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Habitat associations of epigeal spiders in upland calcareous grassland landscapes: the importance for conservation

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Abstract Upland calcareous grassland landscapes are typically comprised of a matrix of calcareous grassland, acid grassland and limestone heath plant communities. This matrix of habitats is produced by a combination of underlying geology, climate and management. These landscapes are typically managed through grazing, with management targeted to maintain particular plant communities in the calcareous grassland habitat, whilst patches of acid grassland and limestone heath are not targeted by conservation management. The biodiversity value of acid grassland and limestone heath patches within the calcareous grassland matrix are unknown. This study provides the first assessment of their biodiversity value by examining aspects of epigeal spider diversity supported by these non-target habitat patches in comparison to calcareous grassland. Spiders were sampled in each habitat from April to August 2014 using pitfall traps across three upland regions in Great Britain. Spider species assemblages were distinct between limestone heath and both grassland types. Distinction in species assemblages are likely due to differences in vegetation structure and microclimate, e.g., humidity, degree of shade. Each habitat type supported several rare species (e.g., *Jacksonella falconeri*, *Agyneta subtilis*) revealing the contribution

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to spider fauna. The distinct spider species assemblage and presence of rare species in limestone heath patches demonstrate their importance in the upland calcareous grassland matrix. This study highlights the value of monitoring biodiversity in non-target habitats within a habitat matrix alongside those that are actively targeted by management.

Keywords Heath · Acid grassland · Limestone · Calcareous grassland matrix · Grazing · Grassland management · Conservation

Introduction

Calcareous grassland, considered among the most species rich and diverse habitats for many species groups in Europe, underwent wide scale loss and degradation following post 1950s agricultural intensification and as such has become the focus of conservation efforts (Willems 2001; Fischer and Stocklin 1997; Poschlod et al. 2005; Poschlod and Wallis de Vries 2002; Roesch et al. 2013; Wallis De Vries et al. 2002). Afforded protection under Annex I of the EU habitats directive, an estimated 595, 973 ha is protected in the Natura 2000 network across EU member states (Calaciura and Spinelli 2008). Their management typically aims to maintain particular plant communities through prevention of succession and domination by one or few species (Willems 2001; Wallis de Vries et al. 2002).

In upland regions of the UK, high stocking densities of sheep were implicated as a major cause of habitat deterioration and the decline of associated plants, invertebrates and birds (Dennis et al. 2008; Fuller and Gough 1999). In an attempt to conserve the characteristic vegetation of rare upland calcareous grassland, which covers just 0.1% (22,000–25,000 ha) of total UK land cover (calculated from Maddock 2008; DEFRA 2013), there has been a reduction in stocking levels within the last decade.

Upland calcareous grassland landscapes are typically comprised of a matrix of calcareous grassland, acid grassland and limestone heath plant communities. This matrix of habitats is produced by a combination of underlying geology, climate and grazing management (Rodwell 1992; Rodwell et al. 2007). Thin, well drained, lime rich soils found on limestone bedrock provide suitable conditions for calcareous grassland (Rodwell et al. 2007; Joint Nature Conservation Committee 2007). Superficial deposits of glacial till or loess among the thin soil overlying the limestone bedrock produce patches of plant communities within the calcareous grassland which are dominated by calcifuge species (Rodwell 1992; Dixon 1982). Under reduced intensity sheep grazing, these patches are either maintained as acid grassland (dominated by *Nardus stricta*) or develop into the climax community of limestone heath [EC Habitats Directive Annex 1 (Joint Nature Conservation Committee 2013)]. The selective grazing behaviour of sheep results in particular vegetation patches experiencing different effective stocking densities (Dennis et al. 2015; Grant et al. 1985). At low stocking densities sheep restrict grazing to vegetation patches containing preferred plant species resulting in effectively ungrazed patches of less preferred vegetation (Hester and Baillie 1998).

Little is known about the biodiversity value of these habitat patches in the calcareous grassland matrix. While the calcareous grassland itself is recognised as a priority habitat for conservation and targeted by conservation management, the value of patches of limestone heath and acid grassland in the grassland matrix is often overlooked, and not targeted by management, despite the former being included under Annex 1 of the EC Habitats Directive (Joint Nature Conservation Community 2013). Such habitats outside of the

calcareous grassland matrix are known to support distinct plant and animal assemblages (Dennis et al. 2001; Littlewood et al. 2006).

Spiders play an important role in the functioning of all ecosystems, occupying an important role in terrestrial food webs as both predators and prey (Turnbull 1973; Uetz 1991). They encompass a wide range of foraging strategies and as such are differentially sensitive to variations in vegetation architecture and disturbance (Barriga et al. 2010; Dielh et al. 2013; Gibson et al. 1992). Differences in foraging strategies are linked to vegetation structure and disturbance (Alderweireldt 1994; Bell et al. 2001; Uetz 1991). Ground hunting species require a heterogeneous sward of open patches to search for prey and taller vegetation for refuge (Maelfait and De Keer 1990), whereas orb web weaving spiders select structurally complex vegetation that provides increased web anchorage points (Dielh et al. 2013; Langellotto and Denno 2004; McNett and Rypstra 2000). The differences in foraging strategy, activity and substrate utilisation amongst species make grouping spiders into guilds a useful tool for examining functional differences among habitats (Corcuera et al. 2015; Schweiger et al. 2005). It would be expected that the contrasting structure and differences in relative stocking densities of the non-target habitats in the calcareous grassland matrix will impact both potential niche availability and microclimate, e.g., humidity and temperature stability, thus providing conditions suited to different species or hunting guilds.

Furthermore, spider diversity correlates with total arthropod diversity over a wide range of cultivated habitats in Central Europe (Duelli and Obrist 2003). Thus, their ecological requirements and relationship with other taxa make them a useful group for studying differences in diversity among contrasting habitat types.

This study is the first to investigate the biodiversity value of non-target habitats within the upland calcareous grassland matrix, using spiders as a model group. Specifically, it will ask:

1. How do spider assemblages differ among habitats in the upland calcareous grassland matrix?
2. How does the proportion of functional guilds, measured by hunting strategy, differ among habitat types in the matrix?
3. Do non-target habitats support species of conservation interest?

Methods

Study sites

Three sites of extensive areas of calcareous grassland (size 35–525 ha, median 76 ha) were selected for study across geographically distinct regions separated by 14–48 km in Northern England (54°29′44.41″N, 002°33′20.03″W) (54°09′03.76″N, 002°06′00.29″W) (54°08′44.37″N, 002°19′17.54″W). Each study site was under the same management of sheep grazing with a stocking intensity of < 0.24 LU ha^{-1} year^{-1} that had been in place for a minimum of 10 years prior to study. Elevation ranged from 213 to 383 m, median 355 m. Soil across the sites was generally base rich with some deposits of glacial till and peat resulting in each site containing three habitat types: a matrix of calcareous grassland, targeted by conservation management, along with scattered patches of *Nardus stricta* grassland and limestone heath, both non-target habitats. The habitats were defined as: calcareous grassland which had a species rich sward with a mean sward height of 8.09 cm over

the sampling period, limestone heath which occurred in patches exceeding 20 m^2 and was dominated by mature stage *Calluna vulgaris*, and acid grassland which was dominated by *N. stricta*, and again occurred in patches exceeding 20 m^2. In addition, though vegetation height in acid grassland and heath was not measured there was an observable distinction, the latter was taller with the canopy always exceeding 30 cm. Further, the ground layer of heath largely lacked vegetation, instead having a covering of heather litter. In contrast, both the calcareous grassland and acid grassland had a well-developed ground layer, with the acid grassland having dense tufts of *N. stricta*.

Three representative samples of each habitat type were selected as replicates at each study site. Each habitat replicate was spaced a minimum of 51 m (median 226 m) from other replicates to ensure statistical independence of samples (Digweed et al. 1995), and a minimum of 50 m away from disturbance, e.g. footpaths, water troughs, etc. Spatial independence of samples was confirmed with Moran's I based on nearest neighbour distances for all 27 locations for spider abundance (Moran's I $\pm$ SD: -0.06 ± 1.14, p = 0.87) (Bivand et al. 2014). Within each site, collections of epigeic spiders were conducted between May and August 2014.

Epigeal spider sampling

Within each habitat replicate, six pitfall traps, spaced 2 m apart, were established to capture epigeal spiders. Traps consisted of a plastic cup approximately 7 cm in diameter and 9 cm deep and covered with a square plastic lid suspended 1 cm from the ground by pegs to prevent rain water and debris from entering. These were filled to 1 cm depth with propylene glycol to act as a killing and preserving agent. To prevent traps being trampled or interfered with by livestock each trap was protected by a secured cage made from 2.5 cm × 2.5 cm gauge mesh. These cages do not affect the trapping rates of ground-dwelling invertebrates (Oxbrough et al. 2012). Where traps were set in patches of acid grassland or limestone heath they were placed in the centre of the patch, where they were set in calcareous grassland they were placed a minimum of 50 m from other habitat types. Traps were set between 05/05/2014 and 21/08/2014 and were changed every 21 days, giving a total of 105 trap days. Samples from five of the traps within each location were pooled for analysis, with the sixth kept as a spare in case of trap loss.

Pitfall traps are a widely used sampling method to catch active ground dwelling invertebrates in grasslands and heathlands (Gardner et al. 1997; Haysom et al. 2004; Lyons et al. 2017). This method estimates relative invertebrate activity rather than an absolute measure of density, reflecting species abundance and movement rates (Greenslade 1964; Mazia et al. 2006). Consequently, they are less likely to capture sedentary species or those occupying higher levels of vegetation. Nevertheless, their high catch rate, ease of setting up and objectivity render their use appropriate in large scale studies with multiple sites (e.g., Oxbrough et al. 2012; Taboada et al. 2010; Niemela et al. 1993).

All adult spiders were identified to species level using Roberts (1993) and nomenclature follows World Spider Catalogue (2017). Since it was not possible to reliably identify most juvenile species these were excluded from the study. Information on conservation status was gathered from Dawson et al. (2008). Spider reference specimens are housed at the Edge Hill University Department of Biology arthropod collection.

Spider hunting guilds

Following identification to species, spiders were separated into five guilds based on hunting strategies suggested by Cardoso et al. (2011): sheet web weavers, ground hunters, space web weavers, ambush hunters and other hunters. However, whilst Cardoso et al.'s (2011) classification includes *Pachygnatha degeeri* as an orb web spinner, in this study since only adult specimens were identified, it is placed in the ground hunter guild in recognition of its active hunting strategy as an adult. The list of spider species and associated guilds is included in Online Resource 1.

Data analysis

Five of the pitfall traps in each habitat replicate were pooled across the full sampling period. To account for differences in trapping effort all samples were standardised to trap day by calculating the abundance of each species at each location and dividing it by the number of actual trap days at that location and then multiplying it by the maximum number of trap days across all locations (105), a standard method used in studies using pitfall trapping (Bergeron et al. 2013; Blanchet et al. 2013: Pinzon et al. 2013).

Statistical analyses were carried out with R statistical software (version 3.2.0.) (R Development Core Team 2016) and EstimateS (version 9.1.0) (Colwel 2013).

Raw spider species data (not standardised by trap day) was used to examine differences in species richness among habitats using sample based rarefaction calculated using EstimateS, version 9.1.0 (Colwel 2013) with rarefaction curves produced in R and scaled by the number of individuals. This technique accounts for differences in sampling effort by standardising species richness for the number of individuals within a sample. Rarefaction estimates the number of species expected in a random sub-sample extracted from a larger sample (Chao 2005; Magurran 1988, 2004).

Differences in spider abundance among habitat types were examined with generalised linear mixed models (GLMMs) performed with negative binomial errors using the glmer function of the lme4 package (Bates et al. 2015). Habitat was modelled as a fixed factor with region modelled as a random factor. Negative Binomial errors were used to combat overdispersion of Poisson errors (dispersion = 43.82) (Thomas 2017). The model was tested for significance using the Anova function of the Car package (Fox and Weisberg 2011) and post hoc Tukey pairwise comparisons were used to test for differences among habitat types, correcting p values for multiple comparisons with the Holm method using the glht function of the multcomp package (Hothorn et al. 2008).

The proportion of each hunting guild among habitats was compared using GLMMs computed with Binomial errors. Habitat was modelled as a fixed factor and region modelled as a random factor. GLMMs were computed for ground hunters and sheet web weavers. Space web weavers, ambush hunters and other hunters were not examined in this way as the abundance of each group was too small and contained too many zero observations. Each model was tested for overdispersion of Binomial errors (dispersion: ground hunters = 14.69; sheet web weavers = 9.77). To correct for overdispersion, observation level random effects were included in the overall model (Harrison 2014). Bonferonni correction was applied to the confidence intervals to account for the multiple testing of the abundance data (e.g., split into five guilds). However, as the number of individuals was not divided equally among the five guilds the confidence intervals at which statistical significance was determined using the Bonferonni correction were not set at equal (e.g., 0.05/5) but rather

as the proportion that each guild comprised of the data set (required confidence intervals to infer significance: ground hunters < 0.02; sheet web weavers < 0.028) following Neuwald and Green (1994). GLMM model outputs are included in Online Resource 2.

Spider species composition was examined through Redundancy Analysis (RDA) computed on Hellinger transformed spider species data using the RDA function in the vegan package in R (Oksanen et al. 2016). Habitat was included as the main term in the model with region included as a random factor. Permutation test, with 9999 permutations, was used to test final significance of the model.

Beta diversity (β), defined as variability in spider species composition (Anderson et al. 2006), among habitats was quantified using the betadisper function in the vegan package in R (Oksanen et al. 2016), followed by permutation test (999 permutations) to test for significance. Betadisper measures β diversity by assessing the variability in average distances from the group centroid among individual sampling units (Anderson et al. 2006). The analysis was conducted on spider species data transformed into a dissimilarity matrix calculated with the Simpson dissimilarity index (bsim) (Koleff et al. 2003). Simpson dissimilarity index is appropriate for use in this instance as it measures differences in species composition independent of richness gradients (Baselga 2007; Koleff et al. 2003). The dissimilarity matrix is presented graphically in a principal coordinate analysis (PCoA) plot based on group centroids.

Significant associations of spider species with each habitat type were determined using indicator species analysis (Dufrene and Legendre 1997) using the indval function of the labdsv package (Roberts 2015). Indicator Species Analysis produces indicator values between 0 and 1, a value of 1 represents a perfect indicator that is always present in a particular treatment and is exclusive to that treatment (McCune et al. 2002). Significance of indicator values was assessed using a Monte Carlo randomisation procedure with 4999 iterations. Significant indicator values infer species associations with each habitat type as a mechanism to characterise habitat use by spiders.

Results

A total of 12,878 individual spiders from 89 species were collected. 4066 (31.57% of overall abundance) of these were juveniles and 103 (0.80%) were damaged specimens. Neither of these groups could be identified and were therefore omitted from the data set. A total of 8709 individuals from 89 species of nine families representing five hunting guilds were included in the following analyses. A full list of species is given in Online Resource 1. Overall, only three species individually made up more than 5% of the total spider abundance, together totalling 29% of the overall catch: *Pardosa pullata* (14.13%), *Pachygnatha degeeri* (8.24%) and *Silometopus elegans* (6.88%).

Spider diversity

Rarefaction curves showed that spider species richness did not differ among habitats (Fig. 1), as indicated by the overlap in confidence intervals. Spider abundance was different among habitats ($\chi^2_{2,N=27} = 9.69$, p < 0.01), with greater abundance in acid grassland and calcareous grassland compared with heath (z = 2.65, p < 0.05; z = 2.71, p < 0.05 respectively) (Fig. 2).

Fig. 1 Sample based rarefaction curves scaled by the number of individuals, indicating spider species richness. *A* acid grassland, *C* calcareous grassland, *H* heath. Grey bars indicate 95% confidence intervals
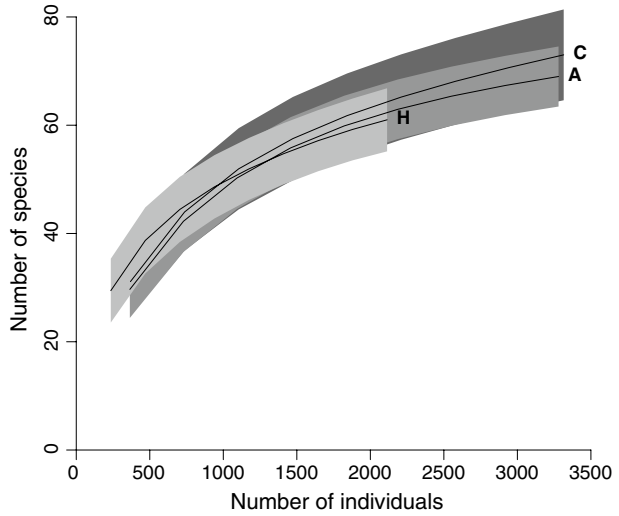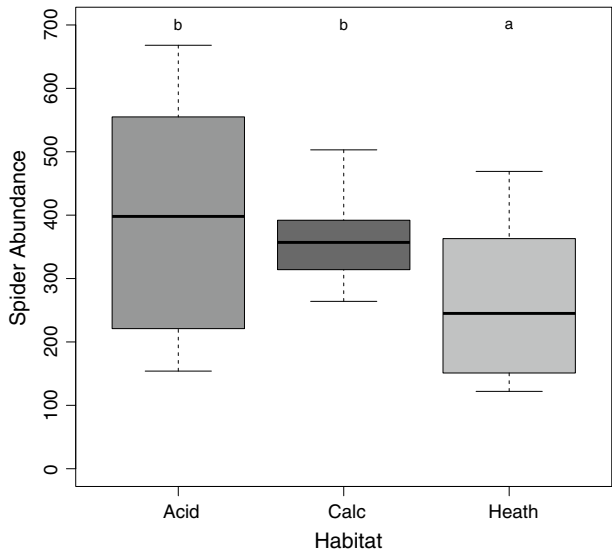

Fig. 2 Spider abundance among habitat types. The letters indicate significance of post hoc Tukey test, where letters are different this indicates a significant difference (p < 0.05)

How do spider assemblages differ among habitats in the calcareous grassland matrix?

Spider species assemblage differed significantly among habitats ($F_{2,22}$ = 5.40, p = 0.001) which accounted for 26.32% of the variability in the overall model. The conditional variable of region accounted for 20.08% of the variability in the overall model. The first two RDA axes accounted for 32.92% of the variation in the model after the contribution of region was removed (Fig. 3). The removal of region enables the comparison of habitat types without the effects of unmeasurable variables which are a product of regional

Fig. 3 RDA of spider assemblage by habitat type. Region partialled out. Variation in the model represented by RDA1 was significant ($F_{1,22} = 8.77$, p = 0.001) whilst RDA2 was not significant ($F_{1,22} = 2.03$, p = 0.081). Circles = calcareous grassland, triangles = acid grassland, squares = heath
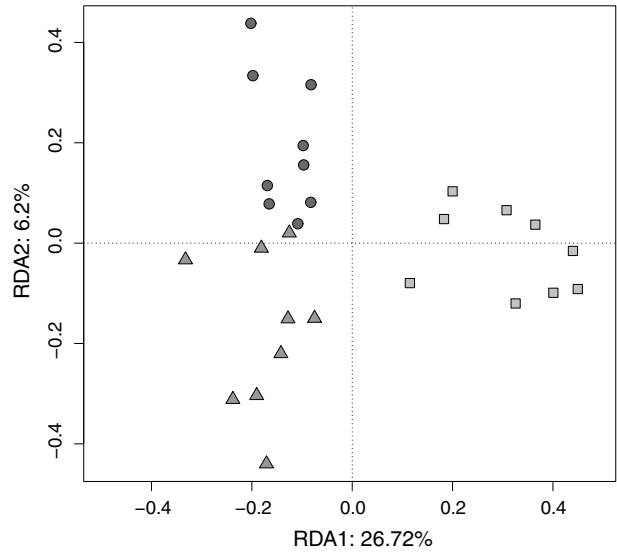
variation. The contribution of RDA axis one to the variation in the model was significant ($F_{1,22} = 8.77$, p = 0.001) and represents a separation of heath from both acid grassland and calcareous grassland (Fig. 3). RDA2 distinguishes acid grassland from calcareous grassland, however, this axis was not significant ($F_{1,22} = 2.03$, p = 0.081).

β diversity was significantly different among habitat types ($F_{2,24} = 4.95$, p = 0.02). Significant differences were found in the pair wise comparisons of the habitats acid grassland and heath (p = 0.043), and calcareous grassland and heath (p = 0.008), but not calcareous grassland and acid grassland (p > 0.05). The PCoA plot (Fig. 4) shows greater spread of

Fig. 4 Principal coordinate analysis plot showing average dissimilarity from individual observations to their group centroids. *H* heath, *A* acid grassland, *C* calcareous grassland. Permutation test: Heath—acid grassland p = 0.04, heath—calcareous grassland p = 0.004, acid grassland—calcareous grassland p = 0.54
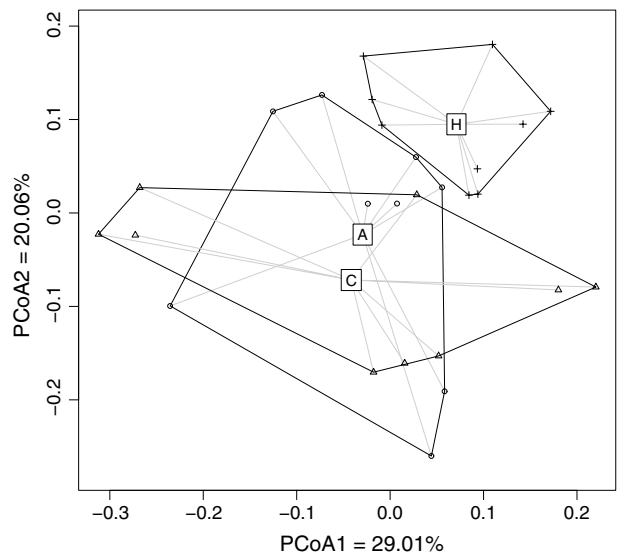
points around the centroid in both acid grassland and calcareous grassland along both axes compared to heath, indicating they have greater β diversity.

How does functional diversity, measured by hunting strategy, differ among habitat types in the matrix?

The most abundant guild was sheet web weavers (5233 individuals, 56.03%), then ground hunters (3783 individuals, 40.51%), other hunters (166 individuals, 1.78%), space web weavers (100 individuals, 1.07%) and ambush hunters (58 individuals, 0.62%).

The proportion of sheet web weavers was significantly different among habitats ($\chi^2_{2,N=27} = 77.44$, p < 0.028) (based on Bonferroni corrected p values) and was driven by a greater proportion in calcareous grassland compared to acid grassland (z = 3.46, p < 0.001) and a greater proportion in heath compared to acid grassland and calcareous grassland (z = 8.75, p < 0.001; z = 5.40, p < 0.001 respectively) (Fig. 5). The proportion of ground hunters was also significantly different among habitats ($\chi^2_{2,N=27} = 52.84$, p < 0.001) with a greater proportion in acid grassland compared to calcareous grassland and heath (z = 0.57, p < 0.01; z = 1.57, p < 0.001 respectively) and a greater proportion in calcareous grassland compared to heath (z = 1.01, p < 0.001) (Fig. 5).
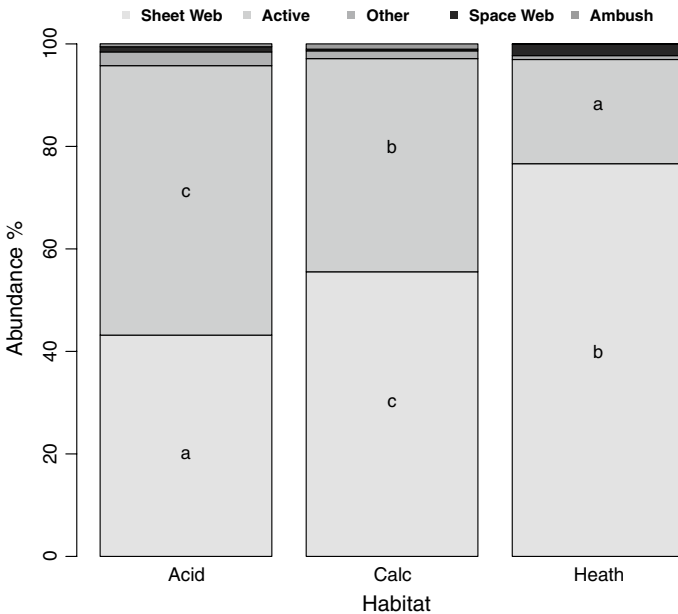

Fig. 5 The proportion that each spider hunting guild makes up in each habitat type. The letters indicate significance of post hoc Tukey test within each guild; where letters are different this indicates a significant difference (p < 0.05) in a guild's proportional abundance among the habitat types. *Sheet Web* sheet web weavers, *Active* ground hunters, *Other Hunter* 'other' hunter, *Space Web* space web weavers, *Ambush* ambush hunters

Do non-target habitats support species of conservation interest?

Indicator species analysis revealed a total of three species associated with acid grassland, four with calcareous grassland and eight associated with heath (Table 1). All three species associated with acid grassland were from the sheet web weaver guild, two of which have a preference for damp habitat conditions. Three of the four species associated with calcareous grassland were from the sheet web guild, including *Jacksonella falconeri* which is classified as endangered by Dawson et al. (2008). All three species have preferences for grassland habitats. The fourth species associated with calcareous grassland belongs to the ground hunter guild and is a generalist species. Of the eight species associated with heath, six were from the sheet web guild, including *Agyneta subtilis* which is classified as vulnerable by Dawson et al. (2008). The further two associated species were from the ground hunter and space web weaver guilds. With the exception of *Walckenaeria acuminata*, all species associated with heath have a known preference for woodland or heathland (Table 1).

Assessment of conservation status according to Dawson et al. (2008) revealed two endangered species: *J. falconeri* (17 individuals) and *Porrhomma egeria* (2 individuals), and six vulnerable species; *A. subtilis* (274 individuals); *Walckenaeria dysderoides* (4 individuals); *Allomengea scopigera* (3 individuals); *Trichopternoides thorelli* (2 individuals); *Walckenaeria inscisa* (1 individual) and *Walckenaeria monoceros* (1 individual) (Table 2).

Discussion

How do spider assemblages differ among habitats in the calcareous grassland matrix?

This study found distinct spider species assemblages between heath and both grassland habitat types, the latter not differing from each other. Additionally, despite there being no difference in species richness, β diversity was greater in both grassland habitat types compared to heath, though again the former did not differ from each other. This indicates that spider species assemblage is driven by turnover of species (both losses and gains) and is not simply a product of recruitment of species, as was also recognised by Dennis et al. (2015) and van Klink et al. (2013) in grasslands under varying management intensities.

Indeed, the differences in species assemblage are likely a result of contrasting habitat structure, which is known to impact spiders (Bell et al. 2001; Morris 2000; Uetz 1991). There is considerable variation in the structure of grasslands and heathlands (García et al. 2010). In the present study, though heath had greater overall vegetation height than the grassland habitats, the ground layer was denser in the latter resulting in greater structural complexity at the ground level in grasslands (personal observation). Indeed, increased structural complexity provides increased potential for niche differentiation (Woodcock et al. 2009). In structurally complex swards containing a full range of phenological structures there is increased potential for resource utilisation for phytophagous prey taxa (Denno 1980; Woodcock et al. 2009; Morris 2000), and greater abundance than in structurally less complex swards (Dennis et al. 1998, 2008). Further, as structural complexity increases, the availability of niches suitable for the construction of different types of webs also increases (Bell et al. 2001; Robinson 1981; Woodcock et al. 2009).

Table 1 Spider species associated with habitat type

Species	Family	Conservation status	Hunting guild	Habitat association	Habitat preference	Indicator value
Walckenaeria vigilax	Linyphiidae	LC	SW	Acid grassland	Moss and grass in wet areas	0.616**
Micrargus herbigradus	Linyphiidae	LC	SW	Acid grassland	Moss, leaf litter, detritus in grassland/woodland/heathland.	0.552*
Walckenaeria antica	Linyphiidae	LC	SW	Acid grassland	Dry woodland litter or moist litter where *W. alticeps* is absent. Aeronaut	0.513*
Hahnia nava	Hahniidae	LC	SW	Calcareous grassland	Moss and other low vegetation and amongst stones	0.711***
Tiso vagans	Linyphiidae	LC	SW	Calcareous grassland	Moss, grass grasslands, wet moorland, heather. Aeronaut	0.683**
Jacksonella falconeri	Linyphiidae	EN	SW	Calcareous grassland	Calcareous grassland, open stony areas of heathland. Uncommon. In decline	0.510*
Trochosa terricola	Lycosidae	LC	GH	Calcareous grassland	Wide range of habitats including: grassland/woodland/heath	0.503*
Tenuiphantes zimmermanni	Linyphiidae	LC	SW	Heath	Woodland/heath.	0.849***
Ceratinella brevipes	Linyphiidae	LC	SW	Heath	Variety: woodland/mature heathland	0.670**
Peponocranium ludicrum	Linyphiidae	LC	SW	Heath	Mature heathland/unimproved grassland	0.666***
Pardosa nigriceps	Lycosidae	LC	GH	Heath	Heathlands/woodlands/grasslands. Partly arboreal	0.647**
Agyneta subtilis	Linyphiidae	VU	SW	Heath	Woodland/mature dry heath	0.629**
Walckenaeria acuminata	Linyphiidae	LC	SW	Heath	Ground zone of almost any habitat	0.610**
Pelecopsis mengei	Linyphiidae	LC	SW	Heath	Ericaceous shrubs	0.571*
Robertus lividus	Linyphiidae	LC	SP	Heath	Woodland/high moorland	0.523*

Indicator species analysis produces an indicator value between 0 and 1, with values closest to 1 signifying a perfect indictor (always present in a particular treatment and exclusive to that treatment). Hunting guilds were gathered from Cardoso et al. (2011). Conservation status was gathered from Dawson et al. (2008) and habitat associations from Harvey et al. (2002)

GH ground hunter, *SW* sheet web weaver, *SP* space web weaver

*p < 0.05; **p < 0.01; ***p < 0.001

Table 2 Spiders of conservation importance with abundance in each habitat type

Species	Guild	Family	Conservation status	Habitat preferences	Acid grassland	Calcareous grassland	Heath
Jacksonella falconeri	SW	Linyphiidae	EN	Calcareous grassland, open stony areas of heathland. Uncommon. In decline	2	13	2
Porrhomma egeria	SW	Linyphiidae	EN	Cavernicolous. Ecology relatively unknown	0	0	2
Agyneta subtilis	SW	Linyphiidae	VU	Woodland/mature dry heath	19	91	164
Allomengea scopigera	SW	Linyphiidae	VU	Wet grasslands and dry heathland	0	0	3
Trichopternoides thorelli	SW	Linyphiidae	VU	Ground level, moss and grass. Damp areas	2	0	0
Walckenaeria dysderoides	SW	Linyphiidae	VU	Heathland, open stony areas. Also on calcareous grassland	0	2	2
Walckenaeria incisa	SW	Linyphiidae	VU	Calcareous grassland, heathland	0	1	0
Walckenaeria monoceros	SW	Linyphiidae	VU	Pioneer of burned heathland. Also under stones in open habitats	0	1	0

Hunting guilds were gathered from Cardoso et al. (2011). Conservation status was gathered from Dawson et al. (2008) and habitat associations from Harvey et al. (2002)

How does the proportion of functional guilds, measured by hunting strategy, differ among habitat types in the matrix?

Overall, differences of the proportions of hunting guilds among habitat types likely reflect habitat structural differences. The dominance of sheet web weavers in heath and the significantly reduced proportion of ground hunters compared to the grassland habitats reflects differences in ground level vegetation structure, differences in microclimate and shade. Differences of shade among heath and grasslands habitats is highlighted by the much lower abundance of *Xysticus cristatus*, a shade intolerant ambush hunter which is rare in woodlands and closed canopy habitats (Spider and Harvestman Recording Scheme 2017). This is further reflected by all but one of the species associated with heath having a habitat preference for woodland or heathland, six of which occupy the ground zone, often casting webs close to the ground, e.g., *Peponocranium ludicrum* (Harvey et al. 2002). The single heath associated species without a particular preference for woodland or heathland, *Walckenareia acuminata* is a habitat generalist, but again occupies the ground zone (Harvey et al. 2002).

The greater proportion of ground hunters in grassland habitats reflects the crucial role of refuges within the sward, such as those of tussock forming grasses, in habitat suitability for ground dwelling predators (Woodcock et al. 2009; Maelfait and De Keer 1990). For example, *Trochosa terricola*, associated with calcareous grassland in the present study, utilises tufts of *Festuca ovina*, the second most abundant plant species in these upland calcareous grasslands (Lyons et al. 2017). Further, in both grassland habitats the ground hunter guild was dominated by *Pardosa* species, a genus known to also utilise different components of vegetation structure for prey capture, overwintering and refuge from predators (Bristowe 1958; Maelfait and De Keer 1990). In contrast, the ground layer of the heather lacked the structural heterogeneity of the grassland habitats and is reflected by the lower proportion of ground hunters. Indeed, *Pardosa nigriceps*, the ground hunter associated in this study with heath, is a semi arboreal species (Vlijm and Kessler-Geschiere 1967) able to utilise the contrasting structural complexity of the mature heather and as such is not as reliant on ground vegetation heterogeneity as other species in the *Pardosa* genus.

The reduced proportion of sheet web weavers in acid grassland compared to calcareous grassland was seemingly replaced by a greater proportion of active hunters, notably due to the greater abundance of *Pachygnatha degeeri*. McFerran et al. (1994) and Maelfait and De Keer (1990) found *P. degeeri* was an indicator species of less intensively managed sites. Their greater abundance in acid grassland in the current study may reflect the lower effective stocking density in this habitat type, which is a product of sheep grazing behaviour. Sheep are preferential grazers, able to select preferred plant species within a sward (Grant et al. 1985). Where preferred vegetation is available sheep avoid *N. stricta* (Grant et al. 1985), the dominant species in the acid grassland habitat. This likely results in a lower effective stocking density in the acid grassland habitat compared to the calcareous grassland, thus providing suitable conditions for *P. degeeri*.

Do non-target habitats support species of conservation interest?

Both calcareous grassland and the non-target habitats of acid grassland and heath supported several notable species. Though some of these species were rare in the dataset (occurring as doubletons and singletons), making it difficult to make specific habitat determinations,

this study provides the first evidence of the importance of these landscapes for supporting rare species and highlights the need for further monitoring and research.

Jacksonella falconeri, found in each habitat type (total of 17 individuals) but most abundantly in calcareous grassland (13 individuals), is classed as endangered in Britain (Dawson et al. 2008) (Table 2), and has shown a steep decline over the last 20 years (Spider and Harvestman Recording Scheme 2017). Threats to this species include degradation and loss of calcareous grassland and heathland (Spider and Harvestman Recording Scheme 2017). The close proximity of these two habitat types in the present study may be beneficial for its long-term conservation.

Calcareous grassland also supported four species classed by Dawson et al. (2008) as vulnerable in Britain: *A. subtilis*, *W. dysderoides*, *W. incisa* and *W. monoceros*, the latter two represented exclusively in this habitat by single individuals (Table 2). *W. monoceros*, which occurs under stones in open inland habitats (Harvey et al. 2002) and is also identified as a pioneer species of heather (Merrett 1976), has also previously been recorded in calcareous grassland (Spider and Harvestman Recording Scheme 2017). It has experienced steep decline in Britain over the last 20 years, with both the loss of heathland and the lack of management to maintain early successional stages implicated in this decline (Spider and Harvestman Recording Scheme 2017). *W. dysderoides*, which was found in calcareous grassland and the non-target habitat of heath in the present study, is an uncommon species found in heathland, woodlands and both acid and calcareous grasslands (Harvey et al. 2002). The loss of calcareous grassland and heath have been recognised as potential causes of its long-term decline, though understanding of its ecology remains relatively unknown, rendering it difficult to appreciate the mechanisms of its decline (Spider and Harvestman Recording Scheme 2017).

There were a further two vulnerable species recorded in the non-target habitat of acid grassland (Table 2): *A. subtilis* and *T. thorelli*, the latter represented exclusively in this habitat by two individuals.

In heath two individuals of *P. egeria*, classed as endangered in Britain (Dawson et al. 2008), were recorded (Table 2). *P. egeria* is predominantly a cavernicolous species which usually occurs in low numbers (Harvey et al. 2002) and is noted as having suffered a 70% decline (Spider and Harvestman Recording Scheme 2017).

In addition to the endangered species mentioned, heath also supported three species classed by Dawson et al. (2008) as vulnerable (Table 2); *A. scopigera* which was again exclusive to this habitat, *W. dysderoides* and *A. subtilis*, the latter of which occurs in greater abundance in this habitat (164 individuals) compared to each of the grassland habitat types (acid grassland = 19 individuals; calcareous grassland = 91 individuals). *A. subtilis* has been noted as maintaining high densities in mature heather of dry heath after burning (Merrett 1990). Its comparatively high abundance in heath in the present study again highlights the importance of this habitat type in the calcareous grassland matrix.

Conservation implications

The absence of targeted management of heath patches within the upland calcareous grassland matrix, coupled with the low stocking density of sheep, results in them being relatively undisturbed. Consequently, they support a distinct spider assemblage and a number of notable species. It is suggested therefore, that management recommendations consider the full spectrum of the species pool and their ecological requirements. To this effect,

the current study greatly improves our understanding of rare species and their ecological needs.

Whilst it is acknowledged that due to rarity of some species in this study (doubletons and singletons) specific habitat associations cannot be determined, they do occur in the landscape and as such it is still incumbent to consider their presence in these areas. For example, prior to this study just 85 individual *P. egeria* had been recorded in Great Britain since 1894 (Spider and Harvestman Recording Scheme 2017). Consequently, little is known about its ecological requirements or life history, rendering it difficult to make conservation management recommendations despite their endangered status. It is therefore strongly recommended that rare species such as these are targeted for study in these non-target microhabitats using a range of sampling techniques to discern if they have established populations and what their ecological requirements are. Developing such an understanding will enable recommendations on management practices to enhance conservation efforts to be made.

Further, though this study targeted active epigeal species it is acknowledged that some species may also be found in the higher vegetation layers or will be sedentary. It is unknown how these respond to different habitat patches, although research has shown high congruence between ground dwelling and higher vegetation living spiders in terms of changes in biodiversity between habitats (Oxbrough et al. 2009). Despite this, pitfall trapping is a well-used and robust method for sampling ground-active spiders, rendering the management recommendations presented here an important first step for the conservation of spiders in this important landscape.

Conclusions

The importance of the calcareous grassland habitat mosaic has been demonstrated in this study by the distinct species assemblages between heath and the grassland habitats and by the different proportion of guilds in these assemblages.

This study highlights the value of monitoring biodiversity in non-target habitats within a habitat matrix alongside those that are actively targeted by management. Understanding which species occur within these non-target habitats and their ecology is vitally important in making management decisions. Integrating research outputs into conservation management decisions is vital and further research into the overall biodiversity value of these non-target habitats within the calcareous grassland matrix is urged.

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