# Pattern of local plant species richness along a gradient of landscape topographical heterogeneity: result of spatial mass effect or environmental shift?

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Several processes are hypothesised to mediate the relationship between local (microsite) plant species richness and the topographical heterogeneity of the surrounding landscape. In a topographically heterogeneous landscape with various habitats occurring close to each other, local species richness may be enriched by species from surrounding habitats due to the spatial mass effect (sink-source dynamics). In contrast, increased habitat fragmentation due to spatial heterogeneity may have a negative effect on local species richness. The spatial mass effect is thought to be more pronounced in communities with a higher ratio of generalists, as generalists are more likely to establish viable populations in sink habitats. To reveal the pattern of local species richness along a gradient of landscape topographical heterogeneity at middle altitudes of the Bohemian Massif, we used 2551 forest vegetation plots stored in the Czech National Phytosociological Database. We developed an analytical approach relating the pattern of local species richness of vegetation types to the gradient of landscape topographical heterogeneity. An increase or decrease in species richness with increasing landscape heterogeneity was related to changes in the generalist/specialist ratio, and also to changes in soil reaction and productivity estimated through Ellenberg indicator values. Local species richness along a gradient of increasing landscape heterogeneity increased in nutrient-poor vegetation and decreased in nutrient-rich vegetation. Nutrient-poor vegetation types, such as thermophilous and acidophilous oak forests, also had a high proportion of habitat generalists, supporting the hypothesis that increased richness in heterogeneous landscapes may result from the spatial mass effect. However, the same pattern may be explained by a shift in environmental conditions along the landscape heterogeneity gradient, such as increasing productivity of nutrient-rich vegetation types or increasing soil reaction of most vegetation types in more heterogeneous landscapes. We discuss available evidence and conclude that these two explanations need not be mutually exclusive.

Environmental heterogeneity is considered as one of the most important drivers of biological diversity (Huston 1994, Rosenzweig 1995, Sarr et al. 2005). Topographical heterogeneity is a special case, as it strongly affects other types of landscape heterogeneity, e.g. variation in mesoclimate, natural disturbances, soil conditions or intensity of human impact. The main effect of landscape-scale topographical heterogeneity on local (microsite) species richness can be seen in the control of the spatial configuration of habitats surrounding the target site. In a topographically homogeneous landscape, a site's neighbourhood usually contains the same or similar habitats, while in a heterogeneous landscape very different habitats may be found close to the target site. The effect of spatial configuration of neighbourhood habitats on local species richness has been demonstrated in a number of empirical studies (e.g. Gabriel et al. 2005, Kumar et al. 2006), as well as in simulation models (Palmer 1992, Steiner and Köhler 2003). Fewer

studies have directly evaluated the effect of topographical heterogeneity (Jobbágy et al. 1996, Dufour et al. 2006, Hofer et al. 2008).

There are several processes that may drive local species richness patterns along the gradient of landscape heterogeneity. Increasing topographical heterogeneity results not only in a higher diversity of habitats occurring close to each other, but also in a reduction in the size of particular habitat patches and therefore habitat fragmentation. The theory of island biogeography (MacArthur and Wilson 1967) predicts that increasing habitat fragmentation in heterogeneous landscapes would itself result in decreasing local species richness, as smaller and isolated habitat fragments are more prone to species extinction than large ones (see Fahrig 2003 for a review of the effect of habitat fragmentation on biodiversity). However, habitat fragments in a heterogeneous landscape differ from islands in the sea in that they are rarely surrounded by completely different habitats.

Thus, the spatial mass effect (or vicinism; Shmida and Ellner 1984, van der Maarel 1995, Zonneveld 1995) may play a role here, which is another important process with a contradictory effect on local species richness. It assumes that a species can occur in an unfavourable habitat where it cannot regenerate due to influx of propagules from a vital source population existing in a nearby favourable habitat (Shmida and Ellner 1984). In a heterogeneous landscape, where more habitats occur close to each other, the probability of the spatial mass effect happening increases, and the enrichment of the target habitat for vicinists (species from surrounding habitats) increases too. As a result, local species richness may be higher in a heterogeneous landscape.

In their simulation study, Steiner and Köhler (2003) concluded that the importance of the spatial mass effect on species richness increases with an increasing proportion of habitat generalists in a community, as generalists can survive in a variety of habitats (Holt 1997). Therefore, we hypothesised that the change in the ratio of generalists to specialists along the gradient of landscape heterogeneity, measured within vegetation types, gives an indication that the spatial mass effect plays a role. However, the spatial mass effect and fragmentation may not be the only processes responsible for changes in species richness along the gradient of landscape heterogeneity. There may be a systematic shift in local environmental factors along the gradient of landscape heterogeneity, and these local factors may control local species richness. Here, we particularly focus on the gradual shift in local soil pH and productivity, as both of these variables are known to exert strong controls on species richness. The relationship between soil pH and species richness in the temperate and boreal zones is most frequently reported as positive linear (Pärtel 2002, Gilbert and Lechowicz 2005), although across the entire pH range existing in nature it is ultimately unimodal (Chytrý et al. 2007, Hájek et al. 2007). The pattern of species richness along the productivity gradient is usually reported as unimodal (Waide et al. 1999, Gough et al. 2000, Mittelbach et al. 2001; but see Gillman and Wright 2006). While for the productivity-diversity pattern there are at least two sets of possible interpretations, one based on local biotic interactions (see Grace 1999 for a review) and the other based on the species pool hypothesis (Schamp et al. 2002, 2003), explanation of the pH-diversity pattern is based solely on the species pool hypothesis (Pärtel 2002, Ewald 2003, Peet et al. 2003).

When studying the effect of landscape context on local species richness, it is important to consider different vegetation types separately. There are two reasons for this. First, the magnitude and direction of the effect can vary among vegetation types, and the analysis of pooled data could obscure opposite trends. Second, vegetation types differ in the size of their species pools, therefore comparison of species richness across vegetation types (thus across species pools of different sizes) may reflect the effects of species pools rather than of landscape context. Therefore, we developed a method capable of identifying species richness patterns along the gradient of landscape heterogeneity, based on the separate analyses of data subsets with similar vegetation composition.

In this study, we address the following questions: 1) what is the pattern of local species richness within different vegetation types along the gradient of increasing topographical heterogeneity? 2) Can this pattern result from the spatial mass effect? 3) Can this pattern also be attributed to a systematic shift in local habitat conditions such as soil reaction and productivity?

## Methods

### Vegetation data

All analyses in this paper are based on data from the Czech National Phytosociological Database, which contains >88 000 vegetation survey plots (relevés) of various vegetation types recorded using the Braun-Blanquet approach (Westhoff and van der Maarel 1978) in the Czech Republic (Chytrý and Rafajová 2003). We selected georeferenced forest plots that had been assigned by their authors to phytosociological vegetation units at least at the class level. All of the selected plots represented natural forest vegetation, i.e. that with canopy trees originating from natural regeneration. Plantations of trees that naturally occur in other habitats were excluded. Some of these forests were managed by coppicing in the past, but due to state ownership of Czech forests since the mid 20th century and abandonment of coppicing at the same time or earlier, the effects of forest management were comparable among the plots. To ensure that no forest vegetation type was represented by a disproportionately high number of plots from a small area, and to limit the effect of spatial autocorrelation, which was not controlled further in the analysis, the dataset was geographically stratified (Knollová et al. 2005). This stratification was performed in a geographical grid with cells of 1.25 minutes of longitude × 0.75 minutes of latitude (ca 1.5 × 1.4 km) in the following way: if more than one plot assigned by their authors to the same phytosociological association occurred within the same grid cell, only one of them was selected, with a preference for the most recently sampled plot. Records of bryophytes, lichens, juvenile woody plants and their seedlings were deleted and records of the same species in different vegetation layers were merged. To limit the effect of altitude, only plots from the altitudinal range of 250–480 m a.s.l. were included in further analysis. Plots $<100$ m$^2$ or $>400$ m$^2$ were removed, as well as plots from rare or ecologically extreme forest types (e.g. thermophilous oak forests on base-rich bedrock and peatland pine forests). The resulting dataset used for the analysis contained 2551 plots (Fig. 1).

### Local species richness, soil reaction and productivity

Local species richness, as referred to in the text, is the number of all vascular plant species occurring in the plot. Soil reaction and productivity for each plot were estimated as unweighted mean Ellenberg indicator values (Ellenberg et al. 1992) for soil reaction and nutrients, respectively. Here, Ellenberg indicator values for nutrients are interpreted as a measure of productivity, following Hill and Carey (1997) and Schaffers and Sýkora (2000).
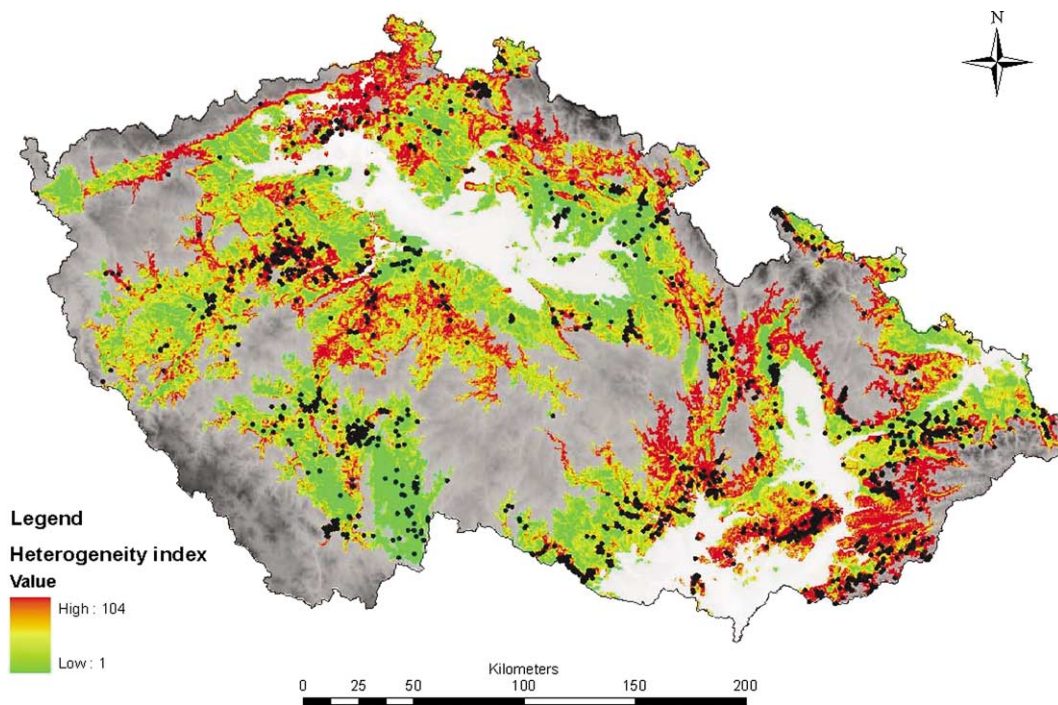
Figure 1. Map of the Czech Republic, with locations of vegetation plots (black dots) used in the analysis and projection of landscape topographical heterogeneity from low (green colour) to high (red colour) in the area falling within the altitudinal range of 250–480 m (the area below or above this range is coloured grey).

## Landscape heterogeneity

The heterogeneity of the landscape surrounding each plot was calculated from the digital terrain model of the Czech Republic (with pixel resolution of $50 \times 50$ m) using the Terrain Ruggedness Index (Riley et al. 1999) and the ArcGIS 8.3 software (ESRI, Redlands, CA, USA). The position of each plot was projected onto the digital terrain model. For a circle of fixed radius around it, the square rooted mean of squared differences between the altitude of the central grid cell and other cells falling within the circle was calculated. We arbitrarily set the circle radius corresponding to the length of six grid cells (300 m), following Kumar et al. (2006), who showed the best predictive power of landscape heterogeneity on local species richness when calculated from circles with a radius of 240 m. The gradient from the plots with low values of landscape topographical heterogeneity ("homogeneous landscape") toward the plots with high values of landscape topographical heterogeneity ("heterogeneous landscape") is further referred to as "gradient of landscape heterogeneity".

## Species habitat specialisation

We used the measure of species habitat specialisation proposed by Fridley et al. (2007), based on the species co-occurrences in large datasets. This measure assumes that, in a large dataset, habitat specialists, which are confined to specific habitats, will systematically co-occur with a limited number of other species, adapted to the same habitat, whereas habitat generalists, which are able to grow in a wide range of habitats, will co-occur with many species. The

metric, called theta ($\theta$), is in fact the beta diversity of the set of plots that contain the target species, accounting for the differences in species frequencies in the dataset: a low $\theta$ value (low beta diversity) indicates a habitat specialist, a high $\theta$ value (high beta diversity) indicates a habitat generalist. The original algorithm (Fridley et al. 2007) used beta diversity based on additive partitioning of diversity, which is, however, affected by the size of the species pool. In this paper, we used a modified version of the original algorithm according to Zelený (2009), which replaces the additive partitioning measure with Whittaker's beta diversity measure, thus removing the confounding effect of species pool size. This algorithm was applied to a geographically stratified dataset of 43 814 plots of all vegetation types from the Czech National Phytosociological Database. The $\theta$ value was calculated for all species with $>10$ occurrences. In the dataset of 2551 plots, one third of species with the highest $\theta$ values were considered as generalists, and the proportion of generalists to the total number of species was calculated for each plot.

## Statistical analyses

As local species richness of different vegetation types is derived from species pools of various sizes, we developed a method which enables an analysis of the pattern of local species richness (and other variables) along the gradient of landscape heterogeneity for each vegetation type separately. For each of the 2551 plots we generated a group including this plot and the 99 plots with most similar species composition according to the Bray-Curtis distances, calculated from the square rooted percentage species covers
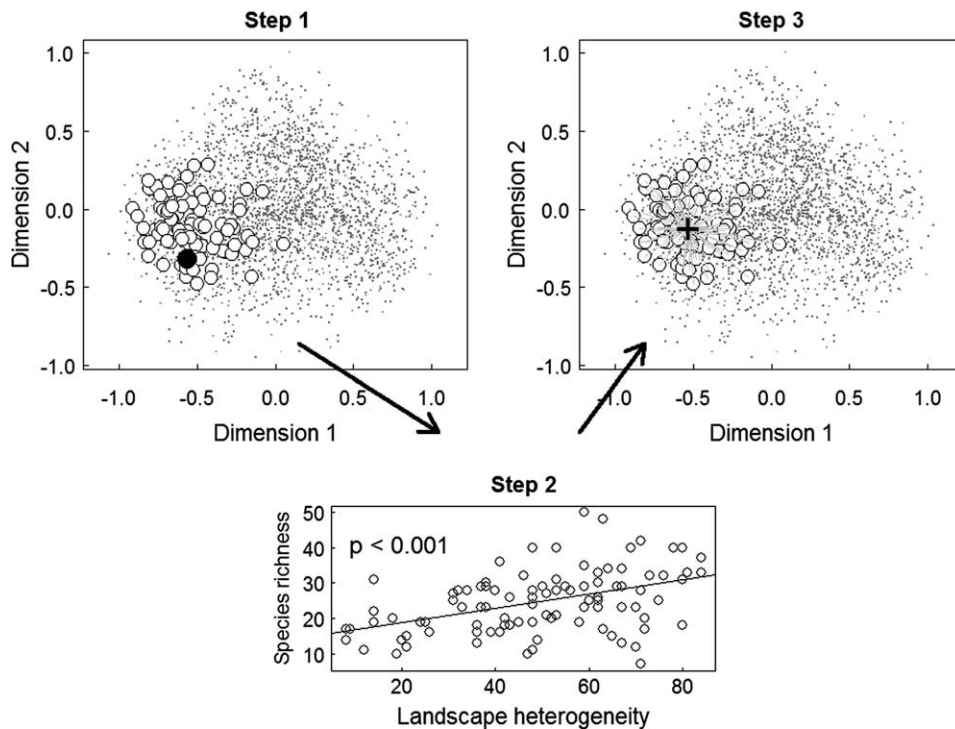
Figure 2. Scheme of the repeated-correlation analysis. The solid dark circle in the upper left part of the figure indicates the position of a randomly selected plot in the space of the NMDS ordination diagram. For this plot, 99 plots with most similar species composition were selected, with their position indicated by empty circles (step 1). The selected plots were used for correlation analysis between species richness and landscape heterogeneity (step 2, for simplicity showing the correlation between species richness and landscape heterogeneity, while in reality we used GLM with the plot area as a covariable). The result of this analysis was significant and positive, and this information was projected back onto the original ordination diagram as a plus symbol in the weighted centroid of the analysed plots (step 3); a minus sign would be projected in the case of a significant negative relationship and an empty circle in the case of a non-significant relationship.

(Fig. 2, step 1). For further analyses, we compared all groups with each other and if two groups shared more than two thirds (i.e. >66) of plots, we randomly deleted one of these groups; after this procedure, 1684 groups were left for further analyses. To allow interpretation of the pattern at the level of vegetation types as well, we classified all plots into six vegetation types, using cluster analysis with the flexible beta linkage method (beta = −0.25) and the Bray-Curtis distance applied to the square rooted percentage species covers. The method used, the number of resulting vegetation types and their delimitation were selected subjectively based on the preliminary analysis and expert judgment, in order to distinguish the major vegetation types of broadleaf and mixed coniferous forest occurring at middle altitudes of the Czech Republic. Each group of 100 plots was assigned to the vegetation type that was represented by most plots within the group (as a result, 99% of groups were assigned to the type that was represented by at least 33 plots, and 75% of groups to the type represented by at least 50 plots). The result of vegetation classification was projected onto the space of ordination diagram prepared by non-metric multidimensional scaling (NMDS, Minchin 1987, Oksanen et al. 2008) of all 2551 plots, calculated using the Bray-Curtis distances and square rooted percentage species covers. Vectors of Ellenberg indicator values for moisture, nutrients, soil reaction, light and temperature, fitted to the original sample scores of 2551 plots, were projected a posteriori onto this diagram to ease its interpretation.

For plots of each group of 100 plots, we used general linear models (GLM, McCullagh and Nelder 1989) to calculate the relationship between landscape heterogeneity and 1) local species richness (Fig. 2, step 2), 2) soil reaction, 3) nutrients (productivity) and 4) proportion of generalists. Models with local species richness as the dependent variable used a logarithmic canonical link function and also included plot area as a co-variable in order to account for variable plot size (100–400 m$^2$); other models used an identity link function. Signs of the significant correlations ($p < 0.05$) were projected onto the NMDS ordination diagram (Fig. 2, step 3) in the centroid position of each group. Significant results were plotted as plus signs in the case of positive and minus signs in the case of negative correlation; non-significant correlations were indicated by an empty grey circle. This analysis is further referred to as repeated-correlation analysis.

It is important to note that the entire study is designed to reveal patterns in the data rather than to test null hypotheses. We are aware of the fact that phytosociological data, obtained by non-random preferential sampling, may violate the basic assumption of traditional statistical tests, which require that input data are sampled at random. Consequently, the significance values calculated by statistical tests performed on non-randomly sampled data or variables directly derived from them may be unreliable (Lájer 2007). Here, a threshold for significance of correlation analysis (performed by GLM) was set in order to quantify the result of repeated-correlation analysis, which is
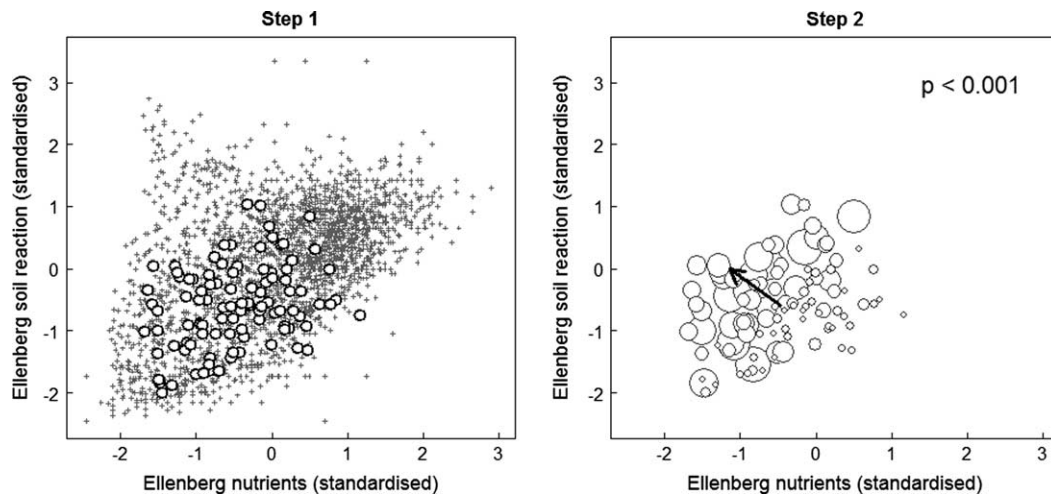
Figure 3. Scheme of the vector analysis, which visualises the complex relationship between landscape heterogeneity and gradients of productivity, soil reaction and species pool size. Two-dimensional ecospace is defined by the gradient of productivity (horizontal axis) and soil reaction (vertical axis), which are represented by transformed and standardised mean Ellenberg indicator values for nutrients and soil reaction, respectively. Step 1 shows the projection of all plots (small grey crosses) onto the ecospace (the position of each plot is defined by its mean Ellenberg indicator value for nutrients and soil reaction) and the projection of 100 plots (empty circles) belonging to one selected group. The pattern of landscape heterogeneity for these 100 plots is shown in step 2, with the circle size increasing with the heterogeneity of the landscape around each plot. The arrow shows the direction of the steepest increase in landscape heterogeneity across the ecospace (with the maximal correlation with particular axes).

interpreted on the basis of the counts of significant ($p < 0.05$) correlations; as a result, these counts may be slightly over- or underestimated. In fact, the repeated-correlation analysis is a multidimensional variant of moving window regression (Walker et al. 2003, Palmer 2006). The original method of moving window regression was designed for one gradient and a moving window sliding along this gradient, with the samples falling within this window in each step subjected to regression analysis. In this study, the sliding was done in a hypothetical multidimensional ecospace, with each window containing plots with similar species composition and two windows close to each other sharing no more than 66% of plots.

As each analysis consisted of 1684 independent correlations, some kind of correction for multiple comparisons was necessary. Therefore we performed the Monte Carlo permutation test for each analysis: values of both dependent and independent variables were randomised and the same set of 1684 correlations was calculated. This procedure was repeated 199 times in order to obtain the distribution of the number of significant correlations from each run. Based on this distribution, we were able to determine the probability that a given number of significant correlations in the analysis resulted from random effects. We are aware that the partial correlations within the repeated-correlation analysis are not independent, as they may share up to 66% of samples, and this fact may unpredictably violate the results of the Monte Carlo permutation test, which requires independent samples. Thus, we treated the results of the Monte Carlo permutation test as a rough indication, without any intention to test and reject a null hypothesis.

The last analysis, hereafter called vector analysis, visualises the relationship between landscape heterogeneity on the one hand and productivity, soil reaction and species pool size on the other hand. We established a two-dimensional ecospace, defined by Ellenberg indicator values

for nutrients and soil reaction (Fig. 3, step 1). As the original distribution of Ellenberg indicator values was strongly skewed, nutrient values were transformed by the second power function and soil reaction values by the third power function, and both were further standardised to the zero mean and unit variance. The position of each of the 2551 plots in this ecospace is given by its mean Ellenberg indicator values for nutrients and soil reaction (small grey crosses in Fig. 3, step 1). For each group of 100 plots, used in the repeated-correlation analysis, we plotted the position of each plot in this ecospace (empty circles in Fig. 3, step 1). Each plot was assigned its value of landscape heterogeneity (indicated by the size of the circle in Fig. 3, step 2) and the direction in the ecospace toward which the landscape heterogeneity increases most rapidly was calculated and indicated by a vector (Fig. 3, step 2). The significance of the fitted vectors was assessed by the Monte Carlo test based on 199 permutations of heterogeneity values among plots within each group and the criterion of goodness of fit based on the squared correlation coefficients (Oksanen et al. 2008); the length of the vector is proportional to this squared correlation coefficient. This procedure was repeated for all 1684 groups and only significant vectors ($p < 0.05$) were considered in further analysis. Of these, we selected only the vectors for groups that had a significant correlation between species richness and landscape heterogeneity and also significant correlation between either nutrients and landscape heterogeneity or soil reaction and landscape heterogeneity; these vectors were projected onto the ecospace, separately for positive and negative correlations of species richness and landscape heterogeneity. Additionally, we drew the isolines of estimated species pool size within the ecospace. This estimate was based on the information from the geographically stratified dataset extracted from the Czech National Phytosociological Database including 4644 forest plots from the altitudinal

range of 250–480 m, which were projected onto the ecospace according to their mean Ellenberg indicator values for nutrients and soil reaction. Then we generated 1000 random locations within the ecospace, took one of them, surrounded it by a circle of constant diameter, randomly selected 10 plots falling within this circle and counted the number of species occurring in these plots as an estimate of species pool size in the given location of ecospace. This procedure was repeated for all 1000 locations and the results were fitted by a smooth surface using thin plate spline fitting (Oksanen et al. 2008). This procedure can visualise the trends of increase or decrease in the species pool size related to the gradients of productivity and soil reaction.

All statistical analyses were carried out in the R program (R Development Core Team 2008). Plot data were edited and mean Ellenberg indicator values were calculated in the JUICE 6.5 program (Tichý 2002), and vegetation classification was done in the PC-ORD 5 program (McCune and Mefford 1999).

## Results

The NMDS ordination diagram (Fig. 4) reveals the relationships between the distinguished forest vegetation types in terms of main ecological gradients, described by Ellenberg indicator values. The first ordination axis is correlated with nutrients and moisture, separating (from the left to the right) oak forests, oak-hornbeam forests, ravine forests and alluvial forests. The second axis is correlated with soil reaction, light and temperature, with thermophilous oak forests placed in the warmer and base-rich part of the gradient (bottom) and beech forests in colder and more acid conditions (top).

Nutrient-poor vegetation types (such as thermophilous and acidophilous oak forests) situated on the left of the ordination diagram tend to be locally more species-rich in heterogeneous than in homogeneous landscapes (prevalence of positive correlations in Fig. 5). In contrast, nutrient-rich vegetation types (such as beech and ravine forests) on the right of the ordination diagram have lower local species richness in heterogeneous than in homogeneous landscapes. The exception from this pattern is alluvial forests, which are extremely rich in nutrients, but have a positive correlation between local species richness and landscape heterogeneity.

The differences between vegetation types in the proportion of generalists are similar to the pattern of local species richness along the gradient of landscape heterogeneity (Fig. 6). Both thermophilous and acidophilous oak forests have a high proportion of generalists, while beech forests, oak-hornbeam forests and ravine forests have a high proportion of specialists. The proportion of generalists is mainly negatively correlated with landscape heterogeneity in the nutrient-rich (right) part of the vegetation continuum, with a few positive correlations in the nutrient-poor (left) part (Fig. 7a–b). However, when only those groups (of 100 plots) that have significant correlations between the proportion of generalists and landscape heterogeneity (Fig. 7a), and between species richness and landscape heterogeneity (Fig. 5a), are selected, it appears that no vegetation type has a markedly increased proportion of generalists in a heterogeneous landscape related to changes in local species richness, and only alluvial and ravine forests and partly also thermophilous oak forests have a remarkable decrease in the proportion of generalists (Fig. 7b).

Soil reaction, as expressed by Ellenberg indicator values, generally increases with increasing landscape heterogeneity (Fig. 7c–d). If we select only the groups (of 100 plots) with a significant species richness–landscape heterogeneity relationship, the pattern of increasing soil reaction along the gradient of increasing landscape heterogeneity is the most apparent for both thermophilous and acidophilous oak forests, while it is least apparent for beech forests. In contrast, correlations between Ellenberg indicator values for nutrients and landscape heterogeneity (Fig. 7e–f) change along the gradient of increasing productivity from negative to positive (with the exception of alluvial forests at the right end). If only groups (of 100 plots) with a significant species
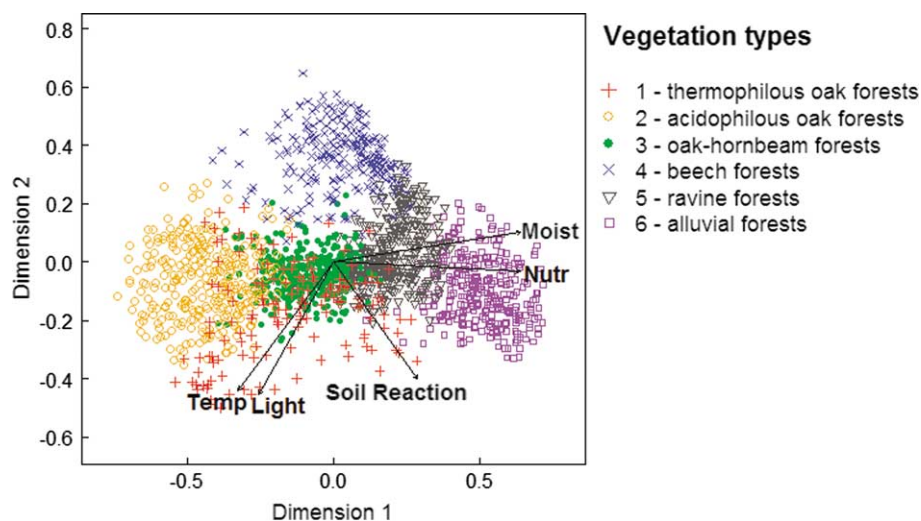


Figure 4. Vegetation types in the space of the NMDS ordination diagram, with passively projected Ellenberg indicator values for moisture (Moist), nutrients (Nutr), soil reaction, light and temperature (Temp). Each symbol represents groups of 100 plots. Vegetation types: 1 – thermophilous oak forests, 2 – acidophilous oak forests, 3 – oak-hornbeam forests, 4 – beech forests, 5 – ravine forests and 6 – alluvial forests.

**(a) Species richness vs heterogeneity**

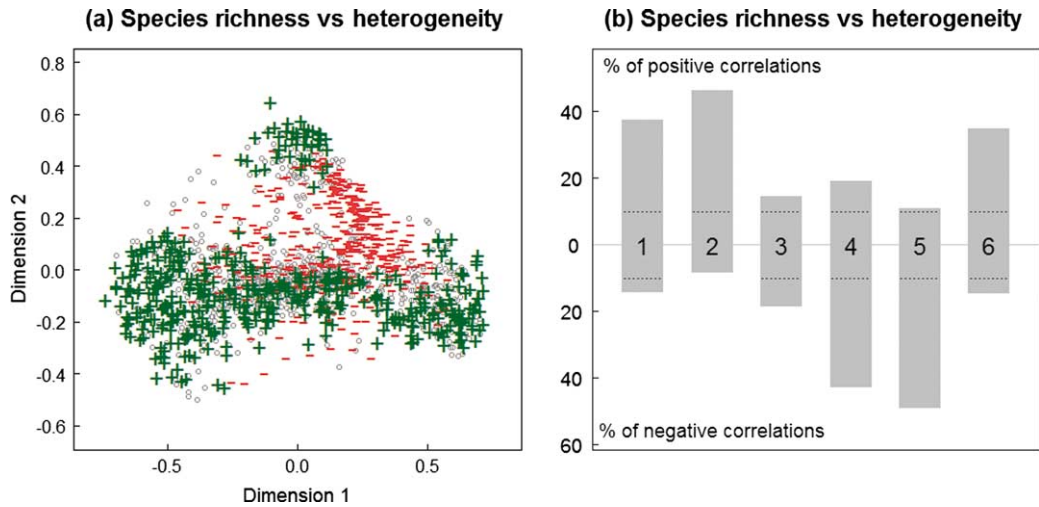**(b) Species richness vs heterogeneity**

Figure 5. Results of the repeated-correlation analysis between species richness and landscape topographical heterogeneity projected onto the NMDS ordination diagram (a) and expressed as the percentage of positive or negative correlations within a particular vegetation type (b). Plus symbols on the left of the diagram indicate significant positive correlations within each group of 100 plots, minus symbols indicate significant negative correlations and open grey circles indicate non-significant correlations. The height of the bars in (b) reflects the percentage of significant positive (upwards) or negative (downwards) correlations; the dotted lines indicate the interpretation threshold (10%) set up by the Monte Carlo test. Vegetation types: 1 – thermophilous oak forests, 2 – acidophilous oak forests, 3 – oak-hornbeam forests, 4 – beech forests, 5 – ravine forests and 6 – alluvial forests.

richness–landscape heterogeneity relationship are selected, both thermophilous and acidophilous oak forests have prevailing negative correlations between productivity and landscape heterogeneity, while ravine and beech forests have prevailing positive correlations, and oak-hornbeam and alluvial forests show no trend.

Vector analysis (Fig. 8) illustrates how the changes in landscape heterogeneity are related to the changes in local productivity and soil reaction and the size of the species pool. Each arrow in Fig. 8 represents the group of 100 plots and points toward the direction of increasing landscape heterogeneity within this group. Green arrows (Fig. 8a) represent the groups in which species richness significantly increases along the gradient of landscape heterogeneity, while red arrows (Fig. 8b) represent groups in which species richness significantly decreases along the gradient of landscape heterogeneity (corresponding to green plus signs and red minus signs in Fig. 5a). The direction of the arrows also illustrates how the gradient of increasing landscape heterogeneity is related to the gradient of local productivity (horizontal axis) and soil reaction (vertical axis). For example, the arrow in Fig. 3 (step 2) indicates that increasing landscape heterogeneity within this group corresponds to decreasing productivity (arrow is pointing left) and increasing soil reaction (arrow is pointing up). In addition, the direction of the arrows shows how the changes in both productivity and soil reaction (along the gradient of increasing landscape heterogeneity) are associated with the changes in the size of the species pool (isolines on the figure background). Figure 8 reveals a clear pattern: 1) most of the vectors in Fig. 8a (representing mainly thermophilous and acidophilous oak forests) point toward higher soil reaction and lower productivity, which means that the increase in species richness towards more heterogeneous landscapes is associated with both increasing local soil reaction and decreasing productivity within these vegetation types; 2)

most vectors in Fig. 8b (mainly ravine and beech forests) point toward higher productivity, meaning that the decrease in species richness in more heterogeneous landscapes is associated mainly with increasing local productivity within these vegetation types in more heterogeneous landscapes. Projection of the species pool size, estimated on the basis of a large vegetation database, onto the ecospace of Fig. 8 suggests a link between the species pool size and local species richness (most of the vectors in Fig. 8a point toward a larger species pool, while most of the vectors in Fig. 8b point toward a smaller species pool).
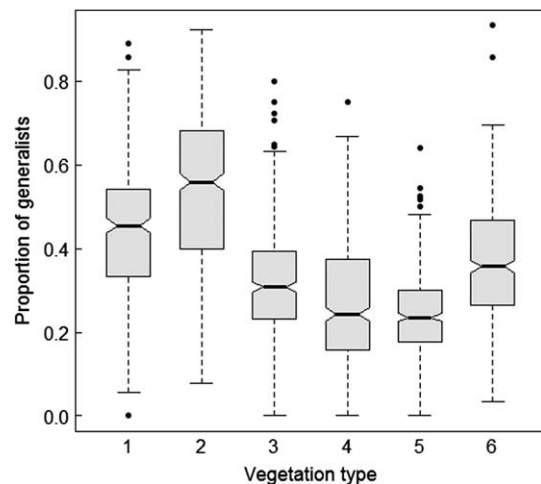


Figure 6. Proportion of generalists in plots of different vegetation types. Notches in the boxes indicate the significance of between-group differences: if notches of two groups do not overlap this is strong evidence that medians of these groups differ significantly. Vegetation types: 1 – thermophilous oak forests, 2 – acidophilous oak forests, 3 – oak-hornbeam forests, 4 – beech forests, 5 – ravine forests and 6 – alluvial forests.
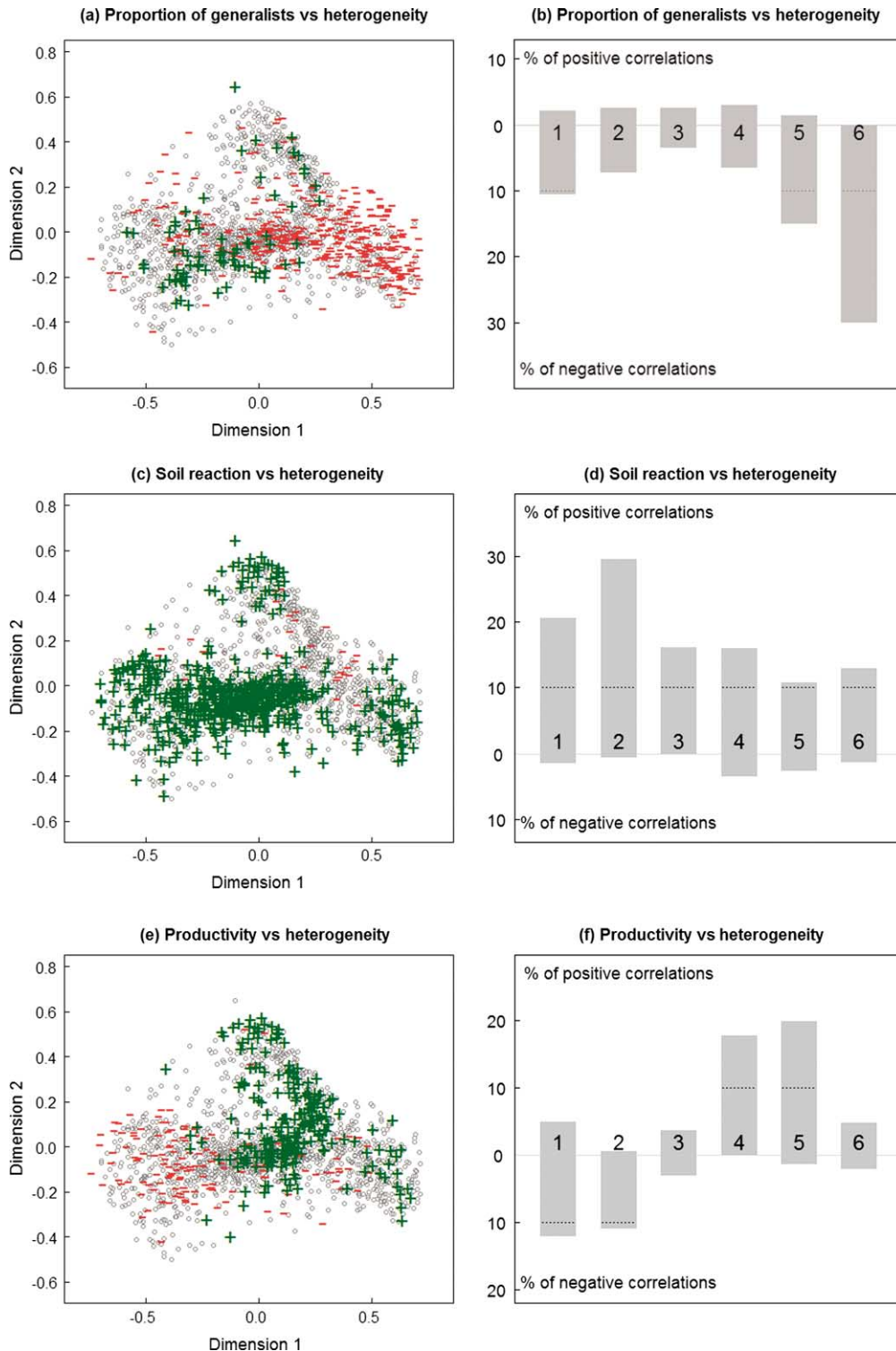
Figure 7. Results of the repeated-correlation analysis projected onto the NMDS ordination diagram (left) and as the percentage of positive or negative correlations within a particular vegetation type (right). Correlations were calculated between the landscape heterogeneity and proportion of generalists (a, b), soil reaction (c, d) and productivity (e, f). Plus symbols on the left-hand diagrams indicate significant positive correlations within groups of 100 plots, minus symbols significant negative correlations and empty grey circles non-significant correlations. The height of the bars in the right-hand diagrams reflects the percentage of significant positive (upwards) or negative (downwards) correlations; the dotted lines indicate the interpretation threshold (10%) set up by the Monte Carlo test. Vegetation types: 1 – thermophilous oak forests, 2 – acidophilous oak forests, 3 – oak-hornbeam forests, 4 – beech forests, 5 – ravine forests and 6 – alluvial forests.

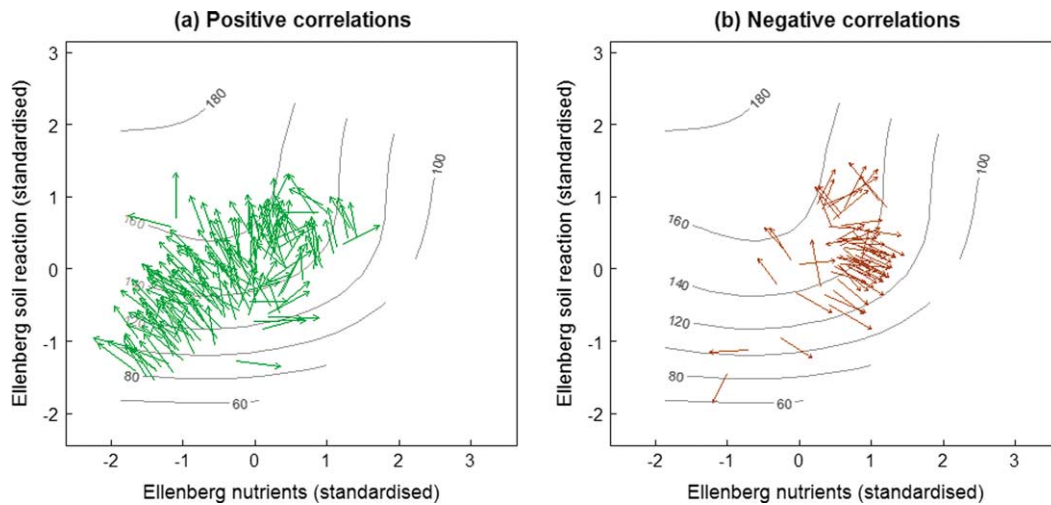**(a) Positive correlations**

**(b) Negative correlations**

Figure 8. Vector analysis illustrating the relationship between landscape heterogeneity and gradients of local productivity, soil reaction and species pool size for particular combinations of productivity and soil reaction. The two-dimensional ecospace is defined by productivity (Ellenberg nutrient values on horizontal axis) and soil reaction (Ellenberg reaction values on vertical axis). Background isolines show the estimated size of the species pool across the ecospace. Each arrow represents a group of 100 plots and points in the direction of increasing landscape heterogeneity within this group. Arrows representing positive (a) and negative (b) significant correlations between local species richness and heterogeneity of the surrounding landscape are plotted separately. See Fig. 3 for more details.

## Discussion

There is no direct way to prove, at least using the available non-experimental data, that local species richness changes along the gradient of landscape heterogeneity as a result of particular processes. The main outcome of this study is description of the pattern of species richness and other variables along the gradient of landscape heterogeneity, and even if this is done using rather advanced statistical methods, it must be emphasized that these methods are basically hypothesis generating and not hypothesis testing. Consequently, we can compare observed patterns with the predictions derived from alternative ecological theories and, while acknowledging the context of the present study, explore which hypothetical underlying processes appear to be more consistent with the data. The hypothetical processes we will consider are the island effect on species extinction in fragmented habitats (MacArthur and Wilson 1967), the spatial mass effect (Shmida and Ellner 1984), the species pool effect (Taylor et al. 1990, Eriksson 1993, Zobel 1997) and the hump-back relationship between species richness and productivity (Grime 1979).

Our original assumption was that changes in species richness along the gradient of landscape heterogeneity are driven by two processes with opposite effects: habitat fragmentation, which is higher in a topographically hetero-geneous landscape and results in lower local species richness, and the spatial mass effect, which results in higher local species richness in a heterogeneous landscape that contains different habitats close to each other. If the habitat fragmentation effect was present and the spatial mass effect was absent, we would expect negative correlations between species richness and landscape heterogeneity across vegetation types, and vice versa. However, the pattern resulting from this study indicates that both processes may play a role, but with different intensities in different vegetation types: negative correlations between local species richness

and landscape heterogeneity (suggesting the fragmentation effect) prevail in nutrient-rich vegetation (except alluvial forests), while positive correlations (suggesting the spatial mass effect) dominate in nutrient-poor vegetation. An analogous pattern was observed in the proportion of generalists, which was low in nutrient-rich and high in nutrient-poor vegetation. Based on the result of their simulation study, Steiner and Köhler (2003) concluded that the spatial mass effect is more likely to result in higher species richness in communities with a higher proportion of generalists, and this gives grounds for interpreting the observed species richness pattern as being a result of the combination of the spatial mass effect and the habitat fragmentation effect.

In addition, we expected that, in the presence of the spatial mass effect, vegetation types with higher local species richness in heterogeneous landscapes would contain more generalists there; however, this pattern did not occur in any vegetation type (Fig. 7a, b). The reason may be that beside the spatial mass effect this proportion can be affected by the function of the heterogeneous landscape (here represented mainly by deep river valleys) as a historical species refuge. From the glacial and postglacial perspective, accumulation of diverse habitats in heterogeneous landscapes may have played an important role for survival of particular species during periods of climatic change. Due to changing climate some habitats may have become unfavourable for species survival, while others may have simultaneously become good alternatives. The spatial proximity of alternative habitats in a heterogeneous landscape facilitated species migration and thus reduced their extinction risk. We suggest that this process is probably more important for habitat specialists than generalists, due to the specialists' higher sensitivity to environmental change, and it may have resulted in a higher proportion of specialists in hetero-geneous landscapes. Our finding that there is no vegetation type with a pronounced increase in the proportion of habitat generalists towards heterogeneous landscapes

suggests the importance of this "refuge effect" in structuring plant communities in heterogeneous landscapes.

The openness of local communities to species enrichment via the spatial mass effect was expected to differ among vegetation types, as documented by both experimental (Foster and Dickson 2004) and observational studies (Cantero et al. 1999). The main controlling factors of local species richness probably change from the species pool effects (e.g. dispersal limitation) to local ecological processes (competition) on the gradient from low-productive to high-productive habitats (Foster and Dickson 2004). The pattern of local species richness observed in this study partly fits this theoretical framework, as the increase in species richness that may be explained by the spatial mass effect occurs mainly in low-productive vegetation types such as thermophilous and acidophilous oak forests. The exception to this rule is alluvial forest, which has higher species richness in more heterogeneous landscapes even though it is extremely productive. Detailed inspection of particular alluvial forest plots revealed a possible explanation for this: these plots frequently contain species from other habitats, mainly from ravine forests, reflecting the topographical vicinity of these vegetation types in heterogeneous landscapes of deep river valleys. Dispersal of propagules from other habitats occurring in deep river valleys to alluvial forests may be considerably enhanced by flood events.

The analysis of changes in local ecological conditions along the gradient of landscape heterogeneity, based on Ellenberg indicator values (Fig. 7c–f), reveals an alternative explanation of the species richness pattern. Soils of the same vegetation type are generally base-richer in heterogeneous than in homogeneous landscapes. This holds true for all vegetation types, although being less pronounced in ravine and alluvial forests. An obvious explanation is that in a topographically heterogeneous landscape, more intensive denudation and erosion causes relief rejuvenation, weathering and cation release, which are absent in a homogeneous landscape. Due to higher erosion in heterogeneous landscapes, chemical properties of the bedrock have a more direct effect on vegetation, while in homogeneous landscapes the bedrock is generally covered by thick, often leached soils, at least in non-arid regions. Because the central European forest flora contains a larger pool of calcicole than calcifuge species (Pärtel 2002, Chytrý et al. 2003, Ewald 2003, Schuster and Diekmann 2005), the higher local species richness of oak forests in a more heterogeneous landscape (Fig. 5a–b) may simply result from the effect of a larger species pool existing for base-rich soils that prevails in heterogeneous landscapes.

However, an increase in local species richness along the gradient of topographical heterogeneity does not occur in all vegetation types, although an increase in soil reaction does. A possible explanation is the effect of productivity, acting independently of the effect of soil reaction. Moving toward more heterogeneous landscapes, habitats of particular vegetation types are shifted toward more extreme ecological conditions: nutrient-poor vegetation types (thermophilous and acidophilous oak forests) become even more oligotrophic, while mesotrophic and nutrient-rich vegetation types (beech and ravine forests) are further enriched in nutrients. This pattern results from the topographical position of particular vegetation types in heterogeneous landscapes, represented here mainly by deep river valleys: while oak forests are restricted to the upper and exposed parts of slopes, the other vegetation types occupy mainly footslopes and lower parts of the valleys (Zelený and Chytrý 2007). Along the gradient of landscape heterogeneity, decreasing species richness in the case of nutrient-rich vegetation types (mainly ravine and beech forests) is coupled with increasing productivity (Fig. 7f). This is consistent with the decreasing right-hand part of the unimodal species richness–productivity relationship, usually attributed to increased competition in more productive habitats (Grime 1979). However, this relationship may be also explained by the effect of smaller species pools of plants adapted to nutrient-rich habitats (Aarssen 2001, Schamp et al. 2002), as suggested by the decreasing size of the species pool toward higher productivity (isolines in Fig. 8). In the case of nutrient-poor vegetation types (oak forests), productivity decreases, but species richness increases along the landscape heterogeneity gradient. When plotted together with soil reaction, it is clear that the decrease in productivity is coupled with the increase in soil reaction (Fig. 8a – most of the arrows point toward lower productivity and higher soil reaction), which is consistent with the empirical linear species richness–soil reaction relationship. Thus, while not important in nutrient-rich vegetation types, soil reaction plays a key role in nutrient-poor types. This provides an evidence of the effect of interaction of productivity and soil reaction on local species richness (Crawley et al. 2005), which requires further scientific attention.

Apart from the spatial mass effect, fragmentation or shift in environmental conditions, we have to acknowledge forest management as another important factor which may influence local species richness but which was not controlled in this study. It may be argued that the intensity of management decreases along the gradient of landscape topographical heterogeneity as a simple consequence of lower accessibility of heterogeneous landscape. The strategy of selection of our dataset was designed to limit variation in management among plots as much as possible, however, this factor was not controlled in the statistical analyses. Quantifying the differences in the intensity and type of management among the plots and their effects on local species richness is not an easy task and falls outside the scope of this study. However, this issue also calls for further scientific evaluation.

## Conclusions

The pattern of local species richness along the gradient of increasing topographical heterogeneity of the landscape that surrounds the target sites differs among vegetation types: low productive vegetation types have higher local species richness, while medium and high-productive types have lower local species richness in heterogeneous landscapes (with alluvial forests being the exception to this rule). We offer two alternative sets of explanations, which are not mutually exclusive (Table 1): the first is based on the combination of processes resulting from the spatial mass effect and habitat fragmentation, and the second points to the fact that the gradient of landscape heterogeneity is coupled with the shift in soil reaction and productivity at

Table 1. Topographically heterogeneous landscape, compared to homogeneous landscape, and their effects on local species richness: summary of results. Plus and minus signs indicate increasing and decreasing local species richness, respectively, in topographically more heterogeneous landscapes.

| Properties of more heterogeneous landscape | Local species richness | Possible explanation for the species richness pattern | Evidence from the current study |
|---|---|---|---|
| Different habitats are closer to each other | + | Historical refuge effect<br>Spatial mass effect | Not studied<br>Consistent (only valid for low-productive vegetation types) |
| Habitats are more fragmented | − | Island effect | No clear evidence |
| Soils are more base-rich | + | Species pool effect | Consistent (valid mainly for low-productive vegetation types) |
| Nutrient-rich soils become richer | − | Hump-back model of diversity-productivity, species pool effect | Consistent (only valid for high-productive vegetation types) |
| Nutrient-poor soils become poorer | +/− | Hump-back model of diversity-productivity, species pool effect | No clear evidence |

local sites, which may be dominant controls of species richness. It may be hard to test the hypotheses presented as a result of the current study experimentally, but further observational studies performed in other areas and different landscape contexts could explore whether the patterns reported here have a more general validity.

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