

## ARTICLE

# A replicated study on the response of spider assemblages to regional and local processes

Jörg Müller<sup>1,2</sup>  | Roland Brandl<sup>3</sup> | Marc W. Cadotte<sup>4,5</sup>  | Christoph Heibl<sup>2</sup> |  
 Claus Bässler<sup>6</sup>  | Ingmar Weiß<sup>2</sup> | Klaus Birkhofer<sup>7</sup>  | Simon Thorn<sup>1</sup>  |  
 Sebastian Seibold<sup>8,9</sup> 

<sup>1</sup>Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Rauhenebrach, Germany

<sup>2</sup>Bavarian Forest National Park, Grafenau, Germany

<sup>3</sup>Department of Ecology - Animal Ecology, Faculty of Biology, Philipps-Universität Marburg, Marburg, Germany

<sup>4</sup>Department of Biological Sciences, University of Toronto–Scarborough, Toronto, Ontario, Canada

<sup>5</sup>Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada

<sup>6</sup>Conservation Biology, Faculty of Biological Sciences, Institute for Ecology, Evolution and Diversity, Goethe-University Frankfurt, Frankfurt am Main, Germany

<sup>7</sup>Department of Ecology, Brandenburg University of Technology Cottbus-Senftenberg, Cottbus, Germany

<sup>8</sup>Technical University of Munich, Freising, Germany

<sup>9</sup>Berchtesgaden National Park, Berchtesgaden, Germany

## Correspondence

Jörg Müller

Email: joerg.mueller@npv-bw.bayern.de

**Handling Editor:** William E. Snyder

## Abstract

Understanding species richness variation among local communities is one of the central topics in ecology, but the complex interplay of regional processes, environmental filtering, and local processes hampers generalization on the importance of different processes. Here, we aim to unravel drivers of spider community assembly in temperate forests by analyzing two independent data sets covering gradients in elevation and forest succession. We test the following four hypotheses: (H1) spider assemblages within a region are limited by dispersal, (H2) local environment has a dominant influence on species composition and (H3) resources, and (H4) biotic interactions both affect species richness patterns. In a comprehensive approach, we studied species richness, abundance, taxonomic composition, and trait-phylogenetic dissimilarity of assemblages. The decrease in taxonomic similarity with increasing spatial distance was very weak, failing to support H1. Functional clustering of species in general and with canopy openness strongly supported H2. Moreover, this hypothesis was supported by a positive correlation between environmental and taxonomic similarity and by an increase in abundance with canopy openness. Resource determination of species richness (H3) could be confirmed only by the decrease of species richness with canopy cover. Finally, decreasing species richness with functional clustering indicating effects of biotic interactions (H4) could only be found in one analysis and only in one data set. In conclusion, our findings indicate that spider assemblages within a region are mainly determined by local environmental conditions, while resource availability, biotic interactions and dispersal play a minor role. Our approach shows that both the analysis of different aspects of species diversity and replication of community studies are necessary to identify the complex interplay of processes forming local assemblages.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Ecological Monographs* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

**KEYWORDS**

assembly mechanism, Bavarian Forest National Park, canopy gradient, community ecology, diversity, LiDAR

## INTRODUCTION

Since the beginnings of ecology, differences in species richness and composition between assemblages has been among the central topics in community ecology (Davies et al., 2009; Hutchinson, 1959; Leibold et al., 2004). However, progress was dauntingly slow, which led Sir John Lawton at the end of the 20th century to the painful judgment that “community ecology is a mess.” Lawton (1999) also noted that the lack of generalizations in community ecology was a result of focusing on local assemblages and experiments. Consequently, he asked why ecologists continue to invest so much time in studying local communities instead of turning towards larger spatial scales, like macroecology. Irrespective of the benefits and achievements of macroecology, understanding the processes determining local communities is crucial for forecasting and dealing with global change in the Anthropocene (Simberloff, 2004; Winter et al., 2013).

Community ecology has identified a plethora of processes influencing local assemblages (Mittelbach & McGill, 2019; Vellend, 2016). The structure of communities depends on a series of hierarchically structured, spatial processes: biogeographical processes determine the regional species pool (Lessard et al., 2012; Zobel, 1997), and dispersal abilities (active or passive) determine which species can colonize a specific habitat patch (Bonte, Vandenbroecke, et al., 2003; Hanski & Heino, 2003; Komonen & Müller, 2018). As the species pool experiences steady turnover across space, taxonomic similarity of species assemblages in habitat patches should decrease with increasing spatial distance between patches, especially in species with low dispersal capacity (distance limitation hypothesis; Chase & Myers, 2011; Hubbell, 2001).

After the arrival of a species to a new habitat patch, local environmental filters (Balmford, 1996) select species based on the match between traits and both local abiotic and biotic environmental conditions (Birkhofer et al., 2017; Cadotte & Tucker, 2017; Cavender-Bares et al., 2009; Müller et al., 2012). Biotic interactions, such as competition, predation, herbivory or mutualism, influence the persistence of species and ultimately their local abundance (Howeth & Leibold, 2010; Wise, 2006). Quantifying the relative importance of environmental filtering and biotic interactions is inherently challenging as different processes could create similar patterns (Kraft et al., 2015). Studying patterns of phylogenetic and functional diversity together with

abundances and traits along environmental gradients, however, is one promising approach (Cadotte & Tucker, 2017). However, species with similar phenotype and only minor niche differences can exclude other, different, species under specific environmental conditions and thus create clustered patterns through competitive exclusion (Mayfield & Levine, 2010). Therefore, it is likely that observational data showing environmental filtering are actually combined effects of environmental filters and local species interactions such as competition or predation (Cadotte & Tucker, 2017).

If ecological traits are phylogenetically conserved, phylogenetic position predicts the traits of species. Thus, phylogenetic clustering suggests that species with similar traits co-occur in a habitat, indicating filtering. In contrast, over-dispersion suggests that co-occurring species differ in traits, indicating competition (Cadotte et al., 2013; Pausas & Verdu, 2010). All these processes determine species composition as well as species richness of an assemblage or community (see Stroud et al., 2015, for the difference between these two concepts).

In addition to the influences of environmental filtering and species interactions on communities, some more fundamental factors affect the richness of a community. First, a very general pattern is that species richness increases with increasing area (Allouche et al., 2012; Coleman, 1981; Connor & McCoy, 1979) or resource availability. Two major hypotheses were proposed to explain this pattern. The more-individuals hypothesis explains the increase of species richness with resources by the amount of energy accessible to organisms (Wright, 1983). With increasing energy, we expect an increase in population size of organisms, thereby allowing more species to sustain viable populations. Alternatively, the habitat-heterogeneity hypothesis predicts that the number of different habitats increases with increasing area and, as long as species have somewhat different habitat requirements, more species can coexist with increasing area (e.g., Allouche et al., 2012; Heidrich et al., 2020; MacArthur & MacArthur, 1961; Tews et al., 2004).

The relative importance and the hierarchy of the above-mentioned drivers of species richness and composition of local assemblages is still a matter of debate (Adler & Collins, 2011; Cadotte & Tucker, 2017; Huston, 1999; Loreau et al., 2001; Mittelbach et al., 2001; Mittelbach & McGill, 2019; Weiher et al., 2011). Key for successfully unraveling drivers of species richness and composition is that patterns are assessed along strong environmental gradients (Cadotte & Tucker, 2017; Laughlin et al., 2012). Two of

the globally most important ecological gradients are elevation (Allouche et al., 2012) and succession (Meiners et al., 2015), along which one might expect a predictable change in the importance of drivers structuring communities. With increasing elevation, climatic conditions change towards a harsher climate and shorter vegetation periods in most regions posing increasingly strong environmental filters on species (Bässler, Cadotte, et al., 2016; Bishop et al., 2015). Successional gradients in forests are typically characterized by increasingly buffered microclimatic conditions over time (Meiners et al., 2015; Zellweger et al., 2020). Thus, communities in early forest successional stages can be expected to show clustered functional composition due to harsh environmental conditions, as indicated by a lower phylogenetic diversity in recently disturbed habitats compared to undisturbed habitats (Dinnage, 2009; Gerisch et al., 2012; Winter et al., 2013).

Here we investigate the hierarchy of processes influencing the local species richness and compositional similarity of spiders in temperate forests along gradients of elevation and forest succession. Forest succession was initiated by natural disturbance removing the tree canopy and thus changing microclimatic conditions (Thom et al., 2020). Both gradients are expected to influence spider communities since microclimate is known to be a major niche axis for spiders (Entling et al., 2007; Hilmers et al., 2018; Zellweger et al., 2020). As predators, spiders occur in a wide range of terrestrial habitats (Entling et al., 2007), with varying strategies for foraging and dispersal (Bell et al., 2005; Eberhard, 1990). Moreover, many traits in spiders are phylogenetically conserved (Cardoso et al., 2011; Michalko & Pekar, 2016) allowing for the use of phylogenies for testing hypotheses regarding environmental filtering (Birkhofer, Smith, et al., 2015). Finally, due to the strictly carnivorous diet of spiders, intra-guild predation, cannibalism, and competition are common in spider assemblages (Rusch et al., 2015; Wise, 2006). Thus, biotic interactions should influence functional diversity and species richness of assemblages in a way that assemblages that are subject to a strong habitat filter on certain guilds, have a lower species richness (number of species corrected to abundance), due to strong intra-guild and intraspecific competition, predation, and cannibalism (Wise, 2006). A number of experiments have provided evidence that food availability can limit spider reproduction and abundances (Spiller, 1984; Wise, 1979). Since insect biomass in temperate European forests decreases with increasing elevation and canopy cover (Kortmann, Müller, et al., 2021), spider richness, if determined by food resources, should be higher in early successional stages and lower elevations.

To evaluate the consistency and generality of our results in terms of the direction and relative importance

of processes influencing the structure of the assemblages, we used data from two independent projects collected in different years and on different plots but within the same region in form of a replicated study. The first data set (BIO) was collected in the BIOKLIM Project (Biodiversity and Climate Change Project; Bässler et al., 2008) along transects covering an elevational gradient of about 1000 m and a broad range of successional stages of forest development after disturbance by bark beetles. The second data set (GAP) originates from an experiment, which aimed to build strong contrasts in the effects of forest disturbance, that is, the formation of canopy gaps and deadwood (Seibold et al., 2016), while spanning an elevational gradient of about 500 m. From the arguments above, we developed four general hypotheses with 11 predictions derived from these hypotheses about how diversity measures of local spider assemblages are determined by regional processes linked to dispersal, environmental filtering, and local processes (i.e., resource availability and biotic interactions; Table 1).

## MATERIAL AND METHODS

### Study area and study design

The study area of both data sets is located in the Bohemian Forest, a low mountain range in southeastern Germany (48°54' N, 13°29' E), which covers ~5000 km<sup>2</sup> between 280 and 1456 m above sea level. The geology is rather homogenous with predominantly acidic soils. The Bavarian Forest National Park is embedded in this area with 24,000 ha ranging from 650 to 1452 m above sea level. A summary of study plots, predictors with range of numerical values, and sampling effort is given in Table 2. The 0.1-ha plots of the BIO data set are predominantly arranged along four transects covering the full elevation gradient of the region and providing a continuous gradient of canopy cover (Bässler et al., 2008). The plots of the GAP experiment are all arranged within the management zone of the Bavarian Forest National Park (Seibold et al., 2016). Here canopy cover was low in gap plots and dense in closed forest plots, but with considerable variation.

### Canopy cover and soil moisture

Canopy cover was estimated on BIO plots by summing the cover of shrub and midstory and overstory tree layers recorded via plant surveys on 200 m<sup>2</sup>. These values ranging from no trees to dense coverage were finally scaled between 0 and 1 using function *decostand* and method

**TABLE 1** Hierarchy of three types of processes influencing local assemblages of spiders across forests

Processes and hypotheses	Predictions	Confirmed
1. Regional process		
H1: Spider assemblages are limited by dispersal	P1: Taxonomic similarity decreases with geographic distance	Partially
2. Environmental filtering		
H2: Local environment determines species composition	P2: Functional clustering of species	Yes
	P3: Positive correlation between environmental and taxonomic similarity	Yes
	P4: Correlation between canopy openness and functional clustering	Yes
	P5: Increase of abundance with canopy openness	Yes
3. Local processes		
H3: Resources determine species richness	P6: Abundance decreases with elevation	Partially
	P7: Species richness decreases with elevation	Partially
	P8: Functional diversity decreases with increasing abundance	Partially
	P9: Species richness decreases with canopy cover	Yes
H4: Biotic interaction determines species richness	P10: Over-dispersion of similarity in respect to functional diversity	No
	P11: Species richness decreases with functional clustering	Partially

*Note:* In this table, we list our main statistical tests used to evaluate the four general hypotheses leading to a number of predictions (P1 to P11). P1 and P3 were tested using matrix models, P2 and P10 using Null models, all other predictions were tested using linear models. The last column indicates if the prediction was supported by both data sets (Yes), only partly by the two data sets (Partially), or showed no or the opposite effect (No).

*range* in *vegan* (Oksanen et al., 2016). The canopy cover of each GAP plot was assessed by airborne laser scanning in summer 2012 (the first sampling year) on a circle with a radius of 40 m around each plot (Kortmann et al., 2018). Again, these values were standardized between 0 and 1 as above, to make both data sets comparable. For both data sets, we estimated soil moisture on each plot using the Ellenberg moisture indicator values for plants (Müller et al., 2009) based on plant surveys with 200 m<sup>2</sup> (Bässler, Müller, Dziöck, 2010), using unweighted means of indicator values across co-occurring plant species.

## Spider sampling and traits

Spiders were sampled using 0.5-L pitfall traps with a transparent plastic roof and copper sulfate as sampling liquid. This sampling method is designed for epigeic animals; species mostly active on trees, in the canopy or building webs in higher vegetation structures are under-represented. However, the sampling method was the same on all plots along the successional gradient and representatives of all guilds including spider species living in trees were collected. The probability of falling into a pitfall trap is affected by the activity and density of spider species. Hence, our abundance measure (number of individuals) is in fact an activity density (e.g., Heydemann 1957). We are aware that ours and most other biodiversity studies concentrate only on a small part of a community (Fauth et al., 1996). Therefore we decided to use the term “assemblage” instead of “community” for our data throughout the paper. Sampling for both data sets was conducted throughout May, July, and September. On BIO plots, one trap was installed per plot at the plot center and on GAP plots, two traps were installed 5 m apart around the plot center. All adult spiders were determined to the species level. We excluded those juveniles (~12%) that could not be determined to the species level from further analyses. We extracted information on ecological traits for all species from literature including hunting strategy, preferred vertical stratum, mobility via ballooning, and mean body size (see Table 3). In addition, we conducted a number of morphological measurements on specimens of all species and extracted three independent morphological traits for further analyses. These traits were standardized by body length of the respective individual by taking the residuals from a linear regression using  $\log_e(\text{trait}) \sim \log_e(\text{body length})$ . If specimens of both sexes of a species were available, we measured traits for both sexes and used the mean value. For a list of species traits, their ecological relevance and the source, see Table 3.

**TABLE 2** Overview of the two data sets and the measured predictors

Research study	BIO	GAP
Number of plots	214	190
Spatial extent	74 km	19 km
Sampling years	2007	2012, 2013, 2014
Number of pitfall traps	One trap per plot	Two traps per plot
Number of spider species/individuals determined to species level	190/8446	206/62,442
Predictor		
Canopy cover	0%–100% derived from vegetation survey, shrub and tree cover combined	0%–100%, derived from airborne laser scanning, penetration ratio 2 m above ground
Elevation	287–1419 m above sea level	717–1209 m above sea level
Soil moisture	Ellenberg soil moisture value from plant survey means between 4.5 and 9	Ellenberg soil moisture value from plant survey means between 4 and 6.6

## Phylogeny of spiders

We estimated the phylogeny of 506 spider species including all species in our data sets based on a data matrix of published DNA sequences assembled with the R package *megaptera* (version 1.0-38) from GenBank and BOLD repositories. Four mitochondrial (*cox1*, *nad1*, 12S rRNA gene, 16S rRNA gene) and three nuclear (H3, 18S rRNA gene, 28S rRNA gene) loci were aligned with the L-INS-I algorithm (MAFFT; Katoh & Standley, 2013); after removing ambiguously aligned nucleotide positions, which are positions identified (and removed) with GBLOCKS (Talavera & Castresana, 2007), sequences were concatenated into a single matrix. Tree topology and branch lengths were modeled in a maximum-likelihood framework (RAxML v8.4.2; Stamatakis, 2014). Sequence evolution was modeled with the GTRCAT approximation for each marker gene separately on a common topology (Stamatakis, 2014). Branch lengths were converted from substitution per site to a relative time scale, thereby making the tree ultrametric, using the function *chronos* in the R package *ape* with a penalized likelihood approach using a relaxed clock model of rate evolution (Paradis, 2013; Sanderson et al., 2002). Because the phylogenetic information of the seven loci cannot be expected to resolve deep nodes in the phylogeny, we imposed a topological constraint on the phylogeny based on recent phylogenomic studies (Bond et al., 2014; Fernandez-Palacios & de Nikolas, 1995; Sharma et al., 2014). For species without any available genetic information we used congeners as proxies (27 species) or, if this was not possible, we added these species randomly to the final topology of the respective genus (121 species). However, these procedures had little effects on the analyses (for the phylogeny, see repository).

## Statistical analyses

All statistical analyses were conducted in R 3.4.3 (www.r-project.com). We tested our 11 predictions by combining three approaches: approach one used similarity metrics (e.g., difference in species composition between plots), approach two was based on raw data of species richness and approach three used null-models for functional-phylogenetic diversity.

To assess overall community assembly patterns, we calculated functional diversity describing divergence, that is, how similar are species within assemblages (Cadotte & Davis, 2016). Functional diversity was calculated as mean pairwise distances (MPD) between functional traits in the functional space of co-occurring species (Mouillot et al., 2012; Webb et al., 2002). To control for variation in number of species in the samples and to obtain a metric on the assembly patterns, we applied a null-model approach to our final functional diversity using the tip-shuffling method (Cadotte & Davis, 2016). This provides standardized effects sizes (SES) of the mean pair-wise distances (SES MPD), which we calculated with 999 randomizations with the function *ses.mpd* in the add-on package *picante* (Kembel et al., 2011). Functional diversity based on species-by-species distance matrices was calculated using Gower distance (Gower, 1971) of abundance data with the *gowdis* function in the add-on package FD (Laliberte & Legendre, 2010). The dissimilarity coefficient of Gower (1971) can combine continuous and categorical traits. In order to take into account traits that consist of several categories, such as species foraging at different strata, these categories have been down-weighted accordingly to give all traits the same weight.

To account for unmeasured traits, we additionally calculated the mean pairwise distances for phylogenetic

**TABLE 3** Traits characterizing the behavior of spider species in response to local environments

Trait	Ecology	Measurement	Source
Stratum	Spiders use different strata in a forest from ground to canopy layer	1/0 coding of the 5 strata: epigaic, herb layer, shrub layer, tree trunk, canopy layer, multiple strata per species possible	Expert knowledge from literature summarized by Ingmar Weiss (IW)
Web type	Spiders use different types of web for foraging	Five categories: no web, web with tangles of stopping threads, horizontal web bottom, horizontal web top, vertical web	Expert knowledge from literature summarized by IW
Ballooning	Some spiders use passive ballooning for long distance dispersal	1/0 coding of the ballooning high and ballooning low probability	Birkhofer, Meub, et al. (2015) and additional information from literature summarized by IW
Body size	Body size decrease from warm and dry to cool and moist conditions, body size increase with habitat complexity	Continuous value from literature	Entling et al. (2010)
Opisthosoma and prosoma breadth <sup>a</sup>	Arthropods are narrower in structurally more complex habitats	Residuals of a linear model $\log_e(y) \sim \log_e(x)$ : Opisthosoma and prosoma breadth (mm) $\sim$ body length (mm) measured	Gibb et al. (2015)
Leg length <sup>a</sup>	Might decrease with latitude and in simple habitats	Residuals of tibia length of first leg as before	Gibb et al. (2015)
Fang length <sup>a</sup>	Fast prey in less complex and warmer environment evokes long fang length	Residuals of chelicera length as before	Gibb et al. (2015)

<sup>a</sup>These traits were measured for the same individuals.

diversity extracting the distance between two species from the phylogeny above. This approach is justified since traits of spiders are phylogenetically conserved (Cardoso et al., 2011) and functional and phylogenetic diversity in our data (Appendix S1: Figure S1) and previous studies (Birkhofer, Smith, et al., 2015) were correlated. To combine information based on traits and phylogeny, we calculated mean-functional-phylogenetic-diversity (MFPD) following Cadotte et al. (2013). The key to MFPD is a weighting parameter,  $a$ , which weights the contributions of phylogenetic and functional distances to MFPD. When  $a = 0$ , MFPD only includes functional distances and when  $a = 1$ , MFPD only includes phylogenetic distance. At intermediate values of  $a$ , both functional and phylogenetic distances contribute to MFPD. Based on these distance matrices, we standardized the effect size of the mean distance between co-occurring species (FPD.ses) within each assemblage based on a null model with tip shuffling (Webb et al., 2002). Values above zero indicate over-dispersion; values below zero indicate clustering (Pausas & Verdu, 2010). For our final model, an  $a$  value of about 5% yielded the highest  $R^2$  value for both data sets. This means that the phylogeny improved the explicatory power of the

functional diversity measure only slightly (Appendix S1: Figure S1). Moreover, the hump-shaped relationship between  $R^2$  and  $a$  indicated that both traits and phylogeny contribute to dissimilarities, supported also by the correlation of functional and phylogenetic diversity (Appendix S1: Figure S1). To test if the means of final FPD.ses differed from 0 for both data sets, we fitted a linear mixed model using the function `lmer` with project as fixed effect and plot as random effect as `lmer(FPD.ses ~ 0 + Project + (1 | Plot))`. The  $p$  values for the linear mixed model were estimated using function `cftest` in package `multcomp` (Hothorn et al., 2008).

For testing the prediction P1 of “Taxonomic similarity decreases with geographic distance” and P3 “Positive correlation between environmental and taxonomic similarity” we first used multiple regression on distance matrices (MRM; Lichstein, 2007) with function `MRM` separately for both data sets (package `ecodist`; Goslee & Urban, 2017). Here the taxonomic dissimilarity of spider assemblages between plots was measured as Bray-Curtis dissimilarities using the function `vegdist` in package `vegan`. The distances in space, canopy cover, and soil moisture between plots were calculated as Euclidian distances using the function `dist` and scaled to zero mean and unit variance to make estimates comparable. For

the three-year data set in GAP we added the distance year to the analyses. Finally, to test for consistencies of the relationships between both data sets, we extracted the pairwise distance between two assemblages and the respective predictors and conducted matrix correlation in the same framework as linear mixed models described below. Here we fitted linear mixed models with taxonomic dissimilarity as response and environmental dissimilarity as predictors. These models included random effects on both plots used repeatedly for measuring the individual distance to account dependence of the observations. We are aware of the fact that using plot identity as random effects to account for the hidden correlations between distance estimates is an ad hoc procedure, which has up to now no convincing theoretical underpinning. However, we applied this possibility for two reasons. First, we wanted to analyze the distance data within the same statistical framework as other biodiversity measures to allow for a direct comparison of the results. Second, using plot identity as a random factor is a suitable way to account for replicated observations from specific plots in mixed models regularly used for the analysis of matrices (e.g., Pool et al., 2016; Yang, 2004). In our case, the results of the two statistical approaches differ only in details.

To test the predictions P4–P9, and P11, we fitted generalized linear-mixed models using data from BIO and GAP in one model, which allows testing for differences in predictor slopes between both data sets. To make estimates comparable among predictors all predictors were scaled to zero mean and unit variance. Temporally replicated measurements in the GAP data were considered by including plot as a random factor. To account for potential over-dispersion in the mixed models with Poisson distribution (abundances, richness), we added an observation specific random factor to the model (Elston et al., 2001). For each model, we first estimated study specific estimates (BIO, GAP) for each predictor and in a second step we tested if differences in slope between the two data sets were significant (see repository). To account for general differences in sampling effort in both data sets we always used study as categorical predictor (factor with two levels). For modeling abundances, we used canopy cover, elevation and soil moisture as predictors, for MFPD we added the  $\log_e(\text{abundance})$  as predictor and for richness we added  $\log_e(\text{abundance})$  as predictors to model true species richness (corrected for sampling effort, see Gotelli & Colwell, 2001) and MFPD to test the prediction “Species richness decreases with functional clustering.” To illustrate the findings of the complex generalized linear mixed models we plotted partial effect size plots with residuals using function *allEffects* in package *effects* (Fox & Weisberg, 2018). Furthermore, in the Appendix S1, we present the pairwise correlation of all

raw data of dependent variables and their predictors in the glmms and the matrix correlations.

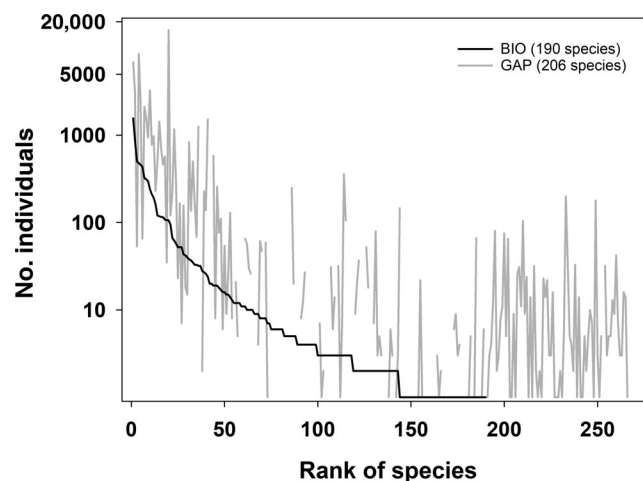
Finally, for illuminating the relation of single traits and environmental variables as well as their consistency among data sets, we calculated the community-level weighted means of trait values using the function *functcomp* in the package *FD*. We then modeled each of these values with canopy cover, elevation and moisture as fixed factors and plot as random factor in a linear mixed model. Again, we estimated project-specific slopes to check for consistency between both data sets (see repository). Furthermore, we investigated the phylogenetic signal of abundances in both data sets separately using the function *phylosig* in the package *phytools* using method “lambda.”

## RESULTS

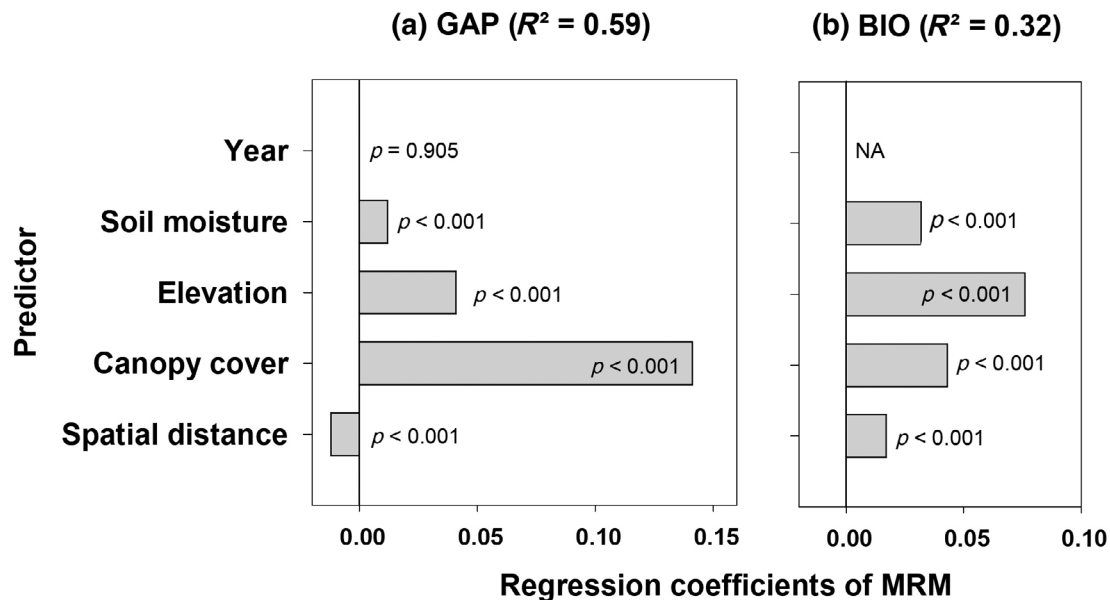
Our two data sets comprised a total of 265 species. The rank abundance curves of both data sets were quite similar for the species recorded in both studies (Figure 1).

### Regional processes

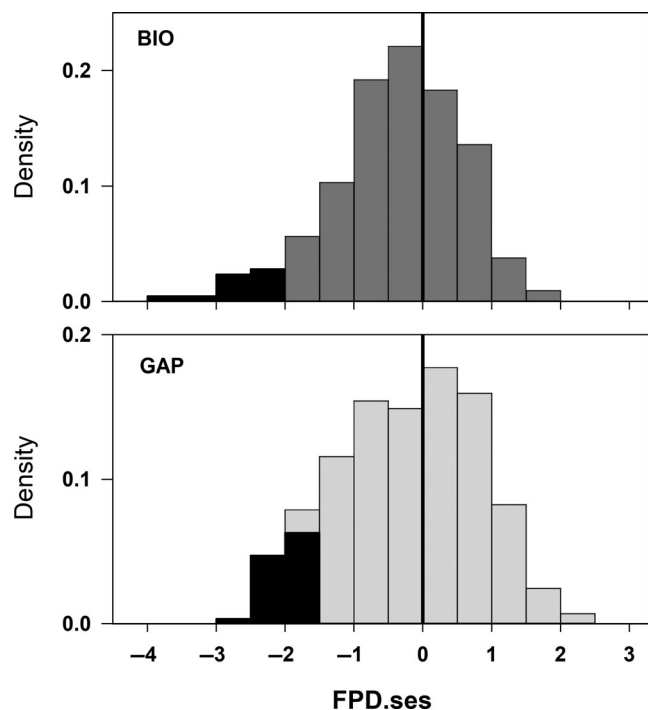
Spatial distances between plots had the weakest effect on species dissimilarity in matrix correlations for BIO and even a slightly negative effect for GAP data (Figure 2). This was also supported by our linear mixed model approach in which spatial distance revealed as sign (Appendix S1: Table S2). These results failed to support



**FIGURE 1** Rank-abundance curve for both data sets with in total 8446 specimens in BIO and 62,442 specimens in GAP. We used the rank-abundance curve of BIO as baseline, because it covers the longer elevation range. Gaps in the gray curve are caused by species occurring only in BIO, curves on the right side ( $x > 190$ ) display species only occurring in the GAP experiment, sorted alphabetically



**FIGURE 2** Results of matrix correlation with spider assemblage composition as target matrix, and spatial distance, elevation, canopy cover, and soil moisture as predictor matrices. Note, in the GAP data set, year was used as additional matrix because spiders were sampled over 3 years, while in the BIO data set, only 1 year was sampled and therefore no year matrix was available



**FIGURE 3** Histogram of FPD.ses values. FPD.ses ist is the standardized effect size of a combined functional-phylogenetic diversity. Mean value of FPD.ses were  $-0.37$  and  $-0.24$  for BIO and GAP data, respectively. FPD.ses ist is the standardized effect size of a combined functional-phylogenetic diversity

our first prediction that taxonomic similarity decreases with geographic distance at the spatial scale of our studies compared to the other predictors.

### Environmental filtering

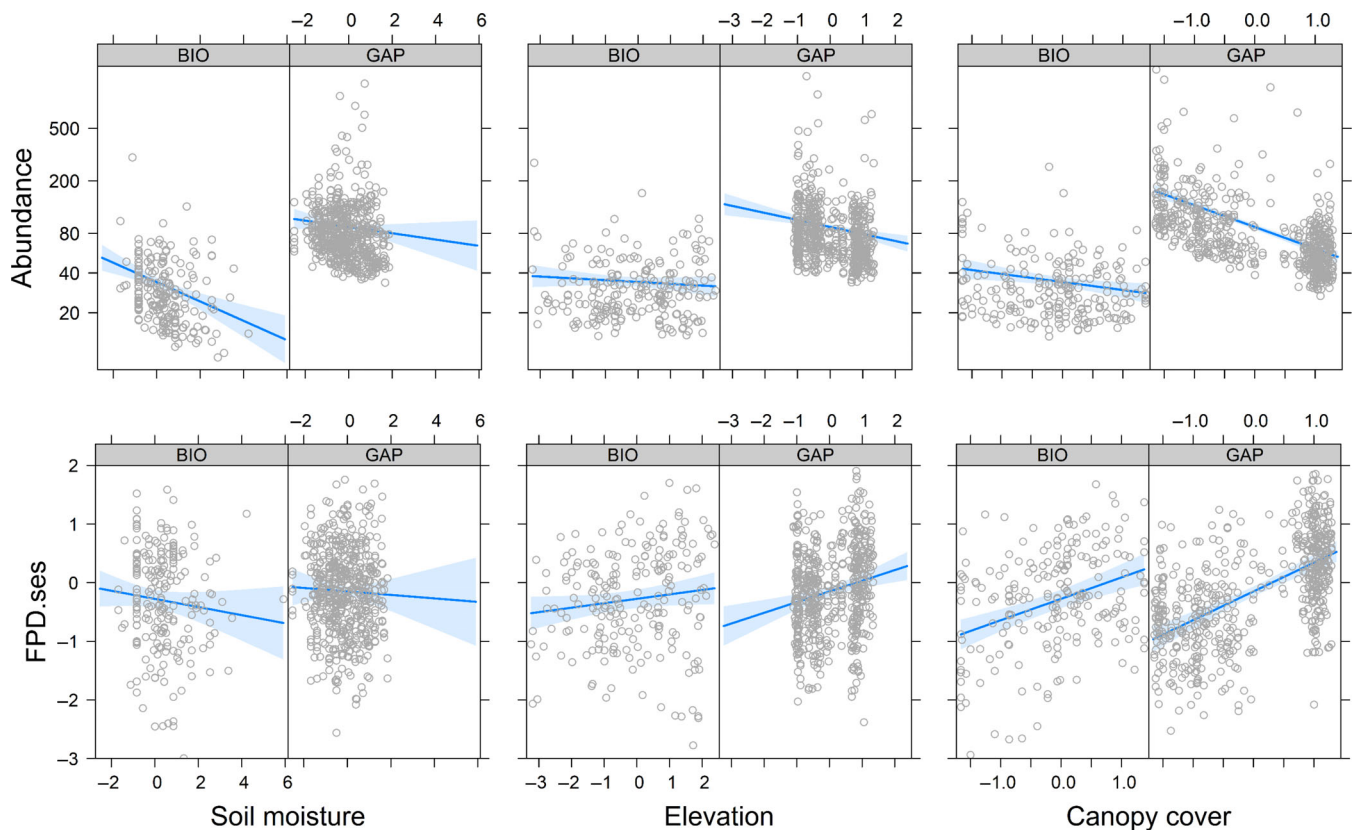
Elevation and canopy cover had strong and soil moisture had moderate effects on species dissimilarity (Bray-Curtis) as shown by the matrix correlations with relatively high  $R^2$  values (Figure 2). This indicates that the environment strongly influenced species composition, thus supporting our prediction P3. The standardized effect sizes of mean pairwise distance of assemblages in a functional-phylogenetic space tended to be more frequently negative (clustering) than positive (overdispersion; Figure 3). Assemblages with significant deviation from zero as indicated by null models were found only for negative values in 13 out of 214 (BIO) and 65 out of 570 (GAP) assemblages. Testing whether the means (Figure 3) differed from zero our linear mixed modeled revealed estimates of  $-0.37$  (BIO) and  $-0.25$  (GAP) both with a  $p < 0.001$  underlining that these values were significantly less than zero. This indicates that spider assemblages show variable patterns but tend towards being clustered, which is consistent with our prediction of functional clustering (P2) by habitat filtering, but we found little support for our prediction of functional over-dispersion by biotic interactions (P10). Functional-phylogenetic diversity increased with canopy cover in line with our prediction P4 (Table 4, Figure 4). The generalized linear mixed model for abundance showed a consistent decrease with increasing canopy cover, in line with our prediction P5 (Table 4, Figure 4).



**TABLE 4** Results of three generalized mixed models for both data sets in one model

Predictors	Data set	Abundance	Prediction	FPD.ses	Prediction	Richness	Prediction
Family		Poisson		Gaussian		Poisson	
Soil moisture	BIO	<b>-0.17***</b>		-0.07		<b>0.03</b>	
	GAP	<b>-0.06</b>		-0.03		<b>0.09***</b>	
Elevation	BIO	<b>-0.03</b>	P6	0.08		-0.02	P7
	GAP	<b>-0.12***</b>	<b>P6</b>	0.18***		-0.05***	<b>P7</b>
Canopy cover	BIO	<b>-0.14**</b>	<b>P5</b>	1.11***	<b>P4</b>	-0.06*	<b>P9</b>
	GAP	<b>-0.37***</b>	<b>P5</b>	1.49***	<b>P4</b>	-0.14***	<b>P9</b>
FPD.ses	BIO					<b>-0.01</b>	P11
	GAP					<b>0.06***</b>	<b>P11</b>
log(individuals)	BIO			<b>0.02</b>	P8	<b>0.36***</b>	
	GAP			<b>-0.34***</b>	<b>P8</b>	<b>0.24***</b>	
Data set	GAP	0.96***		0.13		0.70***	

Note: Estimators show data-set-specific values and are based on standardized predictors. FPD.ses is the standardized effect size of a combined functional-phylogenetic diversity. Estimators in boldface type show significant interactions between data sets. Prediction indicates the respective predictions from Table 1, in boldface type if supporting the prediction. \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .



**FIGURE 4** Partial effect plot for selected predictors of the glmms in Table. Note that predictors were standardized. Blue lines represent the partial fit, gray dots represent the residuals according to the Fox and Weisberg (2018). For full graphs of all predictors and for all three dependent variables of Table 4 see Appendix S1: Figures S2–S6

### Local processes

For the local-level resource-based processes, our prediction that abundance decreases with elevation was

supported only in one data set, but the slope of the effect of elevation did not differ significantly between both data sets (Table 4). The same was true for the observed decrease of species richness with elevation (Table 4).

Functional-phylogenetic diversity in both data sets increased with elevation. Abundance had contrasting effects on functional-phylogenetic diversity in both data sets. While results for GAP were in line with P8, the positive estimate in BIO did not support this prediction. The consistent decrease of species richness with canopy cover supported P9 (Table 4, Appendix S1: Figure S8).

For the influence of biotic interactions on local processes, the standardized effect sizes of functional diversity did not show significantly higher positive values than expected by random, which would have indicated overdispersion (P10). Moreover, we found a decrease in species richness with increasing functional clustering as predicted (P11), but only in the GAP data set (Table 4, Appendix S1: Figure S8). Evaluating the correlation of traits and environment, we found some consistent relationships between the single community weighted means of traits and the three environmental variables in both data sets. We found higher incidence of species foraging in higher vertical strata and of species with web with tangles in closed forests and higher elevations and vice versa higher incidence of species without web in open forests and lower elevations (Table 5). In open forests, species showed higher incidence of ballooning ability and smaller body size. Opisthosoma breadth was wider at higher elevation and prosoma breadth was smaller in open forests. Finally, the fang length was consistently longer in closed forests, but leg length showed the opposite pattern (Table 5).

Testing the phylogenetic signal for abundances in both data sets separately, we found a clear signal in the larger GAP data set with  $\lambda = 0.47$

( $p < 0.001$ ) and a weaker only marginal significant signal in BIO with  $\lambda = 0.26$  ( $p = 0.08$ ). This indicates that successful species tend to be closely related to other successful species, ostensibly because of niche conservatism.

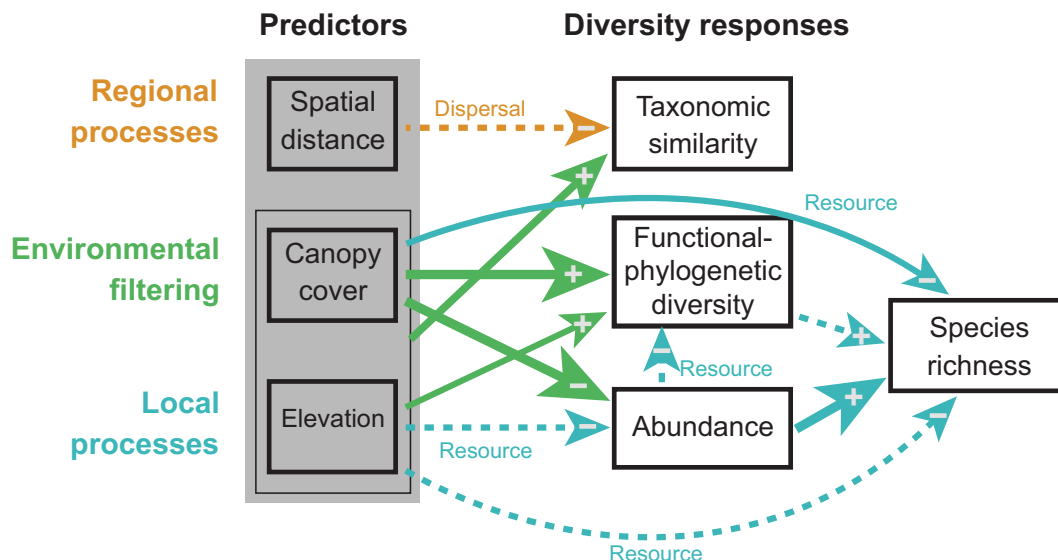
## DISCUSSION

We found full support in both data sets and analyses for five out of 11 predictions, that is, P2–P5 and P9. In two cases (abundance and richness versus elevation; P6 and P7), the directions of the effects were consistent with the prediction in both data sets but only significant in one data set. Nevertheless, the interaction term indicated that the difference between estimates was not significantly different between data sets (Table 4). For two predictions (P8, P11), only one of the data sets showed a significant effect in the predicted direction. In summary (Figure 5), spatial distance was of minor importance for spider community assembly that does not support the hypothesis “Spider assemblages are limited by dispersal” (H1) at least at the scale of 20–70 km. We found consistent and strong support for environmental filtering for abundances, species composition, and functional diversity supporting our hypothesis “Local environment determines species composition” (H2). Our hypothesis “Resources determine species richness” (H3), however, was only partially supported. For the hypothesis “Biotic interaction determines species richness” (H4), we found support only for one of the two derived predictions and for only one of the two data sets.

**TABLE 5** Results of linear mixed models ( $z$  values) predicting community weighted mean values of single traits by canopy cover, elevation, and moisture conditions with plot as random factor

Trait	Canopy		Moisture		Elevation		
	BIO	GAP	BIO	GAP	BIO	GAP	
Vertical niche	Mean values of stratum	<b>6.06</b>	<b>9.366</b>	−1.83	0.21	<b>3.79</b>	<b>4.00</b>
Web types	Web with tangles of stopping threads	<b>2.20</b>	<b>3.70</b>	<b>5.90</b>	1.51	<b>3.55</b>	<b>2.55</b>
	No web	<b>−7.00</b>	<b>−14.5</b>	<b>−4.50</b>	−0.35	<b>−2.06</b>	<b>−3.37</b>
	Horizontal web top	<b>3.09</b>	−0.17	1.35	0.21	−2.47	−0.76
	Vertical web	−0.46	−1.31	−1.46	0.12	−0.36	<b>3.40</b>
Dispersal	Ballooning high probability	<b>−11.0</b>	<b>−15.6</b>	0.80	0.78	1.06	0.40
Morphology	Body size	<b>5.27</b>	<b>6.68</b>	<b>−3.86</b>	−0.74	−1.45	0.12
	Opisthosoma breadth	<b>3.02</b>	<b>−8.39</b>	0.77	<b>−3.21</b>	<b>3.39</b>	<b>5.61</b>
	Prosoma breadth	<b>−2.72</b>	<b>−3.60</b>	−0.08	<b>2.35</b>	<b>2.99</b>	<b>−5.73</b>
	Leg length	<b>−2.81</b>	<b>−2.15</b>	0.80	−0.61	−1.35	−0.14
	Fang length	<b>3.55</b>	<b>2.06</b>	1.00	<b>−1.97</b>	0.27	1.51

Note: Note the predictors were estimated specifically for each project. Bold numbers indicate significant  $t$  values.



**FIGURE 5** Summary of our findings. The size of arrows displays their relative importance; dashed arrows indicate inconsistent results between both data sets (direction of effect opposite or one not significant). Signs (i.e., + and -) indicate the direction of effect

### Low effects of space on taxonomic dissimilarity

Despite a spatial extent of about 20 and 70 km, respectively, in the two data sets, distance explained consistently low amounts of variation in species composition compared to environmental gradients. Hence, the distance limitation hypothesis provides no strong explanation for the composition in the assemblages of spiders at a regional scale. This is not really surprising. Spiders evolved an effective dispersal strategy: ballooning. The majority of species in both data sets are capable or probably capable of ballooning, allowing them to reach suitable habitats to hundreds of kilometers by wind (Weyman, 1993). Furthermore, theoretical work has shown that cursorial movement is a successful strategy of spiders in colonizing new habitats over short distances (Bonte, Lens, et al., 2003).

Ballooning has been shown to link habitats in multiple systems and different spider taxa. For example, Greenstone (1982) found that the species living in unpredictable open habitats near water showed a higher frequency of ballooning than species living in more stable prairie habitat. Birkhofer, Smith, et al. (2015) further showed that spider assemblages in grasslands and crop fields are characterized by species with higher dispersal ability than assemblages in forest. Similarly, spider communities colonizing deadwood also showed very little response to spatial proximity (Müller et al., 2020), much like in this study here. Overall, this supports the view that spiders have an effective strategy to colonize

ephemeral habitats at the regional scale. However, other reasons can lead to similar low dissimilarity patterns in space. Homogenization of habitats can reduce dissimilarity (Gossner et al., 2016). Another reason might be that assemblages became isolated only recently. In our study region, habitat heterogeneity across space is high and forests have long existed in this region. Thus, dispersal is the most parsimonious explanation for the observed pattern.

### Canopy cover determines species richness

A major finding of our study is that decreasing canopy cover is the only consistent factor that significantly increased species richness (controlled for abundance). Our results suggest that mechanisms related to environmental heterogeneity are driving this pattern. In principle, Stein and Kreft (2015) identified three potential mechanisms behind positive environmental heterogeneity (EH)-richness relationships: (1) diversification in an evolutionary context by promotion of adaptation, diversification, and speciation with dispersal limitations, in topographic EH and on larger scales, (2) persistence of species through EH, for example, by improved shelter from predators or unfavorable conditions like cold or heat, and (3) improved coexistence of species in a local community by an increase in available niche space and more diverse resources due to increasing EH. In our study, abundance-corrected species richness was higher in forest with open canopy, which supports the idea of

more resources or niches for spiders in open forests. In fact, more insect prey is found in the herb layer of open compared to closed forests (Kortmann, Müller, et al., 2021). Moreover, open forests may represent a more complex habitat, at least at the forest floor, due to a diverse and dense ground vegetation, presence of bare soil and deadwood features, which might support coexistence of more species, as predicted by the habitat heterogeneity hypothesis (Heidrich et al., 2020) and shown in experiments (Robinson, 1981). Another mechanism might be the interaction of habitat complexity, prey availability and cannibalism. Wagner and Wise (1996) showed higher cannibalism rates in more complex habitats with sufficient food. Such a “higher intraspecific population regulation” can also produce higher richness.

On the other hand, assemblages in open forests were functional-phylogenetically more similar, which at first sight does not support the hypothesis that richness increases due to increased dissimilarity. However, various spider species have a very specialized diet (Pekar & Toft, 2015) and thus narrow niches despite overall similar phenotypes. Such subtle specialization on different prey might allow congenetics to coexist in a specific habitat (Mezofi et al., 2020; Pekar et al., 2012) and to exclude other species ending up in a combined effect of environmental filtering and a habitat effect on competition (Cadotte & Tucker, 2017). Eco-evolutionary simulations frequently show the emergence of clusters of similar species coexisting due to extremely small niche differences as a stable outcome (Scheffer & van Nes, 2006).

Another way to support coexistence of species in a specific habitat, particularly in taxa with competition between species, is an increasing dissimilarity, as indicated by functional overdispersion in species-rich assemblages as shown for deadwood inhabiting fungi (Bässler, Müller, et al., 2016). In our study, decreasing canopy cover decreased functional-phylogenetic diversity but increased species richness, which does not seem to indicate that competitive effects were important in open forests, unless similar species are better competitors than others, as discussed above. A pattern of greater species richness but functionally more closely related spider communities has previously been observed only in permanent grassland habitats also rich in vegetation structure (Birkhofer, Meub, et al., 2015). However, when testing for an effect of functional-phylogenetic diversity on richness together with the other predictors, we observed an increase of richness with increasing functional-phylogenetic diversity only in the GAP data set. The GAP data set comprised more samples due to the three sampling years and more specimen per sample due to the higher number of pitfall traps per plot. Hence, it is possible that the subtle effects of competition are only detectable in large samples sizes.

The open canopy seems to favor larger population sizes of many spider species, supporting the persistence of higher abundances of spiders. In line with the more individual hypothesis, a higher number of individuals due to higher resource availability drives species richness. Indeed, the number of individuals was the most important driver of species richness in our model (Table 4). One possible explanation for the observed higher spider abundance in open compared to closed forests (e.g., almost threefold more individuals) is higher resource availability (arthropod prey) in open forest (Birkhofer et al., 2010; Chen & Wise, 1999; Lehnert et al., 2013; Sereda et al., 2012). Additionally, higher availability of sunlight and temperature at the forest floor can promote the development of spider offspring (Weiß, 1995). Finally, ground-living spiders, which are more susceptible to bird predation than web-building spiders (Gunnarsson & Wiklander, 2015), might experience a reduced predation risk in open forest due to a more complex soil surface with vegetation and deadwood increasing the survival.

## Species richness declines with elevation

Elevation and latitude are among the most prominent predictors of species richness globally (Gillooly & Allen, 2007), generally showing a decrease of richness towards harsh environments in which only specialists can survive (Hodkinson, 2005; Pellissier et al., 2012; Peters et al., 2016). We found support for this pattern along the studied elevation gradient, but previous studies focusing on larger latitudinal gradients on national scales did not observe such a pattern (Germany [Finch et al., 2008], Sweden [Arvidsson et al., 2016]). Other predictors in our analyses were more important for explaining local richness, particularly canopy cover. These results suggest that spider richness may not only be influenced by macroclimatic conditions, but also by microclimate, which in forests is very much determined by the canopy. The interplay of macro- and microclimate is increasingly considered in climate change studies (Bässler, Müller, Dziock, et al., 2010; Dulle et al., 2016; Zellweger et al., 2020) as well as in spider studies (Malumbres-Olarte et al., 2018; Matevski et al., 2020).

Similar to the effects of canopy cover, elevation had also a number of indirect effects on species richness. First, spider abundance decreased consistently with increasing elevation in both data sets, although not significant for BIO. This indicates that the less favorable conditions in higher elevations support fewer individuals, which in turn reduces species richness in accordance with the more individuals hypothesis. Another indirect

effect might act via higher functional diversity allowing more species to coexist at higher elevation. We found functional diversity to increase with elevation consistently in both data sets, but species richness decreased with elevation not supporting the hypothesis of higher richness due to higher functional diversity. In a study of spider communities along a tropical elevation gradient, Dolson et al. (2020) observed the opposite with lowest functional diversity at higher elevations, underlining that our finding from a temperate forest cannot be generalized.

## Environmental filtering important for spider assemblages

Overall, we found broad support for the hypothesis that environmental filtering (H2) drives local spider assemblages. However, identifying processes from patterns of phylogenetic or functional diversity alone is hampered by simultaneously acting processes and identical patterns created by different processes (Gerhold et al., 2015; Kraft et al., 2015; Mayfield & Levine, 2010). Comprehensive analyses of changes of phylogenetic diversity and traits along underlying environmental gradients can help to identify the processes driving community assembly (Cadotte & Tucker, 2017). We combined here dissimilarity based on traits and phylogeny to extract as much as possible variation among species, including unmeasured traits. This functional-phylogenetic diversity consistently decreased with canopy cover indicating that open forest conditions are an important filter. Comparable to our results, Kosulic et al. (2016) found higher species numbers but lower functional diversity of spider assemblages in oak forests with an open canopy compared to oak forests with dense canopy (see also Ziesche & Roth, 2008). High habitat complexity in the ground stratum caused by the herb layer, tree stumps, branches, open soil, moss and leaf litter might provide a higher number of niches that could allow closely related species to coexist (Podgaiski & Rodrigues, 2017). Moreover, open forests are characterized by higher, small-scale variation in soil and litter moisture (Stein & Kreft, 2015) due to the loss of mature trees. Habitat heterogeneity at the ground level can positively affect the number of species and individuals in forest spider communities (Sereda et al., 2012; Stanska et al., 2016).

The harshness of environmental conditions increases with elevation and habitat filters should become more important with elevation leading to a decrease of functional diversity with increasing elevation as shown for lichens (Bässler, Cadotte, et al., 2016). However, our results suggest the opposite as functional diversity

increased with elevation. Hence, in temperate forests the canopy seems to be the major habitat filter for spider communities.

Because competition can produce patterns similar to those of habitat filtering (Mayfield & Levine, 2010), Kraft et al. (2015) challenged approaches to identify environmental filtering by analyzing phylogenetic or functional diversity patterns. Cadotte and Tucker (2017) therefore proposed a stepwise approach before clustering can be attributed to environmental filtering: (1) identify clustering, (2) attribute the degree of clustering to a clear environmental gradient, and (3) relate environmental conditions where species show clustering to species traits. Following this approach, we were able to identify a clustering pattern that could be attributed to the environmental gradient of canopy cover and linked the environmental gradients successfully to traits, such as ballooning and some morphological attributes. Moreover, the phylogenetic signal in then observed abundances as an indicator of species performance supports the link between clustering and the environment. Our results, thus, strongly suggest that an environmental filter is a major driver of spider community assembly in open forests. The dominance of canopy as critical environmental gradient, followed by moisture supports an earlier study identifying environmental niche axis for spiders in Europe, but previously excluding elevation (Entling et al., 2007).

In arthropods, the relationship between morphological traits and environmental gradients is still insufficiently understood. For spiders, Olive (1980) developed predictions on morphology in relation to environment based on observations of two orb-weaving spider species: for instance, spiders specialized on rapidly escaping prey types, such as Diptera and Lepidoptera, should have short legs and long fangs, while the opposite is expected for species specialized on dangerous or slowly escaping taxa, such as Hymenoptera, Orthoptera, or Homoptera. In our data, we found this combination with the latter in forests with an open canopy. This matches the observation of more species of these groups with increasing bark beetle infestation (Beudert et al., 2015; Kortmann, Roth, et al., 2021). Gibb et al. (2015) expanded the prediction based on Olive (1980) and further studies on beetles and ants (Barton et al., 2011; Gibb & Parr, 2013; Sarty et al., 2006) predicting that arthropods are broader and have shorter legs and shorter fangs in less complex habitats. In our data, only fang and prosoma breadth were in line with this prediction. The question remains, what kind of complexity matters for our assemblages under study? Open forests are much more complex near ground, but the total three-dimensional complexity of forests increases towards mature forests. This might support the narrower prosoma, larger fang as well as a higher overall

functional diversity of spiders in vertically more complex dense forests due to mature trees (Brändle & Brandl, 2001; Heidrich et al., 2020).

The mean body size increased as forest and canopy density increased, which is in line with the prediction that body size increases with increasing habitat complexity (Entling et al., 2010). Again, this supports the view, that the pronounced three-dimensional structure of mature forests (Davies & Asner, 2014) forms the habitat complexity for this arthropod group. An alternative mechanism might be an increase in mean body size from cool/moist to warm/dry environments due to changes in metabolic rate, desiccation resistance, and community interactions as shown for European spiders (Entling et al., 2010). However, we found no consistent response of body size to soil moisture or elevation in line with this prediction. Mean and extreme values might counteract here. It has been shown that open forests are characterized by higher temperature extremes than closed forests (Thom et al., 2020), but also by higher humidity due to the absence of trees.

## Limitations of the study

Observational studies always have limitations. First, multiple processes form local assemblages hampering the identification of individual mechanisms. The classical view that clustered assembly patterns suggest habitat filtering and over-dispersed patterns suggest competition has been challenged by studies identifying different mechanisms leading to these patterns (Kraft et al., 2015). There is evidence that trophic interactions can drive over-dispersion and competition can lead to clustered communities as well. Further, over-dispersed communities can arise from local heterogeneity (Gallien, 2017; Herben & Goldberg, 2014; Mayfield & Levine, 2010).

However, these situations, where different mechanisms drive such patterns are very specific. The critical point is, whether measured traits control niche differentiation or the position in a competitive hierarchy. The traits we measured seem to be much more linked to the niche differentiation in temperate forests (Entling et al., 2007) and not as suggested for competition in sessile organism as plants (Mayfield & Levine, 2010). Nevertheless, diverse types of competitive interactions hamper the identification of the presence of competition in natural communities, and might not be detectable with existing methods (Gallien, 2017). We followed the suggestion by Cadotte and Tucker (2017) to identify habitat filtering by combining information on species traits, abundances, species numbers, and well-known environmental gradient. Based on the combination of results, we are convinced that our

interpretation is well founded, even if further mechanisms such as indirect competition cannot be measured.

The second limitation of this study is that we sampled near ground level and thus likely observed incomplete communities since the species in the canopy of closed forests are underrepresented. However, the finding that species of the canopy are found in closed forest plots but not in the gaps supports the view that the functional range of species is well covered. Nevertheless, using a full three-dimensional sampling of the environment, which does not exist at the moment for all types of forests from openings to dense forests, might show higher abundances in closed forests due to canopy dwellers.

Finally, arthropod sampling in general suffers from imperfect detection of species in a local assemblage. Our GAP data set consist of much more individuals due to higher local sampling effort. Moreover, our methods broadly considered this by null model approaches and the control of species richness using the abundance as covariate (see suggestion by Gotelli & Colwell, 2001). Finally, community patterns used in the matrix correlation are rather robust to imperfect detection. Interestingly, the major patterns were highly robust for both data sets despite differences in sampling intensity in GAP and BIO, except for biotic interactions. Here the larger sample size in BIO enabled us to identify currently potentially hidden patterns. In summary, we see the strength of our study here in a truly replicated community analysis, conducted in different years at different plots, but along similar major environmental gradients.

## CONCLUSION

Our approach combining abundance, taxonomic and functional (phylogenetic) diversity in one framework helped to test four major hypotheses about how richness is determined in a diverse arthropod assemblage. The assemblages of spiders in forests along gradients of elevation, moisture and canopy cover and replicated in two independent data sets showed that, from the plethora of processes influencing local assemblages, some can be identified as being consistently of major importance. In the studied temperate forests, habitat filtering seems of major importance while dispersal seems to be of lower importance. Resource limitation and biotic interactions might have some impact on local spider assemblages but are of lower importance compared to habitat filtering and therefore more difficult to identify.

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Müller, 2021a) are available in Dryad at <https://doi.org/10.5061/dryad.sn02v6x4r>. R codes (Müller, 2021b) are available in Zenodo at <https://doi.org/10.5281/zenodo.5523394>.

## ORCID

Jörg Müller  <https://orcid.org/0000-0002-1409-1586>

Marc W. Cadotte  <https://orcid.org/0000-0002-5816-7693>

Claus Bässler  <https://orcid.org/0000-0001-8177-8997>

Klaus Birkhofer  <https://orcid.org/0000-0002-9301-2443>

Simon Thorn  <https://orcid.org/0000-0002-3062-3060>

Sebastian Seibold  <https://orcid.org/0000-0002-7968-4489>

## REFERENCES

- Adler, P. B., and S. L. Collins. 2011. "Productivity Is a Poor Predictor of Plant Species Richness." *Science* 334: 905.
- Allouche, O., M. Kalyuzhny, G. Moreno-Rueda, M. Pizarro, and R. Kadmon. 2012. "Area-Heterogeneity Tradeoff and the Diversity of Ecological Communities." *Proceedings of the National Academy of Sciences of the United States of America* 109: 17495–500.
- Arvidsson, F., L. J. Jonsson, and K. Birkhofer. 2016. "Geographic Location, Not Forest Type, Affects the Diversity of Spider Communities Sampled with Malaise Traps in Sweden." *Annales Zoologici Fennici* 53: 215–27.
- Balmford, A. 1996. "Extinction Filters and Current Resilience: The Significance of Past Selection Pressures for Conservation Biology." *Trends in Ecology & Evolution* 11: 193–6.
- Barton, P. S., H. Gibb, A. D. Manning, D. B. Lindenmayer, and S. A. Cunningham. 2011. "Morphological Traits as Predictors of Diet and Microhabitat Use in a Diverse Beetle Assemblage." *Biological Journal of the Linnean Society* 102: 301–10.
- Bässler, C., M. Cadotte, B. Beudert, C. Heibl, M. Blaschke, J. Bradtka, T. Langbehn, S. Werth, and J. Müller. 2016. "Contrasting Patterns of Lichen Functional Diversity and Species Richness across an Elevation Gradient." *Ecography* 39: 689–98.
- Bässler, C., B. Förster, C. Moning, and J. Müller. 2008. "The BIOKLIM-Project: Biodiversity Research between Climate Change and Wilding in a Temperate Montane Forest – The Conceptual Framework." *Waldökologie, Landschaftsforschung und Naturschutz* 7: 21–33.
- Bässler, C., J. Müller, M. W. Cadotte, C. Heibl, J. H. Bradtka, S. Thorn, and H. Halbwachs. 2016. "Functional Response of Lignicolous Fungal Guilds to Bark Beetle Deforestation." *Ecological Indicators* 65: 149–60.
- Bässler, C., J. Müller, and F. Dziöck. 2010. "Identification of Climate Sensitive Zones for Plants in Montane Forests." *Folia Geobotanica* 45: 163–82.
- Bässler, C., J. Müller, F. Dziöck, and R. Brandl. 2010. "Microclimate and Especially Resource Availability Are more Important than Macroclimate for Assemblages of Wood-Inhabiting Fungi." *Journal of Ecology* 98: 822–32.
- Bell, J. R., D. A. Bohan, E. M. Shaw, and G. S. Weyman. 2005. "Ballooning Dispersal Using Silk: World Fauna, Phylogenies, Genetics and Models." *Bulletin of Entomological Research* 95: 69–114.
- Beudert, B., C. Bässler, S. Thorn, R. Noss, B. Schröder, H. Dieffenbach-Fries, N. Foullois, and J. Müller. 2015. "Bark Beetles Increase Biodiversity while Maintaining Drinking Water Quality." *Conservation Letters* 8: 272–81.
- Birkhofer, K., M. Gossner, T. Diekötter, C. Drees, O. Ferlian, M. Maraun, S. Scheu, et al. 2017. "Land-Use Type and Intensity Differentially Filter Traits in above- and below-Ground Arthropod Communities." *Journal of Animal Ecology* 86: 511–20.
- Birkhofer, K., C. Meub, K. Stötzel, V. Wolters, and T. Diekötter. 2015. "Optimizing Arthropod Predator Conservation in Permanent Grasslands by Considering Diversity Components beyond Species Richness." *Agriculture, Ecosystem & Environment* 211: 65–72.
- Birkhofer, K., S. Scheu, and T. Wiegand. 2010. "Assessing Spatio-temporal Predator-Prey Patterns in Heterogeneous Habitats." *Basic and Applied Ecology* 11: 486–94.
- Birkhofer, K., H. G. Smith, W. W. Weisser, V. Wolters, and M. M. Gossner. 2015. "Land-Use Effects on the Functional Distinctness of Arthropod Communities." *Ecography* 38: 889–900.
- Bishop, T. R., M. P. Robertson, B. J. van Rensburg, and C. L. Parr. 2015. "Contrasting Species and Functional Beta Diversity in Montane Ant Assemblages." *Journal of Biogeography* 42: 1776–86.
- Bond, J. E., N. L. Garrison, C. A. Hamilton, R. L. Godwin, M. Hedin, and I. Agnarsson. 2014. "Phylogenomics Resolves a Spider Backbone Phylogeny and Rejects a Prevailing Paradigm for Orb Web Evolution." *Current Biology* 24: 1765–71.
- Bonte, D., L. Lens, J. P. Maelfait, M. Hoffmann, and E. Kuijken. 2003. "Patch Quality and Connectivity Influence Spatial Dynamics in a Dune Wolfspider." *Oecologia* 135: 227–33.
- Bonte, D., N. Vandenbroecke, L. Lens, and J. P. Maelfait. 2003. "Low Propensity for Aerial Dispersal in Specialist Spiders from Fragmented Landscapes." *Proceedings of the Royal Society B: Biological Sciences* 270: 1601–7.
- Brändle, M., and R. Brandl. 2001. "Species Richness of Insects and Mites on Trees: Expanding Southwood." *Journal of Animal Ecology* 70: 491–504.
- Cadotte, M., H. A. Cecile, and S. C. Walker. 2013. "The Ecology of Differences: Assessing Community Assembly with Trait and Evolutionary Distances." *Ecology Letters* 16: 1234–44.
- Cadotte, M., and T. J. Davies. 2016. *Phylogenies in Ecology*. Princeton, NJ: Princeton University Press.
- Cadotte, M. W., and C. M. Tucker. 2017. "Should Environmental Filtering Be Abandoned?" *Trends in Ecology & Evolution* 32: 429–37.
- Cardoso, P., S. Pekár, R. Jocqué, and J. A. Coddington. 2011. "Global Patterns of Guild Composition and Functional Diversity of Spiders." *PLoS One* 6: e21710.
- Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. "The Merging of Community Ecology and Phylogenetic Biology." *Ecology Letters* 12: 693–715.
- Chase, J., and J. Myers. 2011. "Disentangling the Importance of Ecological Niches from Stochastic Processes across Scales." *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2351–63.
- Chen, B., and D. H. Wise. 1999. "Bottom-Up Limitation of Predaceous Arthropods in a Detritus-Based Terrestrial Food Web." *Ecology* 80: 761–72.

- Coleman, B. D. 1981. "On Random Placement and Species-Area Relations." *Mathematical Biosciences* 54: 191–215.
- Connor, E. F., and E. D. McCoy. 1979. "Statistics and Biology of the Species-Area Relationship." *American Naturalist* 113: 791–833.
- Davies, A. B., and G. P. Asner. 2014. "Advances in Animal Ecology from 3D-LiDAR Ecosystem Mapping." *Trends in Ecology & Evolution* 29: 681–91.
- Davies, K. F., M. Holyoak, K. A. Preston, V. A. Offeman, and Q. Lum. 2009. "Factors Controlling Community Structure in Heterogeneous Metacommunities." *Journal of Animal Ecology* 78: 937–44.
- Dinnage, R. 2009. "Disturbance Alters the Phylogenetic Composition and Structure of Plant Communities in an Old Field System." *PLoS One* 4: e7071.
- Dolson, S. J., M. McPhee, C. F. Viquez, W. Hallwachs, D. H. Janzen, and M. A. Smith. 2020. "Spider Diversity across an Elevation Gradient in Area de Conservacion Guanacaste (ACG), Costa Rica." *Biotropica* 52: 1092–102.
- Dulle, H. I., S. W. Ferger, N. J. Cordeiro, K. M. Howell, M. Schleuning, K. Bohning-Gaese, and C. Hof. 2016. "Changes in Abundances of Forest Understorey Birds on Africa's Highest Mountain Suggest Subtle Effects of Climate Change." *Diversity and Distributions* 22: 288–99.
- Eberhard, W. G. 1990. "Function and Phylogeny of Spider Webs." *Annual Review of Ecology and Systematics* 21: 341–72.
- Elston, D. A., R. Moss, T. Boulinier, C. Arrowsmith, and X. Lambin. 2001. "Analysis of Aggregation, a Worked Example: Numbers of Ticks on Red Grouse Chicks." *Parasitology* 122: 563–9.
- Entling, W., M. H. Schmidt, S. Bacher, R. Brandl, and W. Nentwig. 2007. "Niche Properties of Central European Spiders: Shading, Moisture and the Evolution of the Habitat Niche." *Global Ecology and Biogeography* 16: 440–8.
- Entling, W., M. H. Schmidt-Entling, S. Bacher, R. Brandl, and W. Nentwig. 2010. "Body Size–Climate Relationships of European Spiders." *Journal of Biogeography* 37: 477–85.
- Fauth, J. E., J. Bernardo, M. Camara, W. J. Resetarits, Jr., J. van Buskirk, and S. A. McCollum. 1996. "Simplifying the Jargon of Community Ecology: A Conceptual Approach." *The American Naturalist* 147: 282–6.
- Fernandez-Palacios, J. M., and J. P. de Nikolas. 1995. "Altitudinal Pattern of Vegetation Variation on Tenerife." *Journal of Vegetation Science* 6: 183–90.
- Finch, O. D., T. Blick, and A. Schuldt. 2008. "Macroecological Patterns of Spider Species Richness across Europe." *Biodiversity and Conservation* 17: 2849–68.
- Fox, J., and S. Weisberg. 2018. "Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals." *Journal of Statistical Software* 87: 1–27.
- Gallien, L. 2017. "Intransitive Competition and its Effects on Community Functional Diversity." *Oikos* 126: 615–23.
- Gerhold, P., J. F. Cahill, M. Winter, I. V. Bartish, and A. Prinzing. 2015. "Phylogenetic Patterns Are Not Proxies of Community Assembly Mechanisms (They Are Far Better)." *Functional Ecology* 29: 600–14.
- Gerisch, M., V. Agostinelli, K. Henle, and F. Dziock. 2012. "More Species, but all Do the Same: Contrasting Effects of Flood Disturbance on Ground Beetle Functional and Species Diversity." *Oikos* 121: 508–15.
- Gibb, H., D. Muscat, M. R. Binns, C. J. Silvey, R. A. Peters, D. I. Warton, and N. R. Andrew. 2015. "Responses of Foliage-Living Spider Assemblage Composition and Traits to a Climatic Gradient in Themeda Grasslands." *Australian Ecology* 40: 225–37.
- Gibb, H., and C. L. Parr. 2013. "Does Structural Complexity Determine the Morphology of Assemblages? An Experimental Test on Three Continents." *PLoS One* 8: e64005.
- Gillooly, J. F., and A. P. Allen. 2007. "Linking Global Patterns in Biodiversity to Evolutionary Dynamics Using Metabolic Theory." *Journal of Ecology* 88: 1890–4.
- Goslee, S. C., and D. L. Urban. 2007. "The Ecodist Package for Dissimilarity-Based Analysis of Ecological Data." *Journal of Statistical Software* 22: 1–19.
- Gossner, M. M., T. M. Lewinsohn, T. Kahl, F. Grassein, S. Boch, D. Prati, K. Birkhofer, et al. 2016. "Land-Use Intensification Causes Multitrophic Homogenization of Grassland Communities." *Nature* 540: 266–9.
- Gotelli, N. J., and R. K. Colwell. 2001. "Quantifying Biodiversity: Procedures and Pitfalls in the Measurement and Comparison of Species Richness." *Ecology Letters* 4: 379–91.
- Gower, J. C. 1971. "A General Coefficient of Similarity and Some of its Properties." *Biometrics* 27: 857–71.
- Greenstone, M. H. 1982. "Ballooning Frequency and Habitat Predictability in Two Wolf Spider Species (Lycosidae: Pardosa)." *Florida Entomologist* 65: 83–9.
- Gunnarsson, B., and K. Wiklander. 2015. "Foraging Mode of Spiders Affects Risk of Predation by Birds." *Biological Journal of the Linnean Society* 115: 58–68.
- Hanski, I., and M. Heino. 2003. "Metapopulation-Level Adaptation of Insect Host Plant Preference and Extinction-Colonization Dynamics in Heterogeneous Landscapes." *Theoretical Population Biology* 64: 281–90.
- Heidrich, L., S. Bae, S. Levick, S. Seibold, W. Weisser, P. Krzystek, P. Magdon, et al. 2020. "Heterogeneity-Diversity Relationships Differ between and within Trophic Levels in Temperate Forests." *Nature Ecology & Evolution* 4: 1431–1.
- Herben, T., and D. E. Goldberg. 2014. "Community Assembly by Limiting Similarity Vs. Competitive Hierarchies: Testing the Consequences of Dispersion of Individual Traits." *Journal of Ecology* 102: 156–66.
- Hilmers, T., N. Friess, C. Bässler, M. Heurich, R. Brandl, H. Pretzsch, R. Seidl, and J. Müller. 2018. "Biodiversity along Temperate Forest Succession." *Journal of Applied Ecology* 55: 2756–66.
- Hodkinson, I. D. 2005. "Terrestrial Insects along Elevation Gradients: Species and Community Response to Altitude." *Biological Reviews* 80: 489–513.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. "Simultaneous Inference in General Parametric Models." *Biometrical Journal* 50: 346–63.
- Howeth, J. G., and M. A. Leibold. 2010. "Prey Dispersal Rate Affects Prey Species Composition and Trait Diversity in Response to Multiple Predators in Metacommunities." *Journal of Animal Ecology* 79: 1000–11.
- Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.
- Huston, M. A. 1999. "Local Processes and Regional Patterns: Appropriate Scales for Understanding Variation in the Diversity of Plants and Animals." *Oikos* 86: 393–401.
- Hutchinson, G. E. 1959. "Homage to Santa-Rosalia or why Are there So Many Kinds of Animals." *American Naturalist* 93: 145–59.



- Katoh, K., and D. M. Standley. 2013. "MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability." *Molecular Biology and Evolution* 30: 772–80.
- Kembel, S. W., D. D. Ackerly, S. P. Blomberg, W. K. Cornwell, P. D. Cowan, M. R. Helmus, H. Morlon, and C. O. Webb. 2011. "Picante - R Tools for Integrating Phylogenies and Ecology." Version 1.3-0.
- Komonen, A., and J. Müller. 2018. "Dispersal Ecology of Deadwood Organisms: Implications for Connectivity Conservation." *Conservation Biology* 32: 535–45.
- Kortmann, M., M. Heurich, H. Latifi, S. Rösner, R. Seidl, J. Müller, and S. Thorn. 2018. "Forest Structure following Natural Disturbances and Early Succession Provides Habitat for Two Avian Flagship Species, Capercaillie (*Tetrao urogallus*) and Hazel Grouse (*Tetrastes bonasia*)." *Biological Conservation* 226: 81–91.
- Kortmann, M., J. C. Müller, R. Baier, C. Bässler, J. Buse, O. Cholewińska, M. I. Förstner, et al. 2021. "Ecology Versus Society: Impacts of Bark Beetle Infestations on Biodiversity and Restorativeness in Protected Areas of Central Europe." *Biological Conservation* 254: 108931.
- Kortmann, M., N. Roth, J. Buse, J. Hilszczański, T. Jaworski, J. Morinière, R. Seidl, S. Thorn, and J. C. Müller. 2021. "Arthropod Dark Taxa Provide New Insights into Diversity Responses to Bark Beetle Infestations." *Ecological Applications*. <https://doi.org/10.1002/eap.2516>
- Kosulic, O., R. Michalko, and V. Hula. 2016. "Impact of Canopy Openness on Spider Communities: Implications for Conservation Management of Formerly Coppiced oak Forests." *PLoS One* 11: e0148585.
- Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015. "Community Assembly, Coexistence and the Environmental Filtering Metaphor." *Functional Ecology* 29: 592–9.
- Laliberté, E., and P. Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91: 299–305.
- Laughlin, D. C., C. Joshi, P. M. van Bodegom, Z. A. Bastow, and P. Z. Fule. 2012. "A Predictive Model of Community Assembly that Incorporates Intraspecific Trait Variation." *Ecology Letters* 15: 1291–9.
- Lawton, J. H. 1999. "Are there General Laws in Ecology." *Oikos* 84: 177–92.
- Lehnert, L. W., C. Bässler, R. Brandl, P. J. Burton, and J. Müller. 2013. "Highest Number of Indicator Species Is Found in the Early Successional Stages after Bark Beetle Attack." *Journal for Nature Conservation* 21: 97–104.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. "The Metacommunity Concept: A Framework for Multi-Scale Community Ecology." *Ecology Letters* 7: 601–13.
- Lessard, J.-P., J. Belmaker, J. A. Myers, J. M. Chase, and C. Rahbek. 2012. "Inferring Local Ecological Processes amid Species Pool Influences." *Trends in Ecology & Evolution* 27: 600–7.
- Lichstein, J. W. 2007. "Multiple Regression on Distance Matrices: A Multivariate Spatial Analysis Tool." *Plant Ecology* 188: 117–31.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, et al. 2001. "Ecology - Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges." *Science* 294: 804–8.
- MacArthur, R. H., and J. MacArthur. 1961. "On Bird Species Diversity." *Ecology* 42: 594–8.
- Malumbres-Olarte, J., L. Crespo, P. Cardoso, T. Szuts, W. Fannes, T. Pape, and N. Scharff. 2018. "The Same but Different: Equally Megadiverse but Taxonomically Variant Spider Communities along an Elevational Gradient." *Acta Oecologica-International Journal of Ecology* 88: 19–28.
- Matevski, D., A. Cvetkovska-Gjorgjievska, D. Prelic, S. Hristovski, M. Naumova, and C. Deltchev. 2020. "Distribution and Community Structure of Araneocoenoses (Araneae) along an Altitudinal Gradient on Kozuf Mountain (North Macedonia)." *Biologia* 75: 1963–76.
- Mayfield, M. M., and J. M. Levine. 2010. "Opposing Effects of Competitive Exclusion on the Phylogenetic Structure of Communities." *Ecology Letters* 13: 1085–93.
- Meiners, S. J., M. W. Cadotte, J. D. Fridley, S. T. A. Pickett, and L. R. Walker. 2015. "Is Successional Research Nearing its Climax? New Approaches for Understanding Dynamic Communities." *Functional Ecology* 29: 154–64.
- Mezofi, L., G. Marko, C. Nagy, D. Koranyi, and V. Marko. 2020. "Beyond Polyphagy and Opportunism: Natural Prey of Hunting Spiders in the Canopy of Apple Trees." *PeerJ* 8: e9334.
- Michalko, R., and S. Pekar. 2016. "Different Hunting Strategies of Generalist Predators Result in Functional Differences." *Oecologia* 181: 1187–97.
- Mittelbach, G. G., and B. McGill. 2019. *Community Ecology*. Oxford: Oxford University Press.
- Mittelbach, G. G., C. F. Steiner, S. M. Scheiner, K. L. Gross, H. L. Reynolds, R. B. Waide, M. R. Willig, S. I. Dodson, and L. Gough. 2001. "What Is the Observed Relationship between Species Richness and Productivity?" *Ecology* 82: 2381–96.
- Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. Bellwood. 2013. "A Functional Approach Reveals Community Responses to Disturbances." *Trends in Ecology & Evolution* 28: 167–77.
- Müller, J. 2021a. "Forest Spider Data to Study the Response of Assemblages to Regional and Local Processes." Dryad, Dataset. <https://doi.org/10.5061/dryad.sn02v6x4r>
- Müller, J. 2021b. "Forest Spider Data to Study the Response of Assemblages to Regional and Local Processes." Zenodo, Software. <https://doi.org/10.5281/zenodo.5523394>
- Müller, J., C. Bässler, C. Strätz, B. Klöcking, and R. Brandl. 2009. "Molluscs and Climate Warming in a Low Mountain Range National Park." *Malacologia* 51: 133–53.
- Müller, J., M. Mehr, C. Bässler, M. B. Fenton, T. Hothorn, H. Pretzsch, H.-J. Klemmt, and R. Brandl. 2012. "Aggregative Response in Bats: Prey Abundance Versus Habitat." *Oecologia* 169: 673–84.
- Müller, J., M. Ulyshen, S. Seibold, M. Cadotte, A. Chao, C. Bässler, S. Vogel, et al. 2020. "Primary Determinants of Communities in Deadwood Vary among Taxa but Are Regionally Consistent." *Oikos* 129: 1579–88.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2016. "Vegan: Community Ecology Package." <https://cran.r-project.org/web/packages/vegan/index.html>
- Olive, C. W. 1980. "Foraging Specialization in Orb-Weaving Spiders." *Ecology* 61: 1133–44.

- Pausas, J. G., and M. Verdu. 2010. "The Jungle of Methods for Evaluating Phenotypic and Phylogenetic Structure of Communities." *Bioscience* 60: 614–25.
- Pekar, S., J. Smerda, M. Hruskova, O. Sedo, C. Muster, P. Cardoso, Z. Zdrahal, et al. 2012. "Prey-Race Drives Differentiation of Biotypes in Ant-Eating Spiders." *Journal of Animal Ecology* 81: 838–48.
- Pekar, S., and S. Toft. 2015. "Trophic Specialisation in a Predatory Group: The Case of Prey-Specialised Spiders (Araneae)." *Biological Reviews* 90: 744–61.
- Pellissier, L., K. Fiedler, C. Ndribe, A. Dubuis, J. N. Pradervand, A. Guisan, and S. Rasmann. 2012. "Shifts in Species Richness, Herbivore Specialization, and Plant Resistance along Elevation Gradients." *Ecology and Evolution* 2: 1818–25.
- Peters, M. K., A. Hemp, T. Appelhans, C. Behler, A. Classen, F. Detsch, A. Ensslin, et al. 2016. "Predictors of Elevational Biodiversity Gradients Change from Single Taxa to the Multi-Taxa Community Level." *Nature Communications* 7: 13736.
- Podgaiski, L. R., and G. G. Rodrigues. 2017. "Spider Community Responds to Litter Complexity: Insights from a Small-Scale Experiment in an Exotic Pine Stand." *Iheringia Serie Zoologia* 107: e2017007.
- Pool, T. K., J. Cucherousset, S. Boulêtreau, S. Villéger, A. L. Strecker, and G. Grenouillet. 2016. "Increased Taxonomic and Functional Similarity Does Not Increase the Trophic Similarity of Communities." *Global Ecology and Biogeography* 25: 46–54.
- Robinson, J. V. 1981. "The Effect of Architectural Variation in Habitat on a Spider Community—An Experimental Field-Study." *Ecology* 62: 73–80.
- Rusch, A., K. Birkhofer, R. Bommarco, H. G. Smith, and B. Ekbom. 2015. "Predator Body Sizes and Habitat Preferences Predict Predation Rates in an Agroecosystem." *Basic and Applied Ecology* 16: 250–9.
- Sanderson, M. J. 2002. "Estimating Absolute Rates of Molecular Evolution and Divergence Times: A Penalized Likelihood Approach." *Molecular Biology and Evolution* 19: 101–9.
- Sarty, M., K. L. Abbott, and P. J. Lester. 2006. "Habitat Complexity Facilitates Coexistence in a Tropical Ant Community." *Oecologia* 149: 465–73.
- Scheffer, M., and E. H. van Nes. 2006. "Self-Organized Similarity, the Evolutionary Emergence of Groups of Similar Species." *Proceedings of the National Academy of Sciences of the United States of America* 103: 6230–5.
- Seibold, S., C. Bassler, P. Baldrian, L. Reinhard, S. Thorn, M. D. Ulyshen, I. Weiss, and J. Muller. 2016. "Dead-Wood Addition Promotes Non-saproxyllic Epigeal Arthropods but Effects Are Mediated by Canopy Openness." *Biological Conservation* 204: 181–8.
- Sereda, E., T. Blick, W. Dorow, V. Wolters, and K. Birkhofer. 2012. "Spatial Distribution of Spiders and Epedaphic Collembola in an Environmentally Heterogeneous Forest Floor Habitat." *Pedobiologia* 55: 241–5.
- Sharma, P. P., S. T. Kaluziak, A. R. Pérez-Porro, V. L. González, G. Hormiga, W. C. Wheeler, and G. Giribet. 2014. "Phylogenomic Interrogation of Arachnida Reveals Systematic Conflicts in Phylogenetic Signal." *Molecular Biology and Evolution* 31: 2963–84.
- Simberloff, D. 2004. "Community Ecology: Is it Time to Move on?" *American Naturalist* 163: 787–99.
- Spiller, D. A. 1984. "Competition between 2 Spider Species—Experimental Field Study." *Ecology* 65: 909–19.
- Stanska, M., T. Stanski, A. Gladzka, and M. Bartos. 2016. "Spider Assemblages of Hummocks and Hollows in a Primeval Alder Carr in the Bialowieza National Park—Effect of Vegetation Structure and Soil Humidity." *Polish Journal of Ecology* 64: 564–77.
- Stein, A., and H. Kreft. 2015. "Terminology and Quantification of Environmental Heterogeneity in Species-Richness Research." *Biological Reviews* 90: 815–36.
- Stroud, J. T., M. R. Bush, M. C. Ladd, R. J. Nowicki, A. A. Shantz, and J. Sweatman. 2015. "Is a Community Still a Community? Reviewing Definitions of Key Terms in Community Ecology." *Ecology and Evolution* 5: 4757–65.
- Talavera, G., and J. Castresana. 2007. "Improvement of Phylogenies after Removing Divergent and Ambiguously Aligned Blocks from Protein Sequence Alignments." *Systematic Biology* 56: 564–77.
- Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. "Animal Species Diversity Driven by Habitat Heterogeneity/Diversity: The Importance of Keystone Structures." *Journal of Biogeography* 31: 79–92.
- Thom, D., A. Sommerfeld, J. Sebald, J. Hagge, J. Müller, and R. Seidl. 2020. "Effects of Disturbance Patterns and Deadwood on the Microclimate in European Beech Forests." *Agricultural and Forest Meteorology* 291: 108066.
- Vellend, M. 2016. *The Theory of Ecological Communities*. Monographs in Population Biology, Vol 57. Princeton, NJ: Princeton University Press.
- Wagner, J. D., and D. H. Wise. 1996. "Cannibalism Regulates Densities of Young Wolf Spiders: Evidence from Field and Laboratory Experiments." *Ecology* 77: 639–52.
- Weiber, E., D. Freund, T. Bunton, A. Stefanski, T. Lee, and S. Bentivenga. 2011. "Advances, Challenges and a Developing Synthesis of Ecological Community Assembly Theory." *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2403–13.
- Weiß, I. 1995. "Spinnen und Weberknechte auf Baumstämmen im Nationalpark Bayerischer Wald." In *Proceedings of the 15th European Colloquium of Arachnology*, Budweis, 184–192.
- Weyman, G. S. 1993. "A Review of the Possible Causative Factors and Significance of Ballooning in Spiders." *Ethology Ecology & Evolution* 5: 279–91.
- Winter, M., V. Devictor, and O. Schweiger. 2013. "Phylogenetic Diversity and Nature Conservation: Where Are we?" *Trends in Ecology & Evolution* 28: 199–204.
- Wise, D. H. 1979. "Effects of an Experimental Increase in Prey Abundance upon the Reproductive Rates of 2 Orb-Weaving Spider Species (Araneae, Araneidae)." *Oecologia* 41: 289–300.
- Wise, D. H. 2006. "Cannibalism, Food Limitation, Intraspecific Competition and the Regulation of Spider Populations." *Annual Review of Entomology* 51: 441–65.
- Wright, D. H. 1983. "Species-Energy Theory—An Extension of Species-Area Theory." *Oikos* 41: 496–506.
- Yang, R. C. 2004. "A Likelihood-Based Approach to Estimating and Testing for Isolation by Distance." *Evolution* 58: 1839–45.
- Zellweger, F., P. de Frenne, J. Lenoir, P. Vangansbeke, K. Verheyen, M. Bernhardt-Romermann, L. Baeten, et al. 2020. "Forest Microclimate Dynamics Drive Plant Responses to Warming." *Science* 368: 772–5.

- Ziesche, T. M., and M. Roth. 2008. "Influence of Environmental Parameters on Small-Scale Distribution of Soil-Dwelling Spiders in Forests: What Makes the Difference, Tree Species or Microhabitat?" *Forest Ecology and Management* 255: 738–52.
- Zobel, M. 1997. "The Relative Role of Species Pools in Determining Plant Species Richness; an Alternative Explanation of Species Coexistence?" *Trends in Ecology & Evolution* 12: 266–9.

### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Müller, Jörg, Roland Brandl, Marc W. Cadotte, Christoph Heibl, Claus Bässler, Ingmar Weiß, Klaus Birkhofer, Simon Thorn, and Sebastian Seibold. 2022. "A Replicated Study on the Response of Spider Assemblages To Regional and Local Processes." *Ecological Monographs* e1511. <https://doi.org/10.1002/ecm.1511>