
Do organisms use landscapes at certain spatial scales? A null model for diversity pattern in relation to the spatial extend of landscapes

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Summary. Recent studies on the way species diversity is influenced by the surrounding landscape structure have formed the paradigm that species have a ‘characteristic scale’ of response to their environment. The reasoning is based on regressing species diversity data against measures of landscape composition at various spatial scales (i.e. buffer sizes) around the sampling points. In most of these studies, model fit (usually measured as coefficient of determination) peaks at some landscape segment size. In this study, we propose a null model for this phenomenon. We assume that diversity is related to habitat area *in the entire landscape*, and that habitat area is better predicted by large landscape segment sizes than by small. Hence, as landscape segment size is increased, model fit should increase as well. Running simulations of this null model both on artificial and real landscapes indeed resulted (among others) in humpshaped curves. Additionally, since Shannon’s diversity is statistically related to habitat area in the entire landscape it may produce spurious relationships between diversity and landscape scale. Overall, our null model is cautioning against relying on the new paradigmatic way of detecting characteristic species scales, without a proper formulation of landscape structure-induced, species independent pattern. The pattern observed may be more to do with the distribution of relevant habitats in the landscape than with the ‘perception’ of the landscape by the group of organisms under focus.

Key words: landscape structure, null model, species-area relationship

1 Introduction

Organisms, it has been said, ‘perceive and respond to the environment at different scales’ (Fleishman et al., 2003, p. 675). Already in 1992, Holling has forcefully argued that the morphology of communities is a reflection of the ecosystem morphology itself. However, only in the last years have studies attempted to explicitly detect the scale at which certain groups ‘perceive and respond to’ the landscape.

Several recent studies claim to have found evidence of diversity of different groups of insects being related to a certain spatial scale of the surrounding landscape (e.g. Steffan-Dewenter et al., 2002; Thies et al., 2003; Westphal et al., 2003; Söderström & Pärt, 2000; Kremen et al., 2004; Holland et al., 2004). The indications are derived

from regressing species richness against some measure of landscape composition (e.g. Shannon diversity of land use types, percentage arable land or alike). When the spatial extend of the landscape described is increased, model fit first increases, reaches an optimum and then (often, but not always) decreases again. The spatial scale of optimum model fit was interpreted as the scale relevant to the organisms (for review see Holland et al., 2004, and references therein).

To evaluate if this pattern is indeed the footprint of the way organisms perceive, and interact with, their environment, an appropriate null model (Gotelli & Graves, 1996) needs to be specified. We argue that these null models are able to reproduce this and other apparent pattern, without being related to the ecology and biology of the organisms investigated. Additionally, we show that

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for the particular case of Shannon's diversity of land use types at various sizes of landscape sections, a humpshaped curve can be attributed to the statistical interrelationship of species diversity and habitat diversity.

A verbal sketch of the null model

We perceive the key issue in analyzing the species richness-landscape composition relationship to be the way landscape description changes with spatial extend. As we increase the section under consideration (i.e. the buffer size in a GIS), a parameter describing the proportion of land use types will increasingly accurately represent the 'true' (i.e. large-scale) landscape composition. Imagine a landscape description, starting from the 100 m² patch where the fly traps for bees have been placed. At this small spatial extend, only few land use types are present, and their relative area is far from representative for the entire landscape (i.e. hundreds of square kilometers). As the section under consideration increases in size, so will its representativeness for the entire landscape. Hence, we would expect that a landscape composition descriptor, such as land use type diversity, will become a better predictor of the percentage of each land use type, as spatial extend is increased. This would yield an increasing asymptotic curve of model fit over spatial extend.

Land use types comprised of mostly small patches should be predictable at smaller spatial scales. Also should their contribution to a diversity measure such as Shannon's H decrease with spatial extend. Hence, it is perceivable that at larger spatial extends small-patched land use types are less well predicted than at medium extends.

Assuming that (1) for most species semi-natural habitats will be most species-rich, and that (2) in agriculture-dominated landscapes semi-natural habitats are generally of low proportion and small patch size, it seems plausible that (3) species diversity may simply be related to habitat area, which, in turn, is for small-patched habitats best predicted at medium to large spatial extend.

If this reasoning were correct, we could reproduce a humpshaped, in any case an increasing asymptotic curve without invoking behaviour or perception of the organisms studied, solely on

the way habitat area can be predicted at different spatial extends. We will now illustrate these ideas using simulated and real landscapes.

2 Methods

Assumptions and realization of the null model

We assume that species diversity is a function habitat area (also known as species richness-area relationship, SAR). Most reported SARs are power functions, but at small intervals of spatial extend (e.g. from 1 to 100 km²), a linear increase of species richness with habitat area is a reasonable approximation (compare SAR figures over one order of magnitude e.g. in Gaston and Blackburn, 2000; Gaston & Blackburn, 2000). The exact shape of this function is of little relevance for our argument, however, since it is not used to construct the data for the null model and only affects the scaling of the y-axis (by translating area of bee habitat differently into bee numbers).

Furthermore, we assume that all sites within a landscape share a common distribution of patch size frequencies and overall proportion of land use types. That means, the sites where species richness has been investigated are assumed to be different 'realizations' of a homogeneous landscape. This assumption is not overly important, however. Using qualitatively different landscapes will reduce the overall model fit, without affecting any of our other findings (see results).

For verbal and ecological convenience, we think of bees as our target group, their preferred land use type simply called 'bee habitat'. In this example we pretend to know what our target group demands, while in reality this may not be the case.

Building the null model now follows these steps:

1. Draw buffers of different size centered on the sample point.
2. For each buffer size, calculate the percentage cover of bee habitat, and/or the Shannon diversity of land use types.
3. Calculate the percentage of bee habitat for the landscape, i.e. across the largest buffer size, for all sites separately. As species diversity is proportional to the area of bee habitat in the

landscape, we can use bee habitat cover as surrogate for bee diversity.

4. Regress bee diversity for each site against percentage cover of bee habitat at a given buffer size. Thereby one generates the model fit values (r^2) to be plotted against buffer size.

Artificial landscape

The artificial landscape consists of 10 land use types, each with its own patch size-frequency distribution (from land use types dominated by small patches, e.g. dry grassland, to those consisting mainly of large patches, e.g. forests) and different absolute shares of the total landscape (5–17%). We chose ten land use types in line with the number usually reported in the studies cited in the introduction. We implemented ‘triangular distributions’ with some maximum and symmetric decreases to both sides (except for distributions with maximum close to 0, in which case we chose a linear decrease to 0. These distributions are rather different from those found in nature (see below), but the similarity of results suggests that the precise shape is of limited relevance.

To assemble the landscape, we randomly chose a land use type and a size from the land use types size-frequency distribution to go with it. This procedure was repeated for 1000 patches to yield one site, and we produced 20 different sites. These 20 sites thus represent the 20 different points at which diversity has been sampled in our virtual landscape. Note that these landscapes are *not* spatially explicit. That means we have no graphical visualization of the artificial sites, but rather use the sequence of randomly drawn patches to simulate the increase in buffer size.

In the artificial landscape, landscape section size around the virtual sample point for species richness was increased in 1000 small steps.

Weißer Elster catchment

The second landscape is based on real data from the Weißer Elster catchment in central Germany. Land use was summarized in eight types. Their frequency distribution differed from the triangular distributions of the null model by being log-normal distributions (data not shown). 10 sites

were selected hap-hazardly for even spacing in the real landscape.

In the real landscape circles of 500 m radius (increased in 20 steps by 500 m to a maximum radius of 10 km) were used (Fig. 1). As we were solely interested in investigating the pattern, we did not attempt to make the units of artificial and real landscape comparable.

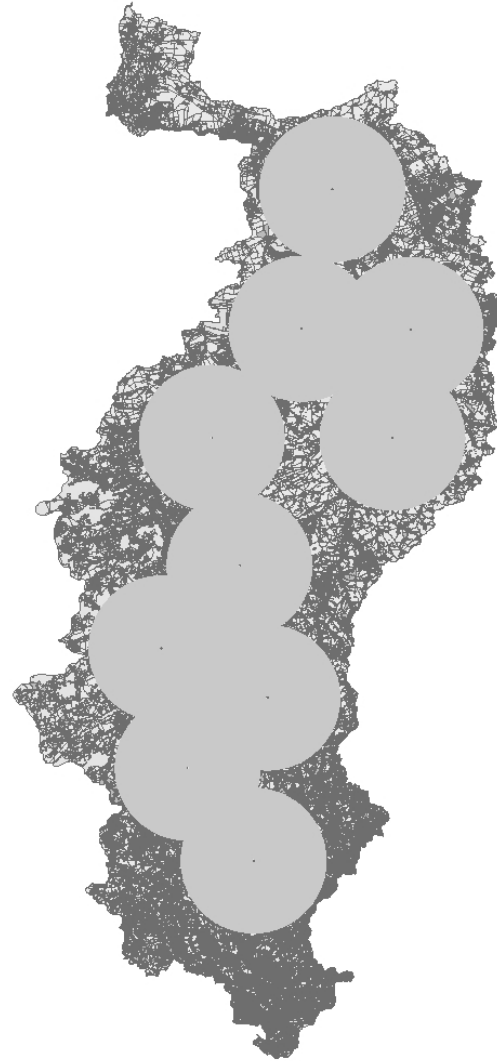


Fig. 1. Orientation of the ten buffers in the Weißer Elster catchment. Only the largest circles with 10 km radius are shown.

All simulation and analyses were carried out using the software package R (R Development Core Team, 2004), while the data provided by the Weißer Elster were processed in ARCInfo.

3 Results

Artificial landscape

We found different types of relationships between model r^2 and landscape segment size in the artificial landscape scenario (Fig. 2). Humpshaped curves were common (4) among the ten land use types investigated, but increasing (3) and indifferent (3) relationships also occurred. There was no tendency for rare land use types to be less well predicted by Shannon's H , although this is what we had expected. For all land use types an almost periodic oscillation of r^2 -values could be observed (depicted only for one land use type in Fig. 2). The cause of this pattern remained obscure.

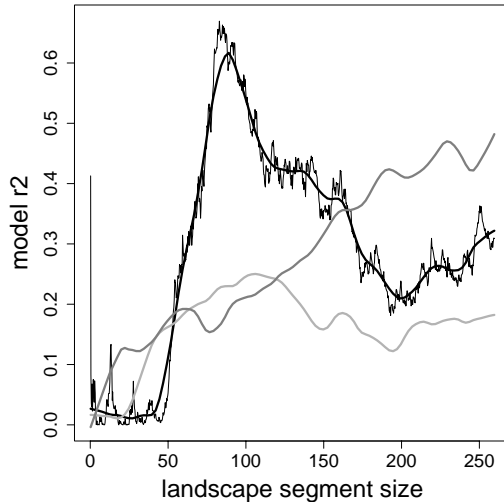


Fig. 2. Artificial Landscape: The relationship between model r^2 and buffer size for three differently common land-use types (17, 5 and 7% represented by black, grey and light grey, respectively). Lines are smoothed to give a more transparent graph, apart from the thin line around the most common land use type, which depicts the raw data for illustration.

Weiße Elster catchment

For the real landscape, we found a similar pattern. Here again, different relationships between model r^2 and segment size were detectable (Fig. 3): 4 were approximately humpshaped, 2 increasing, one U-shaped and one indifferent. The oscillation pattern of the artificial landscape was not apparent here, most likely because step size was much

larger (20 different segment sizes, compared to the 1000 segment sizes for artificial landscapes).

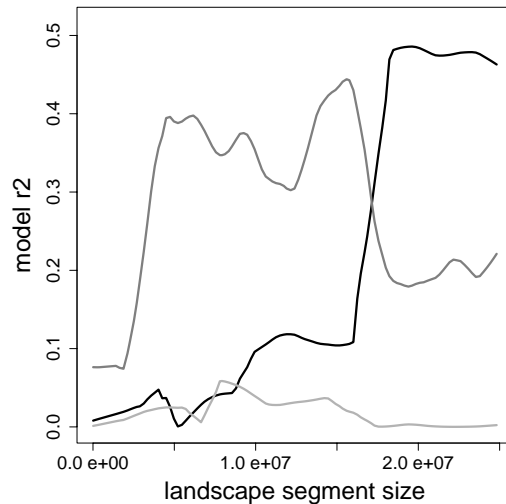


Fig. 3. Weiße Elster catchment: The relationship between model r^2 and buffer size for three different land-use types. Lines are smoothed.

4 Discussion of simulation results

Our simple simulations in artificial and real landscapes have shown that the proposed null model is able to replicate the observed relationships between model fit and landscape scale *without* invoking organismic behaviour. It thus can thus serve as a benchmark against which to test the pattern observed in field studies. We acknowledge that our approach is not entirely satisfactory, as its assumptions are possibly violated in some field studies. For example any study along a climatic or elevational gradient will not follow our prerequisite of a homogeneous generic landscape, from which the field sites are random realizations. However, as we detail later, our approach can be used on a site-by-site basis, where the null model is constructed for each segment size at each site from the observed data at that site.

Furthermore, species diversity for a specific group may not simply be a function of habitat available, but rather of, e.g., food availability (Westphal et al., 2003). In this case, our null model would have to include the land use type 'mass crop' to be useful. In fact, the findings of Westphal et al. (2003) indicate a possible condition when landscape structure rather than organ-

isms produce the observed humpshaped relationship: these models may simply have missed an important aspect of the ecology of the investigated group. Only by using cover of mass crops as explanatory variable could bumble bee diversity be successfully related to landscape structure. Their attempts to relate bumble bee diversity to percentage of semi-natural habitat was not successful, but may as well have resulted in the spurious relationships of Figs. 2–4.

5 Are humpshaped model fit-landscape scale relationships statistically spurious?

Along a completely different line, one could argue that landscape diversity is no appropriate predictor variable, as it is related to the cover of its contributing land use types. Let us look at the example of Shannon's H :

$$H = - \sum_{i=1}^n p_i \ln p_i$$

where p_i is the proportional cover in the buffer. Hence, H is indirectly related to the cover of our bee habitat, which is one of the terms to be summed over. Clearly when regressing bee diversity against landscape diversity, and if indeed bee diversity is a function of bee habitat area (p_{bee}), then this term p_{bee} stands on both sides of the regression equation and some relationship will inevitably occur. This need not be a humpshaped relationship, however.

We used data from the Weiße Elster (as above) to investigate this relationship. We simply calculated Shannon's H for each buffer size in each of the 10 sites and then analysed the relationship between proportion of bee habitat in the buffer and H . Figure 4 shows the familiar humpshaped relationship between model r^2 and buffer size for three different land use classes (i.e. three differently common bee habitats). The humpshaped relationship occurred in 4 of 8 cases, others were U-shaped (3) or increasing (1).

We hence conclude that, under the assumption of a \pm linear richness-area-relationship, a humpshaped function of model r^2 with size of landscape segment is not statistically inevitable, but it is a *likely* shape.

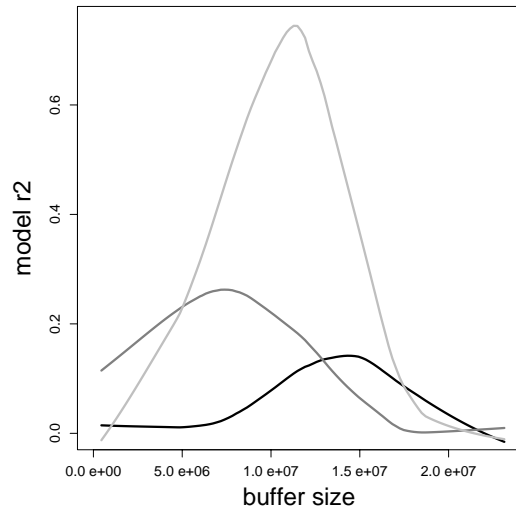


Fig. 4. Illustrating the possibility of humpshaped relationships between model r^2 and buffer size. For details see text.

6 Implications for null model construction in landscape-species diversity studies

This study shows that landscape pattern of diversity may be more complex and indirect than we might expect (see also Purtauf et al., 2005). Carefully constructed null hypotheses will allow the clear differentiation of statistical artefacts and ecological processes. With the above results we illustrated that a humpshaped r^2 -buffer size-relationship in itself is insufficient to document that organisms have a preferred landscape scale. It may simply reflect landscape structure, which in turn also determines species richness. To detect an 'organismic' landscape scale, one needs to contrast the observed pattern with a null model as we have developed here.

The null model can be constructed along the following lines:

1. calculate, for each buffer size in each site, the percentage cover of all land use types;
2. calculate, for each buffer size in each site, your preferred target measure of landscape structure (e.g. Shannon's diversity index H or percentage arable land);
3. construct, for each buffer size, your model explaining species richness by your land-

scape variable from step 2; store model r^2 and buffer size;

4. repeat step 3 but with cover of one land use type instead of species richness as response variable; do this for all land use types;
5. construct a new model, regressing model r^2 s from step 3 against buffer size, but using model r^2 s from step 4 as covariate. If you have not enough degrees of freedom to simultaneously fit all land-use type model r^2 s, then fit only one at a time, and later pick the most conservative model.

Only if buffer size is still significant *after* accounting for land use type-model r^2 s there is indeed sound evidence for species operating at preferred landscape scales.

This recipe for building the null model is somewhat different from the one illustrated in methods and results. It has the additional advantage of relying only on the land-use cover distributions found in the respective buffer segment, and can hence be applied to sites across rather different landscape compositions.

The test for both the proposed null model and the studies claiming to have found the ‘characteristic scale’ (Holland et al., 2004, 2005) of organismic landscape perception is its implementation with data from the field. Although we demonstrated that landscape pattern alone can produce a similarly shaped relationship than the studies mentioned in the introduction, we also found null model r^2 s to be usually lower. This would mean that landscape structuring plays a role, but may not necessarily dominate diversity pattern in the landscape.

Overall, this paper argues that relevant habitats are distributed in the landscape in way that is characteristic for the landscape. Species diversity is only dependent on these relevant habitats and hence shows the same pattern (‘spatial dependence’ *sensu* Legendre et al., 2002). Hence acclaimed ‘proofs’ of characteristic landscape perception of organisms have to be re-analyzed to correct for landscape composition effects.

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