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Niches and noise—Disentangling habitat diversity and area effect on species diversity

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ABSTRACT

The species–area curve is generated by niche-related factors and stochastic factors like neutral processes or dispersal. Even though the use of environmental variables is widespread to predict the spatial distribution of species richness, it remains difficult to distinguish the relative importance of habitat heterogeneity and the area effect on total species richness. In our study, we used different types of species–area curves to disentangle the habitat heterogeneity effect and the area effect on vascular plant species richness. We generated three types of sample rarefaction curves: (1) a randomly aggregated rarefaction curve, (2) a rarefaction curve for which areas of similar habitat types were aggregated and (3) a rarefaction curve, for which areas of dissimilar habitat types were aggregated. These analyses were made on three data sets separately with different grain sizes to investigate if this had an effect on the observed pattern. The classification of the habitat types was based on three environmental variables (mean annual temperature, mean moisture index and the slope of the terrain). A consistent pattern of sample rarefaction curves was found with all three data sets. While the aggregation of dissimilar habitat types showed the highest species accumulation rates and saturation levels, the lowest accumulation rates and saturation levels were found when similar habitat types were aggregated. Depending on the grain size, the habitat heterogeneity effect accounted for 20–30% to the total species richness. However, this effect was not statistically significant. The results indicate, that effects of niche related factors on the species–area curve are scale dependent and that effects related to the area are at least as important in explaining the species richness.

1. Introduction

Species richness is likely determined by multiple processes operating at different spatial scales (Shmida and Wilson, 1985; Turner and Tjørve, 2005). The number of species found in small areas (micro-scale) depends on the size and growth form of the species (Crawley and Harral, 2001). On a small scale, species richness increases rapidly as it is likely to encounter individuals of new species within a specific habitat type. Once the area is large enough to contain all potentially detectable species the species richness increases further with area as the chance of inclusion of different habitat types carrying different species compositions increases (Deshaye and Morisset, 1988; Kohn and Walsh, 1994). In addition, with increasing area of suitable habitats, the extinction probability of single populations and the effects of stochastic noise decreases and the chance of immigration of new species increases, thus leading to a further increase of the species–area curve (Mac Arthur and Wilson, 1963, 1967). On a large scale, species richness increases with area, as different species pools, which evolved independently, are aggregated (Preston, 1960; Rosenzweig, 1995; Ricklefs et al., 2004). The interplay of these processes leads to the well known pattern of the species–area relationship, which was first described by Arrhenius (1921) and Gleason (1922).

It is generally assumed, that the species–area curve follows a power law function (Arrhenius, 1921; Preston, 1960, 1962) rather than an exponential function (as proposed by Gleason, 1922). However, as shown by Tjørve (2003) other types of mathematical functions are suitable to fit the shape of species–area curves (see also Dengler, 2009). The slope of species–area curves depends on the habitat where the species richness was observed (Crawley and

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Harral, 2001). But species richness does not only differ between different habitat types. Studies from Ricklefs et al. (2004) showed that even between areas of a similar environment, the species richness can considerably differ. Therefore, it can be assumed that on a meso-scale species richness is not only a result of niche differentiation and habitat diversity (Qian et al., 2007). According to the unified neutral theory (Hubbell, 2001), the species–area relationship is even considered as independent of the environmental heterogeneity and seen as solely the consequence of ecological drift. Thereby random dispersal is viewed as the key mechanism for the spatial distribution of species richness. Theoretical models show that increased dispersal leads to lower species turnover and higher homogenization of species compositions (Hubbell, 2001; Gravel et al., 2006). Hence, within the framework of neutral theory the shape of species–area curves is thought to depend mainly on the dispersal rate of the species (Hubbell, 2001; Hovestadt and Poethke, 2005; Rosindell and Cornell, 2009). Neutral models are not the only ones resulting in a power-law species–area relation without including habitat heterogeneity (see Harte et al., 1999; Leitner and Rosenzweig, 1997; McGill and Collins, 2003). On the other hand, empirical studies have reported a positive correlation between habitat heterogeneity and species richness (Kohn and Walsh, 1994; Ricklefs and Lovette, 1999; Rosenzweig, 1995).

These contradictory findings lead to the view, that it seems unwise to oppose the gradient niche theory to the neutral community theory (Stokes and Archer, 2010). Taking the neutral theory as a null model, which is influenced by niche differentiating (and potentially other) processes, seems to be a more realistic perspective (Leibold and McPeek, 2006). According to this view, the niche and neutrality theory present the two extreme ends of a continuum from competitive to stochastic exclusion (Gravel et al., 2006). With increasing niche overlap and dispersal rate, a community is more likely driven by neutral processes (Stokes and Archer, 2010), and thus a potential effect of habitat heterogeneity is reduced. In other words, the "pure" area effect is expected to increase with increasing niche overlap and dispersal rate. However the main issue in the debate about the effects of area and habitat heterogeneity on species richness is that area and habitat diversity are strongly correlated (Kohn and Walsh, 1994; Ricklefs and Lovette, 1999; Simberloff, 1976). Consequently, species richness can readily be predicted by either of the two parameters (Báldi, 2008; Pyšek et al., 2002). The area effect "per se" cannot be easily disentangled from the habitat diversity effect and so it is difficult to quantify the interrelationship. In addition, the area effect is often confounded with the sampling effort (Cam et al., 2002; Connor and McCoy, 1979). The detection probability of new species increases with the size of area, and therefore independently of the habitat heterogeneity and equilibrium processes, a higher number of different species is found within larger areas.

The aim of our study was to test the effect of habitat diversity and to disentangle the contributions of habitat diversity and area effect on vascular plant species richness at different grain sizes. Therefore we constructed three types of sample rarefaction curves (Gotelli and Colwell, 2001): (1) a randomly aggregated rarefaction curve (random curve); (2) a rarefaction curve for which areas of similar habitat types are aggregated (similar curve); and (3) a rarefaction curve, for which areas of dissimilar habitat types are aggregated (dissimilar curve). If habitat diversity is indeed a driver of species richness, then we expect that the shape of the three constructed curves should differ significantly. Based on classical niche theory (Hutchinson, 1957), we expect the highest accumulation rate for aggregation of dissimilar habitat types (Palmer et al., 2002). Low saturated species richness is expected when similar habitats are aggregated, whereas the random aggregation of habitat types (considered as a null model) should result in an intermediate species–area curve. The proportion of the difference of the saturation levels of the dissimilar curve and the similar curve to the total species richness (dissimilar curve) is assumed to indicate the contribution of habitat diversity to the total species richness. To detect scale dependent patterns, we estimated the effect of habitat heterogeneity on three different grain sizes.

2. Materials and methods

2.1. Study area

The study area encompassed Switzerland. The climate is generally humid temperate with rather mild winters and moderately warm summers. Annual mean temperature ranges from ca. 1.5 °C (in high alpine valleys) to 11.5 °C (in the southern part of Switzerland). The mean annual precipitation sums vary between 600 mm and 2900 mm. The topographic relief ranges from ca. 190 m to 4634 m a.s.l.

2.2. Species richness data

In order to investigate a potential scale effect, we made separate analyses of species–area curves, using three different data sets, which covered the same geographical extent, but differed in grain sizes. Two data sets are from the biodiversity monitoring program of the Swiss Federal Office for the Environment (Plattner et al., 2004). In this monitoring program, vascular plant composition was recorded in circular plots with an area of 10 m^2 (radius = 1.8 m; plot data) and on a transect basis with length of 2.5 km and width of 5 m (transect data). In both data sets the sampling design is a regular grid with mesh size 6 km × 4 km ($n = 422$) and 12 km × 8 km ($n = 270$) respectively (see Fig. 1). The initial points of the grids were generated randomly. Urban areas and inappropriate growing conditions such as lakes and glaciers were excluded. The third data set contains grasslands only and originates from the dry meadows and pastures survey of the Swiss Federal Office for the Environment (dry meadow data; Eggenberg et al., 2001). The plots ($n = 13{,}911$) were recorded based on phytosociological methods. They include vegetation types of four alliances: Mesobromion, Xerobromion, Stipo-Poion and Cirsio-Brachypodion (according to Delarze et al., 1999). The number of plant species was recorded within a circular area of ca. 28 m^2 (radius = 3 m). The spatial distribution of the plots is given in Fig. 1.

2.3. Habitat classification

Temperature, water and light as well as nutrients are the most important factors for a plant to grow. Therefore we used the following three environmental parameters as surrogates for the habitat classification: mean annual temperature, mean moisture index, and the slope of the terrain. The slope was derived from a digital elevation model (DEM) with a spatial resolution of 25 m. The same DEM was used to generate the climatic layers from meteorological measurements (for details see Zimmermann and Kienast, 1999). The mean annual temperature was derived from monthly Normals of the period 1961–1990 (Zimmermann and Kienast, 1999). Mean monthly moisture indexes were derived from the difference of the monthly precipitation sum and the mean monthly potential evapotranspiration. As the species richness was most responsive to the moisture index of the month May, the analyses were based on the mean moisture index of this month. The environmental parameters for the dry meadow and plot data

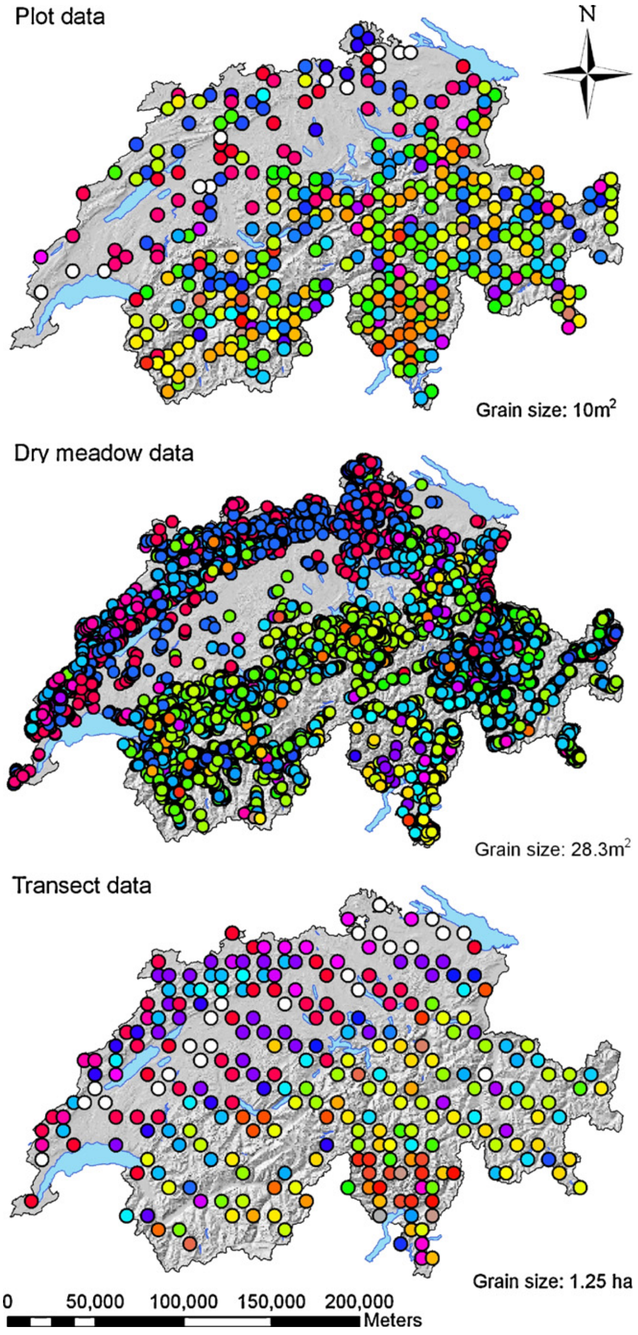

Fig. 1. Sampling design of the 3 data sets used for the analysis. The grain size increases from the plot data (10 m^2) to the transect data (1.25 ha). The dots' colour represents the specific habitat type, to which the according vegetation record belongs to. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

were directly obtained by the climatic layers with a resolution of 25 m. For the analysis of the transect data, where each transect covers an area of 12,500 m^2, we took the focal mean of all 25 m × 25 m pixels within windows of 100 m × 100 m and resampled the predictor grids to a resolution of 100 m. Intersecting these layers at the centre-coordinates from each transect field resulted in the environmental parameters for the transect data.

We classified each of the three environmental parameters into five classes of equal interval length, i.e. we split the range of a parameter (the difference of the maximal and minimal value) in five classes. This way, we divided the 3-dimensional environmental parameter space spanned by the three parameters into 125 ($n = 5^3$) hyper-cubes. Each hyper-cube was considered as one potential habitat type. Based on the temperature, moisture and slope of the geographic position of a vegetation recording, it was assigned to a specific environmental habitat type. By this procedure, we produced a habitat map where each pixel was assigned to one of the possible 125 environmental habitat types. In Fig. 1 each habitat type to which the vegetation recordings belong to, is represented by a specific colour.

The spatial analyses were carried out with Arc Info Version 9.2 (Environmental Systems Research Institute, Inc., 380 New York Street, Redlands, CA 92373-8100, USA).

2.4. Constructing sample based rarefaction curves

We constructed three types of sample based rarefaction curves: a randomly aggregated rarefaction curve which served as a null model (random curve), a rarefaction curve of dissimilar habitat types (dissimilar curve) and a rarefaction curve of similar habitat types (similar curve). The "random curve" was built by randomly selecting among all vegetation records to build rarefaction curves. As a consequence of random selection, the overall frequency of habitat types is reflected in the vegetation records of the random curve. The "dissimilar curve" was built by aggregating vegetation records from dissimilar habitat types. This means that from each of the potential 125 habitat types only one vegetation record per habitat type was randomly drawn for the aggregation procedure. The number of aggregated records was restricted to the number of habitat types for which we had a vegetation record. In order to have a roughly equally number of hyper-cubes of a similar environmental character, as there are available for the drawing for the random- and dissimilar curve we superimposed a coarser scale hypercube on the existing system. Therefore we divided the 3-dimensional parameter space of the 125 hyper-cubes into 8 hyper-cubes only ($n = 2^3$), representing 8 broader defined habitat types. We assumed that each of the 8 habitat types assembled similar of the finer habitat types defined above. For each of these 8 hyper-cubes a sample rarefaction curve was constructed by aggregating randomly drawn vegetation records from within one hyper-cube. The similar curve was then defined as the mean of the 8 curves.

In order to get smoothed species–area curves and to estimate confidence intervals, the curves were iterated 100 times. Calculating the mean of the 100 iterations showed that 100 iterations were enough to get stable results.

All the algorithms were written in the statistical software environment R (version 2.4.1; R Development Core Team, 2006), which was also used for all statistical analyses performed.

2.5. Quantification of the habitat heterogeneity effect

As we had hypothesized that habitat diversity and area both contribute to explain species richness in our plots, we quantified how much each of these two important drivers add to explain species richness. To do so, we compared the rarefaction curve of "dissimilar habitats" (which is hypothesized to accumulate the largest richness because it is both influenced by area and habitat diversity) against the curve from "similar" habitats (influenced solely by area as no habitat diversity is of influence). To quantify the habitat heterogeneity effect, we calculated the difference of curves of "similar" and "dissimilar" habitats. The ratio of this difference to the "dissimilar" curve served as a measure for the habitat effect.

3. Results

A consistent pattern of sample rarefaction curves was found with all three data sets (see Fig. 2). As expected from the niche theory, the aggregation of dissimilar habitat types resulted in the highest species accumulation rates and saturation levels. The aggregation of similar habitat types resulted in the lowest species accumulation rates and saturation levels. A difference between the curves of aggregated dissimilar and similar habitat samples is visible in the plot data. However, the difference is only marginal significant. The pattern gets clearer in the dry meadow data, where the similar and dissimilar curves differ significantly (see Fig. 2, non overlapping confidence intervals). The curves from the transect data however showed no significant difference between the species–area curve of similar and dissimilar habitat types.

The contribution of habitat diversity to total species richness accounted for 20% in the plot data and 21% in the transect data. In the case of the dry meadow species, the contribution of habitat diversity to species richness was 27% (see Fig. 3). However, the 95% confidence interval of the calculated habitat effects are larger than the effects, and thus only in the case of the dry meadow data, the effect comes close to being significant (see Fig. 3a).

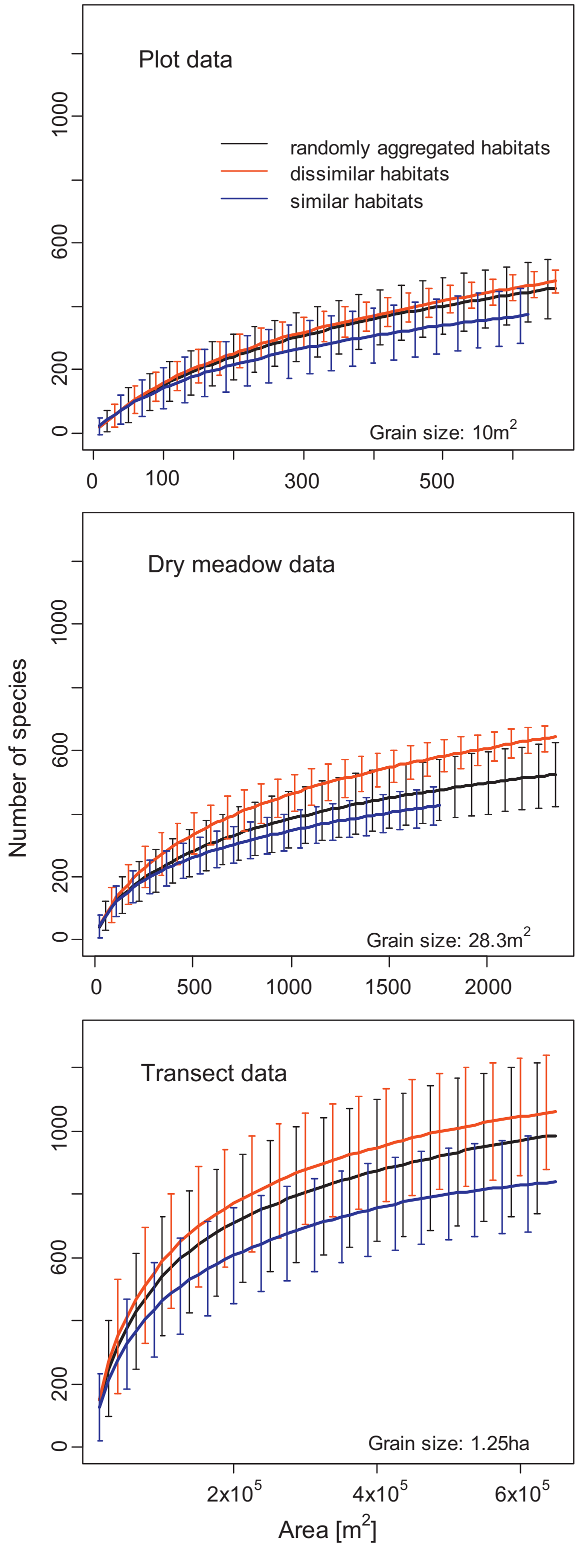

Fig. 2. Three types of sample rarefaction curves are compared on three different scales of grain sizes (10 m^2, 28.3 m^2 and 1.25 ha). The extent was held constant, including the area of Switzerland. Error bars indicate the 95% confidence intervals.

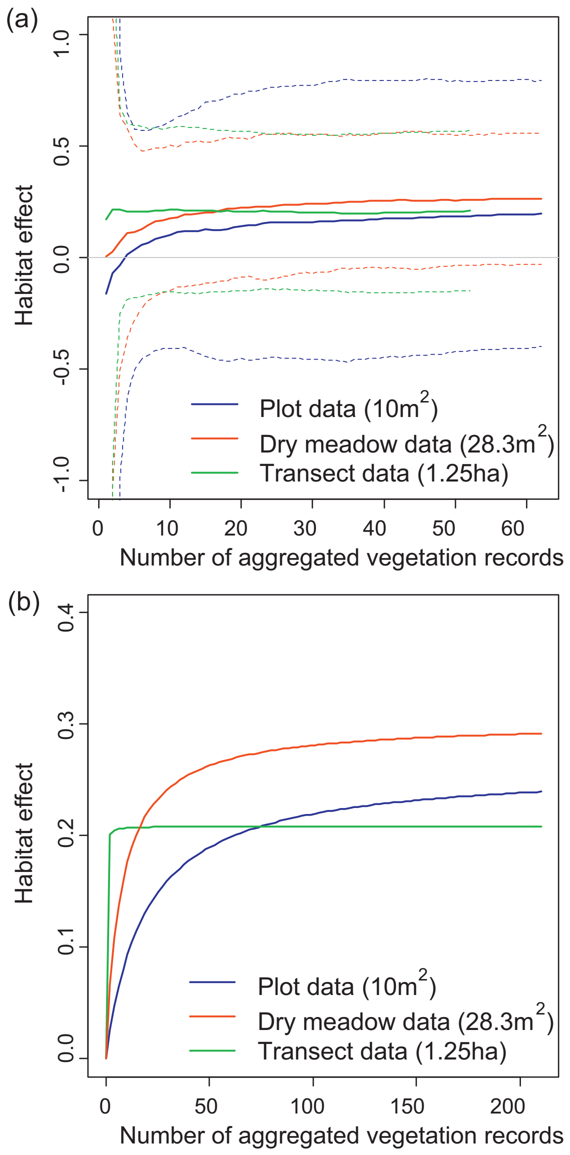

Fig. 3. The habitat effect calculated as the proportion of the difference between the species number sampled within dissimilar and similar habitats to the number of species found within dissimilar habitats. (a) Habitat effect calculated from the data directly. (b) Habitat effect calculated from curves fitted to a Monod function. Blue lines correspond to the plot data, the red lines to the dry meadow data and the green line to the transect data. The dotted lines indicate the 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

As it is not clear from Fig. 2, whether the sample rarefaction curves did reach the saturation level, we extrapolated the curves to the tenfold length. We fitted three functions to the data: an Arrhenius function, an exponential function and a Monod function. The Monod function showed the best fit in terms of minimised squared residuals and therefore it was used for the extrapolation procedure. Recalculating the contribution of habitat diversity to species richness from the extrapolated functions showed that the habitat effect of the plot data converges to a value of 25% and to 30% for the dry meadow data (see Fig. 3b). The same procedure applied to the transect data did not change the contribution of habitat diversity to species richness, showing, that the saturation level of the sampled rarefaction curve was already reached by the data

4. Discussion

With our method of classifying the environmental space into habitat types, we estimated a habitat diversity effect between 20 and 30% compared to the area effect on total species richness. It thus indicates that more than 70% of the species richness pattern was explained by the size of the area. This result is in line with the study of Crist and Veech (2006). Using a power-law regression, they found that area explained 73% of the variation in moth species richness. In a path analysis of plant species richness, Pyšek et al. (2002) found that the direct habitat effect and the area effect were both equal in size. However, the total effect of area, when direct and indirect effects were summed, slightly exceeded the effect of habitat in their study. A similar result was found by Kohn and Walsh (1994) for dicotyledonous plant species.

Due to the large standard deviation of the ratio between the difference of the dissimilar and similar curve to the level of the dissimilar curve, the effect of habitat diversity was not found to be significant. This result might further support the view that the area effect on species richness is more important compared to the habitat heterogeneity effect (Simberloff, 1976). However, our habitat classification was based on three environmental variables only, and thus might be too simple to comprise a realistic measure for habitat heterogeneity structuring the plant community. As there are many more potential factors that can generate environmental heterogeneity, it is possible, that with our approach we are not able to fully separate the effect of habitat heterogeneity from the area effect. On the other hand, as the environmental parameters used in the present study are related to space, it is possible, that the habitat heterogeneity captures some of the variation, which is in reality generated by dispersal related factors.

Our method of estimating the habitat heterogeneity effect is sensitive to the total species richness of the area and the mean species richness found within similar habitats. If the total species richness is underestimated or the mean species richness within similar habitats is overestimated, the habitat effect is underestimated, as it is estimated by the ratio of the difference of the two richness estimates to the total species richness. As showed by Ugland et al. (2003), traditional methods of generating species–area curves underestimate the species richness.

Generating total species projection curves (the smoothed curve through the average total number of species of different subsets of species–area curves, see Ugland et al., 2003 for details) might give a better reflection of the reality. However, if the traditional method used in this study underestimates both the similar and the dissimilar species richness curve, then the relative contribution of the habitat heterogeneity is likely overestimated. On the other side, it is also possible, that we underestimated the habitat heterogeneity effect as a matter of scaling. The weak signal might result from a habitat classification system, for which the number of classes is too low or the class width is chosen too wide. Wider classes contain a larger part of the environmental gradient, and thus the separation of the real potential niches is less precise. If the class widths are chosen too large, they contain too many species occupying partly different niches. Consequently the saturation level of the sample rarefaction curve of similar habitat types is too high, and the estimated contribution of the habitat heterogeneity to total species richness is then underestimated. Especially in the case of the transect data, where plots of the size of 2.5 km × 5 m were aggregated, the niche definition is likely imprecise and the grain size might be so large that it sometimes contains species data from different vegetation types.

Furthermore, the rectangular form of the transect data might lead to an overestimation of the species richness within similar habitat types, as it is known, that the shape of plots has an effect on plant species diversity (Keeley and Fotheringham, 2005). Rectangular sampling plots, especially when the direction of the long side is parallel to a local environmental gradient, bear more heterogeneous vegetation, which potentially contains more species compared to an analogous shape with a squared form (Bormann, 1953). Therefore it seems unsurprising, that the transect data indicate only a small habitat heterogeneity effect with a larger uncertainty (large confidence interval of the ratio).

Another scaling issue concerns the way the species–area curves are constructed. Using individual-based rarefaction curves instead of sample-based rarefaction curves might lead to a more pronounced habitat effect (Colwell et al., 2004). Individual-based rarefaction curves have the advantage, that confounding effects of differing densities and sizes of individuals are excluded (Colwell et al., 2004). In addition, spatial autocorrelation (patchiness) in species occurrence would be excluded as well (Gotelli and Colwell, 2001). Patchiness and other confounding effects related to density might especially introduce random noise in data, where the grain size is small, such as it is the case with the plot- and dry meadow data. However, as we have presence absence data only, we are not able to construct individual based rarefaction curves.

The habitat heterogeneity effect in the dry meadow data was more pronounced compared to the plot- and transect data. This finding might result for several reasons: first, per definition, the dry meadow data contained a reduced set of species, which mainly belong to the Mesobromion and Xerobromion habitat types. Thus, the data contain primarily annual- and perennial herbs and grasses, which are similar in size. Therefore effects from differing species sizes are more likely excluded (McGeoch and Gaston, 2002; Niklas et al., 2003) in the dry meadow data, whereas the presence of trees and shrubs might introduce random noise in the plot data, as these woody species are large in size, relative to the grain size of 10 m^2 in this data set. A second reason for the more pronounced habitat heterogeneity effect in the dry meadow data might lie in the more uniform land use of the sampling area of this data set compared to the other two data sets. While the plot and transect data are spread over varying land use types, the dry meadow data are restricted to locations of pastures and meadows only. Thereby plots belonging to bioclimatic similar habitat types can still contain varying vegetation types in the case of the plot and transect data set (leading to an overestimation of the species–area curve where similar habitat types are aggregated), and thus the habitat heterogeneity effect in those two cases is underestimated. In contrast, sampling plots of the dry meadow data belonging to bioclimatic similar habitats contain more uniform vegetation, as they belong to the same land use type.

Yet, within a bioclimatic constant area, not only land use, but also land management (Klimek et al., 2007; Myklestad and Sætersdal, 2004,), soil type (Sebastiá, 2004), the age of the habitat (Cousins and Eriksson, 2008; Waesch and Becker, 2009) as well as the presence of ecosystem engineers (Badano and Cavieres, 2006;

Jones et al., 1994) have an effect on the species richness and species density. By using the slope angle as one factor for the habitat classification, we may indirectly take land management and soil quality partially into account, as the land use tends to be less intensive in hilly regions with steep slopes (Klimek et al., 2007).

The more pronounced habitat heterogeneity effect in the dry meadow data might give a more realistic estimation of the habitat heterogeneity effect, compared to the other two data sets. I.e. the simple classification system of the present study might generally underestimate the habitat heterogeneity effect, as it does not take anthropogenic and biotic interactions into account.

It remains a challenge, to define an appropriate system that stands for surrogates of real niches to estimate habitat heterogeneity effects. This is especially so, because the size of real niches depends on the individual species, and so does the habitat heterogeneity effect (Laliberté et al., 2009). With increasing size of the realised niches and with increasing degree of overlap, the estimated effect of habitat heterogeneity on the species–area relationship will decrease and be less precise, as a simple consequence of aggregating similar sample areas containing a higher number of different species. For this reason we support the view of Ricklefs and Lovette (1999) that strong habitat-diversity effects are likely found in taxa that show a high degree of habitat specialization, while area effects are more important in taxa with weak habitat specialization. However, as our sampling plots are non-contiguous, we cannot evaluate the area effect on species richness in respect to island theory.

In conclusion our results indicate a rather weak habitat heterogeneity effect compared to the area effect. It is possible, that the simple classification of the environment into potential habitat types used in this study does not contain the features structuring the plant community. However, as all analyses of the three different data sets show the same basic pattern consistently across a range of scales, we assume that the system does reflect realistic processes in nature. The weakness of the habitat heterogeneity effect and its dependence on the grain size might be the reason, why climatic- and topographic variables used to predict the spatial species distribution vary in their explanatory power, depending on the grain size and extent as well as the organisms used in the reported studies (Willis and Whittaker, 2002).

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