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Abundance and co-occurrence patterns of core and satellite species of ground beetles on small lake islands

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15 lake islands and two mainland sites of Mamry lake in Poland were sampled to investigate community structures and patterns of co-occurrences of ground beetles (Carabidae). The total ground beetle metacommunity of 71 species was divided into a group of core species occupying at least half of all study sites and of satellite species, which occurred at two sites or less. This division is mirrored by reduced dispersal abilities and non-random patterns of site occupancy. Core and satellite species also differed in patterns of relative abundance. The core group followed a lognormal distribution, the satellite group a power function as predicted by the self-similarity model of occurrence. We conclude that the division into core and satellite species is not a sample artefact but reflects different life history strategies. We also conclude that current models of niche division and co-occurrence might miss important aspects of community structure if they do not refer to patterns of dispersal.

From these findings we infer that the regional distribution of core species might be shaped by species interactions and processes of niche divisions whereas the spatial distribution of satellite species are best interpreted as stemming from random dispersal.

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The question what makes species common or rare is central to community ecology and conservation (Gaston 1994, Kunin and Gaston 1997). It has long been known that at smaller ecological scales and in temporary or ephemeral habitats species can be divided into core and satellite (Hanski 1982, 1999, Hanski and Gyllenberg 1993, McGeoch and Gaston 2002). The first group consists mostly of species which are widely distributed and often abundant within local patches. The second group is made up of mostly rare species occurring only at a limited number of sites. This distinction has long been discussed in a metapopulation context (for an overview cf. Hanski 1999). Recent investigations have revealed very similar patterns in large scale presence–absence matrices (Storch and Šizling 2002, Selmi and Boulinier 2004). Storch and Šizling attributed their finding to metapopulation dynamics at the regional scale and habitat fragmentation and showed that the pattern cannot simply be dismissed as a pure sampling artefact stemming from lognormal or log-series species abundance distributions (SADs) (Nee et al. 1991a, McGill 2003).

The original core-satellite distinction referred to the spatial distribution (patch occupancies) of species where high numbers of species in the first and last occupancy class cause a bimodal species number–occupancy distribution (Hanski 1982). SADs of core and satellite species have not been studied so far. However, Magurran and Henderson (2003) found that the spatially defined core–satellite distinction has a temporal counterpart.

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Using a long-term survey of estuary fish assemblages they showed that the commonness and rarity of species is closely related to their permanence in time (cf. Guo et al. 2000 for a similar pattern in plants). Temporary persistent (core) species appeared to follow a log-normal SAD in line with traditional niche orientated models (Sugihara 1980, Tokeshi 1999, Fesl 2002), whereas for temporary occasional (satellite) species Magurran and Henderson (2003) predicted a log-series distribution as traditionally assumed from sample theory for assemblages under the strong influence of dispersal (Fisher et al. 1943). However, in a subsequent study Ulrich and Ollik (2004) reported for satellite species a power function SAD in line with current fractal models (Solé and Alonso 1998, Mouillot et al. 2000). Present evidence suggests therefore that current models of species abundances might dismiss important aspects of species assemblage if they do not include the distinction between temporally defined core and satellite species. This calls for a rethinking of these models and for tests whether spatially defined core and satellite species also differ in their species abundance distributions.

If the occurrence of satellite species is mainly governed by dispersal, co-occurrence patterns should in most cases be either random or overdispersed (in the case of differences in habitat suitability) but not underdispersed as would be expected from competitive interactions (Diamond 1975, Weiher and Keddy 1999, Gotelli and McCabe 2002, but see Ulrich 2004a, Bell 2005). Instead, for common species traditional assembly rules predict species underdispersion (Diamond 1975, Weiher and Keddy 1999). Hence, the study of species co-occurrences might be crucial to the interpretation of observed patterns of abundance across sites. Underdispersion refers to a situation where species tend to avoid each other. This should result in a reduced number of co-occurrences and a higher number of mutual exclusions across sites with respect to a random distribution of occurrences. In the case of overdispersion a reversed pattern is expected.

Up to now SADs were mainly studied from a within habitat perspective (Tokeshi 1999, Magurran 2004). Macroecological studies of SADs at a regional (between habitat) scale have been performed for some vertebrates (Nee et al. 1991b, Gaston and Blackburn 2000, Azeria 2004) but still relied on simple model fitting of whole assemblages. The possible heterogeneity of assemblages with respect to SADs and patterns of spatial distribution calls for a regional perspective that takes patterns of dispersal and spatial distribution into account.

The present paper aims in this direction. We use data of ground beetle assemblages of 15 lake islands and two mainland sites in northern Poland (Zalewski 2000, 2004) to relate SADs to patterns of site occupancies. We will show that ground beetle assemblages can be divided into core and satellite species and that this division is not only manifest in patterns of relative abundance and co-occurrences but can also be seen in the distribution of body sizes and the relation between site abundance and occupancy. From these findings we infer that the regional distribution of core species might be shaped by species interactions and processes of niche division whereas the spatial distribution of satellite species are best interpreted as stemming from random dispersal.

Material and methods

15 island and two forested mainland sites (variants of Tilio-Carpinetum and Carici elongatae-Alnetum associations) from the largest archipelago of islands in Poland – the Mazurian Lake Mamry (21°30′–21°52′ E, 54°00′–54°10′ N) were sampled using pitfall traps (0.5 l plastic mug, mouth diameter 120 mm, wooden roof). Existing maps of forest habitats and soil types (1:25 000) were used to place trap lines in every habitat type per study site (three traps per site in line at a distance of 25 m; at the smallest island only two traps were placed) to allow for a stratified sampling design (Krebs 1989, Digweed et al. 1995). Between 2 and 21 traps were used per site, depending on its habitat diversity and size making up a total of 107 traps. Traps were operated from June to September 1997 and 1998 and were emptied monthly and refilled with fresh glycol (Zalewski 2000).

All carabid species except the genus *Europhilus* were identified to species level using the keys of Hürka (1996) and Lindroth (1985). Nomenclature follows Hürka (1996). Life history and morphological characteristics are based on den Boer et al. (1980), Lindroth (1985), and Hürka (1996).

According to the occurrence pattern of the 71 species found we divided the species into those that were found in at least 8 of the 17 study sites (core species, 20 species) and those that were found in at most two sites (satellite species, 31 species). The present paper is mainly based on these two groups. Total species numbers per study site were estimated by rarefaction (Heck et al. 1975) and using the jackknife I and II estimators (Burnham and Overton 1978, Brose et al. 2003).

For studying relative abundance distributions we fitted three types of stochastic models to the observed species abundances. We used a normally distributed random number at a logarithmic scale to fit the lognormal to rank order–log abundance plots. The distribution has a single shape generating parameter, the variance. By adjusting this variance the distribution can be fitted to a given data set (Ulrich 2002, Ulrich and Ollik 2004). Secondly we applied the random assortment algorithm of Tokeshi (1990) to approximate the log-series (Ulrich and Ollik 2004). This sequential breakage model is defined by

$$A_i = A_{\min(i-1)} \mathrm{ran}^z \quad (1)$$

where A_i is the abundance of species i. $A_{\min(i-1)}$ is the smaller breakage product of species $i-1$, ran is a linear random number between 0 and 1 and z is a shape generating parameter (Ulrich 2002). Lastly, we approximated the self-similarity model (the power function) by a stochastic version (Mouillot et al. 2000) defined by

$$A_i = (\mathrm{ran} + X)^{-z} \quad (2)$$

where X and z are two shape generating parameters (Ulrich 2002).

For assessing the goodness of fit we used the 95% confidence limit method of Tokeshi (1990) and counted, for abundance – rank order plots (Whittaker plots), the number of data points that ranged outside the 95% confidence limits of the model to be fitted. We determined the respective confidence limits from 100 randomizations of each model. Because this method does not provide a ranking of models we further used the sum of all squared log-residuals r_{test} of model expectation and observed values to infer the best fit model. Hence

$$r_{test} = \sum_{i=1}^{S} (\mathrm{obs} - \mathrm{exp})^2 \quad (3)$$

with obs and exp being the log transformed observed and expected abundances and S the number of species. The smaller r_{test} is, the better does a given model fit to a given dominance rank order distribution (Ulrich 2002, Ulrich and Ollik 2004). Fits to species number–octave plots (Preston plots) were assessed using conventional χ^2 tests.

We studied species co-occurrence patterns of presence-absence matrices using standardized C-scores (Stone and Roberts 1990) and species combination scores (Pielou and Pielou 1968). The C-score measures species underdispersion between sites (checkerboard patterns), the species combination score by contrast screens for unique species combinations (Gotelli 2000). Standardized scores are Z-transformed and should have a mean of 0 and a standard deviation of 1 (errors given below refer always to standard deviations). Significant species underdispersion or overdispersion, on the other hand, should result in Z-transformed scores above 1.96 or below -1.96 (at the 5% error level). Random matrices for generating standardized scores and significance levels were computed with EcoSim 7.72 (Gotelli and Entsminger 2005). We used fixed sum row and column constraints (Connor and Simberloff 1979) and the sequential swap algorithm for randomization. Gotelli (2000) advocated these constraints for the study of island data because such constructed random matrices seem to be least prone to type I and type II errors. Standard deviations of scores were computed from 5000 null matrices.

The use of the swap algorithm and of Z-scores has been criticized for possible biases introduced by the algorithm and subsequent inflated type I error levels (Sanderson et al. 1998, Gotelli 2001, but see Miklós and Podani 2004). Additionally sampling artefacts due to differences in species abundances and detection probabilities might affect score values (Peres-Neto 2004). To account for these possible error sources we constructed 200 random matrices each for the core and the satellite species by placing the number of trapped individuals per species at random but in accordance with the observed frequency distribution of total individual numbers into the 17 sites. For each of these individual based random matrices we performed the above analyses and compared the resulting distribution of Z-scores with the observed values.

Additionally, we used the abundance based variance test of Schluter (1984) to infer whether the variance patterns of the abundance matrices deviated from expectation (Schluter 1984). This test is potentially influenced by site characteristics and area that might result in species aggregation on larger and more suitable sites. To correct for this, we used relative abundances per site instead of absolute captures. In essence, the test used in this way is a measure whether species rank orders between sites are similar (V-score >0) or dissimilar (V-score <0). Null model index values and standard deviations were computed from 1000 random matrices using the program ComStruc (Ulrich 2005a; sequential swap algorithm, equiprobable row and column constraints). For comparison we computed also 1000 randomized matrices using the sum-of-squares reduction algorithm proposed by Miklós and Podani (2004). However, the latter algorithm gave higher Z-score and inflated significance values in all runs compared to the sequential swap (data not shown). The sequential swap appears therefore to be the more conservative test as already suggested by Gotelli (2000) and Miklós and Podani (2004). Therefore, below we show only the swap-scores.

To assess differences in size ratios we used the Simberloff and Boecklen (1981) test. The null hypothesis of this test is that size ratios per site (either at a linear or at a logarithmic scale) are randomly drawn from the body sizes of the metacommunity. Lower or higher variances in the distribution of the ordered sequence of species with respect to the random expectation point to a segregated or aggregated pattern of size distributions. We computed this variance for mean body length differences ($L_n - L_{n-1}$; variance test) and for the ratio of body length (L_n/L_{n-1}; ratio test) for each site and compared the observed ratio with those of 1000 random samples of the same species number taken from the whole species pool (Ulrich 2005b). As above we used Z-scores to infer whether the observed size distributions differ from expectation.

The computer programs Random, ComStruc and Structure used in this study are available at the home page of WU (www.uni.torun.pl/∼ulrichw).

Results

In total we trapped 12793 individuals out of 71 species of ground beetles at the 17 study sites (Table 1). Because the sites differed in number of traps placed, we first looked whether these differences resulted in different proportions of species trapped. However, irrespective of study site and trap number, between 77 to 89% (mean 84 ± 3%) of the estimated number of species were trapped as inferred from rarefaction and from the estimates of the jackknife I and II estimators (Table 2). The present results should therefore not be biased by unequal trap numbers.

Species–area (Fig. 1A) and individuals–area (Fig. 1B) relationships of the ground beetles were well described by power functions with slopes of 0.13 and 0.38, respectively. The residuals from the species–area relationship were neither correlated with site area nor with the degree of isolation as measured by the index of Hanski (1994, 1999)($R^2 < 0.09$, $p > 0.3$), hence more isolated islands were not depauperate in species. When classified into $\log_2$ occurrence classes (Fig. 2) the ground beetle species could be divided into two groups (inferred from a comparison with a Bernoulli distribution according to the method of Tokeshi (1992) ($p < 0.01$)): one group of core species, which occurred at least at half of all sites (20 species), and one group of satellite species, which occurred at most at two of the sites (31 species). Below, these two classes are used to study species dominance rank orders and patterns of co-occurrences.

The whole community (all trapped individuals combined) was not well fitted by any of the three SAD models tested (Fig. 3A, 4A). However, the core species closely followed a lognormal distribution with a shape generating parameter $a = 0.32$ (Fig. 3 B, 4B), a value that is higher than the canonical value of 0.2 (May 1975). For this group all data points of the Whittaker plot (Fig. 3B) ranged inside the 95% confidence limit of the model. On the other hand the random assortment and the self-similarity model fitted worse. In both cases more than 10% of the data points ranged outside the 95% confidence limits (data not shown). The r_{test} value of the lognormal (2.30 ± 0.34) was significantly lower than those of the random assortment (13.50 ± 1.52) and the self-similarity model (7.2 ± 1.19) as inferred from 100 randomizations of the fits.

The satellite species, on the other hand, were well fitted by the self-similarity model (Fig. 3C, 4C). For this group all data points of the Whittaker plot ranged inside the model's 95% confidence limits (Fig. 3C), whereas this was not the case for both other models (data not shown). The r_{test} value of the self-similarity model (6.63 ± 0.58) was significantly lower than those of both other models (lognormal: 125.8 ± 5.7; random assortment: 94.9 ± 3.2). The Preston plot of the satellite species (Fig. 4C) was well fitted by the self-similarity model, but not by the random assortment model (data not shown). The lognormal fitted under the assumption that the distribution mode was well behind the veil line (the left side truncation of the lognormal, Preston 1962), which implicates a total of more than 80 satellite species. This would be in contradiction to the total ground beetle species richness of about 90 species (Table 2) and to the whole faunal SAD pattern (Fig. 3A, 4A). In summary, core and satellite species appeared to follow different species abundance distributions.

The core species showed a clear non-random pattern of site colonisation when applying the C- and V-score (Table 3). The presence–absence pattern (C-score) gave a strong signal ($p < 0.0001$) towards underdispersion. The abundance based variance test (V-score) instead pointed to a strongly aggregated pattern of abundances and therefore to similar SADs across the study sites ($p < 0.0001$). However, the species combination score did not significantly differ from zero ($Z = 0.499$). Therefore, there where no more exclusive species combinations than expected by chance (Table 3). In the satellite species, on the other hand, the signs of the C- and V-scores indicate patterns contrary to those of the core species. The V-score of −2.51 points to significant ($p < 0.05$) dissimilarities of the SADs across the sites. The negative C-score of $Z = -0.36$ does not significantly deviate from the null model expectation of zero (Table 3). Again, there were no more exclusive species combinations than expected by chance (Table 3).

The core species showed a strong ($p(t) < 0.01$) positive allometric abundance–occupancy relationship (Fig. 5) with a slope of 0.11. In the satellite species such a relation per definition does not exist. Subsequent Kruskal–Wallis ANOVAs by ranks for differences in mean abundances between the species occupying 1, 2, 3, ...to 17 sites revealed a significant ($p < 0.05$) abundance–occupancy relationship only after including those species which occupied at least eight study sites. This is exactly the group of core species.

Core and satellite species differed also in morphological traits. Satellite species had a significantly higher proportion of fully winged species than the core species (Table 4: $p(\chi^2) = 0.01$). However, we could not detect any differences with respect to spring and autumn breeders. Lastly, differences between core and satellite species appeared from the comparison of body size ratios (Fig. 6). The core species seem to be more evenly distributed along the body size axis than expected from the random distribution null model (Fig. 6A, 6B; although this pattern is not significant at

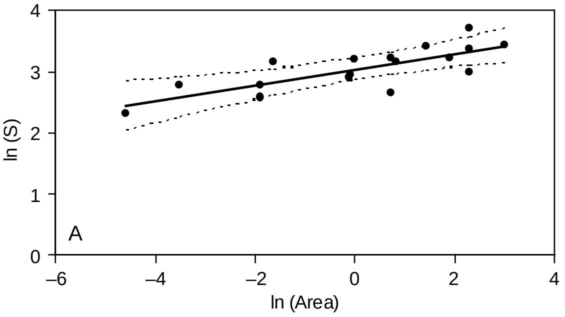
Table 1. Carabid species sampled at the 17 study sites. Abbreviations: flight ability: m: macropterous; b: brachypterous; d: dimorphic. Seasonality: a: autumn breeders; s: spring breeders; x: complex life cycles. Mean body lengths in mm. Occurrences refer to the number of study sites colonized.

Species	Flight ability	Breeding season	Length	Individuals	Occurrences
Agonum duftschmidi Schmidt	m	s	8.75	4	3
Agonum lugens (Duftschmid)	m	x	9.5	12	7
Amara aulica (Panzer)	m	a	12.5	1	1
Amara brunea (Gyllenhal)	m	a	5.7	84	9
Amara communis (Panzer)	m	s	6.6	32	6
Amara plebeja (Gyllenhal)	m	s	6.8	13	5
Amblystomus sp.	m	?	3.15	1	1
Anisodatylus binotatus (Fabricius)	m	s	11.1	2	1
Badister bullatus (Schrank)	m	s	5.4	26	8
Badister dorsiger (Duftschmid)	m	s	5.1	1	1
Badister sodalis (Duftschmid)	m	s	4.3	8	4
Badister unipustulatus Bonelli	m	s	7.5	11	4
Bembidion articulatum (Panzer)	m	s	3.4	1	1
Bembidion doris (Panzer)	m	s	3.4	1	1
Bembidion sp.	m	?	–	1	1
Calathus fuscipes (Goeze)	b	a	11.7	6	1
Calathus melanocephalus (Linnaeus)	d	a	7.2	5	4
Calathus micropterus (Duftschmid)	b	a	7.9	79	2
Calathus mollis (Marsham)	d	a	7.75	10	2
Carabus cancelatus Illiger	b	s	23.5	1	1
Carabus granulatus Linneus	d	s	19.5	684	15
Carabus hortensis Linnaeus	b	a	26	236	3
Carabus nemoralis Muller	b	s	23.5	85	11
Chlaenius nigricornis (Fabricius)	m	s	10.9	1	1
Clivina collaris (Herbst)	m	s	5.4	2	1
Clivina fossor (Linnaeus)	d	s	6.9	11	7
Dischirius globosus (Herbst)	d	s	2.5	4	1
Dischirius sp.	m	?	–	2	1
Epaphius secalis (Paykull)	b	a	3.9	169	7
Harpalus 4-punctatus Dejean	m	x	10.5	879	10
Harpalus froelichi Sturm	m	x	9.4	1	1
Harpalus latus (Linnaeus)	m	x	9.3	47	7
Harpalus rufipalpis Sturm	m	s	9.9	1	1
Harpalus solitaris Dejean	m	x	9.6	2	2
Harpalus xanthopus winkleri Schauberger	m	s	7.7	11	3
Lasoitrechus discus (Fabricius)	m	a	5	2	2
Leistus ferrugineus (Linnaeus)	d	a	7.2	1	1
Leistus rufomarginatus (Duftschmid)	d	a	8.9	99	6
Leistus terminatus (Hellwig)	m	a	6.9	51	12
Loricera pilicornis (Fabricius)	m	x	7.4	16	6
Nebria brevicolis (Fabricius)	m	a	11.5	189	5
Notiophilus biguttatus (Fabricius)	d	s	5	7	5
Notiophilus palustris (Duftschmid)	d	s	5.2	20	8
Oodes gracilis A_Villa & G_B_Villa	m	s	8.9	10	6
Oodes helopioides (Fabricius)	m	s	8.7	24	5
Oxypselaphus obscurus (Herbst)	d	x	5.5	986	14
Panagaeus cruxmajor (Linnaeus)	m	s	8.1	1	1
Paranchus albipes (Fabricius)	m	x	7.8	2	1
Patrobus atrorufus (Stroem)	b	a	8.5	571	12
Phonus sp.	m	?	–	1	1
Platynus assimilis (Paykull)	m	x	11	337	11
Poecilus cupreus (Linnaeus)	m	s	12.1	3	2
Poecilus versicolor (Sturm)	m	s	10.7	2	1
Pseudoophonus rufipes (De Geer)	m	a	13.8	135	13
Pseudoophonus calceatus (Duftshmid)	m	a	12.6	1	1
Pterostichus antracinus (Illiger)	d	s	11	370	10
Pterostichus aterrimus (Herbst)	m	s	13.9	3	1
Pterostichus diligens (Sturm)	d	s	5.7	67	13
Pterostichus gracilis Dejean)	m	s	8.9	1	1
Pterostichus longicollis (Duftschmid)	m	?	6	2	1
Pterostichus melanarius (Illiger)	d	a	15.7	3624	15
Pterostichus minor (Gyllenhal)	d	s	7.4	120	10
Pterostichus niger (Schaller)	m	a	18.5	1166	7
Pterostichus nigrita (Paykull)	m	s	11	274	13
Pterostichus oblongopunctatus (Fabricius)	m	s	11.4	1802	15
Pterostichus strennus (Panzer)	d	s	6.1	216	15
Pterostichus vernalis (Panzer)	m	s	6.7	33	6
Stenolophus mixtus (Herbst)	m	s	5.9	1	1
Stomis pumicatus (Panzer)	b	s	6.9	76	8
Synuchus vivalis (Illiger)	d	a	7.4	145	12
Trechus sp.	m	?		1	1

Table 2. The study sites. Area in ha, observed species numbers (Sobs), rarefied species numbers (rarefied S and its standard deviation) based on total catches, estimated species numbers using the jackknife I and II estimators, and the total number of individuals sampled per site.

Study site	Area (ha)	No. of traps	Sobs	Rarefied S	SD	Sexp		Individuals
						Jackknife I	Jackknife II	
Sosnowy Ostrów	20.09	21	31	45	3	35	34	1704
Gilma	9.9	15	40	46	3	48	54	1895
Dębowa Górka	6.84	9	25	33	2	29	31	505
Lipka	4.19	9	30	43	3	34	34	1410
Wyspa Kormoranów	2.3	9	23	52	3	26	29	3450
Poganackie Kępy III	2.1	6	25	26	2	30	31	206
Switalowy Ostrów	2.08	3	14	20	2	17	18	91
Ilmy Wielkie	1	3	24	30	2	29	32	342
Wyspa Helena	0.92	6	19	30	2	23	25	325
Poganackie Kępy II	0.9	3	18	23	2	22	24	149
Mala Ilma	0.2	3	23	38	3	28	29	829
Kępa Wronia N	0.15	2	16	24	2	19	19	160
Kępa Wronia S	0.15	2	13	20	2	16	16	98
Terra Dobia	0.03	2	16	21	2	19	19	102
Poganackie Kępy I	0.01	2	10	16	2	13	13	55
Main land I		6	29	39	3	34	37	996
Main land II		6	20	33	2	24	27	476
Total		107	71			88	97	12793

$p < 0.05$ for single comparisons). The constancy of this pattern among the study sites strongly calls for an ecological explanation. Meanwhile, the body size distributions of the other species (those occurring in at most seven study sites) did not deviate from the null expectation.



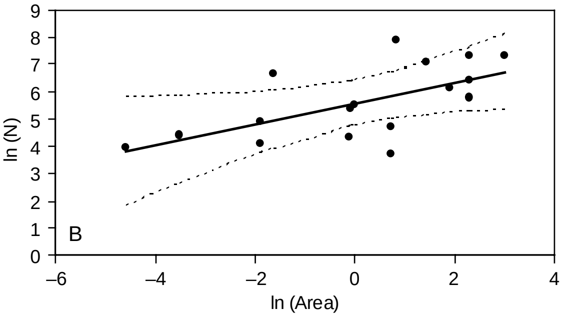


Fig. 1. Species–area (A) and individuals–area (B) relationships of ground beetles on the 15 island sites studied. A: $S = 20.6A^{0.13}$; $R^2 = 0.62$, $p < 0.01$. B: $N = 267.3A^{0.38}$; $R^2 = 0.38$, $p < 0.01$. Note that values are ln-transformed. Given are also 95% confidence limits.

Discussion

The present study shows for the first time how species abundance distributions are related to patterns of co-occurrences and the distinction into core and satellite species. By this we link important aspects of regional community structure. It seems that our core species represent rather the classical community type in which niche division processes result in lognormal type species abundance distributions (May 1975, Sugihara 1980, Connolly et al. 2005). In such communities competition could lead to non-random patterns of co-occurrence according to some assembly rules (Diamond 1975, Gotelli and Graves 1996, Weiher and Keddy 1999), and to non-random patterns of resource allocation which manifest in certain body size distributions (Hutchinson 1959, Gotelli and Graves 1996, Siemann and Brown 1999). Indeed, our results link the lognormal SAD with spatial underdispersion (as measured by the

Fig. 2. Numbers of ground beetle species per binary occupancy class (number of study sites occupied: 1, 2, 3 to 4, 5 to 8, 9 to 17). The distribution is significantly bimodal ($p < 0.01$).

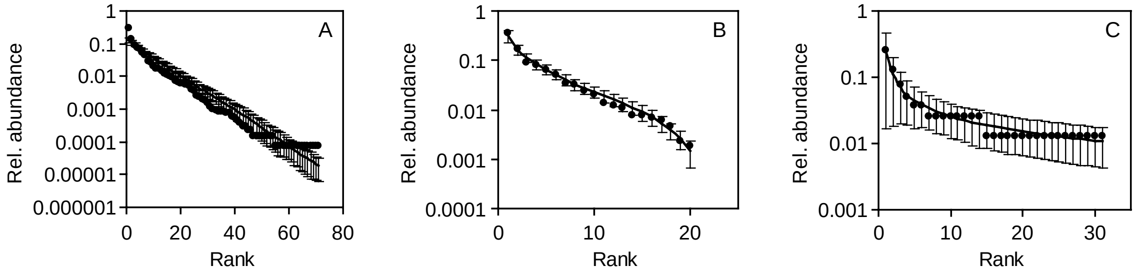


Fig. 3. (A) Abundance–rank order (Whittaker) plot of all ground beetle species sampled (metacommunity SAD). 63% of all species abundances range outside the 95% confidence limit of the best fit model, the random assortment (the fits of the log-normal and the power function model are not shown). (B) The SAD of core species is best fitted by a log-normal distribution. (C) The satellite species are best fitted by a power function model. In (B) and (C) all species abundances range inside the 95% confidence limit of the respective model.

C-score, Table 3) and more regular size distributions with respect to the null model used (Fig. 6). Additionally, we found that flight ability is not randomly distributed across the core and the satellite species (Table 4). However, whether these non-random patterns have to be related to competitive interactions or to other, for instance stochastic, processes (Ulrich 2004a, 2004b, Bell 2005) remains an open question. Ground beetle communities are generally viewed as being not shaped by competition (Loreau 1990, 1992, Niemelä 1993). Under this premise we might speculate that differences in dispersal ability between core and satellite species are responsible for the observed differences. Our satellite species seem to represent a more dynamic assemblage, chiefly structured by dispersal as judged from the low percentage of morphologically dispersal limited species (Table 4). It is no wonder that these species did not show significant non-random patterns of co-occurrence (Table 3) and body size distributions (Fig. 6).

There has been some discussion about the shape of SADs under the influence of dispersal. In their classic paper Fisher et al. (1943) derived the log-series distribution under a random sample assumption that leads to a Poisson distribution of species turnover. If Poisson processes governed local species turnover rates and abundances, the variance-mean ratio should be approximately 1 ($\sigma^2 \sim \mu$). However, temporal and spatial variability follows, at least in insects, more often Taylor's power law (a pattern of proportional rescaling) with $\sigma^2 \sim \mu^z$ and z being around 2 (Taylor 1961, Taylor et al. 1980, Kilpatrick and Ives 2003). Magurran and Henderson (2003) used the variance–mean ratio to test whether their satellite fish assemblages follow log-series and found z-values around 1 in accordance with a Poisson distribution. Instead, both, the core and the satellite species of the present study closely follow Taylor's power law (core species: $z = 2.33 \pm 0.11$, $R^2 = 0.96$, $p < 0.001$; satellite species: $z = 2.29 \pm 0.09$, $R^2 = 0.95$, $p < 0.001$). Both z-values are even higher than the proportional rescaling value of 2.0. From this we conclude that neither the core nor the satellite species follow Poisson dispersal patterns. Instead we have to assume that spatial patterns of variability are in accordance with Taylor's power law. How Taylor's power law translates into relative abundance distributions has, as far as we know, not been studied although the results of Banavar et al. (1999) indicate that Taylor's power law is consistent with the assumption of self-similar spatial distributions and therefore with a power function SAD. However, the fact that both the core and the satellite species have very similar variance–mean ratios despite their different SADs does not point to a simple translation mechanism. Nevertheless, it seems not probable that core and satellite species under the regime of Taylor's power law will exhibit log-series SADs.

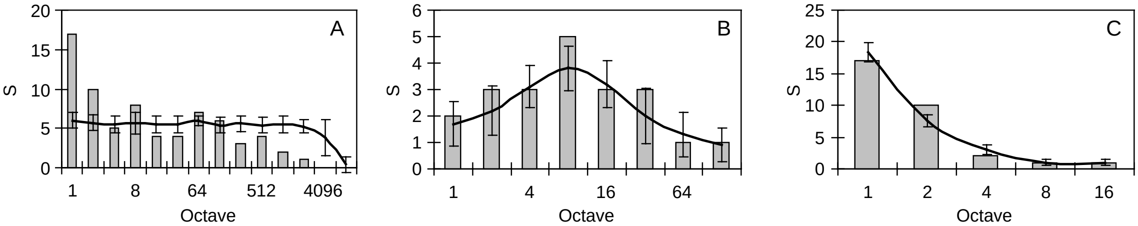


Fig. 4. (A) Species number–octave (Preston) plot of all ground beetle species sampled (metacommunity SAD). The best fit model (black line), the random assortment significantly deviates from the observation ($p(\chi^2) < 0.0001$) (the fits of the log-normal and the power function model are not shown). (B) The core species are well fitted by a log-normal distribution ($p(\chi^2) > 0.5$). (C) The satellite species are best fitted by a power function model ($p(\chi^2) > 0.5$).

Table 3. C-scores, V-scores, and species combination scores of core and satellite species of the 17 study sites. Higher values for C-scores indicate underdispersion of species, V-scores show whether SADs differ between sites: similar SAD ($V > 0$); dissimilar SAD ($V < 0$). Note that all these scores are Z-transformed values that should have a mean of 0 and a variance of 1 for random matrices. The scores of the abundance based simulations refer to the 200 random matrices generated from the observed frequency distributions of species described in the text.

	Observed values		Abundance based simulations						Abundance based variance test V-score
	C-score	Species combination score	C-score			Species combination score			
			Mean	SD	Skewness	Mean	SD	Skewness	
Core	6.499	0.499	−0.141	0.707	0.952	0.001	0.654	−0.399	13.69
Satellite	−0.36	0.298	0.078	0.919	0.592	0.012	0.857	−2.928	−2.51

The occurrence of power function SADs has been attributed to self-similar patterns of species spatial or temporal distribution (Moulliot et al. 2000, Magurran and Henderson 2003, Ulrich and Ollik 2004) although the original work of Harte et al. (1999) does not explicitly refer to this point. Indeed, in a recent paper Harte et al. (2005) showed that non-self-similar species spatial distribution patterns may also lead to power function species–area relationships and to power function SADs for the species in the tail of the Whittaker plot. These are exactly the satellite species defined in the present study.

The occurrence of core and satellite species in ecological assemblages has been attributed as being a pure statistical artefact (Nee et al. 1991a, Novotny and Drozd 2001). Indeed, in a forthcoming study (W. Ulrich and M. Zalewski, unpubl.) we will show that random draws from the overall species pool resulted also in core – satellite patterns but in any case with more core species than observed. However, random draws could not explain the observed SARs, SADs, and patterns of co-occurrence. This finding is similar to the results of Dolman and Blackburn (2004) on British birds. Storch and Šizling (2002) and Selmi and Boulinier (2004) also rejected the random draw hypothesis to explain spatial distribution patterns of bird communities. Indeed a simple random draw should generate a random spatial distribution irrespective of whether a species is satellite or core. The present results instead show that core and satellite species differ in patterns of spatial distribution and body size ratios. These findings strongly call for a biological interpretation instead of a purely statistical one.

However, we should mention that the above picture is not as unequivocal as it seems. The first cautionary note refers to the observed body size distributions. None of the single study site size distributions of the core species did significantly (at $p < 0.05$) deviate from a random pattern although it is highly improbable that all sites deviate from the expectation in the same way. Such a consistent deviation might stem from a systematic bias in the null model. However, such a bias should be visible for the satellite species too. Of importance is the difference between core and satellite species with respect to size distributions using the same null model. It is also possible that the observed difference in size ratio distributions between core and satellite species stems from non-independence of data due to phylogenetic constraints (Knouft 2003, Butler and King 2004). A selective sampling of core and satellite species should be evident in different species per genus (S/G) ratios. We tested for this by comparing the observed S/G ratios with the expectation obtained from 1000 random samples of 20 and 31 species, respectively, out of the total pool. The S/G ratios of both groups did not deviate from the random expectation (core species: $S/G = 1.54 \pm 1.59$; satellite species: $S/G = 1.72 \pm 0.99$; null model: $S/G = 1.41 \pm 0.18$).

Secondly, the C- and the V-score statistics that measure co-occurrence gave contrasting results while

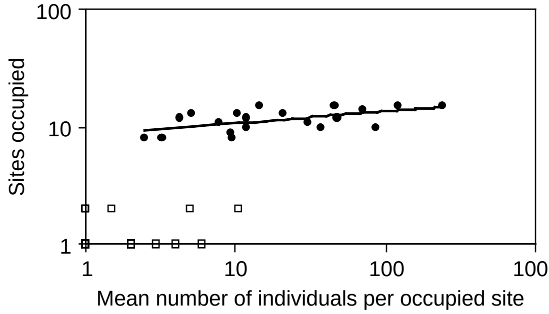


Fig. 5. The number of sites occupied in dependence on the mean number of individuals trapped per site. Black dots: core species. Regression: $I = 8.2\ N^{0.11}$; $R^2 = 0.38$; $p(t) < 0.01$. Open squares: satellite species.

Table 4. Core and satellite species: numbers of macropterous, brachypterous and dimorphic species and of autumn breeders, spring breeders and species of unknown or complex life cycles. Flight ability is not randomly distributed across core and satellite species: $p(\chi^2) = 0.01$.

Type	Core	Satellite
Brachypterous	3	3
Dimorphic	9	3
Macropterous	8	25
Spring breeders	11	15
Autumn breeders	6	7
Complex	3	9

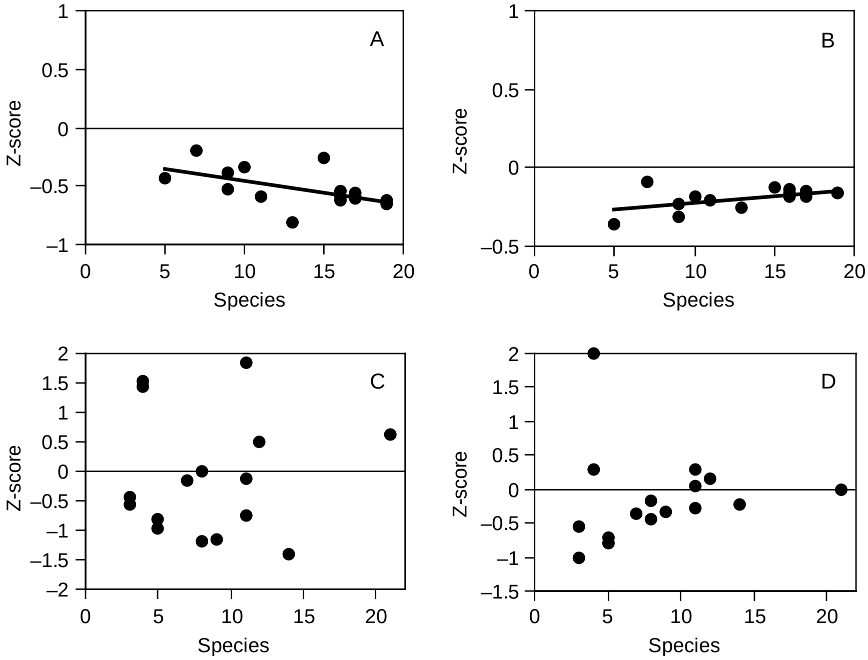


Fig. 6. Size ratio tests: Z-scores of the variance test (A, C) and the ratio test (B, D) for core species (A, B) and all other species (C, D) in dependence of the respective species numbers per study site. Note that we used all non-core species instead of the satellite species to avoid a possible bias due to too low species numbers and to have species numbers that are comparable to those of the core species.

the species combination score was for core and for satellite species insignificant. Gotelli and McCabe (2002) reported a similar pattern in their meta-analysis. The C-score is based on average co-occurrences (Gotelli 2000), whereas the species combination score is based on absolute counts of unique species combinatons. Gotelli (2000), Gotelli and McCabe (2002), and Ulrich (2004a) showed already that these measures are only weakly correlated and measure different aspects of co-occurrence and species assembly. Further, we computed the V-score that measures similarities in abundances between sites using relative abundances to account for differences in total sampling due to unequal sample sizes. Nevertheless, the score gave a strong signal towards common trends in abundance and similarities of the SADs across the sites.

An interesting side effect of the present study is the difference between core and satellite species with respect to the interspecific abundance–occupancy relationship (AOR). The core species showed a strong positive correlation between local abundance and regional occupancy (Fig. 5) as predicted by current theory (Hanski 1999, Gaston and Blackburn 2000, Kotze et al. 2003). That we could not observe this pattern in the satellite species might indicate that the assumed mass effect responsible for the AOR pattern (Hanski 1999, Bell 2001, Hubbell 2001) is too weak for locally rare species to generate a positive AOR.

Lastly, the present results might have implications for the current discussion about neutral macroecological models (Bell 2001, Hubbell 2001, Ulrich 2004b). Although we did not aim to test these models explicitly, we feel that the above described differences between core and satellite species call for a rethinking as to what these classes of models refer. Current neutral models refer to biologically indistinguishable lineages of similar trophic position. This contrasts with the differences in flight ability between core and satellite species (Table 4) although the members of both groups are apparently similar with respect to resource usage. Despite the fact that neutrality is able to generate non-random patterns of species co-occurrence (Ulrich 2004a, Bell 2005) it is not clear under what types of metacommunity structure and speciation regimes this is possible. It remains to be shown whether neutral models are able to generate lognormal types of SADs and non-randomness in co-occurrence (Bell 2005). It is therefore tempting to refer neutral models in particular to satellite species, where apparently dispersal plays a major role.

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References

Azeria, E. T. 2004. Community dynamics of insular biotas in space and time. – Thesis, Univ. Uppsala, Sweden.

Banavar, J. R., Green, J. L., Harte, J. et al. 1999. Finite size scaling in ecology. – Phys. Rev. Lett. 83: 4212–4214.

Bell, G. 2001. Neutral macroecology. – Science 293: 2413–2418.

Bell, G. 2005. The co-distribution of species in relation to the neutral theory of community ecology. – Ecology 86: 1757–1770.

Brose, U., Martinez, N. D. and Williams, R. J. 2003. Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. – Ecology 84: 2364–2377.

Burnham, K. P. and Overton, W. S. 1978. Estimation of the size of a closed population when capture probabilities vary among animals. – Biometrika 65: 623–633.

Butler, M. A. and King, A. A. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. – Am. Nat. 164: 683–695.

Connolly, S. R., Hughes, T. P., Bellwood, D. R. et al. 2005. Community structure of corals and reef fishes at multiple scales. – Science 309: 1363–1365.

Connor, E. F. and Simberloff, D. 1979. The assembly of species communities: chance or competition. – Ecology 60: 1132–1140.

Den Boer, J. P., van Huizen, T. H. P., den Boer-Daanje, W. et al. 1980. Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera, Carabidae). – Entomol. Genet. 6: 107–134.

Diamond, J. M. 1975. Assembly of species communities. – In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities. Harvard Univ. Press, pp. 342–444.

Digweed, S. C., Currie, C. R., Carcamo, H. A. et al. 1995. Digging out the 'digging – in effect' of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Col., Carabidae). – Pedobiol. 39: 561–576.

Dolman, A. M. and Blackburn, T. M. 2004. A comparison of random draw and locally neutral models for the avifauna of an English woodland. – BMC Biol. 4: 8.

Fesl, C. 2002. Niche-orientated species-abundance models: different approaches of their application to larval chironomid (Diptera) assemblages in a large river. – J. Anim. Ecol. 71: 1085–1094.

Fisher, A. G., Corbet, S. A. and Williams, S. A. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. – J. Anim. Ecol. 12: 42–58.

Gaston, K. J. 1994. Rarity. – Chapman and Hall.

Gaston, K. J. and Blackburn, T. M. 2000. Pattern and process in macroecology. – Blackwell.

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

Gotelli, N. J. 2001. Research frontiers in null model analysis. – Global Ecol. Biogeogr. Lett. 10: 337–343.

Gotelli, N. J. and Graves, G. R. 1996. Null models in ecology. – Smiths. Inst. Press.

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

Gotelli, N. J. and Entsminger, G. L. 2005. EcoSim: null models software for ecology. Version 7.72. – Acquired Intelligence Inc. & Kesey-Bear.

Guo, Q., Brown, J. H. and Valone, R. J. 2000. Abundance and distribution of desert annuals: are spatial and temporal patterns related? – J. Ecol. 88: 551–560.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. – Oikos 38: 210–221.

Hanski, I. 1994. A practical model of metapopulation dynamics. – J. Anim. Ecol. 63: 151–162.

Hanski, I. 1999. Metapopulation ecology. – Oxford Univ. Press.

Hanski, I. and Gyllenberg, M. 1993. Two general metapopulation models and the core-satellite species hypothesis. – Am. Nat. 142: 17–41.

Harte, J., Kinzig, A. P. and Green, J. 1999. Self-similarity in the distribution and abundance of species. – Science 284: 334–336.

Harte, J., Conlisk, E., Ostling, A. et al. 2005. A theory of spatial-abundance and species-abundance distributions in ecological communities at multiple spatial scales. – Ecol. Monogr. 75: 179–197.

Heck, K. L., van Belle, G. and Simberloff, D. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. – Ecology 56: 1459–1461.

Hubbell, S. P. 2001. The unified theory of biogeography and biodiversity. – Princeton Univ. Press.

Hürka, K. 1996. Carabidae of the Czech and the Slovak Republics. – Karabourek.

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

Kilpatrick, A. M. and Ives, A. R. 2003. Species interactions can explain Taylor's power law for ecological time series. – Nature 422: 65–68.

Knouft, J. H. 2003. Convergence, divergence, and the effect of congeners on body size ratios in stream fishes. – Evolution 57: 2374–2382.

Kotze, D. J., Niemelä, J., O'Hara, R. B. et al. 2003. Testing abundance-range size relationships in European carabid beetles (Coleoptera: Carabidae). – Ecography 26: 553–566.

Krebs, C. J. 1989. Ecological methodology. – Harper Collins.

Kunin, W. E. and Gaston, K. J. (eds) 1997. The biology of rarity. – Chapman and Hall.

Lindroth, C. H. 1985. The Carabidae (Col.) of Fennoscandia and Denmark. – Fauna Entomologica Scandinavica, Scand. Sci. Press.

Loreau, M. 1990. Competition in a carabid beetle community. – Oikos 58: 25–38.

Loreau, M. 1992. Spcies abundance patterns and the structure of ground beetle communities. – Ann. Zool. Fenn. 28: 49–56.

Magurran, A. E. 2004. Measuring biological diversity. – Blackwell.

Magurran, A. E. and Henderson, P. A. 2003. Explaining the excess of rare species in natural species abundance distributions. – Nature 422: 714–716.

May, R. M. 1975. Patterns of species abundance and diversity. – In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities. Belknap, pp. 81–120.

McGeoch, M. A. and Gaston, K. J. 2002. Occupancy frequency distributions: patterns, artefacts and mechanisms. – Biol. Rev. Cambr. Philos. Soc. 77: 311–331.

McGill, B. J. 2003. Does Mother Nature really prefer rare species or are log-left-skewed SADs a sampling artefact? – Ecol. Lett. 6: 766–773.

Miklós, I. and Podani, J. 2004. Randomization of presence – absence matrices: comments and new algorithms. – Ecology 85: 86–92.

Moulliot, D., Lepretre, A., Andrei-Ruiz, M. C. et al. 2000. The fractal model: a new model to describe the species accumulation process and relative abundance distribution (RAD). – Oikos 90: 333–342.

Nee, S., Gregory, R. D. and May, R. M. 1991a. Core and satellite species: theory and artefacts. – Oikos 62: 83–87.

Nee, S., Harvey, P. H. and May, R. M. 1991b. Lifting the veil on abundance patterns. – Proc. R. Soc. Lond. B 243: 161–163.

Niemelä, J. 1993. Interspecific competition in ground beetle assemblages (Carabidae): what have we learned? – Oikos 66: 325–335.

Novotny, V. and Drozd, P. 2001. Sampling error can cause false rejection of the core-satellite species hypothesis. – Oecologia 126: 360–362.

Peres-Neto, P. R. 2004. Patterns in the co-occurrence of fish species in streams: the role of site suitability, morphology and phylogeny versus species interactions. – Oecologia 140: 352–360.

Pielou, D. P. and Pielou, E. C. 1968. Association among species of infrequent occurrence: the insect and spider fauna of *Polyporus betulinus* (Bulliard) Fries. – J. Theor. Biol. 21: 202–216.

Preston, F. W. 1962. The canonical distribution of commonness and rarity. Part I and II. – Ecology : 185–215 43: 410–432.

Sanderson, J. G., Moulton, M. P. and Selfridge, R. G. 1998. Null matrices and the analysis of species co-occurrences. – Oecologia 116: 275–283.

Schluter, D. 1984. A variance test for detecting species associations, with some example applications. – Ecology 65: 998–1005.

Selmi, S. and Boulinier, T. 2004. Distribution-abundance relationship for passerines breeding in Tunisian oases: test of the sampling hypothesis. – Oecologia 139: 440–445.

Siemann, E. and Brown, J. H. 1999. Gaps in mammalian body size distributions re-examined. – Ecology 80: 2788–2792.

Simberloff, D. S. and Boecklen, W. 1981. Santa Rosalia reconsidered: size ratios and competition. – Evolution 35: 1206–1228.

Solé, R. and Alonso, D. 1998. Random walks, fractals and the origins of rainforest diversity. – Adv. Complex Syst. E 62: 8466–8484.

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

Storch, D. and Šizling, A. 2002. Patterns of commonness and rarity in Central European birds: reliability of the core-satellite hypothesis within a large scale. – Ecography 25: 405–416.

Sugihara, G. 1980. Minimal community structure: an explanation of species abundance patterns. – Am. Nat. 116: 770–787.

Taylor, L. R. 1961. Aggregation, variance and the mean. – Nature 332: 721–722.

Taylor, L. R., Woiwod, I. P. and Perry, J. N. 1980. Variance and the large scale spatial stability of aphids, moths and birds. – J. Anim. Ecol. 49: 831–854.

Tokeshi, M. 1990. Niche apportionment or random assortment: species abundance patterns revisited. – J. Anim. Ecol. 59: 1129–1146.

Tokeshi, M. 1992. Dynamics and distribution in animal communities; theory and analysis. – Res. Popul. Ecol. 34: 249–273.

Tokeshi, M. 1999. Species coexistence. – Blackwell.

Ulrich, W. 2002. RAD – a FORTRAN program for the study of relative abundance distributions. – www.uni.torun.pl/~ulrichw.

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

Ulrich, W. 2004b. Neutral macroecology – ecology without biology? – Ecol. Quest. 4: 113–126.

Ulrich, W. 2005a. ComStruc – a FORTRAN program for comparing ecological communities. – www.uni.torun.pl/~ulrichw.

Ulrich, W. 2005b. Structure – a FORTRAN program for ecological pattern analysis. – www.uni.torun.pl/~ulrichw.

Ulrich, W. and Ollik, M. 2004. Frequent and occasional species and the shape of relative abundance distributions. – Div. Distr. 10: 263–269.

Weiher, E. and Keddy, P. A. (eds) 1999. Ecological assembly rules: perspectives, advances, retreats. – Cambridge Univ. Press.

Zalewski, M. 2000. Colonization, extinction and species richness of ground beetles (Carabidae, Coleoptera) on Islands of Mazurian lakes. – Thesis.

Zalewski, M. 2004. Do smaller islands host younger populations? A case study on metapopulations of three carabid species. – J. Biogeogr. 31: 1139–1148.