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β-diversity decreases with increasing trophic rank in plant – arthropod food chains on lake islands

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Contrasting trophic theories of island biogeography try to link spatial patterns in species distribution and richness with dietary preferences, arguing that the spatial turnover of species among habitat patches changes with trophic rank causing a systematic change in the proportion of plants, herbivores, and predators across habitats of different size. Here we test these predictions using quantitative surveys of plants, spiders, and herbivores as well as of omnivorous and predatory ground beetles on undisturbed Polish lake islands. We found decreased proportions of predators and habitat generalists on larger islands. Environmental niches and niche overlap were highest in predators. Variability in environmental niche width among species increased at higher trophic levels. Our results confirm models that predict a decrease in spatial species turnover (β-diversity) with increasing trophic level. We speculate that the major trigger for these differences is a reduced dispersal ability in plants at basal trophic ranks when compared to higher trophic levels.

Current approaches to ecological community assembly based on niche[1,2] and neutral[3] theories do not explicitly consider the trophic position of a species (but see[4]). Implicitly, they refer to species of the same trophic level. In turn, trophic network approaches to community assembly[5] have highlighted the importance of trophic position in the formation of ecological interactions[6] and community stability[7]. For instance, study of predator-prey richness relationships (e.g.[8,9]) has indicated the need to include community assembly processes and also spatial grain into trophic network models. Consequently, recent models on the influence of trophic position on community assembly[10,11] and on the influence of assembly processes on trophic network structure[12] have pointed to differential assembly processes acting at each trophic level. Gravel *et al.*[10] and Holt[11] have further introduced colonization and extinction dynamics into these trophic models to predict patterns of local (α-diversity) and of spatial species turnover (β-diversity) within a meta-community framework.

Gravel *et al.*[10] introduced two simple extensions to the island biogeographic model of community assembly[3,13]: (1) a predator species can only colonize an island if its prey is already present, and (2) the predator goes extinct if his prey has gone extinct. These two extensions directly link trophic complexity to α-diversity and to the slope of the species-area relationship, *SAR*, giving rise to a trophic theory of island biogeography (TTIB). As the SAR slope quantifies how fast species richness increases with increasing spatial scale it has frequently been used as a measure of β-diversity[14]. From their simulations Gravel *et al.*[10] found that low trophic connectance within a local food web might reduce α-diversity. They further predicted a decreased β-diversity at higher trophic levels (predators) in

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comparison to herbivores. The latter prediction is equivalent to a negative correlation between β-diversity and trophic rank. In turn, Holt[11] extended island biogeographic theory from the notion that predators have generally lower population sizes than their prey. Consequently, they should face higher extinction probabilities, particularly on smaller islands. This observation leads directly to the prediction that predators have increased spatial species turnover (β-diversity) in comparison to their prey species[11]. Both contrasting predictions still await critical comparison. Importantly, any change in β-diversity among trophic levels also implies changing patterns of species occurrences with respect to habitat size.

Below we study the trophic aspect of β-diversity using a power function *SAR* model. Let $S_P = S_{P,0}A^{z_P}$ and $S_H = S_{H,0}A^{z_H}$ being the *SARs* of predators and herbivores, respectively (S_P, S_H denoting species richness in area of size A, $S_{P,0}$, $S_{H,0}$, the species richness per unit area, and z_P, z_H the *SAR* slopes). According to Gravel *et al.*[10], predator SARs have shallower slopes (smaller slope values) than the respective SARs at lower trophic levels: $z_P < z_H$ and $A^{z_P - z_H} < 1$. It follows that

$$\frac{S_P}{S_H} = \frac{S_{P,0}}{S_{H,0}}A^{z_P - z_H} \tag{1}$$

and

$$\pi_H = \frac{S_P}{S_{P,0}} \bigg/ \frac{S_H}{S_{H,0}} = A^{z_P - z_H} < 1 \tag{2}$$

As $A^{z_P - z_H}$ decreases with increasing area *A*, Eq. 2 predicts that the proportion of species in a higher trophic level should decrease in larger areas with respect to the proportion in a lower trophic rank.

The model of Gravel *et al.*[10] can be extended to also cover habitat generalists and specialists. If we define habitat generalists as those that occur in the majority of habitats and assume that habitat diversity increases with area, the richness of generalist predator and herbivore species, G_P and G_H respectively, can also be described by the power function SAR model: $G_P = G_{P,0}A^{z_P}$ and $G_H = G_{H,0}A^{z_H}$. Where $G_{P,0}$ and $G_{H,0}$ denote the respective richness at unit area. Assuming again $A^{z_P - z_H} < 1$ it follows that $\frac{G_P}{G_{P,0}} = \frac{G_H}{G_{H,0}}A^{z_P - z_H} < \frac{G_H}{G_{H,0}}$ and

$$\frac{G_P}{G_{P,0}} - 1 = \frac{G_P - G_{P,0}}{G_{P,0}} < \frac{G_H}{G_{H,0}} - 1 = \frac{G_H - G_{H,0}}{G_{H,0}} \tag{3}$$

Thus the proportion of predator species that do not occur in the majority of habitats, i.e. $\frac{G_P - G_{P,0}}{G_{P,0}}$; habitat specialists should be lower than the respective proportion of herbivores $\left(\frac{G_H - G_{H,0}}{G_{H,0}}\right)$. This is a direct consequence of the shallower predator SAR slope and implies a trend towards decreasing habitat specialization at higher trophic levels.

Further, dividing the generalist predator SAR by that of the herbivore results in $\frac{G_P}{G_{P,0}}\frac{G_{H,0}}{G_H} = A^{z_P - z_H} < 1$. After a simple transformation, this results in

$$\pi_G = \frac{\frac{G_P - G_{P,0}}{G_{P,0}}}{\frac{G_H - G_{H,0}}{G_{H,0}}} = \frac{G_H A^{z_P - z_H} - G_{H,0}}{G_H - G_{H,0}} < 1 \tag{4}$$

π_G defines the proportion of habitat specialist predators with respect to that of herbivores. Because $A^{z_P - z_H}$ and consequently the right part of Eq. 4 decreases with increasing area, we predict π_G to be area dependent and to become smaller in larger areas. In other words, predators should have a wider distribution than herbivores.

The above line of argument focuses on richness proportions along food chains (the vertical dimension) but does not consider trophic niche width, that is the degree of trophic specialization. We might include the horizontal dimension of food webs with the additional observation that species of narrow habitat demands also have, on average, a narrow diet (e.g.[15,16]). With this assumption our prediction on the proportions of generalist predators can be interpreted as a hypothesis that habitat generalists exhibit a lower β-diversity with respect to habitat specialists. Consequently, the proportion of specialists should be higher in the regional than in the local species pool. This is not a simple tautology. Within this framework, generalists cannot be conflated with widely occurring species. The latter might well be habitat specialists. Therefore, to test the trophic biogeographic theory, the data on species occurrences need to be linked to respective data on environmental conditions.

Here we take advantage of a recently developed eigen-ellipsoid method to compare environmental demands of species with respective patterns of co-occurrences[17]. This method calculates the *n*-dimensional eigenvector ellipsoid based on the distribution of *n* environmental characters observed in the habitats where the focal species occurred (similar to Hutchinson's *n*-dimensional niche volumes[18,19]). The size of this ellipsoid defines the degree of environmental generalism while the relative overlap between pairs of species quantifies the degree of niche turnover. For a meta-community spread among a number of sites, the average overlap defines the degree of species functional segregation (functional β-diversity[17]).

We applied this method to an extraordinary data set on plant and arthropod species on Northern Polish lake islands including quantitative surveys of ground beetles of three different trophic levels (herbivore, omnivore, and predatory as assessed stable isotopic analyses[20]), predatory spiders, and plants. This trophic diversity allowed us to test basic predictions regarding diversity patterns at different trophic levels. According to Eq. 2 we (1) predict
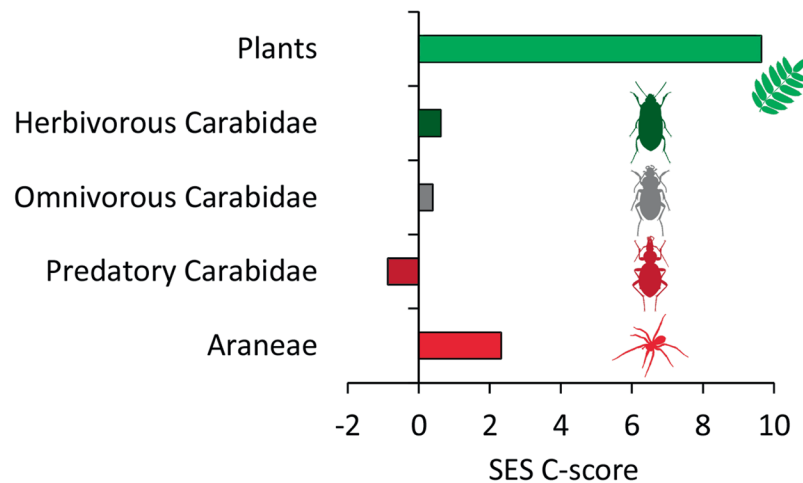
Figure 1. Standardized effect sizes SES (with respect to the fixed-fixed null model expectation) of the C-score of species co-occurrence of five trophic guilds (plants, and herbivorous, omnivorous, and predatory Carabidae and Araneae) on Lake Wigry islands. Positive SES scores point to spatial segregation. Figure prepared by Ivo Bogucki.

that predators exhibit lower species spatial turnover than species of lower trophic rank. From Eq. 4 we (2) further predict that the proportion of habitat specialist predators decreases with increasing island area. Finally, we (3) assess differences in environmental niche overlap between trophic levels to test whether β-diversity increases with increasing trophic rank as predicted by Holt[11].

Results

Spatial patterns of community assembly. The pattern of species co-occurrence of plant and, to a lesser degree, spider species across the 15 study sites was significantly segregated (high β-diversity) with respect to the fixed-fixed null standard while ground beetles did not deviate from the random co-occurrence expectation (Fig. 1). In line with Eqs 2 and 4 the proportion of trophically higher ranking species π_H (Fig. 2a) and the proportion π_G of habitat specialist species (Fig. 2b) significantly decreased in larger islands with respect to the proportion at unit area.

Environmental niche overlap at different trophic position. Species eigen-ellipsoid volume and number of occurrences were positively correlated in all three taxa (plants: $r^2 = 0.66$, ground beetles: $r^2 = 0.46$; spiders: $r^2 = 0.31$). Species co-occurrences (β_{Soer}) were significantly ($P(F_{1,96}) < 0.001$) positively correlated with ellipsoid volume and overlap, and negatively with centroid distances (Table 1).

We found significant differences in species environmental niche overlap and volumes between the four trophic levels (Table 1, Fig. 3) even after accounting for differences in the numbers of occurrences between species (Table 2). Spiders and predatory ground beetles had on average larger environmental niches than plants and herbivorous ground beetles (Fig. 3). Furthermore, these predators also had significantly (all $P(F) < 0.001$) higher ellipsoid overlap and lower centroid distances than plants (Fig. 3). Herbivorous and omnivorous ground beetles ranked intermediate, showing large variability in ellipsoid overlap and distance (Fig. 3). In turn, average degrees of pairwise species co-occurrence (β_{Soer}) did not significantly differ between the trophic groups (Fig. 3).

Discussion

Our study corroborates the view that knowledge about trophic relationships is essential for a full understanding of macroecological patterns[10,11,21,22]. We found strong support for the hypothesis that the patterns of species spatial occurrences (Fig. 1), species-area relationships (Fig. 2), and the distribution of trophic niches (Fig. 3) change along the trophic hierarchy.

The taxon wide degree of plant spatial co-occurrences was significantly segregated (Fig. 1) and contrasted to Carabidae and Araneae. Such a strong segregated pattern is equivalent to high level of β-diversity[14] and corroborates our first starting hypothesis concerning the decreased β-diversity in predatory species. A high β-diversity is also equivalent to a steep SAR slope as the slope quantifies the increase in species richness with increasing space[23]. Thus, our co-occurrence analysis indicates differences in spatial species turnover and consequently in the compositional similarity of local communities between plants and different groups of arthropods. Regarding the possible mechanisms that trigger this difference, we note that the spiders, whose mobility is on average intermediate between plants and the mostly winged Carabidae, were also intermediate in the degree of species spatial segregation (Fig. 1). Consequently, we speculate that differences in dispersal ability are responsible for the observed differences in species co-occurrences. Indeed, neutral, ecological drift models[8] predict a similar mechanism. Particularly, a high dispersal ability should be linked to random species co-occurrences as in the case of Carabidae found here (Fig. 1).

In line with our first starting hypothesis, we found also support for the model of Gravel et al.[10] predicting shallower slopes of SARs at higher trophic level and decreasing proportions of predators on larger islands (Fig. 2a).
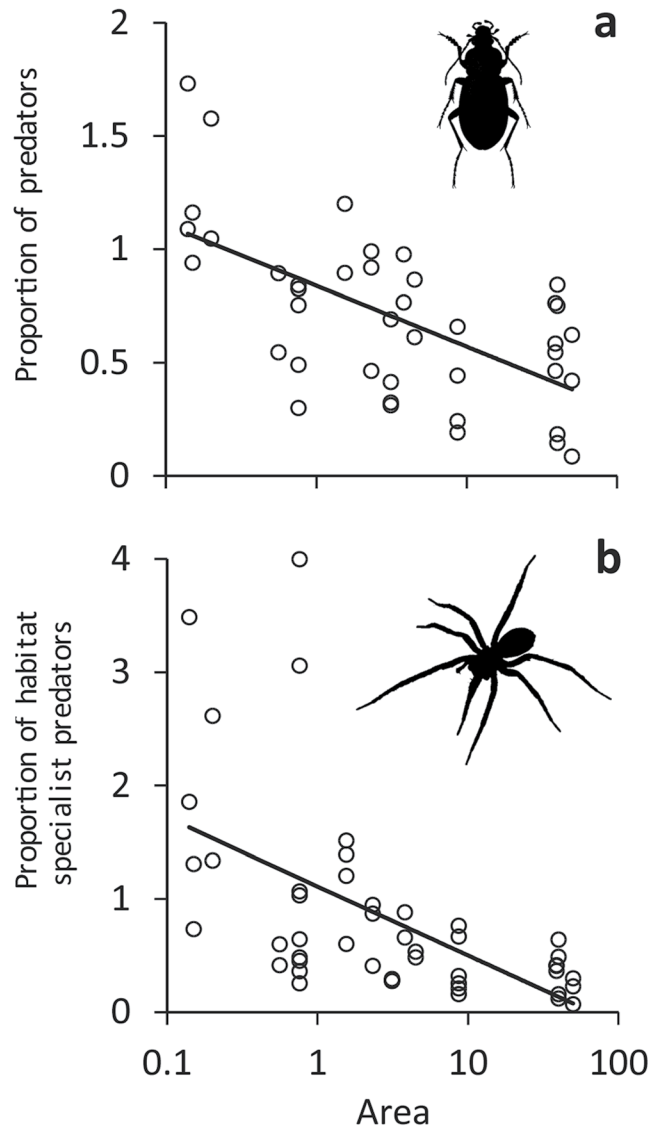
Figure 2. The proportion of predators π_H (a: calculated according to Eq. 2) and the proportion of habitat specialist predators π_G (b: Eq. 4) decreased logarithmically with area on Lake Wigry islands. a: $r^2 = 0.31$, $P(F_{1,62}) < 0.001$; b: $r^2 = 0.38$, $P(F_{1,51}) < 0.001$. Figure prepared by Ivo Bogucki.

Variable	df	Overlap	Distance	Volume
β_{Soer}	1	(+) 0.49***	(−) 0.60***	(+) 0.10*
Trophic level	4	0.03	0.01	0.11*
r^2 (model)		0.50***	0.61***	0.21**

Table 1. General linear modelling based on pairwise comparisons of all 96 species using eigen-ellipsoid overlap, centroid distance, or eigen-ellipsoid volume (larger volume of a focal pair) as response and trophic level (as a random categorical effect) as predictor variable. The degree of pairwise overlap in species occurrences (measured by the Sørensen coefficient β_{Soer}) of both species of the focal pair served as metric covariate. Given are partial η^2-values with *$P < 0.05$; **$P < 0.001$; ***$P < 0.001$. Error degrees of freedom df = 96. Positive (+) and negative (−) signs of the model parameters for β_{Soer} are given in brackets.

The observation that habitat specialist predators also decreased with increasing island area (2b) corroborates our second starting hypothesis. Consequently, we reject the model of Holt[11], our third hypothesis, that predicts increased β-diversity at higher trophic levels. We interpret this negative result as evidence that predator – prey dynamics are not the major factor shaping richness patterns on islands as assumed by the Holt model.

SARs are a very general description of biogeographic richness patterns[23,24] as they contain information on α-, β-, and γ-diversity. Being generally best described by power functions, these can easily be combined to infer
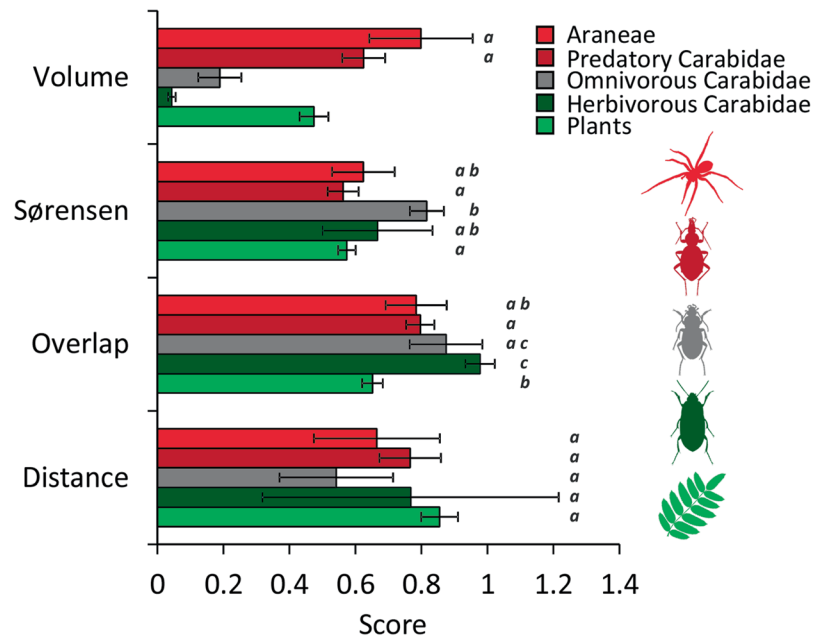
Figure 3. Average eigen-ellipsoid volumes, Sørensen dissimilarity in species co-occurrence eigen-ellipsoid overlap, and respective centroid distances for plants, herbivorous, omnivorous, and predatory Carabidae and Araneae on Lake Wigry islands. Araneae and predatory ground beetles had significantly larger eigen-ellipsoid volumes than omnivores, herbivores, and plants (all P(F) < 0.01. They also significantly differed from plants with respect to overlap (both P(F) < 0.05). Error bars denote two parametric standard errors. Bars that do not significantly differ at the 1% error level are marked by the same characters (a, b, c). Included are species with at least five occurrences within the focal archipelago. Figure prepared by Ivo Bogucki.

Variable	df	partial η^2	P(F)
Occurrences	1	0.68	<0.001
Trophic level	4	0.07	<0.05
r^2 (model)		0.71	<0.001

Table 2. General linear modelling detected significant differences in environmental niche volumes between members of five trophic levels (random categorical effect) after accounting for differences in the number of occurrences (metric covariate). N = 96.

changes in proportions of taxa and ecological guilds. With this approach we found decreases in the proportion of trophically higher ranking species and particularly of trophic specialists in larger islands (Fig. 2). Early work on proportions of prey and predator species in a variety of locations had focused on the observed linear relationship between prey and predator richness (reviewed by Schoenly et al.[25]) leading to the argument that the proportion of predator species in food webs is invariant of spatial scale (reviewed by Warren and Gaston[26]). In turn, Spencer et al.[27], similar to Holt[28], focused on differential community assembly processes that influence the slopes of prey and predator SARs, and predicted increased proportions of freshwater predator species at larger spatial scales. In grassland arthropod herbivore-predator systems, Sieman et al.[29] have reported a higher β-diversity of herbivores compared to predators resulting in a respective increased proportion of predators. However, these and comparable studies on predator-prey ratios did not explicitly refer to the area but rather to gradients in food plant abundance and richness. Our results from island systems are in contrast to these findings (Fig. 2). Proportions of predator ground beetles and spiders significantly decreased at a larger spatial scale. Such a pattern is in line with species-area relationships that vary among trophic guilds. High-ranking guilds have the lowest slopes (β-diversity) (Eqs 2 and 3).

These contrasting results raise the question whether a general predictable pattern exists. Trophic island biogeography (TTIB) aims at providing a respective model. However, the theory is built on a number of assumptions, which in turn need empirical confirmation. Most basically, Gravel et al.[10] and Holt[28] assume the existence of well-defined trophic levels. This might be justified for producers (plants) and some groups of herbivores and predators, but is questionable for numerous groups at higher trophic levels as we generally don't have information about dietary opportunism and the degree of omnivory.

Second, both mentioned models as well as our own data are species-centred and do not consider intraspecific or even individual variability in diet preferences, which might blur patterns in diversity across trophic levels (reviewed in Violle et al.[30]). In a previous paper[20], we found high intraspecific trophic variability in predatory and

omnivorous ground beetles within the present archipelago. Again, if trophic levels significantly overlap, this high variability might make the testing of any sound hypothesis challenging.

Empirical support for the trophic biogeographical model of Gravel et al.[10] so far comes mainly from relatively trophically simple coral reef fish meta-communities[31]. Species-rich and often complex terrestrial systems require precise knowledge of specific feeding relationships. Our study system was able to circumvent this hurdle due to the availability of sufficient environmental data, which allowed us to apply a new approach in assessing environmental niche width (habitat generality) based on observed ranges of environmental variables[17] (Fig. 3). This method enables an assessment of niche overlap and turnover among species within and among trophic levels. Respective comparisons of ellipsoid overlap and distances (Fig. 3) confirmed our third hypothesis that the spatial patterns of resource use change along the trophic hierarchy from plant and herbivores towards predators. Importantly, ellipsoid volumes that measure the habitat width and can be seen as proxis to the degree of habitat generalism significantly differed between trophic levels, being widest for predators and very small for herbivores (Fig. 3). That both predator taxa also had the highest niche overlap is another confirmation that, at least in our study system, the proportion of habitat generalists increases at higher trophic levels. Based on this finding we speculate that a similar gradient exists for diet width.

Finally, our results (Figs 1 and 3) indicate that communities of producers and consumers are assembled by different mechanisms. Plants species occurred spatially segregated; their habitat niches were on average well separated. Such a pattern indicates a relatively high degree of specialisation and possibly narrow habitat niches (Fig. 3). While plants are sessile, they must be efficient in acquiring local resources in order to withstand competitors. Consequently plant communities might rather be governed by competitively driven niche-based assembly rules[32,33]. In turn, animals, particularly flying insects, are able to move in order to search for resources and to avoid competition interactions[34]. Consequently, we found much lower degrees of spatial species (Fig. 1) and niche segregation (Fig. 3).

In addition to our starting hypotheses, our study points to another gradient in trophic hierarchy, the increasing variability in environmental niche width at higher trophic levels (Fig. 3). Plants and herbivorous ground beetles scattered significantly less around the group average than omnivores and predators (Fig. 3, unequal variance test: $P(F) < 0.001$). Such an increased variability might be an indirect sign of interspecific habitat and feeding generalism among member of a focal trophic guild. However, increasing variability might also be caused by higher intraspecific variability in feeding and habitat relationships. Intraspecific gradients in niche width are clearly insufficiently studied[35,36]. Our study does not allow for a disentangling of the effects of intra- and interspecific variability in food web structure. However, in a previous study on a similar island system[20] we found high intrapopulation variability in ground beetle feeding relationships. Future studies have to show whether this variability systematically changes with trophic position.

Methods

Species sampling. We studied ground beetles, spiders, and plants on 13 lake islands and two adjacent mainland sites of Lake Wigry in Suwalki Lake District, North-Eastern Poland (hereafter called islands). Island sizes span a range from 0.14 to 38.82 ha[37]. Sampling took place monthly from June to September in 2004 and 2005 using pitfall traps (0.5 l plastic mug, mouth diameter 120 mm, wooden roof, emptied every month and refilled with new glycol). Detailed sample protocols are already contained in[38,39]. Sampling intensity was proportional to island size[39]; note that while Zalewski et al.[39] was conducted on Mamry Lake archipelago this study was conducted on Wigry Lake archipelago, the sampling protocol was identical. Quantitative floristic samples of 100 m² were taken around each trap. In total, we found 64 ground beetle, 201 spider, and 160 plant species. Sample sizes, site characteristics, and species identities and occurrences are contained in the electronic supplement A. All carabids, except the genus *Europhilus*, were identified to species level using the keys in Hürka[40] and Lindroth[41,42]. The carabid nomenclature follows Hürka[40]. Most carabids appear to be omnivorous feeding opportunists[43] although precise trophic relationships are often unknown. Based on prior analyses of stable isotopic relationships (complete raw data in[20,44]) and field observations, we classified carabid species as being omnivore (that is, possibly feeding on animals, plants, or dead organic matter, 9 species) unless they were known to be either true herbivores (9 species) or predators (46 species) (Appendix A). Spiders (predators) were classified into species according to World Spider Catalog (2018)[45]. We arranged the species of each guild in ordinary species × islands presence - absence matrices.

In order to estimate average island conditions and habitat variability on the islands we estimated three habitat characteristics known to be important for the occurrence of ground beetles[43], using average standard Ellenberg plant indicator values[46]: temperature (*T*), soil fertility (nitrogen demand *N*), and organic material content (*OMC*). Raw data are contained in Appendix A.

Statistical analysis. For each species at each trophic level (plants, herbivores, omnivores, predators) we calculated three-dimensional environmental eigenvector ellipsoids (axes from *T*, *N*, and OMC) and their centroid position in environmental space according to Ulrich et al.[17]. This method uses the variance-covariance dissimilarity matrix Σ of environmental characteristics at those *k* sites where the focal species occurs to calculates respective eigenvector ellipsoid E(C,r) from

$$E(C, r) = (x - c)^T U^T \Lambda^{-1} U(x - c) \leq L \tag{5}$$

where the vectors x denote the vector of environmental characteristics and c the ellipsoid centre, U and Λ are the eigenvector and eigenvalues, respectively, of the variable dissimilarity matrix Σ, and L is the 99% quantile of a χ^2 distribution with *k* degrees of freedom. We calculated these ellipsoids for average environmental conditions. Such ellipsoids characterise environmental niche width. Ulrich et al.[17] showed that a plot of the variability in ellipsoid

spatial distances vs. average ellipsoid overlap (calculated from all pairwise comparisons) allows for a niche-based classification of community assembly. In this respect, low niche overlap points to spatial niche segregation while high variability in ellipsoid distance marks a modular assembly containing groups of species with similar environmental niche. Estimates for ellipsoid volumes become increasingly unsure at low numbers of species occurrences. Therefore, in this analysis we used only species with at least five occurrences leaving 16 ground beetles, 23 plant species, and 57 spiders (in total 96 species). All calculations were done with the Fortran software application *NicheNew*[17] that is freely available from the website of WU (www.keib.umk.pl).

We used two metrics to compare the pattern of spatial species distribution among trophic guilds. As a measure of species spatial turnover (spatial segregation[14]), we calculated the common C-score, a matrix-wide normalized metric of reciprocal pairwise species exclusion[47]. As the absolute values of this metric depend on matrix size and fill, we used a null model approach and compared the standardised effect sizes of the metrics (SES = Δscore/σ_{null}; Δscore = observed score − null model average and σ_{null} is the standard deviation of the null model distribution). Positive SES score point to species spatial segregation[47]. We used the fixed-fixed null model[48] that retains matrix marginal totals during randomization and that is increasingly recommended as being least biased in comparison to matrices of different size and fill[49–51].

We used parametric ANOVA and general linear mixed modelling to relate ellipsoid volume and overlap of all species pairs, as well as species pairwise co-occurrence (Sørensen index) to trophic level, numbers of species occurrences. As pair-wise comparisons might bias the statistical inference due to non-independence of data points we artificially reduced the error degrees of freedom from 1911 (the total number of pairs within each trophic level) to 96, the number of species included in the analyses. Errors refer to parametric standard errors.

Data Availability
All data analyzed during this study are included in this published article (and its Supplementary Information file).

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M.Z. proposed and planned the fieldwork and initiated this study. M.Z., W.C., and I.H. conducted the fieldwork. I.H., M.S., P.S., and W.C. organized the material and P.T., D.D.-G. and W.U. prepared the final database. W.U. conducted the statistical analyses and wrote the first draft. W.U. and M.Z. prepared the final version. I.H. and M.S. commented on the text.

Additional Information

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