included in 92% of all possible models. Moss layer had a weight of 0.74, building heather had a weight of 0.71 and pioneer heather had a weight of 0.66, all other variables had a weight of less than 0.48. *Alopecosa pulverulenta*, in relation to the independent variable of habitat type, showed no significant difference between the habitat types (ANCOVA $F(2, 25) = 2.80$, $p = 0.080$) (see Table 11 & 12).

3.4.2ii Analysis and subsequent ANCOVA results for the next three most abundant species

For *Alopecosa barbipes* the best model included building heather, moss layer and all shrubs with Akaike weight of 0.376. The second-best model included building heather, mature heather, pioneer heather, all shrubs and vegetation height and did not differ appreciably from the best model (delta AICc: 0.188). Building heather was negatively correlated and all shrubs were positively correlated with this species, both appeared in all the five top-ranking models with Akaike weight of 1.0 (delta AICc < 2.0; see SI2 Table S8). Moss layer appeared in three out of the five top-ranking models and had a weight of 0.74 while all other variables had a weight of less than 0.50. *Alopecosa barbipes* in relation to the independent variables, mean percentage cover of all shrubs (ANCOVA $F(1, 22) = 6.08$, $p=0.022$) showed significant association but there were no differences between habitat types (ANCOVA $F(2, 22) = 1.64$, $p= 0.217$) (see Table 11 & 12).

For *Haplodrassus signifer* the best model included all graminoids, litter layer and habitat type with Akaike weight of 0.664. The second-best model included all variables from the top model as well as mature heather and did not differ appreciably from the best model (delta AICc: 0.336). All graminoids, litter layer and habitat type appeared in both top-ranking models with Akaike weight of 1.0. All graminoids were positively correlated and litter layer was negatively correlated with this species (delta AICc < 2.0; see SI2 Table S8). Mature heather appeared in 1 out of the 2 top-ranking models while all the other variables had a weight of below 0.40. There were overall significant differences in the dependent variable, *Haplodrassus signifer* in relation to the independent variable, habitat type (ANCOVA $F(2, 24) = 4.93$, $p= 0.016$), but Tukey tests showed no individual differences between the habitat types ($p = >0.050$, see Table 11 & 12).

For *Drassyllus praeficus* the best model included bare ground and vegetation height which were negatively correlated, with Akaike weight of 0.145. The second-best model, which did not differ appreciably from the best model (delta AICc: 0.1), included building heather which had a negative correlation and bare ground. Bare ground appeared in eight out of the 12 top-ranking models while vegetation height appeared in seven, both always negatively correlated (delta AICc < 2.0; see SI2 Table S8). The combined Akaike weights for bare ground was 0.74 i.e. it was included in 74% of all possible models. Vegetation height had a weight of 0.62, while the other variables had a weight of below 0.50. Habitat type did not appear in the top models therefore no ANCOVA was conducted.

3.4.2iii Analysis and subsequent ANCOVA results for the next three most abundant species

For *Drassodes cupreus* the best model included building heather, all forbs, moss layer and SSSI condition with Akaike weight of 0.436. The building heather, all forbs and moss layer had negative relationships with this species. The second-best model included building heather, moss layer, all forbs only and did not differ appreciably from the best model (delta AICc: 0.201). Building heather, all forbs and moss layer appeared in all the four top-ranking models (delta AICc < 2.0; see SI2 Table S9) with Akaike weight of 1.0. SSSI condition had a weight of 0.80 while all other variables had a weight of less than 0.4. Habitat type did not appear in the top models therefore no ANCOVA was conducted.

For *Aelurillus v-insignitus* the best model included bare ground, all forbs, moss layer, all graminoids, habitat type and SSSI condition with Akaike weight of 0.301. Bare ground, moss layer and all graminoids had positive relationships with this species, while all forbs was negatively correlated. The second-best model included bare ground, all graminoids and habitat type and did not differ appreciably from the best model (delta AICc: 0.263). Habitat type appeared in all the five top-ranking models with Akaike weight of 1.0. Both bare ground and all graminoids appeared in four of the five top-ranking models (delta AICc < 2.0; see SI2 Table S9). Bare ground had a weight of 0.88, all graminoids had a weight of 0.83, all forbs had a weight of 0.47 and moss layer had a weight of 0.30. There were no significant relationships between the dependent variable, *Aelurillus v-insignitus* in relation to the independent variables, and Tukey tests did not show any differences between the habitat types ($p = >0.05$, see Table 11 & 12).

For *Dysdera erythrina* the best model included vegetation height only which had a positive relationship, with Akaike weight of 0.193. The second-best model included building heather, vegetation height and SSSI condition and did not differ appreciably from the best model (delta AICc: 0.9). Vegetation height appeared in eight of the nine top-ranking models and was always positively correlated with this species (delta AICc < 2.0; see SI2 Table S9). Vegetation height had a combined Akaike weight of 0.89, i.e. it is included in 89% of all possible models while all the other variables had a weight of less than 0.25. There was a significant relationship between the dependent variable, *Dysdera erythrina* and the independent variable, vegetation height (ANCOVA $F(1, 27) = 8.14$, $p = 0.008$), and differences with habitat type (ANCOVA $F(2, 27) = 4.64$, $p = 0.019$), with Tukey tests showing differences between the wet and restored dry habitat types ($p = 0.019$, see Table 11 & 12). This is as expected as the abundance was higher in the restored dry (10) in relation to the wet (1).

3.4.2iv Analysis and subsequent ANCOVA results for five of the most abundant species

For *Dictyna arundinacea* the best model included litter layer and all shrubs which had negative relationships and moss layer with a positive relationship with Akaike weight of 0.104. The second-best model included litter layer, mature heather and all shrubs and did not differ appreciably from the best model (delta AICc: 0.1). Litter layer appeared in all the 16 top-ranking models (delta AICc < 2.0; see SI2 Table S10). The Akaike weight for litter layer was 1.0, i.e. it is included in 100% of all possible models. Building heather had a weight of 0.47, habitat type had a weight of 0.43 while the other variables had a weight of less than 0.25. There was a significant relationship between the dependent variable, *Dictyna arundinacea* in relation to the independent variable, mean percentage cover of litter layer (ANCOVA $F(1, 23) = 5.37$, $p = 0.030$) as well as all shrubs (ANCOVA $F(1, 23) = 6.58$, $p = 0.017$). Additionally, there were significant differences between habitat type (ANCOVA $F(2, 23) = 6.0$, $p = 0.008$), with Tukey tests showing differences between the wet and restored dry habitat types ($p = 0.019$, see Table 11 & 12).

For *Zelotes latreillei* the best model included all shrubs which had a positive relationship and SSSI condition, with Akaike weight of 0.169. The second-best model included all graminoids and SSSI condition and did not differ appreciably from the best model (delta AICc: 0.04). SSSI condition appeared in all the nine top-ranking models with an Akaike weight of 1.0. All shrubs appeared in five of the nine top-ranking models (delta AICc < 2.0; see SI2 Table S10) with a weight of 0.52 while the other variables had a weight of less than 0.48. Habitat type did not appear in the top models therefore no ANCOVA was conducted.

For *Zora spinimana* the best model included building heather, all forbs and vegetation height with Akaike weight of 0.483. The second-best model included all variables from the top model plus habitat type and did not differ appreciably from the best model (delta AICc: 47.1). Building heather, all forbs and vegetation height appeared in all three of the top-ranking models with Akaike weights of 1.0 and showed positive relationships with this species (delta AICc < 2.0; see SI2 Table S10). The other variables had a weight of less than 0.30. There was a significant relationship between the dependent variable, *Zora spinimana* in relation to the independent variable, mean percentage cover of all forbs (ANCOVA $F(1, 24) = 5.73$, $p = 0.025$) although there were no significant differences between habitat type (ANCOVA $F(2, 24) = 0.95$, $p = 0.401$) (see Table 11 & 12).

For *Trochosa terricola* the best model included all graminoids with a positive relationship and Akaike weight of 0.149. The second-best model included all graminoids and moss layer which did not differ appreciably from the best model (delta AICc: 0.29). All graminoids appeared in eight of the 12 top-ranking models and pioneer heather appeared in four of the 12 top-ranking models and was also positively correlated with this species (delta AICc < 2.0; see SI2 Table S10). The combined Akaike weight for all graminoids was 0.63, i.e. it is included in 63% of all possible models. Pioneer heather had a weight of 0.29 while the other variables had a weight of less than 0.25. Habitat type did not appear in the top models therefore no ANCOVA was conducted.

For *Asagena phalerata* the best model was the intercept with Akaike weight of 0.117. The second-best model included mature heather and SSSI condition and did not differ appreciably from the best model (delta AICc: 0.57). Both mature heather and SSSI condition appeared in five out of the 15 top-ranking models and mature heather positively correlated with this species (delta AICc < 2.0; see SI2 Table S10). The Akaike weight for mature heather was 0.36, i.e. it is included in 36% of all possible models. SSSI condition had a weight of 0.33 while all the other variables had a weight of below 0.25. Habitat type did not appear in the top models therefore no ANCOVA was conducted.

Table 11 Subset of the best models (within <2AICc's) for individual species and the relative importance of each predictor (vegetation characteristics) examined by summing the Akaike weights for each model where that variable appeared

	BG	Bd	Fb	Gd	LL	Mt	ML	Pr	Sh	Vh	HbTyp	HStag	SSSICon
<i>Aelurillus v-insignitus</i>	0.88		0.47	0.83			0.30				1.00	0.12	0.42
<i>Alopecosa barbipes</i>	0.14	1.00			0.14	0.33	0.67	0.19	1.00	0.48	0.14		
<i>Alopecosa pulverulenta</i>	0.24	0.71		0.08		0.24	0.74	0.66	0.92	0.92	0.08		
<i>Asagena phalerata</i>	0.05	0.07	0.05	0.18		0.36		0.07	0.07	0.22			0.33
<i>Dictyna arundinacea</i>	0.13	0.47	0.14	0.09	1.00	0.15	0.15		0.40	0.23	0.43	0.08	0.12
<i>Drassodes cupreus</i>	0.18	1.00	1.00		0.19		1.00						0.80
<i>Drassyllus praeficus</i>	0.74	0.37		0.10	0.18				0.14	0.62			
<i>Dysdera erythrina</i>		0.21	0.08	0.10	0.11	0.13				0.89	0.11		0.16
<i>Haplodrassus signifer</i>				1.00	1.00	0.34					1.00		
<i>Mangora acalypha</i>			0.20			1.00		1.00	1.00			0.70	
<i>Pardosa nigriceps</i>		0.22		1.00	0.25		1.00	1.00	1.00				1.00
<i>Pardosa pullata</i>	1.00		1.00	1.00						1.00	1.00	1.00	
<i>Trochosa terricola</i>			0.13	0.63	0.07		0.20	0.29	0.13				0.06
<i>Zelotes latreillei</i>	0.09		0.18	0.47				0.21	0.52				1.00
<i>Zora spinimana</i>		1.00	1.00		0.22					1.00	0.29		
Total number in best models	9	9	10	11	9	7	7	7	9	8	8	4	8

Table 12 ANCOVA and Tukey results from the extracted best models of the MuMIn dredge for the most abundant species in relation to the habitat type (significant influences in bold)

	Mean Abundance for each Habitat Type			ANCOVA for Habitat Type			Tukey Pairwise	
	Dry	Restored Dry	Wet	D	F	P	Pairwise	P
<i>Aelurillus v-insignitus</i>	1.63	1.00		2	3.14	0.061		
<i>Alopecosa barbipes</i>	1.86	2.13	1.40	2	1.64	0.217		
<i>Alopecosa pulverulenta</i>	1.20	2.50	1.17	2	2.80	0.080		
<i>Asagena phalerata</i>	1.00	1.00	1.00					
<i>Dictyna arundinacea</i>	1.00		1.50	2	6.00	0.008	wet-restored dry	0.019
<i>Drassodes cupreus</i>	1.40	1.14	1.00					
<i>Drassyllus praeficus</i>	2.00	1.00	1.00					
<i>Dysdera erythrina</i>	1.00	1.43	1.00	2	4.64	0.019	wet-restored dry	0.019
<i>Haplodrassus signifer</i>	1.83	1.20	1.00	2	4.93	0.016		
<i>Mangora acalypha</i>	1.33	1.00	1.53					
<i>Pardosa nigriceps</i>	2.32	2.65	1.96					
<i>Pardosa pullata</i>	1.90	2.57	6.48	2	1.12	0.344		
<i>Trochosa terricola</i>	1.00	1.50	1.25					
<i>Zelotes latreillei</i>	1.00	1.00	1.25					
<i>Zora spinimana</i>	1.00	1.67	1.00	2	0.95	0.401		

4: Discussion

This study investigated the spiders in lowland heathland in terms of differences in their functional diversity, total and individual species abundance and their relationship with heathland structure and habitat type. In addition, it explored which variables had significant influence on these differences across thirty sites in Purbeck, Dorset. The results suggest that the vegetation structure between the sites and habitat types, especially the sites categorised as wet habitat type, were significantly different. There were significant differences in nine out of the thirteen vegetation characteristics across three of the different functional trait groups (guilds, prey capture method, web type and daily activity) as well as significant associations between traits (ground, no web, diurnal, prefer ground) and the wet habitat type. The wet habitat had a significantly higher number of spider functional traits, species richness and total abundance. The vegetation characteristics; moss layer, pioneer heather, all forbs, all graminoids and habitat type can also predict the probability of the presence of specific spider functional traits. Specific spider species were significantly influenced by vegetation structure variables of vegetation height, the wet habitat type and all graminoids. In addition, the most abundant individuals recorded had the following functional traits: ground hunter, capture of prey through pursuit, no use of a web, nocturnal and ground dwellers.

In this study, vegetation height and percentage cover of all shrubs (which includes heather stands) was significantly different between the habitat types. Wet heath had the lowest vegetation height and coverage of all shrubs, and the restored dry heath the highest. Another important finding is that the percentage cover of both pioneer heather and graminoid species was highest in the wet heath and lowest in the dry heath., potentially due to the effect of grazing being easier on dry land. With this in mind, as the heathland structure changes from pioneer (bare ground) to maturity following management, an increase in web spinning families (e.g., Dictynidae, Pisauridae, Agelenidae, Araneidae) would be expected, alongside a decrease in ground dwelling families (e.g., Gnaphosidae, Lycosidae, Zodariidae) i.e. the hunting strategy changes as the heathland matures (Merrett 1976, Pedley *et al.* 2023). This investigation found that in both the building and the mature heather stages the most predominant prey capture method trait present was the pursuit spiders and in the frequency of the web types the functional trait 'none' was the most frequent and abundant. This would be as expected due to most pursuit predators not using a web (Bee *et al.* 2020). Another finding was that the pioneer stage lacked the presence of any Specialists (Dysderidae) or Space Web Weavers (Dictynidae & Theriididae). Therefore, it seems that overall, the ground, pursuit, ambush, and specialist spider families, were low the pioneer stage of heather growth, This would be expected to occur, as the vegetation is low and more open with higher risk of predation themselves which is in accord with other studies (Avila *et al.* 2017, Bell *et al.* 1998, Canard 1990). These observations may therefore support the hypotheses that heterogeneity can maintain and stabilise ecosystem services in any given habitat (Wilcox *et al.* 2017).

Prior studies have noted the importance of vegetation structure on the spider communities present (Byriel *et al.* 2022, Maelfait *et al.* 1990, Webb and Hopkins 1984). This study found that when a variety of vegetation structure characteristics and habitat types were examined together in relation to their influence on spider functional traits, the most included influential variables were moss layer, pioneer heather, all forbs, all graminoids and habitat type. More specifically, the wet and restored dry habitats were significant factors in relation to the presence of the trait's specialists from the functional group of guilds, capture web from the functional group prey

capture method and tangled cribellate from the functional group of web type. It was not surprising to see that all forbs and moss layer had an inverse relationship with ground hunter spiders whose preferred spatial location was, as expected, on the ground. This observed correlation might be explained by the fact that the Lycosidae were the most abundant family recorded across all the habitat types and they use open spaces for predation, which were more prevalent in the wet habitat. Lyons *et al.* (2018) reported similar differences in spider assemblages between different habitat types of acid and calcareous grassland and limestone heaths in UK uplands. This was corroborated by the findings from Byriel *et al.* (2022) which looked at heathland succession, concluding that management on heathlands should contain a mix of the successional stages in order to increase invertebrate diversity. In general, it can thus be suggested that spider functional diversity could infer the effect of conservation management and restoration of heathlands.

Several reports have suggested vegetation structure plays an important role in shaping the spider communities present and discussed the implications for heathland management (Maelfait *et al.* 1990, Buchholz 2010, Dennis *et al.* 2015). One study investigating different management practices in grassland and the influence of the resulting vegetation structure on spiders, suggest that areas with a higher vegetation height were more abundant and diverse in terms of spider fauna (Gibson *et al.* 1992). Similarly, in this study, the vegetation characteristics, in relation to structure, of the mean percentage cover of all forbs and moss layer, had a negative relationship with the ground hunting trait, who's individuals were more abundant than in any other trait within the functional group of spider guilds. Ground hunting families have been found to be more abundant in areas with a low litter layer depth in forests (Uetz 1979). As expected, in this study, they were more abundant in the pioneer stage as it generally tends to have more open ground and low vegetation (up to 10cm) for hunting in. For the functional group web type there were three significant associations with the vegetation structure; the mean percentage cover of mature heather was lower for the trait 'none' than for the trait 'tangled sticky', mean percentage cover of all forb species was lower for the trait 'none' than for 'tangled cribellate' and all graminoid species was lower for the trait 'tangled sticky' than for the trait 'tangled cribellate'. Similar findings have also been documented in a study focused on habitat complexity that concluded complex habitats with tall vegetation were more likely to support spiders that construct webs and less complex structured habitats would contain more spiders that hunt on the ground (Rypstra *et al.* 1999). The results from this study were also in agreement with Urák *et al.* (2023) where the heather and plant structure influenced spider diversity. It is known that ground hunters are more likely to use open areas for capturing their prey and use areas with higher vegetation for predator protection and concealment to enable their sit and wait strategy (Langellotto and Denno 2004, DeLong *et al.* 2023). According to the findings reported here, the data does concur with and supports previous studies, and the traits present can be related to habitat structure (Popatov *et al.* 2020).

This study set out to examine the influence of habitat type and structure on spider functional traits. In recent literature, a strong relationship between the habitat type and diversity has been reported for other taxa like Coleoptera (Harry *et al.* 2022) and soil moisture also influences differences in insect communities (Wallis de Vries *et al.* 2016). In this study, an important finding is that one of the variables with the most significant relationships and influence on the presence of specific functional traits is the habitat type. In this study the most abundant functional traits in the wet habitat type were; ground hunter, pursuit, none, diurnal and ground dwellers. One unanticipated finding was that it also contained the funnel web spiders that are usually associated with gorse and heather vegetation (Bee *et al.* 2020). Another important finding is that

the wet habitat was more species rich, functionally diverse and had higher abundance of spiders compared to other habitat types. These findings may reveal something about the nature of the wet heath in relation to its structure and available prey resources. Another factor could be the proximity of the wet heath to the other habitat types and the combined heterogeneity of these habitats driving the functional response recorded. The findings broadly support the work of other studies in this area of linking response traits to phenotype (fitness) and the abundance of particular functional traits to community level impacts (Chacón-Labelle *et al.* 2023, Hacala *et al.* 2024, Langelotto and Denno 2024). The findings reported here suggest that the presence of functional traits associated with ground dwelling spiders could be an indicator of how diverse the wet heath is (Byriel *et al.* 2023), as their abundance can be related to the available prey resource (Schmitz 2006).

At an individual species level, the best models (i.e. the variable or combinations of them with a probability of influence) contained vegetation height, habitat type, all shrubs and all forbs. Surprisingly though, the top five most abundant species, classified as associated with dry habitats in previous literature, were found in all three of the habitats but were more abundant in wet or the restored dry sites. Spider species habitat preferences and the evidence of them overlapping has been stated historically on the Dorset heaths (Snazell 1982 and Merrett 1976) as well as on other habitat types like limestone (Bell *et al.* 1998) and grasslands (Hamřík *et al.* 2023). So, does this finding suggest that the species have changed their habitat preferences due to abiotic factors, climate change, the availability of suitable habitat or a specific combination of them? Habitat association change in other species has been recorded at both a local and microclimate level (Suggitt *et al.* 2015) and positive responses of invertebrates in the UK to change in climate in terms of abundance (Pateman *et al.* 2012) have also been found. Further support of this idea in relation to Aranea and response to biotic and abiotic conditions was suggested by Buchholz (2010). Spider responses to changes in climate annually and over time could have had an influence on this study as the collection period from May to June was particularly dry. In the UK, on average, May was 1.0°C and June was 2.5°C warmer (Met Office May and June 2023). Information on the meteorological conditions over time and when studies are undertaken, are important factors to consider with climate change predicting warm wet winters and hot dry summers in the UK (Met Office 2020).

Spiders have been used successfully to predict overall species richness and diversity at a landscape scale (De Mas *et al.* 2009) and they have also been used successfully as ecological indicators (Churchill T.B. 1997, Maelfait and Hendrickx 1998). A strong relationship between several species present and their potential as indicator species has previously been reported. Webb (1994) examined the differences in presence of eight heathland indicator species (used by Moore 1962) across twelve heathland sites between two time periods, 1960 and 1980-87. He concluded that developing lists of indicator species would be of use to assess heathland habitat quality and presented lists of species that could be used as indicators for Aranea, Lepidoptera, Carabids, Hemiptera and plants. This was supported by Scott *et al.* (2006), who suggest that the total number of bog specialist spider indicator species present can be an acceptable substitute for the conservation value of bog habitat. An interesting finding from the results of this study is the presence of two species, in the wet habitat type only, from that list of bog specialists, occurring in low numbers over three sites, namely *Arctosa leopardus* and *Piratula latitans*. These two species are recorded in the literature as preferring and occurring in wet habitats (Scott *et al.* 2006). These two were not included in the species-level analyses due to low numbers, however there were a total of nine out of the fifteen species analysed that would be considered bog appropriate and in the entire dataset a total of sixteen were cited as occurring

in dry habitats. This finding was unexpected and suggests that if indicator species can drift and occur across different habitat types within a landscape in a dry versus a wet year or vice versa, their presence might not actually indicate the habitat type that we think it does, rather the conditions encountered in that particular year. However, it should be noted that SSSI condition appeared in eight out of the fifteen species best models, although the probability of influence was low. These results support the work of other studies who have highlighted spiders and their potential for use as focal species as their abundance is significantly correlated with habitat structure in sand ecosystems (Buchholz 2010), in peat bogs the vertical microhabitats present can contain indicator species (Urák *et al.* 2023) and that different aged heathland contains specific related species (Byriel *et al.* 2022).

The vegetation variables with the most significant relationships and influence on the spider functional traits and species were mean percentage cover of moss layer, pioneer heather, mean vegetation height and the wet habitat type. The functional traits ground hunter, capture of prey through pursuit, no use of a web, nocturnal, and ground dwellers were the most significant and abundant in the study. The relationship between different vegetation heights and structure influencing an abundance of ground predators, concurs with other studies (Chacón-Labella *et al.* 2023, Hacala *et al.* 2024, Langellotto and Denno 2024). The presence, abundance and significance of different traits can reflect community response to environmental conditions, for example, a change in plant community or structure can be the result of changes in the abiotic environment such as light, humidity or water levels. This is reflected in this study with the direct relationship of orb-web weaver traits and the inverse relationship of ground hunter traits with the vegetation height. Chacón-Labella *et al.* (2023) have suggested an approach to trait-based ecology that this study has aspired to as well as built upon the work of Cadotte *et al.* (2011). There were more web builder types recorded in the sweep net than in the pitfalls as they are associated with a preference for occurring on vegetation and as expected, the ground dwellers are more frequently recorded and abundant in the pitfall traps. Using a combination of different sampling methods will capture different species with different functional traits which when analysed can contribute to a better understanding of how and where these communities are responding to the conservation and restoration efforts (László *et al.* 2018, Churchill and Aurther 1999, Merrett 1975). These results provide further confirmation that there is a benefit to using more than one survey technique when examining functional traits when studying invertebrates.

4.1 Limitations of this study

There was limited data on historical management methods and time periods which could have been of benefit to enable some solid conclusions on its success for maintaining and improving habitat condition for spiders and biodiversity in general. Due to unforeseen circumstance, there was an interruption to the total length of time taken for the sampling period. This has made my study truncated with the lack of early autumn species emergence and therefore this study may not be a fully representative sample of all functional traits present on the Purbeck heathlands. In terms of methods used, the combination of both pitfall and sweep net survey methods enabled a more comprehensive dataset of the functional diversity present. If the pitfall method had been used in isolation, there would have been limited functional traits recorded and potentially a challenge to reject the null hypotheses. The use of suction sampling was restricted to sites that were located near the road and therefore this has limited the dataset. The data recorded was not included as the sampling was not across all the sites and therefore not representative. As well as this, the majority of the sweep net samples contained juveniles that could not be identified to species, which excluded a comparison between the other corresponding sites. Another collection method, namely litter layer sieving, was not undertaken and there is potential that the

dataset is missing those associated species (Bultman T.L. *et al.* 1982, Bultman T.L. *et al.* 1984). Finally, my ethical consideration of pooting out only spiders and carabids from sweep samples rather than putting the sample directly into 70% ethanol may have missed some of the smaller individuals of both taxa. These factors combined may limit the knowledge of the full range of functional traits across the Purbeck Heathlands and could have strengthened the evidence base in terms of management success. The data set that has been used for the analyses also does not include the family Linyphiidae. Their identification may have added to the composition of functional traits however, all the samples have been retained for future research and reanalysis if their identification becomes possible.

4.2 Recommendations for further research

Ideally, as mentioned as limitations, the inclusion of different methods would enhance the dataset and potentially enrich the current knowledge base of the functional diversity of spiders on the Purbeck Heathlands. Consideration of pitfall protection from weather and using a mesh size that is slightly bigger would aid the capture of larger bodied spiders like species in the Agelenidae family, again enhancing the current information known on the species that are present, but there is a trade off with likelihood of capturing vertebrates such as sand lizards, which are present on the heaths. Due to the truncated sampling time in this study, I would suggest a longer sampling period (April to October) to capture a clearer picture of the spider phenology, and the inclusion of litter layer and suction sampling would likely record other spider families, increasing the knowledge of other functional traits present.

In addition to these, and in hindsight, I would consider the use of different functional traits that could help with determining the habitat complexity, quality and potential suitability for other migrant species to occupy. These could include habitat and microhabitat specificity as, for example, a specialist can suggest the stability or quality of a particular habitat or when specifically associated with litter layer an assumption of the habitat complexity could be determined. Another set of traits could be moisture and or thermal tolerance with the presence of specific species suggesting the quality of the microhabitat. Also, the inclusion of a species prey diversity (i.e. generalist or specialist) and specifics where changes in the prey available could indicate the complexity of the habitat. Furthermore, the inclusion of other taxa like coleoptera and isopods could broaden and aid the understanding of how conservation and restoration efforts affect biodiversity as a whole and can indicate habitat quality.

Finally, further study across the wider landscape of the PHNNR as well as across the Dorset Heaths could be targeted for use as a comparison of spider functional diversity recorded in 1976, 1982 and by this study in 2023. A study with a wider range of sites and potentially habitat types, with data analysis focused on differences and the change between years, might be revealing in terms of species shifts as well as habitat and climate change effects.

4.3 Implications for Conservation Management

In terms of conservation management, it is generally thought that the physical works, planning and resulting good habitat quality needs to incorporate multispecies groups in combination with indicator species (Maes and Dyck 2005). To infer if conservation and restoration management has been a success, I would suggest that further research is required over a more sustained period, however this snapshot has hopefully informed how historical and recent management approaches have the power to drive the functional diversity and resulting ecosystem services that our protected heathlands should be providing.

However, it should be noted that the benefit and effect of restoration management can only be measured over time. For spiders, the early restoration phases will support eurytopic species like some of mobile species of Lycosidae and Gnaphosidae, with typical heathland spider communities developing over time (Crisifoli 2010). Hawkes *et al.* (2020) reported the benefit of novel approaches like using scrape rotation on heathlands to mimic succession for biodiversity and some suggest that 'wilding' is random enough for systems to recover (Oyarzabal *et al.* 2023) but fragmented habitats require a balanced approach that incorporates a combination of these elements.

Ideally, the management for all sites and habitat types included in this study, would include a rotational management system, where all stages of heathland development are present on the one site at the same time. The mosaic approach to heathland management is highly recommended for our spider communities as each stage of heather growth will be the preferred habitats for their different traits and therein families. With a variety of micro habitats present encouraging such a range of spider fauna will result in a site that is both diverse and species rich.

4.4 Conclusion

The influence of heathland structure and habitat type on the functional diversity and abundance of spiders on a lowland heathland in Dorset has been demonstrated in this study by the significant relationships between specific traits and the environmental variables.

This study has highlighted the relationship and influence of heathland structure, in particular moss layer, pioneer heather, all forbs, all graminoids, vegetation height and habitat type on the presence of specific functional traits of spiders. The influence on the diversity and abundance of spider functional traits, generates additional evidence to support the importance of heterogeneity and the mosaic theory of heathland management. In addition, the wet habitat type in this study was a significant variable for specific functional traits and species present. Wet heath, with the presence of rare and or known indicator species of habitat quality recorded in the sample, suggests the diversity of spider fauna would benefit from restoration of the wet and humid areas of heathland as part of the mosaic.

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