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Research article

Temporal variation in spider trophic interactions is explained by the influence of weather on prey communities, web building and prey choice

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Generalist invertebrate predators are sensitive to weather conditions, but the relationship between their trophic interactions and weather is poorly understood. This study investigates how weather affects the identity and frequency of spider trophic interactions over time, alongside prey community structure, web characteristics and prey choice. Spiders (Linyphiidae and Lycosidae) and their prey were collected from barley fields in Wales, UK, from April to September 2017–2018. The gut contents of 300 spiders were screened using DNA metabarcoding, analysed via multivariate models and compared against prey availability using null models. When linyphiids were collected from webs, the height and area of webs were recorded and compared against weather conditions. Trophic interactions changed over time and with weather conditions, primarily related to concomitant changes in prey communities. Spiders did, however, appear to mitigate the effects of structural changes in prey communities through changing prey preferences according to prevailing weather conditions, possibly facilitated by adaptive web construction. Using these findings, we demonstrate that prey choice data collected under different weather conditions can be used to refine inter-annual predictions of spider trophic interactions, although prey abundance was secondary to diversity in driving the diet of these spiders. By improving our understanding of the interaction between trophic interactions and weather, we can better predict how ecological networks are likely to change over time in response to variation in weather conditions and, more urgently, global climate change.

Keywords: climate, dietary analysis, metabarcoding, meteorology, network ecology, predictive modelling

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Introduction

Trophic interactions are fundamental to ecosystem functioning, energy transfer and biodiversity maintenance (Logan et al. 2006). Weather can profoundly affect the frequency and diversity of trophic interactions over time by modifying habitat suitability (Kuntner et al. 2014), emergence times (Thackeray et al. 2016) and encounter rates (Moya-Laraño et al. 2012) among many other factors. These effects can arise through rapid short-term (i.e. weather fluctuations) and gradual long-term change (i.e. climate change; Ovadia and Schmitz 2004, Thackeray et al. 2016) and can vary across trophic levels, with lower trophic levels exhibiting the greatest sensitivity to change, leading to the uncoupling of links in ecological networks through phenological trophic mismatches (Thackeray et al. 2016). Phenological mismatches between tree budburst, caterpillar emergence, and the arrival and reproduction of migratory birds which feed on these caterpillars, for example, illustrate this (Bell 2014), although weather can also impact consumers independent of resource availability (Finch et al. 2022). With weather conditions predicted to become increasingly variable with climate change (Kareiva et al. 1993, Stemkovski et al. 2022), it is important to understand how changes to highly stochastic weather processes may influence spatial and temporal dynamics of consumer trophic ecology.

Spiders have often been used as model invertebrate predators given that they are abundant generalist predators and the prey encounter rates of web-building spiders have traditionally been easily estimated from webs (Welch et al. 2016). Given their substantial contributions to biocontrol (Sunderland et al. 1986, Michalko et al. 2019, Cuff et al. 2022a), much interest has surrounded the trophic dynamics of spiders in agricultural systems. Spiders are known to respond to weather changes (Ovadia and Schmitz 2004), with open pits on their tarsal organs thought to detect changes in humidity and temperature (Barth 2001). Changes in these conditions have been shown, for example, to alter the frequency and timing of discrete behaviours such as ballooning, the act of dispersing long distances using silk to move through the air (Greenstone 1990, Weyman 1993, Suter 1999, Bell et al. 2005, Reynolds et al. 2007). Alongside humidity and temperature, spiders respond strongly to changes in solar radiation (Høye and Forchhammer 2008). How spiders more generally respond to temporal variation in weather, particularly in terms of their trophic ecology, is, however, poorly understood (Aitchison 1984).

Dietary intake by spiders, and its variation over time, is likely to be affected by weather, climate and prey availability (Crouch and Lubin 2000), with the results dictating development and survival (Li 2002). Spiders are known to be thermally tolerant and many remain active throughout the winter months although their prey capture rates are reduced at low temperatures (Aitchison 1984, Korenko et al. 2010, Boreau De Roincé et al. 2013). The dietary specialism and trophic niche breadth of spiders appears to remain stable across temperature gradients, but the identities of their prey change (Eitzinger et al. 2021). Spiders more evenly exploit prey in warmer environments with smaller fluctuations in precipitation, and the identity of prey changes along temperature and precipitation gradients (Birkhofer and Wolters 2011). Spiders can mitigate some of the effects of weather change by adapting their web-building behaviours and web characteristics (Napiórkowska et al. 2021); for example, *Argiope keyserlingi* (Araneae: Araneidae) decorate their webs more at lower temperatures, possibly to overcome reduced prey activity (Herberstein and Fleisch 2003). The ability of spiders to adaptively respond, however, is finite and extreme conditions such as heavy dew can exceed the loading capacity of webs, and reduce prey capture (Brackenbury 2009).

Although we understand how the trophic and behavioural ecology of spiders responds to a selection of weather conditions, we lack information surrounding the interactive effects of changes in weather conditions on the interactions between spiders and their prey, and how spiders can adapt to these fluctuations. In this study, we assess how the trophic interactions of linyphiid and lycosid spiders change with temporal variation in weather conditions and whether observed differences are likely to be driven by prey community changes. We specifically investigate temporal covariation of weather and the identities of spider trophic interactions, prey community structure, web characteristics and prey choice. We hypothesised that:

1. Temporal variation in spider trophic interactions is related to weather conditions.
2. Covariance in weather conditions and spider trophic interactions is related to the abundance of prey taxa.
3. Web area and height differ with weather, suggesting that variability in spider trophic interactions over time is reduced by adaptive web-building under variable weather conditions.
4. Including relationships between weather and prey choice in prey choice models will improve predictions of spider trophic interactions over time.

Material and methods

Fieldwork and sample processing

Field collection and sample processing has been described previously by Cuff et al. (2022a), but is briefly described in Supporting information. In short, money spiders (Araneae: Linyphiidae) and wolf spiders (Araneae: Lycosidae) were collected from occupied webs and the ground in barley fields between April and September 2018. Linyphiids occupying webs (n = 78) were prioritised for collection, but ground-active linyphiid and lycosid spiders were also collected. For each linyphiid taken from a web, the height of the web from the ground (mm) and its approximate dimensions were recorded, the latter calculated as approximate web area (mm^2). To obtain data on local prey density, ground and crop stems were suction sampled using a 'G-vac' for approximately

30 s at each 4 m^2 quadrat from which spiders were collected. Extraction, amplification and sequencing of DNA, and bioinformatic analysis, is described by Cuff et al. (2022a) and Drake et al. (2022), and is also detailed in Supporting information. Amplification was carried out using two complementary PCR primer pairs: one targeting invertebrates generally, and one intended to exclude amplification of spider DNA to reduce the prevalence of 'host' reads in the data output (Cuff et al. 2023). Amplicons were sequenced via Illumina MiSeq V3 with 2 × 300 bp paired-end reads. The resultant sequencing read counts were converted to presence–absence data of each detected prey taxon in each individual spider. Given the prevalence of sequencing reads associated with each spider analysed, and the impossibility of disentangling these from detections of intraspecific predation (i.e. cannibalism), all such reads were removed (Cuff et al. 2023), although intrageneric and intrafamilial predation were still detected and retained.

Weather data

Weather data were taken from publicly available reports from the Cardiff Airport weather station (6.6 km from the study site) via 'Wunderground' (Wunderground 2020), to represent local weather conditions. This does not necessarily reflect smaller-scale effects (e.g. microclimate-scale; Holtzer et al. 1988, Bell 2014), but the timescale of detection for dietary metabarcoding reduces the value of that resolution, given that spiders may forage across multiple microclimates. We collated data from 1 January 2018 to 17 September 2018 (the last field collection). Weather data were also separately extracted for the week preceding each of the two 2017 collection dates (3–9 August and 29 August to 4 September 2017; detailed below). Specifically, daily average temperatures (°C), daily average dew point (°C), maximum daily wind speed (km h^{-1}), daily sea level pressure (hPa) and day length (min; sunrise to sunset) were recorded. Precipitation data were downloaded via the UK Met Office Hadley Centre Observation Data (UK Met Office 2020) as regional precipitation (mm) for south-west England and Wales. Weather data were converted to mean values for the seven days preceding each collection of spider samples to correspond with the longevity of DNA in the guts of spiders (Greenstone et al. 2014).

Statistical analysis

All analyses were conducted in R ver. 4.0.3 (www.r-project.org). To assess how weather affects spider trophic interactions over time, we analysed dietary changes across weather gradients using multivariate models. To identify whether this was likely to be driven by changes in prey abundance, we assessed the corresponding changes in the prey communities and then used null models to ascertain whether spiders were responding to prey abundance changes through prey choice. Given the dependence of linyphiid spiders on webs for foraging, we also compared web height and area over weather gradients to assess whether this may be a component of adaptive foraging. To assess the inter-annual consistency of prey choices in response to weather conditions, we also assessed whether prey preference data could be used to improve the predictive power of prey choice models. For this, we generated null models for 2017 data with prey abundance weighted by prey preferences estimated with the 2018 data. This allowed us to assess the consistency of prey choice under similar conditions, but also provided insight as to whether this framework can be used to predict predator responses to diverse prey communities under dynamic conditions. We detail the specific stages of this analytical framework in the sections below.

Sampling completeness and diversity assessment

To assess the diversity represented by the dietary analysis and the invertebrate community sampling, and the completeness of those datasets, coverage-based rarefaction and extrapolation were carried out, and Hill diversity calculated (Chao et al. 2014, Roswell et al. 2021). This was performed using the 'iNEXT' package with species represented by frequency-of-occurrence across samples (Chao et al. 2014, Hsieh et al. 2016, Supporting information).

Relationships between weather, spider trophic interactions and prey community composition

Prey species that occurred in only one spider individual were removed before further analyses to prevent outliers skewing the results. Spider trophic interactions were related to temporal and weather variables in multivariate generalized linear models (MGLMs) with a binomial error family (Wang et al. 2012). Trophic interactions were related to temporal variables and their pairwise interactions (including spider genus to account for any confounding effect), weather variables and their pairwise interactions, and weather variables and their interactions with spider genus and time (to account for any confounding effects) in three separate MGLMs. These variables were separated into different models (Temporal model, Weather interaction model and Confounding effects model) to improve model fit and reduce singularity. Invertebrate communities from suction sampling were related to temporal and weather variables in identically structured MGLMs (excluding the spider genus variable) with a Poisson error family.

All MGLMs were fitted using the *manyglm* function in the 'mvabund' package (Wang et al. 2012). 'Temporal model' independent variables were calendar day (*day*), mean day length in minutes for the preceding week (*day length*), spider genus (for dietary models only, to ascertain any effect of spider taxonomic differences on dietary differences over time and day lengths) and all two-way interactions between these variables. 'Weather interaction model' independent variables were mean temperature, precipitation, dewpoint, wind speed and pressure for the preceding week, and pairwise interactions between weather variables. 'Confounding effects model' independent variables were day (to investigate the interaction between time and weather), spider genus (for dietary models only, to ascertain any effect of spider taxonomic differences on dietary differences over time and day lengths), mean

temperature, precipitation, dewpoint, wind speed and pressure for the preceding week, and two-way interactions of each weather variable with day and genus.

Trophic interaction and community differences were visualised by non-metric multidimensional scaling (NMDS) using the *metaMDS* function in the 'vegan' package (Oksanen et al. 2016) in two dimensions and 999 simulations, with Jaccard distance for spider diets and Bray–Curtis distance for invertebrate communities. For the dietary NMDS, outliers (n = 21; samples containing rare taxa) obscured variation on one axis and were thus removed to facilitate separation of samples and achieve minimum stress. For visualization of the effect of continuous variables against the NMDS, surf plots were created with scaled coloured contours using the *ordisurf* function with the 'ggplot2' package (Wickham 2016).

Relationships between web characteristics and weather variables

Web area and height were compared against weather and temporal variables using a multivariate linear model (MLM) with the 'manylm' command in 'mvabund' (Wang et al. 2012). Log-transformed web area and height comprised the multivariate dependent variable and day, spider genus, temperature, precipitation, dewpoint, wind, pressure and two-way interactions between each of these and with day and genus comprised the independent variables.

Variation in spider prey choice across weather conditions

To separately represent spiders from different weather conditions in prey choice analyses, sample dates for every spider were clustered based on the mean weather conditions (temperature, precipitation, dewpoint, wind and pressure) of the week before collection (seven days, to align approximately with spider gut DNA half-life; Greenstone et al. 2014). Alongside data from 2018 (n = 24 collection dates), two sampling periods from 2017 were included in the clustering to ascertain similarity of weather conditions for additional interannual prey choice analyses described below (see Supporting information for description of clustering process). Five clusters were generated: high pressure (HPR), hot (HOT), wet low dewpoint (WLD), dry windy (DWI), wet moderate dewpoint (WMD), and 2017 (2017 sampling periods).

Prey preferences of spiders in each of the weather clusters were analysed using network-based null models in the 'econullnetr' package (Vaughan et al. 2018) with the 'generate_null_net' command. Consumer nodes in this case represented spiders belonging to each of the weather clusters. 'econullnetr' generates null models based on prey abundance, represented here by suction sample data, to predict how consumers will forage if based on the abundance of resources alone. These null models are then compared against the observed interactions of consumers (i.e. interactions of spiders within each weather cluster with their prey) to ascertain the extent to which resource choice deviated from random (i.e. density dependence). The trophic network was visualised with the associated prey choice effect sizes using 'igraph' (Csardi and Nepusz 2006) with a circular layout, and as a bipartite network using 'ggnetwork' (Briatte 2021, Wickham 2016). The normalised degree of each weather cluster node was generated using the 'bipartite' package (Dormann et al. 2008) and compared against the normalised degree of the same node in the null network to determine whether spiders were more or less generalist than expected by random. Prior to the prey choice analysis, an hemipteran prey identified no further than order level through dietary analysis was removed due to the inability to pair it to any present prey taxa with certainty.

Validating and predicting relationships between years

To test how generalisable the results are and the extent to which weather drives prey preferences, we used a measure of prey preference (observed/expected values; observed interaction frequencies divided by interaction frequencies expected by null models) from the above prey choice analysis to assess whether we could more accurately predict observed trophic interactions under similar weather conditions for data from a linked study at the same location in 2017. These additional data represent a subset of the spider taxa analysed above (*Tenuiphantes tenuis* and *Erigone* spp.) collected using the same methods by the same researchers and in the same locality (Cuff et al. 2021b).

The similarity in weather conditions between the 2017 study period and each of the five 2018 weather clusters was determined via NMDS of the weather data in two dimensions with Euclidean distance. Centroid coordinates for each 2018 weather cluster and the 2017 data were extracted and pairwise distances calculated between weather clusters:

$$\text{distance} = \sqrt{\left((x2 - x1)^2 + (y2 - y1)^2\right)}$$

In order, the most proximate weather clusters to the 2017 weather data were HPR (mean Euclidean distance = 8.845), HOT (9.290), WMD (13.626), DWI (13.817) and WLD (18.682, Supporting information).

To facilitate comparison between the two years, observed/expected values from the 2018 prey choice models were extracted separately for each of the weather clusters and scaled between 0.1 and 1. For this, 0.1 was used as a minimum since 0 would result in interactions being excluded altogether in the null models, and one as a maximum given the limits of 'econullnetr', but also because this is a multiplier applied to the prey abundances, so greater values would skew prey abundances beyond realistic proportions. Scaling was achieved by the following equation:

$$\text{Scaled value } x = \frac{x - \min(x)}{\max(x) - \min(x)} \times 0.9 + 0.1$$

Missing values (e.g. prey that were absent in certain weather conditions) were represented as 1 to prevent transformation of their abundances in the null models; this treats prey for which data were absent naively, but could increase perceived preferences for them. The scaled values were used to weight

the abundance of prey available to the spiders in the 2017 data using the weighting option in 'econullnetr', whereby values ≤ 1 proportionally reduce the probability of that taxon being predated in the null models. This effectively redistributes the 2017 relative prey abundance data according to the preferences calculated for each of the 2018 weather clusters. If prey preferences are similar between the 2017 spiders and those from the weather cluster being used to weight the model, the composition of simulated diets should more closely resemble observed diets and fewer significant deviations from the null model should be found.

Null models were generated as in the section Variation in spider prey choice across weather conditions, but based on the prey availability and trophic interactions from 2017 samples. Three types of model were run: 1) a conventional model based on observed prey abundances; 2) a model with prey abundances set to be equal across all prey taxa; and 3) observed prey abundances weighted by prey preferences determined for each of the weather clusters in the 2018 prey choice analysis. A separate model was run for each 2018 weather cluster with abundances weighted by the corresponding scaled observed/expected values. The unweighted conventional model was compared against weighted models to ascertain whether the prey preference weightings from 2018 improved the predictive power of the null models. To compare effect sizes between the unweighted and each other null model for each resource taxon, mean standardised effect size (SES) values were calculated from the paired 'pre-harvest' and 'post-harvest' data from each model, and paired t-tests were carried out with these between the unweighted and each weighted model. The SES values were plotted for each model and joined between taxa to visualise these paired differences using 'ggplot' (Wickham 2016). Null model-predicted trophic interactions were generated via a modified 'econullnetr' function (*generate_null_net_indiv*) which produces outputs at the individual level to generate simulated diets for individual spiders to compare dietary composition between null model predictions and observed data. These models were run with 2300 simulations to represent 50 simulations per individual spider in the 2017 dataset (n = 46). Null diets were associated with sample IDs by aggregating the 50 simulations per sample and retaining a mean incidence of prey (i.e. mean occurrence across all 50 simulations). A visualisation of the per-sample differences in null model and observed data was generated via NMDS. Mean centroid coordinates for the observed 2017 data and the predicted diets of each model were extracted and the Euclidean distance between the observed data centroid and that of each model was calculated (as above for weather conditions).

Results

Relationships between spider trophic interactions and weather variables

Following bioinformatics, sequencing yielded 7 351 188 and 6 574 698 reads for the general invertebrate and spider exclusion PCR primers, respectively. Dietary analyses identified prey in the guts of 244 of the 300 spiders, comprising 89 taxa across 45 families. Additional details on dietary composition and comparison of these diets across biological traits (taxon, sex and age) are reported by Cuff et al. (2022a). Sample coverage across all spiders was estimated to be 94% and the trophic interactions largely comprised common prey (Supporting information).

Spider trophic interactions were related to both temporal and weather variables (Fig. 1), varying across the study period and in relation to day length (Fig. 1, Supporting information). The interaction between day and day length, as well as the interactive effects of sample day and spider genus, and day length and spider genus, were also significant (Supporting information). There were a number of taxon-specific relationships, most of which involved springtails and thrips (specifically with calendar day, day length and their interactive effects, Supporting information). Whilst interactions between day and day length with spider genus were significant, no specific prey abundances were significantly related to these interactive effects. Spider trophic interactions were also significantly related to temperature, precipitation, dewpoint, wind and pressure (Supporting information), and interactions between temperature and precipitation, temperature and pressure, dewpoint and wind, dewpoint and pressure, and wind and pressure (Fig. 1, Supporting information). Again, several specific prey taxa were significantly related to these variables, most of which were springtails, thrips and rove beetles (specifically with all of the overall significant variables and interactions except the interaction between dewpoint and wind, Supporting information). The relationship between spider trophic interactions and weather does, however, change over time and with different spider genera (Supporting information), although no specific taxa were related to these interactions (Supporting information).

Relationships between prey community composition and weather variables

Invertebrate surveys identified 72 taxonomic families, across 11 orders. Across all communities, sample coverage was estimated to be 99% and the communities were dominated by common families, yet there was a relatively high incidence of rare taxa (Supporting information).

Invertebrate community structure was temporally variable and related to weather variables (Fig. 2), with variation related to calendar day and day length (Fig. 2), but also the interaction between these variables (Supporting information). In total, 63 significant taxon-specific relationships between abundance and temporal variables were identified (Supporting information). Invertebrate communities were also significantly related to temperature, precipitation, dewpoint, wind and pressure (Fig. 2), and interactions between temperature and precipitation, temperature and dewpoint, precipitation and wind, and wind and pressure (Supporting information). Specific taxa were related to each of these variables and interactions with the exception of the interaction

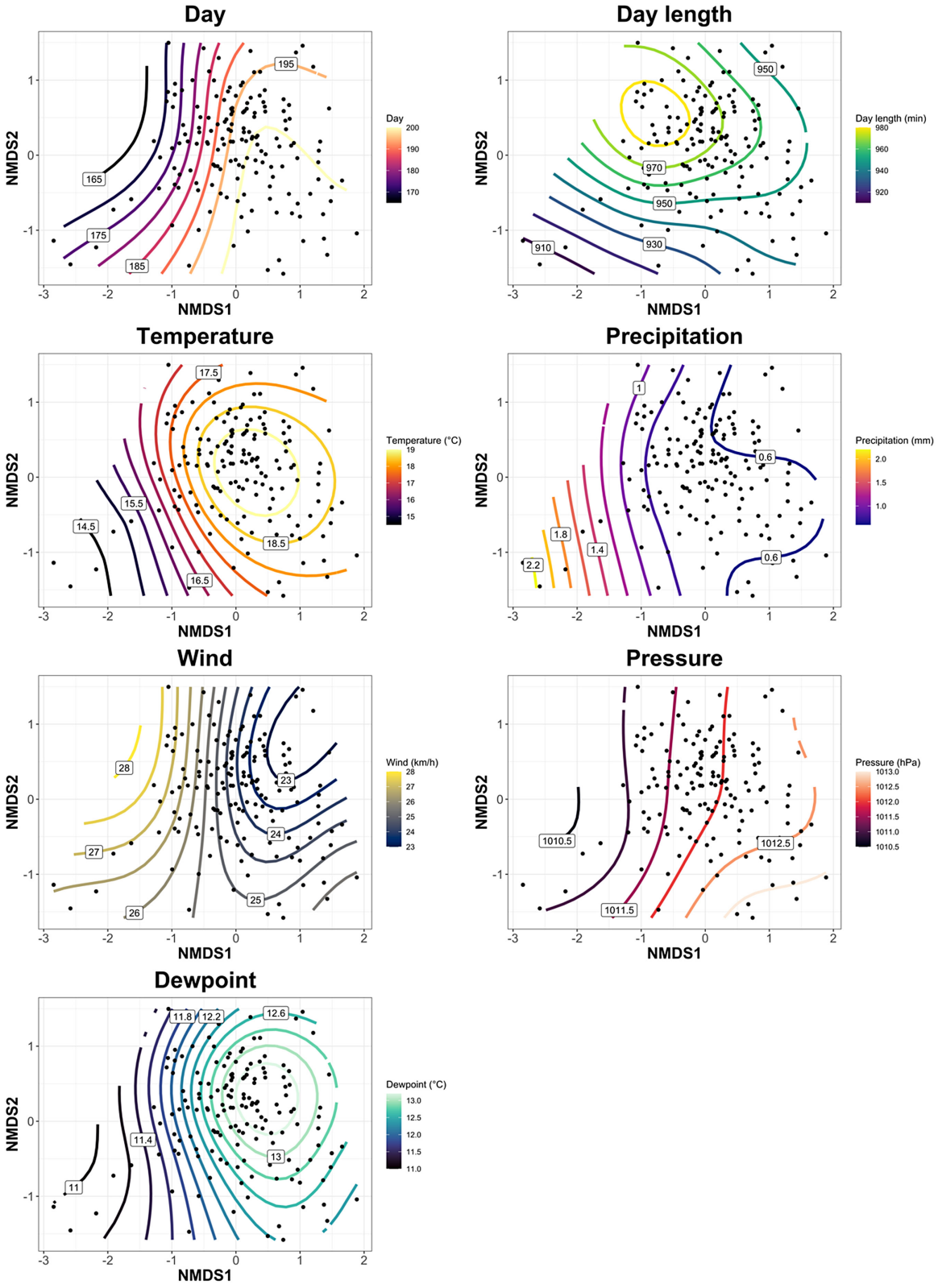

Figure 1. Non-metric multi-dimensional scaling of spider diets with contours representing an approximate relationship between continuous variables and dietary data. Axes represent two-dimensional variation in spider diets. Each point represents the dietary composition of a single spider, with distance between them indicating their dissimilarity (i.e. proximate points are similar, distant points are dissimilar). Numbers in boxes denote the value associated with the linked contour. See Supporting information for an alternative plot with taxon labels.

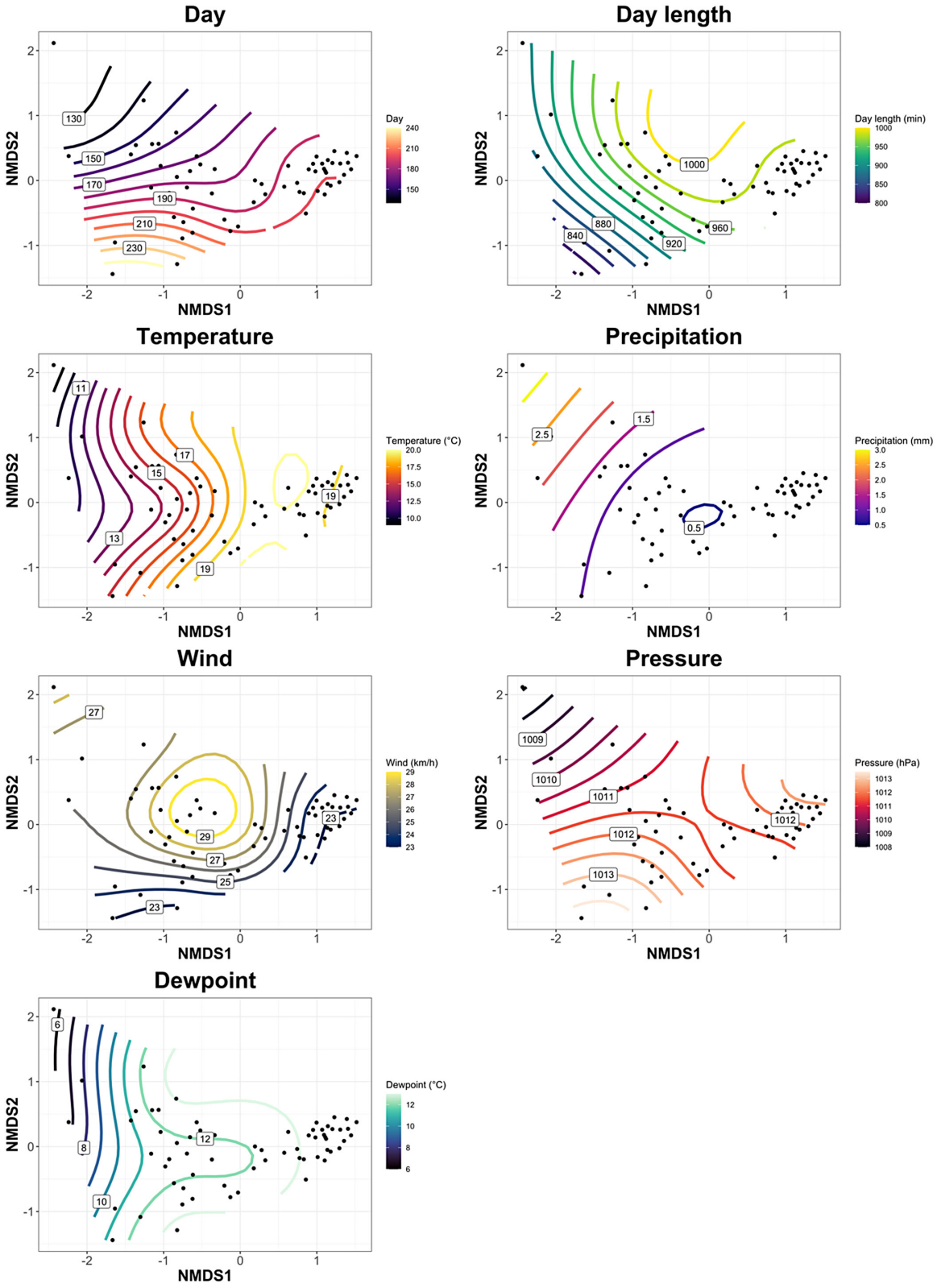

Figure 2. Non-metric multi-dimensional scaling of invertebrate communities with contours representing an approximate relationship between continuous variables and community data. Axes represent two-dimensional variation in invertebrate communities. Each point represents the composition of a single community, with distance between them indicating their dissimilarity (i.e. proximate points are similar, distant points are dissimilar). Numbers in boxes denote the value associated with the linked contour. See Supporting information for an alternative plot with taxon labels.

between wind and pressure, but there were specific taxa related to the interaction between precipitation and pressure despite the absence of a significant effect at the community level (Supporting information). The relationship between invertebrate communities and weather does, however, change over time (Supporting information), and 22 significant relationships were identified between specific prey taxa and these interactions (Supporting information).

Relationships between web characteristics and weather variables

Spider web characteristics significantly differed in relation to dewpoint, but also the interaction between dewpoint and day (Supporting information). Web characteristics also significantly differed in relation to interactions between spider genus and precipitation, day and temperature, day and precipitation, day and wind, and day and pressure (Supporting information). Web height and area also separately significantly related to all of the weather variables and interactions that significantly related to web characteristics as a multivariate dependent variable, i.e. only dewpoint of the weather variables, which had a non-linear relationship with web height and area, and otherwise six interactions (Supporting information).

Variation in spider prey choice across weather conditions

Significant taxon-specific deviations from density-dependent prey choice were identified, which differed across the five different weather clusters (Fig. 3, 4). The normalised degree (i.e. number of interactions per node) of spiders in WLD (SES = 2.579, observed = 0.128, null = 0.087 ± 0.032), HPR (SES = 2.299, observed = 0.410, null = 0.317 ± 0.083) and DWI (SES = 2.569, observed = 0.308, null = 0.225 ± 0.068) were higher than expected (Fig. 4).

Validating and predicting relationships with preference data

By using the observed/expected values from the weather cluster-based 2018 prey choice models as weightings for prey abundances in a 2017 dataset, deviations from foraging expected by null models were altered, the directionality of the change depending on the prey taxon and the weather cluster used (Fig. 5). The weightings derived from the weather cluster most similar to 2017, HPR, altered the significance of deviation from the null model for three interactions. For Cicadellidae, the HPR effect size weighting resulted in non-significant deviations from random foraging that were otherwise significant. For Cecidomyiidae and Thripidae, however, significant deviations from random were determined when using the HPR effect size weighting that were not previously significant. The significance of the effect sizes for the remaining ten prey taxa remained unchanged. Null models weighted by preference data for the other weather clusters resulted in similar changes to the significance of differences between the null model and observed interactions, with the notable exception of DWI (the second most dissimilar cluster to 2017), for which there were many more differences. The equal prey abundance model resulted in the greatest number of significant prey preferences, but no significant avoidances.

Prey preference effect sizes did not significantly differ from those in the unweighted model for the HPR (paired t-test: mean difference = −0.025, t = −0.278, df = 93, p = 0.781), WMD (paired t-test: mean difference = −0.075, t = −0.655, df = 93, p = 0.514), HOT (paired t-test: mean difference = −0.119, t = −1.346, df = 93, p = 0.182), WLD (paired t-test: mean difference = −0.108, t = −1.246, df = 93, p = 0.216), DWI (paired t-test: mean difference = −0.048, t = −0.456, df = 93, p = 0.650) nor equal prey abundance (paired t-test: mean difference = 1.305, t = 1.707, df = 22, p = 0.102) models. The SESs in the weather cluster preference weighted models inconsistently differed from the unweighted model (Supporting information). The compositions of diets predicted by null models were generally similar but did differ in their similarity to the observed diets. The equal prey abundance model predicted diets most compositionally similar to the observed data (mean Euclidean distance = 0.337), followed by the DWI (0.463), WMD (0.495), HPR (0.500), WLD (0.513), HOT (0.514) and unweighted (0.526) predictions, respectively (Supporting information).

Discussion

We show that spider trophic interactions change over time and in relation to weather, likely driven by changing prey community structure. The effects of these prey community changes on spider diet are, however, seemingly mitigated by selective foraging possibly facilitated in the case of web-building spiders by adapting web structures depending on weather conditions. Using prey choice data across different weather conditions, we were able to validate the consistency of prey preferences across weather conditions, suggesting that further assessment of the relationship between weather and prey choice could improve our capacity to predict changing trophic interactions into the future.

Interactive effects of time and weather on prey availability and consumption

Relationships between weather, spider diets and prey communities over time were complex, with many interactions between weather variables and time related to the availability of prey to spiders and the prey that were consumed. Similar interactions between weather variables were related to both dietary and prey community composition (i.e. temperature and precipitation, temperature and dewpoint, and wind and pressure), but some were specific to diet (i.e. temperature and pressure, dewpoint and wind, and dewpoint and pressure) or prey community (i.e. precipitation and wind). This suggests that interactive weather effects on dietary composition were

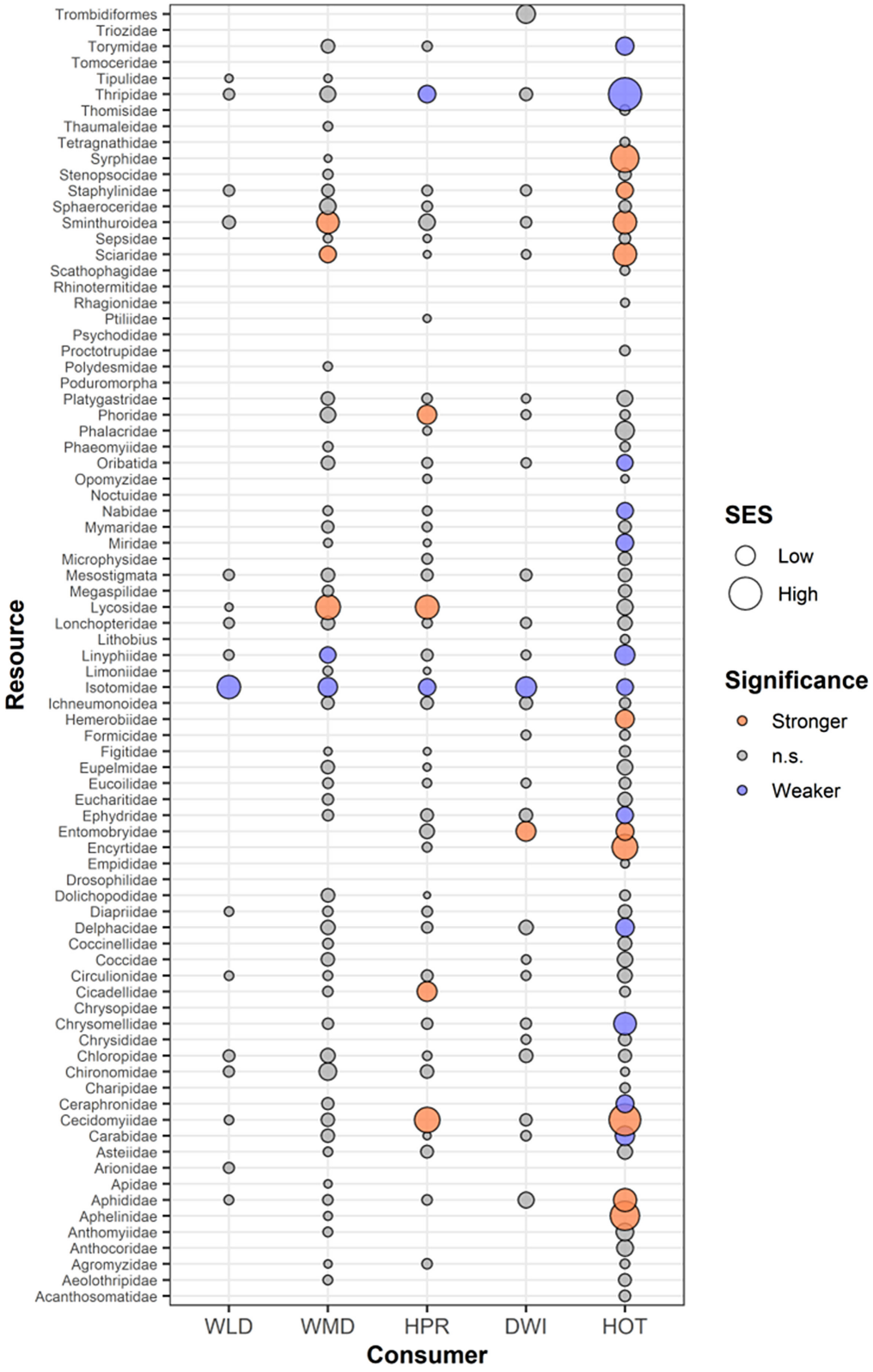

Figure 3. Prey choice standardised effect sizes (SESs) are given between each prey taxon and each consumer weather cluster. Larger points reflect larger deviations of SESs from zero (zero indicating the absence of preference). Orange, grey and blue points denote stronger (preference), non-significant (density-dependent) and weaker (avoidance) interactions compared to the null model, based on 95% confidence intervals. Absent points are those for which data were not available. These data are presented as a bipartite network in Fig. 4.

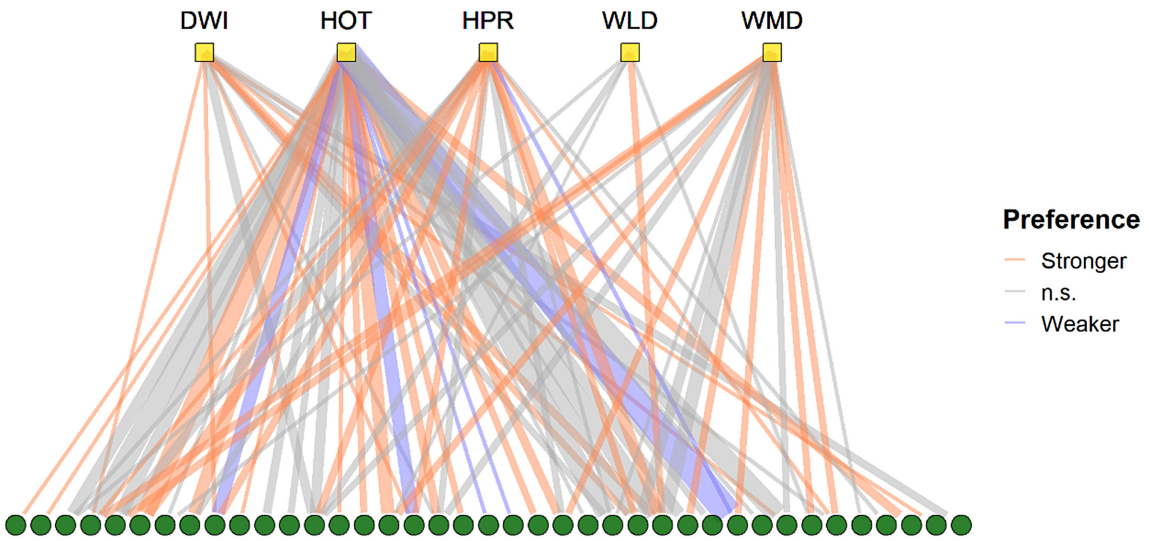

Figure 4. The 2018 interaction network between spiders in the five weather clusters and their prey, with prey abundance data incorporated to assess the selectivity (i.e. density dependence) of prey choice. Orange, grey and blue links denote interactions more, equally or less frequent than expected based on the null model, respectively. Yellow squares represent the spiders within each weather cluster, and green circles represent prey taxa. WLD = Wet, low dewpoint; WMD = wet, moderate dewpoint; HPR = high pressure; DWI = dry, windy; HOT = hot. Individual taxon responses are represented in Fig. 3.

not solely driven by weather-related changes in prey availability but instead by changes in the ecology and behaviour of both predator and prey.

Whilst weather conditions can directly determine the outcome of predator–prey interactions (Holtzer et al. 1988), invertebrate populations can be regulated by competition for resources more so than weather-related factors such as temperature (Ferguson and Joly 2002), contrary to the top–down hypothesis (Hairston et al. 1960). Here we show that weather influences even these effects. Whilst the abundance of specific prey taxa was associated with the interactive effects of time and weather, the prevalence of those taxa in the diet of spiders was inconsistently affected, suggesting that spiders are able to overcome some of the effects of short-term weather changes on the prey available to them. This suggests that the previously reported unimodal relationship of trophic interaction strength with weather conditions, in which trophic interactions are more frequent in benign conditions, may be in effect here (Spiller and Schoener 2008) and that the identity and frequency of spider trophic interactions will be less resilient to larger changes. The higher-than-expected normalised degree of spiders in WLD, HPR and DWI also suggests that spiders will expand their trophic niche under some conditions, likely driven by changes in prey availability and predator state. Given that temperature is likely to affect spider metabolism, differences in prey diversity across temperatures could reflect changes in DNA half-lives, but our data show an increase in detections at higher temperatures in line with increased prey abundance (determined via suction sampling), suggesting that this was not a significant issue (Supporting information).

The weather-dependent web characteristics and selectivity for different prey regardless of their abundance highlighted here suggest that spiders adapt their foraging based on weather-related changes in prey abundance through adaptive web building and prey switching. The ecological mechanisms through which spiders and their prey respond to these heterogeneous weather conditions are likely dependent on taxon-specific behaviours and the interaction of multiple weather variables (Table 1). The resultant highly complex and dynamic systems across weather gradients demonstrate the highly adaptable foraging ecology of these generalist predators, although the individual mechanisms underlying this require further study. Higher trophic levels are increasingly sensitive to weather effects (Voigt et al. 2003), possibly affecting the incidence of intraguild predation, although this appears inconsistent in this study. Non-consumptive effects on prey behaviour can also profoundly impact trophic networks through trophic cascades (Beckerman et al. 1997), but the interaction of weather with these effects remains poorly understood.

Validating and predicting spider prey preferences

Prey choice null models provide valuable insight into the trophic ecology of consumers in different contexts. In this study they also provided the basis for validating the consistency of prey preferences under heterogeneous weather conditions to improve predictions of trophic interactions. By applying weightings based on the effect sizes from the most similar weather cluster in the 2018 model (HPR) to prey availability and spider dietary data from 2017, it was possible to assess the inter-annual consistency of trophic interactions in response to weather. The prey preference effect sizes did not significantly differ between weighted and unweighted models, but the identity of interactions that significantly deviated from

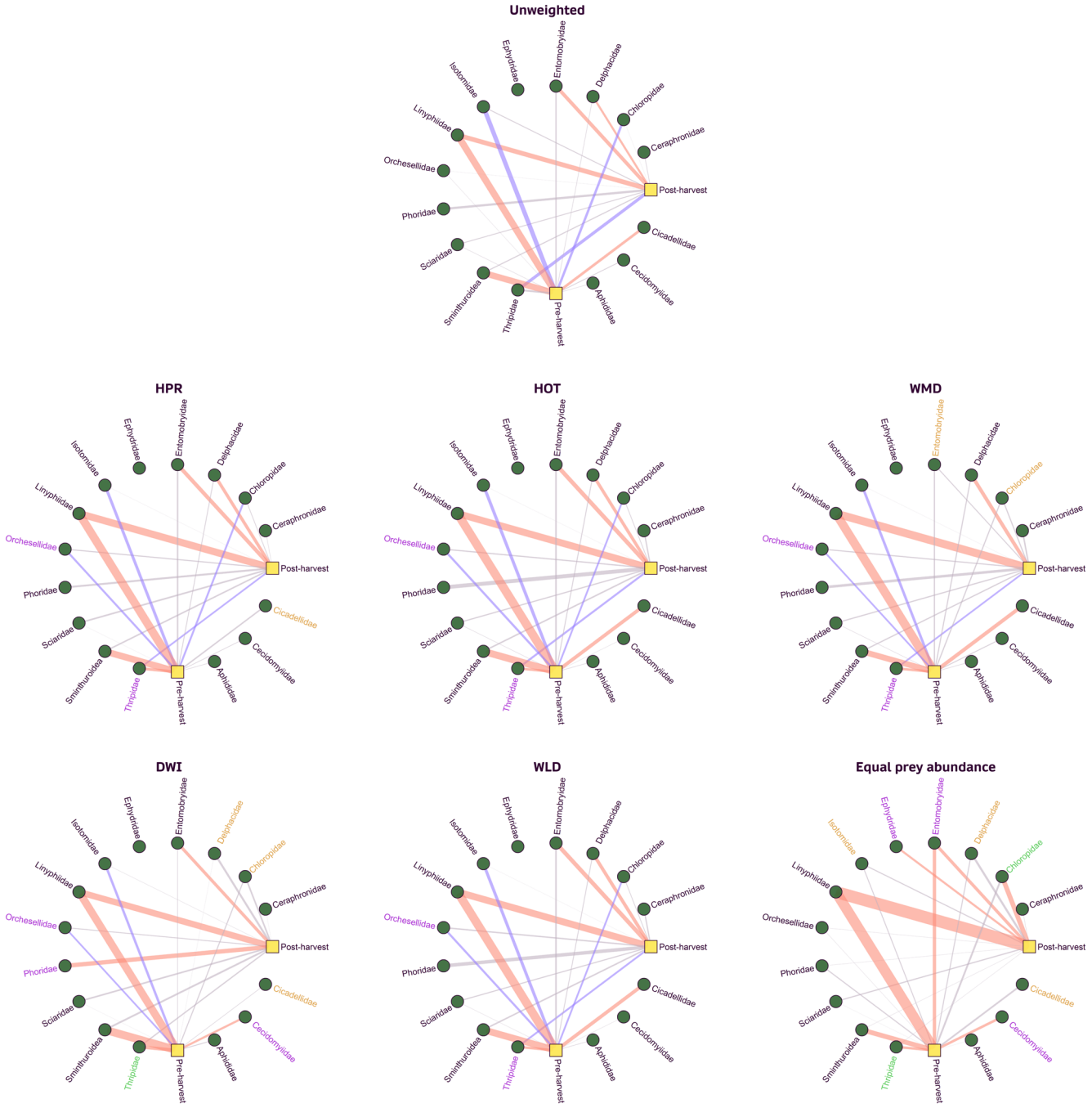

Figure 5. Network plots of 2017 spider trophic interactions with prey choice data incorporated. Blue, grey and red links denote interactions less, equally or more frequent than expected based on the associated null model, respectively. Link weights represent the standardised effect size (i.e. the strength of preference/avoidance). Yellow squares represent the two spider sampling periods, and green circles represent prey taxa. Coloured text denotes taxa for which the significance of their deviation from the null model differed from the unweighted model, with purple, green and yellow denoting more significant differences, inconsistent changes (i.e. the two spider groups vary in their difference to the unweighted model) and fewer significant differences, respectively. Prey choice is assessed without prey abundance weightings in the top network. Each other network assessed prey choice with prey abundance weighted based on effect sizes from each of the weather clusters used in the 2018 prey choice analysis, or with prey abundances represented equally (final network). Networks are ordered according to the proximity of the weather conditions of their corresponding weather cluster to the 2017 study period weather, followed by the equal prey abundance model.

Table 1. Potential mechanisms driving spider trophic interactions in this study. Supporting literature is provided when available.

Driver	Group	Ecological mechanism	Example	Reference
Temporal patterns	Prey	Phenology	Peak abundance of *Oscinella* sp. is in July, coinciding with their consumption	Vickerman (1980)
		Negative phototaxis	Many springtails are likely less abundant during summer months due to their avoidance of light	Fox et al. (2007)
		Host plants	Consumption and abundance of Thripidae species relating to day length suggests crop senescence may drive abundance decreases	This study
Temperature	Prey	Avoidance of arid conditions	Springtails (*Hypogastrura viatica* and *Isotomurus* sp.) are more commonly predated by spiders in cooler conditions given the difficulty involved in catching them at higher temperatures	Birkhofer and Wolters (2011), Frampton et al. (2001)
		Activity-density	*Limothrips denticornis* are more available to spiders at higher temperatures	Hamdy and Salem (1994), Gao et al. (2022)
	Predator	Community structure	Temperature can influence spider community structure and spatial dynamics even more than prey availability, ultimately altering competition and co-occurrence with prey	Meineke et al. (2017), Cuff et al. (2021a)
		Avoidance of arid conditions	Increased preference for smaller flying prey and avoidance of ground-running invertebrates	This study
		Activity	Spider activity increases at higher temperatures, converse to other generalist predators (e.g. carabid beetles)	Kruse et al. (2008)
		Susceptibility to pesticides and predation	Increased susceptibility to pesticides (e.g. deltamethrin) and predation (e.g. from birds) at higher temperatures may alter the identity and frequency of trophic interactions, even via non-consumptive effects of predator cues	Avery and Krebs (1984), Everts et al. (1991), Mestre et al. (2020)
Precipitation	Prey	Avoidance of waterlogging	Springtails exhibit climbing behaviour in response to precipitation	Frampton et al. (2001)
	Predator	Spatial adjustment of webs	Spiders spatially adjust their webs in response to rain	Haberkern et al. (2020)
Dewpoint	Prey	Adhesion of prey to surfaces	Small prey are immobilised when they make contact with dew	Eberhard (2018)
	Predator	Web restructuring	Spiders adjust webs either to overcome mechanical strain from dew or to exploit dew as an adornment or adhesive	Brackenbury (2009), Zheng et al. (2010), Eberhard (2018)
Wind	Prey	Dispersal	Effects on the efficiency of aerial dispersal and abundance in arthropod prey	Waiganjo et al. (2008)
	Predator	Ballooning	Wind speeds below 3 m s^{-1} promote spider dispersal by ballooning, whereas higher windspeeds prohibit it	Vugts and Van Wingerden (1976), Simonneau et al. (2016)
		Exploitation of non-flying prey	Spiders may switch to non- or poor-flying prey such as rove beetles and entomobryid springtails	This study
Pressure	Prey	Dispersal	Effects on the efficiency of flight by insect prey (e.g. thrips), modifying their abundance	Fournier et al. (2005), McFarlane et al. (2015), Smith et al. (2016)
		Grounding of flying insects	Parasitoids are grounded by rapid drops in pressure, increasing their availability to predators	Fournier et al. (2005)
	Predator	Ballooning	Pressure can determine the viability of ballooning for dispersal by spiders	Vugts and Van Wingerden (1976), Simonneau et al. (2016)

the null model and the composition of null model-predicted diets did differ. The prey composition of the simulated trophic interactions was only marginally more similar to the observed trophic interactions than the unweighted model, and less similar than models weighted by preference data from other weather conditions. This suggests that the predictions were not improved qualitatively, and factors other than weather influence these differences. In fact, a null model in which all prey were assumed to be equally abundant generated simulated diets more similar in composition to those observed, suggesting that prey abundance is secondary to diversity in driving the diet of these spiders. Prey abundance weightings based on prey choice data from similar weather conditions are therefore unlikely to completely account for the foraging behaviours of spiders. These findings are, however, based on a single network and further investigation may yield greater results, particularly if they incorporate more contextual data.

Whilst this use of weather-based prey choice data to weight simulations shows some potential (i.e. in removing significant differences between null models and observed

interactions), the outcome was imperfect. Importantly, the data used were selected solely based on proximity of weather conditions without any consideration of other factors known to influence the trophic interactions of the spiders, such as their taxonomy, life stage and sex (Cuff et al. 2022a). By incorporating increasingly data-rich approaches to the analysis of prey choice and trophic interactions, it may be possible to further improve the predictive power of null models, particularly in long-term single-species studies with temporally consistent sampling on small spatial scales. This would facilitate more accurate and meaningful testing of specific hypotheses regarding the factors determining prey choice and diet. The cluster-based approach used here has potential to introduce stochasticity between poorly replicated or misaligned contexts (e.g. disparate weather conditions), thus the importance of careful data selection when applying weights to such models cannot be overstated.

Conclusions

We have shown that weather and time modify the identities of spider trophic interactions. Given the concurrent variation in prey community structure, this appears to be elicited through variation in prey availability, mitigated to some degree by density-independent prey choice of some taxa and avoidance of others. The weather-dependent variation in web height and area also suggests that the web-building linyphiids analysed engage in adaptive web building, which may facilitate the selectivity of spiders in different environmental conditions, but this requires further investigation. Interactions between spiders and some prey taxa were particularly impacted by weather, most notably springtails and thrips, two of the most prevalent prey groups. We provide a framework through which data can be analysed and used in a predictive manner in the assessment of consumer choices in natural systems. Using weather-based prey choice data, interannual predictions of trophic interactions were adjusted, but weather is not the only driver of these interactions and prey abundance appears to be secondary to diversity in driving the dietary responses to weather. By understanding how weather impacts the identities and frequencies of trophic interactions, particularly in a predictive framework, we can begin to understand how ecological networks may change as weather becomes increasingly unpredictable and variable with global climate change.

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Data availability statement

Data are available from Zenodo Digital Repository: https://doi.org/10.5281/zenodo.7291565 (Cuff et al. 2022b).

Supporting information

The Supporting information associated with this article is available with the online version.

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