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LANDSCAPE HETEROGENEITY AND SPECIES RICHNESS AND COMPOSITION: A MIDDLE SCALE STUDY

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Abstract

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The aim of this study was to confirm and prove the influence of habitat heterogeneity to species composition and richness of 4 taxa: higher plants, spiders, butterflies and true bugs. We also wanted to analyze the role of a biotope identity in species richness and composition of observed taxa on various biotopes, e.g. whether the biotope itself weakens or forcens the effect of habitat heterogeneity.

The research was taken place in the years 2003–2004 in Bochov in Doupovske vrchy, a military training zone in Western Bohemia. 4 transect lines (each 6 km long) were established here and each transect was divided into 20 rectangles, each 300 m long. True bugs, spiders and butterflies were collected here using swepping net, ground traps and transect walks. The data about higher plants were collected using classical vegetational relevés.

Habitat heterogeneity strongly affects the species richness of the observed taxons, especially butterflies and true bugs. After adding the biotope identity to the model the impact of habitat heterogeneity dies away. But, on the contrary, species richness of higher plants and spiders were not so affected by the biotope identity. From heterogeneity predictors, the species richness of higher plants was mainly affected by number of segments and borders and butterfly species richness was strongly affected by number of segments and diversity. By true bugs the strongest impact had number of segments and diversity, similarly as by spiders, which species richness was also strongly affected by borders. Habitat heterogeneity also affects the species composition of the taxons. In large distance the most affected taxons were true bugs and plants even after adding the effect of biotope identity. The effect of biotope is very important in assessing the species richness and it can strongly affect the results.

Key words: habitat heterogeneity, transects, agroenvironmental schemes, cultural landscape, landscape diversity

Introduction

Habitat heterogeneity is among the most discussed theme in ecology. On the macroscale the heterogenity of the landscape is predicted e.g. by the distance of large regions in one state or continent (Fischer et al., 2006; Kerr, Cihlar, 2004), global diversity of tropical rainforests (Kerr, Burkey, 2002), climatic energy (Kerr, Curie, 1999) and the heterogeneity of biomas in one continent (Kerr et al., 1998).On middle scale, the basic predictors of species richness are e.g. valley sides, tops of slopes and wood edges (Dennis, Sparks, 2005) and even the island isolation(Dennis et al., 2000). On the other hand, at local scales, heterogeneous habitats provide more resources, or niches, allowing local co-existence of more species. For instance, recent analyses from butterflies (Konvička et al., 2006) illustrate that as majority of species utilise more resource types during their lifespan, structurarly diverse environments are essential conditions for their persistence (Zimmermann et al., 2005). Especially for many invertebrate species (Krauss et al., 2003; Dennis, Sparks, 2005; Konvička et al., 2005) the existence of mosaique landscape is very important, because they need some refugia where they live and where they lay their eggs, where to find a nectar sources, etc. For example some butterfly species need the shrubs where they hide during hot weather and open landscape with extensively managed meadows, where they find some nectar supplies (Zimmermann et al., 2005; Dennis, 2004; Dennis, Sparks, 2005). Each invertebrate species also needs something else to survive, so the patchy landscape is much more rich in invertebrate species, than the uniform landscape. Increase of habitat heterogeneity can also cause highest migration of the species from surroundings. On the oposite side it is also known, that the lack of habitat heterogeneity causes the extinction of some in the past very common species of invertebrates, especially butterflies (Štorch et al., 2003).

From conservation point of view, the crucial issue is the effect of heterogeneity on species richness and composition at middle scale of individual landscapes (decades of km^2, i.e. farms, districts, national parks etc.). It is the scale, which is unlike the heterogeneity on the level of whole states and continents practically appliable to the conservation policy. But simultaneously, there also appear the problems, which are not important on the local scale – the diversity of owners relations, etc. Regardless, there is a strong theoretical (Hanski, 2005; Zartmann, Shaw, 2006) and empirical (Hula et al., 2004; Franzen, Ranius, 2004) evidence, that without accent to the conservation in large scales we do not stop the loss of biodiversity.

As a response, multiple studies focusing on landscape level heterogeneity recently appeared across Europe. Söderström et al. (2001) studied the diversity in 31 seminatural grassland in Sweden. They compared richness of plants, birds, butterflies, bumble bees, ground beetles and dung beetles and found, that both the landscape pattern and the way of management is very important for many species. Bengtsson et al. (2005) analysed the effects of organic farming (i.e. without pesticides and artificial fertilizers) on species richness and abundance. They learned, that organic farming was beneficial, but the way of farming itself had only partial influence if compared to average size of field, i.e., landscape heterogeneity. Weibull et al. (2000) also compared the diversity of butterflies in organic and conventional farmlands, finding negligible effect of organic farming, but strong effects of landscape grain size. Ouinn et al. (2004)

studied in western France, whether butterfly use of herbaceous patches depends on the nature of those patches and their management and whether they prefer any. They came across that the butterflies need more patches, because of their different behavioral strategy during day and that is why they need a patchy landscape. Burel et al. (1998) compared the biodiversity in contrasted landscape units in selected region in western France. They measured biodiversity of small mammals, birds, insects and plants using Shannon´s diversity index, equitability and similarity indices. They wanted to study the effect of the agricultural intensification to landscape grain size and the effect of grain size to the diversity of these taxons. They learned, that the intensification of agriculture does not always lead to a decrease in species richness, but to several functional responses according to taxonomic groups, either no modification, or stability by replacement of species, or loss of species.

The major hindrance in studies of effects of habitat heterogeneity on species richness is distinguishing heterogeneity effects from effects biotope identity. Only a few studies about habitat heterogeneity did not forget, that the richness of various biotopes is different and that in heterogeneous landscape there will be also rich biotopes, which can be missing in the homogeneous landscape (Burel et al., 1998; Nikodemus et al., 2005; Herzog et al., 2001).

The second problem is a space autocorrelation (Lennon, 2000). There are only a few studies about habitat heterogeneity, which use this method. Correlation between an autocorrelated response variable and each of a set of explanatory variables is strongly biased in favour of those explanatory variables that are highly autocorrelated – the expected magnitude of the correlation coefficient increases with autocorrelation even if the spatial patterns are completely independent. Similarly, multiple regression analysis finds highly autocorrelated explanatory variables „significant“ much more frequently than it should. The chances of mistakenly identifying a „significant“ slope across an autocorrelated pattern is very high if classical regression is used. Consequently, under these circumstances strongly autocorrelated environmental factors reported in the literature as associated with ecological patterns may not actually be significant. It is likely that these factors wrongly described as important constitute a red-shifted subset of the set of potential explanations, and that more spatially discontinuous factors are actually relatively more important than their present status suggests.

This thesis contributes to the debate by studying effects of landscape heterogeneity on species richness and composition of four taxonomic groups, plants, butterflies, true bugs and spiders and it tries to solve this problem partially. We want to bring some pieces of evidence, that the impact of landscape structure is very important for the species richness and also to bring some possible solution to this very difficult and highly discussed theme.

Material and methods

Study area

The study was carried out in Bochov, Karlovy Vary district, northwestern Czech Republic (50°10’ N, 13°01’ E, 700 m a.s.l.). The wider region, southern foothills of the volcanic Doupovské vrchy? Mts, is characterised by particularly low intensity of land use. It adjoins the Hradiště military training range, but even the land outside the range is sparsely populated. The entire region is a mosaic of both traditionally managed and improved meadows and pastures, fields, small woodlots, fish ponds and alluvial wetlands. The climate is mildly warm and mildly damp, the mean air temperatures do not exceed 7 °C. The coldest month is January (3 °C), the warmest one is July (16.7 °C).

The bedrock is formed by gneiss with unique amphibolite lens with ascendent peaks of basalt eruptions. Slightly inclined bottoms of their walleys which form the protuberances going to the higher placed areas are formed with the uphill rocks. In the valleys along the rivers and in the erosion cuts are alluvial sediments.

The region is renown for high diversity of plants and animals of traditionally used submontane grasslands, hosting, e.g., strong populations of the critically endangered Marsh Fritillary butterfly (Hula et al., 2004).

Field methods

Insect and plant diversity were surveyed in 2003 along four parallel transects, situated 300 metres apart and crossing the area in an approximate NW–SE direction. Each of the transects consisted of twenty sections, each 300 m long, thus giving a lattice of 20*4 sections (Fig. 1). The four taxonomic groups were recorded as follows.

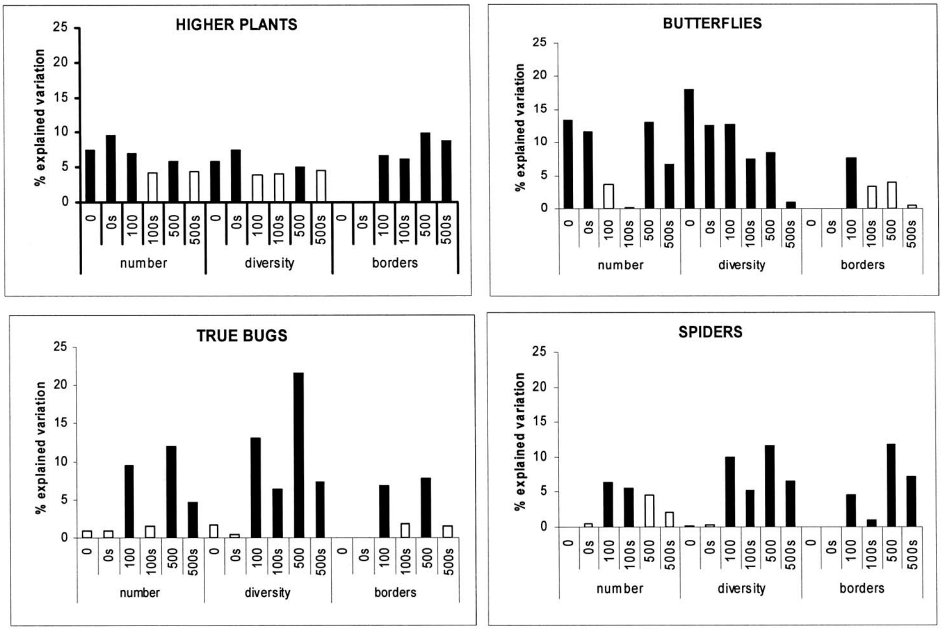

Fig. 1. Residual variation attributable to the three measures of heterogeneity, as returned by the GLM multiple regression models. The analysis without the effect of biotopes. Black columns stand for significant nominally results ($P < 0.05$) and white columns stand for non-significant results. Numbers from 0-500 are the distance from the transect line. "s" by the numbers means, that space was included in the model.

Higher plants

A skilled botanists (L. Filipova) walked the transect in late June and again in mid July, recording all species of higher plants growing in approximate 5 metres strip along the transect path (Appendix 1). It took twenty person-days to complete the survey. Nomenclature follows Kubát (2002).

Butterflies and burnets (Lepidoptera: Papilionoidea, Hesperioidea and Zygaenidae – Recorded by M. Konvicka and Z. Fric.

Sixteen transect walks (Pollard, 1977) were carried out along the lattice, in approximately 10-days intervals, between 6th May and 20th August. All butterflies and burnets were identified to species, usually by sight, more difficult species were net-captured for identification. The walks were limited 9:30 a.m. and 4:60 p.m. (C European summer time) and to weather appropriate for counting butterflies; they were interrupted if the weather worsened. Under fine weather, it took two person-days to complete one lattice.

Terrestrial bugs (Heteroptera)

We sampled the bugs in early July by sweping herbaceous and (where appropriate) shrubby vegetation along the transects. Fifty sweps, distributed regularly along its length, were taken from each section, and care was paid to include all distinct vegetation types in proportions relatively equal to their representations along the sections. The bugs were killed en masse and subsequently sorted and identified in a laboratory. The sweping took ten person-days, the sorting/identifying ca 50 person-days. Nomenclature follows Aukema and Rieger (2004).

Spiders

Spiders originated from the sweeping described above. They were identified by a specialist (V. Hula), the nomenclature follows Buchar and Růžička (2002).

Landscape variables

Biotopes along the transect were distinguished in field and subsequently measured using aerial 1: 1000 photographs. We distinguished: extensively managed meadow (unfertilised, mown at most once a year), intensively managed meadow (fertilised and mown twice a year), steppe grassland, ponds, intravillan, scrub, pastures, ruderal grasslands and forests. The program ArcView3.x was used for the measurements.

Biotope heterogeneity was analysed at three distance from the transects (i) „zero", i.e., the right at the transect; (ii) 100 m, i.e. the heterogeity in 200*300 m rectangles dissected by individual transect sections with the width of 100 m; (iii) 500 meters, i.e. the heterogeity in 1000*300 m rectangles dissected by individual transect sections with the width of 500 m.

Out of numerous possible ways to describe biotope heterogeneity, we used three simple measures. (a) Numbers of segments of distinct biotope categories within the given rectangle (or at the transect line in case (i)), herein number. (b) Simpson's diversity of distinct biotope categories, computed as $D = 1\text{-}\Sigma\ (n/N)2$, where n is the area of one biotope in the rectangle and N is the area of the whole rectangle, herein diversity. (c) Summed length of borders of the above biotope segments, herein borders.

Because lengths of individual sections, despite much care, sometimes deviated from 300 m, we used lengths of sections or (if appropriate) areas of the analysed rectangles as covariables in all analyses.

Regression analyses of species richness

Generalised linear models (GLM) regressions were used to study patterns in species richness. The analyses were carried out separately for each taxonomic group, distance from the transect and predictor of heterogeneity. The link function was gaussian (identity link) for higher plants, butterflies and true bugs, and poisson's (log link) for spiders. All data vectors except for serial numbers of transects and ordination scores (see below) were transformed by substracting their mean and dividing by standard deviation. The analyses always followed the same routine.

(i) The length of section was entered ontoa null model (Y ~ +1) to control for effects of unequal lengths on species numbers, thus obtaining covariate model.

(ii) Separate effects of number, diversity and borders were tested by entering these predictors onto the covariate models, assessing for significant residual difference using F-tests.

(iii) Spatial autocorrelation was controlled for by defining models that contained, besides of section length, predictors describing positions of the sectoins relative to other sections. These spatial models were obtained by entering serial numbers of transect (1–4) and section (1–20), their 2nd-degee polynomials (transect2, section2), and all possible additive (transect+section, transect2+section, transect+section2, transect2+section2) and interaction (transect*section, transect2*section, transect*section2, transect2*section2) combinations, onto the covariate models. The most appropriate model was that achieving the lowest AIC value, compared to covariate model.

(iv) As a next step, number, diversity and borders were entered onto the spatial models to test for significant resitual differences (i.e., difference due to heterogeneity after considering spatial position of sections).

(v) The above tests did not control for identity of biotopes along the transects. To do so, we computed the Principal component analysis (PCA) from biotope data, using CANOCO, version 4.5 (Ter Braak, Šmilauer, 2000). Then, we used scores of individual sections at the four PCA axes as predictor variables, which I sequentially entered onto the covariate models for individual taxonomic groups. AIC and F-tests were used to define minimum-terms biotope identity models, i.e. models that could not be further improved by adding further PCA terms.

(vi) Entering spatial terms (see iii, above) onto the above models that controlled for both biotopes along the transects and spatial autocorrelation (spatial biotope identity models).

(vii) Finally, I tested for a residual variation explicable to number, diversity and borders by entering these variables onto the biotope identity and spatial biotope identity models.

Multivariate analyses of species composition

To asses whether heterogeneity, besides of species richness, affected patterns of species composition, I used the Redundancy analysis (RDA), a linear ordination method that ordinates samples according to species composition, subject to constraints by external „environmental“ predictors. I again used CANOCO version 4.5 (Lepš, Šmilauer, 2000), which allows for partial ordination analyses that include covariate terms, and tests the significance of models via the Monte Carlo tests. All permutations were computed using torroidal shifts within the 20*4 rectangle to account for the spatial structure of the data. They were again carried out separately for each taxonomic group and distance from the transect.

We first tested for separate efffects of the three predictors of habitat heterogenity. These analyses had transect length as the only covariable, and number, diversity or borders as environmental variable. Second, we tested for partial effects of heterogeneity in models that already included identity of biotopes. To do so, we computed RDAs that contained lenghts of individual biotopes along individual transect sections, using the CANOCO forward selection procedure to construct minimum adequate models. Next, we entered the variables selected by the forward selection as covariables onto the models, and checked for resitual variation explicable to number, diversity and borders.

Results

Together, the data refer to 348 species of higher plants, 54 species of butterflies, 45 species of spiders and 37 species of true bugs. Means/medians per section were 51.95 ±19.2 SD/53.0 (plants), 14.45 ± 4.95 SD/14.0 (butterflies), 3.0 ± 3.0 SD / 3,0 (spiders), 3.96 ± 2.028 SD/4.0 (true bugs). The values of species richness per section was all corellated (Pearson’s correlation, all $P < 0.05$). The same applied to the values of the three variables describing heterogeneity (all $P < 0.001$).

Species richness

Length of transect sections did not affect the species richness of plants, true bugs and spiders; it possitively influenced richness of butterflies (b = 0.24, F1,78 = 4.94, $P < 0.05$, explained deviance: 5.9%). The terms that entered spatial models were transect2 for plants, transect*section for butterflies and true bugs, and transect*section2 for spiders, fitting, respectively, 6.1, 16.2, 25.9 and 13.2 per cent of original deviance in species richness data (compared to covariate models, all $P < 0.05$).

In the models not controlling for biotope identity, the three predictors of heterogeneity exhibited positive effects on species richness, although the exact patterns differed among predictors and groups (Fig. 1). The explained variation in butterflies and true bugs was higher than in higher plants and spiders. In higher plants, diversity at 100 meters did not influence species richness, and effects of all predictors at 100 meters were weaker than at „zero“ and 500 meters. In butterflies, the predictors with no detectable effects were number (100 m) and borders (500 m), and all the effects were strongest, sustaining controls for spatial position, at 100 meters. In true bugs, no effects were detected at „zero“ meters, while the strongest effects were found at 500 meters. In spiders, there were no again significant effects at „zero“ meters; number increased the species richness at 100 m distance, while diversity and borders did so at both 100 and 500 metre distance.

The PCA ordination of biotopes used for preparing the biotope identity models (Fig. 2) pointed to three main gradients, the first (32.5% of variation in analysed data) distinguishing intensively managed and extensively managed non-arable biotopes, the second (18.15%) distinguishing non-arable biotopes and crop fields, and the third axis (16.7%) distinguishing biotopes with uniform herbaceous vegetation (both types of meadows, fields) from biotopes containing both short turf and scrub (pastures, steppe, clearings). Importantly, entering measures of heterogeneity to the PCA (as „additional environmental variables“, i.e. variables not affecting ordination resulsts) showed that heterogeneity increased with increasing proportions of „natural“ habitats, such as extensively managed meadows, wetlands or forest margins (Fig. 2).

The biotope identity models contained the first (plants), first plus second (butterflies), second (true bugs) and third (spiders) PCA axes. In these groups, they fitted 5.8, 22.19, 13.0 and 4.2 per cent of variation in species richness, respectively; the fits were significant in all cases but spiders, in which $P = 0.08$. The construction of spatial biotope identity models selected the following spatial terms: section2 (plants), transect2, transect*section (true bugs) and transect2*section (spiders). The respective fitted deviations were 7.4, 0.5, 13.8 and 13.2 per cent of null model deviation.

Entering heterogeneity predictors onto the biotope controlled models (Fig. 3) resulted, in higher plants, into loss of significance of heterogeneity at 100 meters, an exception being diversity if controlled for both biotopes and spatial autocorrelation. In butterflies, the positive effects of heterogeneity at 100 and 500 m were largely lost, except for number, 500 m, and border, 100 m. In true bugs, the effects of borders were lost, but effects of number

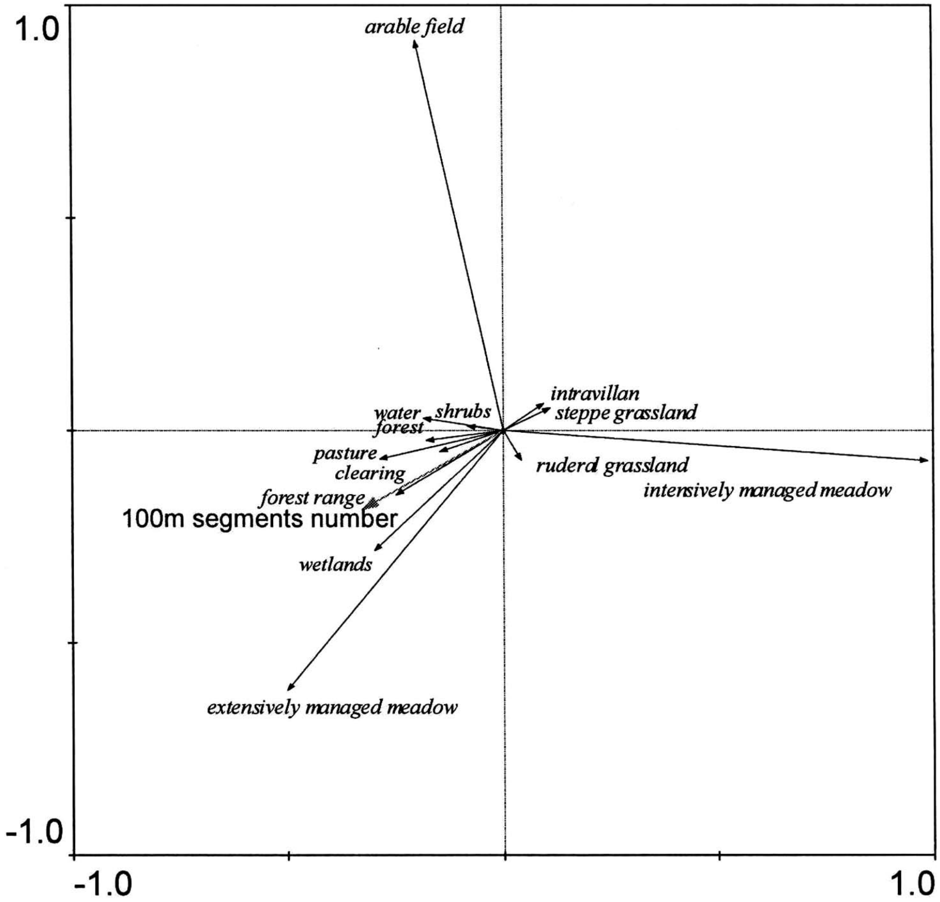

Fig. 2. PCA ordination biplot of effect of biotopes in 100 m. First canonical axis explained 32.5% of variability, the second axis explained 18.5% of variability, third axis explained 16.7% of variability and the fourth axis explained 3.9% of variability. The first ordination axis leads from intensively managed to extensively managed habitats and the second differentiates between arable field and shrubs and clearings.

and diversity remained significant and more important in larger (500 m) distance. Finally in spiders, the effects were largely similar, albeit weaker, to effects in models not controlled for biotope identity.

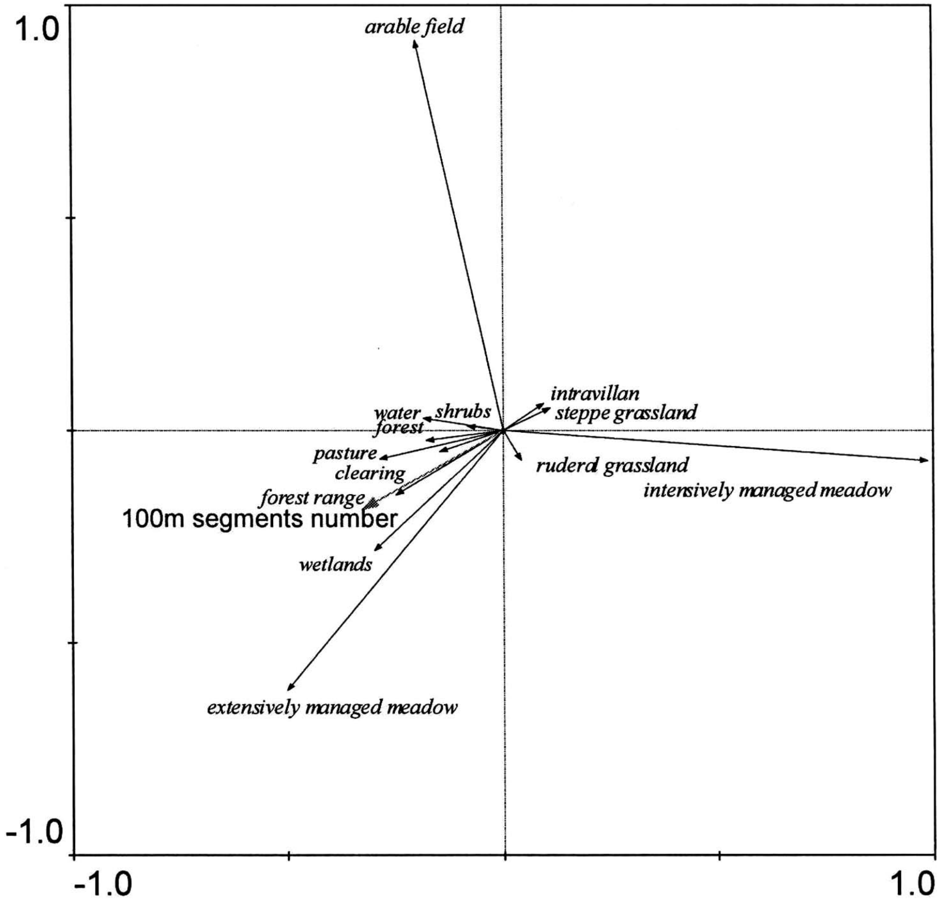

Fig. 3. Residual variation attributable to the three measures of heterogeneity, as returned by the GLM multipe regression models. The analysis with the effect of biotopes. Black columns stand for significant nominally results (P < 0.05) and white columns stand for non-significant results. Numbers from 0-500 are the distance from the transect line. "s" by the numbers means, that space was included in the model.

Species composition

Regarding species composition (Table 1), all descriptors of heterogeneity had significant effects on plants in 0 and 100 m; at 500 m, the effect of diversity was lost. Species associated with high values of heterogeneity tended to be plants of seminatural meadows and wetland biotopes (e.g., *Trollius europaeus, Caltha palustris, Bistorta major*). In contrast, agricultural weeds and ruderal species were associated with low heterogeneity values (e.g., T a b l e 1. Results of two kinds of RDA ordination analyses for the number of segments, Simpson´s Diversity of the rectangles, the lenghth of segment borders and the distance from the transect as the environmental variable and the area and biotopes as covariables. It show the influence of presence/absence of habitat and of the habitat heterogenity to the species diversity of butterflies, true bugs, flowering plants and spiders. The first figure shows a sum of all eigenvalues, the second one show the sum of all canonical eigenvalues. The third values is p. B before the distance means, that there were used biotopes as covariable.

Distance from transect (m)	**0**			**100**			**500**			**B0**			**B100**			**B500**		
BUTTERFLIES																		
number	0.979	0.033	***	0.984	0.028	*	0.980	0.052	**	0.803	0.018	***	0.803	0.015	ns	0.834	0.015	ns
diversity	0.979	0.045	***	0.984	0.046	*	0.980	0.032	*	0.803	0.019	***	0.803	0.012	ns	0.834	0.015	ns
lenght				0.984	0.042	*	0.980	0.039	*				0.803	0.016	ns	0.834	0.016	ns
TRUE BUGS																		
number	0.984	0.011	ns	0.986	0.037	*	0.981	0.035	**	0.890	0.008	ns	0.890	0.026	*	0.890	0.023	*
diversity	0.984	0.018	ns	0.986	0.034	*	0.981	0.047	**	0.890	0.009	ns	0.890	0.018	ns	0.834	0.008	ns
lenght				0.986	0.029	*	0.981	0.045	*				0.890	0.021	*	0.890	0.025	*
PLANTS																		
number	0.983	0.020	***	0.980	0.021	*	0.981	0.025	*	0.759	0.013	ns	0.759	0.015	ns	0.759	0.018	*
diversity	0.983	0.028	***	0.980	0.023	*	0.981	0.021	ns	0.759	0.014	ns	0.759	0.011	ns	0.759	0.013	ns
lenght				0.980	0.023	*	0.981	0.023	*				0.759	0.018	**	0.759	0.019	*
SPIDERS																		
number	0.988	0.014	ns	0.985	0.020	ns	0.986	0.013	ns	0.974	0.014	ns	0.974	0.021	ns	0.974	0.013	ns
diversity	0.988	0.020	ns	0.985	0.020	ns	0.986	0.018	ns	0.974	0.017	ns	0.974	0.017	ns	0.974	0.017	ns
lenght				0.985	0.015	ns	0.986	0.028	*				0.974	0.015	ns	0.974	0.026	ns

	Selected variables	**1st axis trace**	**1. st axis F, p**	**all axes trace**	**All axes F, p**
Plants	arable field, wetland, intensively managed meadow, extensively managed meadow, steppe grassland, forest, ruderal grassland, ponds	0.07	F=5.96 **	0.24	F=2.80 **
Butterflies	extensively manager meadow, steppe grassland, wetland, shrubs, forest range, ponds	0.13	F=9.66; ***	0.30	F=2.19; ***
Bugs	wetland, forest range, arable field	0.06	F=4.99; **	0.11	F=3.12; **
Spiders	clearing	0.05	F=3.34; ns	0.21	F=1.35; **

Table 2. Results of RDA analysis using forward Selection to select the biotopes for a biotope identity model. For each taxonomic group the selected biotopes were different.Table 1. Results of two kinds of RDA ordination analyses for the number of segments, Simpson´s Diversity of the rectangles, the lenghth of segment borders and the distance from the transect as the environmental variable and the area and biotopes as covariables. It show the influence of presence/absence of habitat and of the habitat heterogenity to the species diversity of butterflies, true bugs, flowering plants and spiders. The first figure shows a sum of all eigenvalues, the second one show the sum of all canonical eigenvalues. The third values is p. B before the distance means, that there were used biotopes as covariable.

Lamium album, Carum carvi, *Centaurea cyanea*). In butterflies, all heterogeneity predictors exhibited effects in all distances, and it was notable that species responding positively to heterogeneity were those associated with such habitats as forest edges (e.g., *Anthocharis cardamines, Melitaea athalia*). In contrast, generalists of agricultural landscapes (*Pieris rapae, Coenonymha pamphillus*) tended to respond negatively. Species composition of true bugs showed no response to heterogeneity in short distances, but the effects manifested in longer distances. The positively responding species tended species characteristic to weedy, ruderal vegetaion (*Rhopalus subrufus, Graphosoma lineatum*), whereas against diversity were the species of extensively managed meadows. Finally, the composition of spiders did not show any clear pattern. Only in 500 m the effect of segment borders appeared as significant.

The minimum adequate models constructed by the RDA forward-selection of biotopes explained, in average, 13% of variation in species data (minimum 11% for spiders, maximum 24% for butterflies) (Table 2). Including these forward-selected predictors as covariables onto the ordinations dramatically changed the heterogeneity patterns. In plants, heterogeneity retained its effects in 100 (borders) and 500 (borders and number) m. In butterflies, only local herogeneity remained important. The situation in true bugs was alike in plants, showing significant effect of heterogeneity in 100 and 500 m. In spiders the situation was similar as in the model without biotope identity, but there were no significant results.

Discussion

Responses of individual taxa

The study showed strong importace of habitat heterogeneity for species richness, but the effects are different for different taxa and at different scales. It also attempted to partition the influences of biotope identity from the heterogeneity itself. Some authors (Ewers, Didham, 2006) observed that the influence of habitat heterogeneity can be confounded by many other factors as the climate, trophic strategie, etc., but vast majority of them do not realize, that there is necessary to deal with the biotope identity, which can change dramatically the results of the analyses. It seems that it can weaken the impact of habitat heterogeneity to species composition and richness, as it also appeared in our analyses.

If evaluated without control for biotope identity, response of butterflies and true bug to the habitat heterogeneity were stronger (in terms of explained variation) than in case of spiders and plants. The strong importance of heterogeneity has already been noted, for true bugs, by Duelli (2001), and for butterflies, e.g., by Krauss et al. (2004). It is also expectable from life histories of individual representatives of these groups, which may depend on different resources (adult vs. pre-adult sources, basking, hiding, and mate-locating places etc.) during different phases of their developent (Dennis et al., 2003). Spiders, as a predatory group, and sessile plants, are more likely to obtain all resources from a given habitat, which may decrease the importance of dense clumping of various biotopes types for their persistence.

Regarding scale, the three animal taxa exhibited the strongest responses at intermediate scale tested of 100 m, whereas plants responded to heterogeneity either right at the transects or at the largest distances tested of 500 m. This pattern conforms to known ranges of lifetime home range movements of „average“ butterfly, true bug or spider, which occur at a scale of tens to hundreds meters in these groups (e.g., butterflies: Van Dyck, Baguette, 2005; bugs:

Schooley, Wiens, 2004; spiders: Winder, 2004). In plants, the patterns of heterogeneity were rather strong at „zero“ distances- it is not surprising: the biotope types were defined by vegetation and the more vegetation types, the more constituing species. At the large distances, however, the pattern likely reflects a more profound effect of richness of species pool available as sources of propagules (Bruun, 2006; Bruno, 2004).

Inclusion of biopope identities considerably changed the outcomes. The effects of heterogeneity weakened considerably, suggesting that some of the positive responses of species richness to heterogeneity reported in literature (Weibull et al., 2000; Bergman et al., 2004) could be, at least in part, inflated due to not controlling for biotope effects. Still, heterogeneity increased species richness, although different taxa responded to different heterogeneity measures. The residual positive responses to heterogeneity thus confirms its importance for maintaining high species richness in human dominated landscapes.

The highest decrease of explained variance occured in butterflies. Reversing this argument, they exhibited strongest response to biotopes. A likely reason stems from the scale of the transect study, and biotope delimitaiton. Both were designed primarily for butterfly monitoring (cf. Zimmermann et al., 2005) and thus, for instance, distinguished between meadows mown once and twice. Mowing regimes have profound effect on butterflies (Louault et al., 2005; Saarinen et al., 2005) but hardly on other higher plants or bugs. As a result, fitting biotope identity explained the highest proportions of variation for butterflies. Recall that the biotope identity model for butterflies contained two sets of ordination axes scores, whereas the models for other taxa contained just one axis. The point is also illustrated by exact composition of the biotope identity models. First (or „most important“) PCA axis passed only for butterflies, second axis passed for three groups, whereas third axis passed as the only predictor for spiders. Clearly, richness different taxa responded to different environmental gradients.

Whereas the influence of heterogeneity to the species richness was discussed by many authors, there is a minimum of studies focused on its impact to the species composition. In our analyses, the effect of heterogeneity was strong, closely tied to biotopes involved. Control for biotope identities preserved some heterogeneity effects only for butterflies, local situation at the transect), true bugs and plants (both intermediate and large distances). Notably, the predictor that most often remained significant was length, suggestiong that there were some edge specialists in these three groups that responded to high amount of edges rather than to areas of particular biotopes. Edges may be important, e.g., as mate-locating sites for butterflies (Conradt, Roper, 2006), or as biotopes of some „weedy“ or „ecotonal“ plants attracting specialised Heteroptera (Schooley, 2004).

Still, the the heterogeneity effects on species composition decreased more markedly than the effects on species composition. This suggests that only few species require heterogeneity per se, much more respond to biotopes, and it is mainly the richness of biotopes in heterogeneous regions that generates high diversity. Indeed, the fact that biotopes more valuable from a conservation point of view (extensive grasslands, wetlands) (Wood, 2001) were more heterogeneous than less valuable biotopes (intensive meadows, fields) (Fig. 4.) shows that the two patterns are strongly interrelated.

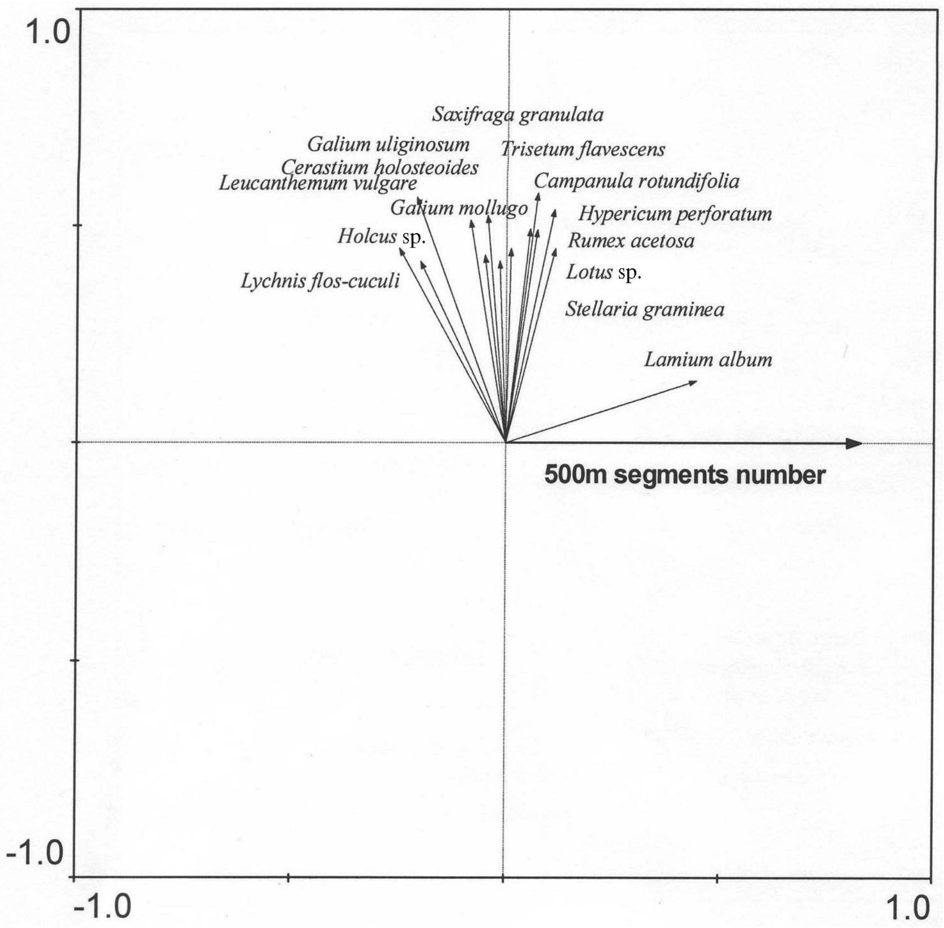

Fig. 4. RDA ordination biplot showing the effect of number of segments to species diversity of plants in 500 m distance from the transect line, with an area as a covariable. First axis explained 2.5% of variability, second axis explained 10.5% of variability, third axis 6.7% and fourth axis explained 4.7% of variability.

Conclusion

Habitat heterogeneity strongly affects the species richness of the observed taxons, especially butterflies and true bugs. After adding the biotope identity to the model the impact of habitat heterogeneity dies away. But, on the contrary, species richness of higher plants and spiders was not so affected by the biotope identity.

From heterogeneity predictors, the species richness of higher plants was mainly affected by number of segments and borders and butterfly species richness was strongly affected by number of segments and diversity. By true bugs the strongest impact had number of segments and diversity, similarly as by spiders, which species richness was also strongly affected by borders.

Habitat heterogeneity also affects the species composition of the taxons. In large distance the most affected taxons were true bugs and plants even after adding the effect of biotope identity.

The effect of biotope is very important in assessing the species richness and it can strongly affect the results. Point of view is very important factor, i.e. the identity of a biotope from a butterfly point of view is not the same as, e.g., by spiders.

Translated by the authors

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