Ground beetles on islands: on the effects of habitat and dispersal

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Neutral theory focuses on random dispersal and species equivalence, and challenges views on the ecological importance of life history traits and habitat properties in explaining community assembly and the spatial distribution of species. Ground beetles are a popular model taxon to test predictions of contrasting macroecological theories. Here we investigate the effects of habitat properties and life history on the occurrence and community structure of 71 carabid beetle species inhabiting 15 lake islands in NE Poland. Island properties, particularly area and habitat quality, were positively linked to the occurrences of 42% of the species and correlated with species richness and β-diversity. Life history traits (hibernation type, dispersal ability and average abundances) significantly influenced species occurrences. Thus, site and species properties influence the spatial distribution of species and macroecological patterns on islands.

Introduction

Are species randomly distributed among sites or do site properties and species characteristics influence occurrences? This basic question re-appeared at the centre of ecological debates along with the neutral theory (Pueyo 2006). In essence, neutral community ecology assumes species equivalence within trophic levels. Furthermore, random dispersal and local coloniza-tion/extinction dynamics are of key importance with direct consequences for community structure (Hubbell 2001). In this context, the relative roles of a species' habitat requirements and dispersal abilities are seen as central to our understanding of the forces that structure communities (Cottenie 2005, Kadmon & Allouche 2007).

Ground beetles on islands are a model system for the theory of island biogeography (MacArthur & Wilson 1967), which is often

cited in ecology textbooks (Rosenzweig 1995, Hanski 1999, Gaston & Blackburn 2000). Despite clear habitat requirements and distinct life-history traits of many ground beetle species (e.g. Thiele 1977), a number of studies on islands have suggested that spatial distributions and, therefore, patterns of colonization are largely random (Ulrich & Zalewski 2007), that these beetles have broader habitat tolerances on islands (Niemelä *et al.* 1988, Kotze 2008), and that habitat properties are of minor importance in shaping island communities (Nilsson *et al.* 1988, Ås *et al.* 1997, Kotze *et al.* 2000, Zalewski & Ulrich 2009). It is, therefore, hypothesized that carabid beetle island communities are moulded largely by neutral colonization–extinction events as predicted by island biogeography (MacArthur & Wilson 1967).

Recent models have attempted to balance both neutral and niche oriented approaches to diversity and community structure (Kadmon & Allouche 2007). In particular, Triantis *et al.* (2003), Kadmon and Allouche (2007) and Hortal *et al.* (2009) proposed the integration of area *per se* (neutral) and habitat diversity (niche based) hypotheses in explaining spatial patterns of community structure. While Carabidae are extensively present in community-assembly studies, the role of habitat for ground beetles on islands is still unclear (Nilsson *et al.* 1988, Ås *et al.* 1997, Kotze *et al.* 2000, Zalewski & Ulrich 2009). Studies on ground beetles that dismissed the role of habitat on islands often lacked precise measurements of local environmental conditions (Niemelä *et al.* 1987, Niemelä *et al.* 1988, Leśniak 1993, Kotze *et al.* 2000). In the present study we assessed (1) how average local environmental conditions affected species occurrence, and (2) how differences in habitat conditions on particular islands were linked to species richness. These measures of habitat conditions (1 and 2) are likely to affect species occurrence and richness in different ways. We expected local habitat conditions to determine species occurrence, while variation in these conditions to affect species richness and diversity. Further, island area should have a twofold influence on beetle communities, through area *per se* and through the link with habitat diversity (Rosenzweig 1995).

As with studies on habitat effects, research on carabid beetle dispersal on islands also challenges established views. Because ground beetles differ in dispersal ability (there are winged, wingless and wing-dimorphic species, den Boer *et al.* 1980) they are a popular model in island ecology (e.g. Ås 1984, Niemelä *et al.* 1987, Brose 2003, Lövei & Sunderland 2006, Hatteland *et al.* 2008, Kotze 2008). The isolation of islands in the Baltic Sea (ranging from 0.5 to 27 km) does not prevent colonization by both winged (macropterous) and wingless (brachypterous) species (Ås 1984, Kotze *et al.* 2000, Kotze and Niemelä 2002). This lack of dispersal superiority of winged species contrasts with results from habitat islands where many wingless species experience difficulties in reaching isolated habitats (Turin & den Boer 1988, de Vries *et al.* 1996, Šerić-Jelaska & Durbešić 2009). Furthermore, wingless species are more abundant on Baltic islands than on the mainland (Ås 1984, Kotze *et al.* 2000), and wingless beetles, on average, colonize more islands than winged species (Zalewski & Ulrich 2006).

We attempt to investigate dispersal from a species-level perspective (Hanski 1992, Lomolino 2000) by analysing how species with different dispersal strategies are affected by island properties: isolation, area and habitat conditions. Additionally we examine whether hibernation type affects species persistence. As such, this is the first time the importance of species characteristics and island properties in explaining carabid beetle occurrences is studied.

Material and methods

Study sites and collecting method

Fifteen islands (from 0.01 to 20.09 ha in size) and two forested mainland sites (variants of *Tilio-Carpinetum* and *Carici elongatae-alnetum* associations) in the largest archipelago of islands in Poland — the Masurian Lake Mamry (21°30´–21°52´E, 54°00´–54°10´N) — were sampled monthly from June to September in 1997 and 1998, using pitfall traps (0.5-l plastic mug, mouth diameter 120 mm, wooden roof, emptied every month and refilled with new
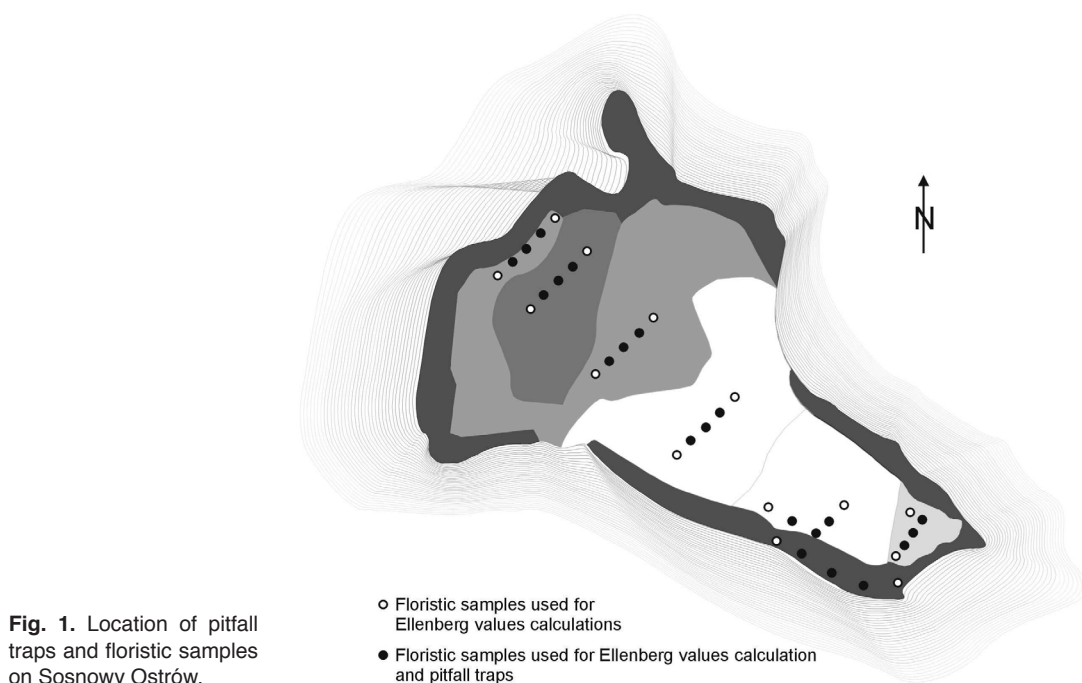
Fig. 1. Location of pitfall traps and floristic samples on Sosnowy Ostrów.

○ Floristic samples used for Ellenberg values calculations

● Floristic samples used for Ellenberg values calculation and pitfall traps

glycol). Existing maps of forest habitats and soil types (1:25 000), and thorough botanical investigations of the islands allowed us to distinguish 13 habitat types within the archipelago (Zalewski 2004). A single main line (following one of the eight main geographical directions) crossing all habitat types on an island was chosen and then perpendicular trap lines were placed in each habitat (Fig. 1). Trap lines consisted of three traps place 25 m apart (Digweed *et al.* 1995). On the smallest islands, it was possible to accommodate only two traps. Depending on habitat diversity and size, between 2 and 21 traps were used per island. The total number of traps was 107, distributed over 37 trapping lines on 15 islands and at two mainland sites.

Insects

We collected 11 321 carabid individuals (71 species) on the islands and 1472 individuals (31 species) on the mainland. A complete species list together with life history traits and abundance data is given in Ulrich and Zalewski (2006) and Zalewski and Ulrich (2006). All carabids, except the genus *Europhilus*, were identified

to species level using the keys in Hürka (1996) and Lindroth (1985, 1986). The nomenclature follows Hürka (1996). Life history and morphological characteristics are based on den Boer *et al.* (1980), den Boer and den Boer-Daanje 1990, Lindroth (1985, 1986) and Hürka (1996). In particular, all species were classified into flight ability (winged, wingless, dimorph) and hibernation type (hibernating as larvae, hibernating as imagines and species of more complex strategy) categories. Regional proportions of dispersal types (winged, wingless, dimorph) on the Masurian mainland were calculated from Burakowski *et al.* (1974).

Habitat variables

In order to estimate both average island conditions and habitat variability on the islands, using standard Ellenberg values (Ellenberg *et al.* 1992) adapted to the Polish flora by Zarzycki *et al.* (2002) we estimated seven habitat characteristics known to be important for the occurrence of ground beetles (Thiele 1977): L = insolation, T = temperature, Tr = soil fertility (rich/poor in minerals), W = soil wetness, R = soil acidity, D =

soil dispersion (rock/clay), H = organic material content. This method relies on tabulated habitat requirements (given as ranks) of plants according to their response to specific environmental gradients. A local index, for instance of soil wetness, is then calculated by averaging the respective plant indices within the sample. A floristic sample of 100 m² was taken around each trap, with additional sample taken 25 m away from the first and the third traps along each trapping line.

Habitat variability was expressed using coefficient of variation (CV) of species-specific Ellenberg scores. Log-transformed elevation was used as an additional measure of habitat variability, assuming that more elevated islands have more habitats (Ricklefs & Lovette 1999). Island isolation was expressed as the log-transformed distance to the closest mainland.

Statistical analyses and procedures

Due to a limited number of islands and species occurrences, we used a recently developed (Gotelli *et al.* 2011) non-parametric procedure (hereafter called impact test) to assess the impact of environmental variables on species occurrence. For each species i we calculated the

Table 1. Principal Components Analysis of habitat diversity. Variables with high loading (> 0.6) are set in boldface. L = insolation, T = temperature, Tr = soil fertility, W = soil wetness, R = soil acidity, D = soil dispersion, H = organic material content.

Variables	ABIOTIC$_{cv}$	SOIL$_{cv}$
Eigenvalue	4.12	2.46
Variance explained (proportion)	0.46	0.27
	Coefficients of variation	
Log$_{10}$area	0.89	0.09
Log$_{10}$elevation	0.83	−0.22
***L*$_{cv}$**	0.88	0.14
***T*$_{cv}$**	0.84	−0.07
***W*$_{cv}$**	0.77	0.35
Tr$_{cv}$	0.62	0.43
***R*$_{cv}$**	0.39	0.81
***D*$_{cv}$**	−0.04	0.84
***H*$_{cv}$**	0.16	0.85

average sum $P_i = \Sigma V_{i,\text{present}}/n_{i,\text{present}}$ and the average sum $A_i = \Sigma V_{i,\text{absent}}/n_{i,\text{absent}}$; where $V_{i,\text{present}}$ is the environmental variable that acts on i and $n_{i,\text{present}}$ is the number of sites species i is present. $V_{i,\text{absent}}$ is the environmental variable without species i and $n_{i,\text{absent}}$ is the number of sites where the species was absent. The difference $D_i = P_i - A_i$ is a test metric that describes the effect of the environmental variable on species i (Gotelli *et al.* 2011). We compared this difference D_{obs} with a null distribution of 1000 differences D_{exp} obtained from 1000 randomised orderings of islands. We then used Z-transformed scores — $Z = (D_{\text{obs}} - D_{\text{exp}})/\text{SD}_{\text{exp}}$, where SD_{exp} is the standard deviation of the expectation — to assess whether a species correlated positively or negatively with the respective environmental variable.

We measured local, trap level (α) and island level (γ) species diversities using Hurlbert's PIE:

$$\Delta_1 = [N/(N-1)](1 - \Sigma S_{i=1}p_i^2)$$

where N = is the number of individual specimens in the sample; $p_i = n_i/N$ is the proportion of species in the sample, and S is the species richness Hurlbert's PIE was chosen because it is unbiased with respect to sample size (Olszewski 2004). In this case, α-diversity was calculated as the average of the diversity of individual sampling units, whereas γ-diversity was calculated by pooling all species. β-diversity was measured as a difference between the weighted mean PIE of individual collections and PIE of the composite sample as described in detail in Olszewski (2004). Due to sample size constraints it was not possible to calculate Hurlbert's PIE for different dispersal groups. The jackknife 1 estimator (Burnham & Overton 1978) was used to estimate species richness of macropterous, dimorphic and brachypterous species. Species–area plots were constructed in log-log space (Rosenzweig 1995). Lastly, we used principal components analysis (PCA) to reduce the number of variables describing habitat variability (Table 1) as well as average local habitat conditions (Table 2). For variables quantifying habitat variability, the PCA clearly identified two main environmental principal components: PCAV1 correlates highly with area, elevation and variation of climatic factors: insolation,

temperature, humidity and soil fertility (abbreviation: $ABIOTIC_{cv}$). We interpret PCAV2 mainly from its correlation with the variability of soil characteristics: acidity, dispersion and organic matter content (abbreviation: $SOIL_{cv}$). The PCA applied to variables describing average local habitat conditions distinguished three significant principal components: PCA1 (named LWH_{mean}) correlated highly with insolation, organic matter content and soil humidity, PCA2 ($TTrR_{mean}$) with soil fertility, soil acidity and temperature while PCA3 (D_{mean}) with soil dispersion (Table 2).

Results

Because the sites differed in numbers of traps, we tested whether these differences resulted in different proportions of species trapped. Irrespective of the study site and number of traps, between 77% and 89% (mean 84.9%) of the estimated number of species were trapped as inferred from the estimates of jackknife I. Unequal trap numbers should therefore not bias our results.

Of the 71 species, 15 (8 significantly) reacted positively or negatively to $ABIOTIC_{cv}$ (Table 3). This is significantly more than expected from a binomial distribution at the two-tailed 5% error level ($p < 0.001$). Eleven species reacted to LWH_{mean}. In total, 42% of the species occurrences were affected by at least one of the six island properties. This is 10% of all 426 possible correlations and therefore slightly more than expected at $p = 0.05$. Responses to environmental factors were unevenly distributed among species of different hibernation types. In particular, species with a complex hibernation strategy reacted positively to variation in soil characteristics ($SOIL_{cv}$) (Table 4). Dispersal type did not correlate with island properties (Table 5).

The presence of a species on an island might be predicted by its average abundance in an archipelago. We found a strong correlation between a species' average island abundance and the number of colonized islands (Pearson's $r = 0.87$, $p < 0.001$). Dispersal ability plays a role in this pattern. By comparing wingless species *vs.* flying ones, we observed an important difference in the ability to colonize islands (Fig. 2).

Brachypterous species displayed narrower distributions for their average abundance while the distributions of flying species were a function of their abundances. ANCOVA confirmed that flight ability affected the number of occupied islands independently of the general abundance of the species (Table 6), and the model explained 81% of the variance in the number of inhabited islands ($p < 0.001$).

To test whether a species' abundance on the surrounding mainland affected island colonization, we regressed average mainland abundance against the number of colonised islands. There were neither statistically significant relationships for all species nor for any of the dispersal groups ($p > 0.1$).

The fraction of wingless species did not differ between island communities and the community in the surrounding mainland landscape. Macropterous species were slightly (1.5 times) less represented on islands. However, a sharp difference was observed for dimorphic beetles (Fig. 3). Species with a flexible dispersal strategy represented, on average, 45.4% of the species of the island communities, but only 15.1% of the mainland communities.

A correlation analysis (Table 7) showed that the species richnesses of carabid beetle dispersal groups were positively influenced by the

Table 2. Principal Components Analysis of local average habitat conditions. Variables with high loading (> 0.6) are set in boldface. L = insolation, T = temperature, Tr = soil fertility, W = soil wetness, R = soil acidity, D = soil dispersion, H = organic material content.

	PCA1 LWH_{mean}	PCA2 $TTrR_{mean}$	PCA3 D_{mean}
Eigenvalue	2.61	1.98	1.41
Variance explained (proportion)	0.37	0.28	0.20
Variable		Means	
L_{mean}	**0.93**	0.22	0.22
T_{mean}	0.25	**0.74**	−0.23
W_{mean}	**0.97**	0.20	0.01
Tr_{mean}	−0.44	**0.66**	0.27
R_{mean}	0.21	**0.92**	0.20
D_{mean}	0.03	0.07	**0.96**
H_{mean}	**0.71**	−0.27	−0.51

Table 3. *Z* scores of the impact test for each of the 71 ground-beetle species in this study. For PCA scores of average habitat variables refer to Tables 1 and 2. Negative scores indicate a negative response of a species to island isolation or a specific PCA variable, positive scores indicate positive responses. At the $p < 0.05$ of the scores are either < -1.96 or $> +1.96$ (normal approximation) (set in boldface).

Species	Variability in habitat variables		Mean habitat variables			Isolation
	$ABIOTIC_{cv}$	$SOIL_{cv}$	LWH_{mean}	$TTrR_{mean}$	D_{mean}	
Agonum duftshmidi	−1.80	0.56	1.95	0.60	−0.71	0.18
Agonum lugens	−1.26	0.04	**2.45**	0.11	−0.63	−0.99
Amara aulica	−0.29	1.52	0.18	−0.24	−0.65	0.64
Amara brunea	1.61	−0.26	−1.07	−1.35	−1.02	**−1.98**
Amara communis	−0.36	−0.36	1.23	−0.43	0.26	−0.55
Amara plebeja	**2.60**	−0.73	−1.70	**−1.98**	−0.12	**−1.98**
Harpalus sp.	−1.19	−0.34	1.02	0.83	1.34	1.25
Anisodatylus binotatus	−0.63	−0.29	0.48	1.20	1.06	0.22
Badister bullatus	**2.40**	−0.66	−1.69	−1.24	−0.75	−1.96
Badister dorsiger	1.36	−0.27	−0.63	−0.53	−0.19	−1.16
Badister sodalis	0.58	−0.34	0.27	1.23	−0.77	−1.26
Badister unipustulatus	**2.16**	−0.78	−1.52	**−2.16**	0	−1.85
Bembidion articulatum	−0.63	−0.29	0.48	1.20	1.06	0.22
Bembidion doris	−0.63	−0.29	0.48	1.20	1.06	0.22
Bembidion sp.	−0.35	**2.11**	0.86	−0.99	−1.39	−0.62
Calathus fuscipes	0.91	−0.78	−1.00	−0.14	1.57	**2.88**
Calathus melanocephalus	−0.30	−0.73	0.39	1.55	0.33	1.33
Calathus micropterus	0.36	−1.38	−1.20	−0.19	0.32	−0.55
Calathus mollis	−0.63	−0.29	0.48	1.20	1.06	0.22
Carabus cancelatus	0.36	−1.38	−1.20	−0.19	0.32	−0.55
Carabus granulatus	1.83	0.63	−1.68	−0.73	−1.95	−0.60
Carabus hortensis	1.36	−0.27	−0.63	−0.53	−0.19	−1.16
Carabus nemoralis	**2.43**	0.49	−1.46	−1.38	−0.67	−0.28
Chlaenius nigricornis	−1.91	−0.55	1.75	−0.21	1.60	0.58
Clivina collaris	−0.63	−0.29	0.48	1.20	1.06	0.22
Clivina fossor	−0.36	0.72	0.53	0.88	−1.50	−0.88
Dischirius globosus	−0.63	−0.29	0.48	1.20	1.06	0.22
Dischirius sp.	1.73	1.23	−0.23	**−2.21**	−0.07	−0.39
Epaphius secalis	1.79	−0.38	−0.87	−1.06	0.61	−0.67
Harpalus 4-punctatus	**2.48**	1.58	**−2.41**	−1.01	−0.80	0.38
Harpalus froelichi	−0.76	1.33	−0.82	0.26	−0.53	0.61
Harpalus latus	1.74	0.84	−1.86	−1.54	0.21	0.95
Harpalus rufipalpis	0.80	−0.72	−1.55	**2.01**	−0.38	−0.07
Harpalus solitaris	1.36	−0.27	−0.63	−0.53	−0.19	−1.16
Harpalus xanthopus winkleri	0.22	1.61	−0.78	−0.31	−0.89	0.01
Lasiotrechus discus	−1.33	−0.45	1.11	1.49	1.72	1.10
Leistus ferrugineus	1.36	−0.27	−0.63	−0.53	−0.19	−1.16
Leistus rufomarginatus	**2.12**	0.21	−1.82	−0.68	−0.52	−0.85
Leistus terminatus	**2.75**	1.10	**−2.88**	−1.49	−0.85	−0.24
Loricera pilicornis	0.15	0.37	−0.18	1.31	−1.00	−0.87
Nebria brevicolis	**2.50**	−0.65	−1.73	−1.72	0.91	0.34
Notiophilus biguttatus	1.59	−1.48	**−2.08**	0.74	−0.16	−1.14
Notiophilus palustris	**2.08**	−0.57	−1.60	−0.93	0.15	0.25
Oodes gracilis	−1.02	−0.76	1.69	1.42	0.73	−0.25
Oodes helopioides	−0.60	1.10	1.36	0.55	−0.20	0.41
Ophonus sp.	−0.74	−0.09	1.20	1.40	**−1.97**	−0.94
Oxypselaphus obscurus	−0.27	0.26	1.92	−0.86	0.60	0.39
Panagaeus cruxmajor	0.36	−1.38	−1.20	−0.19	0.32	−0.55
Paranchus albipes	1.36	−0.27	−0.63	−0.53	−0.19	−1.16

Table 3. Continued.

Species	Variability in habitat variables		Mean habitat variables			Isolation
	ABIOTIC$_{cv}$	SOIL$_{cv}$	LWH$_{mean}$	TTrR$_{mean}$	D_{mean}	
Patrobus atrorufus	1.90	1.09	−1.49	**−2.73**	−0.80	−0.57
Platynus assimilis	**2.34**	0.44	**−2.37**	0.17	−1.11	0.22
Poecilus cupreus	1.95	0.32	−0.88	−1.73	1.10	1.75
Poecilus versicolor	0.36	−1.38	−1.20	−0.19	0.32	−0.55
Pseudoophonus calceatus	0.91	−0.78	−1.00	−0.14	1.57	**2.88**
Pseudoophonus rufipes	1.10	0.02	−1.35	0.73	0.21	0.70
Pterostichus anthracinus	−0.92	−1.56	−0.37	**2.27**	1.36	1.34
Pterostichus aterrimus	−0.74	−0.09	1.20	1.40	**−1.97**	−0.94
Pterostichus diligens	1.77	−1.55	−1.83	0.12	−0.32	−0.45
Pterostichus gracilis	1.36	−0.27	−0.63	−0.53	−0.19	−1.16
Pterostichus longicollis	1.36	−0.27	−0.63	−0.53	−0.19	−1.16
Pterostichus melanarius	1.70	−1.11	−1.92	0.89	−0.11	0.03
Pterostichus minor	−1.37	1.29	**2.88**	−0.60	−0.35	−0.61
Pterostichus niger	**2.15**	0.38	−1.26	**−2.08**	0.31	0.31
Pterostichus nigrita	−0.96	0.24	1.44	−0.01	0.16	−0.48
Pterostichus oblongopunctatus	**2.25**	0.65	**−1.98**	−0.48	**−2.19**	−1.36
Pterostichus strennus	**2.25**	0.65	**−1.98**	−0.48	**−2.19**	−1.36
Pterostichus vernalis	−0.98	0.93	**2.19**	−0.10	−0.70	−0.62
Stenolophus mixtus	−1.19	−0.34	1.02	0.83	1.34	1.25
Stomis pumicatus	**3.09**	−0.16	**−2.48**	−0.65	0.17	0.39
Synuchus vivalis	**2.67**	−0.16	**−3.11**	−0.34	0.43	0.22
Trechus sp.	−0.74	−0.09	1.20	1.40	**−1.97**	−0.94
Significant scores	15	1	11	7	5	**4**

Table 4. Kruskal Wallis *H* and associated probability levels (*p*) for differences in *Z* scores (*see* Table 3) between species of different hibernation types. *S* = number of species.

Hibernation type	Number of species	Variability in habitat variables		Average habitat variables			Isolation
		ABIOTIC$_{cv}$	SOIL$_{cv}$	LWH$_{mean}$	TTrR$_{mean}$	D_{mean}	
Hibernating as larvae	18	1.27	−0.26	−1.11	−0.39	0.03	0.16
Hibernating as imagines	37	0.44	−0.21	−0.23	0.08	−0.08	−0.36
Complex life cycle	9	0.79	0.48	−0.5	−0.29	−0.4	−0.18
H		3.82	7.21	3.38	2.03	4.45	1.81
p		0.15	0.03	0.18	0.36	0.11	0.40

Table 5. Kruskal Wallis *H* and associated probability levels (*p*) for differences in *Z* scores (*see* Tables 3) between species of different dispersal ability. *S* = number of species.

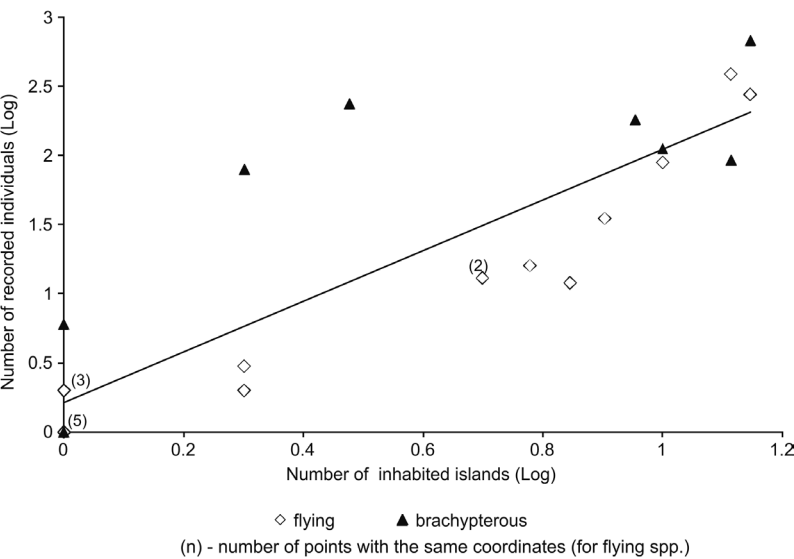| Hibernation type	Number of species	Variability in habitat variables		Average habitat variables			Isolation
		ABIOTIC$_{cv}$	SOIL$_{cv}$	LWH$_{mean}$	TTrR$_{mean}$	D_{mean}	
Macropterous	47	0.45	0.07	−0.19	−0.08	−0.11	−0.23
Dimorphic	16	0.81	−0.27	−0.65	0.23	−0.14	−0.19
Brachypterous	8	1.52	−0.35	−1.29	−0.86	0.16	−0.06
H	4.32	2.16	4.87	3.82	0.74	0.03	
p	0.12	0.34	0.09	0.15	0.69	0.98	

Fig. 2. Mean abundance–island occupancy relationship (log-log scale) for macropterous and brachypterous carabid species. Reduced Major Axis regression: $y = 0.08 + 2.1x$, $r = 0.87$, $p < 0.001$. Triangles = brachypterous species, squares = macropterous species with proven ability to fly.
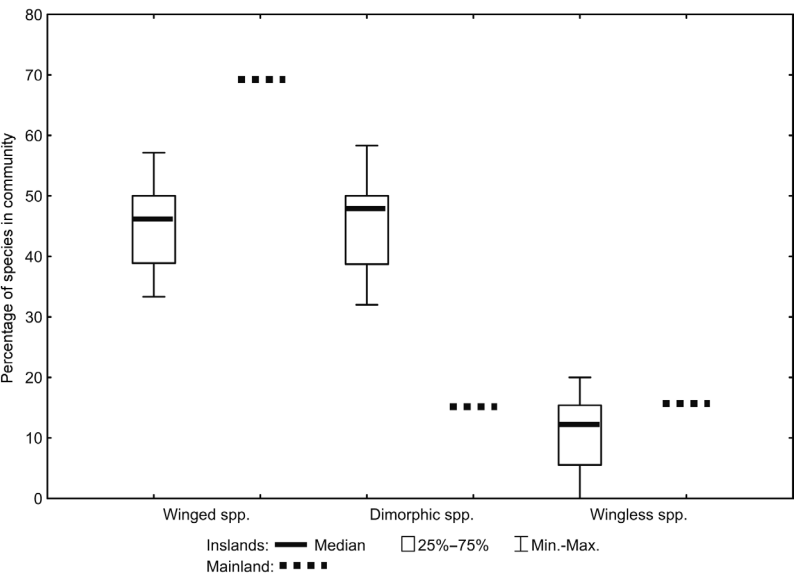

Fig. 3. Proportion of winged, dimorphic and wingless species on the studied islands (box plots) and on the Masurian mainland (dashed lines).

Table 6. ANCOVA results of the relationships between species abundance (log$_{10}$-transformed) and flight ability on the number of occupied islands (log$_{10}$-transformed).

	SS	df	MS	F	p
Constant	0.30	1	0.30	1.39	0.25
Abundance	22.3	1	22.3	101.92	< 0.001
Flight ability	1.59	1	1.59	7.26	0.013
Error	5.02	23	0.22		

diversity of abiotic conditions (ABIOTIC$_{cv}$); the strongest relationships occurred for less mobile, wingless carabids. Additionally LWH$_{mean}$, correlated negatively with the number of brachypterous species. This correlation is likely to reflect successional change of the habitat: from islands with open habitats, which are sometime partly flooded to forested islands with a closed canopy where wingless species are more common.

Carabid beetle β-diversity was measured on each island to determine whether communi-

ties on larger islands are composed of more distinctive groups of species than on smaller islands. Our analysis confirmed that β-diversity is higher on larger and more habitat-diverse islands (Table 7). Additionally we note that the γ-diversity of beetles on islands was significantly lower on more fine-grained soils (D_{mean}, Table 7).

Discussion

The island biogeography of ground beetles yields a number of unexpected and interesting patterns that influence general ecology (Ås 1984, Kotze *et al* 2000). Many authors emphasized the role of dispersal and population size (e.g. Turin & den Boer 1988, Ås *et al*. 1997, Kotze *et al*. 2000, Ulrich & Zalewski 2007). Our results, in turn, indicate that island habitat characteristics are important for the distribution of a significant part of the community. Almost half of the ground beetles (30 species) in our study differed significantly in occurrence probability in relation to habitat conditions (Table 3).

Ground beetle occurrences were mostly affected by factors related to island size (ABIOTIC$_{cv}$) and local habitat conditions (LWH$_{mean}$). Island size plays a significant role in classical island biogeography (MacArthur & Wilson 1967) and appears to be of major importance in the persistence of ground beetle populations (e.g. den Boer 1987, de Vries *et al*. 1996). However, the importance of island habitat (LWH$_{mean}$) was unexpected (Zalewski & Ulrich 2009), since beetle occurrence was believed to be mainly shaped by colonization–extinction trade-offs (Niemelä *et al*. 1988, Nilsson *et al*. 1988, Ås

et al. 1997, Kotze *et al*. 2000) and ecological drift (Ulrich & Zalewski 2007). Our analysis showed that also variability in soil properties (SOIL$_{cv}$) influenced the colonization success of species with different life history traits. While Carabidae hibernate either as larvae or as imagines, the latter being more resistant to varying environmental conditions (den Boer & den Boer-Daanje 1990), hibernation type affects population size and viability (van Dijk & den Boer 1992, Zalewski 2004). This result highlights the link between local habitat conditions, life history and, consequently, population persistence.

Previous studies failed to show that habitat conditions influence species occurrence and richness on islands (e.g. Turin & den Boer 1988, Ås *et al*. 1997, Kotze *et al*. 2000, Zalewski & Ulrich 2009) despite clear habitat requirements of the species involved. A probable explanation for this contradiction involves species persistence. If extinctions are stochastic and frequent, they can mimic random species occurrences and mask underlying habitat effects, even if habitat choice plays a major role. Indeed Den Boer (1985, 1987, 1990) showed that local island and mainland populations of numerous ground beetle species do not survive more than 8–10 years. Extinction times of island populations may be even shorter as previously reported (Zalewski 2000, 2004).

The relative effect of area *per se vs*. habitat heterogeneity on species–area relationships (SARs) has been the subject of intense discussions amongst plant (Kohn & Walsh 1994), animal (Rosenzweig 1995) and even microbial ecologists (Peay *et al*. 2007). Studies on ground beetles (Nilsson *et al*. 1988, Ås *et al*. 1997, Magura *et al*. 2001) are important in this

Table 7. Pearson correlation coefficients (* and ** denote significance at $p < 0.05$ and $p < 0.01$, respectively) for relationships between habitat variables and the number of species in three dispersal groups as well as island β- and γ-diversity.

Habitat variable	Macropterous	Dimorphic	Brachy-pterous	β-diversity	γ-diversity
ABIOTIC$_{cv}$	0.59*	0.56*	0.75**	0.60*	0.38
SOIL$_{cv}$	0.12	–0.17	–0.06	0.12	0.46
LWH$_{mean}$	–0.28	–0.45	–0.60*	–0.44	–0.25
TrR$_{mean}$	–0.20	0.14	–0.44	–0.44	–0.29
D_{mean}	–0.18	–0.10	0.03	–0.20	–0.60*
DISTANCE (log)	–0.34	–0.17	–0.11	–0.32	–0.46

debate. While habitat diversity seems to be the major driver of mainland SARs (Tews *et al.* 2004), its importance in island SARs is less clear and sometime questioned (e.g., Simberloff 1976, Nilsson *et al.* 1988, Sullivan *et al.* 2000, Welter-Schultes & Williams 1999). Kohn and Walsh (1994) showed separate effects of area and habitat diversity for plant species richness on the Shetland Islands while Ricklefs and Lovette (1999) identified biological traits that might be responsible for strong or weak correlations between habitat diversity and species richness. Finally Triantis *et al.* (2003), Kadmon and Allouche (2007) and Hortal *et al.* (2009) proposed ways to integrate both area *per se* and habitat diversity into SAR models. Our analyses show that at least part of the variability in occurrence and species richness of carabids can be traced back to habitat diversity (Tables 3 and 7).

Analyses of *β*-diversities corroborate the concept that different parts of large islands host different sub-communities while small islands have rather homogeneous communities. Of course, whether the higher *β*-diversity on larger islands stems from local habitat differences or from random population trends, leading to differences in species composition, remains uncertain (Armsworth & Roughgarden 2005). Furthermore, we showed that species richness of wingless species was more influenced by island characteristics (e.g. $\mathrm{ABIOTIC_{cv}}$) than was richness of dispersive species (Table 7). Such a difference between dispersive and more sedentary species seems to be a general pattern among plants and animals (Wiens 1994, Ewers & Didham 2006, Marini *et al.* 2010).

Zalewski and Ulrich (2006) argued that ground beetles might be grouped into those of low local abundance and a limited number of colonized habitat patches and those of high local abundance and broad distribution. In line with these findings, our results (Fig. 2) are consistent with the hypothesis that most wingless carabids had broad regional distributions due their very high densities. This is the well-known mass effect. However, the strong relationship between abundance and spatial distribution was not present in the island–mainland comparison (for similar findings cf. Ranta & Ås 1982, Niemelä *et al.* 1985, 1988). A strong mainland abundance–island occupancy relationship is expected from island biogeography (MacArthur & Wilson 1967), invasion ecology (Kolar & Lodge 2001), random sampling hypotheses (Connor & McCoy 1979), and neutral community models (Hubbell 2001). Our contrasting finding might stem from different evolutionary trends for dispersal ability on islands and the mainland. Zalewski (2004) demonstrated — in the same archipelago — a strong selection for dispersal ability in island populations and selection against dispersal on the mainland for three carabid species. If such selection also applies to other species, one can presume that island population dynamics is more dependent on migrants originating from islands rather than from large mainland populations where migrants are very sparse. Nieminen and Hanski (1998) and Hanski *et al.* (2004) favoured a similar argument in explaining regional distributions of moths and butterflies.

Varied colonization success of species with different dispersal abilities resulted in different community structures of the three dispersal groups. Dimorphic species were three times as frequent on islands than on the mainland (Fig. 3). These species probably benefit from having winged individuals during dispersal and take advantage of having a higher proportion of wingless individuals while on the island. Due to the strong trade-off between wing development and the number of offspring (Roff 1986, but *see* Aukema 1991 for a contrary pattern) a flexible strategy allows the allocation of resources to dispersal during the migration phase and to reproduction during the population establishment phase. High colonization success of dimorphic species was also shown for mainland communities by Gutiérrez and Menéndez (1997), Kotze *et al.* (2003), Kotze and O'Hara (2003), and Barbaro and van Halder (2009), who attributed their finding to a better ability of these species to withstand habitat fragmentation. The success of species with flexible ecological strategies might be a general rule with respect to the regional distribution of animals and plants (Guo *et al.* 2003, Ulrich *et al.* 2012). It seems that the well-known and paradoxical predominance of wingless species on Baltic islands (Ås 1984, Kotze *et al.* 2000, Kotze & Niemelä 2002) seems not to be a universal island rule. Our results (Fig. 3)

and a North American lake archipelago study (Will *et al.* 1995) do not support this pattern. The Baltic pattern might rather stem from differences between habitat types on archipelagos and the mainland: island forests being less frequently logged and islands missing riparian habitats. Both factors reduce winged species numbers on islands and might be the reason for this pattern as already suggested by Kotze (2008).

Conclusions

The question whether environmental and life history traits or neutral community assembly are of greater importance for the spatial distributions of species and community structure are hotly debated in biogeography. Our results favour a balanced perspective where habitat characteristics should be implemented in dispersal focused models of species richness and spatial distribution.

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