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ORIGINAL ARTICLE

Habitat heterogeneity overrides the species–area relationship

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ABSTRACT

Aim The most obvious, although not exclusive, explanation for the increase of species richness with increasing sample area (the species–area relationship) is that species richness is ultimately linked to area-based increases in habitat heterogeneity. The aim of this paper is to examine the relative importance of area and habitat heterogeneity in determining species richness in nature reserves. Specifically, the work tests the hypothesis that species–area relationships are not positive if habitat heterogeneity does not increase with area.

Location Sixteen nature reserves (area range 89–11,030 ha) in central Hungary.

Methods Four-year faunistic inventories were conducted in the reserves involving *c.* 70 fieldworkers and 65 taxonomists. CORINE 50,000 land-cover maps were used for calculating the heterogeneity of the reserve landscape (number of habitat types, number of habitat patches and total length of edges).

Results Large reserves were less heterogeneous than small reserves, probably because large reserves were established in large blocks of unproductive land whereas small reserves tended to be in more fertile land. In total, 3975 arthropod species were included in the analysis. The slope of the species–area relationship was positive only for Neuroptera and Trichoptera. There was no significant relationship in the other nine taxa examined (Collembola, Acari, Orthoptera, Thysanoptera, Coleoptera, Araneae, Diplopoda, Chilopoda, Diptera). The density (number of species ha^{-1}) of all species, however, showed a positive correlation with heterogeneity.

Main conclusions The general lack of fit of species–area relationships in this study is inconsistent with most previous published studies. Importantly, and unlike many other studies, habitat heterogeneity was not correlated with reserve area in the studied system. In the absence of this source of covariation, stronger relationships were identified that suggested a fundamental link between species richness and habitat heterogeneity. The results indicate that habitat heterogeneity rather than area *per se* is the most important predictor of species richness in the studied system.

Keywords

Arthropods, central Hungary, community ecology, faunal survey, island ecology, land cover, species–area relationship.

INTRODUCTION

Species–area relationships are amongst the most studied ecological phenomena (Connor & McCoy, 1979; Rosenzweig, 1995; Whittaker, 1998; Báldi & McCollin, 2003; Horner-Devine *et al.*, 2004; Martin & Goldenfeld, 2006). They encapsulate the general pattern that larger islands/areas contain more species than smaller ones (e.g. MacArthur & Wilson, 1967). Although there is strong evidence for the generality of this pattern, and several mechanisms have been

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identified as being important, no single underlying process has been found (McGuinness, 1984; Rosenzweig, 1995). The simplest explanation assumes no mechanism at all; this is the passive sampling or random placement hypothesis, which states that if individuals are distributed at random, larger samples will contain more individuals, and thus more species (Connor & McCoy, 1979; Whittaker, 1998). The most popular explanation assumes mechanisms, namely a dynamic equilibrium between immigration and extinction rates (the equilibrium theory of island biogeography), and that the species richness is influenced by island/habitat area and its degree of isolation (McGuinness, 1984; Whittaker, 1998), even though the original proponents of the equilibrium theory also recognized the role of habitat heterogeneity (MacArthur & Wilson, 1967). The habitat heterogeneity hypothesis predicts higher species richness because of the higher habitat heterogeneity of larger areas. Some authors identify this mechanism as the ultimate determinant of species richness (Rosenzweig, 1995; Tews *et al.*, 2004), at least at coarse spatial scales measured in many hectares (Williamson *et al.*, 2001). Area and habitat heterogeneity are usually positively correlated (MacArthur & Wilson, 1967; Rosenzweig, 1995), which frequently confounds attempts to distinguish their respective influences on species richness (Mac Nally & Watson, 1997). However, some studies have attempted to determine the relative contributions of area and habitat heterogeneity to variation in species richness. For example, plant species richness in meadows in Norway was found to be correlated with habitat diversity, not area (Myklestad & Saetersdal, 2004), whereas the persistence of butterflies in UK landscapes is determined by high-quality habitat rather than by area (Thomas *et al.*, 2001). Area and habitat heterogeneity effects were found to be roughly equal in determining plant species richness in Czech nature reserves (Pyšek *et al.*, 2002). Experiments may provide a way to compare directly the effect of area vs. heterogeneity on species richness (Whittaker, 1998). At coarser spatial scales, where experiments are not feasible, a promising avenue for testing these relationships involves the study of a system where habitat heterogeneity decreases with increasing area. In such a situation, if species richness increases with area, this correlation indicates that probably area *per se* has an overriding effect on species richness. If, however, species richness decreases with area, then heterogeneity alone probably accounts for any species richness patterns found. Finally, if there is no correlation between species richness and area, then habitat heterogeneity and area probably both influence species richness. We cannot exclude, however, that there may be some other factors, as yet undetermined (e.g. connected with the quality of the habitat), influencing the relationship.

Herein, I analyse a system of nature reserves in central Hungary, where measures of habitat heterogeneity (e.g. patch and edge density) are negatively correlated with area. In this region most of the diverse and highly productive habitats (mostly forests and marshes) have been converted to agricultural land, and semi-natural habitats of this type only survive as small fragments, many of which have been designated as reserves. The less productive sandy or alkaline grassland habitats are less intensively managed and some still persist in large blocks, many of which are also designated as reserves. Due to the unbalanced size distribution of reserves on productive vs. non-productive lands, there is a tendency to have small reserves of the former type and larger reserves of the latter type. As a consequence, the general underlying positive correlation of area with heterogeneity is violated, thus providing an excellent test system to examine the relative contribution of area vs. heterogeneity to species richness.

MATERIALS AND METHODS

Study area

The analysis was based on intensive faunal surveys of 16 reserves in central Hungary (Fig. 1) belonging to the Pannon biogeographical zone. Central Hungary is a flat region 100–150 m above sea level. Area, habitat and isolation vary greatly across sites (Table 1 & Fig. 1).

Surveys

The aim of the survey team (about 70 experts participated in the field survey from 1977 to 1980) was to compile as complete a list of the fauna as possible. A variety of taxon-specific

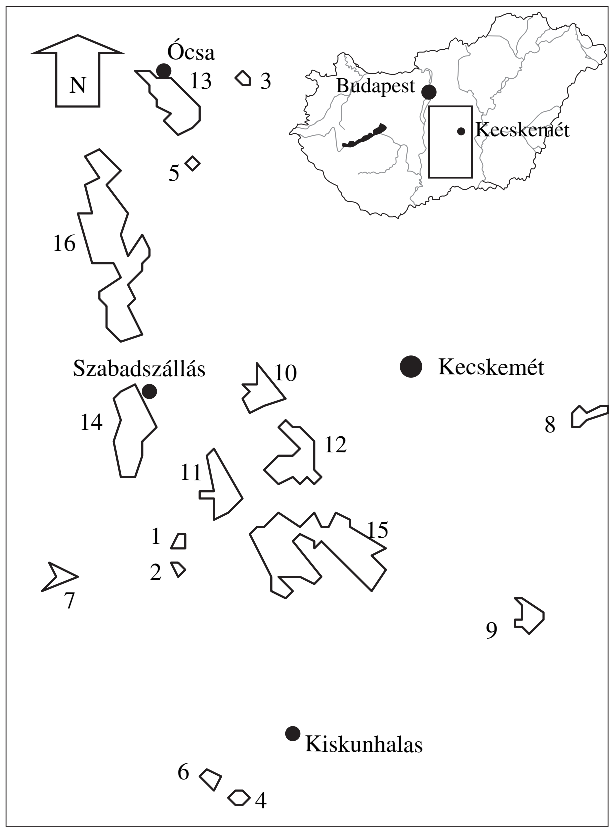

Figure 1 Map of central Hungary with the location of the 16 surveyed reserves. The reserve numbers refer to those in Table 1.

Table 1 Area, main land-cover types and measures of area heterogeneity in the 16 surveyed reserves in central Hungary. Reserves are arranged by increasing size.

Reserve name	Area (ha)	Artificial (% of total)	Grassland (% of total)	Woodland (% of total)	Arable land (% of total)	Marshland (% of total)	Water (% of total)	Number of land-cover types	Number of patches (polygons)	Edge length (km)
1. Marshy ash woodland, Tabdi	89	0.0	34.6	40.0	0.3	25.3	0.0	6	8	29.7
2. Woodland, Kiskörös	92	0.0	12.4	50.4	0.6	36.8	0.0	5	6	22.0
3. Juniper forest, Csévharaszt	105	0.0	0.0	100.0	0.0	0.0	0.0	5	9	14.0
4. Forest, Kunfehértó	120	0.0	0.3	99.4	0.3	0.0	0.0	9	11	16.2
5. Meadows, Dabas	148	0.0	55.1	23.3	4.3	17.4	0.0	7	14	32.2
6. Sand dunes, Kéleshalom	168	0.0	9.9	87.4	2.9	0.0	0.0	8	18	25.2
7. Lake Szelidi	359	0.8	20.9	19.2	29.6	14.2	15.4	13	27	67.2
8. Tőserdő, gallery forest at the River Tisza	382	0.0	12.9	67.1	5.2	8.4	6.3	13	28	82.6
9. Lake Péteri	684	0.0	27.6	6.6	11.5	33.5	20.9	16	48	113.8
10. Sand dunes, Fülöpháza	1665	0.0	35.2	19.5	24.7	17.3	3.3	23	110	266.4
11. Lake Kolon	2728	0.2	46.4	10.6	1.9	40.8	0.1	17	69	201.9
12. Meadows, Orgovány	2953	0.1	53.0	7.0	16.5	23.4	0.0	22	120	375.0
13. Swamps, Ócsa	3576	0.9	13.6	34.2	32.5	18.3	0.5	20	104	375.7
14. Alkaline lakes, northern Kiskunság	3903	0.3	37.3	0.1	37.6	14.9	9.8	13	162	596.3
15. Sand dunes and grasslands, Bócsa-Bugac	10,920	0.4	37.5	55.9	4.8	0.6	0.8	26	341	1097.6
16. Alkaline grasslands, northern Kiskunság	11,030	0.5	72.9	0.6	22.4	2.1	1.4	24	162	7469.4

sampling techniques were applied across different habitats. This approach provided the most taxonomically complete species lists (Stohlgren *et al.*, 1995; Longino *et al.*, 2002). Sixty-five taxonomists from around the world were involved in the identification of the material. The results were published as species lists (Mahunka, 1986, 1987) containing approximately 8900 taxa, of which 8200 were arthropods – Coleoptera, Lepidoptera, Diptera and Hymenoptera had more than 1000 species listed (Báldi, 1999).

For the present study, however, due to inconsistencies in the species lists, not all the taxa were used in the analyses. I selected only those taxa for which lists were based on the 1977–80 surveys as some authors combined historical and literature records with their own collection data, and these were impossible to separate. A taxon was included only if data from at least five reserves were available. Due to these criteria, almost half of the species on the lists were excluded. Eleven major taxa with full species lists were included, with species numbers ranging from 9 to *c.* 2500. The analysis was conducted using the species as the base taxonomic unit; subspecies were pooled.

Environmental data

Habitat heterogeneity was evaluated using the CORINE 50,000 (CLC50) land-cover maps. CORINE (Co-ordination of Information on the Environment) is a programme of the European Environment Agency, which has generated Europe-wide environmental data, including land-cover data for 26 European countries (Büttner *et al.*, 2002). CLC50 (scale 1 : 50,000) has about 80 land cover (or habitat) categories applicable to Hungary. The number of habitat types, number of habitat patches (land-cover polygons) and total length of edges (border between habitats) were calculated for each reserve using standard GIS techniques. Heterogeneity was measured as the density of these variables (e.g. number of habitat types ha^{-1}).

Analytical techniques

From data for each of the taxa in Table 2 I constructed the most common form of species–area curves, when both axes are (base 10) logarithmically transformed. Although these may not always be the best fit models (McGuinness, 1984; Báldi & Kisbenedek, 1999), my aim was to get comparable results to similar analyses in the literature. I calculated the linear regression and the Pearson's product–moment correlation coefficients to test for relationships between the invertebrate groups, habitat area and habitat heterogeneity. I tested for possible effects of habitat heterogeneity on species richness by analyses of the relationship between the density of habitat types (number of habitat types ha^{-1}) and the density of species (number of species ha^{-1}). All analyses were carried out using SPPS for Windows (SPSS, 1999). Normality was achieved by the logarithmic transformation of area and species richness variables.

Table 2 The recorded total number of species of the analysed taxa, their estimated species richness in Hungary (Korsós & Mészáros, 1998) and the proportion they represent of the Hungarian fauna in the studied localities. The number of sites included, the slope (*z* value of the log–log regression), intercept of the log–log regression line, R^2 and significance of the species–area regression using the log–log transformed power function model is given.

Taxon	Recorded total no. of species	Species richness in Hungary	Representation of the Hungarian fauna, % of species known/estimated	Site number	Slope	Intercept	R^2 (P)
Collembola	33	150–200	16.5	11	–0.136	1.208	0.071 (0.427) n.s.
Acari	169	*c.* 1500	11.3	13	0.327	0.144	0.131 (0.225) n.s.
Neuroptera	26	120–125	20.8	12	0.296	–0.519	0.719 (0.004)**
Orthoptera	60	125	48.0	9	0.437	–0.197	0.392 (0.071)*
Trichoptera	23	250–270	8.5	9	0.343	–0.381	0.573 (0.018)**
Thysanoptera	47	180	26.1	5	0.489	–0.920	0.063 (0.684) n.s.
Coleoptera	2413	10,000	24.1	16	0.164	2.187	0.142 (0.150) n.s.
Araneae	182	*c.* 1100	16.6	12	–0.08	1.689	0.025 (0.624) n.s.
Diplopoda	9	87	10.3	13	–0.162	0.845	0.165 (0.169) n.s.
Chilopoda	9	50	18.0	14	–0.05	0.610	0.017 (0.654) n.s.
Diptera	1004	9500	10.6	15	0.439	0.666	0.129 (0.173) n.s.
Total	3975	*c.* 23,200	17.1	16	0.195	2.268	0.191 (0.090)*

$^*P < 0.1$; $^{**}P < 0.05$; n.s., non-significant.

RESULTS

The recorded number of species of a taxon in the reserves ranged from 8.5% to 48.0% of the known species richness of that taxon in Hungary (Table 2). The species–area relationship had a negative slope for Collembola, Araneae, Chilopoda and Diplopoda, but none of these relationships were statistically significant. Positive relationships were found for seven taxa, but these were significant only for Neuroptera and Trichoptera (Table 2 & Fig. 2).

Habitat heterogeneity, measured as the density of habitat types, patches and edges for each reserve, was strongly and

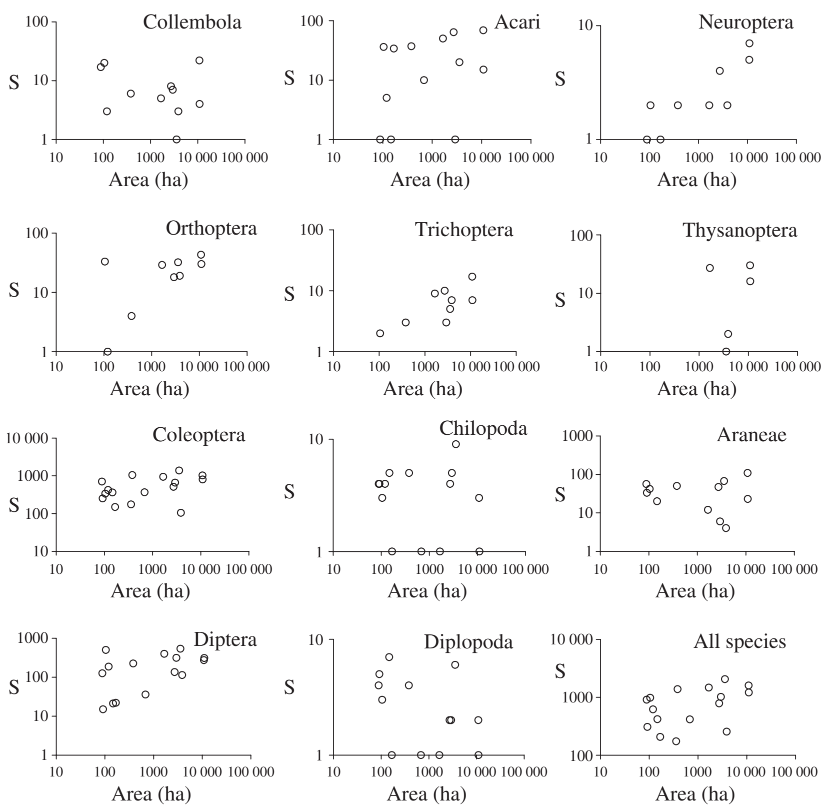

Figure 2 Species–area curves of 11 arthropod taxa and all species in 16 reserves in central Hungary (note that the range of the *y*-axes varies).

negatively correlated with reserve area (area–habitat type density, $r = -0.980$, $P < 0.0001$; area–density of patches, $r = -0.811$, $P < 0.0001$; area–density of edges, $r = -0.740$; $P < 0.001$) (Fig. 3). This shows that larger reserves were more homogeneous than small ones.

The density of habitat types, as a measure of heterogeneity, showed a strongly significant positive correlation with the density of species (Fig. 4) ($r = 0.893$, $n = 16$, $P < 0.0001$). This clearly indicates that a more heterogeneous habitat will have more species per unit area. The position of the reserves in

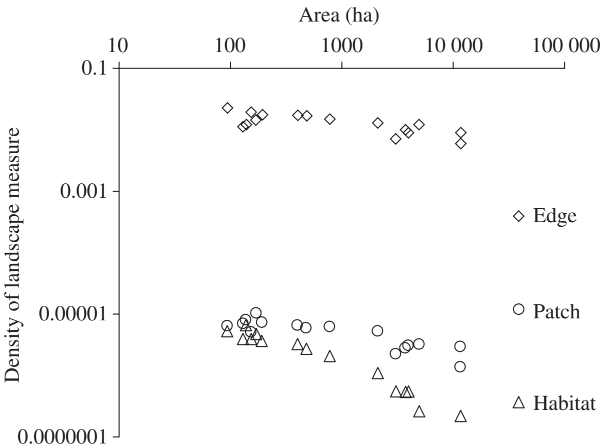

Figure 3 Relationship between reserve area (ha) and measures of landscape heterogeneity per unit area (number of habitat types, patches and edges ha^{-1}) in 16 central Hungarian reserves.

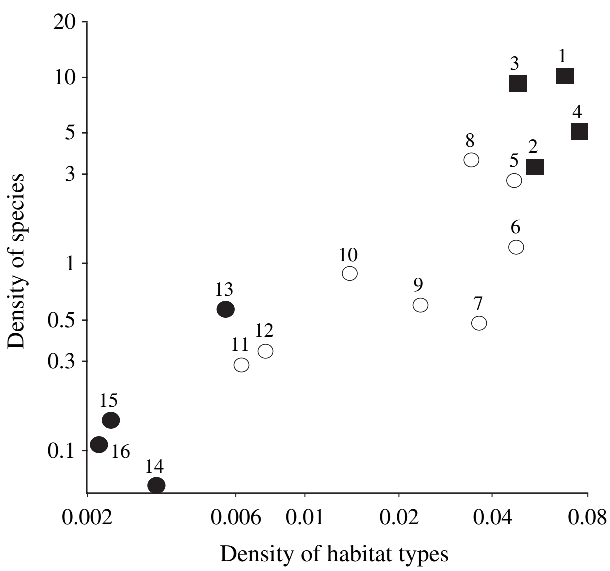

Figure 4 Correlation between the density of habitat types (number of habitat types ha^{-1}), as a measure of heterogeneity, and the density of species (number of species ha^{-1}) based on data from 16 central Hungarian reserves. Reserves falling into the top quartile by size are represented by squares, and those in the lowest quartile by filled circles. The labels refer to the number of reserves from Table 1.

Fig. 4 indicates a trend, with small but heterogeneous reserves at the upper right end of the graph and large but homogeneous reserves at the lower left end.

DISCUSSION

Although the species–area relationship is one of the basic laws in ecology, it does not generally apply across this system of reserves. This probably cannot be attributed to biased sampling of animal taxa, because, as a 'rule of thumb', sampling artefacts are predicted to play no role in determining the species–area curves (Rosenzweig, 1995, p. 204).

The explanation for the lack of a significant species–area relationship for the studied taxa is difficult to identify. Species-rich groups like Coleoptera (2413 species in this analysis) and Diptera (1004 species) probably lack significant species–area relationship due to their diverse species pools, which harbour species with different life-history and habitat selection strategies (Papp & Darvas, 2000; Magura *et al.*, 2001; Lövei *et al.*, 2006). Consequently, they can 'fill' any available habitat patch with species, irrespective of the available resource types, quantities or degree of isolation. The lack of significant species–area relationships for beetles does not particularly contradict earlier studies that have reported a significant positive relationship (e.g. Magura *et al.*, 2001), since most of those studies were restricted to family level, e.g. carabids, tenebrionids, or others, usually with a few hundred species, and thus did not include the whole diversity of Coleoptera. The survey used in this analysis recorded 101 Coleoptera families (Báldi, 2003). The species richness patterns for the less species-rich taxa, which contain soil-living groups such as Collembola, Acari, Chilopoda and Diplopoda, were probably highly influenced by localized small-scale soil properties. The smaller, more heterogeneous reserves, with more productive and wet soils (and more forest cover, Table 1), already provide favourable living conditions for representatives of these groups. Consequently, the resulting relatively high species richness in small reserves tends to decrease the slope of the species–area relationship from that generally expected across systems of this kind.

Significant positive species richness–area relationships were observed in Neuroptera and Trichoptera. Species in both orders have good dispersal (flying) ability in the adult stage. Similarly, good dispersal ability could also explain the positive trend shown by species of Orthoptera. Most orthopteran species also fly or have good dispersal ability – at least compared with the other taxa involved in this study. Therefore, dispersal may be an important factor structuring the species–area relationships in these cases.

The 'SLOSS' problem, whether a single large or several small reserves are more efficient in maintaining diversity, is a long-running debate in conservation biology (e.g. Pullin, 2002). In the present study system, the set of the smallest reserves contained more species than were found in the single largest reserve, indicating that in this case several small reserves are superior in terms of species richness to the large ones. This observation, however, must not be used as a management guideline to neglect large reserves. The conservation of arthropods in the studied system requires the conservation of both small and large reserves. In central Hungary, large reserves are usually unique alkaline and sandy 'puszta' grasslands, with specialist arthropod assemblages harbouring rare and unique species (Rakonczay, 1990).

The explanation for the general lack of species–area relationships in this study may be that species richness is not directly linked to area; area is simply a surrogate of the ultimate factors that determine species richness (MacArthur & Wilson, 1967). MacArthur & Wilson (1967), Rosenzweig (1995), Whittaker (1998) and Tews *et al.* (2004) suggested that habitat heterogeneity could be the most important factor that shapes species–area relationships. Larger areas usually have more habitats and greater heterogeneity, both of which are generally positively correlated with species richness. The present analysis supports this claim from another angle. In the studied situation, the large reserves generally had lower-productivity soils and habitats, e.g. sandy or alkaline soils with grasslands, while several of the small reserves were on more productive meadow soils and were covered by forests (Table 1, Reich *et al.*, 2001; Falge *et al.*, 2002). Consequently, small reserves had higher heterogeneity than large ones, and the usual trend of increasing species number with area was not found. Crawley (1987) found a similar pattern in the English counties, where large administrative areas were large simply because they were barren. Therefore, the lack of a species–area relationship in the present analysis may be attributed to the lower habitat heterogeneity and productivity of larger reserves compared with smaller ones. These findings suggest a dominant role for habitat heterogeneity and probably productivity (which may not always be reflected by area) in determining species richness (Kalmar & Currie, 2006). Therefore, notwithstanding the lack of significant species–area relationships for most taxa in the present analysis, the results support a key role for habitat heterogeneity in the distribution of species richness.

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BIOSKETCH

András Báldi is a research biologist interested in the ecology and conservation of animal communities, especially the effects of habitat area and edges on the organization of assemblages, of a diverse range of taxa. He is also interested in the effects of grassland management on biodiversity.

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