Research Article

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

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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 quantif ed the concept of habitat specif city 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 stratif cation provided an unbiased estimate of relative specif city, whereas unstratif ed 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 m^2 to landscape species richness than more frequently disturbed ones. Contrary to expectation, patch size was negatively correlated to specificit per m^2 for arable f elds, whereas patch shape appeared to be unrelated to the specif city per m^2 both for arable f elds and for meadows. The specif city 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 classificati n 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 specificit . Generalist plant species will occur in many or most habitats, whereas specialist species may be restricted to a specif c 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 specif city is basically a continuum, as Gaston (1994) reasoned for other dimensions of rarity.

For successful, scientifically-ba ed 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 significanc 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 specif city 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 fir t case study, we investigate whether specificit 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-
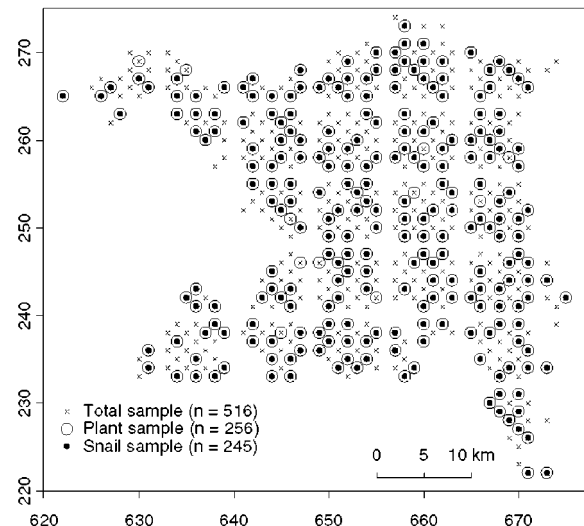

Figure 1. Sampling design and realized sample for land-use, vascular plants, and molluscs of the LANAG biodiversity-monitoring program of the Canton of Aargau, Switzerland.

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 specif city 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 m^2 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 dm^3 and an above ground space volume of 130 dm^3. 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 ×
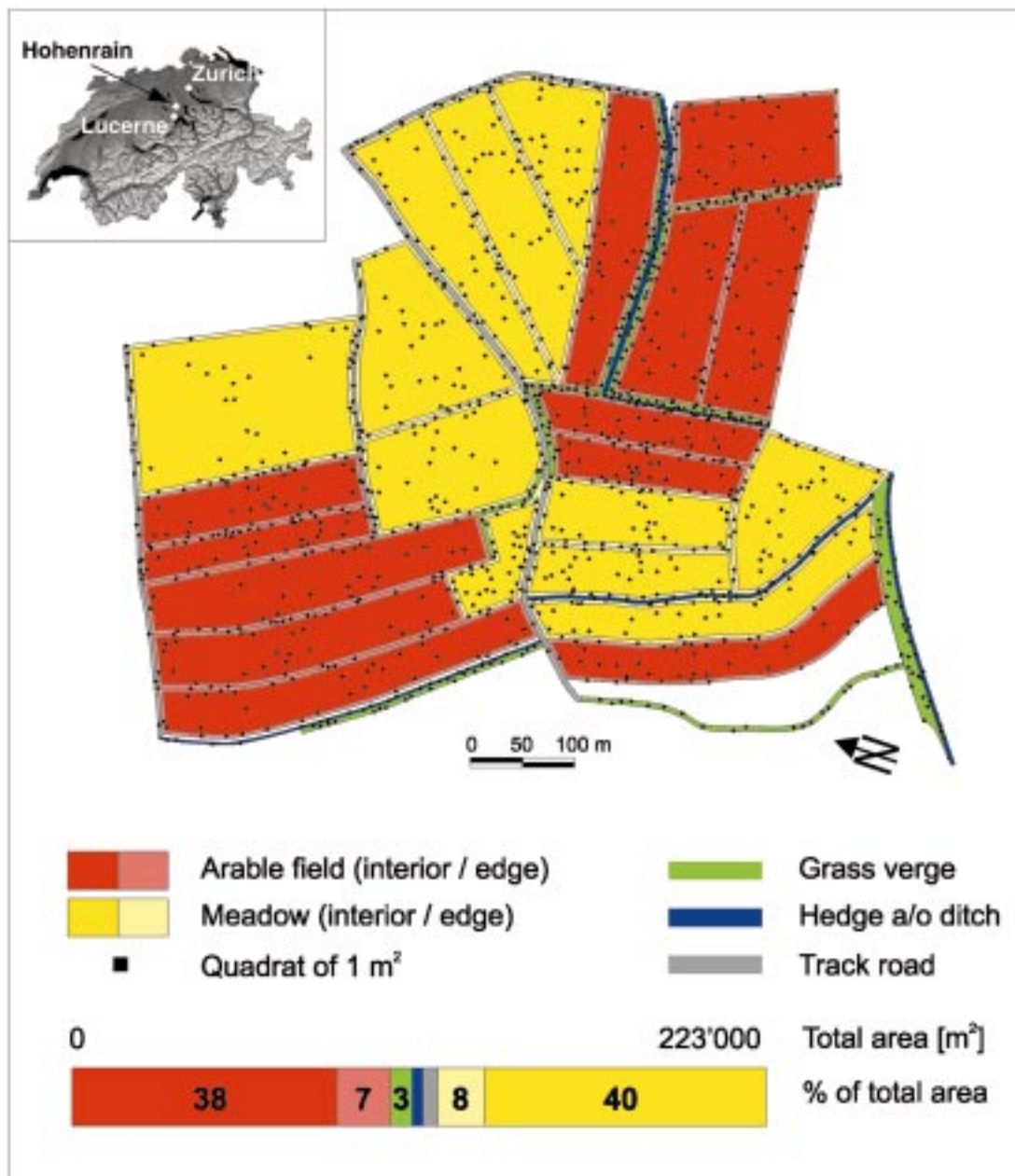
Figure 2. Pattern of land use and stratifie sample of the study area near Hohenrain, Switzerland. The stacked barplot shows for every type of land use its proportional area within the study area.

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 verifie for each grid point during the fir t 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 km^2 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, f ve hedgerows, and f ve track roads (Wagner et al. 2000). The sampling design contained the con-straints 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 fiel 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 be-cause 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.

Specific ty

The meaning of specificit (*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 multif orum* was more or less abundant in all habitats of the Hohenrain study area, *Filipen-dula ulmaria* was generally sparse and restricted to the hedges and grass verges. Thus in the case of *Lolium* there is a low specificit , while for *Filipendula* the specificit for certain habitats is rather high.

The f rst step in calculating the specificit *S* is to give equal weight to all species, irrespective of their abundance. This is achieved by setting the to-tal 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 specif city, which they used as an input variable for calculating indicator values. We defin the speci-ficit S_{ij} of a species *i* to a spatial element *j* as the proportion of its occurrence, or of the local population, that is concentrated in that element. By adding up the specificit scores S_{ij} of all observed species, we as-sess how much of the total occurrence of all observed species, per unit area (S_j^{aq}) or in total (S_j^{aj}), 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).
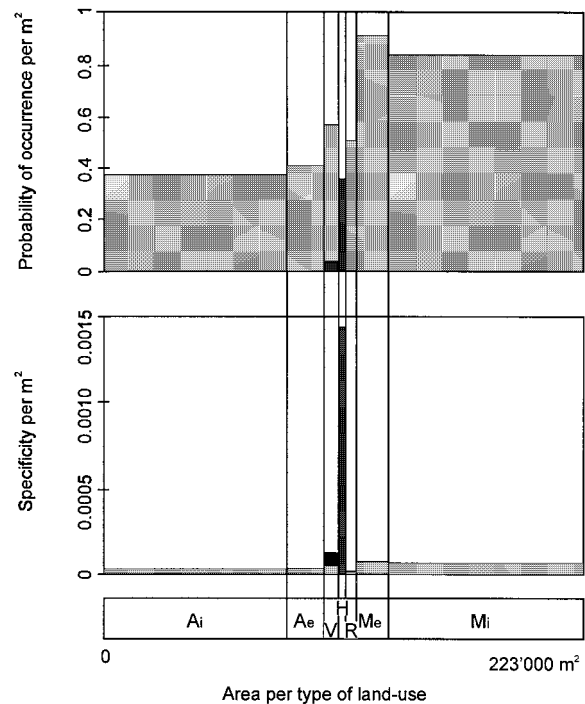

Figure 3. A plot of the relative frequency of occurrence per m² (top) and of the specif city per m² (bottom) of *Lolium multiflo um* (grey) and of *Filipendula ulmaria* (black) versus the area of the various habitat types of the study area near Hohenrain, Switzerland. The product of the relative frequency of occurrence per m² and the area corresponds to the estimated total occurrence, the product of the specif city per m² and the area indicates the total specif city of a species and is 1 by definition The habitat types are: interior (*Ai*) and edge (*Ae*) of arable f elds, grass verge (*V*), hedge (*H*), track road (*R*), and meadow edge (*Me*) and interior (*Mi*).

Robustness of specific ty estimates

We investigated the sensitivity of specificit 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 specificit estimates depend on the sampling de-sign. We resampled the sampling units without re-placement and evaluated the relative specificit 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 specificit estimates and used the 5% and the 95% quantiles to construct a 90% enve-lope. In addition, we simulated a stratifie sample by resampling the three types of land-use with equal in-

Table 1. Mathematical def nition of specif city scores.

Symbol	Description	Mathematical def nition
x_{ijq}	The number of observations of species i in quadrat q within spatial element j	
$\bar{x}_{ij}$	The mean number of observations (individuals or occurrences) of species i in all the n_j quadrats within the spatial element j	$\bar{x}_{ij} = \sum_q \dfrac{x_{ijq}}{n_j}$
	For presence-absence data, $\bar{x}_{ij}$ is the relative frequency of occurrence per unit area q	
	For abundance data, $\bar{x}_{ij}$ is the average density per unit area q	
ω_j	The weight w_j of the spatial element j is proportional to its area a_j	$\omega_j = \dfrac{a_j}{\sum_j a_j}$
S_{ij}	The specif city of species i to spatial element j, i.e., the estimated proportion of the occurrence or population that falls into j	$S_{ij} = \dfrac{\omega_j \bar{x}_{ij}}{\sum_j \omega_j \bar{x}_{ij}}$
S_j^{aj}	The total specif city of the spatial element j of size a_j	$S_j^{aj} = \sum_i S_{ij}$
S_j^{aq}	The specificit per unit area a_q, i.e., quadrat size, of the spatial element j	$S_j^{aq} = S_j^{aj} \dfrac{a_q}{a_j}$
S_j	The relative specif city of the spatial element j	$S_j = \dfrac{S_j^{aj}}{\sum_j S_j^{aj}}$

tensity and evaluated S_j at sample sizes 3×10, 3×20, and 3×30.

Results

Robustness of specific ty estimates

Do specif city 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 specif city 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 specificit estimates to sample size? There is a consistent bias in the estimated relative specificit S_j for the plant data when based on an unstratifie sample (Figure 5 top left). However, a stratifie sample where all land-use types were sam-
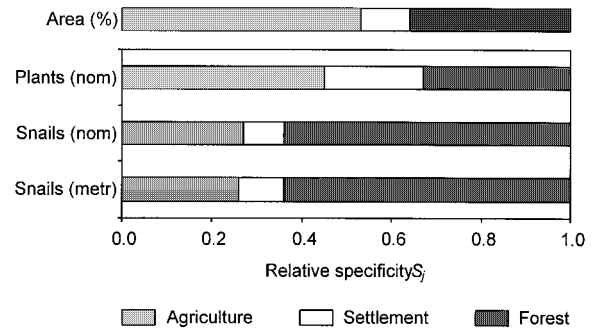

Figure 4. The proportional contribution of the three main types of land use, i.e., agricultural land, forest and settlement area, to the total observed species richness of the Aargau data sets. The snail data was analyzed with the original abundance data (*metr*) and with presence-absence data (*nom*).

pled 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 stratifie samples gave consistently higher specif city values to the least abundant habitat than did the unstratifie . An increase in sample size generally decreased the variance, and for a given sample size, stratificatio reduced variance. The resampling results for the snail data showed a similar, but less marked difference between unstratifie
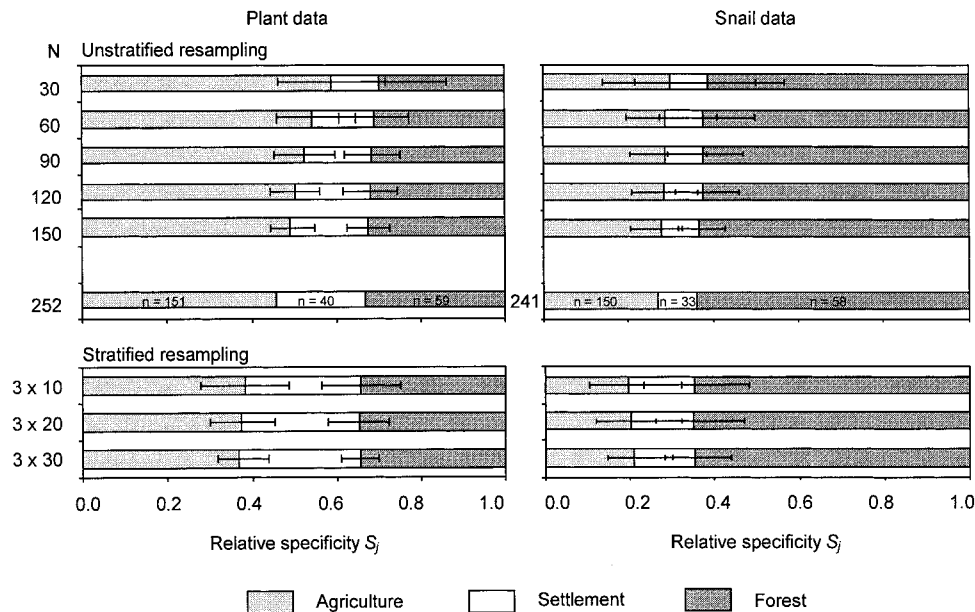
Figure 5. Sensitivity of the relative specificity S_j to sample size as dependent on the sampling strategy. Each bar shows the mean of 99 estimates of S_j derived by unstratified (top) and stratified (bottom) resampling from the Aargau data sets for plants (left) and for snails (right), based on presence-absence data. The whiskers indicate the 5% and the 95% quantiles of the estimates.

(Figure 5, top right) and stratified samples (Figure 5, bottom right).

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^{aj} 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 m² 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 m² (S_j^{aq}) was strongly correlated with the frequency of disturbance (Spearman rank correlation $r_s = -0.38$, $n = 66$, $p = 0.0021$). Hedges had the
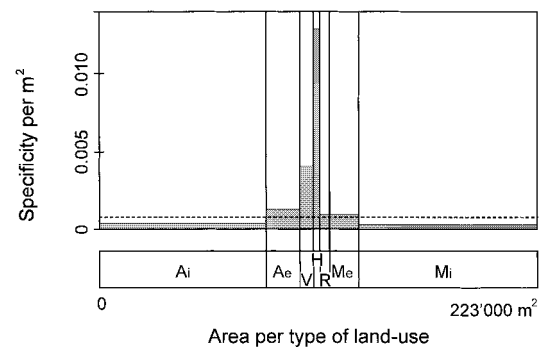

Figure 6. Sum of the specificity values of all 179 observed species per m² (y-axis) and in total (shaded area) for each habitat type in the study area at Hohenrain, Switzerland. The dashed line marks the specificity per m² expected under the null hypothesis, i.e., the number of observed species divided by the total area. The habitat types are explained in the legend to Figure 3.

highest average, and the largest variance of specificity per m², S_j^a. 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 m².

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 m², S_j^{aq}, of the patch interior was clearly negatively correlated with patch size (Figure 7, top
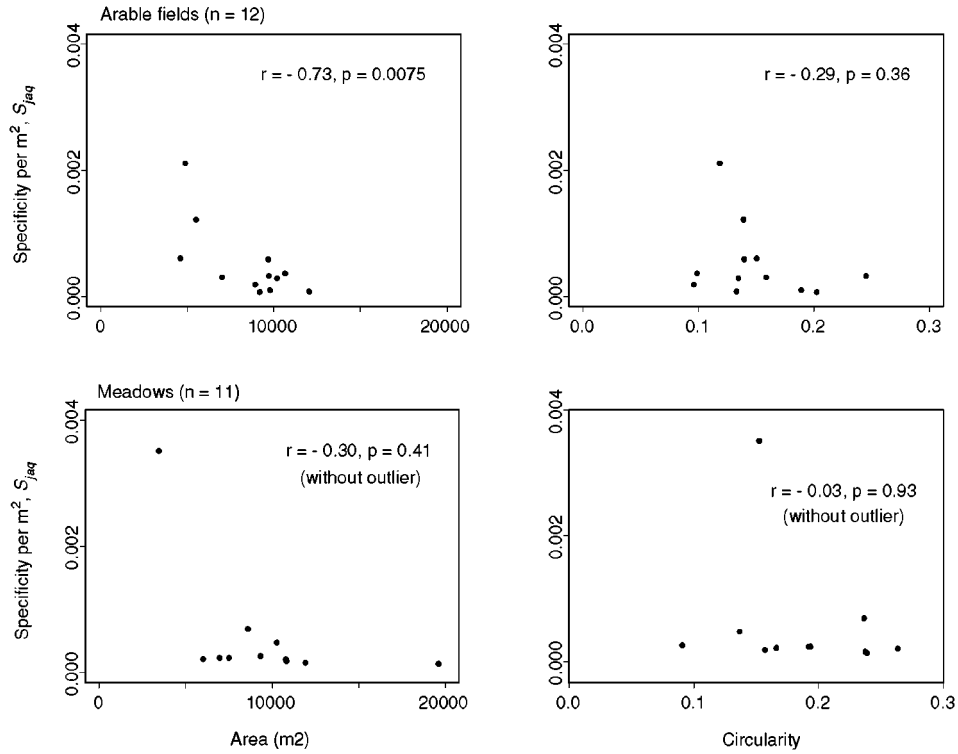
Figure 7. A scatterplot of the specif city per m² of patch interior, i.e., neglecting a 3-m wide edge, S_j^{aq}, and patch area (left) and circularity (right), for the 12 arable field (top) and for the 11 meadows (bottom) in the Hohenrain study area.

left). For the 11 meadows, there was no evidence of a correlation (Figure 7, bottom left). Only one meadow that was managed less intensively under a conservation program showed a markedly higher specif city per m² than the other meadows.

Do more circular or square-shaped f elds contribute more to landscape species richness per unit area than more elongated f elds? We quantif ed the circularity C_j of patch j as a function of its area a_j and its perimeter p_j (Griff th 1982; Davis 1986):

$$C_j = \frac{4a_j}{p_j^2}.$$

Circularity C_j was not significa tly correlated to the specificit per m², S_j^{aq}, of the patch interior, neither for the arable f elds (Figure 7, top right) nor for the meadows (Figure 7, bottom right). It seems unlikely that a positive correlation exists that did not become statistically significan due to small sample size, as for the arable f elds, the empirical correlation was clearly negative (Figure 7, top right).

Discussion

Robustness of the specific ty method

This paper demonstrates how we can quantify the contribution of an area to larger-scale species richness based on the habitat specif city of individual species. The estimated proportion of the occurrence of a species that falls into a spatial element is a measure of the species' specificit 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 specif c 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 specificit 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 conf rms the f ndings 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 butterf ies, 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 specif 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 specif 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 stratif cation is essential for obtaining reliable estimates of specif 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 specif city scores per m^2 than patches that contain only edge species. However, for the Hohenrain data set, fiel size was unrelated to specificit per m^2 for meadows and even negatively correlated for arable fiel s.

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 m^2 both for arable field 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 per m^2. The lack of a positive effect of f eld size and shape on specif city per unit area suggests that interior species play a negligible role in the arable f elds 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 f elds 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 defi ed in the Hohenrain case study. However, alternative models may be more successful at explaining the species richness of arable f elds. In terms of a source-sink model, agricultural practices are aimed at creating homogeneous sink conditions throughout the f eld, but will be less efficien 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 classif cation and assumes that all habitat types are equally different from each other so that the specifi composition of a landscape does not matter. However, we observed strong differences
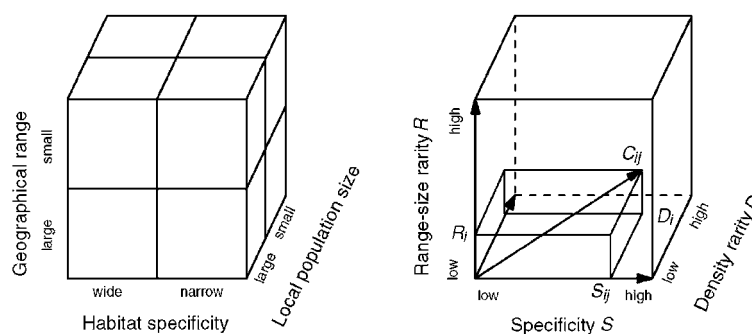
Figure 8. The rarity types by Rabinowitz (1981) depicted as segments of a cube (left), and the concepts of range-size rarity (*R*) and density-rarity (*D*) as def ned by Williams (1999), and specif city (*S*) as define in this paper (right). A combination of specificit , range-size rarity and possibly density-rarity could be used to derive a conservation value C_{ij} of a species i in a spatial element j. The contribution of an area j to conservation goals formulated at regional, national, or global level may then be assessed by summing the C_{ij} over all species i, choosing an appropriate reference area for range-size.

between habitat types in their relative contribution to the overall plant species richness of the Hohenrain study area. Thus specif city 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 f elds. As implied by Duelli's (1997) definitio of natural, semi-natural and cultivated land, less frequently disturbed habitat types (hedgerows, grass verges) contributed more per m^2 to landscape species richness than more frequently disturbed ones (arable f elds, 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 suff ciently large portion of a constantly repeated landscape pattern is covered. The estimated specificit 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 specificit 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 specif city depends on landscape composition. The specificit 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 refine by species-specifi constraints on landscape structure. We could thus localize potential key elements responsible for the species richness of a larger area that has been identifie 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 reflec 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 specifi 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 specificit , 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

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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. Specificit as define here quantifie the dimension of habitat specif city as a continuous variable, while keeping range size and local abundance constant (Figure 8, right).

The specificit 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 specif ed by giving unequal weight to the dimensions of range-size rarity and habitat specif city, or by including a weight for density rarity (Figure 8, right).

Conclusions

Specificit as defi ed 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 specificit scores of different patches of a habitat type can be summed to obtain the contribution of the habitat type, etc. The specif city 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 stratifie 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.

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. Spatially

explicit models of specificit 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 identifie as a biodiversity hotspot at a much coarser spatial resolution.

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