



UK Centre for  
Ecology & Hydrology

# Temporal trends in spider communities at the UK Environmental Change Network Cairngorm field station, 2007-2019

## Data Analysis Report

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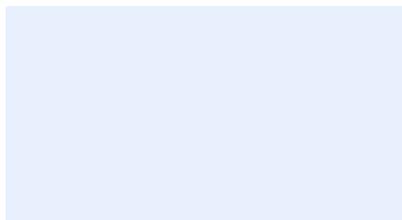
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## Summary

This report details the trends in spider abundance at the Environmental Change Network (ECN) Cairngorms site over 13 years (2007-2019). Spiders were collected from pitfall traps in three habitats (pine woodland, wind-clipped heath, bog) in the Allt a'Mharcaidh catchment near Feshiebridge in the Western regions of the Cairngorms National Park, Scotland. Data was collected using standard ECN protocol, and all collected spider specimens were identified by the same expert araneologist for consistency.

The spider communities were diverse, but typical of upland sites in the region, whilst a number of species present were either nationally rare, scarce, or amber listed due to nationwide declines. Over the relatively short period of monitoring none of the 96 species recorded at the site were found to be declining in abundance, whilst 16 species increased.

The woodland community had the highest richness of species, consistent with this habitat being the most ecologically accessible to generalist species. Overall, however, abundances were similar across spider communities occupying the woodland, bog and heath habitats. The woodland community also appears to be becoming increasingly stable over time, relative to the heath and bog communities, both of which appeared to show extensive community change in 2013, which lasted for five years. This is likely a response to environmental extremes that occurred during the autumn of 2012 and spring / summer of 2013, but further exploratory research is required.

# 1 Introduction

## 1.1 Role of spiders in monitoring environmental change

Terrestrial arthropods are considered valuable biological indicators due to their sensitivity to habitat change, rapid response to disturbance and for the relative simplicity and low cost at which they can be sampled (e.g. Hodkinson et al., 2002; Hodkinson & Jackson, 2005, Gardner et al., 2008 and others).

Historically, the use of spiders as ecological indicators has been particularly in relation to nature conservation and management (Maelfait, 1996), in addition to assessments of anthropogenic disturbance such as heavy metal pollution and habitat fragmentation (Maelfait, 1998). More recently, Borchard et al. (2014) demonstrated their use as bioindicators of environmental and structural habitat change, whilst Schwerdt et al (2018) demonstrated their use as indicators of grassland health.

## 1.2 Environmental Change network (ECN)

The ECN is the UK's long-term, integrated environmental monitoring and research programme. It is focussed on the systematic collection, analysis and interpretation of a wide range of long-term data from a network of sites, with a mission to: "To develop and maintain a multi-agency network and early-warning system to detect, present, interpret and predict long-term ecosystem change and help society mitigate and adapt to global change."

Data used in this study are available on request from either the ECN Central Coordination Unit (<http://www.ecn.ac.uk/data>), or for the meteorological data, from published datasets (Rennie et al, 2020)

## 1.3 Aim of this report

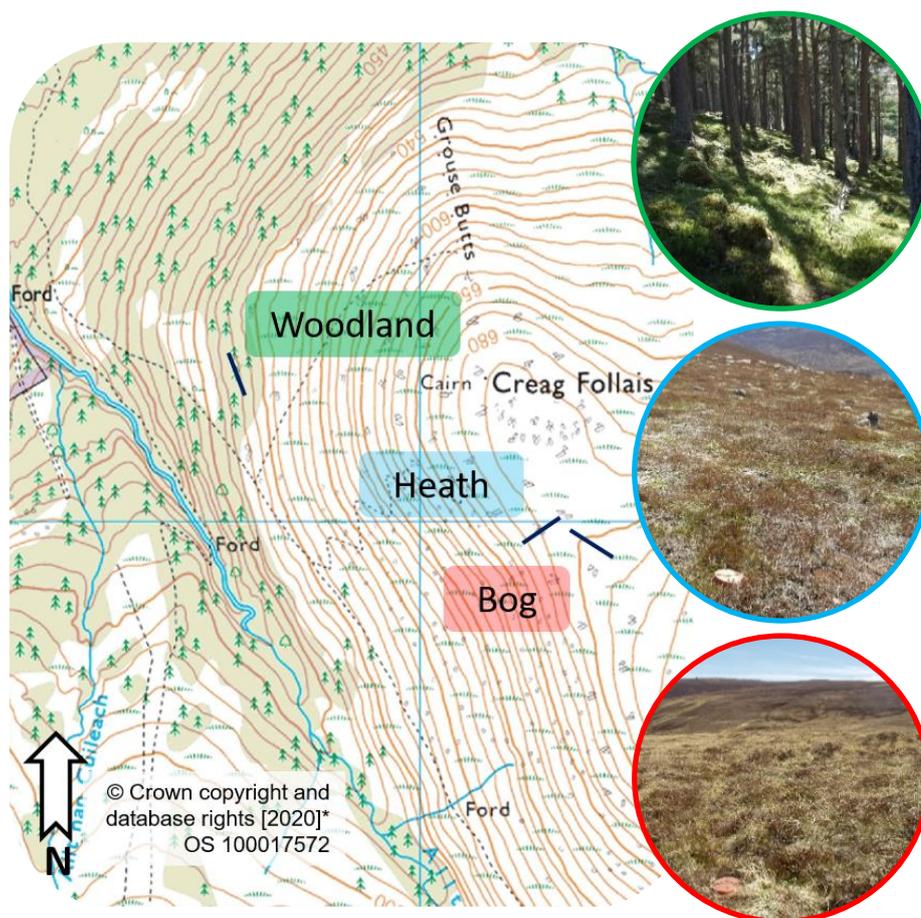
This report is one of a series detailing interim analysis of trends in environmental and ecological variables in the ECN Cairngorm long-term monitoring site (Allt a'Mharcaidh catchment). Spider sampling at the site can be regarded as an opportunistic dataset, as the spiders are sampled as by-catch from the pitfall traps established for recording ground beetles. It is recognised that single method sampling is not ideal for recording a full spider assemblage, but that useful data has been recorded for the ground-dwelling spider assemblage (see section 4.1).

## 2 Methods

### 2.1 Study area

The spider monitoring was conducted in the Allt a'Mharcaidh catchment near Feshiebridge in the Western regions of the Cairngorms National Park, Scotland (57:10:13N 3:51:08W) (fig 1). The catchment rises from 320m to 1111m above sea level, covering approximately 10km<sup>2</sup> and includes part of the Invereshie and Inchriach NNR. Due to logistical constraints, transect sampling was focused on west facing slopes to the north of the catchment, taking in three habitat types located between 460m and 690m.a.s.l. Soils on the western face are generally of peaty podzols overlying pinkish biotite granite (Bayfield and Nolan, 1998). Study habitats were as follows:

- I. Woodland transect – situated at 460m.a.s.l in woodland of mature Scots Pine (*Pinus sylvestris*) with *Vaccinium myrtillus* (L.) dominating the shrub layer.
- II. Heath transect – situated at 690m.a.s.l in predominately wind-clipped *Calluna-Cladonia* sp. dry heath with patches of bare ground.
- III. Bog habitat – situated at 690m.a.s.l in an area of blanket mire dominated by *Eriophorum vaginatum* (L.) and *Molinia caerulea* ((L.) Moench).



**Figure 1** Map showing location of spider sampling transects (as dark lines) located in mature semi-natural *Pinus sylvestris* woodland,

*wind-clipped Calluna-Cladonia heath, and Calluna-Eriophorum raised bog within the Allt a'Mharcaidh catchment, Cairngorms NP, Scotland. Transect photographs inset.*

## 2.2 Sampling protocol

In each habitat a 100m transect line consisting of 10 pitfall traps separated by 10m was set up (see ECN protocol, Sykes & Lane, 1996). A trap was a polypropylene pot (75mm×105mm) buried until flush with ground and part filled with ethylene glycol to a depth of 30mm. To prevent the inadvertent catch of small mammals and amphibians a galvanized wire mesh (mesh size approx 20mm<sup>2</sup>) was inserted into the top of each trap. Each trap was covered by a 140mm plastic rain cover to prevent trap washout, with a gap of approximately 30mm between the cover and the ground.

Sampling frequency was fortnightly, circa April to end October from 2007-2019, with the start date being dependant on snow free ground. On collection, spiders were aggregated into a single sample for each habitat. All spider specimens collected over the duration were identified to species and sex by the same expert araneologist for consistency. All specimens have been stored at UKCEH Edinburgh for future research needs.

A habitat survey was undertaken in 2017 to provide information on the complexity of the vegetation comprising each habitat. At each pitfall trap four 1m<sup>2</sup> quadrats arranged in a 2x2m grid and centred on the trap were sampled for percentage cover of eight major groups (Gramminoids, Ericaceous, Bryophyte, Lichen, tree's, litter, exposed rock and bare ground). The percentage cover of the forty 1m<sup>2</sup> quadrats in each habitat were then averaged to provide a representative vegetation ground cover.

Air temperature was recorded throughout the sampling period using a Campbell Scientific automatic weather station (AWS) situated adjacent to the heath and bog habitats. As a consequence of sporadic problems in the measurement of precipitation at the ECN AWS, precipitation data was taken from the Met Office weather station at Aviemore, approximately 10km North of the sampling area (Met Office, 2012).

## 2.3 Statistical analysis

To check the completeness of sampling across habitats we estimated the absolute species richness using the nonparametric estimator, Chao1 (ChaoRichness – Chao, 1984), by way of the R package iNEXT (Hsieh et al., 2016). Rarefaction curves were generated for each habitat based on the seamless rarefaction and extrapolation of Hill numbers. Hill numbers of the order  $q=0$  were used in both calculations, meaning species were counted equally, without regard to their relative abundances.

A number of diversity indices were used to explore differences in spider assemblages between the habitats, with all analyses undertaken using R (R Core Team, 2018) and graphics using the package ggplot2 (Wickham, 2016). For each habitat the following were calculated for each year of sampling:

**Abundance:** the total abundance of each species of spider standardised across years by the total number of weeks between spring trap installation and final autumn collection each year (wk/yr). This appears a more reliable measure of sampling effort than number of collections, as once a trap was in-situ each spring it trapped continuously until removed in the autumn, irrespective of any missed collections during the season.

Abundance data was then used within the codyn package (Hallett et al., 2016) to calculate temporal community diversity indices for:

**Richness:** the total number of species in each community

**Evenness:** the frequency of each species in each community. The community evenness index, Evar, was used because it is based on the variance in abundance among the species, is independent of species richness, and is balanced with regards to rare or dominant species (Smith & Wilson, 1996).

**Diversity:** a comparative measure of species richness and abundance using Shannon's diversity index (H).

**Species turnover:** the total proportion of species that differ between years:

$$\text{Total turnover} = \frac{\text{Species gained} + \text{Species lost}}{\text{Total species observed in both timepoints}}$$

**Mean rank shifts (MRS):** a temporal analogue for species rank-abundance distributions, indicating the degree of species re-ordering between two years (Collins et al., 2008). Calculated as the average difference in species' ranks between consecutive time periods for species that are present across the entire time series.

Community indices were compared for differences between habitats using ANOVA and Tukey's HSD post-hoc test, with statistical significance considered to be below 5%. The effect of time on indices and species abundances was completed using linear regression. For species, only species-habitat combinations with a minimum of five years of occurrences between 2007 and 2019 were considered for temporal analyses.

To further quantify species-level year-to-year changes in communities, we utilised the codyn package to calculate changes in community rank abundance curves (RAC) (Avolio et al., 2019) for each spider community. This provided twelve paired year-to-year changes per community for: (a) species richness change (change in richness (length of RAC slope) between years divided by the total number of unique species in each year); (b) evenness change (steepness of RAC slope); (c) species rank change (reordering of species as the absolute value of the average change in species ranks between years, divided by the total number of unique species in both years); and (d) species losses and gains (the change in the number of species present/absent between each year, divided by the total number of unique species each year). For richness and evenness change, a positive change value represents an increase between years, and negative a decrease. Changes in species richness, including gains and losses, were further analysed using Pearson's correlation to examine whether seasonal mean temperatures, or total precipitation, could explain the year-to-year variation for each spider community.

## 3 Results

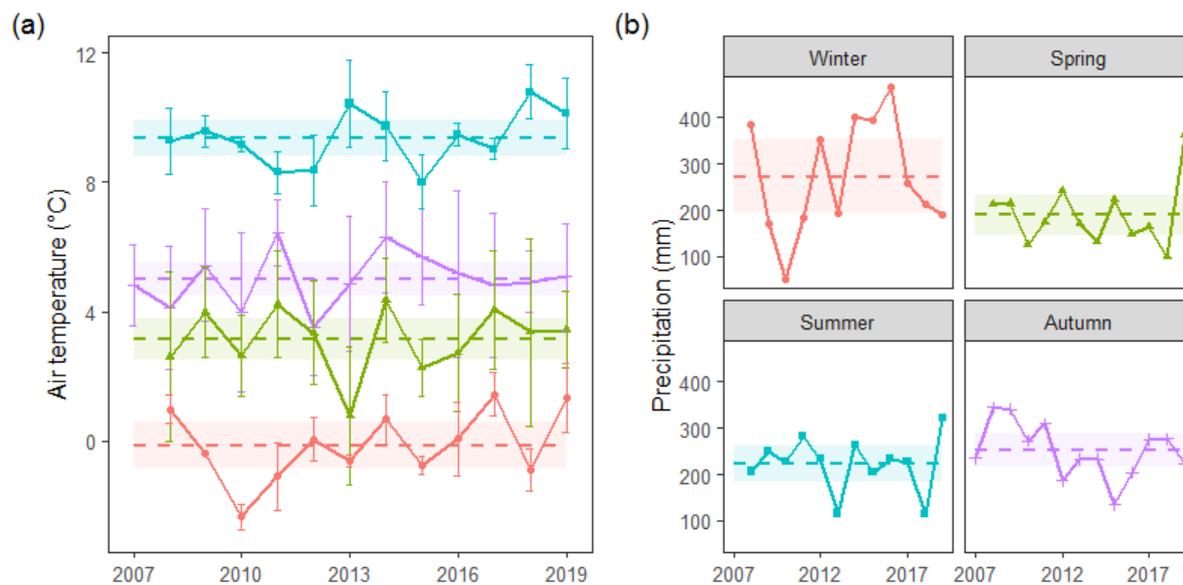
### 3.1 Habitat and environment

The bog and heath habitats are closely co-located above the treeline at 690m.a.s.l. The woodland site is situated some 230m lower and approximately 600m distant. Whilst the bog and heath transects are separated by only 15m at their closest point, their ground cover assemblages are very different. Whereas the bog is more or less equally dominated by graminoid and ericaceous species (39 and 37% respectively), the heath is almost entirely dominated by wind-clipped ericaceous species (71%) with additional areas of *Cladonia* lichens and bare earth (table 1). The woodland shows a more distributed assemblage, with ericaceous species such as *Vaccinium myrtillus* and *V. vitis-idaea* being most dominant, followed by grasses and woodland litter.

**Table 1** Mean percentage cover of eight groups that make up the ground cover assemblage for three habitats in the Allt a'Mharcaidh catchment, Cairngorms NP, Scotland.

	Bog %	Heath %	Wood %
GRAMMINOID	39.08	0.1	21.85
ERICACEOUS	37.45	71.05	42.78
BRYOPHYTE	12.28	0.03	6.45
LICHEN	10.5	14.35	0
TREE	0	0	6.1
LITTER	0	0	18.25
ROCK	0	2.8	2.7
BARE GROUND	0.7	11.58	1.88

The mean minimum air temperature and total precipitation of each month varied substantially from year to year, but showed no directional change between 2007 and 2019 (fig 2).



**Figure 2** (a) Mean minimum air temperature (Winter= red, Spring= green, Summer= turquoise, Autumn= purple) and (b) total precipitation for each season between 2007 and 2019 for the Allt a'Mharcaidh catchment, Cairngorms NP, Scotland. Error bars show standard error. Absolute seasonal mean (dashed line) and 95% CI (shaded area) are shown.

### 3.2 Community composition

Between 2007 and 2019 ground dwelling spiders were collected using pitfall traps from the three habitats. In total 10,768 individuals were collected and identified to species, representing some 97 species belonging to 14 different families (table 2).

**Table 2** Number of species and individuals (in parenthesis) for families of spiders collected from three upland habitats between 2007-2019. The total column represents the unique number of species of a given family recorded across all three habitats, and the total number of individuals collected for that family.

Family	Number of Species (individuals)			Unique total
	Bog	Heath	Wood	
Amaurobiidae	1 (2)	0 (0)	1 (160)	1 (162)
Araneidae	0 (0)	1 (1)	0 (0)	1 (1)
Clubionidae	1 (3)	1 (39)	1 (4)	1 (46)
Dictynidae	1 (1)	0 (0)	1 (365)	1 (366)
Gnaphosidae	1 (1)	3 (6)	3 (6)	5 (13)
Hahniidae	1 (1)	1 (1)	1 (4)	1 (6)
Linyphiidae	37 (3434)	38 (1573)	55 (3284)	70 (8291)
Liocranidae	1 (5)	1 (7)	2 (25)	2 (37)
Lycosidae	4 (294)	5 (1313)	6 (91)	7 (1698)

Mimetidae	0 (0)	0 (0)	1 (3)	1 (3)
Salticidae	0 (0)	1 (1)	2 (2)	2 (3)
Segestriidae	0 (0)	0 (0)	1 (1)	1 (1)
Theridiidae	1 (1)	1 (6)	2 (6)	2 (13)
Thomisidae	1 (2)	1 (114)	2 (12)	2 (128)
<i>Habitat total</i>	<i>49 (3744)</i>	<i>53 (3061)</i>	<i>78 (3963)</i>	<i>97 (10768)</i>

Seventy of the 97 species belonged to the family of Sheet-web spiders, Linyphiidae,, accounting for 77% of all individual spiders recorded. The wolf-spider family (Lycosidae) was the second most abundant family, with seven species, and a further 15.8% of recorded specimens. Ground spiders (Gnaphosidae) were the third most represented family with five species, but only 0.12% of individuals, whilst the Dictynidae, with only a single species (*Cryphoeca silvicola*), accounted for 3.4% of specimens collected. In the heath and woodland habitats five species accounted for >70% of all individuals collected (table 3), whilst in the bog the most abundant five species accounted for >80%. *Tenuiphantes zimmermanni* was the most abundant species overall, occurring in all three habitats, and accounting for 27.8% of all individuals collected. *Alopecosa pulverulenta* (14.6%) and *Oryphantes angulatus* (11%) were the only other species to account for more than 10% of the total catch. A full list of species and abundances can be found in the supplementary material (table S1).

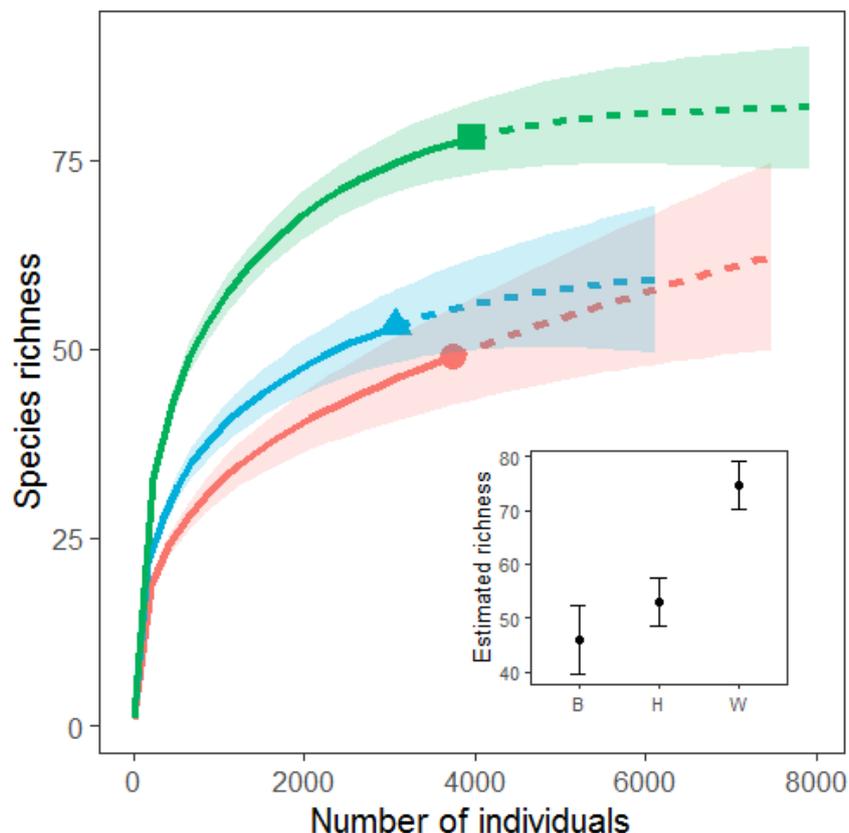
**Table 3** Five most abundant spider species (as percent of catch per habitat) collected from three upland habitats (raised bog, wind-clipped heath, mature semi-natural pine-woodland) in the Allt a'Mharcaidh Catchment, Cairngorms NP between 2007 and 2019.

Habitat	Family	Species	% of total catch per habitat
BOG	Linyphiidae	<i>Oryphantes angulatus</i>	27.75
	Linyphiidae	<i>Tenuiphantes zimmermanni</i>	27.46
	Linyphiidae	<i>Centromerus arcanus</i>	10.04
	Linyphiidae	<i>Palliduphantes ericaeus</i>	10.04
	Lycosidae	<i>Alopecosa pulverulenta</i>	7.61
		<b>SUM</b>	<b>82.90</b>
HEATH	Lycosidae	<i>Alopecosa pulverulenta</i>	41.07
	Linyphiidae	<i>Centromerita concinna</i>	14.11
	Linyphiidae	<i>Tenuiphantes zimmermanni</i>	6.34
	Linyphiidae	<i>Tenuiphantes mengei</i>	5.49
	Linyphiidae	<i>Gonatium rubens</i>	4.48
		<b>SUM</b>	<b>71.49</b>
WOOD	Linyphiidae	<i>Tenuiphantes zimmermanni</i>	44.90

Dictynidae	<i>Cryphoeca silvicola</i>	11.09
Linyphiidae	<i>Tenuiphantes alacris</i>	5.56
Amaurobiidae	<i>Amaurobius fenestralis</i>	4.99
Linyphiidae	<i>Gonatium rubellum</i>	3.40
<b>SUM</b>		<b>69.94</b>

Fifty-two species (54%) were recorded at a frequency of less than 10 individuals over the 13 years of sampling, with 18 having only a single specimen recorded. Forty-four species were unique to a single habitat, with unique diversity highest in the woodland (27 unique species; 35% of all woodland species), followed by the heath (12; 23%) and the bog (5; 10%).

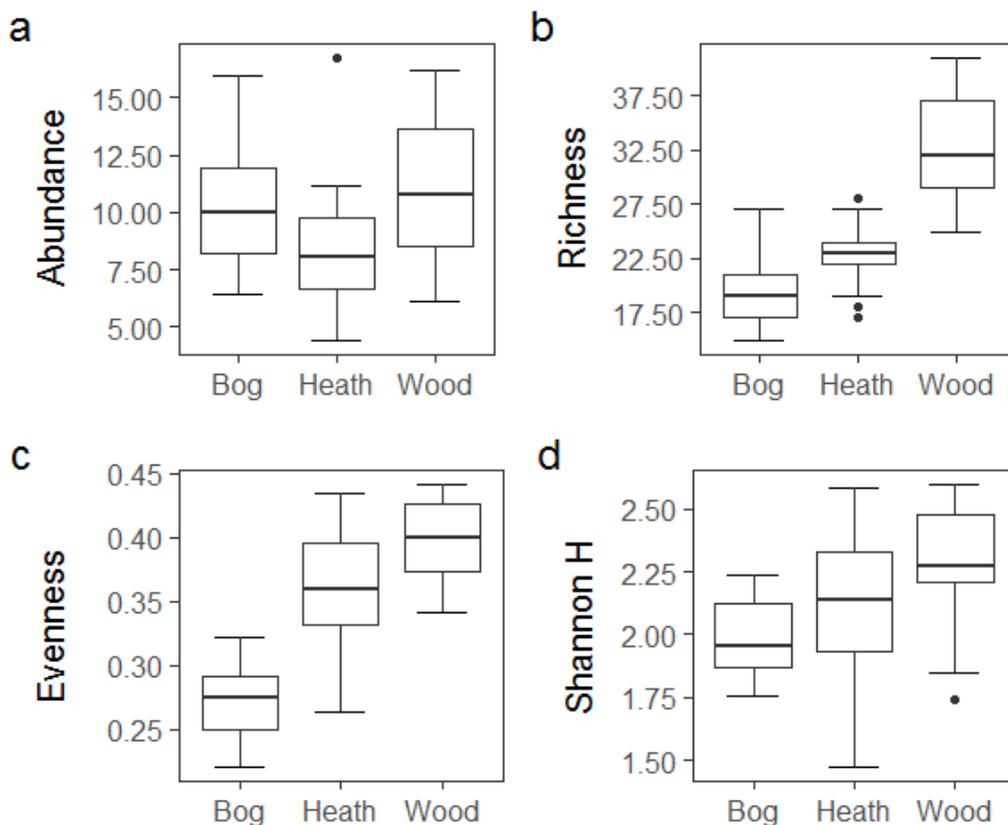
Rarefaction and extrapolation analysis of aggregated sample data across all sites and years (fig 3), suggests that the spider community has been effectively sampled in the heath and woodland habitats, so that it is likely that only very rare species have been missed to date. Indeed the abundance based estimator, Chao1, predicted the species richness for the heath and woodland habitats at  $61 \pm 6$  (s.e.) and  $82 \pm 3$  species respectively. The number of species recorded therefore represent some 87% of expected species in the heath, and 95% in the woodland habitats. Sampling did not however appear as complete in the bog habitat. Here the expected richness was  $98 \pm 37$  (s.e.), but with only 50 species observed, it suggests half the species, probably including a few commoner ones may still be found with future sampling.



**Figure 3** Individual based rarefaction (solid line) and extrapolation (dotted line) curve with 95% confidence intervals for aggregated data from three upland habitats (raised bog (red); dry heath (blue); pine woodland (green)) in the Cairngorms NP, Scotland. The solid marker represents the observed samples. Inset plot shows the estimated richness  $\pm 95\%$  CI for each habitat based on 3061 individuals and Hill numbers of order  $q=0$ .

## 3.2 Community diversity

Overall diversity indices varied between habitats during the study period (fig 4). Whilst abundance of spiders was broadly similar across habitats, species richness ( $F(2,36)=44.71$ ,  $p < 0.001$ ), community evenness ( $F(2,36)=32.54$ ,  $p < 0.001$ ) and Shannon diversity ( $H$ ) ( $F(2,36)= 3.29$ ,  $p = 0.049$ ) differed significantly.



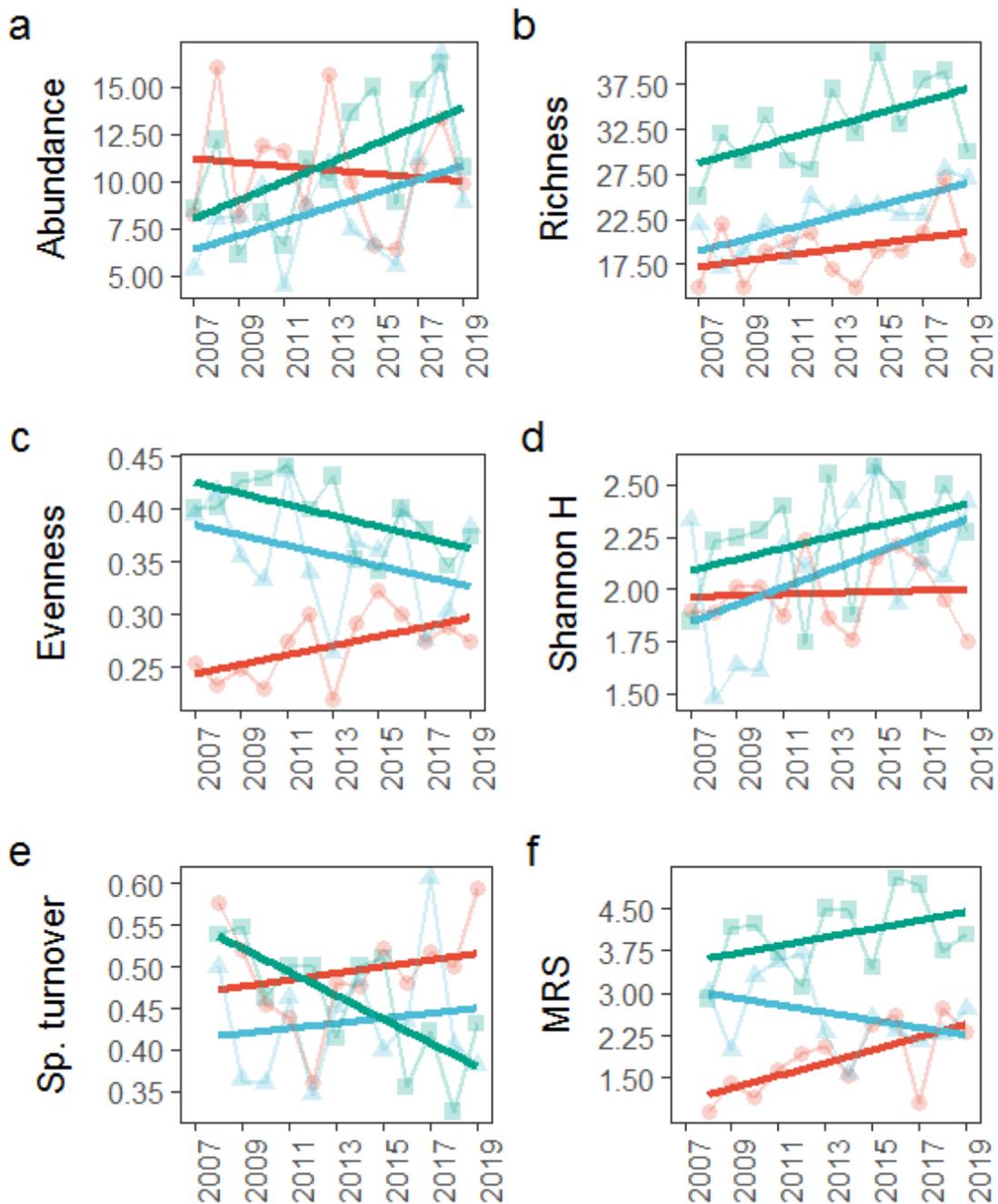
**Figure 4** Annual richness (a, b) and diversity (c, d) indices for communities of ground dwelling spiders in three upland habitats (raised bog, wind-clipped heath, mature semi-natural pine-woodland) in the Allt a'Mharcaidh Catchment, Cairngorms NP, Scotland. (a) abundance corrected for sampling period (as individuals per week per year); (b) species richness; (c) community evenness; (d) Shannon's diversity index.

Tukeys post-hoc analysis showed spider species richness to be significantly higher in the woodland (mean number of species =  $33 \pm 5$  (sd);  $p < 0.001$ ) compared to communities occupying heath ( $23 \pm 3$ ) and bog ( $19 \pm 3$ ), which were not found

(marginally) to statistically differ from each other ( $p= 0.056$ ). Post-hoc analysis for spider community evenness found the community occupying the bog habitat to be significantly less even ( $0.27\pm 0.03$  (sd);  $p= <0.001$ ) than communities on the heath ( $0.36\pm 0.05$  (sd)) or in woodland ( $0.39\pm 0.03$  (sd)), which were marginally not statistically different to one another ( $p= 0.052$ ). Significant differences in Shannon diversity existed only between the bog ( $1.98\pm 0.16$  (sd)) and woodland ( $2.25\pm 0.27$  (sd)) habitats ( $p= 0.039$ ).

### 3.3 Temporal diversity change

Changes in spider community metrics between 2007 and 2019 varied by metric and habitat. The woodland community showed the most change across multiple diversity metrics, with both abundance ( $F(1,11)= 5.701$ ,  $p= 0.036$ ) and species richness ( $F(1,11)= 5.146$ ,  $p= 0.044$ ) increasing significantly over the duration, whilst community evenness ( $F(1,11)= 6.502$ ,  $p= 0.027$ ) and total species turnover ( $F(1,10)= 11.34$ ,  $p= 0.007$ ) significantly decreased (fig 5).



**Figure 5** Temporal changes in community structure for ground dwelling spiders in three upland habitats (raised bog (red circle); dry heath (blue triangle); pine woodland (green square)) in the Cairngorms NP, Scotland, over 13 years between 2007 and 2019. (a) annual abundance corrected for sampling period (as individuals per week per year); (b) annual species richness; (c) community evenness; (d) Shannon's diversity index; (e) species turnover; (f) mean rank shift (MRS).

In the bog habitat, spider community evenness was found to have increased significantly ( $F(1,11)= 4.893$ ,  $p= 0.049$ ), as did species MRS ( $F(1,10)= 7.654$ ,  $p=$

0.020). In the heath habitat only species richness was found to have a significant trend ( $F(1,11)= 15.34$ ,  $p= 0.002$ ), increasing by 0.63 species per year over the duration. Overall, no significant change was observed for Shannon's diversity index for spider communities residing in any habitat, at least in part due to large inter-annual variations.

Analysis of changes in the community rank abundance curves has shown that the rate of year-to-year changes in the species rank order (the re-ordering of the community) has significantly increased in the bog habitat, but decreased in the woodland habitat between 2007 and 2019 (table 4). Overall, year-to-year species re-ordering differed between communities ( $F(2,36)= 6.672$ ,  $p= 0.004$ ), with Tukey's HSD post-hoc analysis showing significantly lower rank change in the bog community (mean rank change =  $0.14 \pm 0.02$  (sd)) than in the heath ( $0.17 \pm 0.02$  (sd);  $p= 0.022$ ) or woodland ( $0.17 \pm 0.01$  (sd);  $p= 0.004$ ).

**Table 4** Linear regression outputs for year-to-year change in five different rank abundance curve metrics, for spider communities occupying three habitats (raised bog, wind-clipped heath, mature semi-natural pine-woodland) between 2007-2019 at the Allt a'Mharcaidh Catchment, Cairngorms NP.

Habitat	RAC Metric	$r^2$	$p =$
Bog	Richness change	-0.16	0.62
	Evenness change	-0.058	0.86
	Rank change	0.62	0.031*
	Species gains	-0.081	0.8
	Species losses	0.22	0.5
Heath	Richness change	0.14	0.67
	Evenness change	0.15	0.65
	Rank change	-0.054	0.87
	Species gains	0.27	0.4
	Species losses	-0.039	0.9
Wood	Richness change	-0.29	0.36
	Evenness change	-0.076	0.81
	Rank change	-0.76	0.004**
	Species gains	-0.55	0.065
	Species losses	-0.049	0.88

$*P= <0.5$ ,  $**P= <0.01$

### 3.4 Temporal change – species

Seventy-seven species-habitat combinations met the threshold for temporal analysis (five or more years of occurrences), with 16 showing a significant change in relative

abundance over time (table 5). A full table for all 77 species can be found in the supplementary material (table S2).

**Table 5** Statistically significant results of linear regression analysis examining the effect of year on relative abundance (per week per year) of spiders from three habitats (raised bog, wind-clipped heath, mature semi-natural pine-woodland) between 2007-2019 at the Allt a'Mharcaidh Catchment, Cairngorms NP. Species marked with an \* are nationally scarce across the UK. A full table of all results is provided in the supplementary material.

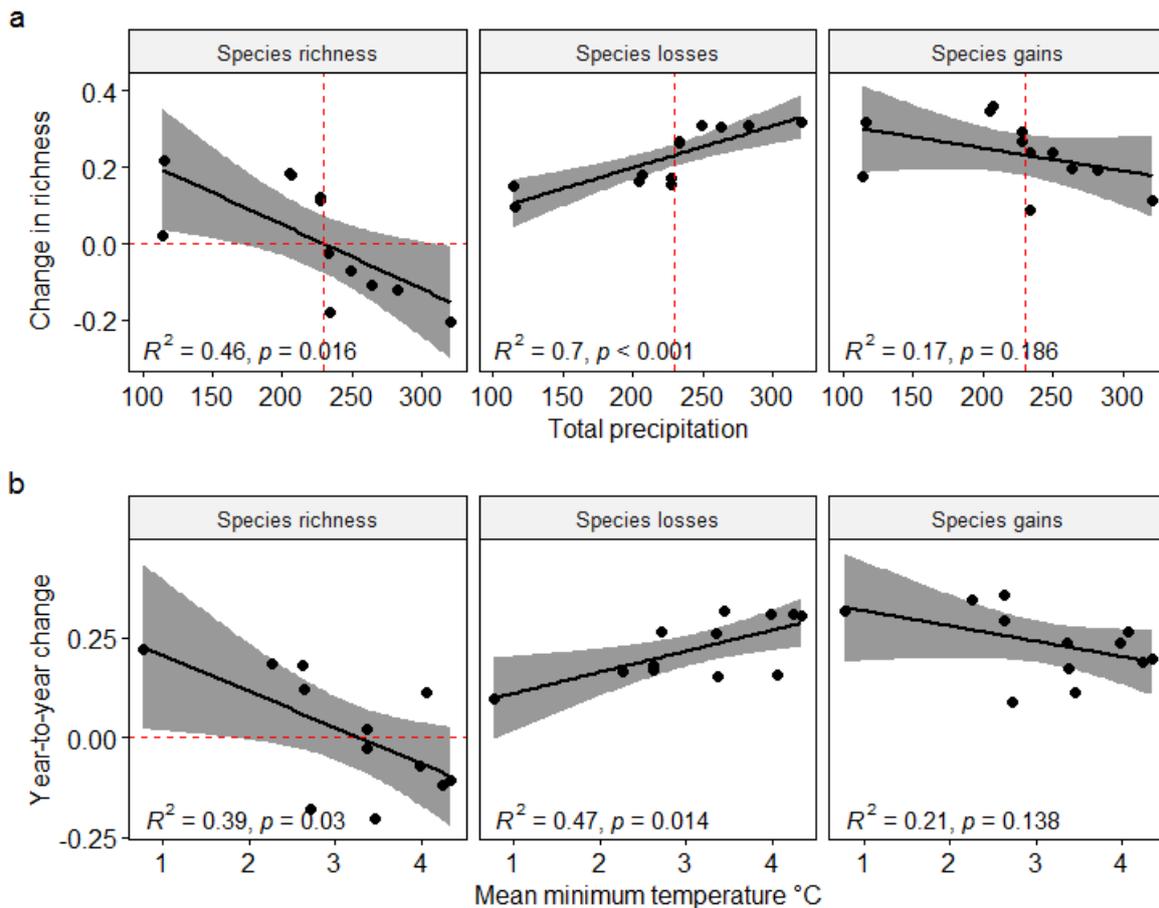
Habitat	Species	$r^2$	$p =$	Direction of change
Bog	<i>Bolyphantes luteolus</i>	0.40	0.020	↑
	<i>Walckenaeria nudipalpis</i>	0.33	0.038	↑
Heath	<i>Gonatium rubens</i>	0.43	0.016	↑
	<i>Hilaira frigida</i>	0.39	0.023	↑
	<i>Robertus lividus</i>	0.58	0.002	↑
	<i>Scotinotylus evansi</i> *	0.33	0.042	↑
	<i>Tenuiphantes mengei</i>	0.32	0.042	↑
Wood	<i>Centromerus arcanus</i>	0.36	0.029	↑
	<i>Centromerus sylvaticus</i>	0.43	0.015	↑
	<i>Gonatium rubellum</i>	0.40	0.021	↑
	<i>Micrargus apertus</i>	0.55	0.004	↑
	<i>Monocephalus fuscipes</i>	0.34	0.037	↑
	<i>Tenuiphantes alacris</i>	0.77	<0.001	↑
	<i>Tenuiphantes mengei</i>	0.37	0.027	↑
	<i>Trochosa terricola</i>	0.37	0.026	↑
	<i>Walckenaeria acuminata</i>	0.31	0.049	↑

In all cases of significant temporal change, relative abundance was found to have increased between 2007 and 2019. Of particular interest from this list is *Scotinotylus evansi* collected from the heath habitat, a montane species considered as nationally scarce in the UK (Harvey et al., 2017).

### 3.5 Drivers of change

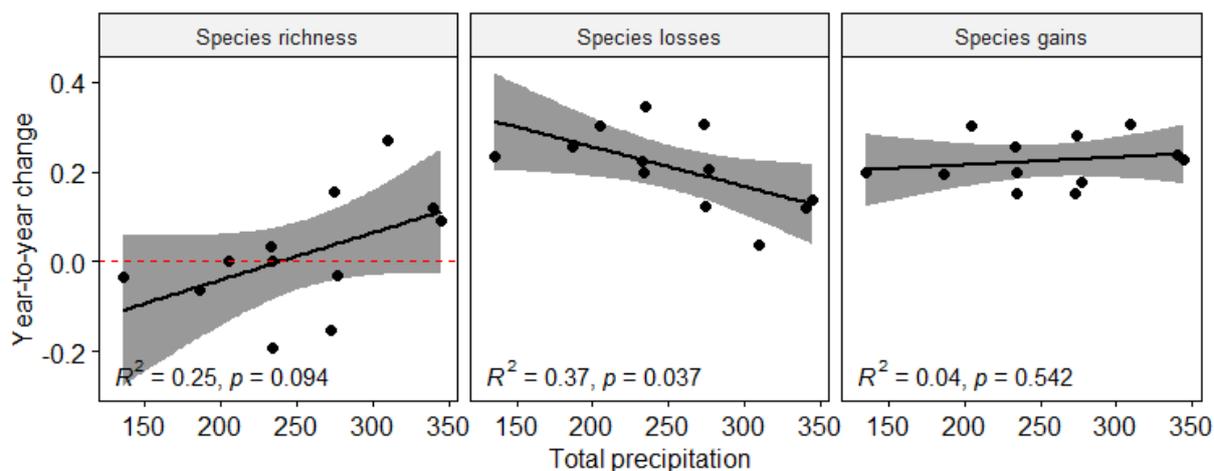
The between year change for species richness in the woodland community was significantly correlated with total summer rainfall ( $r = -0.68$ ,  $p = 0.016$ , fig 6a) and spring mean minimum temperature ( $r = -0.62$ ,  $p = 0.03$ , fig 6b). Increased summer rainfall had the effect of reducing species richness relative to the previous year ( $F(1,10) = 8.429$ ,  $p = 0.016$ ,  $r^2 = 0.46$ ). A threshold of approximately 230 mm of summer rainfall was also apparent. When total summer rainfall was greater than 230 mm, species richness declined relative to the previous year (negative change value), whereas rainfall of less than 230 mm resulted in increased species richness (positive change value). There

was some evidence this was driven to species losses ( $F(1,10)= 23.38$ ,  $p= 0.001$ ,  $r^2= 0.7$ ), which were also higher with increasing summer rainfall, rather than species gains, which were unaffected by rainfall or temperature from any season. The effect of spring mean minimum temperature on species richness ( $F(1,10)= 6.354$ ,  $p= 0.03$ ,  $r^2= 0.39$ ) and losses ( $F(1,10)= 8.954$ ,  $p= 0.014$ ,  $r^2= 0.47$ ), although significant, appears to be unduly influenced by a single data point representing the exceptionally cold spring of 2013. The relationship between temperature and richness change should therefore be treated with a degree of caution.



**Figure 6** Year-to-year change in spider species richness, gains and losses plotted against (a) total summer precipitation (May-July) and, (b) mean minimum spring temperature; for a spider community dwelling in upland pine woodland in the Allt a'Mharcaidh catchment, Cairngorms, Scotland. Regression fit, significance and 95% confidence interval (shaded) shown. Horizontal dashed line for species richness represents no change between years. Change values above this line represent an increase in richness relative to the previous year, and below a decrease relative to the previous year. Vertical dashed line is 230mm of rainfall.

In the heath dwelling spider community, only year-to-year species losses and total autumn precipitation were significantly correlated ( $r= 0.6$ ,  $p= 0.038$ , fig 7). This relationship was opposite to that seen in the woodland community with summer precipitation, with species losses decreasing as autumnal precipitation increased.



**Figure 7** Year-to-year change in spider species richness, gains and losses plotted against previous autumn total rainfall (Sept-Nov); for a spider community dwelling in upland pine woodland in the Allt a'Mharcaidh catchment, Cairngorms, Scotland. Regression fit, significance and 95% confidence interval (shaded) shown. Horizontal dashed line for species richness represents no change between years. Change values above this line represent an increase in richness relative to the previous year, and below a decrease relative to the previous year.

## 4 Discussion

### 4.1 Overview of sampling and communities

Over 670 spider species belonging to 34 families are known to exist across Great Britain (Merrett et al., 2014). In Scotland the number of known species is estimated to be 441 (Davidson, 2010). The 96 species recorded between 2007 and 2019 across three upland habitats in the Allt a'Mharcaidh therefore equate to some 22% of the Scottish species list, and includes 50% of the known families found in Scotland. With 72% (69 species) of all species recorded at the site belonging to the Linyphiidae, the family composition is similar to other studies on upland sites in Scotland and the Northern Pennines (Cherrett, 1964; Coulson & Butterfield 1986; Downie et al., 1995). In most of these studies the actual proportion of species belonging to the Linyphiidae was over 80%, and in some cases, such as on Glas Maol in the southern Cairngorms, over 90%. This agrees with unpublished data from the wider Allt a'Mharcaidh site, where spiders collected using the same pitfall technique but at higher altitude (approximately 950m.a.s.l. on the upper slopes of Sgoran Dubh Mor), had a family composition consisting of 95% Linyphiidae (unpublished research). Indeed, it has been shown that this family becomes increasingly important at northern latitudes irrespective of habitat (Arvidsson et al., 2016) as well as in arctic and sub-arctic regions (Bristowe, 1939 in Cherrett, 1964). Such biomes can be found in the UK around the Cairngorm massif. It is not clear whether the increased representation of Linyphiidae at higher latitudes is an artefact caused by the reduction of non-Linyphiidae species, as shown by Coulson & Butterfield (1986) for elevation, or whether it is driven by other factors.

In our study collection of specimens involved using pitfall traps only. Using a single sampling method to investigate species assemblages can be problematic and result in biases in the kind of species detected (Standen, 2000). The main advantage of using pitfall traps for monitoring ground-dwelling invertebrates is that they continuously trap between visits, and in our case, from spring and late autumn. However, some careful interpretation of results is required given that what they do capture is a product of both the abundance and activity of each species present (Luff 1975, Topping & Sunderland, 1992), which leads to problems relating data to actual population densities, or when comparing traps/transects in varying habitat vegetation structure (Sunderland & Topping, 1995). Pitfall trapping by its nature selects against web building spiders and favours hunting and nocturnal spiders which are actively mobile at ground level (Standen, 2000; Sunderland & Topping, 1995; Bali, 2019). To mitigate these bias's, pitfall trapping would ideally be undertaken alongside vacuum and/or sweep netting (e.g. Merrett & Snazell, 1983; Bali, 2019), but for logistical reasons that was not possible during this long-term monitoring study. It has however been shown that pitfall traps can provide realistic estimates of the number of spider species in a community (Uetz & Unzicker, 1976; Curtis, 1980).

Regardless, we found that the numerous web-spinning spiders of the Linyphiidae accounted for over 77% of individuals caught. However they were much more prevalent in the bog (>93% of catch) and wood (>82%) habitats, which offer more structure for web-spinning spiders, than in the low vegetation of the wind-clipped heath

(51%). Without comparative sampling methods, it is impossible to know whether these abundances represents an underestimate of web-spinning spiders.

Our second most abundant family was the larger active hunters of the Lycosidae, although these were only prevalent in the wind-clipped heath where the vegetation is short, and consists mainly of wind scoured heather (*C. vulgaris*) and *Cladonia* lichens, with occasional patches of bare soil. Here, the Lycosidae account for some 43% of all captured spiders, compared to only 8% in the bog habitat only a few metres away, and 2% in the woodland further down the hill. Whether or not the lower abundances of Lycosidae outside of the heath habitat is an artefact of reduced trapping efficiency of active hunters, in denser more structured vegetation (e.g. Lang 2000; Lafage et al., 2019), or, is an accurate representation of the species abundances in those habitats, is unknown.

Sixteen of the 97 species recorded in the Allt a'Mharcaidh are considered nationally scarce in Great Britain (Harvey et al. 2017), whilst one species, *Hilaira nubigena*, is considered nationally rare. *Oryphantes angulatus*, considered as nationally scarce, was the third most abundant species present across all three habitats, although most common in the bog habitat where it accounted for over 27% of all spiders recorded. Six species recorded in the catchment (*Agyneta subtilis*, *Allomengea scopigera*, *Diplocentria bidentata*, *Leptothrix hardyi*, *Mecynargus morulus*, *Walckenaeria clavicornis*) are amber listed due to recent national declines since 1993, but are still currently widespread (Harvey et al. 2017). Of particular interest is *Scotinotylus evansi* that occurred in the heath habitat. This nationally scarce species (Harvey et al., 2017) has increased significantly in abundance at the site over the years. However, whether its scarcity is a product of under-recording due to inhabiting relatively inaccessible sites, or whether it is genuinely scarce, is yet to be established.

## 4.2 Diversity changes

Increasing abundance and richness of spiders in the woodland habitat, coupled with decreasing evenness and species turnover, suggests that despite an increasing influx of new species into the community, a relatively small number of species were becoming increasingly dominant in the spider community. Indeed, nine species (10%) in the woodland habitat were found to have significantly increased in abundance between 2007 and 2019. Two of which, *Gonatium rubellum* and *Tenuiphantes alacris* were amongst the top five common species collected here, although due to the dominance of *Tenuiphantes zimmermanni*, between them they still accounted for less than 10% of spiders captured. However, as the rate at which species are increasing/decreasing in abundance relative to other species is declining over time, it appears that the woodland community is becoming increasingly stable. Species losses in the woodland spider community appear to be related to increased summer precipitation; however, the underlying mechanism driving this is not immediately apparent without further research. Possible drivers could be the mechanical action of rain suppressing the ability of some species to hunt and/or disperse, reduced prey availability, or that sampling efficiency of pitfall traps was reduced under heavy rain.

In the heath habitat, only the total number of species in a year significantly changed over time. However, there appeared to be substantial community change between

2012 and 2013, followed by a five-year period of relative community stability between until 2018. This was evidenced by year-to-year changes in species reordering within the community, which peaked in 2011/12, before remaining at lower and a more stable state. At the same time between year variations in species richness is greatly reduced, suggesting a balance between species gains and losses. As these community responses do not appear to be driven by obvious changes in the more dominant species present, it is likely a response to changes in more marginal species following 2012 that influencing the community change.

Without further analysis it is not possible to identify the cause of this change, however, it is possible that climate played some role in the community reordering in the heath habitat. Due to its exposed location, thin soils, and with only low wind-clipped vegetation, communities occupying the heath are particularly exposed to prevailing weather. The climate between 2012 and 2013 appears to have been especially volatile. Although the winter temperature was unremarkable and similar to the long-term average, the summer and autumn of 2012 were much colder than average, with temperatures 1°C and 1.5°C below the long-term mean respectively. This was followed in 2013 by an exceptionally cold spring, some 2.4°C below the long-term mean, and thereafter one of the warmest and driest summers of the period with temperatures 1.1°C above the long-term mean, and rainfall only 50% of expected. These stressors could be particularly challenging to the more generalist species occupying the heath habitat, and is likely to favour some of the mountain specialists such as *Hilaira frigida*, which are more tolerant of drier habitats. However, a fuller analysis of the relationship between environmental conditions and species and community responses is still to be undertaken.

In the bog habitat the spider community appears to have responded differently to that in the heath. Both evenness and community re-ordering appeared to increase more consistently across the years. However, the community evenness was severely reduced in 2013 in a comparable manner to the heath community, suggesting increasing dominance of a few species on that year. Evenness appears to then strongly increase before stabilising thereafter, whilst community re-ordering continues to increase, but with greater year-to-year variation.

## 4.3 Summary

Spiders communities were monitored in three habitats in the Allt a'Mharcaidh catchment between 2007 and 2019. Spider communities appeared to be diverse, but typical of upland sites in the region, whilst a number of species present are either nationally rare, scarce, or amber listed due to nationwide declines. However, of the 96 species recorded at the site, none were found to be declining in abundance, whilst 16 species were found to be increasing.

Unsurprisingly, the woodland community, being more ecologically and climatologically accessible to generalist species, had the highest richness of species. The woodland community also appears to be becoming increasingly stable over time, relative to the heath and bog communities, both of which appeared to show some community change in 2013 which lasted for five years. The cause of this community change has not been

established, but coincides with a period of extreme climatic events and further exploratory research is required.

The spider community represented here is limited by only using a single sampling method (pitfall), which likely over emphasises ground dwelling spiders within the community. However, this is only a concern if the community represented here was being considered as the true species assemblage for the site. They are not. Although resources have not made it possible to date, a more accurate species assemblage could be achieved through additional complimentary collection methods (e.g. sweep netting/suction sampling or hand collection). Further study looking at functional trait based community responses may also be necessary to fully understand community change, whilst an in depth analysis of the effects of weather and climate on spider communities, will help us better understand the likely long-term impacts of predicted climate change.

## 5 Acknowledgements

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## Supplementary material

### Table S1

Table showing total numbers of each species of spider collected from three upland habitats (raised bog, wind-clipped heath, mature semi-natural pine-woodland) in the Allt a'Mharcaidh Catchment, Cairngorms NP between 2007 and 2019. The percentage of each species for each habitat is shown in parenthesis (). The most abundant species for each habitat is shown in bold.

Family	Species	Bog	Heath	Wood	Total
Amaurobiidae	<i>Amaurobius fenestralis</i>	2 (0.05)	0 (0)	155 (3.96)	157 (1.46)
Araneidae	<i>Singa pygmaea</i>	0 (0)	1 (0.03)	0 (0)	1 (0.01)
Clubionidae	<i>Clubiona trivialis</i>	3 (0.08)	39 (1.27)	4 (0.1)	46 (0.43)
Dictynidae	<i>Cryphoeca silvicola</i>	1 (0.03)	0 (0)	362 (9.25)	363 (3.39)
Gnaphosidae	<i>Drassodes cupreus</i>	0 (0)	3 (0.1)	3 (0.08)	6 (0.06)
	<i>Drassodes lapidosus</i>	0 (0)	0 (0)	2 (0.05)	2 (0.02)
	<i>Gnaphosa leporina</i>	1 (0.03)	0 (0)	0 (0)	1 (0.01)
	<i>Haplodrassus signifer</i>	0 (0)	2 (0.07)	1 (0.03)	3 (0.03)
	<i>Zelotes latreillei</i>	0 (0)	1 (0.03)	0 (0)	1 (0.01)
Hahniidae	<i>Hahnia montana</i>	1 (0.03)	1 (0.03)	4 (0.1)	6 (0.06)
Linyphiidae	<i>Agyphantes expunctus</i>	0 (0)	0 (0)	3 (0.08)	3 (0.03)
	<i>Agynera ramosa</i>	0 (0)	0 (0)	1 (0.03)	1 (0.01)
	<i>Agynera subtilis</i>	1 (0.03)	0 (0)	17 (0.43)	18 (0.17)
	<i>Allomengea scopigera</i>	4 (0.11)	0 (0)	2 (0.05)	6 (0.06)
	<i>Bathyphantes approximatus</i>	0 (0)	0 (0)	1 (0.03)	1 (0.01)
	<i>Bathyphantes gracilis</i>	12 (0.32)	2 (0.07)	5 (0.13)	19 (0.18)
	<i>Bolyphantes alticeps</i>	1 (0.03)	3 (0.1)	36 (0.92)	40 (0.37)
	<i>Bolyphantes luteolus</i>	15 (0.4)	11 (0.36)	21 (0.54)	47 (0.44)
	<i>Centromerita bicolor</i>	0 (0)	9 (0.29)	0 (0)	9 (0.08)
	<i>Centromerita concinna</i>	54 (1.44)	432 (14.11)	7 (0.18)	493 (4.6)
	<i>Centromerus arcanus</i>	376 (10.04)	9 (0.29)	26 (0.66)	411 (3.84)
	<i>Centromerus dilutus</i>	1 (0.03)	1 (0.03)	0 (0)	2 (0.02)
	<i>Centromerus prudens</i>	4 (0.11)	8 (0.26)	20 (0.51)	32 (0.3)
	<i>Centromerus sylvaticus</i>	0 (0)	0 (0)	31 (0.79)	31 (0.29)
<i>Ceratinella brevipes</i>	15 (0.4)	16 (0.52)	27 (0.69)	58 (0.54)	

Spider community and species trends at the UK Environmental Change Network Cairngorm field station, 2007-2019

<i>Dicymbium tibiale</i>	0 (0)	0 (0)	3 (0.08)	3 (0.03)
<i>Diplocentria bidentata</i>	20 (0.53)	0 (0)	2 (0.05)	22 (0.21)
<i>Dismodicus bifrons</i>	0 (0)	0 (0)	3 (0.08)	3 (0.03)
<i>Erigonella hiemalis</i>	0 (0)	0 (0)	7 (0.18)	7 (0.07)
<i>Gonatium rubellum</i>	3 (0.08)	0 (0)	155 (3.96)	158 (1.47)
<i>Gonatium rubens</i>	8 (0.21)	137 (4.48)	2 (0.05)	147 (1.37)
<i>Gongylidiellum vivum</i>	1 (0.03)	0 (0)	0 (0)	1 (0.01)
<i>Hilaira excisa</i>	0 (0)	0 (0)	9 (0.23)	9 (0.08)
<i>Hilaira frigida</i>	65 (1.74)	88 (2.87)	2 (0.05)	155 (1.45)
<i>Hilaira nubigena</i>	1 (0.03)	0 (0)	0 (0)	1 (0.01)
<i>Labulla thoracica</i>	0 (0)	0 (0)	1 (0.03)	1 (0.01)
<i>Lepthyphantes alacris</i>	1 (0.03)	0 (0)	0 (0)	1 (0.01)
<i>Leptothrix hardyi</i>	0 (0)	5 (0.16)	0 (0)	5 (0.05)
<i>Lophomma punctatum</i>	0 (0)	1 (0.03)	1 (0.03)	2 (0.02)
<i>Macrargus carpenteri</i>	55 (1.47)	136 (4.44)	2 (0.05)	193 (1.8)
<i>Macrargus rufus</i>	9 (0.24)	0 (0)	76 (1.94)	85 (0.79)
<i>Mecynargus morulus</i>	0 (0)	8 (0.26)	0 (0)	8 (0.07)
<i>Meioneta gulosa</i>	0 (0)	2 (0.07)	0 (0)	2 (0.02)
<i>Meioneta mossica</i>	0 (0)	2 (0.07)	0 (0)	2 (0.02)
<i>Micrargus apertus</i>	2 (0.05)	2 (0.07)	17 (0.43)	21 (0.2)
<i>Micrargus herbigradus</i>	0 (0)	0 (0)	4 (0.1)	4 (0.04)
<i>Microlinyphia pusilla</i>	0 (0)	1 (0.03)	0 (0)	1 (0.01)
<i>Minyriolus pusillus</i>	0 (0)	0 (0)	2 (0.05)	2 (0.02)
<i>Monocephalus castaneipes</i>	0 (0)	1 (0.03)	47 (1.2)	48 (0.45)
<i>Monocephalus fuscipes</i>	1 (0.03)	2 (0.07)	67 (1.71)	70 (0.65)
<i>Oedothorax retusus</i>	1 (0.03)	0 (0)	0 (0)	1 (0.01)
<i>Oreonetides vaginatus</i>	50 (1.34)	8 (0.26)	17 (0.43)	75 (0.7)
<i>Oryphantes angulatus</i>	<b>1039 (27.75)</b>	127 (4.15)	10 (0.26)	1176 (10.97)
<i>Palliduphantes ericaeus</i>	376 (10.04)	79 (2.58)	79 (2.02)	534 (4.98)
<i>Palliduphantes pallidus</i>	0 (0)	0 (0)	17 (0.43)	17 (0.16)
<i>Pelecopsis nemoralis</i>	0 (0)	0 (0)	2 (0.05)	2 (0.02)
<i>Peponocranium ludicrum</i>	3 (0.08)	2 (0.07)	0 (0)	5 (0.05)
<i>Pocadicnemis juncea</i>	0 (0)	1 (0.03)	0 (0)	1 (0.01)

Spider community and species trends at the UK Environmental Change Network Cairngorm field station, 2007-2019

	<i>Pocadicnemis pumila</i>	0 (0)	0 (0)	4 (0.1)	4 (0.04)
	<i>Poecilonea variagata</i>	1 (0.03)	0 (0)	2 (0.05)	3 (0.03)
	<i>Porrhomma montanum</i>	0 (0)	1 (0.03)	0 (0)	1 (0.01)
	<i>Porrhomma pallidum</i>	0 (0)	2 (0.07)	2 (0.05)	4 (0.04)
	<i>Saaristoa abnormis</i>	0 (0)	2 (0.07)	25 (0.64)	27 (0.25)
	<i>Scotinotylus evansi</i>	5 (0.13)	21 (0.69)	1 (0.03)	27 (0.25)
	<i>Stemonyphantes lineatus</i>	0 (0)	0 (0)	5 (0.13)	5 (0.05)
	<i>Tapinocyba pallens</i>	1 (0.03)	0 (0)	57 (1.46)	58 (0.54)
	<i>Tapinopa longidens</i>	0 (0)	0 (0)	2 (0.05)	2 (0.02)
	<i>Tenuiphantes alacris</i>	4 (0.11)	0 (0)	260 (6.65)	264 (2.46)
	<i>Tenuiphantes mengei</i>	140 (3.74)	168 (5.49)	58 (1.48)	366 (3.42)
	<i>Tenuiphantes tenebricola</i>	1 (0.03)	0 (0)	105 (2.68)	106 (0.99)
	<i>Tenuiphantes tenuis</i>	0 (0)	7 (0.23)	3 (0.08)	10 (0.09)
	<i>Tenuiphantes zimmermanni</i>	1028 (27.46)	194 (6.34)	<b>1760 (44.99)</b>	<b>2982 (27.82)</b>
	<i>Walckenaeria acuminata</i>	95 (2.54)	34 (1.11)	152 (3.89)	281 (2.62)
	<i>Walckenaeria antica</i>	7 (0.19)	6 (0.2)	1 (0.03)	14 (0.13)
	<i>Walckenaeria atrotibialis</i>	0 (0)	0 (0)	1 (0.03)	1 (0.01)
	<i>Walckenaeria capito</i>	0 (0)	0 (0)	2 (0.05)	2 (0.02)
	<i>Walckenaeria clavicornis</i>	12 (0.32)	43 (1.4)	0 (0)	55 (0.51)
	<i>Walckenaeria cucullata</i>	1 (0.03)	0 (0)	60 (1.53)	61 (0.57)
	<i>Walckenaeria cuspidata</i>	0 (0)	1 (0.03)	5 (0.13)	6 (0.06)
	<i>Walckenaeria nudipalpis</i>	21 (0.56)	1 (0.03)	16 (0.41)	38 (0.35)
Liocranidae	<i>Agroeca brunnea</i>	0 (0)	0 (0)	14 (0.36)	14 (0.13)
	<i>Agroeca proxima</i>	5 (0.13)	7 (0.23)	11 (0.28)	23 (0.21)
Lycosidae	<i>Alopecosa pulverulenta</i>	285 (7.61)	<b>1257 (41.07)</b>	26 (0.66)	1568 (14.63)
	<i>Pardosa lugubris</i>	0 (0)	0 (0)	8 (0.2)	8 (0.07)
	<i>Pardosa nigriceps</i>	3 (0.08)	28 (0.91)	7 (0.18)	38 (0.35)
	<i>Pardosa palustris</i>	0 (0)	6 (0.2)	0 (0)	6 (0.06)
	<i>Pardosa prativaga</i>	0 (0)	0 (0)	1 (0.03)	1 (0.01)
	<i>Pardosa pullata</i>	5 (0.13)	18 (0.59)	4 (0.1)	27 (0.25)
	<i>Trochosa terricola</i>	1 (0.03)	4 (0.13)	44 (1.12)	49 (0.46)
Mimetidae	<i>Ero furcata</i>	0 (0)	0 (0)	3 (0.08)	3 (0.03)
Salticidae	<i>Heliophanus flavipes</i>	0 (0)	1 (0.03)	0 (0)	1 (0.01)

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	<i>Neon reticulatus</i>	0 (0)	0 (0)	1 (0.03)	1 (0.01)
Segestriidae	<i>Segestria senoculata</i>	0 (0)	0 (0)	1 (0.03)	1 (0.01)
Theridiidae	<i>Robertus lividus</i>	1 (0.03)	6 (0.2)	2 (0.05)	9 (0.08)
	<i>Theonoe minutissima</i>	0 (0)	0 (0)	4 (0.1)	4 (0.04)
Thomisidae	<i>Ozyptila trux</i>	0 (0)	0 (0)	7 (0.18)	7 (0.07)
	<i>Xysticus cristatus</i>	2 (0.05)	114 (3.72)	5 (0.13)	121 (1.13)
<b>TOTAL</b>		<b>3744</b>	<b>3061</b>	<b>3912</b>	<b>10717</b>

## Table S2

Table showing regression co-efficients, significance ( $p$ ) and closeness of fit ( $r^2$ ) for the effect of year on spider abundance (standardised by sampling duration per year) between 2007-2019. Sampling occurred in three upland habitats (raised bog, wind-clipped heath, mature semi-natural pine-woodland) in the Allt a'Mharcaidh Catchment, Cairngorms NP, and only species which occurred on at least five years in a given habitat are included. Significant change ( $<0.05$ ) is shown in bold. Species marked with an \* are those considered either nationally scarce, rare or are amber listed in the UK according to Harvey et al. (2017).

Habitat	Species	estimate	S.E.	$p=$	$r^2$
Bog	<i>Alopecosa pulverulenta</i>	-0.0452	0.0419	0.303	0.1
	<i>Bathyphantes gracilis</i>	-0.0029	0.0026	0.283	0.1
	<b><i>Bolyphantes luteolus</i></b>	<b>0.0101</b>	<b>0.0037</b>	<b>0.02</b>	<b>0.4</b>
	<i>Centromerita concinna</i>	0.0104	0.0084	0.241	0.12
	<i>Centromerus arcanus</i>	-0.1	0.052	0.081	0.25
	<i>Ceratinella brevipes</i>	0.0009	0.0035	0.794	0.01
	<i>Diplocentria bidentata*</i>	-0.0021	0.0044	0.635	0.02
	<i>Hilaira frigida</i>	0.0039	0.0102	0.709	0.01
	<i>Macrargus carpenteri*</i>	0.0059	0.0163	0.724	0.01
	<i>Oreonetides vaginatus*</i>	0.0139	0.008	0.108	0.22
	<i>Oryphantes angulatus*</i>	-0.0438	0.1147	0.71	0.01
	<i>Palliduphantes ericaeus</i>	-0.0179	0.0361	0.629	0.02
	<i>Pardosa nigriceps</i>	0.0013	0.0007	0.111	0.21
	<i>Pardosa pullata</i>	0.0005	0.0014	0.707	0.01
	<i>Scotinytus evansi*</i>	-0.0016	0.0013	0.24	0.12
	<i>Tenuiphantes menzei</i>	-0.0175	0.0163	0.306	0.09
	<i>Tenuiphantes zimmermanni</i>	0.0726	0.1144	0.539	0.04
	<i>Walckenaeria acuminata</i>	-0.0011	0.0116	0.924	0
	<i>Walckenaeria antica</i>	-0.0012	0.0021	0.569	0.03
	<i>Walckenaeria clavicornis*</i>	-0.0043	0.0034	0.232	0.13
	<b><i>Walckenaeria nudipalpis</i></b>	<b>0.0087</b>	<b>0.0037</b>	<b>0.038</b>	<b>0.33</b>
Heath	<i>Alopecosa pulverulenta</i>	0.0332	0.1545	0.834	0
	<i>Centromerita concinna</i>	0.0883	0.0499	0.105	0.22
	<i>Centromerus arcanus</i>	0.0011	0.0029	0.712	0.01
	<i>Ceratinella brevipes</i>	0.0073	0.0038	0.081	0.25
	<i>Clubiona trivialis</i>	0.0003	0.0054	0.958	0
	<b><i>Gonatium rubens</i></b>	<b>0.0405</b>	<b>0.0142</b>	<b>0.016</b>	<b>0.43</b>
	<b><i>Hilaira frigida</i></b>	<b>0.0385</b>	<b>0.0145</b>	<b>0.023</b>	<b>0.39</b>
	<i>Macrargus carpenteri*</i>	0.023	0.0236	0.351	0.08
	<i>Mecynargus morulus*</i>	-0.0005	0.0023	0.822	0

	<i>Oreonetides vaginatus*</i>	0.0043	0.0024	0.108	0.22
	<i>Oryphantes angulatus*</i>	0.0077	0.0105	0.479	0.05
	<i>Palliduphantes ericaeus</i>	0.0126	0.0135	0.37	0.07
	<i>Pardosa nigriceps</i>	0.0075	0.0074	0.329	0.09
	<i>Pardosa palustris</i>	0.0015	0.0018	0.439	0.06
	<i>Pardosa pullata</i>	-0.0022	0.0038	0.573	0.03
	<b><i>Robertus lividus</i></b>	<b>0.0037</b>	<b>0.0009</b>	<b>0.002</b>	<b>0.58</b>
	<b><i>Scotinytus evansi*</i></b>	<b>0.0093</b>	<b>0.004</b>	<b>0.042</b>	<b>0.33</b>
	<b><i>Tenuiphantes mengei</i></b>	<b>0.0448</b>	<b>0.0195</b>	<b>0.042</b>	<b>0.32</b>
	<i>Tenuiphantes tenuis</i>	-0.0001	0.0021	0.974	0
	<i>Tenuiphantes zimmermanni</i>	0.032	0.0337	0.363	0.08
	<i>Walckenaeria acuminata</i>	-0.0036	0.0057	0.544	0.03
	<i>Walckenaeria clavicornis*</i>	0.011	0.0089	0.242	0.12
	<i>Xysticus cristatus</i>	-0.0092	0.0204	0.662	0.02
Wood	<i>Agroeca brunnea</i>	-0.0002	0.0032	0.959	0
	<i>Agyneta subtilis*</i>	0.0025	0.0039	0.535	0.04
	<i>Alopecosa pulverulenta</i>	-0.0017	0.005	0.736	0.01
	<i>Amaurobius fenestralis</i>	-0.0134	0.0222	0.559	0.03
	<i>Bolyphantes alticeps</i>	-0.0084	0.0056	0.162	0.17
	<i>Bolyphantes luteolus</i>	0.0072	0.0051	0.185	0.15
	<b><i>Centromerus arcanus</i></b>	<b>0.0164</b>	<b>0.0066</b>	<b>0.029</b>	<b>0.36</b>
	<i>Centromerus prudens</i>	0.0045	0.0038	0.261	0.11
	<b><i>Centromerus sylvaticus</i></b>	<b>0.0164</b>	<b>0.0057</b>	<b>0.015</b>	<b>0.43</b>
	<i>Ceratinella brevipes</i>	0.0091	0.0068	0.205	0.14
	<i>Cryphoeca silvicola</i>	-0.0226	0.0303	0.472	0.05
	<i>Erigonella hiemalis</i>	-0.0025	0.0016	0.154	0.18
	<b><i>Gonatium rubellum</i></b>	<b>0.0542</b>	<b>0.0202</b>	<b>0.021</b>	<b>0.4</b>
	<i>Hilaira excisa</i>	0.0006	0.0024	0.802	0.01
	<i>Macrargus rufus</i>	-0.0005	0.0174	0.976	0
	<b><i>Micrargus apertus</i></b>	<b>0.0108</b>	<b>0.0029</b>	<b>0.004</b>	<b>0.55</b>
	<i>Monocephalus castaneipes*</i>	-0.0019	0.0058	0.751	0.01
	<b><i>Monocephalus fuscipes</i></b>	<b>0.0256</b>	<b>0.0108</b>	<b>0.037</b>	<b>0.34</b>
	<i>Oreonetides vaginatus*</i>	0.0018	0.0031	0.577	0.03
	<i>Palliduphantes ericaeus</i>	0.0145	0.0118	0.245	0.12
	<i>Palliduphantes pallidus</i>	0.0069	0.0032	0.058	0.29
	<i>Pardosa nigriceps</i>	-0.0014	0.0023	0.559	0.03
	<i>Saaristoa abnormis</i>	0.0064	0.0042	0.149	0.18
	<i>Stemonyphantes lineatus</i>	-0.0012	0.0014	0.393	0.07
	<i>Tapinocyba pallens</i>	0.0174	0.0109	0.14	0.19

<b><i>Tenuiphantes alacris</i></b>	<b>0.1112</b>	<b>0.0182</b>	<b>&lt;0.001</b>	<b>0.77</b>
<b><i>Tenuiphantes mengei</i></b>	<b>0.0244</b>	<b>0.0096</b>	<b>0.027</b>	<b>0.37</b>
<i>Tenuiphantes tenebricola</i>	0.0078	0.0134	0.572	0.03
<i>Tenuiphantes zimmermanni</i>	0.1548	0.1328	0.268	0.11
<b><i>Trochosa terricola</i></b>	<b>0.0133</b>	<b>0.0052</b>	<b>0.026</b>	<b>0.37</b>
<b><i>Walckenaeria acuminata</i></b>	<b>0.0344</b>	<b>0.0156</b>	<b>0.049</b>	<b>0.31</b>
<i>Walckenaeria cucullata</i>	-0.009	0.0069	0.218	0.13
<i>Walckenaeria nudipalpis</i>	0.0064	0.0032	0.074	0.26

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