From $m^2$ to $km^2$:

Scaling of the plant species diversity of an agricultural landscape

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Preface

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Abstract

From m² to km²:
Scaling of the plant species diversity of an agricultural landscape.

This study aims at integrating measures of plant species diversity and its main aspects, richness and evenness, at different spatial scales so as to gain a better picture of the overall plant diversity of an agricultural landscape and its potential for biodiversity conservation. The first chapter quantifies the effects of habitat variability and habitat heterogeneity based on the partitioning of landscape species diversity into additive components. We derived components of within- and between-community diversity at four scale levels (quadrat, patch, habitat type, and landscape) for three diversity measures (species number, Shannon index, and Simpson diversity). The approach is illustrated with a case study from central Switzerland, where we recorded the occurrence of vascular plants in a stratified random sample based on the land-use pattern. The diversity components depended strongly on the habitat type and on the diversity measure. Landscape composition had a strong influence on landscape species richness, but not on evenness. In the second chapter, we simulated how the four non-parametric richness estimators Jack1, Jack2, Chao2 and ICE are affected by the abundance distribution and by spatial heterogeneity. In contrast to other simulation studies, we fitted different models of species abundance to real data and, instead of assuming a global aggregation factor, modeled for every species the effects of spatial autocorrelation, of an environmental gradient and of a boundary zone (edge effect). Spatial structures and species abundance distribution influenced the performance of richness estimators via sample representativeness. The sampling design should be adapted to obtain random samples of ecological conditions instead of geographical space. The third chapter is concerned with the concept of habitat specificity and quantifies the contribution of the various spatial elements to the total occurrence of individual species. The robustness of specificity estimates was investigated with vascular plant and mollusc data from a biodiversity-monitoring program in the Swiss Canton of Aargau. With the case study from chapter I, we tested hypotheses on the effect of landscape structure on landscape species richness. Resampling results suggested that unbiased estimates of relative specificity may be obtained by an adequately stratified sampling design. Specificity can be combined with measures of other aspects of the rarity of a species to obtain an integral measure of the contribution of a landscape element to a hierarchical set of conservation goals as formulated in a national biodiversity strategy.
Zusammenfassung


Mit Hilfe von Simulationen wird im zweiten Kapitel untersucht, wie räumliche Muster sowie die Häufigkeitsverteilung der Arten die Effizienz von vier nicht-parametrischen Methoden zur Schätzung der Artenzahl (Jack1, Jack2, Chao2 und ICE) beeinflussen. Im Gegensatz zu anderen Simulationsstudien passten wir verschiedene Häufigkeitsverteilungen an reale Daten aus der Fallstudie von Kapitel I an und modellierten, anstelle eines globalen Aggregierungsfaktors, für jede Art die Effekte räumliche Autokorrelation, eines Standorts-Gradienten und einer Nutzungsgrenze (Randeffekt). Eine Varianzanalyse des Schätzfehlers für einigermassen vollständige Stichproben ergab dass Jack1 und Jack2 die wahre Artenzahl leicht überschätzen, während ICE zur Unterschätzung neigt. Die Methoden unterschieden sich stark in der Streuung, sodass bei der Methodenwahl sorgfältig zwischen Schätzfehler und Streuung abgewägt werden muss. Alle Schätzer versagten für Häufigkeitsverteilungen, die dem geometrischen Modell folgen, sowie in Gegenwart eines simulierten Randeffekts, während räumliche Autokorrelation und ein Standorts-Gradient kaum Einfluss auf die Qualität der Schätzung hatten.
Im dritten Kapitel wird das Konzept der Habitat-Treue (Spezifität) quantifiziert, um das Vorkommen der beobachteten Arten den Landschaftselementen zuzuordnen. Mit Gefäßpflanzen- und Molluskendendaten eines Biodiversitäts-Monitorings aus dem Kanton Aargau wurde untersucht, wie zuverlässig sich der Beitrag eines Landschaftselements zur Gesamtartenzahl der Landschaft schätzen lässt. Der Datentyp (Präsenz-Ab¬
senz-Daten vs. Zähldaten) hatte kaum einen Einfluss auf den Beitrag der drei Hauptnutzungstypen zur Gesamtartenzahl, das Resultat hing jedoch stark davon ab, ob man Pflanzen oder Schnecken betrachtete. Mittels Resampling der Pflanzendaten konnte gezeigt werden, dass eine stratifizierte (d.h. geschichtete) Stichprobe offenbar eine un¬
verzerrte Schätzung erlaubt, während ohne Stratifizierung sogar umfangreiche Stich¬
proben zu einer verzerrten Schätzung führten. Mit Daten der Fallstudie aus Kapitel I wurden ferner Hypothesen über den Einfluss der räumlichen Verteilung der Land¬
schaftselemente auf die Artenzahl einer Landschaft getestet. Pro Quadratmeter trugen seltener gestörte Nutzungstypen mehr zur Artenzahl der Landschaft bei als häufiger gestörte. Anders als erwartet korrelierte die Flächengrösse der Äcker negativ mit der Spezifität pro m², während die Flächenform von Äckern und Wiesen mit der Spezifität pro m² nicht korrelierte.

Die Bedeutung dieser Ergebnisse für die Erfassung der Artenvielfalt auf Landschafts¬ebene werden diskutiert. Die Artenzahl einer Landschaft hängt stark vom Landschaftsmuster ab (Variatiblität und Heterogenität der Nutzungstypen), während gemischte Diversitätsmasse wie der Shannon-Index oder die Simpson-Diversität v.a. auf Hetero¬
parametrische Schätzverfahren setzen eine Zufallsstichprobe einer diskreten, räumlich homogenen Artengemeinschaft voraus, welche eine klar begrenzte Fläche einnimmt. Räumliche Muster und die Häufigkeitsverteilung der Arten beeinflussen die Qualität der Schätzung über den Anteil der erfassten Arten (sample representativeness). Wir empfehlen, die Stichprobe so zu stratifizieren, dass eine repräsentative Stichprobe der Standortsbedingungen anstatt des geographischen Raumes resultiert.

Der Spezifitäts-Ansatz zur Erfassung des Beitrags einer Einzelfläche oder eines Nut¬
zungstyps zur Artenzahl der Landschaft eignet sich sehr gut, um Hypothesen über den Einfluss der Zusammensetzung und Struktur einer Landschaft auf die Artenzahl zu testen. Spezifität als Messgrösse sollte aus zwei Gründen weiter untersucht werden. Erstens weisen unsere Resampling-Analysen darauf hin, dass eine geeignete Stratifizie¬
Summary

This study aims at integrating measures of plant species diversity and its main aspects, richness and evenness, at different spatial scales so as to gain a better picture of the overall plant diversity of an agricultural landscape and its potential for biodiversity conservation. The three main chapters deal with the following problems: (i) How can we quantify species richness and evenness at different spatial scales so that the diversity components can be compared? (ii) How can we estimate components of species richness in a mosaic landscape? (iii) How can we evaluate diversity measurements with respect to conservation goals specified at a larger spatial scale? By addressing these basic problems of biodiversity assessment, we hope to contribute to the success of the growing efforts to enhance the biodiversity of agricultural landscapes through ecological compensation programs.

The first chapter quantifies the effects of habitat variability and habitat heterogeneity based on the partitioning of landscape species diversity into additive components. We derived components of within- and between-community diversity at four scale levels (quadrat, i.e. sampling unit; patch, i.e. management unit; habitat type, i.e. type of land-use; and landscape, i.e. land-use mosaic) for three diversity measures (species number, Shannon index, and Simpson diversity). The approach is illustrated with a case study from central Switzerland where we recorded the presence of vascular plant species in a stratified random sample of 1'280 quadrats of 1 m² within a total area of 0.23 km². The results suggest that the values of the individual diversity components depend on the habitat type and on the chosen diversity aspect. One habitat may be more diverse than another at patch level, but less diverse at the level of habitat type. Landscape composition is a key factor for explaining landscape species richness, but affects evenness only little.

In the second chapter, we simulated how the four non-parametric richness estimators Jack1, Jack2, Chao2 and ICE are affected by variations in the abundance distribution and by different types of spatial heterogeneity. Our approach differs in two ways from other simulation studies. Firstly, we fitted different models of species abundance to the same real data (data for four different habitat types from the case study in chapter 1). Secondly, we explicitly modeled, independently for every simulated species, the effects of spatial autocorrelation, of an environmental gradient and of a boundary zone between neighboring patches (edge effect). An ANOVA of relative bias showed that for reasonably complete samples, Jack1 and Jack2 were positively biased and ICE was negatively biased. The estimators differed markedly in their variance, leading to a trade-off between bias and variance. All estimators failed for communities simulated under the geometric model and were considerably affected by a simulated edge effect, whereas spatial autocorrelation, an environmental gradient, and differences between community types had little effect on estimator performance.
The third chapter is concerned with the concept of habitat specificity and quantifies the contribution of the various spatial elements to the total occurrence of individual species. The robustness of estimates of the contribution of an area to larger-scale species richness was investigated with vascular plant and mollusc data from a biodiversity-monitoring program in the Swiss Canton of Aargau. The relative contribution of the three main types of land use to species richness at regional level did not depend on the data type, i.e. presence-absence or abundance data, but differed strongly between plants and snails. Resampling of the plant data suggested that stratification provides an unbiased estimate of relative specificity, whereas unstratified sampling caused bias even for large samples. With the case study from chapter I, we tested hypotheses on the effect of landscape structure on landscape species richness. Less frequently disturbed habitat types contributed more per m² to landscape species richness than more frequently disturbed ones. Contrary to expectations, field size was negatively correlated to specificity per m² for arable fields, whereas field shape appeared to be unrelated to the specificity per m² both for arable fields and meadows.

The implications of these findings for investigating species diversity at the landscape level are discussed. Landscape species richness is mainly determined by heterogeneity at relatively high scale levels (habitat variability, habitat heterogeneity), whereas mixed diversity measures such as Shannon index and Simpson diversity respond to heterogeneity at lower scale levels (within-patch). Attempts at linking landscape structure quantitatively to species diversity should therefore concentrate on species richness. However, the estimation of richness components at patch, habitat type or landscape level is problematic. Non-parametric estimators of species richness assume that the quadrats represent a random sample from a discrete, spatially homogeneous community that occupies a discrete area. Spatial structures and species abundance distribution influence estimator performance via sample representativeness. We strongly advise adapting the sampling design so as to obtain random samples of ecological conditions instead of geographical space.

The specificity approach to assessing the contribution of a landscape element to landscape species richness is ideally suited for testing hypotheses about the effect of landscape composition and structure on landscape species richness. Specificity should be thoroughly explored for two reasons. Firstly, our resampling study suggests that unbiased estimates of relative specificity may be obtained by an adequately stratified sampling design. Secondly, specificity can easily be combined with measures of other aspects of the rarity of a species to obtain an integral measure of the contribution of a landscape element to a hierarchical set of conservation goals as formulated in a national biodiversity strategy.
Introduction

Objectives

The 1992 Rio convention brought a global commitment to maintain and enhance biodiversity from local to global level. The convention has triggered not only a multitude of research programs, but also a never-ending discussion about what biodiversity actually is. According to Gaston (1996b), the confusion arises because there are a variety of viewpoints about biodiversity and many users assume that everyone shares the same intuitive definition. Fig. 1 illustrates the three main viewpoints identified by Gaston (1996b): those who regard biodiversity as a concept; those who regard it as a measurable entity; and those who regard it as predominantly a social or political construct.

This thesis takes a quantitative view of biodiversity but aims at building bridges towards biodiversity as an abstract, all-encompassing concept and towards biodiversity as a normative value. However, quantifying biodiversity as the 'variety of life', or any other definition of biodiversity per se, is clearly beyond the scope of this study. Several schemes have been suggested to distinguish the major features of biodiversity, and the divisions between genetic, species and ecosystem diversity have become almost conventional (Gaston 1996b). Species diversity is the most commonly used level (Suter et al. 1998). It contains the two aspects species richness, i.e., the number of species, and evenness, i.e. how equally abundant the species are (Magurran 1988). One problem with diversity research is that patterns of diversity, and especially species richness, are known to be highly scale dependent (e.g. Palmer and White 1994). Relatively little is known about patterns of species diversity in agro-ecosystems, as most research deals with natural habitats. Nevertheless, there is an urgent need for objective and efficient methods of evaluating the biodiversity of agricultural landscapes (Duelli 1997). The thesis focuses on some methodological problems associated with the scaling of plant species diversity in an agricultural landscape.

The three main chapters deal with the following problems:

- How can we quantify different aspects of species diversity at a range of scale levels so that the diversity components can be compared directly (chapter I)?

- How can we estimate components of species richness in a mosaic landscape (chapter II)?

- How can we evaluate diversity components according to conservation goals specified at larger spatial scales and in complex landscapes (chapter III)?
Integration of diversity components (Chapter I)

Early authors (Whittaker 1960, 1977; Allan 1975) defined components of species diversity at a number of spatial scales and described the relationship between individual components in mathematical terms. Recent studies are often limited to single variables (Gaston 1996b), which commonly are interpreted as one of Whittaker's components of alpha, beta and gamma diversity. Lande (1996) further developed Allan's approach and emphasized it as a unifying framework with which to measure diversity at different levels of spatial organisation. Duelli (1992; 1997) proposed the mosaic concept as an alternative to the theory of island biogeography (MacArthur and Wilson 1976) for predicting the species diversity of agricultural landscapes. The first chapter uses the methods proposed by Lande (1996) as a basis for quantifying the key parameters of the mosaic concept. The effects of habitat variability and habitat heterogeneity are assessed based on the partitioning of landscape species diversity into additive components. The approach is tested with data from a case study in central Switzerland.
Estimation of species richness (Chapter II)

Because reasonably complete species lists can only be obtained for small areas, we have to rely on estimates for determining the species richness of larger areas (Palmer 1995; Gaston 1996a). Several methods have been proposed for estimating plant species richness from a sample (Bunge and Fitzpatrick 1993; Colwell and Coddington 1994; Palmer 1995). Empirical comparisons of their performance suggest that the non-parametric methods often perform better than the other methods. While the label non-parametric may suggest that a method makes few or no assumptions, these estimators rely on a homogeneous community with some arbitrary type of abundance distribution (Bunge and Fitzpatrick 1993). The second chapter uses simulations to investigate the effect of different types of spatial patterns and of different abundance distributions on the performance of several non-parametric estimators of species richness. This study differs from other simulations of estimator performance in two ways. Firstly, it adopts a systematic approach to spatial heterogeneity as outlined by Legendre (1993) based on hierarchy theory (Allen and Starr 1982). Secondly, the necessary parameters are derived from real data so as to make the simulations as realistic as possible.

From species counts to conservation value (Chapter III)

The model developed in chapter I facilitates the comparison of diversity components between habitat types and scale levels, but it does not tell us which landscape elements are most important for larger-scale species richness. The potential value of an area to overall plant biodiversity conservation may depend on which rather than how many plant species the area contains (Gaston 1996b). A large body of landscape ecological literature deals with the question of how the species richness of a habitat patch is related to landscape structure (Forman 1995). Can the same models also predict the significance of a patch for the overall species richness of the landscape? Species richness components are inflated by generalist species that occur in most of the habitat types, whereas specialist species that may be restricted to a single type receive little weight. Based on an approach by Dufrene and Legendre (1997), the third chapter quantifies the concept of habitat specificity to assess how much each spatial element contributes to the total occurrence of all observed species. The robustness of the method is investigated with plant and mollusc data from a biodiversity-monitoring program in the Swiss Canton of Aargau. The method is then applied to test hypotheses on the effect of the structure and composition of a landscape on its plant species richness using the case study from chapter I. The question is discussed of how habitat specificity can be combined with measures of other aspects of rarity (Rabinowitz 1981; Gaston 1994; Williams et al. 1996) to obtain a measure of conservation value that is consistent with a hierarchical system of conservation goals as recommended by Suter et al. (1998).
Significance

This study aims at quantifying different aspects of plant species diversity across a range of scale levels and integrating these measurements so as to gain a better picture of the overall plant diversity of a landscape and its potential for biodiversity conservation. An important idea is that these measures are only relevant to biodiversity management under certain conditions, which has several implications for their practical application. Firstly, we need to combine measures of a range of diversity components into an integrated assessment of the overall biodiversity of a larger area. Secondly, it is not enough to know how many species were observed in a sample. We lack objective ways of relating this information to conservation goals formulated at regional, national, or global level. Thirdly, any reliable assessment of larger-scale species richness is bound to be costly. Therefore, we need models that predict the significance of a landscape element for larger-scale biodiversity taking account of the structure and composition of the landscape. By addressing these basic problems of biodiversity assessment, the study seeks to contribute to the success of the growing national and international efforts that aim to enhance the biodiversity of agricultural landscapes through ecological compensation programs.

References


Additive partitioning of plant species diversity in an agricultural mosaic landscape


Abstract – In this paper, we quantify the effects of habitat variability and habitat heterogeneity based on the partitioning of landscape species diversity into additive components and link them to patch-specific diversity. The approach is illustrated with a case study from central Switzerland, where we recorded the presence of vascular plant species in a stratified random sample of 1'280 quadrats of 1 m² within a total area of 0.23 km². We derived components of within- and between-community diversity at four scale levels (quadrat, patch, habitat type, and landscape) for three diversity measures (species richness, Shannon index, and Simpson diversity). The model implies that what we measure as within-community diversity at a higher scale level is the combined effect of heterogeneity at various lower levels. The results suggest that the proportions of the individual diversity components depend on the habitat type and on the chosen diversity aspect. One habitat type may be more diverse than another at patch level, but less diverse at the level of habitat type. Landscape composition apparently is a key factor for explaining landscape species richness, but affects evenness only little. Before we can test the effect of landscape structure on landscape species richness, several problems will have to be solved. These include the incorporation of neighborhood effects, the unbiased estimation of species richness components, and the quantification of the contribution of a landscape element to landscape species richness.

Introduction

A natural habitat obtains its characteristics from environmental factors such as climate, soil or topography, from natural succession, and from the frequency and type of natural disturbance. In agro-ecosystems, human actors deliberately modify environmental conditions through agricultural practices such as preparations for crop and pasture seeding, crop management (i.e. actions which directly benefit or protect the crop such as fertilizer and pesticide application), harvesting method and grazing management. In an agricultural landscape, the habitat thus depends strongly on the spatial and temporal pattern of disturbance by agricultural practices.
Approaches that evaluate the biodiversity of a landscape based on its structure often rely on the equilibrium theory of island biogeography by MacArthur and Wilson (1976). It predicts that the biodiversity on an island is positively correlated with the area of that island and negatively correlated with the distance to the nearest continent. Applied to an agricultural landscape, an evaluation of biodiversity would have to be based on the surface area of each habitat island and the distance to the nearest patch of the same habitat type (Duelli 1997). In a review of empirical studies of species richness and patch size in terrestrial landscapes, Forman (1995) stated that in most cases, larger patches have more species than smaller patches, and area is more important than isolation, patch age, and many other variables in predicting species richness. However, it was observed that while the area of patch interior is positively related to the number of specialized interior species (i.e. species primarily distant from the perimeter), patch size can not explain the number of edge species (i.e. species primarily near the perimeter of a landscape element; Forman 1995). If we assume that intensively cultivated land hosts only few specialized interior species, the species richness of an agricultural landscape without natural habitats depends strongly on the edge species and can not be predicted by patch size. According to Duelli (1997), the factors most pertinent to predict and evaluate biodiversity in an agricultural mosaic landscape are (1) habitat variability, i.e. the number of biotope types per unit area; (2) habitat heterogeneity, i.e. the number of patches and the length of ecotones per unit area; and (3) the surface proportions of natural, semi-natural and intensively cultivated areas. Duelli (1992, 1997) proposed the use of the mosaic concept as an alternative approach to explain patch species richness in cultural landscapes. The mosaic concept predicts that the species diversity in an area increases with habitat variability and with habitat heterogeneity.

In order to test the predictions of the mosaic concept, we need a quantitative description of landscape species diversity that partitions overall diversity into the contributions of habitat variability, habitat heterogeneity and patch-specific diversity. Whittaker (1977) proposed to link diversity components between ecological scales by multiplication, so that landscape or gamma diversity is the product of the mean alpha diversity and beta diversity. In contrast to Whittaker’s (1977) multiplicative model, Allan (1975) applied an additive linkage of diversity components to compare the Shannon index measured at microsites, at different sites and for the whole sample. Applied to Whittaker’s diversity components, gamma diversity is partitioned into the sum of the average alpha diversity and the beta diversity. Lande (1996) extended the approach to species richness and to Simpson diversity and recommended it as a unifying framework with which to measure diversity at different levels of organization. In contrast to the multiplicative model, all diversity components are measured in the same way and expressed in the same units so that they can directly be compared.
In most of the above approaches, diversity is equated to species richness. In the present paper, we use species diversity as a broad term encompassing the two aspects of richness and evenness, while we refer to their combination as mixed diversity. In an empirical study on the diversity of invertebrates and flowering plants in a cultivated landscape, Duelli and Obrist (1998) found that for most taxonomic groups, the mixed diversity measures Shannon index and Simpson diversity were only weakly correlated with patch-specific species richness. An interesting question is therefore whether habitat variability and habitat heterogeneity affect different aspects of species diversity in a similar way.

In this paper, we quantify the effects of habitat variability and habitat heterogeneity based on the partitioning of landscape species diversity into additive components and link them to patch-specific diversity measurements. The approach is tested with data from a case study in central Switzerland. Amongst the questions we address are: (1) how is the partitioning of diversity within the landscape affected by the measure of diversity which is used?; (2) how does the partitioning differ according to the type of land-use?; and (3) how important are spatial effects such as the differentiation between edge and patch interior?

**Material and methods**

**Model approach**

The landscape model we apply consists of a mosaic of different habitat types. Each type can be fragmented into patches, which we suppose to be internally homogeneous. A habitat type corresponds to a type of land-use with a typical set of agricultural practices, and a patch to a management unit, e.g. a field. Linear structural elements are treated as patches with a specific width and a distinct border with each neighboring patch. This is the most parsimonious landscape model that accounts for habitat variability and habitat heterogeneity.

We define a new, consistent terminology of diversity components (figure 1). This is necessary because compared to Whittaker (1977), we introduced an intermediate level of habitat type between patch and landscape and we imply an additive linkage of diversity components. Whittaker (1977) equated MacArthur's (1965) within- and between-habitat diversity to alpha and beta diversity, though MacArthur (1965) had not suggested any function to link these components. MacArthur's (1965) concepts of within- and between-habitat diversity can be generalized to within-community and between-community diversity. As Begon et al. (1996) noted, a community can be defined at any...
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<th>Within-community diversity</th>
<th>Between-community diversity</th>
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<td>Landscape (land-use mosaic)</td>
<td><strong>Within-landscape diversity</strong> diversity of a land-use mosaic</td>
<td><strong>Between-type diversity</strong> variability between different types of land-use</td>
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<td>Habitat type (type of land-use)</td>
<td><strong>Within-type diversity</strong> diversity of a type of land-use</td>
<td><strong>Between-type diversity</strong> variability between patches of the same type of land-use</td>
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<td>Patch (management unit)</td>
<td><strong>Within-patch diversity</strong> diversity of a management unit</td>
<td><strong>Between-patch diversity</strong> variability between patches of the same type of land-use</td>
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<td>Sampling quadrat</td>
<td><strong>Within-quadrat diversity</strong> diversity of a sample quadrat</td>
<td><strong>Between-quadrat diversity</strong> variability between quadrats of the same management unit</td>
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Fig. 1. The proposed hierarchical model of species diversity, where the scale-specific components of within- and between-community diversity are linked additively to form the diversity at the next higher level. In italics the corresponding factors of the mosaic concept as defined by Duelli (1992).

size, scale or level within a hierarchy of habitats. Figure 1 shows the definitions of the scale-specific components of within- and between-community diversity for the levels sampling quadrat, patch, habitat type, and landscape.

As indicated in figure 1, habitat variability and habitat heterogeneity defined by Duelli (1992) lead to between-type diversity and between-patch diversity, and patch-specific diversity corresponds to within-patch diversity.

Within-quadrat diversity equals Whittaker’s (1977) point diversity, within-patch diversity corresponds directly to alpha diversity and within-landscape diversity to gamma diversity. In a broader sense, between-quadrat and between-patch diversity are comparable to Whittaker’s (1977) point diversity and beta diversity.

So far, our diversity model does not assume any specific diversity measure. If we accept richness and evenness as distinct aspects of species diversity, the question is no longer how to combine them into a single measure, but how to compare them. An ad-
Additive partitioning of a pure evenness measure has not been developed. Peet (1974) distinguished two groups of mixed diversity measures. Type I measures are most affected by rare species, while Type II measures are most sensitive to changes in the abundance of the dominant species. Magurran (1988) showed that various measures correlate significantly within these groups but not between the groups, and that Type I measures stress richness while Type II measures stress evenness. By comparing diversity patterns in a sequence from pure species richness over a Type I measure to a Type II measure, we will be moving along a gradient from richness towards evenness.

Study site

The study area at Hohenrain (Swiss plateau) is situated in a highly structured agricultural landscape with both arable and grassland farming. We classified the study area into 5 types of land-use. These included arable fields, meadows, verges, hedgerows and ditches, and roads (Fig. 2). We combined hedgerows and ditches to a single type, because they often occurred together within the same management unit. The agricultural landscape of the region contained two other frequent types of land-use, forests and farm yards, which were not represented in the study area.

Data collection

Within an area of 0.23 km², we recorded the presence of vascular plants for a stratified random sample of 1'280 quadrats of 1 m² size (Fig. 2). For this purpose, we mapped the management units from a rectified aerial photograph and classified them according to present (i.e., summer 1997) land-use. To check for spatial interactions, we subdivided the meadows and arable fields into a 3-m wide boundary strip (edge) and the rest of the field (core). Within every patch or subdivision, we sampled 20 quadrats of 1 m² randomly from a 1-m grid. We kept a minimum distance of 5 m between quadrats of the same patch in order to prevent spatial dependence. To achieve an even representation of ecotones, we subdivided patches with a width up to 10 m into 1-m wide strips and required an even distribution of the 20 quadrats over the strips. In summer 1997, we recorded the presence of vascular plant species for each quadrat between the last herbicide application and harvesting. For the grass verges, the main period of observation lay in June, for the arable fields in July, for the meadows in August, and for the hedgerows and the roads between mid-August and mid-September. Three ecotone patches shorter than 100 m were sampled with 10 quadrats only, and two patches were plowed before they could be sampled.
Fig. 2. The management units included in the sample and of the surrounding area near Hohenrain (Switzerland) are classified into 7 types of land-use, namely arable fields, meadows, verges, roads, hedgerows and ditches, farm yards (not sampled) and forests (not sampled). For one meadow, the subdivision into a 3-m wide edge and a core area is indicated together with the random sample of 20 quadrats within each stratum.
Data processing and statistics

We divided the total species diversity observed in the stratified sample of 1'280 quadrats according to the model in Figure 1. For each of the three diversity measures species number, Shannon index and Simpson diversity, we derived separate diversity components for the total area and for each type of land-use applying the formulae in Lande (1996).

The observed number of species \( S \) is a pure richness measure. Let \( W \) and \( B \) denote components of within- and between-community diversity. Within-quadrat species richness \( S_{Wq} \) is the number of species found in quadrat \( q \), and \( S_{Wp} \), \( S_{Wt} \) and \( S_{Wl} \) are the numbers of species found in the pooled quadrats of patch \( p \), type \( t \) and the total landscape \( l \) respectively. Let \( S_{Wq} \) denote the arithmetic mean of the number of species \( S_{Wq} \) of all quadrats \( q \), so that between-quadrat diversity \( S_{Bq} \) is derived as:

\[
S_{Bq} = S_{WP} - S_{Wq}
\]  

Similarly, between-patch species richness \( S_{Bp} \) is the difference between \( S_{WP} \) and \( S_{Wp} \), and between-type species richness \( S_{Bt} \) is the difference between \( S_{Wt} \) and \( S_{WP} \).

Shannon index \( H \) and Simpson diversity \( D \) are both functions of the proportional abundance \( \pi_i \) of species \( i \). We derived the proportional abundances \( \pi_{ip} \) of species \( i \) in patch \( p \) by dividing the number \( f_{ip} \) of quadrats in \( p \) that contained \( i \) by their sum \( f_p \):

\[
\pi_{ip} = \frac{f_{ip}}{f_p}
\]

We calculated the pooled proportional abundance \( \pi_t \) of \( i \) in type \( t \) and \( \pi_l \) in landscape \( l \) as the weighted sums of the \( \pi_{ip} \)'s (cf. formulae 3a and 3b). On type level, we defined the weight of patch \( p \) in type \( t \) as the area \( a_{pt} \) of \( p \) in \( t \) divided by the total area \( a_t \) of all patches in \( t \). For the total area, the weight of patch \( p \) in landscape \( l \) equaled the area \( a_{pl} \) of \( p \) in \( l \) divided by the total area \( a_l \) of \( l \):

\[
\pi_{it} = \sum_{p} \frac{a_{pt}}{a_t} * \pi_{ip} 
\]

\[
\pi_{il} = \sum_{p} \frac{a_{pl}}{a_l} * \pi_{ip} 
\]
The Shannon index $H$ is a Type I measure of mixed diversity:

$$H = -\sum_i \pi_i \ln \pi_i$$

(4)

The Type II measure Simpson diversity $D$ is a function of the dominance $\lambda$. Two different functions are used in the literature. The reciprocal form ($D = 1/\lambda$) cannot be divided into additive components (Lande 1996). Therefore we applied the form that is also known as the Gini Index:

$$D = 1 - \lambda = 1 - \sum_i \pi_i^2$$

(5)

Let within-patch Shannon index $H_{Wp}$ be the Shannon index calculated from the $\pi_p$'s, $H_{Wt}$ and $H_{Wl}$ the Shannon index based on the pooled proportional abundance $\pi_y$ and $\pi_q$. $H_{Wt}$ is the weighted mean of the $H_{Wp}$ of all patches $p$ (with weights proportional to area), so that between-patch Shannon index $H_{Bp}$ is derived as:

$$H_{Bp} = H_{Wt} - H_{Wp}$$

(6)

Similarly, between-type Shannon index $H_{Bt}$ is the difference between $H_{Wt}$ and $H_{Wl}$. The components of Simpson diversity $D$ were derived in the same way as for $H$, applying formula (5) instead of (4).

Results

Figure 3 shows the additive components of the observed plant species diversity for species number $S$, Shannon index $H$ and Simpson diversity $D$. For species number $S$, the total of 179 species that were observed ($S_{tot}$) can be divided into a mean within-type richness $S_{Wt}$ of 80 and the between-type richness $S_{Bt}$ of 99 species. $S_{Wt}$ consists again of a mean within-quadrat richness $S_{Wq}$ of 29 and the between-patch richness $S_{Bp}$ of 51 species. $S_{Wq}$ consists of a mean within-quadrat richness $S_{Wq}$ of 9 and the between-quadrat richness $S_{Bq}$ of 20 species.

Fig. 3. Each bar shows the species number $S$ (top), Shannon index $H$ (middle) or Simpson diversity $D$ (bottom) for a particular type of land-use and for the study area as a whole, partitioned into the mean $S$, $H$ or $D$ per quadrat, the mean $S$, $H$ or $D$ per patch, for every type of land-use the total $S$, $H$ or $D$ observed in the type, and for the whole study area the mean $S$, $H$ or $D$ per type and the total $S$, $H$ or $D$ observed in the entire sample.
For the Type I measure Shannon index $H$, the within-landscape $H_{Wl}$ of 3.5 is composed of the between-type $H_{TB}$ of 0.4 and a mean within-type component $H_{WT}$ of 3.1. The latter again is the sum of a mean within-patch $H_{WP}$ of 2.5 and the between-patch $H_{BP}$ of 0.6. For the Type II measure Simpson diversity $D$, the within-landscape $D_{Wl}$ of 0.96 is composed of the between-type $D_{TB}$ of 0.02 and a mean within-type $D_{WT}$ of 0.94. The latter is the sum of a mean within-patch $D_{WP}$ of 0.89 and the between-patch $D_{BP}$ of 0.5.

The percentages of the total landscape diversity attributed to patch-specific diversity, habitat heterogeneity and habitat variability are therefore 12 : 27 : 61 for $S$, 71 : 18 : 11 for $H$ and 93 : 5 : 2 for $D$. For $D$, and to a lesser degree for $H$, the components become smaller with higher scale levels. The opposite is the case for $S$, where diversity components increase with higher scale levels. This reversed diversity pattern for $S$ as compared to the mixed diversity measures occurs within all types.

The proportions of diversity components vary between the different types of land-use. For example, while the verges have a much higher within-quadrat $S_{WQ}$ than the hedges, their between-quadrat $S_{DQ}$ is considerably lower. The core areas of arable fields and meadows give another example of how the comparison of different types depends on the scale level. The meadows show higher within-patch $H_{WP}$ and $D_{WP}$, but considerably lower between-patch $H_{BP}$ and $D_{BP}$ than the arable fields. Thus, while the average meadow appears to be more diverse than the average arable field, this relation is reversed at the type level. Also for species richness, the meadows have a higher within-quadrat $S_{WQ}$ but smaller between-quadrat $S_{DQ}$ and between-patch $S_{BP}$ than the arable fields, which results in a lower within-type $S_{WT}$.

There is a marked difference in diversity between the edge and the core area both of meadows and arable fields. This difference is rather large compared to the overall difference between meadows and arable fields. The edges are generally more diverse, with higher within-quadrat, within-patch and within-type components for all three diversity measures. But they have a smaller between-patch $H_{BP}$ and $D_{BP}$ than the core areas, which means that the edges are more similar to each other. As to the number of interior species, only 12 species were restricted to the 460 quadrats from the core area of meadows and arable fields.
Discussion

We propose a model that provides a quantitative description of the diversity within and between landscape elements at various scales. The model makes no assumption about the processes that determine these patterns, but provides a useful basis for investigating and understanding them. The contributions of habitat variability, habitat heterogeneity and patch-specific diversity to landscape diversity are quantified and can directly be compared, since all components are measured in the same units.

The question arises why Allan’s (1975) additive model of diversity has been generally neglected and Whittaker’s (1977) multiplicative model has been largely reduced to the individual diversity components over the last twenty years. Whittaker’s (1977) model implies that alpha-type and beta-type diversity cannot be expressed in the same units and are therefore not comparable. While alpha, beta and gamma diversity are often quantified individually, their multiplicative linkage is generally not interpreted as a mathematical operation but as a sign of their independence. As Gaston (1996) noted, the distinctions between genetic, species and ecosystem diversity are becoming increasingly conventional. Although genes correlate with species and species with ecosystems, they are often treated as discrete ecological scales in the sense of hierarchy theory (Allen and Starr 1982; O’Neill et al. 1986). This theory predicts that for a hierarchically structured landscape, patterns are unrelated between domains of scales as they are caused by processes isolated at discrete scales (O’Neill et al. 1991).

Our model implies that what we measure as within-community diversity at a higher scale level is the combined effect of heterogeneity at various lower levels. The case study suggests that these are not equally important for all types of habitat. For a given measure of diversity, the type-specific sizes of the diversity components were not proportional, but varied considerably. The question which habitat type is the most diverse will depend on the level of comparison. While one might identify an appropriate scale for studying a specific phenomenon in a specific habitat, we recommend using several scale levels simultaneously for comparing different habitats.

The case study indicates that the way in which the total diversity is divided strongly depends on the chosen diversity aspect. Landscape composition apparently is a key factor for explaining landscape species richness, but has little effect on evenness. Both measures of mixed diversity were little affected by habitat variability and habitat heterogeneity, with the exception of arable fields. The dominance of the crop species caused low within-patch diversity, whereas crop variability induced a large between-patch diversity component. This effect might even be stronger if the abundance is measured in terms of biomass or cover. As expected, the Type II measure of mixed diversity, Simpson diversity, was more affected by a change of the dominant species than the Type I measure Shannon index.
Before we can test the effect of landscape structure on landscape species richness, several problems must be solved: (1) the incorporation of neighborhood effects; (2) the unbiased estimation of species richness components; and (3) the quantification of the contribution of a landscape element to landscape species richness.

The proposed model links species diversity to landscape composition, but does not account for the spatial arrangement of landscape elements. A marked difference in diversity patterns was observed between the edge and the core area for arable fields and meadows, with the edge being generally more diverse than the core. This effect can probably best be explained in the context of spatial vicinism. That is, the diversity within a patch depends not only on the conditions within the patch, but a neighboring patch can provide a source of rhizomes and diaspores over a short distance (Zonneveld 1995). In order to account for such effects, a modified landscape model is needed which contains information on the spatial arrangement of landscape elements, and the diversity model should be extended to include neighborhood effects.

If we want to proceed from a surrogate approach, i.e., an intuitive estimate based on theories, models or concepts, to a truly correlative approach, i.e., a statistically testable estimate (Duelli 1997) of the species diversity of a landscape, we need unbiased estimates of the true size of diversity components. In the case study, which served for explorative purposes only, we approximated the true species diversity by the observed diversity of the sample. For a given diversity measure, we assumed that comparability was granted by the sampling design. Of the three measures, species number is the most sensitive to sample size, followed by Shannon index (Magurran 1988). Simpson diversity is not only the most robust of the three, but also the only one for which an unbiased estimator exists (Lande 1996). Colwell and Coddington (1994) reviewed extrapolation methods for the species richness of a simple random sample. The approaches should be extended to stratified samples and should not rely on unrealistic assumptions about the spatial distribution and abundance of species. Once the methodological problems are solved, we can estimate landscape species richness from a standardized sample representing the pattern of land-use, which can be derived from remote sensing.

So far, we have not discriminated between species. The model facilitates the comparison of diversity components between habitat types and scale levels, but it does not tell us which landscape elements contribute most to landscape species diversity. Species richness components are inflated by generalist species that occur in most of the habitat types, whereas specialist species that are restricted to a single type receive little weight. Appropriate weighting to adjust for specificity could help us proceed from mere counting to assessing conservation value and deriving strategies for biodiversity management.
Acknowledgments

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Literature


Spatial heterogeneity and abundance distribution affect non-parametric estimators of species richness

Helene H. Wagner and Otto Wildi. Submitted to Ecology.

Abstract – Species richness is an important and intuitive aspect of biodiversity, but it is difficult to determine for a larger area. Several non-parametric estimators have been developed for estimating population size from trapping data. These methods are also used for estimating plant species richness from a spatial sample. While the label non-parametric may suggest that a method makes little or no assumptions, these estimators are known to rely on a homogeneous community with a certain type of abundance distribution.

We investigated by simulation how the four non-parametric richness estimators $Jack_1$, $Jack_2$, $Chao_2$ and $ICE$ are affected by variations in the abundance distribution and by different types of spatial heterogeneity. Our approach differs in two ways from other simulation studies: (1) we fitted different models of species abundance (geometric series, lognormal and broken-stick models) to the same real data that describe the occurrence of vascular plants in four different habitat types of an agricultural landscape in central Switzerland, and (2) we explicitly modeled, independently for every simulated species, the effects of spatial autocorrelation, of an environmental gradient and of a boundary zone between neighboring patches (edge effect).

An ANOVA of relative bias showed that for reasonably complete samples, $Jack_1$ and $Jack_2$ were positively biased and $ICE$ was negatively biased. The estimators differed markedly in their variance, leading to a trade-off between bias and variance. All estimators failed for communities simulated under the geometric model and were considerably affected by a simulated edge effect, whereas spatial autocorrelation, an environmental gradient, and differences between community types had little effect on estimator performance.

The non-parametric estimators of species richness assume that the quadrats represent a random sample from a discrete, spatially homogeneous community that occupies a discrete area. Spatial structures and species abundance distribution influence estimator performance via sample representativeness, which may be increased by adapting the sampling design. We recommend using the first order jackknife $Jack_1$ or the incidence-based coverage estimator $ICE$ for samples that contain at least 80% of the species.
Introduction

Before we can evaluate the success of biological conservation, restoration, or reserve design, we must find rigorous yet feasible ways to monitor biodiversity (Palmer 1995). Species richness is a central aspect of biodiversity, and unlike other aspects, it has the advantage that its meaning is generally understood and there is no need to derive complex indices to express it. However, species richness is not as readily measurable as it seems, and estimators for the absolute species richness of a larger area remain poorly explored (Gaston 1996). Because plants are sessile and comparably easy to identify, plant species richness is often used as a relatively cheap and robust indicator for the species richness of a reserve, habitat or region. Although flowering plants do contribute less to overall species richness than invertebrates, they are a good correlate for overall species richness in cultivated areas (Duelli and Obrist 1998). Because reasonably complete species lists can only be obtained for areas up to the size of some hectares, we have to rely on estimates for determining the species richness of larger areas (Palmer 1995). A further practical difficulty is that estimation methods that require the counting of discrete individuals are not appropriate for plants because of clonal reproduction (Palmer 1990). A common procedure is to record presence of each species in randomly located quadrats, i.e., in spatial units of a specific size and shape.

Several methods have been proposed for estimating species richness based on quadrats (for a review, see Bunge and Fitzpatrick 1993; Colwell and Coddington 1994; Palmer 1995). The numerous techniques fall into four categories: (1) number of observed species; (2) extrapolation of species-area curves, (3) integration of the log-normal distribution; and (4) non-parametric estimators (Palmer 1995). Empirical comparisons of their performance, either by simulation (Heltshel and Forrester 1983; Chao and Lee 1992; Baltanás 1992; Mingoti and Meeden 1992; C. Frampton unpublished manuscript; and Chazdon et al. 1998) or by application to real data sets (Palmer 1990, 1991; Colwell and Coddington 1994; and Chazdon et al. 1998) suggest that in general the non-parametric methods perform better than the other methods.

Assumptions of non-parametric estimators

Quadrat-based non-parametric methods were originally proposed for estimating the size of a closed population of small mammals captured and recaptured in a trap on consecutive days (Burnham and Overton 1978; Chao 1987). By replacing individuals by species, time by space, and the probability of being trapped by the probability of being observed in a quadrat, we can apply the same model to the situation where we want to estimate the total number of plant species from a sample of quadrats of a constant size (Burnham and Overton 1979). However, there are two potential problems in this appli-
cation of the method. The first is that capture-recapture models assume that individual capture probabilities in a population are either all equal, or follow an arbitrary probability distribution. At the community level, species abundances are known to strongly differ (Burnham and Overton 1979), and are often thought to follow a specific distribution that reflects community structure (Whittaker 1970; Magurran 1988). The second problem is that capture-recapture models assume a closed population, where no gains or losses due to birth, death or migration occur during trapping (Burnham and Overton 1979). This assumption corresponds to the assumption of spatial homogeneity in a plant community, where the probability that a species is observed in a quadrat does not depend on the location of the quadrat.

**Abundance distribution**

The four non-parametric estimators compared in this paper (see table 1) were all designed to deal with unequal capture probabilities. As Otis et al. (1978) noted, this does not mean that they are good estimators regardless of the distribution in the population under study. Several simulation studies (Burnham and Overton 1979; Lee and Chao 1994; C. Frampton unpublished manuscript) suggest a general pattern, where a more uneven abundance distribution will result in a lower estimate and thus in a larger negative bias of an estimator.

Abundance distributions in biotic communities commonly differ strongly and systematically from the situation where all species are equally abundant. According to Sugihara (1980), a majority of communities studied by ecologists display a lognormal distribution of abundances. All distributions are expected to fall into the range between a geometric series, where a few species are dominant with the remainder fairly uncommon, and a broken stick model, where the abundances are more evenly distributed than in most observed communities (Magurran 1988). However, as Wilson et al. (1998) demonstrated by simulation, it is often impossible to identify the true species abundance model from a sample for reasons of the practical limitations of sample size. Before we can choose an appropriate estimator for a specific community, we must know how the different estimators behave within the expected range of abundance distributions.

**Spatial heterogeneity**

Because biotic communities are rarely spatially homogeneous, some authors added to their simulations a patchiness or aggregation factor intended to mimic the clumping of individuals of the same species within spatial units or groups of neighboring units (Baltanás 1992; Chazdon et al. 1998; C. Frampton unpublished manuscript). Chazdon et
Table 1. The compared estimators of species richness. The notation is adopted from Colwell (1997).

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Mathematical definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S_{obs}$</td>
<td>The number of species observed in the total sample</td>
<td>$S_{jack1} = S_{obs} + Q_1 \left( \frac{m - 1}{m} \right)$</td>
</tr>
<tr>
<td>$J_1$</td>
<td>The first order jackknife estimator (Burnham and Overton 1978, 1979; Helshe and Forrester 1983)</td>
<td>$S_{jack2} = S_{obs} + \frac{Q_1(2m - 3)}{m} - \frac{Q_2(m - 2)^2}{m(m - 1)}$</td>
</tr>
<tr>
<td>$J_2$</td>
<td>The second order jackknife (Burnham and Overton 1978, 1979; Smith and van Belle 1984)</td>
<td>$S_{Chao2} = S_{obs} + \frac{Q_1^2}{2Q_2}$</td>
</tr>
<tr>
<td>$ICE$</td>
<td>The incidence-based estimator proposed by (Chao 1987)</td>
<td>$S_{ICE} = S_{freq} + \frac{S_{infr}}{C_{ice}} + \frac{Q_1}{C_{ice}^2}$</td>
</tr>
<tr>
<td>$ICE$</td>
<td>The incidence-based coverage estimator by Lee and Chao (1994)</td>
<td>$S_{ICE} = S_{freq} + \frac{S_{infr}}{C_{ice}} + \frac{Q_1}{C_{ice}^2}$</td>
</tr>
</tbody>
</table>

where:

- $Q_j$ Number of species that occur in exactly $j$ quadrats
- $m$ Total number of quadrats
- $S_{freq}$ Number of frequent species (found in more than 10 quadrats)
- $S_{infr}$ Number of infrequent species (found in 10 or fewer quadrats)
- $C_{ice}$ Sample incidence coverage estimator $C_{ice} = 1 - Q_1 / N_{infr}$
- $N_{infr}$ Total number of occurrences of infrequent species $N_{infr} = \sum_{j=1}^{10} jQ_j$
- $\gamma_{ice}^2$ Estimated coefficient of variation of the $Q_j$'s for infrequent species $\gamma_{ice}^2 = \max \left\{ \frac{S_{infr}}{C_{ice} (m_{infr} - 1)} \left( \frac{\sum_{j=1}^{10} j(j - 1)Q_j}{N_{infr}^2} \right) - 1, 0 \right\}$

al. (1998) reported that the effect of aggregation on the estimate depends strongly on the estimator. Baltanás (1992) suggested that the effect may be non-linear so that a small amount of aggregation may even improve the estimate, whereas higher levels of aggregation affect it negatively.
Legendre (1993) outlined a general approach to spatial heterogeneity based on hierarchy theory (Allen and Starr 1982). The environment is regarded as structured primarily by large-scale physical processes that, through energy inputs, cause the appearance of gradients on the one hand, and of patchy structures separated by discontinuities (as in a mosaic) on the other (Legendre 1993). Within these relatively homogeneous zones, smaller scale contagious biotic processes take place such as growth, reproduction, mortality, and migration (Legendre 1993). Due to such contagious processes, nearby samples tend to be more similar than distant ones. This phenomenon has been referred to as spatial autocorrelation, spatial dependence or distance decay.

In most empirical studies we will encounter a combination of different types of heterogeneity with varying predominance. A systematic approach to spatial patterns of species occurrence and to their effect on the performance of species richness estimators may enable us to choose the most robust estimator for a specific situation and to improve the estimate by adjusting the sampling design.

Simulation of estimator performance

The evaluation of species richness estimators is inherently problematic, whether it is based on real data or on simulations (Palmer 1995). The true number of species is generally unknown for real-world data, and even reasonably complete data sets are limited to small areas. Furthermore, if we wanted to identify by observation the relevant factors that govern estimator performance, we would need many extensive data sets from different areas that represent a broad range of conditions. The problem with simulations, on the other hand, is that a large number of parameters have to be chosen more or less arbitrarily, so that the simulated patterns may not mimic the real world (Palmer 1995).

In this paper we use simulations to investigate the effect of different types of spatial patterns and of different abundance distributions on the performance of several non-parametric estimators of species richness. To make the simulations as realistic as possible, we derive the necessary parameters from real data sampled within different habitat types. Amongst the questions we address are: (1) how susceptible are the non-parametric estimation methods to spatial heterogeneity and to differences in the abundance distribution; (2) how does spatial heterogeneity affect the performance of non-parametric estimators; and (3) are some estimators better suited to deal with specific spatial patterns or types of abundance distribution?
Real data
presence of vascular plants in
\(n = 1160\) quadrats of 1 m\(^2\)

Fitted species
abundance models
3 model families

Median rank-abundance distributions
4 community types

Averaged spatial
distributions
parameters
6 spatial patterns

Randomised
spatial parameters

Local probability
of occurrence
\(p_i(x,y)\)

\(3 \times 4 \times 6\) simulated data sets
occurrence of \(S_{true}\) species
in a grid of 100 x 50 cells

20 samples of size
\(n = 500\) cells

4 sub-samples
of 20, 50, 100 and 500

5 estimators
of species richness

Performance:
• relative bias
• relative variance

Fig. 1. Summary of the simulation procedure.
Methods

In this section, we emphasize the modeling of spatial patterns of species occurrence. We hope that the systematic approach to spatial heterogeneity and some new methods described here will be useful for studying spatial phenomena in other contexts. We provide a brief summary of the simulation procedure below. All simulations and analyses were done in S-Plus (Becker et al. 1988).

Overview

Fig. 1 summarizes how we simulated estimator performance. From real data, we derived the median rank-abundance distributions of four different types of communities. (Fig. 2). For every reference community, we fitted three species abundance models that have a theoretical background in community ecology (Fig. 3). The resulting distributions describe for every species in the model the probability that it occurs in a quadrat of 1 m². Next, we modified this probability of occurrence independently for every species according to various spatial patterns (Fig. 4). Based on these local probabilities, we simulated the occurrence of each species in every single m² of a hypothetical field of 100 x 50 m². This resulted in 72 simulated data sets, one for each combination of four community types, three model families and six spatial patterns. From every simulated field, we took a random sample of 500 quadrats and estimated species richness based on the first 20, 50, 100 and 500 quadrats sampled. This sampling process was repeated 20 times. Finally, we compared the estimates obtained with different estimators to the true number of species in the simulated data sets. We evaluated estimator accuracy, measured as relative bias, and estimator precision, measured as relative variance.
Reference communities

Wherever feasible, we derived parameters from real data that represent different habitat types of an agricultural landscape. The main data set consists of a spatial random sample of 20 quadrats of 1 m² from each out of 12 arable fields, 11 meadows, seven grass verges, and five hedgerows, in a study site of 0.23 km² near the village Hohenrain, Canton of Lucerne, Switzerland (for further details see Wagner et al., in press). 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 fields 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, and a set of 3 x 3 adjacent quadrats from the center of selected patches. For each quadrat we recorded the species of vascular plants present shortly before the harvest in summer 1997.
For every community type, we derived a median rank-abundance distribution by first ranking the species per patch by their frequency, i.e., the number of quadrats they occupied, and then taking the median frequency for each rank (Fig. 2). Fig. 2 suggests that the reference communities reflect the four possible combinations of higher and lower species richness, with the hedgerows and verges being far more rich in species than the arable fields or meadows, and of higher and lower dominance, with a larger number of abundant species in meadows and verges than in arable fields or hedges.

**Fitted species abundance models**

For every reference community, we fitted three species abundance models (Fig. 3): (1) a broken-stick model, with one optimized parameter; (2) a general lognormal model, with one fixed and two optimized parameters; and (3) a geometric series, with two optimized parameters. We optimized the parameters by minimizing the squared deviation from the observed median distribution (for details of the procedure see Wilson, 1991). We constrained the predicted abundance values to a maximum of 20.

A Pearson correlation of the reference community and the fitted models showed a relatively good fit for all 12 combinations, with values of $R^2$ between 0.89 and 0.97. For arable fields, meadows and grass verges, the geometric series fitted best, whereas for the hedgerows, both the broken-stick and the lognormal models provided a better fit than the geometric series.

**Spatial patterns**

We developed an independent model for each type of spatial structure, i.e., spatial autocorrelation, a continuous environmental gradient, and an edge effect as it may occur in a patchy environment. The three structures were then combined to form six different spatial patterns.

*The binomial model of species occurrence (Fig. 4 A)*

We modeled the occurrence of a species in a sample of $n$ quadrats as an independent binomial variable $x$, that takes the value 1 if species $i$ is present in a quadrat and zero if it is absent.

$$x_i \sim bin(n, p_i) \ (i = 1, ..., s)$$

The fitted species abundance models predict for a set of species the frequency of occurrence in a sample of 20 quadrats. Hence we obtained the parameter $p$, by dividing the predicted frequency by 20.
Spatial autocorrelation (Fig. 4 B)

As Nekola (in press) showed, species with different growth forms or dispersal types differ considerably in their spatial autocorrelation patterns. We modelled the spatial autocorrelation for every simulated species by an individual variogram function. An empirical variogram is a plot of the semi-variance, i.e., half the squared difference, of two observations against their distance in space. The usual procedure is to plot the mean semi-variance for a range of distance classes against distance and then iteratively fit a variogram function (Isaaks and Srivastava 1989, Cressie 1991, Haining 1997). The four parameters needed for the fitting of a simple variogram function are (see also Fig. 5): (1) the model family (commonly a spherical, an exponential or a Gaussian model is assumed); (2) the sill, i.e., the average semi-variance of independent observations; (3) the range, i.e., the maximum distance at which pairs of observations will influence each other; and (4) the nugget effect, i.e., the offset at a distance very close to zero.

In case of a binary variable \( x \sim \text{bin}(n, p) \), the sill is equal to the variance, that is \( p_i(1-p_i) \). Fitting the other parameters to a binary variable requires a large number of observations. A variogram for the entire community may reveal an average spatial autocorrelation pattern in a community. To avoid multivariability in the computation of a variogram of species composition, Palmer (1988) suggested fitting a variogram for the coordinates of every quadrat on the first axis of detrended correspondence analysis (DCA; Hill and Gauch 1980). We propose a more explicit approach, based on species composition as the sum of independent binomial variables of species occurrence. The details are given in the appendix.

The variogram of species composition (community variogram, see appendix) has an expected sill at

\[
\sum_i p_i (1 - p_i) = \sum_i p_i - \sum_i p_i^2
\]
The left-hand term is the expected number of species found only in the first of a pair of independent quadrats. On the right side of the equation, we find the expected mean number of species per quadrat minus the expected number of species shared by two independent quadrats. We could use either side to construct an empirical variogram. However, we achieved the best results when plotting for each distance class $h$ the difference between the overall mean number of species per quadrat and the average number of species shared by two quadrats.

Fig. 5 shows the empirical community variogram and the fitted spherical model for a sugar beet field at Hohenrain. We fitted similar models to three other communities, a barley field at Hohenrain and a grass verge and a hedgerow near Ruswil, Canton of Lucerne, Switzerland. The distinct sills and the approximately linear behavior of the means near zero distance suggested a spherical model. The fitted models all had a range of approximately 7 m, while the nugget effect varied between 0.15 and 0.55 of the respective sill.

Based on these results, we assumed an average range of $a = 7$ m for our simulated communities. For every species, we obtained a randomized individual range parameter $a_i$ from a lognormal distribution with parameters $lnorm(7, 0.5^2)$. We assumed a spherical model with a sill of $p_i(1-p_i)$ and a nugget effect of one third of the sill:

$$\gamma_i(h) = \begin{cases} 0 & h = 0 \\ p_i(1-p_i) + \frac{2p_i(1-p_i)}{3} \left( \frac{3h}{2a_i} - \frac{1}{2} \left( \frac{h}{a_i} \right)^2 \right) & 0 < h \leq a_i \\ p_i(1-p_i) & h > a_i \end{cases}$$
For every simulated species \( i \), we generated a spatially explicit model of spatial autocorrelation within a 100 x 50 m grid by randomly selecting points from within the grid boundary, keeping a minimum distance of \( a_i \) between points. At these points, we simulated the presence or absence of \( i \) as the outcome of a binomial process with parameters \( bin(1, p_i) \). By kriging with the variogram function \( \gamma(h) \), we interpolated the probability of occurrence \( p_{i_{\text{inh}}}(x, y) \) of \( i \).

**Gradient (Fig. 4 C)**

We generated two different situations mimicking a strong and a weak environmental gradient. The rate of species turnover along a gradient can be expressed as a turnover distance \( d_t \), that is the distance at which on average all species of a community have been exchanged once. For a weak gradient, we assumed a turnover distance \( d_t \) of five times the extent, while for a strong gradient, we set \( d_t \) equal to the extent.

As with spatial autocorrelation, we modeled the response to an artificial gradient for every species independently. Organisms typically respond to a linear gradient in environmental conditions in a non-linear way (Gauch 1982; Kolasa and Rollo 1991). The distribution of individuals along an environmental gradient is often assumed to follow a normal distribution (Gauch 1982). The Gaussian logit curve has a similar shape, but is better suited for modeling probabilities as it can not take values larger than one (Jongman et al. 1995). We generated a Gaussian logit curve for every species \( i \):

\[
p_{i_{\text{grad}}}(x) = \frac{p_i e^{-0.5(x-u_i)^2/t_i^2}}{1 + p_i e^{-0.5(x-u_i)^2/t_i^2}}
\]

For every simulated species, we randomized the two parameters tolerance \( t_i \), i.e., the ecological amplitude, and mean \( u_i \), i.e., the optimum. The tolerance \( t_i \) was sampled from a lognormal distribution with parameters \( \text{lnorm}(d_t / 3, 0.5^2) \), the mean \( u_i \) from a uniform distribution with parameters \( U(-1.5 t_i, 1.5 t_i) \).

**Edge effect (Fig. 4 D)**

In a mosaic-like structure, relatively homogeneous zones (patches) are separated by discontinuities (boundary zones). Edge refers to the part of a patch that belongs to the boundary zone and is influenced by the neighboring patch. Often the edge has a high population density and diversity of species, a phenomenon that is referred to as edge effect in the landscape ecological literature (Forman 1995). The simplest form of a boundary zone is that of an ecotone, where species abundance changes from one side to the other analogous to a compressed gradient (Forman 1995). As with any environmental gradient, different species will respond to it in different ways.
We individually modeled the behavior of every species in the boundary zone of two simulated patches. We determined an average edge width \( w \) by analysis of the real data. For the pooled samples from 12 arable fields, the mean number of species per quadrat increased towards patch border over a distance of 5 m. The pooled samples from the 11 meadows showed no edge effect in quadrat species richness.

To every species with probability \( p_j \) in the simulated patch \( j \), we assigned a corresponding probability \( p_k \) for the adjacent patch \( k \). To simulate realistically the degree of rank consistency, we ordered all species in the original data set by their overall frequency and sampled for every rank \( i \) a probability of occurrence \( p_i \) from the vector of observed probabilities of the \( i \)th species within the individual patches, selecting patches with probability proportional to size.

We generated a logit curve that describes the behavior in the boundary zone as a function of the distance \( d_b \) to the border.

\[
p_i^\text{edge}(d_b) = \frac{e^{rd_b}}{1 + e^{rd_b}} \text{abs}(p_{ij} - p_{ik}) + \min(p_{ij}, p_{ik})
\]

Assuming a median edge width of \( w = 5 \) m, we randomized the individual edge width \( w_i \) of species \( i \) by sampling it from a lognormal distribution with parameters \( \text{lnorm} (\log(5/3), 0.5^2) \).

**Simulations**

For every combination of community type and species abundance model, we modeled six different spatial patterns: (1) a homogeneous model \( H \); (2) a spatial autocorrelation model \( A \); (3) a weak gradient model \( Gw \); (4) a strong gradient model \( Gs \); (5) an edge effect model \( E \); and (6) a combined model \( C \) with spatial autocorrelation, a strong gradient and an edge effect. Apart from the homogeneous model \( H \), all models contain spatial dependence. The parameter combinations are listed in table 2.

To obtain additive effects for the three spatial structures, we re-scaled the local probabilities \( p_i^{\text{auto}}(x, y) \), \( p_i^{\text{grad}}(x) \) and \( p_i^{\text{edge}}(d_b) \) so that each of them summed to zero for the total of 100 x 50 grid cells. The effects were added up by species and grid cell (Fig. 4 E):

\[
p_i(x, y) = p_i + p_i^{\text{auto}}(x, y) + p_i^{\text{grad}}(x) + p_i^{\text{edge}}(d_b)
\]

with the restriction that

\[
0 \leq p_i(x, y) \leq 1
\]
Table 2: Parameter combinations of the simulated spatial patterns.

<table>
<thead>
<tr>
<th>Type of heterogeneity</th>
<th>Parameter</th>
<th>H</th>
<th>A</th>
<th>Gw</th>
<th>Gs</th>
<th>E</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autocorrelation</td>
<td>median range</td>
<td>-</td>
<td>7 m</td>
<td>7 m</td>
<td>7 m</td>
<td>7 m</td>
<td>7 m</td>
</tr>
<tr>
<td>Gradient</td>
<td>median turnover distance</td>
<td>-</td>
<td>500 m</td>
<td>100 m</td>
<td>-</td>
<td>100 m</td>
<td></td>
</tr>
<tr>
<td>Edge effect</td>
<td>median edge width</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5 m</td>
<td>5 m</td>
</tr>
</tbody>
</table>

For every species with \( p_i \geq 0.0002 \), we simulated the occurrence in each cell \((x,y)\) of a 100 \( \times \) 50 m grid as the outcome of a binomial process with parameters \( bin(1,p_i(x,y)) \). This was repeated for every combination of four community types, three species abundance models and six spatial patterns. The resulting 72 simulated data sets contained between 19 and 148 species \( (S_{true}) \).

From every simulated data set, we sequentially sampled 500 cells at random and estimated patch species richness based on the first 20, 50, 100 and 500 cells. The process of sampling and estimating was repeated 20 times per data set.

**Estimator performance**

We compared the performance of the first- and second-order jackknife estimators \( \text{jack1} \) and \( \text{jack2} \), an incidence-based estimator commonly referred to as \( \text{Chao2} \), and the incidence-based coverage estimator known as \( \text{ICE} \) (table 1). As these are empirical corrections of the observed number of species \( S_{obs} \), we used \( S_{true} \) as a reference in the analysis of estimator performance.

An estimator should be *accurate*, i.e., unbiased, and *precise*, i.e., have a small variance (Palmer 1991). Because the simulated communities varied considerably in their species richness, we scaled bias and variance in terms of the true number of species \( S_{true} \). We measured accuracy by relative bias, i.e., the proportional deviation, \( PD \), of the estimate \( S_{est} \) from the true number of species \( S_{true} \):

\[
\text{Relative bias } PD = \frac{S_{est} - S_{true}}{S_{true}}
\]

The mean \( PD \) will be positive if the estimator overestimates and negative if the estimator underestimates \( S_{true} \).
Table 3: The true number of species $S_{true}$ in the simulated data sets. For every combination of community type and species abundance model, the true number of species is averaged separately for spatial patterns with and without edge effect. The spatial patterns are defined in table 2.

<table>
<thead>
<tr>
<th>Spatial pattern</th>
<th>Model</th>
<th>Meadow</th>
<th>Arable</th>
<th>Verge</th>
<th>Hedge</th>
</tr>
</thead>
<tbody>
<tr>
<td>Without edge effect</td>
<td>Broken-stick</td>
<td>19</td>
<td>21</td>
<td>42</td>
<td>52</td>
</tr>
<tr>
<td>(H, A, Gw, Gs)</td>
<td>Lognormal</td>
<td>19</td>
<td>21</td>
<td>42</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td>Geometric</td>
<td>47</td>
<td>50</td>
<td>112</td>
<td>143</td>
</tr>
<tr>
<td>With edge effect</td>
<td>Broken-stick</td>
<td>27</td>
<td>29</td>
<td>47</td>
<td>54</td>
</tr>
<tr>
<td>(E, C)</td>
<td>Lognormal</td>
<td>27</td>
<td>29</td>
<td>47</td>
<td>54</td>
</tr>
<tr>
<td></td>
<td>Geometric</td>
<td>52</td>
<td>55</td>
<td>113</td>
<td>140</td>
</tr>
</tbody>
</table>

We measured precision by the relative variance, i.e., the square proportional deviation, $SPD$, of the estimate $S_{est}$ from the true value $S_{true}$ as proposed by Palmer (1991).

$$Relative\ variance\ SPD = \left( \frac{S_{est} - S_{true}}{S_{true}} \right)^2 = PD^2$$

The mean $SPD$ measures the proportional closeness of $S_{est}$ and $S_{true}$. Estimators with a small mean $SPD$ are more precise than those with large mean $SPD$.

In a multi-factorial ANOVA of relative bias $PD$, we compared the effects and interactions of estimation method, sample size, spatial pattern, species abundance model and community type. In the interpretation, we focused on the magnitude of differences in group means. Statistical significance and sum of squares statistics are less important, as the first can easily be manipulated by the number of replicates in the simulation and the second by the arbitrary choice of factor levels.

**Results**

The complete ANOVA model with all possible main effects and interactions of the five factors estimator, sample size, spatial pattern, species abundance model, and community type, explained 82% of the variance of relative bias $PD$. The species abundance model had the largest effect on relative bias $PD$ (52 % SS), followed by sample size (11 % SS), estimator (3.3 % SS), spatial pattern (1.4 % SS) and community type (0.2 % SS). None of the interactions between three or more factors explained more than 0.5 % SS, therefore we did not examine them any further.
The effect of the abundance distribution

In our simulations, we did not control the species richness of a community. Table 3 shows that for a given combination of community type and spatial pattern, communities simulated under a broken-stick or a lognormal model contained a similar number of species, whereas the communities simulated under the geometric model were between two and three times richer in species. The simulated meadows and arable fields had far fewer species than the grass verges and hedgerows. An artificial edge effect resulted in a considerable increase in species, especially for otherwise species-poor communities. Under the geometric model, an edge effect did not increase species richness.

Fig. 6 shows that the large effect of the species abundance model on relative bias was mainly due to a very large negative bias for the geometric model. The estimates for the broken stick model were on average slightly lower than those for the lognormal model, but this difference was smaller than the differences between estimators or between spatial patterns. Graphical analysis revealed no systematic interaction between the broken-stick and the lognormal models and the other factors, therefore we did not further discriminate between them.

Each of the three species abundance models was fitted to data from four different community types. Although the community types differed in species richness and in the dominance of the most abundant species, the average relative bias $PD$ differed only slightly between the four different community types (Fig. 6).

The effect of spatial heterogeneity

Overall, the spatial patterns seemed to play a minor role for explaining the relative bias of species richness estimates. The differences between individual spatial patterns were comparable to the differences between the four non-parametric estimators (Fig. 6). However, the spatial patterns without edge effect ($H, A, Giv, Gs$) differed very little in their average estimates.

Fig. 7 shows that a simulated edge effect lead to lower estimates and thus to an increase in relative bias and variance. This effect was rather strong in the case of the simulated meadows and arable fields, but less so for the species richer communities representing grass verges and hedgerows. The effect of an edge on estimator performance was strongest for small samples. The second-order jackknife $Jack2$ seemed to suffer less from an increase in variance. However, without an edge effect, $Jack2$ had the largest variance of all estimators, and this variance originated from a positive bias. Any lower estimate due to an edge effect would therefore partly compensate the positive bias and thus reduce variance.
Spatial autocorrelation appeared to increase the estimate, so that it reduced any negative bias and reinforced a positive one. This effect was reduced when a gradient was added, irrespective of gradient type.

**Differences between estimators**

The estimators did not differ systematically in their response to spatial pattern (Fig 7 bottom). Fig. 8 shows that estimator performance is closely related to *sample representativeness*, i.e., the proportion of species observed in the sample, at least up to a representativeness of 90%. Up to a sample representativeness of 80%, all estimators had a
Fig. 7. Interaction plots of the mean relative bias PD (left), and of the mean relative variance SPD (right), with spatial pattern and with each of sample size (top), community type (middle), and estimator (bottom), for all samples based on the Broken-stick or the Lognormal model. The meaning of the factor levels is explained in the legend of Fig. 6.
strong negative bias. Sample representativeness explained most of the relative bias of Jack1 ($R^2 = 0.94$) and of ICE ($R^2 = 0.92$), but considerably less for Jack2 ($R^2 = 0.75$) and for Chao2 ($R^2 = 0.66$). The residuals for Jack2 were unskewed, but Jack2 quite often predicted less species than were present in a sample. All other estimators had a lower bound of the observed number of species, $S_{\text{obs}}$, and thus a somewhat skewed distribution of residuals. Chao2 frequently predicted far too many species, irrespective of sample representativeness.
In the simulations under the geometric model, sample representativeness ranged from 30 - 90%. Samples simulated under the lognormal or the broken-stick models were more complete, with a representativeness of 50 - 100% with edge effect and of 70 - 100% without. The scatterplots in Fig. 8 suggest that four groups were confounded within the range of 30 - 80% representativeness. Further analysis confirmed that these groups correspond to different sample sizes. For a given sample size, estimates increased faster with sample representativeness than suggested by the overall curve.

The dependence of estimator performance on sample size for reasonably complete samples is illustrated in Fig. 9. *Jack1* and *Jack2* were positively biased, whereas *ICE* was negatively biased (see also Fig. 8). *Chao2* was very little biased even for small samples of 20, but then it had a large variance. *Jack2* had a large variance even for samples of 100. *Jack1* and *ICE* clearly had the smallest variance for samples of 20. However, for samples of 50 and more, their variance around the true value $S_{true}$ was not smaller than for $S_{obs}$. 

*Fig. 9. Interaction plot of the mean relative bias PD (left), and the mean relative variance SPD (right), sample size and estimator for the simulations without edge effect under the lognormal and the broken-stick models.*
Discussion

We investigated by simulation how the four non-parametric richness estimators Jack1, Jack2, Chao2 and ICE are affected by variations in the abundance distribution and by different types of spatial heterogeneity. Our approach differs in two ways from other simulation studies: (1) we fitted different species abundance models to the same real data from different types of communities, and (2) we explicitly modeled, independently for every simulated species, the effects of spatial autocorrelation, of an environmental gradient and of an edge effect as expected to occur in a patchy environment.

The ANOVA results suggested that the chosen species abundance model had by far the largest influence on relative bias of the estimates, followed by sample size and by differences between estimators, spatial patterns and community types.

Effect of the abundance distribution

We fitted three species abundance models to the same averaged data sets from four different types of communities. For a given species abundance model, communities with a stronger dominance of the most abundant species, and thus a more uneven abundance distribution, resulted in a lower estimate. This is consistent with the results from other simulation studies (Burnham and Overton 1979; Lee and Chao 1994; C. Frampton unpublished manuscript), where for a constant number of species in a community, a more uneven abundance distribution generally resulted in a lower estimate and thus caused a negative bias in various non-parametric estimators.

We did not control species richness, but fitted the species abundance models to the same data. The communities simulated under the geometric model were between two and three times richer in species than the corresponding communities simulated under the lognormal and the broken-stick model. All estimators performed reasonably well under the lognormal and the broken-stick models, but had a large negative bias under the geometric model. We showed that the large bias of estimates for the geometric model can be explained by sample representativeness, i.e. the proportion of species observed in the sample. Our result supports the findings by Heltshe and Forrester (1983) and Baltanás (1992) that estimator performance depends to a large degree on sample representativeness.

Simulation studies that control for the number of species are likely to obscure some fundamental problems in the estimation of species richness. In our simulations, the lognormal and the broken-stick models predicted a limited set of species, whereas for the same reference community, the geometric model predicted an indefinite number of species with a non-zero probability of occurrence, i.e., an unlimited species pool. The first prediction is compatible with a community approach to vegetation, the latter with...
the continuum concept. A second problem arises if the community under study is not delimited in space. In such a situation, a random sample of the study area can be interpreted as a clustered sample from a larger area, and a true species richness cannot be defined. When using a non-parametric estimator for estimating species richness from a spatial sample, we assume that (1) there is a discrete community, and (2) the community occupies a discrete area. The extrapolation of a species-area curve, on the other hand, is not compatible with these assumptions.

**Effect of spatial heterogeneity**

The three simulated spatial structures, i.e. spatial autocorrelation, an environmental gradient and an edge effect, had very different effects on estimator performance. A simulated edge effect considerably increased both bias and variance, especially for species poor communities where the proportion of additional species due to edge effect was relatively high. This result can again be explained by sample representativeness. Spatial autocorrelation tended to increase the estimate of species richness. This is compatible with the results by Baltanás (1992) where a small amount of aggregation increased estimates and thus reduces bias, while a higher degree aggregation again increased negative bias. The addition of a gradient compensated the effect of autocorrelation. Because a strong gradient basically had the same effect as a weak gradient, this negative effect of the gradient cannot be explained by an overall higher degree of aggregation.

Two fundamental differences in the modeled spatial structures may account for the large differences in their effect on estimator performance. The first is zonation; we assumed that spatial autocorrelation modifies the pattern of occurrence of every species independently, whereas environmental heterogeneity in the form of gradients or patches and their boundary zones causes a simultaneous zonation in many species. Independent small-scale aggregation at the species level may increase the difference between observations and thus enhance sample representativeness, as long as observations are not too close in space. The second difference concerns the presence of rare habitats. In simulating an environmental gradient, we assumed that the species are evenly distributed along a linear gradient across the field. Thus different sections of a gradient were evenly represented in the field. In simulating an edge effect, on the other hand, we assumed that the edge habitat occupies about 28% of our simulated field. Hence the edge habitat was likely to be represented in the sample with much fewer quadrats than the core, and sample representativeness was prone to be low especially when a large proportion of the species were restricted to the edge.
Heltshe and Forrester (1983) reviewed the general problem that a spatial random sample is not necessarily a random sample of environmental conditions or of biological entities. To achieve a better representation of biological variation, Gaston (1996) proposed stratification based on environmental variables and gradient-directed transect sampling (Gillison and Brewer 1985; Austin and Heyligers 1989). Neave et al. (1997) compared these strategies to random sampling and found no significant difference in estimation success, though this may have been due to insufficient environmental data.

Based on the general approach to spatial heterogeneity outlined by Legendre (1993), we propose three ways adapting the sampling design so as to maximize sample representativeness. (1) In the case of continuous environmental change, the quadrats should be spread evenly over the main gradients. Ideally, the environmental gradient would be rescaled into units of species turnover. (2) In a patchy environment, the sample should be stratified by habitat types. Ideally, the sample size within a habitat type would be proportional to its expected contribution of biotic entities, i.e., its difference from the other habitat types. Further research is needed to develop the details and test the effect of this kind of stratified sampling. (3) A minimum distance should be kept between quadrats to account for spatial autocorrelation (Palmer 1988; Palmer and White 1994). The community variogram presented in this paper can be used for determining a minimum distance. However, it should be investigated how the range of the community variogram is related to the range of the individual species.

**Choosing between estimators**

The four non-parametric estimators of species richness that we compared responded to differences in the abundance distribution and to spatial heterogeneity in a similar way. All estimators were strongly biased for samples that contained up to 80% of the species. For reasonably complete samples, Jack1 and Jack2 were positively and the ICE was negatively biased. Chao2 was least biased, but had a very large variance due to frequent and substantial overestimates. The estimators differed markedly in their variance, leading to a trade-off between bias and variance. For general application, we recommend Jack1 or ICE, or even a combination of the two, because of their relatively high precision even for small samples of 20. As Heltshe and Forrester (1983) described for Jack1, the non-parametric estimators did not perform better than the observed number of species, $S_{obs}$ for larger samples of 50 and more.

In theory, the non-parametric estimators have the advantage over $S_{obs}$ that their variance can be estimated with an appropriate formula (see Colwell 1997), so that a classical confidence interval can be constructed. However, several simulation studies showed that the nominal level of the confidence interval is rarely achieved, i.e., far too many estimates were found outside of the interval (Burnham and Overton 1979; Chao
1987; Mingoti and Meeden 1992). On the other hand, the observed number of species $S_{obs}$ can safely be interpreted as a lower bound to species richness, whereas the non-parametric estimators may under- or overestimate species richness, and $Jack2$ may even predict less species than observed in the sample.

**Conclusions**

The quadrat-based non-parametric estimators of species richness assume that the quadrats represent a random sample from a spatially homogeneous community that occupies a discrete area. Non-parametric estimators of species richness are only recommended for samples that contain at least 80% of the species. Spatial structures and the species abundance distribution influence estimator performance via sample representativeness. Further research is needed to develop methods for and test the effect of different strategies which aim to maximize sample representativeness by adjusting the sampling design to continuous and patchy structures in the environment and to spatial autocorrelation.

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Literature


Appendix: The community variogram

In the absence of spatial heterogeneity, the probability $p_{ia}$ that species $i$ occurs in a spatial unit of size $a$ is a constant. The number of independent spatial units $x$ of a given size $a$ occupied by species $i$, $x_{ia}$, is a binomial

$$x_{ia} \sim \text{bin}(n, p_{ia}) \quad (i = 1, \ldots, s)$$

with $p_{ia}$ the probability of occurrence of $i$ in one unit and $n$ the number of units. An expansion of quadrat size $a$ will obviously increase $p_{ia}$.

The parameter $p_{ia}$ can be estimated from a sample of $n$ quadrats of size $a$ by:

$$\hat{p}_{ia} = \frac{x_{ia}}{n}$$

Assuming further that the species are independent, the number of species observed in a quadrat, $S_a$, is a binomial sum that depends on $P_{ia}$ the distribution of the probabilities of occurrence (Burnham and Overton 1979; Bunge and Fitzpatrick 1993).

$$S_a = \sum_i x_{ia}$$

If the species are independent, the first and second moment of $S_a$ are:

$$E[S_a] = \sum_i E[x_{ia}] = \sum_i p_{ia} \quad (n=1)$$

$$\text{Var}(S_a) = \sum_i \text{Var}(x_{ia}) = \sum_i p_{ia}(1 - p_{ia})$$

An omni-directional empirical variogram is constructed by calculating the moment of inertia $\gamma(h)$ for a range of distance classes $h$; (Cressie 1991; Isaaks and Srivastava 1989):

$$\gamma(h) = \frac{1}{2N_h} \sum_{j,k|h_jk=h} (x_j - x_k)^2$$

where $N_h$ is the number of pairs of quadrats $j$ and $k$ separated by $h$. In our case, $x_j$ and $x_k$ are not two realizations of a single random variable $X$, but vectors of two realizations of $s$ binomial variables. Let $z_{jk}$ denote their squared Euclidean distance:

$$z_{jk} = (x_j - x_k)^2 = \sum_i (x_{ij} - x_{ik})^2 = \sum_i z_{ijk}$$

then $z_j$ is a binomial:
Thus \( z_{ijk} \) is equal to the number of species present in \( j \) or \( k \) but not in both. Hence we can construct an empirical variogram of species composition (a community variogram) by plotting for each distance class the mean number of species present only in one quadrat of a pair against the mean distance between the two quadrats.

For independent quadrats, the expected value of \( z_{jk} \) is derived as

\[
p(z_{ijk} = 1) = 2p_i (1 - p_i)
\]

\[
E[z_{jk}] = \sum_i E[z_{ijk}] = \sum_i 2p_i (1 - p_i)
\]

Thus the expected moment of inertia \( \gamma(h) \) for independent quadrats is

\[
E[\gamma(h)] = \sum_i p_i (1 - p_i) = \sum_i p_i - \sum_i p_i^2
\]

which is equal to the variance of \( S_n \) and to the sum of the variance of the binomial variables.
Specificity as a measure of the contribution of an area to larger-scale species richness


Abstract — Assessing and predicting the species richness of a complex landscape remains an unsolved 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 specificity 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 specificity, 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 specificity per m² for arable fields, whereas patch shape appeared to be unrelated to the specificity per m² for both habitat types. The specificity 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. 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.
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 an unsolved problem (Stohlgren et al. 1997b) for various reasons.

Firstly, there is no simple scaling function of species richness (Palmer and White 1994). Normally, two adjacent quadrats together will host less than twice the number of species observed in a single quadrat. How much less depends on the degree of heterogeneity, which itself is a matter of scale. A mosaic landscape will usually 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., in press).

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 a 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 1996; Suter et al. 1998). However, any reliable assessment of larger-scale species richness is bound to be time-consuming and costly (Duelli 1997; Stohlgren, Chong et al. 1997). 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 (Fig. 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 volume of 130 dm³. The pooled sample contained a soil sample of 11.2 cm x 11.2 cm x 5 cm and an above ground sample of 11.2 cm x 11.2 cm x 130 cm taken at each of eight points located adjacent to the vegetation sample in the compass directions. 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, we took a random sample of 20 quadrats of 1 m² from each out of 12 arable fields, 11 meadows, 10 grass verges, five hedgerows, and five track roads (Wagner et al., in press). 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 fields 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.
Fig. 2. Pattern of land use and stratified 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.
Specificity

The meaning of specificity is best explained by an example. Fig. 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.
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>$x_i$</td>
<td>The number of observations of species $i$ in quadrat $q$ within spatial element $j$.</td>
<td>$x_i = \sum_{q} x_{iq}$</td>
</tr>
<tr>
<td>$\bar{x}_i$</td>
<td>The mean number of observations (individuals or occurrences) of species $i$ in $n_j$ quadrats within the spatial element $j$.</td>
<td>$\bar{x}<em>i = \sum</em>{q} x_{iq} / n_j$</td>
</tr>
<tr>
<td>$\tilde{w}_j$</td>
<td>The weight $\tilde{w}_j$ of the spatial element $j$ is proportional to its area $a_j$.</td>
<td>$\tilde{w}_j = \frac{a_j}{\sum_j a_j}$</td>
</tr>
<tr>
<td>$S_j$</td>
<td>The specificity of species $i$ to spatial element $j$, i.e., the estimated proportion of the occurrence or population that falls into $j$.</td>
<td>$S_j = \frac{\tilde{w}<em>j x</em>{ij}}{\sum_j x_{ij}}$</td>
</tr>
<tr>
<td>$S_j^{a_j}$</td>
<td>The total specificity of the spatial element $j$ of size $a_j$.</td>
<td>$S_j^{a_j} = \sum_j S_j$</td>
</tr>
<tr>
<td>$S_j^{aq}$</td>
<td>The specificity per unit area $a_q$, i.e., quadrat size, of the spatial element $j$.</td>
<td>$S_j^{aq} = \frac{S_j^{a_j} a_j}{a_j}$</td>
</tr>
<tr>
<td>$S_j$</td>
<td>The relative specificity of the spatial element $j$.</td>
<td>$S_j = \frac{S_j^{aq}}{\sum_j S_j^{aq}}$</td>
</tr>
</tbody>
</table>

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 (Fig. 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 the 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 ($S_{ij}^{aq}$) or in total ($S_{ij}^{a_j}$), 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 plant 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 intensity and evaluated $S_j$ at sample sizes 3 x 10, 3 x 20, and 3 x 30.

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? Fig. 4 shows a striking difference between the proportional contribution of the three main habitat types as calculated from the plant and from the snail data. 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 (Fig. 4).

How sensitive are specificity estimates to sample size? Fig. 5 (top left) shows a consistent bias in the estimated relative specificity $S_j$ for the plant data when based on an unstratified sample. 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 (Fig. 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 (Fig. 5, top right) and stratified samples (Fig. 5, bottom right).

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### Fig. 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, based on presence-absence data. The whiskers indicate the 5% and the 95% quantiles of the estimates.

<table>
<thead>
<tr>
<th>Plant data</th>
<th>Snail data</th>
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<tbody>
<tr>
<td>N</td>
<td></td>
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<tr>
<td>30</td>
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<td>3 x 30</td>
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- **Agriculture**
- **Settlement**
- **Forest**

### Table

<table>
<thead>
<tr>
<th>Sample Size</th>
<th>Relative Specificity $S_j$</th>
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<tbody>
<tr>
<td>30</td>
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<tr>
<td>60</td>
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</table>
**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 \( S_f \) differed significantly from the relative area \( \chi^2 = 758, \text{DF} = 6, p = 0.0001 \). 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 (Fig. 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 of meadows, 4 for the interior of arable fields, and 5 for track roads. At the patch level, specificity per m\(^2\) \( S_f \) was strongly correlated with the frequency of disturbance (Spearman rank correlation \( r_s = -0.57, n = 43, p < 0.001 \)). Hedges had the highest average, and the largest variance of specificity per m\(^2\), \( S_f \). 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\(^2\), \( S_f \), of the patch interior was not positively, but clearly negatively correlated with patch size (Fig. 7, top left). For the 11 meadows, there was no evidence of a correlation (Fig. 7, bottom left). Only one meadow that was managed less intensively under a conservation program showed a markedly higher specificity per m\(^2\) than the other meadows.
Do more circular or square-shaped fields contribute more to landscape species richness per unit area than more elongated fields? We quantified the circularity $C_j$ of patch $j$ as a function of its area $a_j$ and its perimeter $p_j$ (Griffith 1982; Davis 1986):

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

Circularity $C_j$ was not significantly correlated to the specificity per m$^2$, $S_j^{\text{int}}$, of the patch interior, neither for the arable fields (Fig. 7, top right) nor for the meadows (Fig. 7, bottom right). It seems unlikely that a positive correlation exists that did not become statistically significant due to small sample size, as for the arable fields, the empirical correlation was clearly negative (Fig. 7, top right).
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 specificity 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 specificity 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 specificity estimates. Estimators of species richness suffer from the same problem (Wagner and Wildi, submitted). However, specificity 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 specificity 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, 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 specificity does discriminate between generalist and specialist species, patches that host interior and edge species should have higher specificity scores per m² than patches that contain only edge species. However, for the Hohenrain data set, field size was unrelated to specificity 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 specificity m² both for arable fields and for meadows. Circularity Cₜ 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 specificity per m². The lack of a positive effect of field size and shape on specificity 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). However, it is also possible 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.

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 re-
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 did not contain any forest patches.

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. Fig. 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 (Fig. 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 (Fig. 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 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 of 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.

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References


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