Research Article

Quantifying habitat specificit to assess the contribution of a patch to species richness at a landscape scale

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Received 9 August 1999; Revised 31 January 2000; Accepted 18 July 2000

Key words: conservation value, habitat specificit, landscape structure, land-use, rarity scaling, species richness

Abstract

Assessing and predicting the species richness of a complex landscape remains a problem because there is no simple scaling function of species richness in a heterogeneous environment. Furthermore, the potential value of an area for biodiversity conservation may depend on which, rather than how many, species the area contains. This paper shows how we can objectively evaluate the contribution of an area, e.g., a habitat patch, to larger-scale plant species richness, e.g., a landscape composed of patches of several habitat types, and how we can test hypotheses that attempt to explain this contribution. We quantified the concept of habitat specificit to assess the proportion of each observed plant population that is concentrated within a given spatial element. A case study of a biodiversity-monitoring program in the Swiss Canton of Aargau showed that the relative contribution of the three main types of land use to the overall species richness differed strongly between higher taxa (vascular plants and molluscs). However, the type of data, i.e., presence-absence or abundance, was not important. Resampling of the plant data suggested that stratification provided an unbiased estimate of relative specificit, whereas unstratified sampling caused bias even for large samples. In a second case study of vascular plants in an agricultural landscape in central Switzerland, we tested whether the type, size or shape of a landscape element can predict its contribution to the species richness of the landscape. Habitat types that were less frequently disturbed contributed more per m² to landscape species richness than more frequently disturbed ones. Contrary to expectation, patch size was negatively correlated to specificit per m² for arable fields, whereas patch shape appeared to be unrelated to the specificit per m² both for arable fields and for meadows. The specificit approach provides a solution to the problem of scaling species richness and is ideally suited for testing hypotheses on the effect of landscape structure on landscape species richness. Specificit scores can easily be combined with measures of other aspects of rarity to assess the contribution of a spatial element to conservation goals formulated at regional, national or global level.

Introduction

Plant species richness is relatively simple to measure for a small area such as a sampling quadrat of a few square meters, and several methods exist for estimating the species richness of an assumedly homogeneous, larger area (Bunge and Fitzpatrick 1993; Colwell and Coddington 1994; Palmer 1995). Landscape ecological theories aim at predicting the species richness of homogeneous patches from landscape composition and landscape structure (Forman and Godron 1986; Forman 1995). However, assessing and predicting the species richness of a complex landscape remains a problem (Stohlgren et al. 1997a) for various reasons.

Firstly, there is no simple scaling function of species richness (Palmer and White 1994). Two adjacent quadrats together will normally host less than
twice the number of species observed in a single quadrat. How much less depends on the degree of heterogeneity, which in itself is a matter of scale. A mosaic landscape will consist of patches of several types of land-use that represent different types of habitat. The scale at which a habitat is relatively homogeneous or heterogeneous strongly depends on the habitat type and on the classification of habitats. This may cause scale effects; e.g., one habitat may be the richest in species at one scale, while another may be markedly richer at a larger scale (Wagner et al. 2000).

A second problem arises from differences in habitat specificity. Generalist plant species will occur in many or most habitats, whereas specialist species may be restricted to a specific habitat type (Forman 1995). Hence a landscape element that hosts many specialist species will contribute more to landscape species richness than another element with the same number of species all of which are generalists. It should be emphasized, though, that habitat specificity is basically a continuum, as Gaston (1994) reasoned for other dimensions of rarity.

For successful, scientifically-based biodiversity management, it is not enough to know how many species were observed in a sample. We need an objective way of relating this information to conservation goals formulated at a larger spatial scale (Gaston 1996b; Suter et al. 1998). However, any reliable assessment of larger-scale species richness is bound to be time-consuming and costly (Duelli 1997; Stohlgren et al. 1997b). Therefore, we need models based on the structure and composition of a landscape that predict the significance of a landscape element for larger-scale species richness. A large body of landscape ecological literature deals with the question of how the species richness of a landscape element is related to its size, shape, and connectivity (Forman 1995). Can the same models also predict the contribution of a patch to the overall species richness of the landscape?

This paper addresses two main questions. Firstly, how can we measure the contribution of an area to larger-scale species richness? Secondly, how can we test hypotheses that predict this contribution? We quantify the concept of the habitat specificity of a species as a continuous variable and apply it for assessing how much of the total occurrence of all observed species a spatial element contains. In a first case study, we investigate whether specificity as a measure of the contribution of a spatial element to landscape species richness is robust towards the choice of the taxonomic group, the choice of data type (presence-absence vs. abundance), and the sampling design. In a second case study, we test whether information on the type, size, or shape of a landscape element can be used to predict its contribution to landscape species richness. We discuss how habitat specificity can be combined with measures of other aspects of rarity to obtain a measure of conservation value consistent with a hierarchical system of conservation goals.

Material and methods

The Aargau data sets

In 1996, the Canton of Aargau, Switzerland started a biodiversity-monitoring program (LANAG) that involves a number of biodiversity measurements based on a regular grid. The grid covers the entire canton with 516 grid points that were selected by taking every second point of a 1 km grid based on the national coordinate system (Figure 1). The data available up to 1998 cover a sub-sample of 256 grid points with no bias as to geographic region or land-use category. A list of vascular plant species present within a circular area of 10 m² was compiled from two visits, one in April/May, one in August/September of the same year. During the second visit, snails (Mollusca) were collected from a pooled soil sample of 5 dm³ and an above ground sample volume of 130 dm³. The pooled sample contained a soil sample of 11.2 cm × 11.2 cm × 5 cm and an above ground sample of 11.2 cm ×
11.2 cm × 130 cm taken at each of eight points located adjacent to the vegetation sample in the compass directions (N, NW, W, etc.). Land use information derived from the Swiss Federal Land Use Statistic (Arealstatistik) was verified for each grid point during the first visit. The 252 grid points that fell into forest, agricultural land or settlement area contained 411 plant species. At 11 locations, it was impossible to take snail samples. The remaining 241 samples from the three main land-use types contained 71 snail species.

**The Hohenrain data set**

In a study site of 0.23 km² near the village Hohenrain, Canton of Lucerne, Switzerland (Figure 2) we
took a random sample of 20 quadrats of 1 m² from each out of 12 arable field, 11 meadows, 10 grass verges, five hedgerows, and five track roads (Wagner et al. 2000). The sampling design contained the constraints that: (1) a minimum distance of 5 m be kept between quadrats; (2) quadrats do not fall into a 3-m wide edge zone within arable field or meadows; and (3) the quadrats be equally dispersed over the main gradient in hedgerows and grass verges. We sampled 20 additional quadrats from the edge of each arable field and each meadow with the same constraints as for hedgerows and grass verges. One track road and two grass verges were sampled with 10 quadrats only because of their small size. For each quadrat we recorded the species of vascular plants present shortly before the harvest in summer 1997. A total of 179 species was observed within the 1280 quadrats.

Specificity

The meaning of specificity (S) is best explained by an example. Figure 3 (top) illustrates how species may respond to the same landscape in very different ways. While Lolium multiflorum was more or less abundant in all habitats of the Hohenrain study area, Filipendula ulmaria was generally sparse and restricted to the hedges and grass verges. Thus in the case of Lolium there is a low specificity, while for Filipendula the specificity for certain habitats is rather high.

The first step in calculating the specificity S is to give equal weight to all species, irrespective of their abundance. This is achieved by setting the total occurrence of a species, or its local population, to 1 (Figure 3, bottom). For this purpose, we extend the approach by Dufrene and Legendre (1997) who presented a basic, unweighted formula for measuring habitat specificity, which they used as an input variable for calculating indicator values. We define the specificity S_{ij} of a species i to a spatial element j as the proportion of its occurrence, or of its local population, that is concentrated in that element. By adding up the specificity scores S_{ij} of all observed species, we assess how much of the total occurrence of all observed species, per unit area (S^{wa}_i) or in total (S^{wj}_i), that the spatial element contains. This sum is interpreted as an estimate of the contribution of the spatial element to the overall species richness of the study area (see Table 1 for the respective formulae).

Robustness of specificity estimates

We investigated the sensitivity of specificity scores to the choice of the taxonomic group and of the data type. For this purpose, we compared the proportional contribution of the three main land-use types in the Aargau data sets as calculated from plant presence-absence data, snail presence-absence data, and snail abundance data.

By resampling the Aargau data, we explored how the specificity estimates depend on the sampling design. We resampled the sampling units without replacement and evaluated the relative specificity per type of land use, S_j, at sample sizes 30, 60, 90, 120, and 150. From R = 99 repetitions, we calculated the mean of the relative specificity estimates and used the 5% and the 95% quantiles to construct a 90% envelope. In addition, we simulated a stratified sample by resampling the three types of land-use with equal in-
Table 1. Mathematical definition of specificity scores.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Mathematical definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$x_{ijq}$</td>
<td>The number of observations of species $i$ in quadrat $q$ within spatial element $j$</td>
<td>$x_{ijq}$</td>
</tr>
<tr>
<td>$\tilde{s}_{ij}$</td>
<td>The mean number of observations (individuals or occurrences) of species $i$ in all the $n_j$ quadrats within the spatial element $j$</td>
<td>$\tilde{s}<em>{ij} = \frac{1}{n_j} \sum</em>{q=1}^{n_j} x_{ijq}$</td>
</tr>
</tbody>
</table>

For presence-absence data, $\tilde{s}_{ij}$ is the relative frequency of occurrence per unit area $q$.

For abundance data, $\tilde{s}_{ij}$ is the average density per unit area $q$.

| $\omega_j$ | The weight $w_j$ of the spatial element $j$ is proportional to its area $a_j$ | $\omega_j = \frac{a_j}{\sum a_j}$ |
| $S_{ij}$ | The specificity of species $i$ to spatial element $j$, i.e., the estimated proportion of the occurrence or population that falls into $j$ | $S_{ij} = \frac{\omega_j x_{ij}}{\sum_{i} \omega_j x_{ij}}$ |
| $S_{aqj}$ | The total specificity of the spatial element $j$ of size $a_j$ | $S_{aqj} = \frac{1}{a_j} \sum_{i} S_{ij}$ |
| $S_{aqj}$ | The specificity per unit area $a_q$, i.e., quadrat size, of the spatial element $j$ | $S_{aqj} = \frac{S_{aqj}}{a_j}$ |
| $S_j$ | The relative specificity of the spatial element $j$ | $S_j = \frac{1}{a_j} \sum_{i} S_{ij}$ |

### Results

**Robustness of specificity estimates**

Do specificity scores depend on the chosen taxonomic group, on the data type or spatial resolution of the study, and on the sampling design? For the Aargau data sets, there is a striking difference between the proportional contribution of the three main habitat types as calculated from the plant and from the snail data (Figure 4). While the forested area appeared to be very important for snail species richness, the settlement area contributed a far larger part of plant species richness than expected based on the percentage area covered by this habitat type. On the other hand, the specificity scores for the snail data did not depend on the data type, the results based on abundance and on presence-absence data being almost identical.

How sensitive are specificity estimates to sample size? There is a consistent bias in the estimated relative specificity $S_j$ for the plant data when based on an unstratified sample (Figure 5 top left). However, a stratified sample where all land-use types were sampled with the same intensity apparently provided an unbiased estimate, i.e., the mean value of the estimates did not depend on sample size (Figure 5, bottom left). Furthermore, the stratified samples gave consistently higher specificity values to the least abundant habitat than did the unstratified. An increase in sample size generally decreased the variance, and for a given sample size, stratification reduced variance. The resampling results for the snail data showed a similar, but less marked difference between unstratified...
Figure 5. Sensitivity of the relative specificity $S_j$ to sample size as dependent on the sampling strategy. Each bar shows the mean of 99 estimates of $S_j$ derived by unstratified (top) and stratified (bottom) resampling from the Aargau data sets for plants (left) and for snails (right), based on presence-absence data. The whiskers indicate the 5% and the 95% quantiles of the estimates.

**Effects of landscape structure**

For the Hohenrain data, we tested the hypothesis that the contribution of a habitat type depends only on its area, but not on the type. In a chi-square goodness of fit test, however, the relative specificity $S_j$ differed significantly from the relative area ($X^2 = 758, DF = 6, p = 0.0001$). The interiors of arable fields and of meadows contributed less, and hedgerows, grass verges and the edges of arable fields contributed more to landscape species richness than expected from their area (Figure 6).

Can we explain the differences between habitat types by the frequency of disturbance? We estimated the rank correlation between the observed specificity per m$^2$ of each management unit and its frequency of disturbance. We defined frequency of disturbance as an ordinal variable with ranks 1 for hedgerows, 2 for grass verges, 3 for the interior and for the edge of meadows, 4 for the interior and for the edge of arable fields, and 5 for track roads. At the patch level, specificity per m$^2$ ($S_{aqj}$) was strongly correlated with the frequency of disturbance (Spearman rank correlation $r_s = -0.38, n = 66, p = 0.0021$). Hedges had the highest average, and the largest variance of specificity per m$^2$, $S_{aqj}$. The grass verges took an intermediate position, whereas the interiors of meadows and of arable fields and the roads did not differ much from each other and generally exhibited a low specificity per m$^2$.

For a given habitat type, do larger patches contribute more to landscape species richness per unit area than smaller ones? For the 12 arable fields, the specificity per m$^2$, $S_{aqi}$, of the patch interior was clearly negatively correlated with patch size (Figure 7, top.
Figure 7. A scatterplot of the specificity per m$^2$ of patch interior, i.e., neglecting a 3-m wide edge, $S_j^{eq}$, and patch area (left) and circularity (right), for the 12 arable fields (top) and for the 11 meadows (bottom) in the Hohenrain study area.

Discussion

Robustness of the specificity method

This paper demonstrates how we can quantify the contribution of an area to larger-scale species richness based on the habitat specificity of individual species. The estimated proportion of the occurrence of a species that falls into a spatial element is a measure of the species' specificity to that element. The sum of these proportions over all species form the contribution of the spatial element to the total observed species richness of the study area.

The method assumes that the individuals rely entirely on the resources offered by the habitat where they were observed and do not require a specific combination of habitats (multi-habitat species). The two taxonomic groups compared in the Aargau case study, vascular plants and molluscs, are relatively immobile and thus well suited to test the method. However, we found that the resulting pattern of specificity depended highly on the taxonomic group. The very different response of plants and snails to land-use is not an artifact of the method, but confirms the findings of Ricketts...
et al. (1999) at a considerably larger scale of 110 terrestrial ecoregions in North America. When comparing the predictive power of nine taxonomic groups, they found that non-tree vascular plants predicted a similar geographic pattern of the overall species richness of ecoregions as butterflies, birds and mammals, whereas land snails belonged to the other major type together with trees and amphibians. (Ricketts et al. 1999).

While the number of species observed in a sampling unit depends highly on its size, our results suggest that specific city estimates are relatively robust to the spatial resolution, i.e., quadrat size. Abundance data can be viewed as the extreme case of a high resolution where every sampling unit contains only one individual. In the Aargau case study, abundance and presence-absence data from pooled samples with an average of 76 individuals of 6.4 species provided almost identical estimates of the relative specificit of the three main types of land-use. This is consistent with a general strong correlation between densities and presence-absence data as reviewed by Gaston (1994).

The results from resampling of the Aargau plant data suggest that an under-representation of rare habitats may strongly affect specific city estimates. The same problem is common to non-parametric estimators of species richness (Wagner and Wildi, submitted). However, specificit estimates may be affected even more strongly, as the method requires the estimation of the relative frequency of occurrence or of the density of each species within every spatial element. We conclude that an appropriate stratification is essential for obtaining reliable estimates of specific city scores.

**Application to landscape ecology**

The theory of island biogeography (MacArthur and Wilson 1976) predicts that the species richness of an island is positively related to its size and negatively to isolation. In a review of the size effect on biodiversity in land mosaics, Forman (1995) concluded that overwhelmingly, larger patches have more species than smaller patches, and area is more important than isolation, patch age, and many other variables in predicting species number. Forman (1995) suggested that exceptions from a positive species-area relationship may occur if other factors co-vary with area, or if there are no specialist interior species present, as the species-area relationship appears to be valid only for interior species, but not for edge species. Small patches often have high species richness, but they contain only common edge species, whereas larger patches contain more specialized interior species. As specificit does discriminate between generalist and specialist species, patches that host interior and edge species should have higher specificit scores per m² than patches that contain only edge species. However, for the Hohenrain data set, field size was unrelated to specificit per m² for meadows and even negatively correlated for arable fields.

Patch shape is a potential confounding variable. A circular patch has a larger core than an elongated patch of the same size and therefore is expected to contain more interior species. Patch shape, however, appeared to be unrelated to the specificit m² both for arable fields and for meadows. Circularity $C_j$ did not co-vary with patch size, but due to the small sample size, we could not investigate any further interaction of the two variables in their effect on the specificit m². The lack of a positive effect of field size and shape on specific city per unit area suggests that interior species play a negligible role in the arable fields and meadows of the Hohenrain study area. Possible interpretations are that either there are no specialized interior species in these habitat types, or that the fields were too small for such species to occur (Forman 1995). It is possible, though, that a positive effect of patch size and circularity existed within subtypes, but was masked by the heterogeneity within the habitat types defined in the Hohenrain case study. However, alternative models may be more successful at explaining the species richness of arable fields. In terms of a source-sink model, agricultural practices are aimed at creating homogeneous sink conditions throughout the field, but will be less efficient close to adjacent seed sources than at large distances from the edge.

Duelli (1992, 1997) suggested that the species richness of an agricultural mosaic landscape could best be explained by the number of habitat types (habitat variability), by the number of habitat patches and ecotone length (habitat heterogeneity), and by the surface proportions of natural (untouched), semi-natural (perennial vegetation or cultures with low input) and intensively cultivated areas (annual crops and monoculture plantations). Although the number of habitat types is apparently simple to quantify, it obviously depends on the habitat classification and assumes that all habitat types are equally different from each other so that the specific composition of a landscape does not matter. However, we observed strong differences
between habitat types in their relative contribution to the overall plant species richness of the Hohenrain study area. Thus specificity shows what is intuitively true: that the elimination of one habitat type, e.g., hedgerows, would most likely affect the plant diversity of this landscape more severely than the lack of another type, e.g., roads or arable fields. As implied by Duelli’s (1997) definition of natural, semi-natural and cultivated land, less frequently disturbed habitat types (hedgerows, grass verges) contributed more per m² to landscape species richness than more frequently disturbed ones (arable fields, meadows, roads). This is also consistent with Forman’s expectation that habitat diversity and disturbance are the most important factors for explaining patch species richness in terrestrial ecosystems (Forman and Godron 1986; Forman 1995). However, the Hohenrain case study does not offer strong evidence, as the extent of the study was rather small and no forest patches were sampled for this data set.

The range of habitats to be compared, and their proportional size, will change with the perimeter of the study area, unless a sufficiently large portion of a constantly repeated landscape pattern is covered. The estimated specificity of a species to a given landscape element will obviously depend on the composition of the landscape under study. This is not necessarily a drawback as the dependence of specificity scores on landscape composition provides a null-model for isolating the effect of landscape structure, i.e., of the size, shape, and spatial arrangement of landscape elements, on landscape species richness. Generalization is possible even if specificity depends on landscape composition. The specificity scores are based on the relative frequency of occurrence or density of a species per unit area. By assuming an average value for every species of the regional species pool, separately for every habitat type, we can simulate the contribution of any landscape element to landscape species richness from landscape composition. This basic model could easily be refined by species-specific constraints on landscape structure. We could thus localize potential key elements responsible for the species richness of a larger area that has been identified as a biodiversity hotspot at a much coarser spatial resolution.

Application to biological conservation

Areas high in biodiversity need not be of the highest priority for conservation action, because priorities must respect other considerations such as level of threat and contribution to a broad conservation goal (Gaston 1996b). Suter et al. (1998) postulated that conservation goals formulated within a national biodiversity strategy should reflect the responsibility of an area for regional, national and global biodiversity. At a species level, such responsibility is often expressed in terms of rarity or endemism, which itself is a specific form of rarity.

Rabinowitz (1981) distinguished seven types of rarity that correspond to seven of the eight possible combinations of large and small range size, wide and narrow habitat specificity, and large and small local population size, i.e., abundance. Figure 8 (left) illustrates the typology in the form of a three-dimensional cube. However, Gaston (1994) warned against dividing the dimensions of rarity into arbitrary classes. He argued that both abundance and range size, which he considered as the primary dimensions of rarity, are essentially continuous variables. Hence he suggested
measuring rarity as the inverse of the magnitude of abundance, of range size, or of some combination of them. Williams (1999) proposed a number of continuous measures of range-size rarity and density-rarity. Specificity as defined here quantifies the dimension of habitat specificity as a continuous variable, while keeping range size and local abundance constant (Figure 8, right).

The specificity of a species $i$ to a spatial element $j$, $S_{ij}$, can be multiplied with the proportion of the occurrence within the region that falls into the study area to obtain the contribution of the spatial element to regional species richness. The conservation value at national level is derived by further multiplication with the proportion of the occurrence of the species within the country that falls into the region, etc. More complex conservation goals may be specified by giving unequal weight to the dimensions of range-size rarity and habitat specificity, or by including a weight for density rarity (Figure 8, right).

Conclusions

Specificity as defined in this paper estimates the proportion of the occurrence of each observed species that is concentrated within a given spatial element and thus provides an intuitive measure of the contribution of a spatial element to larger-scale species richness. Unlike species richness, the specificity scores of different patches of a habitat type can be summed to obtain the contribution of the habitat type, etc. The specificity approach thus provides a solution to the scaling problem that has impeded the quantitative linking of plant species richness with landscape characteristics. Therefore, it is especially suited for testing hypotheses on the effect of landscape structure on species richness at a landscape scale.

The results presented in this paper suggest that we may obtain an unbiased estimate of the proportional contribution of a landscape element to landscape species richness of a given taxonomic group from a stratified sample, even if the true landscape species richness is unknown and the sample contains only a part of the species. Further research is needed to derive optimal sampling strategies for various types of landscape patterns.

Specificity scores can easily be combined with measures of other aspects of rarity to assess the contribution of a spatial element to conservation goals formulated at regional, national or global level. Spatially explicit models of specificity may be developed without local sampling if average densities per species and habitat type are substituted. Thus we can localize the key elements responsible for the species richness of a larger area that has been identified as a biodiversity hotspot at a much coarser spatial resolution.

Acknowledgements

We thank the department of Nature and Landscape of the Canton Aargau, Switzerland, for letting us use their data. The project has partly been financed by the Swiss Agency of the Environment, Forests and Landscape (BUWAL), with the help of Klaus C. Ewald, Nature and Landscape Protection, Swiss Federal Institute of Technology (ETH), Zürich. We profited from suggestions by Darius Weber of Hintermann & Weber in Reinach BL, and by Otto Wildi, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf.

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