Ann. Zool. Fennici 49: 161–173 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 29 June 2012

Spatial distribution and species co-occurrence in soil invertebrate and plant communities on northern taiga islands

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Received 17 Nov. 2011, final version received 23 Feb. 2012, accepted 12 Apr. 2012

Ulrich, W., Zalewski, M. & Uvarov, A. V. 2012: Spatial distribution and species co-occurrence in soil invertebrate and plant communities on northern taiga islands. — *Ann. Zool. Fennici* 49: 161–173.

Geographical gradients of patterns of species associations in ecological communities are largely unknown. Previous evidence indicated nested community assembly — caused mainly by unequal colonization probabilities and habitat capacity — and a tendency towards negative species associations in arid and tropical plant and animal communities. Patterns of community assembly in arctic environments are poorly studied. Here we use a data set on arctic plant and animal species obtained from arctic islands of the Kandalaksha Bay (White Sea), to infer patterns of species association across taxa and trophic groups. We performed co-occurrence and nestedness analyses to study patterns of community assembly and diversity of 1109 plant and animal species grouped according to taxa, dispersal ability, and ecological guild membership. Twelve out of 50 (24%) sufficiently species-rich families and orders on the environmentally relatively stable forested islands showed significantly negative species associations (segregation), while this proportion decreased to less than 13% on less stable heath, rocky, and sea-shore islands. Segregation was not linked to spatial species turnover across islands. Species richness of plants and animals decreased at higher levels of disturbance. We detected evidence for a gradient in species richness and ecological interactions from the most disturbed sea-shore and rocky islands to more stable forested islands. Species spatial distributions appeared to be largely random, in contrast to previous meta-analyses that used mainly communities at lower latitudes. We speculate that in arctic environments spatial turnover of species (vicariant segregation) is of less importance than turnover-independent (checkerboard) segregation. Our data support the view that ecological assemblages in high-latitude environments are less structured by ecological interactions than comparable assemblages in lower latitudes. We also add to the evidence that environmental disturbance regimes work against stable community structures. We notice the need for a formal meta-analysis on latitudinal trends in community structure.

Introduction

The spatial distribution of species and patterns of species co-occurrence across sites have always caught the attention of ecologists (Weiher and Keddy 1999). The recent development of new statistical tools for spatial analysis (Rangel *et al*. 2006), co-occurrence (Ulrich and Gotelli 2007a), and phylogenetic (Emerson and Gillespie 2008) analysis together with the publication of easy-to-use software has resulted in a large number of macroecological studies on spatially-explicit distributions of ecological communities across spatial and temporal scales (Hawkins *et al*. 2007).

Particular interest has been paid to patterns of species segregation (Weiher and Keddy 1999; Ulrich and Gotelli 2007a) and nestedness (Ulrich and Gotelli 2007b) from local to global scales. Species segregation across sites of potential occurrence has often been linked to present or past competitive pressures (Diamond 1975), while aggregation is mainly interpreted in terms of similar environmental requirements (habitat filtering) or phylogenetic constraints (Webb *et al*. 2002, Emerson and Gillespie 2008, Gómez *et al*. 2010). According to the assembly rule concept of Diamond (1975) that is based on competitive exclusion, meta-communities dispersed across sites of relatively stable environments should mainly exhibit negative species associations (segregation) as reported by Gotelli and McCabe (2002) and Ulrich and Gotelli (2010). Segregation might be divided into two not necessarily exclusive patterns. The first is spatial turnover, where species replace each other across a spatial gradient (Leibold and Mikkelson 2002). The second is a checkerboard pattern, the mutual exclusion of species without clearly defined spatial gradients. This pattern is predicted by the principle of competitive exclusion (Diamond 1975).

Recent work on large-scale and local patterns of species co-occurrence across sites found species segregation to be a common phenomenon. Gotelli and McCabe (2002) and Ulrich and Gotelli (2007a, 2010) identified more than 60% of 281 standard binary presence–absence matrices, compiled by Atmar and Patterson (1995), and more than 80 of 185 abundance matrices, compiled by Ulrich and Gotelli (2010), as being significantly segregated, mainly independent of taxonomic identity, biome, or trophic position. A nested pattern and species aggregation in general seem to be a much less frequent pattern. Ulrich and Gotelli (2007b) found less than 20% of the matrices of the Atmar and Patterson data set as being significantly nested under a conservative null assumption and Ulrich and Gotelli (2010) reported less than 5% of empirical abundance matrices as being significantly aggregated, again independent of taxonomic identity, biome, or trophic position.

Gotelli and McCabe (2002) and Ulrich and Gotelli (2010) compared patterns of co-occurrence between taxa and ecological guilds. However, a shortcoming of these studies was the use of data sets from different biotas that were compiled with different methods and across longer time scales. Such data sets integrate over temporal and spatial variability of species occupancy and have too high matrix fill compared with the respective temporal point data sets. This higher matrix fill might cause a bias towards random association or species aggregation. Only a few comparative studies that used small scale point data detected subtle non-random patterns in species co-occurrence after species invasion (Gotelli and Arnett 2000, Sanders *et al*. 2003, 2007). Some of these studies reported community disassembly (towards random patterns of species association) after disturbance (Costa de Azevedo *et al*. 2006, Sará *et al*. 2006, Bhat and Magurran 2007, Ulrich *et al*. 2010). A comparative approach of community assembly across taxa using properly resolved point data is, however, still missing.

Nestedness, a pattern where sites with fewer species are true subsets of sites with more species, is a special case of species aggregation and is particularly caused by environmental gradients to which species react (reviewed in Ulrich *et al*. 2009). Nestedness analysis is therefore a convenient tool in ecological gradient analysis (Ulrich *et al*. 2009). The gradient has to last sufficiently long for species occurrences to respond to this gradient. Hence a nested pattern is particularly expected across temporarily stable sites. The existence of a nestedness is equivalent to the absence of strong species segregation (Almeida-Neto *et al*. 2007) and indicates ordered patterns of colonization and extinction (Atmar and Patterson 1993, Wright *et al*. 1998).

Lastly, random patterns of species occurrences are expected if metacommunities are dominated by species with high colonization ability as predicted by neutral theory (Zalewski and Ulrich 2006, Zillio and Condit 2007). In this case the incidence frequency distribution is expected to follow a Pareto distribution (Nekola and Brown 2007). Metacommunities with high degrees of dispersal should therefore lack the distinction into core or frequent and satellite or temporary species (Magurran and Henderson 2003, Ulrich and Ollik 2004). Thus a random pattern of species co-occurrence and the absence of a core–satellite pattern might indicate dispersal dominated metacommunities.

Here we take the opportunity to test some predictions about patterns of species co-occurrence with an extraordinarily large and complete data set of species occurrences, the survey of soil fauna and flora on 22 nearby islands in the Russian White Sea (Byzova *et al*. 1986). The majority of these islands suffer from severe environmental conditions (*see* below). We study patterns of species co-occurrence, nestedness, and spatial turnover and link the species occurrences to differences in habitat quality. We are able to compare patterns of species co-occurrence across taxa, ecological guilds, and across habitat types and link these patterns to environmental conditions. We refer to broad ecological patterns to test a number of specific hypotheses.

1. On the northern taiga islands of our study with their harsh and unstable environmental conditions and marked environmental heterogeneity we expected to see a high spatial species turnover combined with a significant degree of negative species associations among islands. We also expected to see higher degrees of checkerboard segregation on islands with more stable habitat conditions than among islands.
2. High species turnover is opposite to a nested subset pattern. Thus we expected to see a lack of or even a significantly anti-nested (Almeida-Neto *et al*. 2007) pattern of species occurrences.
3. We predict turnover to occur particularly in meta-communities driven by reciprocal exclusion due to differential habitat requirements.
4. In line with the previous hypotheses and the findings of Gotelli and McCabe (2002) and Ulrich and Gotelli (2010), we predict that arthropod communities composed of comparatively dispersive (mostly flying) species have less pronounced negative patterns of species association than meta-communities composed of low dispersive plants or soil invertebrates.
5. We expected to see a variability of the core–satellite pattern of abundance and occurrence in dependence on dispersal ability and therefore also pronounced differences in the respective distributions of species occupancy.

Material and methods

Study area

The present study is based on a long-term (1971–1988) survey of soil fauna and flora carried out by the Institute of Ecology and Evolution of the Russian Academy of Sciences on 21 (animals) and 22 (plants) islands of the Kandalaksha Bay (White Sea). They are part of a small archipelago consisting of ca. 70 islands between the seashores (at a distance of 1–10 km) of Karelia and the Kola Peninsula (Karpovich 1988, Berger and Naumov 2000) and have the status as protected areas for nature conservation since 1939. The archipelago is located just beyond the Arctic Circle (66°57´–67°08´N, 32°09´– 32°53´E). The islands differ greatly with regard to age, size and elevation. The largest studied island (Ryazhkov) covers 4 km^2 and reaches 76 m above sea level while some small islets are nearly flooded by seawater during tides reaching up to 3 m in the White Sea. The climate of the Kandalaksha Bay is comparatively mild due to warm oceanic currents in the Barents Sea. Permafrost is absent, but the soils are subject to at least 5 months of seasonal freezing. Soil temperatures vary between –8 and 4 °C in January, and between 12 and 16 °C in July. Hydrothermic conditions on the islands are highly variable (Karpovich 1988, Berger and Naumov 2000).

The faunistic and floristic results of this project were summarized by Byzova *et al*. (1986) and made available to us by one of the authors of that study (AVU). Byzova *et al*. (1986) used standard methods of soil invertebrate extraction (Ghilarov 1975, Ghilarov and Striganova 1987) and in total documented 302 species of vascular plants and 807 species of soil associated animals (Table 1).

For the present study, we classified the islands into forested (six islands), heaths (six), sea shore meadows (seven), and rocky islands (three) (Table 1). The forested islands are comparatively larger and covered by pine (*Pinus lapponica*) or Finnish spruce (*Picea fennica)* and by scrub (*Vaccinium myrtillus*, *V. vitis-idaea*). Sporadically, patches of birch (*Betula* spp.) and aspen (*Populus tremula*) occur. Habitat conditions on the forest islands were more stable than on the other types. The smaller heath islands are occupied by *Empetrum* and *Calluna* heaths and mossy/lichenous associations in rocky crevices. The sea shore meadows are made of various halophilous associations and are strongly dependent on the tide regime. The vegetation on the rocky islets is strongly affected by the activities of settling birds (Byzova *et al*. 1986). The littoral and seashore areas of the islands were regularly flooded. To assess the effect of flood disturbance, we used the frequency of salt tolerant plant species on a given island as a proxy to the degree of flood disturbance and classified the islands into six disturbance classes (least to most disturbed). The forest islands appeared to be least disturbed (average score ± SE = 0.83 ± 0.31), followed by the heath (3.50 ± 0.34), rocky islands (4.0 ± 0.6), and sea-shore meadows (4.14 ± 0.26).

Classification of species

We classified plant and animal species into ten trophic guilds: bacteriophages, smaller, medium sized and large predators, phytophages, mycetophages and saprophages, omnivores, parasitoid species, and primary producers (Tables 2 and 3). Apart from guild classification we used

Table 1. Summary information on area, disturbance level, habitat indices and soil animal and vascular plant species richness on 22 White Sea islands.

Island	Habitat	Area (ha)	Disturbance class	Species richness	
				Animals	Plants
Riazkov	Forested	401.1	0	609	284
Kurichek	Forested	8.6	0	250	102
Dievichja	Forested	13.8	1	103	110
Sieviernaja	Forested	6.6	1	102	124
Smorodinnaja	Forested	1.6	1	82	80
Stvornaja	Forested	2.9	2	96	79
Rogovaja	Heaths	0.2	5	70	33
Piervaja Popieriechnaja	Heaths	0.4	4	57	56
Voronichnaja	Heaths	0.45	3	163	61
Irvasiha	Heaths	0.6	3	81	44
Juznaja	Heaths	0.4	3	36	62
Vostochnaja	Heaths	0.3	3	–	62
Nachalnaja	Sea-shore meadows	0.1	5	119	5
Kroshka	Sea-shore meadows	0.1	4	132	12
Peschanaja	Sea-shore meadows	0.5	5	116	31
Malyshka	Sea-shore meadows	0.2	4	208	10
Brevnushka	Sea-shore meadows	0.3	3	142	36
Vieriesovaja	Sea-shore meadows	0.2	4	34	30
Chistikovaja	Sea-shore meadows	0.1	4	32	32
Kulichinaja	Rocky islands	0.2	5	15	1
Dresnoj Baklysh	Rocky islands	0.1	4	31	9
Malaja Gulmaha	Rocky islands	0.2	3	172	29

Table 2. Numbers of genera and species of soil invertebrates and vascular plants found on the 22 White Sea islands sorted according to taxonomic level.

Taxonomic level			Genera	Species
1	2	3		
Nematoda	Araeolaimida		4	9
Nematoda	Dorylaimida		6	9
Nematoda	Enoplida		3	5
Nematoda	Monhysterida		1	3
Nematoda	Rhabditida		14	20
Nematoda	Tylenchida		15	28
Arthropoda	Acarina	Parasitiformes	44	87
Arthropoda	Acarina	Sarcoptiformes	79	113
Arthropoda	Acarina	Trombidiformes	18	18
Arthropoda	Arachnida	Araneae	66	94
Arthropoda	Arachnida	Opilionides	1	1
Arthropoda	Arachnida	Pseudoscorpionides	1	1
Arthropoda	Insecta	Blattodea	1	1
Arthropoda	Insecta	Coleoptera	125	226
Arthropoda	Insecta	Collembola	37	65
Arthropoda	Insecta	Diptera	27	36
Arthropoda	Insecta	Hemiptera	16	17
Arthropoda	Insecta	Hymenoptera	11	23
Arthropoda	Insecta	Neuroptera	1	1
Arthropoda	Insecta	Psocoptera	1	1
Arthropoda	Insecta	Thysanoptera	7	8
Arthropoda	Myriapoda	Chilopoda	4	4
Arthropoda	Myriapoda	Symphyla	1	1
Mollusca	Gastropoda		11	13
Annelida	Oligochaeta	Lumbriculida	11	23
Sum			505	807
Equisetophyta			1	2
Lycopodiophyta			2	5
Polypodiophyta			6	8
Pinophyta			4	7
Spermatophyta			146	280
Total			159	302
Grand total			664	1109

taxonomic classification at the family and order level to assure that members of the respective taxonomic level could be assigned to a particular feeding style according to our guild classification.

Quantitative data on dispersal abilities are not available for the vast majority of species, which excludes a detailed analysis of the influence of dispersal ability on patterns of species-co-occurrence. However flying animals, ballooning spiders, and wind dispersed plants should be comparably good dispersers while the many belowground dwelling animals have rather weak dispersal abilities. Animal dispersed plant spe-

Table 3. Numbers of genera and species of soil invertebrates and vascular plants found on the 22 White Sea islands sorted according to trophic-guild membership.

Trophic guild	Species
Primary producers	302
Bacteriophages	37
Phytophages	109
Mycetophages	82
Saprophages	55
Small predators	108
Intermediate predators	114
Large predators	107
Omnivores	189
Parasitoids	6

cies and aboveground wingless species should be intermediate on average. We used this classification to relate dispersion to community structure.

Species co-occurrence

To study patterns of species co-occurrence, we arranged species occurrences at sites in an ordinary presence–absence matrix where rows (m) denote species and columns (n) sites. We tested patterns of species co-occurrence for all families and orders with at least three species within a given habitat type and which were studied on at least three islands. We used the C-score (Stone and Roberts 1990) (a normalized count of the total number of $\{\{1,0\},\{0,1\}\}$ submatrices within the presence–absence matrix) to assess matrix-wide species segregation. High values of the C-score point to a segregated pattern of species co-occurrence. The NODF (**n**estedness by **o**verlap and **d**ecreasing **f**ill) metric (Almeida-Neto *et al.* 2008) is linked to differences in occurrences across rows and sites (Almeida-Neto *et al.* 2008) and is a widely used metric of nested subset patterns (Ulrich *et al.* 2009). In line with Leibold and Mikkelson (2002) and Presley *et al.* (2010), we studied species turnover using correspondence analysis. Correspondence analysis sorts the sites and species so as to maximize species occurrences along the matrix diagonal. In this way, species become maximally spatially segregated. The coefficient of correlation between row and column positions of species is then a convenient measure of the degree of spatial turnover in the metacommunity.

We assessed the statistical significance of our metrics (C-score, NODF, coefficient of correlation) from the upper and lower two-sided 95% confidence limits of 1000 randomised matrices that were reshuffled according to the independent swap algorithm (Gotelli 2000) that preserves row and column totals ($10 \times m \times n$ swaps for each matrix). This fixed-row–fixed-column null model was shown to best account for the effect of passive sampling introduced by unequal *a priori* occupancy probabilities of species due to meta-community wide differences in abundance (Ulrich and Gotelli 2007a, Ulrich *et al.* 2009). We also used standardized (z-transformed) effect sizes to relate levels of species segregation to species richness. Prior to analysis, we tested for a dependence of the C-score on matrix size and matrix fill (Ulrich and Gotelli 2007a) and found a slight increase in significant scores at matrix sizes $m \times n > 600$ (t-test: $p < 0.01$). To account for a possible size effect we used only summary counts of significances across island types because the four types did not significantly (ANOVA: $p > 0.25$) differ in average matrix size and only three matrices (two from forest and one from heath islands) were larger than $m \times n = 600$. Null model analyses were done with the software applications CoOccurrence (Ulrich 2006) and NODF (Ulrich and Almeida-Neto 2011).

Results

The islands contained between 1 (the smallest rocky island) and 284 (the largest forested island) plant and between 15 and 609 soil-animal species (Table 1). Most species-rich were Coleoptera (226 species), sarcoptiform mites (111), and spiders (94) (Table 2). Predators (327 species) dominated over primary producers (302) and omnivores (189) (Table 3).

Species richness of soil animals (Fig. 1A) and vascular plants (Fig. 1B) increased with island size according to a power function with the slopes of $z = 0.23$ (animals) and $z = 0.39$ (plants), respectively. The trend towards an increase in species richness with area held for all level 3 taxa of animals and plants and all trophic guilds distinguished in Tables 2 and 3 (all slopes positive), although this was not always statistically significant due to the low number of species in some guilds and taxa (not shown).

We classified 527 species as being good, 198 species as being intermediate and 384 species as being weak dispersers (Table 4). Contingency table analysis revealed highly significant (χ^2-test: $p < 0.001$) differences between island types with respect to the fraction of dispersers. The fraction of species of intermediate dispersal ability (most plants and aboveground animals) increased from forested to rocky islands while the fraction of good dispersers (flying insects, wind dispersers) decreased. The frequency of weak dispersers (belowground dwellers) was highest on forested

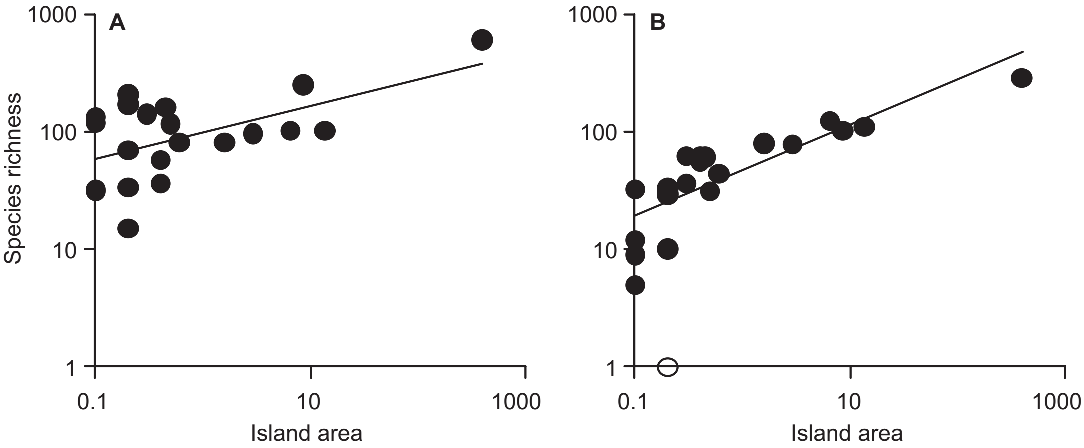

Fig. 1. Species–area relationships for (**A**) soil invertebrates (21 White Sea islands) and (**B**) vascular plants (22 White Sea islands). OLS regressions: (**A**) $S = (98 \pm 4)\text{area}^{0.23 \pm 0.07}$, $r^2 = 0.33$, $p_{(r = 0)} < 0.01$; and (**B**) $S = (47 \pm 8)\text{area}^{0.39 \pm 0.11}$, $r^2 = 0.68$, $p_{(r = 0)} < 0.001$. The rocky island Kulichinaja (circle in **B**) with only one species was excluded.

islands and lowest on the most disturbed sea-shore islands (Table 4). Additionally weak dispersers had on average significantly (χ^2-test: $p < 0.001$) fewer occurrences (0.23 per species and island) than good (0.35) and intermediate dispersers (0.42). This difference indicates that low dispersal rates limit numbers of occurrences.

The occurrence–frequency distributions of plants and soil animals (Fig. 2) could both be fitted by a Pareto distribution with the slopes of $z = -1.5$ (animals: $r^2 = 0.98$) and $z = -1.7$ (plants: $r^2 = 0.76$). Hence, in plants and animals, species with single occurrences dominated: 311 soil animal (39%) and 177 vascular plant species (59%) were found on only one of the islands. Only 13 animal and 3 plant species occurred on more than 20 islands. The occurrence distributions differed with respect to dispersion category (Fig. 2). Highly dispersive species were well fitted by a Pareto distribution ($z = -2.5$, $r^2 = 0.93$). Frequency differences of the less dispersive species were much less pronounced resulting in slopes below $z = -1.6$. However, we did not find any core–satellite pattern with comparably high frequencies of very rare and of common species.

Degree of habitat disturbance and island area were significantly negatively correlated (Spearman's $\rho = -0.78$, $p_{(r = 0)} < 0.001$). Thus species richness of plants and animals decreased at higher levels of disturbance (Fig. 3). However, this trend was statistically significant only for plants (Fig. 3B). For animals, the trend was not at all visible for the islands with disturbance levels 1 to 5, and was only observed when the two large forested islands were included in the analysis (Table 2 and Fig. 3A).

In an all-island analysis 19 out of 70 (27%) sufficiently species rich families appeared to be significantly segregated under the conservative fixed-row–fixed-column null model (Table 5). However, the respective spatial turnover analy-

Table 4. Numbers of species on 22 White Sea islands classified as being high, intermediate, and weak dispersers.

Dispersal ability	Total	Island type			
		Forested	Heaths	Sea-shore	Rocky
High	527	452	150	153	62
Intermediate	198	333	230	216	134
Low	384	196	72	44	27
Total	1109	981	452	413	223

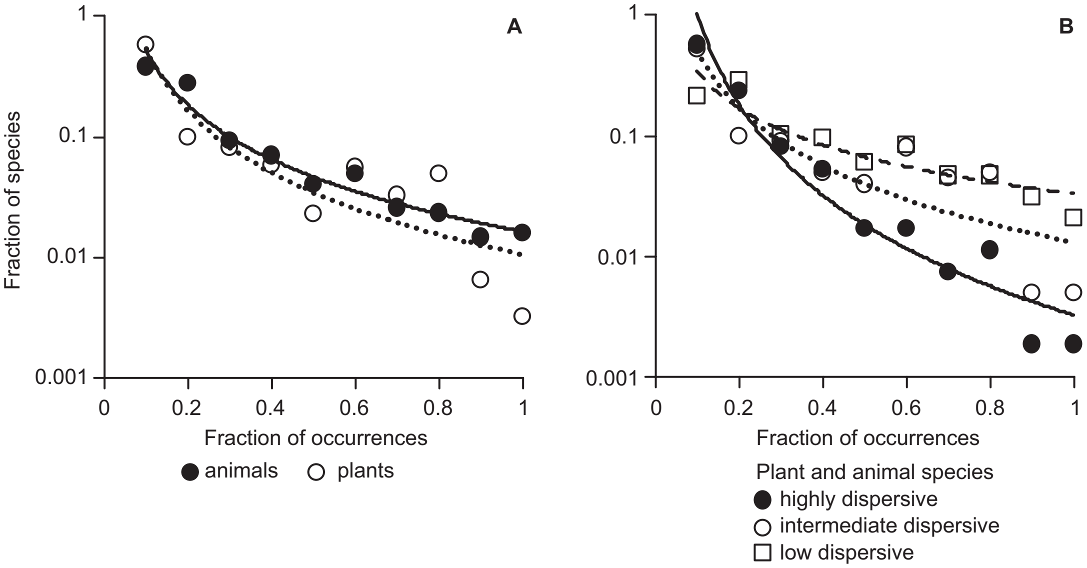

Fig. 2. (**A**) Occurrence–frequency distributions of soil animal and vascular plant species; regressions: animal (solid line): $y = 0.017x^{-1.5}$, $r^2 = 0.98$; plant species (dotted line): $y = 0.011x^{-1.7}$, $r^2 = 0.76$. (**B**) Species of different dispersal ability on 22 White Sea islands; regressions: highly dispersive species (solid line): $y = 0.003x^{-2.5}$, $r^2 = 0.93$; intermediate dispersive species (dotted line): $y = 0.015x^{-1.6}$, $r^2 = 0.71$; low dispersive species (dashed line): $y = 0.039x^{-1.1}$, $r^2 = 0.84$.

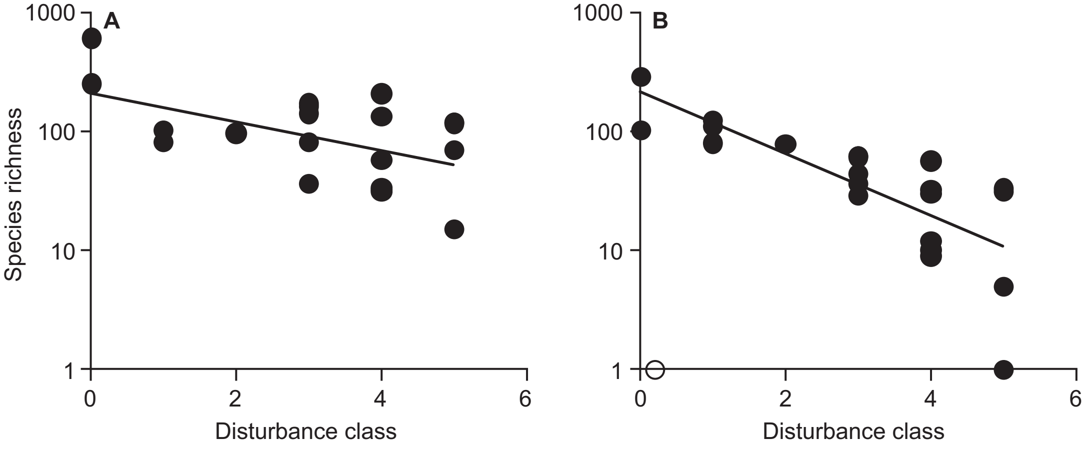

Fig. 3. Dependence of species richness on the degree of disturbance for (**A**) soil invertebrates (Spearman's $\rho = -0.43$, $p_{(r = 0)} > 0.05$), and (**B**) vascular plants (Spearman's $\rho = -0.86$; $p_{(r = 0)} < 0.0001$) on 21 and 22, respectively, islands of the White Sea. The empty circle in **B** indicates to the smallest island not included in the regression.

sis using the coefficient of correlation *r* of row/column positions detected only five taxa (plants, Hymenoptera, Carabidae, Elateridae, and Laelaptidae, all identified also by the C-score as being segregated, not shown) as having significant spatial turnover. For both metrics, six such significances are expected just by chance at the one-sided 5% error level assuming a binomial probability distribution with $p = 0.05$.

Twelve out of 50 sufficiently species rich families and orders on the forested islands (24%) were significantly segregated under the conservative fixed–fixed null model (Table 5), while this proportion decreased to 13% on the heath, 9% on the sea-shore, and 0% on the rocky islands in accordance with increasing habitat instability

Table 5. Species co-occurrence analysis of 70 soil animal and vascular plant taxa (family and order level) on the four types of White Sea islands. Given are the numbers of taxa included in the analysis and numbers of significantly segregated (Segr) or aggregated (Aggr) taxa according to two sided 5% confidence limits of the fixed–fixed null model distribution. Included are only taxa that were studied on at least three islands of a given type and were represented by at least five species.

Guild	All islands			Forested islands			Heath islands			Sea-shore meadow islands			Rocky islands		
	Taxa	Segr	Aggr	Taxa	Segr	Aggr	Taxa	Segr	Aggr	Taxa	Segr	Aggr	Taxa	Segr	Aggr
All	70	19	0	50	12	0	16	2	0	34	3	0	6	0	0
Primary producers	21	4	0	21	6	0	6	2	0	5	1	0	1	0	0
Bacteriophages	3	2	0	0	0	0	0	0	0	2	0	0	0	0	0
Phytophages	11	2	0	5	0	0	0	0	0	3	0	0	0	0	0
Myceto-/saprophages	13	3	0	5	1	0	3	0	0	7	2	0	4	0	0
Omnivores	3	1	0	3	0	0	1	0	0	2	0	0	–	0	0
Small and intermediate predators	11	2	0	6	1	0	3	0	0	7	0	0	2	0	0
Large predators	9	3	0	8	2	0	4	0	0	6	0	0	0	0	0
Winged insects	18	5	0	14	2	0	2	0	0	9	0	0	1	0	0
Soil micro- and mesofauna	27	7	0	12	2	0	7	0	0	17	2	0	4	0	0
Ballooning spiders	4	1	0	4	1	0	1	0	0	3	0	0	0	0	0
Average level of disturbance		3.05			0.83			3.50			4.14			4.00	

(Table 5). For the forested islands maximally five significant taxa are expected to be significant just by chance at the 5% error level. For none of the four island groups did we detect significant spatial species turnover (not shown).

With respect to trophic level, 6 out of 21 plant and 3 out of 14 predator taxa appeared to be significantly more segregated than expected from the null distribution on forested islands. These fractions are higher than expected from a binomial distribution ($p_{(H_0)} < 0.01$). None of the taxa on any island type was significantly aggregated. Low dispersive soil animal taxa (27 taxa) exhibited a similar degree of segregation (7 taxa = 26% significant) to the more dispersive flying insect and ballooning spider taxa (22 taxa, 6 taxa = 27% significant) (Table 5).

Z-transformed C-scores on the forested islands increased significantly with taxon species richness (Fig. 4). Seven out of 15 taxa with more than 20 species were significantly segregated while maximally three such significances were expected just by chance from the binomial probability distribution at the 1% error level and $p = 0.025$. These significant taxa are vascular plants ($z = 6.19$) and the families Asteraceae ($z = 6.34$), Poaceae ($z = 2.01$), and Cyperaceae ($z = 2.23$). Among soil animals Coleoptera ($z = 3.16$), Sarcoptiformes ($z = 8.08$), and Araneae ($z = 2.10$) were significantly segregated. On the other island types only plants (heath and sea-shore islands), were identified as being segregated. For the heath, sea shore, and rocky islands observed numbers of significantly segregated taxa did not differ from the binomial random expectation at the 1% error level.

In line with the absence of significantly aggregated taxa, the nestedness analysis did not point to any significantly nested subset pattern in any taxon and island after sorting the rows and columns according to marginal totals (incidences) (not shown). Per definition this type of sorting should result in the highest degree of nestedness. Accordingly, we did not find any significant degree of nestedness after sorting the islands according to habitat characteristics that define environmental gradients. Thus, we were unable to identify gradients that drive island colonization by plants and animals. In turn, on the forested islands 10 out of 70 taxa (14%)

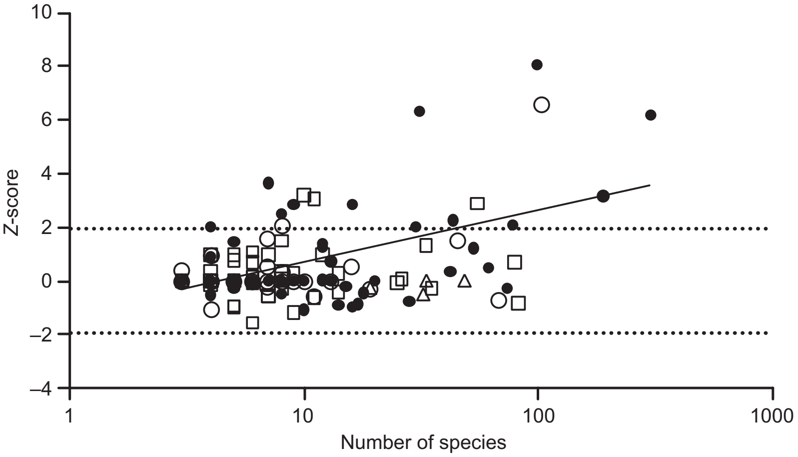

Fig. 4. *Z*-transformed C-scores of presence–absence matrices dependent on species richness of all families (soil invertebrates and vascular plants) under the fixed–fixed null model. Black dots: forested islands; open squares: sea-shore meadow islands; open circles: heath islands; open triangles: rocky islands. Logarithmic regression for forested islands: $r^2 = 0.31$ ($p_{(r^2 = 0)}$ 0) < 0.001. Spearman's ρ for forested islands = 0.29; $p_{(r = 0)} = 0.01$; Dotted lines mark the normal approximations of the upper and lower two-sided 95% confidence limits of *z*-scores.

were significantly anti-nested (again at most five significances are expected just by chance from a binomial distribution at the 1% error level).

Discussion

Recent meta-analyses of species co-occurrences (Wright *et al*. 1998, Gotelli and McCabe 2002, Ulrich and Gotelli 2007a, 2007b, Ulrich and Gotelli 2010) revealed a prevalence of negative species associations in the majority of biogeographic data sets as well as differences between higher taxa in line with our first hypothesis. These studies used large compilations of biogeographic presence–absence matrices provided by Atmar and Patterson (1995) and Ulrich and Gotelli (2010). The data stem from tropical to temperate regions and were obtained using different methods. It is often particularly unclear whether they contain point data that exclude the temporal species turnover or whether they contain pooled species numbers obtained over longer time scales. Such pooled data should overestimate actual species richness of sites and thus potentially underestimate the degree of species co-occurrence. Our data set is one of the few that studies patterns of species co-occurrence across taxonomic hierarchies and guild membership within a single set of islands and within the same type of habitat, the soil. The results allow for a direct comparison of patterns and a testing of our starting hypotheses.

Patterns of co-occurrence could be classified as being random in the majority of taxa. Only a minority of the soil animal and vascular plant taxa (27% of 70 taxa, Table 5) did show a trend towards segregation and spatial species turnover. This finding contrasts with our first three starting hypotheses but is in line with the fourth hypothesis that the single island communities are in the majority dispersal-driven and lack stable interspecific interactions. To interpret our result we reanalysed the well-known biogeographic data set of Atmar and Patterson (1995); 119 out of the 288 presence–absence matrices of this compilation (41%) appeared to be significantly segregated at the 5% error level. The Atmar/Patterson data originate mainly from arid and tropical habitats but nevertheless cover a wide variety of different island and mainland ecosystems. None of these data sets regards high latitude environments. We interpret our results as an indication of increased proportions of random community assembly at high latitudes. We exclude possible matrix size effects because our matrices cover nearly the same size range as the Atmar/Patterson matrices. One explanation for the high degree of random species co-occurrences comes from the stability hypotheses. We speculate that instable habitat conditions and/or high degrees of dispersal and therefore annual species turnover tend to randomize patterns of species co-occurrence.

We note that instability is not the same as heterogeneity. The White Sea islands differ greatly in environmental conditions and we expected this variability to cause a higher degree of species turnover (β-diversity) among islands (hypothesis 3). This was not the case. Neither our nestedness nor the co-occurrence (Table 5) analysis pointed to marked degrees of spatial species turnover. Further, the slopes of species–area relationships (SAR) are common metrics of β-diversity (Tuomisto 2010). At least for the island animals (Fig. 1), the SAR slopes were well within the typical range found for island SARs while plant SARs were on the upper end of empirical slopes (Drakare *et al*. 2006, Sólymos & Lele 2012). These results do not point to increased levels of spatial species turnover across islands.

In line with the above argument, we found, albeit limited, support for our first hypothesis that environmental stability leads to species segregation (Table 5). In accordance with the temporal stability hypotheses, the frequency of significantly segregated taxa was highest on the relatively stable forested islands (24%) while the combined frequency of significantly segregated taxa on the three other types of islands with less stable environments was only 9%.

Our results clearly reject hypotheses of species aggregation across sites due to similar habitat requirements. Our co-occurrences analysis did not point to aggregated patterns of species co-occurrence in any taxon (Table 4). This result is in accordance with the meta-analysis of Gotelli and McCabe (2002) and Ulrich and Gotelli (2010) that were mainly based on animals and adds the same pattern for plants. A nested subset pattern is a special case of species aggregation. According to Wright *et al.* (1998) nestedness is frequent in biogeographic meta-communities. Ulrich and Gotelli (2007b), analysing the same data, showed that in nearly all cases differential regional species abundances caused the nested pattern and our findings are in accordance with these results.

We did not find any significant degree of nestedness in any taxon but we found in total 24 out of 129 taxa (18.6%) to be significantly antinested (that means segregated). The existence of a nested pattern (apart from passive sampling) has often been connected to the influence of environmental gradients that shape community assembly (cf. Ulrich *et al*. 2009). Our results do not point to any specific environmental gradient that determines species occurrences on islands and that might generate nested subset patterns as predicted by our third hypothesis.

Spatial species turnover had only a minor influence on the pattern of species spatial associations. Thus, we did not find indication of reciprocal competitive exclusion due to differential habitat requirements as predicted by our third hypothesis. Again we compared our results with the 288 temporal and tropical data sets of the Atmar/Patterson compilation. Eighty-nine (31%) of these data sets had significant spatial species turnover, while of our 70 arctic data sets only 5 (7%) were significantly spatially segregated. This difference points again to a latitudinal gradient in patterns of community assembly.

The C-score alone as a metric of negative species associations is unable to separate between spatial and non-spatial segregation and this difference and its ecological implications have so far been neglected in the analysis of ecological matrices (but *see* Leibold and Mikkelson 2002). For a correct assessment of the type of species segregation we have to use metrics designed to detect the degree of the non-spatial (checkerboard) and spatial (turnover) parts of segregation. We further propose to term the spatial aspect of species segregation the *vicariant segregation* to emphasize the potential importance for evolutionary processes. Vicariant segregation might result from historical processes, allopatric speciation, or differences in habitat requirements. The degree of vicariant segregation is a measure of spatial species turnover and therefore of β-diversity.

A second part of segregation is not or only slightly connected to spatial turnover. We propose to term this turnover independent part *checkerboard segregation*. The classical assembly rule concept of biogeography envisioned mainly this checkerboard segregation and linked it to negative species interactions, particularly to competition (Diamond 1975). A number of previous studies (Wright *et al.* 1998, Gotelli and McCabe 2002, Ulrich and Gotelli 2007a) that identified high proportions of significant negative species co-occurrences discussed their results in terms of competition theory without acknowledging that a large part of the C-score significances might stem from vicariant segregation without any link to actual species interactions. We call for a meta-analysis that reassesses the importance of vicariant and checkerboard segregation in biogeography.

According to our fourth and fifth hypotheses, we expected to see links between the pattern of species association, colonization frequency, and dispersal ability. The islands lacked clear groups of core species and core–satellite patterns as have been reported in some biogeographic studies (Guo *et al.* 2000, Magurran and Henderson 2003). Ulrich and Ollik (2004) and Zalewski and Ulrich (2006) reported core species to exhibit non-random patterns of species co-occurrence in parasitic Hymenoptera and ground beetles while the infrequent satellite species were characterized by random patterns of species co-occurrence. In our study only 17 out of 1115 (1.5%) plant and animal species occurred on more than half of the islands while in total 488 species (44%) occurred only once. Nevertheless we found weak corroboration for the hypothesis that dispersive species are better described by the power function Pareto distribution than less dispersive species (Zalewski and Ulrich 2006) (Fig. 2).

Contrary to our fourth hypothesis that high dispersion ability is linked to random species co-occurrences (Azeria 2004, Zalewski and Ulrich 2006), we found that the frequency of negative species associations was higher in highly dispersive taxa (19%) compared to taxa with low ability of dispersion (14%) (Table 5). The evidence for gradients in colonization from forested islands that harbour particularly weak and good dispersers to sea-shore and rocky islands with higher degrees of intermediate dispersers needs explanation. Good dispersers were found to have comparably low abundances (Morse *et al.* 1988, Cowley *et al.* 2001) and to be weak colonizers (Azeria 2004). That means there might be a trade-off between dispersal and persistence ability as has been found for ground beetles (Zalewski and Ulrich 2006). This trade-off might differ between dispersal groups and would explain the higher fraction of intermediate dispersers on the severely disturbed sea-shore and rocky islands.

Acknowledgements

This work was supported in part by grants from the Polish Ministry of Science and Higher Education to WU (KBN, 3 P04F 034 22, 2 P04F 039 29), to MZ (PBZ KBN 087 P04 2003 01 20, NN 304 354538), and to AVU (4023/B/PO1/2010/38). Hazel Pearson kindly improved our English.

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