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BIODIVERSITY RESEARCH

Dispersal as a key element of community structure: the case of ground beetles on lake islands

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ABSTRACT

In order to study the influence of dispersal ability on community structure of ground beetles (carabidae), 15 lake islands and 2 mainland sites of the lake Mamry archipelago, northern Poland, were sampled by using pitfall traps. Of the 71 ground beetle species detected, 47 were macropterous, 16 wing-dimorphic and 8 brachypterous. Macropterous species had lower site abundances and occupied fewer sites than dimorphic and brachypterous species. There were trends from macropterous to brachypterous species towards a nested distribution across the sites and towards over-dispersed (aggregated) species co-occurrences. Canonical correspondence analysis pointed to site isolation and area as main factors influencing site abundance and spatial distribution. Our results imply that further studies on species co-occurrences and community assembly have to consider dispersal ability as a key element influencing ecological distributions at the regional scale.

Keywords

Carabidae, wing polymorphism, abundance, species–area relationship, co-occurrences, nestedness.

INTRODUCTION

Many studies have revealed correlations between local population density and regional distribution (the abundance–range size relationship, ARR, cf. Gaston, 1996; Gaston & Blackburn, 2000). One factor generally believed to influence range sizes is dispersal ability (Hanski *et al*., 1993). The question of how dispersal ability shapes the structure of animal communities has been widely discussed and is one of the major themes of macroecology (Brown, 1995; Blackburn & Gaston, 2003), metapopulation ecology (Hanski, 1999) and the discussion around neutral models (Hubbell, 2001, 2005; Chave, 2004; Ulrich, 2004a).

Dispersal ability has been linked to local and regional abundance, particularly to rarity (understood as low abundance) (Gaston, 1994; Kunin & Gaston, 1997). However, critical assessments about the influence of dispersal ability on regional and local community structure are surprisingly scarce. Morse *et al.* (1988) argued for higher frequencies of rarity in species with high mobility, because they might be able to mate and reproduce at comparably low abundance. For butterflies, Cowley *et al.* (2001) showed that more dispersive species had lower mean abundances and were less aggregated because of their migration into less suitable habitats. Such a pattern has been predicted by the aggregation hypothesis of Hartley (1998), developed to explain the positive ARR relationship (Gaston, 1996). In line with this theory, Cowley *et al.* (2001) did not find a significant ARR for weak dispersers, which might be a more widespread phenomenon (Lesica *et al*., 2006).

A second major ecological distribution that is influenced by dispersal is the well-known species–area relationship (SAR). Island biogeography (MacArthur & Wilson, 1967) and metapopulation (Levins, 1969; Hanski, 1999) theory predict local extinction and colonization to be major drivers of species numbers. Species numbers per site should be correlated with dispersal ability and local survival rates and the relationships cause SAR slopes (when using the power function model) to be steeper in less dispersive species (Rosenzweig, 1995; Hovestadt *et al*., 2005).

Third, dispersal ability should influence patterns of co-occurrences. A lower than randomly expected number of co-occurrences of species (underdispersion) has been linked to sites with higher colonization rates (Badano *et al*., 2005). On the contrary, high rates of colonization with respect to local persistence should randomize the faunal composition and cause random patterns of species co-occurrences. However, direct tests of whether and how dispersal ability influences patterns of species co-occurrences are largely missing. Azeria (2004) reported higher numbers of co-occurrences of species (over-dispersion) at medium rates of colonization and local extinction. The study suggests therefore a trade-off between colonization rates and local persistence to influence species co-occurrence.

Ground beetles are particularly suited for studying the influence of dispersal on local community structure because they can be

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divided into groups of winged and wingless species, which differ from each other with respect to dispersal ability (Niemelä, 1988; Den Boer, 1990). Furthermore, most communities contain wing-dimorphic (hereafter dimorphic) species, in which only a part of the population is fully winged. These species exhibit an intermediate dispersal strategy. Flight, and therefore dispersal, ability depends also on other factors, like the development of thoracic muscles (Nelemans, 1987; Den Boer, 1990), although wing size seems to be the best predictor when comparing the dispersal abilities of different carabid species (Den Boer *et al.*, 1980; Gutiérrez & Menéndez, 1997; Gutiérrez *et al.*, 2004; Zalewski, 2004).

The present paper aims at studying whether and how dispersal ability influences patterns of regional distribution, SARs and species co-occurrence. We use data from a 2-year survey of ground beetles on small lake islands in northern Poland (Ulrich & Zalewski, 2006) and show that macropterous, dimorphic and brachypterous species differ in patterns of spatial distribution and co-occurrences.

METHODS

Fifteen 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). Between 3 (on the smallest site only two) and 21 traps were used per site, depending on its habitat diversity and size making up a total of 107 traps. Habitat diversity was assessed according to existing maps and from a survey of soil types. As recommended by Krebs (1989) and Digweed *et al.* (1995), a single main line crossing all habitats of an island was chosen. From this line, perpendicular trap lines were placed (trap distance 25 m). Traps operated from June to September 1997 and 1998 and were emptied monthly and refilled with fresh glycol (Zalewski, 2000; Ulrich & Zalewski, 2006).

All carabid species except the genus *Europhilus* were identified to species level using the keys of Hürka (1996) and Lindroth (1985) (Table 1). Nomenclature follows Hürka (1996). Life history and morphological characteristics are based on Den Boer *et al.* (1980), Lindroth (1985) and Hürka (1996). In particular, we classified species into macropterous (always possessing wings), dimorphic (only part of the population being fully winged), and brachypterous (wingless).

To assess differences of beetle occurrences among sites, we measured the site area and the degree of isolation (distance from nearest mainland). Mean temperature, soil humidity, pH, soil fertility (rich/poor in minerals) and organic material content were assessed using the plant habitat indices of Ellenberg (1979) and Zarzycki *et al.* (2002) calculated from floristic samples of 100 m^2 around each trap.

Bivariate and multivariate comparisons from multi-species assemblages might be influenced by non-independence of data points as a result of phylogenetic constraints (Felsenstein, 2004). There is still no unequivocal phylogenetic system of ground beetles available (Madison *et al.*, 1999) and subfamily and tribe relationships are not well resolved. Hence, we were unable to compute phylogenetic contrasts at the genus level (Felsenstein, 2004). To account at least in part for this possible source of errors, we computed bivariate comparisons and ARRs twice, once using species values and once using genus means. Because of the low number of data points for brachypterous species, we were unable to use genus means for these species.

We used the canonical correspondence analysis (CCA) to refer beetle occurrences to the previously mentioned site characteristics. To account for possible inhomogeneities in the data structure, we used ranked values for all parameters and abundances. Ordination scores were scaled via the optimize species option implemented in PC-ORD version 4.2 (McCune & Mefford, 1999). Significances were inferred by Monte Carlo simulation, assuming no structure in the main matrix. For CCA, assuming unimodal response curves, we first checked for appropriateness by performing a detrended correspondence analysis that provides estimates of axis lengths. The length of our first axis (1.89) was above the minimum length of 1.5 recommended by ter Braak & Prentice (1988) for applying CCA.

We used C-scores (Stone & Roberts, 1990) and species combination scores (Pielou & Pielou, 1968) to study species co-occurrence patterns of presence–absence matrices. The C-score measures mean matrix-wide underdispersion (segregation) between sites (checkerboard patterns), the species combination score by contrast screens for unique species combinations (Gotelli & McCabe, 2002). Both scores therefore measure different aspects of co-occurrence (Gotelli & McCabe, 2002). Standardized scores are Z-transformed and should have a mean of 0 and a standard deviation of 1. Significant species under-dispersion or over-dispersion, 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 & Entsminger, 2005). We used fixed sum row and column constraints and the sequential swap algorithm for randomization as advocated by Gotelli (2000) for the study of island data.

To account for possible sampling errors and bias introduced by the swap algorithm (Sanderson *et al.*, 1998; Gotelli, 2001; Miklós & Podani, 2004; Peres-Neto, 2004), we constructed 200 random matrices each for the macropterous, the dimorphic and the brachypterous 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 previously mentioned 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 random expectation. To correct for differences in site suitability that might result in species over-dispersion on larger and more suitable sites, we used species-relative abundances per site (n_i/N; N being the total catch

Table 1 Carabid species sampled at the 17 study sites

Species	Wing development	Individuals	Occurrences
Agonum duftschmidi Schmidt	m	4	3
Agonum lugens (Duftschmid)	m	12	7
Amara aulica (Panzer)	m	1	1
Amara brunea (Gyllenhal)	m	84	9
Amara communis (Panzer)	m	32	6
Amara plebeja (Gyllenhal)	m	13	5
Amblystomus sp.	m	1	1
Anisodatylus binotatus (Fabricius)	m	2	1
Badister bullatus (Schrank)	m	26	8
Badister dorsiger (Duftschmid)	m	1	1
Badister sodalis (Duftschmid)	m	8	4
Badister unipustulatus Bonelli	m	11	4
Bembidion articulatum (Panzer)	m	1	1
Bembidion doris (Panzer)	m	1	1
Bembidion sp.	m	1	1
Calathus fuscipes (Goeze)	b	6	1
Calathus melanocephalus (Linnaeus)	d	5	4
Calathus micropterus (Duftschmid)	b	79	2
Calathus mollis (Marsham)	d	10	2
Carabus cancelatus Illiger	b	1	1
Carabus granulatus Linneus	d	684	15
Carabus hortensis Linnaeus	b	236	3
Carabus nemoralis Muller	b	85	11
Chlaenius nigricornis (Fabricius)	m	1	1
Clivina collaris (Herbst)	m	2	1
Clivina fossor (Linnaeus)	d	11	7
Dyschirius globosus (Herbst)	d	4	1
Dyschirius sp.	m	2	1
Epaphius secalis (Paykull)	b	169	7
Harpalus 4-punctatus Dejean	m	879	10
Harpalus froelichi Sturm	m	1	1
Harpalus latus (Linnaeus)	m	47	7
Harpalus rufipalpis Sturm	m	1	1
Harpalus solitaris Dejean	m	2	2
Harpalus xanthopus winkleri Schauberger	m	11	3
Lasoitrechus discus (Fabricius)	m	2	2
Leistus ferrugineus (Linnaeus)	d	1	1
Leistus rufomarginatus (Duftschmid)	d	99	6
Leistus terminatus (Hellwig)	m	51	12
Loricera pilicornis (Fabricius)	m	16	6
Nebria brevicollis (Fabricius)	m	189	5
Notiophilus biguttatus (Fabricius)	d	7	5
Notiophilus palustris (Duftschmid)	d	20	8
Oodes gracilis A_Villa & G_B_Villa	m	10	6
Oodes helopioides (Fabricius)	m	24	5
Oxypselaphus obscurus (Herbst)	d	986	14
Panagaeus cruxmajor (Linnaeus)	m	1	1
Paranchus albipes (Fabricius)	m	2	1
Patrobus atrorufus (Stroem)	b	571	12
Phonus sp.	m	1	1
Platynus assimilis (Paykull)	m	337	11
Poecilus cupreus (Linnaeus)	m	3	2
Poecilus versicolor (Sturm)	m	2	1
Pseudoophonus rufipes (De Geer)	m	135	13
Pseudoophonus calceatus (Duftschmid)	m	1	1
Pterostichus antracinus (Illiger)	d	370	10

Table 1 *continued*

Species	Wing development	Individuals	Occurrences
Pterostichus aterrimus (Herbst)	m	3	1
Pterostichus diligens (Sturm)	d	67	13
Pterostichus gracilis Dejean)	m	1	1
Pterostichus longicollis (Duftschmid)	m	2	1
Pterostichus melanarius (Illiger)	d	3624	15
Pterostichus minor (Gyllenhal)	d	120	10
Pterostichus niger (Schaller)	m	1166	7
Pterostichus nigrita (Paykull)	m	274	13
Pterostichus oblongopunctatus (Fabricius)	m	1802	15
Pterostichus strennus (Panzer)	d	216	15
Pterostichus vernalis (Panzer)	m	33	6
Stenolophus mixtus (Herbst)	m	1	1
Stomis pumicatus (Panzer)	b	76	8
Synuchus vivalis (Illiger)	d	145	12
Trechus sp.	m	1	1

Abbreviations: Wing development: m: macropterous; b: brachypterous; d: dimorphic. Occurrences refer to the number of study sites occupied.

per site) instead of absolute captures. In essence, the test used in this way is a matrix-wide measure whether species rank orders between sites are similar (V-score > 0) or dissimilar (V-score < 0) (Ulrich, 2005; Ulrich & Zalewski, 2006). Null model index values and standard deviations where computed from 1000 random matrices using the program COMSTRUC (Ulrich, 2005; sequential swap algorithm, equiprobable row and column constraints).

We assessed differences in species composition and idiosyncratic species and sites from a nestedness analysis (using the nestedness temperature calculator: Atmar & Patterson, 1995; Patterson & Atmar, 2000) that measures whether the faunal composition of different study sites form perfect subsamples from a larger common species pool (a nested pattern) or whether local peculiarities occur.

We estimated species richness with the incidence-based Jackknife I and the abundance based Chao I estimators (implemented in EstimateS, Colwell, 2004). Standard statistical analyses were carried out using STATISTICA version 7.0 (StatSoft, 2005). Regressions were in all cases computed with the nonlinear estimation module of this program using standard least squares. Errors refer always to standard errors.

RESULTS

Overall, 71 species were found at the 17 study sites (Table 1). The two estimators of species richness pointed to a total of 85–90 species (Table 2). Hence, about 80% of the estimated total ground beetle fauna was trapped. Sample covers per site varied between 77% and 89% of the estimated number of species (Table 2).

Forty-seven of the species were macropterous, 16 dimorphic and 8 brachypterous (Table 1). These three groups differed in mean site abundance and occupancy. Macropterous species had a mean site abundance (individuals per species per trap) of 1.6 ± 0.5 individuals, dimorphic species reached 4.7 ± 2.1 individuals, and the brachypterous species 4.4 ± 1.5 individuals. After classifying into $\log_2$ occurrence classes (Fig. 1), contrary trends for macropterous and dimorphic species appeared. Twenty-two of the 47 macropterous species were found at only a single site. Half of the dimorphic species (eight) instead occurred at eight or more sites. Brachypterous species did not show any significant trend with respect to site occurrence.

The above two patterns resulted in a significant positive ARR of the macropterous (Fig. 2a) and the dimorphic (Fig. 2b) species, but not of the brachypterous species (Fig. 2c). Computing the same relationships using genus means produced for macropterous ($R^2 = 0.76$, $P < 0.001$) and dimorphic ($R^2 = 0.69$, $P < 0.01$) species again significant positive ARRs. Furthermore, macropterous species occupied in the mean 4 ± 1, dimorphic 9 ± 1 and brachypterous species 6 ± 2 sites.

All three morphological groups had a significant SAR (Fig. 3). However, brachypterous on one side and the dimorphic and macropterous species on the other side differed significantly with respect to their SAR parameters. The brachypterous SAR had a significantly steeper slope ($z = 0.28$) than that of both other groups [$P(t) < 0.01$; Fig. 3a]. When plotting the mean number of individuals per trap against the site area (individuals–area relationship, IAR) we found individual numbers of macropterous and dimorphic species to be independent of site area (Fig. 3b). Instead, the brachypterous species showed a pronounced IAR with a slope of $z = 0.36 \pm 0.11$. This pattern indicates higher densities of brachypterous species at larger sites but area independence of densities in both other groups.

The CCA segregated macropterous and brachypterous/dimorphic species along axis 1 (Fig. 4), the only axis for which the Monte Carlo randomization gave a significant eigenvalue (E = 0.235). This axis correlated highest with the degree of isolation (the distance from the nearest mainland: inter-set

Table 2 The study sites. Area in hectares, observed species numbers of macropterous, dimorphic and brachypterous species, estimated species numbers using the incidence based Jackknife I and the abundance based Chao I estimators, and the total number of individuals sampled

Study site	Area [ha]	No. of t raps	S_{total}	Macro-pterous species	Dimor-phic species	Brachy-pterous species	Expected S_{total}		Individuals
							Jackknife I	Chao I	
Sosnowy Ostrów	20.09	21	31	18	9	4	35	33	1704
Gilma	9.9	15	40	22	13	5	48	54	1895
Debowa Górka	6.84	9	25	14	7	4	29	29	505
Lipka	4.19	9	30	14	10	6	34	32	1410
Wyspa Kormoranów	2.3	9	23	10	9	4	26	31	3450
Poganackie Kępy III	2.1	6	25	13	9	3	30	28	206
Świtałowy Ostrów	2.08	3	14	8	5	1	17	22	91
Ilmy Wielkie	1	3	24	15	9	0	29	40	342
Wyspa Helena	0.92	6	19	8	9	2	23	25	325
Poganackie Kępy II	0.9	3	18	10	7	1	22	27	149
Mała Ilma	0.2	3	23	13	10	0	28	29	829
Kępa Wronia N	0.15	2	16	6	8	2	19	19	160
Kępa Wronia S	0.15	2	13	7	4	2	16	16	98
Terra Dobia	0.03	2	16	9	6	1	19	21	102
Poganackie Kępy I	0.01	2	10	7	3	0	13	13	55
Mainland I	—	6	29	12	11	6	34	38	996
Mainland II	—	6	20	7	9	4	24	32	476
Total		107	71	47	16	8	88	89	12793

correlation coefficient = 0.89) and less with island area (inter-set correlation coefficient = 0.68). Bivariate comparisons (U-test) of the scores of the first axis revealed that brachypterous species had significantly lower scores than macropterous ($P(U) = 0.02$) and dimorphic ($P(U) < 0.03$) species. This indicates also differences in mean abundance between the three morphological groups with respect to island isolation. In turn, island soil, vegetation and microclimatic variables did not significantly contribute to the resolution of spatial occurrences of the ground beetle fauna.

Site co-occurrences of the carabid species were not random with respect to dispersal ability. The co-occurrence pattern of the macropterous species was significantly underdispersed as inferred from the high C-score of 3.09 (Table 3). The scores point to a trend towards random or even over-dispersed co-occurrences in the dimorphic and brachypterous species. On the other hand, the combination score did not deviate from the null model expectation. These results were not influenced by

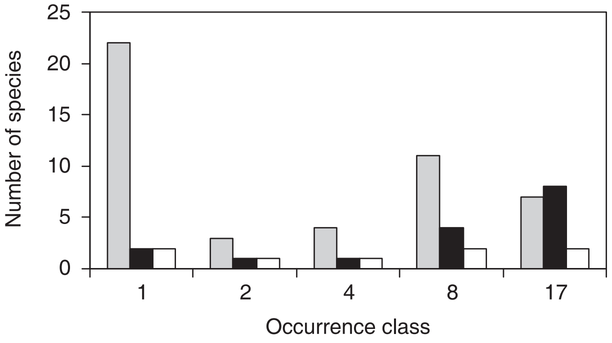

Figure 1 Number of species per $\log_2$ occurrence class in the 17 study sites. Grey bars, macropterous species; black bars, dimorphic species; white bars, brachypterous species. The distribution of the macropterous species is significantly bimodal ($P < 0.01$) as tested by the method of Tokeshi (1992).

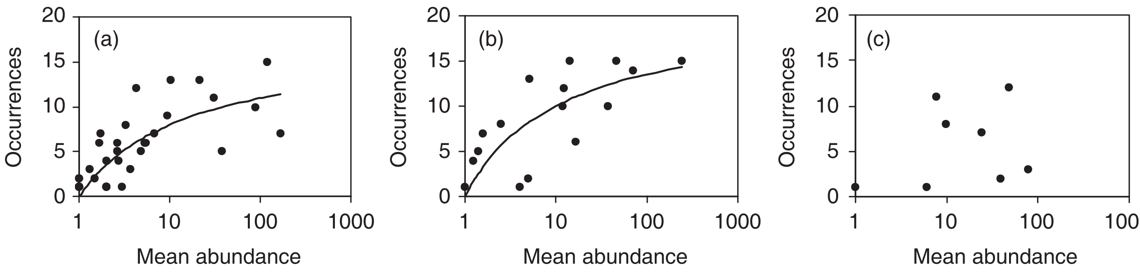

Figure 2 Distribution (number of occurrences at sites) — abundance (mean numbers of individuals in occupied sites) relationships for macropterous (a), dimorphic (b), and brachypterous (c) ground beetles. Regression of the best fit models (the Monod function) in A: Occ. = $(17.7 \pm 4.8)\ln(A)/(2.80 \pm 1.28) + \ln(A)$; $R^2 = 0.64$; $P < 0.05$, in B: Occ. = $(20.7 \pm 8.5)\ln(A)/(2.45 \pm 2.1) + \ln(A)$; $R^2 = 0.51$; $P < 0.05$.

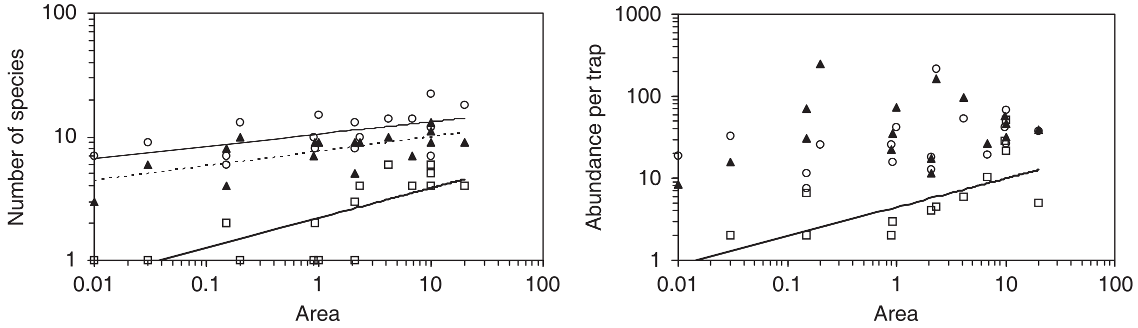

Figure 3 (a) Species–area relationships of macropterous species (open dots, light regression line: S = (10.1 ± 0.04)$A^{(0.10 \pm 0.04)}$; $R^2 = 0.35$; $P = 0.01$), dimorphic species (black triangles, dotted regression line: S = (7.9 ± 0.03)$A^{(0.12 \pm 0.03)}$; $R^2 = 0.41$; $P = 0.01$), and brachypterous species (open squares, bold regression line: S = (2.4 ± 0.04)$A^{(0.28 \pm 0.07)}$; $R^2 = 0.61$; $P < 0.01$). (b) Abundance–area relationships of macropterous species (open dots), dimorphic species (black triangles), and brachypterous species (open squares: S = (1.4 ± 0.4)$A^{(0.36 \pm 0.11)}$; $R^2 = 0.36$; $P < 0.01$). Abundances are mean numbers of individuals per trap. Note that the two mainland sites are omitted because no comparable area could be assigned.

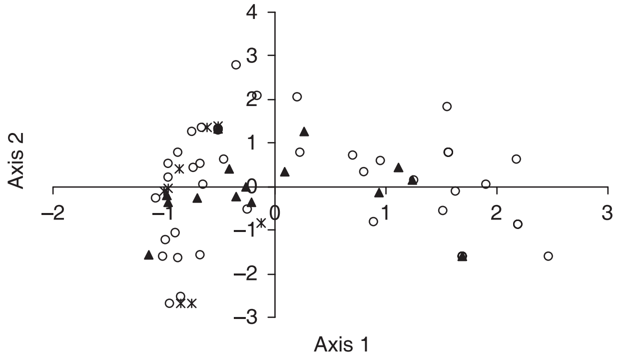

Figure 4 CCA ordination (first two axes) of ranked ground beetle abundances with ranked environmental variables (site isolation, site area, mean temperature, soil humidity, pH, soil fertility and organic material content) using normalized row and columns scores and species scores from linear combination of site characteristics. Shown are entries of macropterous (open dots), dimorphic (black triangles) and brachypterous (stars) species. The three groups differ significantly in their occurrence along axis one (one way ANOVA: $P(F) < 0.05$).

a potential bias of the random matrices as can be seen from the scores of the abundance-based randomizations (Table 3).

The V-score measures matrix-wide similarities in abundance distributions. A similar trend as for the C-score appeared with the macropterous species having independent dominance–rank order distributions across the sites (V = 1.97, $P = 0.05$), whereas the respective distributions of other groups did not significantly differ across the sites.

Different colonization abilities should also be mirrored by patterns of nestedness. Indeed, there was a trend from macropterous to brachypterous species towards a nested distribution across the sites (Fig. 5). Macropterous species were not significantly nested (T = 31.4°; $P(T = T_{null}) > 0.1$), whereas brachypterous species appeared to be highly nested (T = 8.5°; $P(T = T_{null}) = 0.003$). Hence, for brachypterous species, depauperate sites formed nearly perfect subsamples of the species-richer sites, whereas for macropterous species, site occupancies were far less predictable. The macropterous species *Platynus assimilis*, *Harpalus 4-punctatus*, *Oodes gracilis* and *Pseudoophonus calceatus* appeared to have unexpected site occurrences (idiosyncrasies defined by an idiosyncratic species temperature > 70 °C, Atmar & Patterson, 1995). Of the dimorphic species, only *Pterostichus anthracinus* was idiosyncratic and none of the brachypterous species was distinctly idiosyncratic (Fig. 5).

Table 3 Z-transformed C-scores, species combination scores, and V-scores of macropterous, dimorphic, and brachypterous species of the 17 study sites. Values for C-scores and species combination scores above 1.96 indicate significant (at the 5% error level) underdispersion of species. V-scores show whether species rank orders (SRO) differ between sites: similar SRO (V > 0); dissimilar SRO (V < 0)

			Abundance based simulations						
	Observed values		C-score			Combinations		V-score	
Species	C-score	Combinations	Mean	SD	Skewness	Mean	SD	Skewness	Abundance-based variance test
Macropterous	3.09	0.0	0.10	0.94	0.43	0.002	1.24	9.14	1.97
Dimorphic	1.62	0.34	0.44	1.18	0.98	0.006	1.04	−3.89	0.87
Brachypterous	−0.70	0.54	−0.09	0.92	1.23	−0.07	1.01	−0.01	−0.30

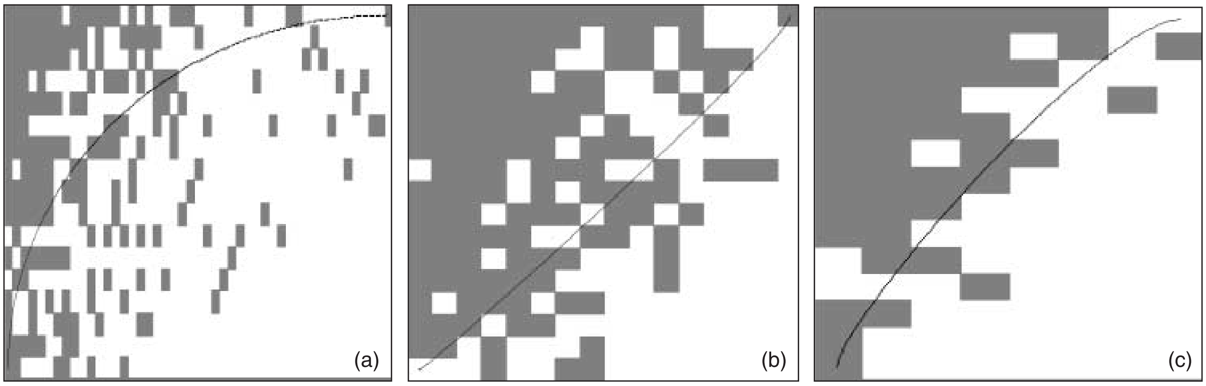

Figure 5 Nestedness analysis of macropterous (a), dimorphic (b) and brachypterous (c) species of the 17 study sites points to a trend towards a nested distribution from macropterous to brachypterous species. Rows are sites and columns are species. Macropterous species: $T = 31.4°$; $T_{null} = 38.3° \pm 4.08°$; ($P$ ($T = T_{null}$) > 0.1). Dimorphic species: $T = 24.3°$; $T_{null} = 33.8° \pm 3.69°$; P ($T = T_{null}$) $= 0.01$. Brachypterous species: $T = 8.5°$; $T_{null} = 24.5° \pm 5.49°$; ($P$ ($T = T_{null}$) < 0.003).

DISCUSSION

Several authors (Hanski *et al.*, 1993; Gutiérrez & Menéndez, 1997) have reported brachypterous and therefore less dispersive ground beetle species to be regionally more widespread than macropterous species. Kotze *et al.* (2003) and Gutiérrez & Menéndez (1997) found dimorphic species to be most widespread and Kotze & O'Hara (2003) attributed this finding to a better ability to withstand habitat fragmentation. Gutiérrez & Menéndez (1997) argued that dimorphic species take advantage of their variable dispersal strategy while being winged during dispersal, and wingless during population persistence. This might not only be a common pattern in insects (Kotze *et al.*, 2003) but be a general rule with respect to the regional distribution of animal and plant species (Guo *et al.*, 2003). Although our scale is smaller than that of the cited studies, we found a similar pattern. Only seven of the 47 macropterous (15%) and two of the eight brachypterous species (25%) were found in more than eight of the study sites, whereas eight of the 16 dimorphic species (50%) were trapped at more than eight sites (Fig. 1). These differences are obviously not sampling artefacts resulting from different site abundances. Of each of the three groups, more than 1200 individuals were trapped, hence in the mean more than 70 per site.

Site occupancy depends on two factors, dispersal and establishment (Gaston, 1994; Kunin & Gaston, 1997). In this view, differences in site occupancy might be explained from a trade-off between dispersal and establishment success (Gutiérrez & Menéndez, 1997). The macropterous species should be the better dispersers and the brachypterous species should be better in survival. Indeed, Den Boer (1985, 1990) reported low persistence times of less than 10 years of winged ground beetles. Furthermore, the flexible strategy of the dimorphic species seems to allow for higher colonization rates and longer site persistence, which would explain the comparably high site occupancies and abundances (Figs 2 and 3).

In their study on ARRs of British butterflies Cowley *et al.* (2001) found low abundances of dispersive species. The present results are in line with this finding. The macropterous species were significantly less abundant than the brachypterous (U-test: $P(U) < 0.01$) and the dimorphic ($P(U) < 0.05$) species. This difference might be explained by two processes. First, animals that disperse are affected by a 'diffusion effect' and by higher mortalities that lower their local abundances. Second, many authors dealing with insect life histories reported a trade-off between wings and associated muscle development and the number of offspring (e.g. Dingle, 1978; Roff, 1986; Langellotto *et al.*, 2000; but see Aukema, 1991 for a contrary pattern in species of the genus *Calathus*). The present results about differences in regional occurrence patterns are in line with these findings and even point to a relationship between fecundity and patterns of regional distribution and co-occurrence. Further studies have to show whether such connections exist and how local differences in fecundity are related to macroecological patterns.

Differences in abundance and site occupancy should also affect patterns of regional species accumulation. Indeed, the brachypterous species deviated from those in both other morphological groups in having much steeper slopes of their species–area and individuals–area relationships (Fig. 3). In other words, smaller sites contained a relatively lower proportion of brachypterous species than larger sites. Additionally, brachypterous species at smaller sites had relatively lower abundances (Fig. 3b). This pattern is predicted by classical island biogeography (MacArthur & Wilson, 1967) but also by metapopulation theory (Hanski, 1999) and by recent neutral models (Hubbell, 2001; Chave, 2004; Ulrich, 2004a). According to these models, winged species on smaller islands persist only because of a continuous immigration (Den Boer, 1970, Brown & Kodric-Brown, 1977).

The present study does not only show how differences in dispersal ability affect site occupancies and abundances. It also shows how this influences patterns of co-occurrence. There was a clear trend from an under-dispersed towards a random or even an over-dispersed pattern of co-occurrence and towards nestedness from the macropterous to the brachypterous species (Fig. 5, Table 3). In other words, macropterous species occurred less often, brachypterous species more often together than expected from our null model. Because the measures used here (Z-scores and matrix temperatures) are matrix size-corrected values and based on randomization procedures that used the actual matrix sizes, the differences in species numbers between the three morphological groups should not influence this result.

The CCA (Fig. 4) showed that the result was also not the result of measured differences in site quality but might be influenced by site isolation and area: factors that are again related to colonization. We are not aware of any other study on ground beetles relating dispersal ability to patterns of co-occurrences. Our results imply that further studies on species co-occurrences and community assembly rules (Gotelli & McCabe, 2002; Ulrich, 2004b; Sfenthourakis *et al.*, 2005) have to consider differences in dispersal ability as a key element influencing ecological distributions at the regional scale.

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