Tourism disassembles patterns of co-occurrence and weakens responses to environmental conditions of spider communities on small lake islands

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Abstract: The impact of disturbance on animal and plant assemblages has been described mainly in terms of aggregate community properties like species richness, abundance, or productivity. However, the question how disturbance acts on species interactions, particularly on patterns of co-occurrence, has received much less attention. Here we use a large pitfall trap sample of spiders from two complexes of lake islands in Northern Poland to show how disturbance by tourist visits affects species richness, composition and co-occurrence. On the pristine and protected islands of Lake Wigry, species co-occurrence was significantly segregated. Further, island species richness and abundances could be predicted from environmental correlates, particularly from island area, soil fertility and humidity. In turn, on the lake islands that are frequently visited by tourists, species co-occurrences were random and environmental correlates other than island area failed to predict species richness and abundances. However, species composition, $\alpha-$, β-, and γ-diversities, as well as average local spider abundances did not significantly differ between both island complexes. Our results show that disturbance disassembles the structure of spider communities prior to visible richness and abundance effects. This result has implications for biological conservation. The detection of community disassembly might be an early sign for factors that act negatively on ecosystem functioning.

Abbreviations: NBM NMDS SAR

Introduction

The impact of disturbance on animal and plant assemblages has been described mainly in terms of aggregate community properties like species richness, abundance, or productivity (Mackey and Currie 2001, Begon et al. 2006, Ulrich et al 2007). Intermediate disturbance regimes are known to increase local diversities (Wilkinson 1999, Shea et al. 2004, but see Mackey and Currie 2001) while severely disturbed habitats nearly always decrease in species richness (Menge and Sutherland 1987, Death 2005). The influence of disturbance on species abundances is less clear and several studies even reported highest abundances in highly disturbed areas (Witman 1992, Scheffler 2005, Rehage and Trexler 2006).

The question how disturbance acts on species interactions, particularly on patterns of co-occurrence, has received much less attention. The assembly rule theory of Diamond (1975) predicts some degree of segregation (underdispersion) of competing species across sites in equilibrium communities. There is a long (Gotelli and Graves 1996) and ongoing discussion whether and to what degree Diamond's assembly rules apply (Gotelli and McCabe 2002, Ulrich 2004) but recent meta-analytical work corroborated at least the basic concept of species segregation. Gotelli and McCabe (2002) and Ulrich and Gotelli (2007) reanalyzed published presence-absence matrices and found the majority of them to be significantly segregated.

In disturbed communities, patterns of species co-occurrence might differ from what is expected in undisturbed communities (Wilbur 1987). Recent studies that used null model approaches are in line with this prediction. Gotelli and Arnett (2000) reported a disassembly of ant communities after invasion by fire ants and Sanders et al. (2007) found ant community structure in burned sites to be less predictable than in unburned sites. A similar disassembly of community structure was reported by Costa de Azevedo et al. (2006) and Bhat and Magurran (2007) in fish communities and Sarà et al.

(2006) in terrestrial vertebrates. However, in each of these studies, disturbance influenced also species richness and abundances. Hence the question remains unsolved as to whether disturbance acts on species co-occurrences through changes in species richness and abundance or whether community disassembly is independent of both or even precedes species loss and changes in abundances.

Classical (Hutchinson 1959) and recent niche theory (Chase and Leibold 2003) links species composition and abundances to limiting environmental factors and species specific traits. In equilibrium communities, species richness and species abundances across sites are therefore predicted to be correlated to sets of environmental variables. Ordination and regression techniques should be able to identify major predictors of the distribution of species across sites. Although there is a discussion around the pitfalls in the use of regression models (Lichstein et al. 2002, Dormann 2007), there is a growing number of studies that demonstrated their predictive value at different ecological scales (Beals 2006, Dormann et al. 2008, Finch et al. 2008). For instance, disturbance might weaken the correlation between richness and environmental variables making richness less predictable. Indeed Taylor et al. (2006) using ordination techniques reported higher correlation of stream fish diversity to environmental variables in stable habitats. In turn, Batáry et al. (2008) applied gradient and correspondence analysis and did not find significant differences in richness and abundance of spiders between habitats of different disturbance level.

In the present paper, we test the above hypotheses on species co-occurrence and environmental correlates. Particularly we ask

- whether disturbance influences island species richness and abundance,

- whether disturbance influences regional species richness,

- whether correlations of species richness and abundances with environmental variables differ between disturbed and undisturbed sites,

- whether disturbance changes patterns of species co-occurrence.

We study these questions using spider communities in two Polish complexes of lake islands that were differently disturbed by tourist visits. Tourists might have various impacts on ecosystems. Prior work (Skłodowski et al. 2006) that studied one of the complexes reported soil densification, damages to trees, and reduced amounts of leaf litter and herb layers due to tourist visits. Each of these changes might directly influence the structure of spider communities and act as the proximate cause for the observed changes. However, there are astonishingly few studies that deal with tourism as an ultimate cause for changes in ecosystem functioning (Christ et al. 2003). These deal mainly with loss in diversity (Hsieh et al. 2003, Laiolo 2004) and invasive species (Reaser et al.

2007). How tourism acts on arthropod species interactions is largely unknown.

Several studies found spiders to be good indicators of agricultural intensity and habitat change (Clough et al. 2005, Schmidt et al. 2005, 2008, Batáry et al. 2008) and disturbance (Bonte et al. 2002, Hsieh et al. 2003, Chen et al. 2004, Buddle et al. 2006, Jung 2008, Matveinen-Huju and Koivula 2008). However, all of these studies focused on species richness and dominance orders. The question how disturbance acts on co-occurrence and species specific traits remains largely unsolved. Here, we show that disturbance disassembles community structure prior to changes in diversity and abundance and makes species richness and abundance less predictable from environmental conditions.

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 (N 54°37' – N 53°46', E 21°31 – E 21°37, hereafter NBM) (Appendix). Lake Wigry is part of the Wigierski National Park and its protected forested islands have a primeval character. NBM form a complex of three connected lakes and are part of the Mazurian Lake District. They are the centre of aquatic tourism in Poland. Consequently, their mixed forested islands are frequently impacted by tourist visits (Skłodowski et al. 2006).

On 13 islands on Wigry, 13 islands on NBM (hence all islands except of a few very distant and inaccessible ones) and four floristically similar sites on the surrounding mainlands, we placed 3 to 15 roof covered Barber traps ($\varnothing$ 12 cm opening) in dependence on island area (Appendix). Placement was done to cover representative parts of the floral composition per site. The distance between the traps was always 25 m (Zalewski and Ulrich 2006). They were monthly controlled from May to October 2004 and 2005. Spiders were classified into species according to Platnick (2009).

Apart from island area and island distances, we estimated seven important habitat characteristics (light, temperature, soil humidity, soil fertility, soil acidity, soil dispersion, and organic matter content, Appendix) from plant habitat indices (Schaffers and Sykora 2000, Dzwonko, 2001, Zarzycki et al. 2002) that rely on habitat requirements of plants (Ellenberg et al. 1992). Respective floristic **samples** of 100 m^2 for index calculation were taken around each trap. The NBM islands appeared to be more fertile than the Wigry islands (fertility: $P_{same} = 0.02$; organic matter content: $P_{same} = 0.001$). Mean temperature and humidity did not significantly differ ($P_{same} > 0.1$) (Appendix).

Islands were divided into four disturbance classes (virgin to highly disturbed) based on the area of island covered with signs of touristic presence like paths, camp sites, camp fires and rubbish. 12 islands/mainland sites at Wigry were classified as being virgin (class 4) and three islands as being

Table 1. Summary statistics of the spider communities on Wigry and NBM lake islands: S_{obs}: observed species richness, S_{exp}: estimated species richness of the first order Jackknife estimator, S_{trap}: average number of species per trap, N: number of individuals caught, N_{trap}: average number of individuals per trap. Joint species refers to the species common to both lakes.

Lake	S_{obs}	S_{exp}	S_{trap}	N	N_{trap}
Wigry	163	183	7.8 ± 0.5	4799	58.2
NBM	157	184	6.7 ± 0.6	5557	60.8
Joint species	118	124	5.1	7737	46.6

slightly disturbed (class 3). At NBM, four islands were given class 4, two islands and two mainlands class 3, two islands class 2 (moderately disturbed) and five islands class 1 (highly disturbed).

Statistical analysis

We arranged species occurrences at sites in an **ordinary** presence - absence matrix with rows as species and columns as sites (in the present case islands and the mainland sites). We used the C-score (Stone and Roberts 1990), and the checkerboard score (Gotelli 2000) to assess matrix-wide species segregation. The third score used, the togetherness score (Stone and Roberts 1992) is a matrix-wide count of common absences and presences. Because common occurrence or absence should be caused by site characteristics we used this metric to assess the degree of common reactions to environmental variables. In a species pair approach, we calculated the C- and the togetherness score of each pair of species. In each case, we assessed statistical significance from the upper and lower confidence limits of 100 randomised matrices that were reshuffled according to the sequential swap algorithm that preserves row and column totals (25000 swaps for each matrix). We also used standardized (Z transformed) effect sizes that can be compared to the standard normal distribution and should have values below -1.96 and above +1.96 at the 5% error level. All computations were done with the software applications *Co-Occurrence* (Ulrich 2006) and *Pairs* (Ulrich 2008, Gotelli and Ulrich 2009).

Species richness was estimated using the 1. order jackknife estimator (Bunge and Fitzpatrick 1993):

$$S_{estimated} = S_{observed} + \frac{S1(n-1)}{n} \qquad (1)$$

where *n* is the number of samples and *S*1 the number of species that occurred in only one **sample.**

Because soil humidity, organic matter content, fertility, and disturbance were spatially autocorrelated (Moran's I (distance class 1): P < 0.05) we used the simultaneous autoregression module of SAM 3.0 for spatial autoregression modelling (Rangel et al. 2006) to infer whether island species richness and single species abundance depend on the aforementioned environmental variables. To standardize for unequal numbers of traps per island, abundances entered the model as average number of individuals per trap. Prior to analysis, we used PCA to avoid undesired effects of high multicollinearity and to reduce the number of variables (Graham 2003). The PCA returned for both island complexes three axes with eigenvalues above 1.0 that could be inter-

preted similarly. In both cases, the first axis loaded high (a > 0.7) with soil humidity, acidity and organic matter content. The second axis loaded high (a > 0.8) with average temperature and the third axis (a > 0.7) with soil mineral richness. We used these three axes and the ln-transformed island area as predictors for ln-transformed species richness in a simultaneous autoregression analysis (Rangel et al. 2006). Because for NBM species richness was significantly (P = 0.04) correlated with the distances between islands (Moran's I = -0.43) we used island longitude and latitude as spatial autocorrelates. In a further test, we used the same modelling approach to infer to which degree species abundances can be explained by the above predictors. For each island complex, we used species abundances of all species that occurred on at least five islands (44 species at Wigry and 40 species at NBM) and compared explained variances in abundance of these species and of the part of species shared by both complexes (17 species). Differences in species composition between the two islands complexes were inferred from non-metric multidimensional (NMDS) scaling using the Sörensen dissimilarity coefficient applied to the presence-absence matrix.

Results

Diversity and abundances

In total, we collected 4799 individuals from 163 species at Wigry and 5557 individuals from 157 species at NBM (Table 1). Separate Jackknife 1 estimates for each sample site showed that sample intensity did not significantly influence species coverage (the quotient of observed to estimated numbers of species). Coverage ranged between 65% and 95% and was neither correlated with the number of traps per site (r = 0.08 n.s.) nor with island area (r = 0.09 n.s.), or with the average number of individuals per trap (r = 0.07 n.s.).

118 species occurred at both complexes (58% of the total of 202 species). Jackknife 1 estimates of species richness at both complexes were nearly identical (183 and 184 species respectively, 124 joint species). Average species numbers per trap and average numbers of individuals per trap did also not significantly differ ($P_{species}$(U) = 0.18) and $P_{individuals}$(U) = 0.90). Species abundances of the 118 joint species were slightly but not significantly (P_{same}(U) > 0.1) higher at NBM (59 individuals/trap) than at Wigry (55 individuals/trap). However, the NMDS analysis revealed a clear difference in species composition between the two island complexes (Fig. 1). The Wigry islands clustered together with respect to species composition while the NBM islands showed a larger variability on the first NMDS axis. The NMDS results reflect the comparably higher numbers of web building species (Wigry: 99; NBM: 107) and lower numbers of vagrant species

Table 2. Significant environmental predictors (ln transformed area and first three PCA scores and the two most important raw variables) of ln transformed spider species richness at Wigry and NBM. B and S.E.: parameter values and their standard errors of the spatial autocorrelation model; p: the associated Bonferroni corrected H_0 probability level.

Wigry Predictor	B	S.E.	p
ln area	0.15	0.03	<0.001
PCA I	0.13	0.02	<0.001
PCA II	-0.02	0.03	n.s.
PCA III	-0.01	0.04	n.s.
Constant	3.52	0.04	<0.001

Wigry Predictor	B	S.E.	p
ln area	0.15	0.02	<0.001
Soil humidity	-0.37	0.07	<0.001
Soil fertility	1.11	0.07	<0.001
Constant	1.21	0.09	<0.001

NBM Predictor	B	S.E.	p
ln area	0.18	0.04	<0.001
PCA I	-0.03	0.05	n.s.
PCA II	0.01	0.06	n.s.
PCA III	0.02	0.08	n.s.
Constant	3.54	0.07	<0.001

NBM Predictor	B	S.E.	p
ln area	0.18	0.04	<0.001
Soil humidity	-0.19	0.19	0.42
Soil fertility	0.01	0.29	0.99
Constant	4.18	0.98	0.002
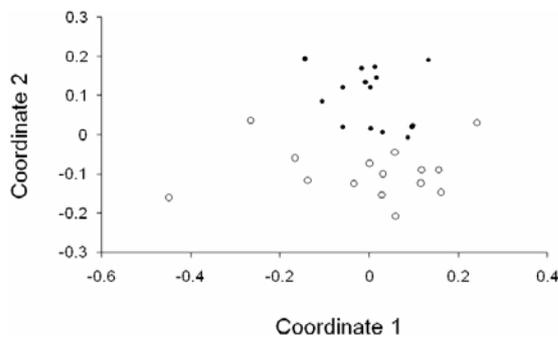
Figure 1. Non-metric multidimensional scaling (Sörensen index) of Wigry (black dots) and NBM (open dots) islands points to differences in the composition of the respective spider fauna.

Table 3. Variance explanation (R^2) of environmental predictors (ln transformed area and first three PCA scores) of ln transformed spider abundances (all species S with at least five occurrences) at Wigry and NBM. The significance level refers to the difference in R^2 between the two assemblages.

Predictor	S	R^2	S.E.	P
All species				
Wigry	44	0.48	0.04	<0.001
NBM	40	0.30	0.03	
Joint species				
Wigry	17	0.46	0.03	<0.001
NBM	17	0.32	0.03	

(Wigry: 64; NBM: 50) at the NBM sites although these differences are statistically not significant ($p(\chi^2) = 0.08$).

At NBM neither environmental variables nor total and mean island species richness and abundance were related to the degree of disturbance (Kruskal-Wallis test: all P > 0.2). Species richness increased with island area at both island complexes in a nearly identical manner. Both species – area relationships (SARs) are best fitted by power functions of the form $S = S_0 A^z$ with slopes of $z = 0.22 \pm 0.04$ (Wigry) and $z = 0.19 \pm 0.03$ (NBM) and species densities $S_0 = 33 \pm 2.0$ (Wigry) and $S_0 = 35 \pm 2.2$ (NBM). Both slopes and species densities are statistically significant at $P(x=0) < 0.001$. Neither species densities nor slopes differed significantly at the 5% error benchmark (two sided t-test).

Environmental correlates

Spatial autoregression analysis revealed that at Wigry total island species richness was highly correlated with area and the first PCA axis that captured important soil properties

(Table 2). A stepwise regression analysis using the raw environmental variables pointed to soil humidity ($P_{uncorrelated} < 0.001$) and soil fertility ($P_{uncorrelated} < 0.001$) as being major predictors of species richness. In contrast, at NBM none of the PCA axes entered the spatial autoregression model at the 5% error benchmark (Table 2). Accordingly, the stepwise analysis using raw data did not point to any environmental variable as being a significant predictor of spider species richness (all $P_{uncorrelated} > 0.05$; Table 2). For both island complexes, total abundances did not significantly depend on the PCA axes or on the raw environmental variables (all $P_{uncorrelated} > 0.05$).

In the species specific approach, we looked at what part of variance of species abundance among islands was explained by area and the first three PCA axes (Table 3). On average the explained variance of species abundances at Wigry was significantly ($P < 0.001$) higher than at NBM. This effect did not depend on species composition because we observed the same effect for the species common to both complexes (Table 3). Of the 17 joint species 14 had higher R^2 values at Wigry ($P(H_0) < 0.01$).

Co-occurrence

The community-wide pattern of species co-occurrence of the Wigry complex was significantly segregated. All three

Table 4. C-, Checkerboard, and togetherness scores of the total spider communities of the Wigry and NBM lake islands and for the subsets of species common to both complexes, the respective lower (LCL) and upper (UCL) 95% confidence limits of the fixed-fixed null model, the Z-transformed values and the probability levels of Z based on the standard normal distribution. In a pairwise approach expected numbers of significant segregated ($Segr_{Exp}$) or aggregated ($Aggr_{Exp}$) species pairs were obtained from 100 randomized matrices and compared to the observed ones.

Wigry						Significant pairs			
Metric	Value	LCL	UCL	Z	p	$Segr_{Exp}$	$Segr_{Obs}$	$Aggr_{Exp}$	$Aggr_{Obs}$
C-score	3.150	2.960	3.090	4.070	<0.0001	17±3	58	1±1	0
Checkerboard score	5383	5060	5369	2.26	0.01	-	-	-	-
Togetherness score	0.110	0.107	0.109	3.550	0.0002	14±2	51	6±2	12

NBM						Significant pairs			
Metric	Value	LCL	UCL	Z	p	$Segr_{Exp}$	$Segr_{Obs}$	$Aggr_{Exp}$	$Aggr_{Obs}$
C-score	3.170	3.080	3.200	1.450	n.s.	15±5	13	1±2	0
Checkerboard score	6270	6069	6321	1.270	n.s.	-	-	-	-
Togetherness score	0.092	0.090	0.092	1.480	n.s.	13±2	29	2±2	1

Joint species only Wigry						Significant pairs			
Metric	Value	LCL	UCL	Z	p	$Segr_{Exp}$	$Segr_{Obs}$	$Aggr_{Exp}$	$Aggr_{Obs}$
C-score	3.15	2.947	3.084	3.737	<0.0001	16±3	44	1±1	0
Checkerboard score	5381	5089	5381	1.96	0.05	-	-	-	-
Togetherness score	0.110	0.106	0.108	3.742	<0.0001	12±2	63	1±1	0

Joint species only NBM						Significant pairs			
Metric	Value	LCL	UCL	Z	p	$Segr_{Exp}$	$Segr_{Obs}$	$Aggr_{Exp}$	$Aggr_{Obs}$
C-score	4.010	3.880	4.045	1.812	n.s,	15±3	14	1±1	1
Checkerboard score	2156	2034	2174	1.350	n.s.	-	-	-	-
Togetherness score	0.113	0.101	0.114	1.860	n.s.	16±2	17	2±2	1

metrics of species co-occurrence (C-score, checkerboard score, and togetherness score) ranged above the upper 99% confidence limit of the fixed –fixed null model (Table 4). In the pairwise approach numbers of segregated species pairs were for the C- and the togetherness score significantly higher than expected by chance ($P(H_0) < 0.0001$). The togetherness score pointed also to a higher number of aggregated pairs than expected by chance ($P(H_0) < 0.001$). At NBM, neither of the matrix-wide metrics pointed to a segregated or to an aggregated pattern of species co-occurrence at the 5% error benchmark (Table 4). Pairwise species co-occurrences were in line with this finding. At Wigry, we observed significantly ($P < 0.001$) more segregated pairs (C-score) than at NBM and than expected by the null model. These findings did not depend on differences in species composition. Using the submatrices for the 118 species common to both complexes pointed again to a highly segregated pattern at Wigry and a random pattern at NBM (Table 4).

Discussion

The major finding of our study is that disturbance might disassemble subtle patterns of community structure prior to apparent changes in species composition and abundances. Average island species richness (α-diversity) and average abundances were similar at both complexes. Hence the observed differences in soil fertility (cf. methods) did not influence local species richness. Further, the regional species turnover (β-diversity) as estimated from both SAR slopes and total species richness of both complexes (γ-diversity) did not significantly differ between the island complexes either. Thus, neither differences in environmental variables nor

tourist visits influenced the patterns of species richness at NBM in comparison to the Wigry complex. These findings are in line with previous studies (reviewed in Schmidt et al. 2008 and Batáry et al. 2008) that reported no or mixed reactions of total spider diversity and abundance to differences in land use. Apparently a clear decrease in richness needs severe changes in habitat suitability. In our study, the NBM complex was only moderately disturbed by tourist visits. Such a disturbance level did not influence richness and abundances.

In contrast to richness and abundance we found significant differences in species composition and co-occurrences between the island assemblages. The NMDS analysis of species composition clearly separated the more pristine Wigry islands from the NBM complex (Fig. 1). Such differences have previously been reported in comparisons of disturbed and undisturbed agricultural landscapes (Schmidt et al. 2005, 2008, Batáry et al. 2008) and forested sites (Larrivee et al. 2005, Gillette et al. 2008). Further, on the Wigry islands abundant and intermediate abundant species occurred in a significantly segregated manner (Table 4) while at NBM species co-occurrence of all abundance classes was random. We assessed statistical significance with the most conservative of the possible null models for co-occurrence analysis, the fixed - fixed algorithm that retains numbers of occurrences and site species richness during randomization (Gotelli 2000). The strong signal for segregation under this null model hence implies major differences in community organization between both island complexes and a disassembly of community structure at NBM. A similar community disassembly has previously been reported in ants after invasion of foreign species

(Gotelli and Arnett 2000, Sanders et al. 2003). In other recent studies, community disassembly was associated with a decrease in species richness (Bhat and Magurran 2007) and major differences in species composition (Sarà et al. 2006).

The present results point also to another aspect of community disassembly. At the disturbed island complex, we observed lower correlations of total species richness (Table 2) and species abundances (Table 3) with environmental variables. Hence species richness and abundance at disturbed sites were less predictable. This fits of course into the notion of a random pattern of species co-occurrence. Quantitative studies on the spatial distribution and abundance of spiders in dependence on habitat properties are rare in comparison to other important terrestrial arthropod taxa. A few local studies reported significant correlations of spider abundance and species richness with habitat architecture and plant species composition (Beals 2006, Rypstra et al. 1999) and humidity (Bonte et al. 2002). Jimènez-Valverde and Lobo (2007) showed that local vegetation complexity influences regional species richness and Finch et al. (2008) found significant correlations of spider species richness with climate and topographic variables. Our results for the pristine complex (Table 2) extend these findings while showing that soil fertility is also an important factor for spider species richness. However, the present study is the first to show that disturbance weakens the effect of habitat properties on spider occurrence (Table 2).

Our work points to tourist visits as the ultimate cause for the observed patterns of species occurrence among islands. However, it does not answer the question about the proximate causes. Tourism altered important habitat properties: particularly soil fertility and organic matter content (cf. Methods section). Prior work (Skłodowski et al. 2006, Mądrzejowska and Skłodowski 2008) on the island banks at NBM additionally reported soil densification and reduced amounts of leaf litter and herb layers. All of these factors might contribute to the randomization of species occurrences among islands. Because we used a co-occurrence and niche approach that requires the simultaneous comparison of both island complexes we were unable to identify precisely the important proximate causes. Future work has to clarify whether disturbance by tourists directly or indirectly via changes in habitat suitability affects the spider communities.

The present study has implications for biological conservation. The detection of community disassembly might be an early sign for factors that act negatively on ecosystems. This signal gives us the opportunity to act counter to these factors prior to more severe changes in diversity and ecosystem functioning. Indeed, internal community organization has been somewhat neglected in the discussion around diversity and ecosystem functioning (Loreau et al. 2002, Ives and Carpenter 2007). In part this is surely caused by the use of low diversity experimental communities in most ecosystem functioning studies (Loreau et al. 2002; but see Tylianakis et al. 2006). Further, they centred on the local scale where patterns of species co-existence are difficult to quantify while studies at regional scales are still scarce (Loreau et al. 2003, Chesson and Kuang 2008). Studies of species occurrence and interaction matrices at the regional scale might be a way to infer the importance of diversity on ecosystem functioning above local scales.

References

Batáry, P., A. Báldi, F. Samu, T. Szűts and S. Erdős. 2008. Are spiders reacting to local or landscape scale effects in Hungarian pastures? *Biol. Conserv.*141: 2062-2070.

Beals, M. L. 2006. Understanding community structure: a data-driven multivariate approach. *Oecologia* 150: 484-495.

Begon, M., C. R. Townsend and J. L. Harper. 2006. *Ecology. From Individuals to Ecosystems.* Blackwell, Oxford.

Bhat, A. and A. E. Magurran. 2007. Does disturbance affect the structure of tropical fish assemblages? A test using null models. *J. Fish Biol.* 70: 623-629.

Bonte, D., L. Baet and J.-P. Maelfait. 2002. Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). *J. Arachnol.* 30: 331-343.

Buddle, C. M., D. W. Langor, G. R. Pohl and J. R. Spence. 2006. Arthropod responses to harvesting and wildfire: implications for emulation of natural disturbance in forest management. *Biol. Conserv.* 128: 346–357.

Bunge J and M. Fitzpatrick. 1993. Estimating the number of species: A review. *J. Am. Stat. Ass.* 88: 364–373.

Chase, J. M. and M. A. Leibold. 2003. *Ecological Niches.* Chicago, Univ. Press, Chicago.

Chen, K.-C. and I.-M. Tso. 2004. Spider diversity on Orchid island, Taiwan: A comparison between habitats receiving different degrees of human disturbance. *Zool. Stud.* 43: 598-611.

Chesson, P. and J. J. Kuang. 2008. The interaction between predation and competition. *Nature* 456: 235-238.

Christ, C., O. Hillel, L. Matus and J. Sweeting. 2003. *Tourism and Biodiversity.* Conservation International, Washington.

Clough, Y., A. Kruess, D. Kleijn and T. Tscharntke. 2005. Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. *J. Biogeogr.* 32: 2007-2014.

Costa de Azevedo, M. C., F. Araujo, A. Pessanha and M. Silva. 2006. Co-occurrence of demersal fishes in a tropical bay in southeastern Brazil: A null model analysis. *Estuar Coastal Shelf Science* 66: 315-322.

Death, R. G. 2005. Predicting invertebrate diversity from disturbance regimes in forest streams. *Oikos* 97: 18-30.

Diamond, M. 1975. Assembly of species communities. In: M . L. Cody and J. M. Diamond (Eds.), *Ecology and Evolution of Communities.* Belknap, Harvard, pp. 342-444.

Dormann, C. F. 2007. Promising the future? Global change projections of species distributions. *Basic Appl. Ecol.* 8: 387-397.

Dormann, C. F., Schweiger, O., Arens, P., Augenstein, I., Aviron, S., Bailey, D., Baudry, J., Billeter, R., Bugter, R., Bukácek, R., Burel, F., Cerny, M., Cock, R.D., De Blust, G., DeFilippi, R.,

Diekötter, T., Dirksen, J., Durka, W., Edwards, P.J., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Liira, J., Maelfait, J.P., Opdam, P., Roubalova, M., Schermann-Legionnet, A., Schermann, N., Schmidt, T., Smulders, M.J., Speelmans, M., Simova, P., Verboom, J., van Wingerden, W. and Zobel, M. 2008. Prediction uncertainty of environmental change effects on temperate European biodiversity. *Ecol. Lett.* 11: 235-244.

Dzwonko, Z. 2001. Effect of proximity to ancient deciduous woodland on restoration of the field layer vegetation in a pine plantation. *Ecography* 24: 198-204.

Ellenberg, H., H. E. Weber, R. Düll, V. Wirth and W. Werner. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18: 1-258.

Finch, O.-D., T. Blick and A. Schuldt. 2008. Macroecological patterns of spider species richness across Europe. *Biodiv. Conserv.* 17: 2849-2868.

Gillette, N. E., R. S. Vetter, S. R. Mori, C. R. Rudolph and D. R. Welty. 2008. Response of ground-dwelling spider assemblages to prescribed fire following stand structure manipulation in the southern Cascade Range. *Can. J. Forest Res.* 38: 969-980.

Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606-2621.

Gotelli, N. J. and A. E. Arnett. 2000. Biogeographic effects of red fire ant invasion. *Ecol. Lett.* 3: 257-261.

Gotelli, N. J. and D. J. McCabe. 2002. Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology* 83: 2091-2096.

Gotelli, N. J. and G. R. Graves. 1996. *Null Models in Ecology*. Smithsonian Inst. Press, Washington.

Gotelli, N. J. and W. Ulrich 2009. The Empirical Bayes approach as a tool to identify non-random species associations. *Oecologia,* in press.

Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84: 2809-2815.

Hsieh, Y. L., Y.-S. Lin and I.-M. Tsao. 2003. Ground spider diversity in a Kenting uplifted coral forest reef forest, Taiwan: a comparison between habitats receiving various disturbances. *Biodiv. Conserv.* 112: 2173-2194.

Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* 93: 145-159.

Ives, A. R. and S. R. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317: 58-62.

Jimènez-Valverde, A. and J. M. Lobo. 2007. Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: climate and altitude vs. habitat structure. *Ecol. Entomol.* 32: 113-122.

Jung, M.-P. 2008. Species diversity and community structure of ground dwelling spiders in unpolluted and moderately heavy metal-polluted habitats. *Water Air Soil Poll.* 195: 15-22.

Laiolo, P. 2004. Diversity and the structure of the bird community in the Himalayan subalpine zone: is conservation compatible with tourism? *Biol. Conserv.* 115: 251-262.

Larrivee, M., L. Fahrig and P. Drapeau. 2005. Effects of a recent wildfire and clearcuts on ground-dwelling boreal forest spider assemblages. *Can. J. Forest Res.* 35: 2575–2588.

Lichstein, J. W., T. R. Simons, S. A. Shriner and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecol. Monogr.* 72: 445-463.

Loreau, M., S. Naeem and P. Inchausti (eds.) (2002). *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives.* Oxford, Univ. Press.

Loreau, M., N. Mouquet and A. Gonzalez. 2003. Biodiversity and spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Science USA* 100: 12765-12770.

Mackey, R. L. and D. J. Currie. 2001. The diversity-disturbance relationship: is it generally strong and peaked? *Ecology* 82: 3479-3492.

Matveinen-Huju, K. and M. Koivula. 2008. Effects of alternative harvesting methods on boreal forest spider assemblages. *Can. J. Forest Res.* 38: 782-794.

Mądrzejowska, K., and J. Skłodowski. 2008. Assemblages of carabid beetles (Coleoptera: Carabidae) as zoo-indicator of water tourism impact on forest-lake ecotones. *Baltic J. Coleopterol* 8: 1-14.

Menge, B. A. and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* 130: 730-757.

Platnick, N. I. 2009. *The World Spider Catalog*, version 9.5. American Museum of Natural History. http://research.amnh.org/entomology/spiders/catalog/INTRO3.html.

Rangel, T. F. L., J. A. F. Diniz-Filho and L. M. Bini. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Glob. Ecol. Biogeogr.* 15: 321-327.

Reaser, J. K., L. A. Meyerson, Q. Cronk, M. De Poorter, L. G. Eldrege, E. Green., M. Kairo, P. Latasi, R. N. Mack, J. Mauremootoo, D. O'Dowd, W. Orapa, S. Sastroutomo, A. Sauners, C. Shine, S. Thrainsson and L. Vaiutu. 2007. Ecological and socio-economic impacts of invasive alien species in island ecosystems. *Env. Conserv.* 34: 98-111.

Rehage, J. S. and J. C. Trexler. 2006. Assessing the net effect of anthropogenic disturbance on aquatic communities in wetlands: community structure relative to distance from canals. *Hydrobiol.* 569: 359-373.

Rypstra, A. L., P. E. Carter, R. A. Balfour and S. D. Marshall. 1999. Architectural features of agricultural habitats and their impact on the spider inhabitants. *J. Arachnol.* 27: 371–377.

Sanders, N. J., N. J. Gotelli, N. E. Heller and D. M. Gordon. 2003. Community disassembly by an invasive species. *Proc. Natl. Acad. Science USA* 100: 2474-2477.

Sanders, N. J., N. J. Gotelli, S. I. Wittman, J. S. Ratchford, A. M. Ellison and E. S. Jules. 2007. Assembly rules of ground-foraging ant assemblages are contingent on disturbance, habitat and spatial scale. *J. Biogeogr.* 34: 1632-1641.

Sarà, M., E. Bellia and A. Milazzo. 2006. Fire disturbance disrupts co-occurrence patterns of terrestrial vertebrates in Mediterranean woodlands. *J. Biogeogr.* 33: 843-852.

Schaffers, A. P. and K. V. Sykora. 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *J. Veg. Sci.* 11: 225-244.

Scheffler, P. Y. 2005. Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *J. Trop. Ecol.* 21: 9-19.

Schmidt, M. H., I. Roschewitz, C. Thies and T. Tscharntke. 2005. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *J. Appl. Ecol.* 42: 281-287.

Schmidt, M. H., C. Thies, W. Nentwig and T. Tscharntke. 2008. Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *J. Biogeogr.* 35: 157-166.

Shea, K., S. H. Roxburgh and E. S. J. Rauschert. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecol. Lett.* 7: 491-508.

Skłodowski, J., J. Sater and T. Strzyżewski. 2006. Impact of water tourism activity in forest/waterside ecotones on the example of the Bełdany Lake. *Sylwan* 10: 65-71 (in Polish).

Stone, L. and A. Roberts. 1990. The checkerboard score and species distributions. *Oecologia* 85: 74-79.

Stone, L. and A. Roberts. 1992. Competitive exclusion or species aggregation? An aid in deciding. *Oecologia* 91: 419-424.

Taylor, C. M., T. L. Holder, R. A. Fiorillo, R. A. Williams, R. B. Thomas and M. L. Warren Jr. 2006. Distribution, abundance, and diversity of stream fishes under variable environmental conditions. *Can. J. Fish. Aquat. Sci.* 63: 43-54.

Tylianakis, J. M., T. Tscharntke and A.-M. Klein. 2006. Diversity, ecosystem functioning, and stability of parasitoid – host interactions across a tropical habitat gradient. *Ecology* 87: 3047-3057.

Ulrich, W. 2004. Species co-occurrences and neutral models: reassessing J. M. Diamond's assembly rules. *Oikos* 107: 603-609.

Ulrich, W. 2006. *CoOccurrence - a Fortran program for species co-occurrence analysis*. www.uni.torun.pl/~ulrichw.

Ulrich, W. 2008. Pairs – a Fortran program for studying pair wise species associations in ecological matrices. www.uni.torun.pl/~ulrichw.

Ulrich, W., M. Almeida-Neto and N. J. Gotelli. 2009. A consumer's guide to nestedness analysis. *Oikos* 118: 3-17.

Ulrich W. and N. J. Gotelli. 2007. Disentangling community patterns of nestedness and species co-occurrence. *Oikos* 116: 2053-2061.

Ulrich W., Zalewski M. and K. Komosiński. 2007. Diversity of carrion visiting beetles at rural and urban sites. *Community Ecol.* 8: 171-181.

Wilbur, H. M. 1987. Regulation of structure in complex systems: experimental temporary pond communities. *Ecology* 68: 1437-1452.

Wilkinson, D. M. 1999. The disturbing history of intermediate disturbance. *Oikos* 84: 145-147.

Wilson, S. D. and D. Tilman. 2002. Quadratic variation in old-field species richness along gradients of disturbance and nitrogen. *Ecology* 83: 492-504.

Witman, J. D. 1992. Physical disturbance and community structure of exposed and protected reefs: a case study from St. John, U.S. Virgin Islands. *Am. Zool.* 32: 641-654.

Zalewski, M. and W. Ulrich. 2006. Dispersal as a key element of community structure: The case of ground beetles on lake islands. *Divers. Distrib.* 12: 767-775.

Zarzycki, K., H. Trzcińska-Tacik, W. Różański, Z. Szeląg, J. Wołek and U. Korzeniak. 2002. *Ecological Indicator Values of Vascular Plants of Poland*. W. Szafer Institute of Botany, Polish Academy of Sciences, Krakow.

Appendix

Sample sites, numbers of traps, species and individuals caught, and basic environmental variables of the islands and mainland sites used in the present study. The values for light, temperature, soil humidity, soil acidity, soil dispersion, and organic matter content are the respective Ellenberg habitat indices. Disturbance categories from 1 (disturbed) to 4 (pristine). Latitude and longitude are given in decimal notation. The file may be downloaded from the web site of the publisher at www.akademiai.com.