



Additive partitioning of plant species diversity in an agricultural mosaic landscape

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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 neighbourhood 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 of 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 neighbouring 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

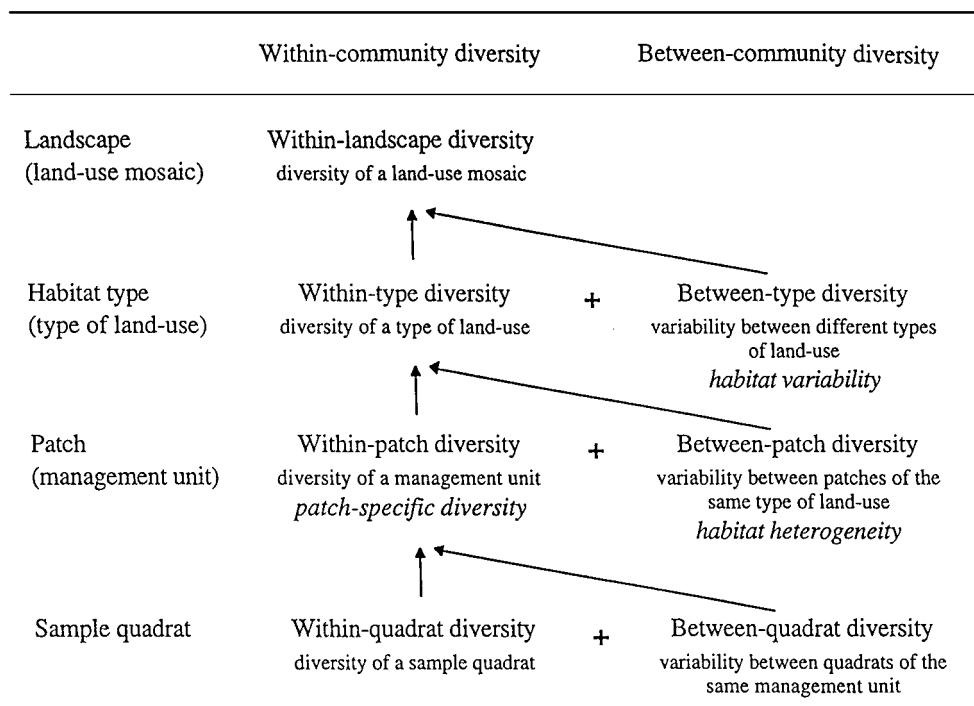


Figure 1. The proposed hierarchical model of species diversity, where the scale-specific components of within- and between-community diversity are linked additively to form the diversity at the next higher level. In italics the corresponding factors of the mosaic concept as defined by Duelli (1992).

defined at any 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 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 (Figure 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.

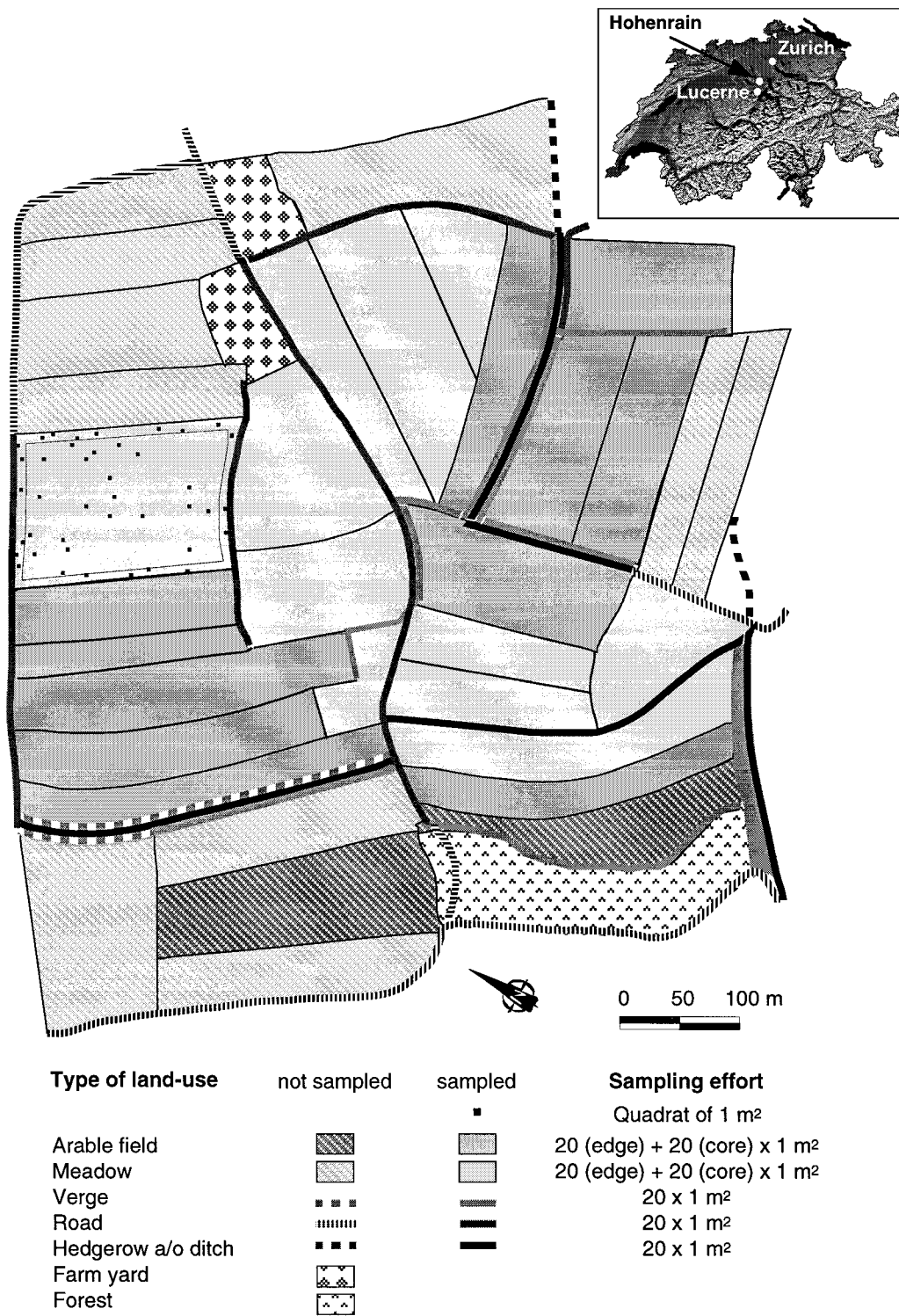


Figure 2. The management units included in the sample and of the surrounding area near Hohenrain (Switzerland) are classified into 7 types of land-use, namely arable fields, meadows, verges, roads, hedgerows and ditches, farm yards and forests. For one meadow, the subdivision into a 3-m wide edge and a core area is indicated together with the random sample of 20 quadrats within each stratum.

Data 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 (Figure 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.

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 \underline{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:

$$S_{Bq} = S_{Wp} - \underline{S}_{Wq}. \quad (1)$$

Similarly, between-patch species richness S_{Bp} is the difference between S_{Wt} and \underline{S}_{Wp} , and between-

type species richness S_{Bt} is the difference between S_{Wl} and \underline{S}_{Wt} .

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

$$\pi_{ip} = \frac{f_{ip}}{f_{\cdot p}}. \quad (2)$$

We calculated the pooled proportional abundances π_{it} of i in type t and π_{il} in landscape l as the weighted sums of the π_{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 :

$$\pi_{it} = \sum_p \frac{a_{pt}}{a_t} * \pi_{ip}, \quad (3a)$$

$$\pi_{il} = \sum_p \frac{a_{pl}}{a_l} * \pi_{ip}. \quad (3b)$$

The Shannon index H is a Type I measure of mixed diversity:

$$H = - \sum_i \pi_i * \ln \pi_i. \quad (4)$$

The Type II measure Simpson diversity D is a function of the dominance λ . 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:

$$D = 1 - \lambda = 1 - \sum_i \pi_i^2 \quad (5)$$

Let within-patch Shannon index H_{Wp} be the Shannon index calculated from the π_{ip} 's, H_{Wt} and H_{Wl} the Shannon index based on the pooled proportional abundances π_{it} and π_{il} . \underline{H}_{Wp} 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:

$$H_{Bp} = H_{Wt} - \underline{H}_{Wp} \quad (6)$$

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

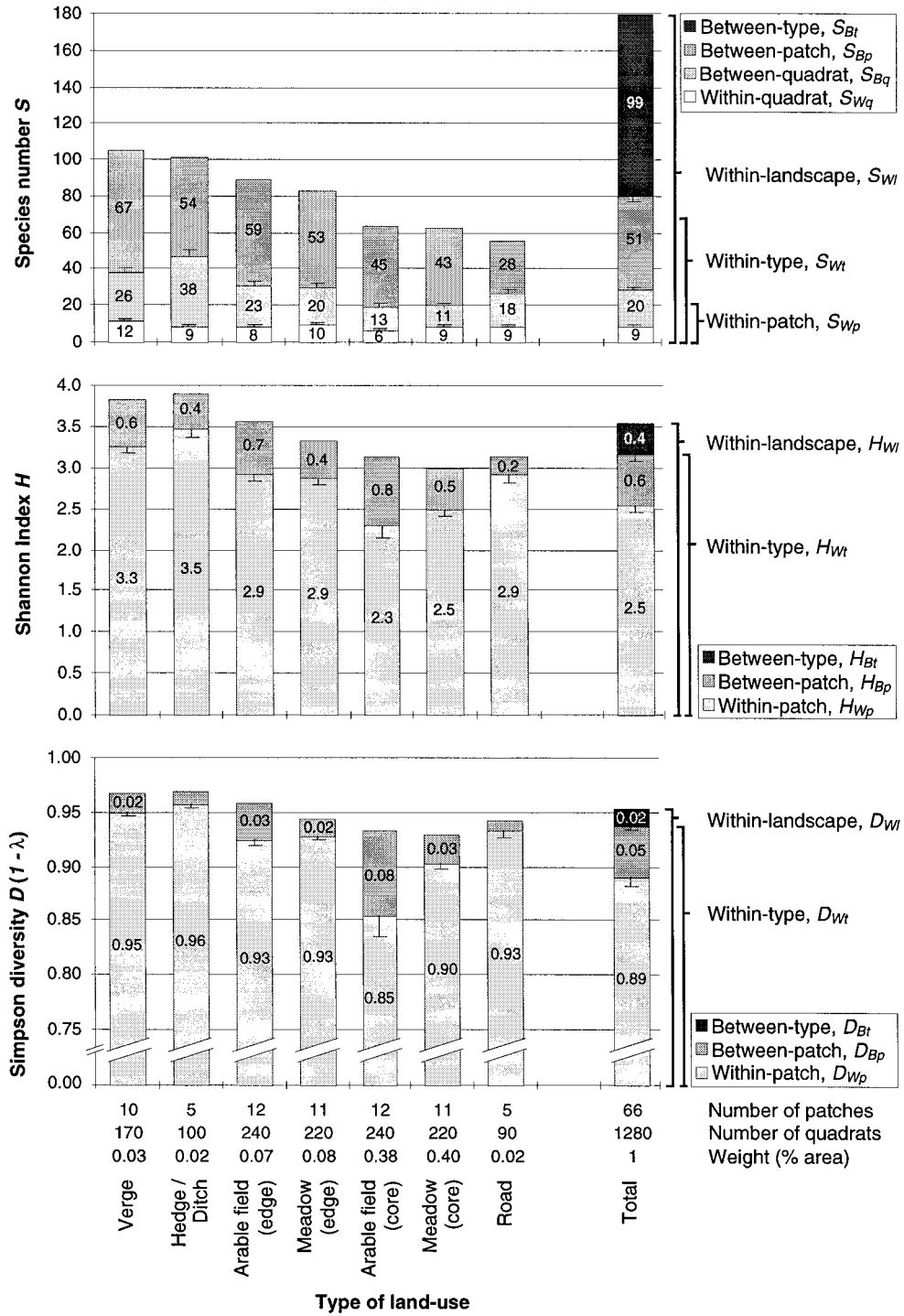


Figure 3. Each bar shows the species number S (top), Shannon index H (middle) or Simpson diversity $D(1-\lambda)$ (bottom) for a particular type of land-use and for the study area as a whole, partitioned into the mean S , H or D per quadrat, the mean S , H or D per patch, for every type of land-use the 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.

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_{Wl}) can be divided into a mean within-type richness \underline{S}_{Wt} of 80 and the between-type richness S_{Bt} of 99 species. \underline{S}_{Wt} consists again of a mean within-patch richness \underline{S}_{Wp} of 29 and the between-patch richness S_{Bp} of 51 species. \underline{S}_{Wp} consists of a mean within-quadrat richness \underline{S}_{Wq} of 9 and the between-quadrat richness S_{Bq} of 20 species.

For the Type I measure Shannon index H , the within-landscape H_{Wl} of 3.5 is composed of the between-type H_{Bt} of 0.4 and a mean within-type component \underline{H}_{Wt} of 3.1. The latter again is the sum of a mean within-patch \underline{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_{Bt} of 0.02 and a mean within-type \underline{D}_{Wt} of 0.94. The latter is the sum of a mean within-patch \underline{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_{Bq} 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_{Bq} 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 neighbourhood effects; (2) the unbiased estimation of species richness components; and (3) the quantification of the contribution of a landscape element to landscape species richness.

(1) 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 neighbouring 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.

(2) 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.

(3) 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. An appropriate weighting to adjust for specificity could help us proceed from mere counting to assessing conservation value and deriving strategies for biodiversity management.

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