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Species assortment or habitat filtering: a case study of spider communities on lake islands

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Abstract Competition theory predicts that species of similar ecological niches are less likely to coexist than species with different niches, a process called species assortment. In contrast, the concept of habitat filtering implies that species with similar ecological requirements should co-occur more often than expected by chance. Here we use environmental and ecological data to assess patterns of co-occurrence of regional communities of spiders distributed across two assemblies of lake islands in northern Poland. We found aggregated and random co-occurrences of species of the same genus and a significant tendency of species segregation across genera. We also found that species of the same genus react similarly to important environmental variables. A comparison of ecological traits of species of the local communities with those expected from a random sample from the regional Polish species pool corroborated partly the habitat filtering hypothesis. On the other hand, we did not find evidence for species assortment. Our results also imply that at least some observed species co-occurrences result from niche differentiation.

Keywords Araneae · Spiders · Habitat filtering · Phylogenetic signal · Species/genus ratios · Canonical correspondence analysis · Ordination

Introduction

Ever since Darwin (1959), ecologists have noticed that closely related species are ecologically more similar than more distantly related ones (reviewed in Wiens and Graham 2005). They are increasingly aware of the potential influence of such phylogenetic signals on the structure of ecological communities (Webb et al. 2002; Donoghue 2008; Losos 2008). Indeed a series of recent studies detected phylogenetic signals in ecological communities, in particular non-random occurrences of species with respect to phylogeny (e.g., Prinzing et al. 2001, 2008; Johnson and Stinchcombe 2007; Kraft et al. 2008) and have tried to develop conceptual models to explain observed patterns (Emerson and Gillespie 2008).

Three contrasting (but by no means mutually exclusive) theories explain structure and composition of ecological communities. The first focuses on interspecific competition and niche differentiation to explain non-random patterns of species occurrences and abundances across sites (Diamond 1975). In this view, species of similar ecological niches are less likely to coexist than species with different niches (Gotelli and Graves 1996). The respective ecological filtering process has been termed species assortment (Emerson and Gillespie 2008). Within this framework, competition theory predicts also fewer numbers of co-occurring closely related species (phylogenetic overdispersion) compared to more distantly related species (Tofts and Silvertown 2000).

In contrast to species assortment, the concept of habitat filtering (Weiher and Keddy 1999; Cornwell et al. 2006) implies that species with similar ecological requirements should co-occur more often than expected

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by chance if only ecologically similar species can coexist in a given habitat. In terms of phylogeny, this concept predicts phylogenetic underdispersion or that closely related species should co-occur more often than expected by chance (Vamosi and Vamosi 2007; Losos 2008).

Both previous concepts a priori assume the non-equivalence of species with respect to persistence within communities and therefore also the existence of species specific traits (Chase and Leibold 2003). In contrast, the third concept of community assembly, neutrality, explicitly does not consider such traits and assumes the equivalence of individuals within communities without the need to refer to species and niches (Hubbell 2001; Chave 2004). In its simplest version (Hubbell 2001), neutral communities are assembled from ecological drift, the process of random birth/death and colonization events of individuals, and random speciation according to Brownian motion, in which the amount of change in any given time interval is comparably small and random in direction. At ecological time and local to regional spatial scales such a model predicts a random assortment of species with respect to the underlying phylogeny (Kembel and Hubbell 2006; Kraft et al. 2007) and random patterns of species co-occurrence (Ulrich and Zalewski 2007).

Based on the compilations of Emerson and Gillespie (2008) and Prinzing et al. (2008), it seems that phylogenetic over- and underdispersion are both common in bacterial, plant, and animal communities. Neutral community structure is much more difficult to detect, because any lack of phylogenetic signal might be caused not only by ecological drift but also by methodological and statistical issues, particularly the power of a test (Kraft et al. 2007). As Webb et al. (2002) and Losos (2008) rightly remark, unequivocal assessment of phylogenetic signals and the distinction between neutrality, species assortment, and filtering must be based on information on the actual phylogenetic distribution of ecological traits and phenotypes of the species involved. Most studies mentioned in Emerson and Gillespie (2008) lack this information.

Therefore, in the present paper we use phylogenetic, environmental, and ecological data to assess the patterns of co-occurrence of regional communities of spiders distributed across two assemblies of lake islands in northern Poland (Ulrich et al. 2009). We ask whether the distribution of spider species across sites contains a phylogenetic signal and whether habitat filtering or species assortment accounts for it. Because the phylogeny of European spiders is still not sufficiently worked out, we use two phylogenetic levels only and compare patterns of co-occurrence within and between genera.

Materials and methods

Study sites and sampling

We sampled spiders from two large complexes of lake islands in northern Poland: the Lake Wigry islands (N 54°00′–N 54°05′, E 22°01–E 22°09) and the Lake Nidzkie, Bełdany, and Mikołajskie islands/mainlands (N 54°37′–N 53°46′, E 21°31–E 21°37, hereafter NBM). Lake Wigry is part of the Wigierski National Park and its protected forested islands have a primeval character. NBM are part of the Mazurian Lake District and are the center of aquatic tourism in Poland.

On 13 islands on Wigry, 13 floristically similar islands on NBM and four sites on the surrounding mainlands, one to five (depending on island area) lines of roof covered Barber traps (∅ 12 cm opening, three traps at 25-m distance) were placed at representative floristic associations and checked monthly from May to October 2004 and 2005. Island sizes span a range from 0.0003 to 38.82 ha.

Spiders were classified into species according to Platnick (2007). In total, we collected 4799 individuals from 163 species and 87 genera at Wigry, and 5557 individuals from 157 species and 84 genera at NBM (Ulrich et al. 2009; Hajdamowicz and Stańska, unpublished data).

We studied habitat filtering from comparisons of observed local species composition at Wigry and NBM with that expected from random samples of the regional species pool. We used the Polish spider fauna as the regional species pool and compiled species/genus (S/G) ratios from the checklist of the Arachnological Section of Polish Zoological Society (2008). To study whether the observed S/G ratios of the two island ensembles differed from a random expectation, we equiprobably resampled the Polish fauna 100 times according to the observed local species richness and compared the obtained S/G ratios to the observed ones. We further calculated expected species richness per genus from regressions of the species numbers per genus at Wigry and NBM on the respective species numbers per genus of the species pool (Fig. 1). We then used the residuals $\Delta S = \Delta S_{\mathrm{obs}} - \Delta S_{\mathrm{exp}}$ of the observed number of species at Wigry and NBM (ΔS_{obs}) and the expected species

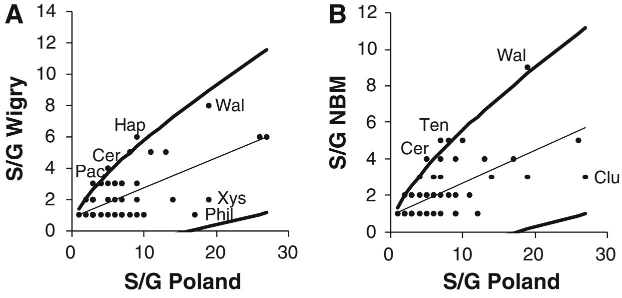

Fig. 1 Species/genus (S/G) ratios at the Wigry (**a**) and the NBM (**b**) island ensembles in comparison to the S/G ratios of the Polish fauna. Hap, *Haplodrassus*; Phi, *Philodromus*; Xys, *Xysticus*; Cer, *Ceratinella*; Wal, *Walckenaeria*; Pac, *Pachygnatha*; Ten, *Tenuiphantes*; Clu, *Clubiona*. *Bold lines* show the expected 99% confidence limits of local S/G ratios obtained from 100 equiprobable random samples from the Polish fauna. The *thin lines* mark the respective maximum likelihood expectations $Y = 0.19X + 0.88$. Regression in B $Y = 0.18X + 0.92$

number ΔS_{exp} in subsequent one-way ANOVA and regression analysis to infer whether S/G ratios depend on life-history traits and ecological variables. ANOVA was applied to ten genus specific life-history traits obtained from literature data (Heimer and Nentwig 1991; Roberts 1995; Uetz et al. 1999; Platen et al. 1999): stratum (ground/vegetation/both), plant use (no/foliage/between plants), mobility (sedentary/frequent site change/mobile); activity (diurnal/nocturnal), cocoon carrying (yes/no), web building (yes/no), web use (no/sitting/hunting off the web), web type (tube/sheet/space/orb), hunting type (ambush/stalk/pursue), microhabitat (stones, holes/grass, herbs, litter, moss/trees). We further regressed ΔS against mean genus body length, regional family species richness, and mean genus abundances (mean numbers of individuals trapped). Significance levels were in all cases Bonferroni corrected by recalculating the test-wise error rate P from an experiment wise error level of 0.05 and $N = 10$ (ANOVA) and 3 (regression), respectively, single tests: $P = 1-(1-0.05)^{1/N}$.

We studied phylogenetic signals at both lake ensembles from comparisons of the patterns of co-occurrence and niche space for species within the same genus (intragenus) and between genera (intergenus). In a first approach we used C-scores (Stone and Roberts 1990) and checkerboard scores (Gotelli 2000) to infer whether species of the same genus differ in patterns of species co-occurrences from species between genera. The degree of nestedness was estimated from the discrepancy metric of Brualdi and Sanderson (1999). We calculated the average scores of all intragenus submatrices c_{intra} and compared this mean with the respective means for the same number of identically sized submatrices composed of randomly assigned species of different genera c_{inter}. We obtained the standard deviation of intergenus means $\mathrm{SD}_{\mathrm{inter}}$ from 100 reshufflings, calculated the respective standardized (Z-transformed) effect sizes [$Z = (c_{\mathrm{intra}} - c_{\mathrm{inter}})/\mathrm{SD}_{\mathrm{inter}}$], and counted how often intragenus means were larger or smaller than intergenus means. Lastly, we inferred the significance of intragenus nestedness and co-occurrences from a comparison with the fixed–fixed null model, where row and column marginal sums are held constant, and which has comparatively low type I and II error rates (Ulrich and Gotelli 2007a, 2007b).

In a second approach, we estimated realized niche spaces from nine environmental variables (cf. Ulrich et al. 2009 for detailed description). Apart from the island area, we estimated seven important habitat characteristics (light, temperature, soil humidity, soil fertility, soil acidity, soil dispersion, and organic matter content) from plant habitat indices (Zarzycki et al. 2002) characterizing habitat requirements of plants (Ellenberg et al. 1992). Respective floristic samples of 100 m^2 were taken around each trap and 25 m apart from the first and third trap. The NBM islands appeared to be more fertile than the Wigry islands (fertility $P_{\mathrm{same}} = 0.02$; organic matter content $P_{\mathrm{same}} = 0.001$). Mean temperature and humidity did not significantly differ ($P_{\mathrm{same}} > 0.1$) (Ulrich et al. 2009). Lastly, we used the division of islands into four classes of disturbance by tourist visits in Ulrich et al. (2009): 12 islands/mainland sites at Wigry were classified as being virgin (class 4) and two islands as being slightly disturbed (class 3). At NBM, four islands obtained class 4, two islands and two mainlands class 3, two islands class 2 (moderately disturbed), and five islands class 1 (highly disturbed).

To assess similarities in niche space we used canonical correspondence analysis (CANOCO) to relate abundance matrices of both island complexes to environmental variables. The Euclidean distances of species within the ordination space are then a measure of niche similarity. We compared mean intragenus and intergenus distances and again assessed the variability in intergenus distance from 100 randomizations of species identity. Lastly, we assessed intra- and intergenus niche overlap from all intra- and intergenus Bray–Curtis distances of species abundance data. Again we compared intra- and intergenus distances from 100 randomizations of species identity.

Results

Phylogenetic niche conservatism

The co-occurrence and nestedness analyses gave strong signals for an aggregated pattern of island occupancy within genera with respect to the observed intergenus pattern (Table 1). At Wigry 21 of the C-, 19 checkerboard, and 22 of the Z-transformed nestedness scores (out of 22 genera) were negative, suggesting intragenus species aggregation (phylogenetic underdispersion). Although only 2 and 3, respectively, of them were statistically significant at the 5% error level (estimated from the tails of the null distributions), the overall tendency is highly significant (cumulative binomial test: P(3 scores

Table 1 Within genus patterns of species co-occurrence (C-score, checkerboard score) and nestedness (BR)

Metric	$Z > 0$	$Z < 0$	$Z > 2$	$Z < -2$
Wigry				
C-score	1	21	0	2
Checkerboard score	3	19	0	2
BR	0	22	0	3
NBM				
C-score	6	20	1	8
Checkerboard score	6	20	1	7
BR	4	22	0	8
Between Wigry and NBM				
C-score	15	28	0	0
Checkerboard score	12	31	0	0
BR	16	27	0	0

Z-transformed scores [$(c_{\mathrm{intra}} - c_{\mathrm{inter}})/\mathrm{SD}_{\mathrm{exp}}$] of mean observed within genus metrics c_{intra} ($N_{\mathrm{NBM}} = 26$; $N_{\mathrm{Wigry}} = 22$) in comparison to between genus metrics c_{inter} of 100 randomized matrices for each genus obtained by randomizing the species ordering of the whole presence–absence matrix of each ensemble

SD_{exp} Standard deviation of expectation positive; 19 negative) <0.001). At NBM 20 (C-, and checkerboard score) and 22 (nestedness) scores out of 26 were negative, 7 and 8, respectively, significantly ($P < 0.05$). Again, the cumulative binomial test pointed for all three metrics to a significant trend [$P(6;20) < 0.01$]. However, within genera, patterns of co-occurrence and nestedness (studied for all genera with more than three species: *Agroeca*, *Bathyphantes*, *Centromerus*, *Clubiona*, *Haplodrassus*, *Neriene*, *Pardosa*, *Pirata*, *Philodromus*, *Tenuiphantes*, *Walckenaeria*, *Xysticus*, *Zelotes*) did not differ from the expectation of the conservative fixed–fixed null model (not shown).

We also compared intra- and intergenus co-occurrences between both island complexes and still found a weak [*C*-score: cumulative binomial $P(15;28) = 0.06$; checkerboard score: cumulative binomial $P(12;31) < 0.01$] trend towards phylogenetic underdispersion (Table 1) but not a nested distribution within genera [BR: cumulative binomial $P(16;27) = 0.12$].

The environmental and abundance-based niche overlap analyses confirmed this trend (Table 2). At both island complexes, species of the same genus membership were on average significantly ($P < 0.001$) closer in ordination space than species of different genera. The intragenus Bray–Curtis distances of island abundances were also significantly ($P < 0.001$) lower than the respective intergenus distances. Hence, species of the same genus were on average more similar in abundance across islands than species of different genera.

Habitat filtering

For both island complexes we did not find clear evidence for non-random species occurrences with respect to the regional (Polish) species pool. At Wigry, the observed S/G ratio was 1.83 (expected 1.47 ± 0.29; $\mu \pm \sigma$) and at NBM 1.84 (expected 1.45 ± 0.29). The S/G ratios for single genera also did not significantly differ from a random sample (Fig. 1). At Wigry, three out of 87 (*Ceratinella*, *Haplodrassus*, *Pachygnatha*) and at NBM three out of 84 (*Ceratinella*, *Tenuiphantes*, *Walckenaeria*) genera had significantly higher local species richness than expected. These genera come from three different families (Tetragnathidae, Linyphiidae, Gnaphosidae), are in part web builders (*Ceratinella*, *Walckenaeria*, *Pachygnatha* (juvenile); active hunters: *Haplodrassus*, *Pachygnatha* (adult) and span a considerable range of body length (1.5–10 mm) and local abundance (0.01–3.2 individuals × trap^{-1}).

ANOVA and regression analysis of ecological traits suggested that at the pristine Wigry islands microhabitat was a highly significant ($P < 0.0001$) environmental filter for spiders (Table 3). On average, species that used stones, holes, walls, and sandy surfaces (six species observed; two expected) or live in the herb layer or leaf litter (137; 125 expected) were overrepresented, while species that use trees were less species-rich than expected by chance (18; 34). At NBM, this microhabitat signal vanished. In turn, the number of web-building species increased (103; 71) with respect to vagrant species (50; 61). Consequently, mobile species decreased in comparison to sedentary species (sedentary/less mobile: 104; 71, mobile: 49; 61). Observed species richness did not differ from a random expectation with respect to activity, stratum, web, or hunting type (Table 1).

Discussion

The spider communities of both island complexes were phylogenetically underdispersed. The nestedness, co-occurrence (Table 1), and niche overlap (Table 2) analyses pointed to a tendency of joint occurrences of species of the same genus. Recent reviews linked phylogenetic underdispersion directly to habitat filtering (Webb et al. 2002; Davies 2006; Emerson and Gillespie 2008) arguing that the effect of competitive exclusion is not strong

Table 2 Average intra- and intergenus Euclidean distances within the CCA ordination space calculated for all environmental axes and for the first two axes only

Axes	Intragenus mean	Intergenus mean	Intergenus SD	Intergenus mean < intragenus mean
Wigry				
CCA axes				
All axes	5.22	6.01	0.11	0
First two axes	2.04	2.16	0.05	3
Bray–Curtis distance	0.89	1.01	0.03	0
NBM				
CCA axes				
All axes	6.53	7.26	0.08	1
First two axes	2.04	2.16	0.05	0
Bray–Curtis distance	0.93	1.05	0.03	0

The intergenus means were obtained from 100 reshuffles of the ordering of species. Intra- and intergenus means refer to 72 species for Wigry and 71 species for NBM. Intergenus mean and SD obtained as before

Intergenus SD Standard deviation of intergenus means, *Bray–Curtis distance* average intragenus and intergenus species niche overlaps (estimated using the Bray–Curtis metrics applied to raw abundance data)

Table 3 ANOVA and linear regression results of the habitat filtering analysis

Trait	NBM		Wigry	
	F	P	F	P
Stratum	3.90 (2;80)	>0.4	2.91 (2;85)	>0.5
Plant use	0.48 (2;80)	>0.5	1.31 (1;86)	>0.5
Mobility	6.76 (2;80)	0.02	0.02 (1;86)	>0.5
Activity	1.37 (1;81)	>0.5	3.68 (1;86)	>0.5
Cocoon carrying	0.34 (1;81)	>0.5	0.14 (1;86)	>0.5
Web building	12.3 (1;81)	0.008	1.19 (1;86)	>0.5
Web use	6.86 (2;80)	0.02	1.70 (2;85)	>0.5
Web type	0.44 (3;56)	>0.5	2.46 (3;57)	>0.5
Hunting type	0.26 (2;20)	>0.5	3.36 (2;25)	>0.4
Microhabitat	4.54 (2;80)	0.13	13.92 (2.83)	<0.00001
	R^2	P	R^2	P
Family richness	0.00	0.99	0.00	0.99
Mean abundance	0.03	0.10	0.01	0.48
Mean body length	0.01	0.46	0.10	0.45

The dependent variable was in both cases the differences $\Delta S = \Delta S_{obs} - \Delta S_{exp}$ between the observed number of species per genus at Wigry and NBM (ΔS_{obs}) and the expected species richness obtained from the function of Fig. 1 (ΔS_{exp}). Coefficients of determination refer for Wigry to $N = 87$ and for NBM to $N = 84$. Probability levels P refer to Bonferroni corrected values

enough to outweigh the tendency of ecologically similar species to enter the same habitats. Such a view tacitly assumes some degree of niche conservatism (Losos 2008). Our results (Table 2) and recent studies on environmental correlates of spider occurrences (Entling et al. 2007) reported a weak but significant signal of niche conservatism in spiders. Although, as the latter authors rightly remark, it may be misleading to predict spider occurrences from the occurrence of closely related species, this weak trend to niche conservatism might well account for the underdispersed phylogenetic signal reported here.

We could not unequivocally detect filtering processes that might cause phylogenetic underdispersion (Table 3). At Wigry, we detected a highly significant signal for microhabitat use. Species associated with stones, holes, the herb layer, and leaf litter were more diverse than expected from a random model. At NBM the signal vanished. Within the NBM complex the number of web-building species increased in comparison to vagrant species. Possibly, in both complexes different filters are at work. Further studies have to show whether these differences can be attributed to the different levels of disturbance.

Our results also confirm that habitat filtering is a diffuse concept and may be difficult to confirm for many taxa. Any test would need precise information on which traits are filtered for and whether these traits are similar across genera and families. On the other hand, we may ask whether the detection of phylogenetic underdispersion in combination with niche conservatism is sufficient to infer some degree of habitat filtering. However, under- and overdispersion might be caused by different mechanisms, for instance by sympatric speciation (Barluenga et al. 2006) or facilitation and mutualism (Verdú and Pausas 2007; Valiente-Banuet and Verdú 2007).

In a previous study (Ulrich et al. 2009) we found significant species segregation across the Wigry islands and a random pattern of co-occurrence across the NBM islands. At Wigry, phylogenetic underdispersion was not as strong as to drive this pattern towards significant aggregation. At NBM, however, more than one-third of the intragenus co-occurrences was significantly aggregated at the 5% error benchmark. It seems likely that the contrasting processes of interspecific competition and habitat filtering resulted in a random pattern of co-occurrence within genera at Wigry while the weaker degree of competition at NBM produced the stronger signal of habitat filtering. Recently, Lovette and Hochatka (2006) reported very similar antagonistic processes in the shaping of communities of North American wood warblers.

The Wigry islands are protected and nearly pristine while NBM are the center of aquatic tourism in Poland and its islands are frequently visited by tourists. Previous results (Ulrich et al. 2009) suggested that the difference in species composition and segregation between the island complexes might result from different disturbance regimes introduced by water tourists. Other factors like plant species composition, soil properties, and climate did not produce significant signals, therefore the differences in phylogenetic signal reported here might also be caused by disturbance. Further studies have to verify this hypothesis and to infer the precise mechanisms of how disturbance influences phylogenetic signals.

Although we found a significant trend towards underdispersion, a large proportion of species co-occurrences were apparently random (Table 1). Hence, we cannot rule out that island colonization is mainly neutral. However, we did not formerly model neutrality (Hubbell 2001) to compare observed and expected patterns of intragenus co-occurrence similar to the approaches of Ulrich and Zalewski (2007) and Zillio and Condit (2007). Such modeling needs information about the abundances of species within the regional pool. These are largely unknown. Taking observed abundance totals across all islands as an approximation would already contain the phylogenetic signal to be modeled. Hence a neutral modeling without detailed knowledge about regional abundance distributions (and dispersal abilities) is unlikely to detect any phylogenetic signal different from that inherent in the model settings. Nevertheless our results indicate that site occupancy of spiders might be governed, at least in part, by some non-neutral traits related to phylogeny. Similarly to our results, Prinzing et al. (2008) reported that functional variability in plant communities generally decreases with increasing phylogenetic dispersion. They explained this finding with competitive interactions and facilitation, thus with non-neutral processes. However, they also did not model neutrality but refer to a pure random sample model. While it is known that ecological drift might generate non-random patterns of species assembly (Ulrich 2004, Bell 2005), the question of whether ecological drift might explain some of the observed patterns needs further study.

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