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ORIGINAL ARTICLE

Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures

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ABSTRACT

Aim In a selected literature survey we reviewed studies on the habitat heterogeneity–animal species diversity relationship and evaluated whether there are uncertainties and biases in its empirical support.

Location World-wide.

Methods We reviewed 85 publications for the period 1960–2003. We screened each publication for terms that were used to define habitat heterogeneity, the animal species group and ecosystem studied, the definition of the structural variable, the measurement of vegetation structure and the temporal and spatial scale of the study.

Main conclusions The majority of studies found a positive correlation between habitat heterogeneity/diversity and animal species diversity. However, empirical support for this relationship is drastically biased towards studies of vertebrates and habitats under anthropogenic influence. In this paper, we show that ecological effects of habitat heterogeneity may vary considerably between species groups depending on whether structural attributes are perceived as heterogeneity or fragmentation. Possible effects may also vary relative to the structural variable measured. Based upon this, we introduce a classification framework that may be used for across-studies comparisons. Moreover, the effect of habitat heterogeneity for one species group may differ in relation to the spatial scale. In several studies, however, different species groups are closely linked to 'keystone structures' that determine animal species diversity by their presence. Detecting crucial keystone structures of the vegetation has profound implications for nature conservation and biodiversity management.

Keywords
Habitat heterogeneity hypothesis, structural diversity, structural heterogeneity, foliage height diversity, species richness, biodiversity, spatial scale, habitat fragmentation.

INTRODUCTION

The 'habitat heterogeneity hypothesis' is one of the cornerstones of ecology (e.g. Simpson, 1949; MacArthur & Wilson, 1967; Lack, 1969). It assumes that structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity (Bazzaz, 1975). In most habitats, plant communities determine the physical structure of the environment, and therefore, have a considerable influence on the distributions and interactions of animal species (reviews in Lawton, 1983; McCoy & Bell, 1991). For example, for bird species diversity in forests, MacArthur & MacArthur (1961) evidenced that the physical structure of a plant community, i.e. how the foliage is distributed vertically, may be more important than the actual composition of plant species.

Although positive relationships between vegetation-shaped habitat heterogeneity and animal species diversity are well documented on both local and regional scales (Davidowitz & Rosenzweig, 1998), empirical and theoretical studies have yielded contradictory results. Depending on the taxonomic group, the structural parameter of the vegetation and the spatial scale, species diversity may also decrease with increase in habitat heterogeneity (e.g. Ralph, 1985; Sullivan & Sullivan, 2001). Moreover, effects of habitat heterogeneity may vary considerably depending on what is perceived as a habitat by the species group studied. Structural attributes of the vegetation that constitute habitat heterogeneity for one group may be perceived as habitat fragmentation by another taxonomic group (e.g. Okland, 1996).

Here we present a selected literature survey on the relationship between habitat heterogeneity of the vegetation and animal species diversity. In our survey habitat heterogeneity is considered as a term for vertical and horizontal vegetation and landscape structure in terrestrial ecosystems. We show which taxonomic groups, vegetation habitats and measurements of habitat heterogeneity have been used at which spatial and temporal study scales. We then present the 'keystone structure concept' which we want to bring forward for future discussion. Our concept explains that the presence of 'keystone structures' of the vegetation may be indicated by positive correlations of the species diversity–habitat heterogeneity relationship along a spatial trajectory. Empirical support for this is given by examples from temporary wetlands in agricultural fields and solitary trees in South African savannas.

DEFINITIONS

While the term 'habitat' is usually defined as a dominant vegetation formation, e.g. forest, meadow or wetland (see e.g. Ricklefs & Miller, 1999), the definition and meaning of 'habitat heterogeneity' varies considerably. Depending on the taxonomic group and spatial resolution of the study, the scale of observation may range from the architecture of single plant species (e.g. Lawton, 1983) to landscape patterns (e.g. Böhning-Gaese, 1997). Yet, even within one species group, e.g. arthropods, 'habitat heterogeneity' may refer to small scale 'complexity of patch borders' (Haslett, 1997) or continental scale 'topographic heterogeneity' (Kerr & Packer, 1997). Given this large heterogeneity and the explicit focus of our study, we did not attempt to provide an in-depth review of definitions of this term.

LITERATURE SURVEY

In the literature survey we screened for publications that correlated habitat heterogeneity or synonyms with animal species diversity. Besides 'habitat heterogeneity', equivalent terms included in an ISI Web of Science search were 'habitat diversity', 'habitat complexity', 'structural diversity', 'structural complexity', 'structural heterogeneity', 'spatial heterogeneity', 'spatial complexity', 'foliage height diversity', 'foliage diversity', 'architectural complexity', 'vegetation complexity' and 'vegetation heterogeneity'. Here, we excluded studies that did not quantify vegetation structure or focused on assemblage structure instead of species number. As this sample of ecological terms cannot be representative of the literature on habitat heterogeneity and animal species diversity as a whole, we strongly emphasize the selective character of our literature survey. For example, a study that used 'complexity of habitat' to describe vegetation structure was missed out in the literature search, while the term 'habitat complexity' was included. In general, we found the study results to be different regarding the sample size and the magnitude of significance they found for the habitat heterogeneity–species diversity relationship. However, due to insufficient data and the high inconsistency of quantitative structural parameters a detailed meta-analysis (see e.g. Gurevitch *et al.*, 1992, 2001) was impossible to conduct. In order to assess general patterns, we therefore used the 'vote-counting' technique (Gates, 2002) with simple counts for respective categories.

GENERAL PATTERNS AND PREFERENCES: SYNONYMS, SPECIES GROUPS AND ECOSYSTEMS

Overall, we found 85 empirical papers published between 1960 and 2003 that used one of the above-mentioned terms. 'Habitat heterogeneity' (22%) together with 'habitat diversity' (20%) covered the majority of applied terms (Fig. 1a). Here, the use of both terms has shifted over time: while 'habitat diversity' has been more widely used in the literature of the 1960s and 1970s, 'habitat heterogeneity' was more common in the 1980s and 1990s. Besides habitat heterogeneity/diversity other less frequently used terms include, e.g. 'structural diversity' (16%) or 'spatial heterogeneity' (11%) (see Fig. 1a).

Concerning the species groups studied, more than one-third of all screened papers comprised studies of avian fauna (Fig. 1b). This is noteworthy as birds make up less than half a per cent of global animal species diversity. A study frequency of 22% was found for mammals, including studies on, e.g. lemurs (e.g. Ganzhorn *et al.*, 1997), macropods (e.g. Southwell *et al.*, 1999) or rodents (e.g. Cramer & Willig, 2002). Overall, our survey indicates that vertebrates, which comprise only 3% of all animal species (May, 1988), are studied with a disproportionate frequency of 61%. In contrast to this, taxonomic groups that account for almost the entire global species diversity are largely ignored. In particular, arthropods were considered in only 39% of all publications in our analysis. Thereof, 19% focused on arachnids, 19% on butterflies, 14% on beetles and 36% on other insects. It is most likely the unease of species counting that prevented hyperdiverse taxonomic groups from being more frequently studied. Some recently evaluated estimation methods (Colwell & Coddington, 1994; Brose *et al.*, 2003), however, may well be used to close this serious gap in our understanding of the relationship between vegetation-shaped habitat heterogeneity/diversity and species diversity.

In terms of ecosystem preferences, forests are by far the most frequently studied system (49%), followed by agricultural systems (16%), prairie, steppe or grassland ecosystems (11%) and scrub/shrublands (6%) (Fig. 1c). With respect to forest ecosystems, there was a slight tendency towards avian

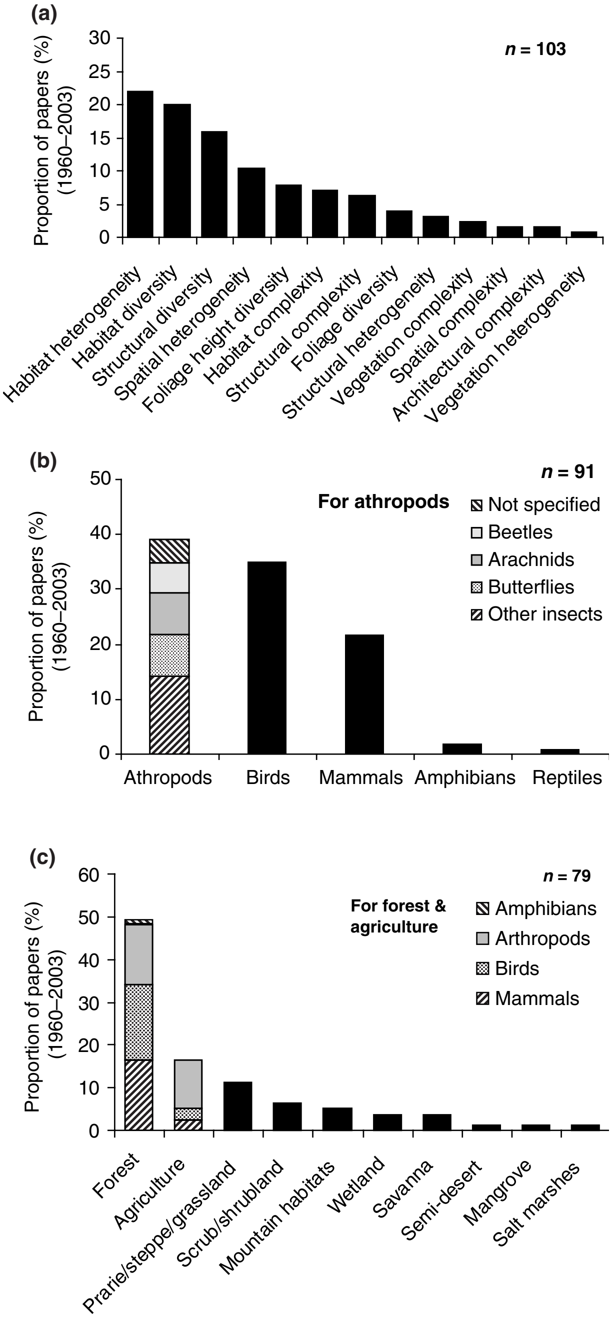

Figure 1 Results of the literature analysis: (a) the proportion of terms used to describe habitat heterogeneity, (b) the proportion of species groups and (c) the proportion of ecosystems. Numbers of counts differ from total number of papers ($n = 85$) as some papers used more than one definition (a, $n = 103$), investigated more than one species groups (b, $n = 91$) or had multiple habitat types due to regional or continental scales (c, $n = 79$).

studies (Fig. 1c). A very significant preference accounts for arthropods in agricultural systems. Here, 70% focused on arthropods as against to 39% in the total data set. Overall, these results show a preference for anthropogenic habitats, whereas habitat heterogeneity effects are less well documented in more natural habitats. Therefore, habitat heterogeneity might have been confounded with anthropogenic disturbances in some studies. For instance, comparative studies on species diversity in cut and uncut forests include effects of habitat heterogeneity, anthropogenic disturbances and habitat fragmentation (see Didham *et al.*, 1998 for a detailed analysis). Considering the high frequency of avian studies, well-known disturbance effects of forest management on bird breeding activity might have a strong effect in such studies.

Together these results indicate that although the relationship between habitat heterogeneity and species diversity is among the best documented patterns in community ecology, there are serious limitations in its empirical support. Particularly troublesome is the bias towards studies of vertebrates in anthropogenic habitats. Recently, the predominance of vertebrate studies has also been emphasized in the field of island biogeography (Báldi & McCollin, 2003).

THE RELATIONSHIP BETWEEN HABITAT HETEROGENEITY AND ANIMAL SPECIES DIVERSITY

In the literature survey 85% of all studies found a positive correlation between species diversity and the structural variable measured (see Table 1). However, we believe that this proportion might have been altered due to the well-known tendency towards the publication of positive results. Positive effects were found for arthropods (e.g. Haslett, 1997; Brose, 2003), birds (e.g. Wiens & Rotenberry, 1981; Thiollay, 1990; Poulsen, 2002), mammals (e.g. Southwell *et al.*, 1999; Williams *et al.*, 2002), amphibians (e.g. Atauri & Lucio, 2001) and reptiles (e.g. Pianka, 1967). Small-scale architectural complexity was shown to be important in studies of, e.g. arboreal arthropods (Halaj *et al.*, 2000), web spiders (Greenstone, 1984), grasshoppers (Davidowitz & Rosenzweig, 1998), epigaeic beetles (Romero-Alcaraz & Avila, 2000) and drosophilids (Tanabe *et al.*, 2001). Bird studies largely confirmed that vegetation physiognomy positively influences species diversity. Particularly in forests, there was strong evidence that vertical partitioning of resources and nesting sites facilitates guild diversity (Poulsen, 2002 and references therein).

However, as opposed to the habitat heterogeneity hypothesis, some studies prove evidence that increase in habitat heterogeneity may also decrease species diversity. This was shown, e.g. for small forest bottom-dwelling mammals (Sullivan & Sullivan, 2001), birds (Ralph, 1985) or butterflies (Hill *et al.*, 1995). In the following, we will discuss the reason for this discrepancy. We will show that the relationship between habitat heterogeneity of the vegetation and animal species diversity generally depend on how habitat heterogeneity is perceived by the animal guild studied (1), the measurement of species diversity (2), the definition (3) and measurement of vegetation structure (4) and the temporal (5) and spatial scale of the study (6).

Table 1 References included in the literature survey investigating the effect of habitat heterogeneity on animal species diversity. For the spatial scale of each study we consider four classes according to 1 (<100 m^2), 2 (100 m^2–1 ha), 3 (1 ha–1 km^2) and 4 (>1 km^2). Effects of habitat heterogeneity on species diversity refers to + for positive, − for negative and ≈ for no significant relationship.

Reference	Species group	Ecosystem	Spatial scale	Effect
Atauri & Lucio (2001)	Invertebrates, arthropods	Multiple types	4	+
August (1983)	Mammals	Forest	3	−
Baz & Garcia-Boyero (1995)	Butterflies	Forest	3–4	+
Berry & Bock (1998)	Birds	Grassland, forest	3	+
Bersier & Meyer (1994)	Birds	Forest	3–4	+
Bestelmeyer & Wiens (2001)	Ants	Steppe, grassland	2	+
Böhning-Gaese (1997)	Birds	Agriculture	4	+
Bowland & Perrin (1993)	Small mammals	Multiple types	3	+
Brooks (1997)	Birds	Multiple types	4	+
Brose (2003a)	Ground beetles	Agriculture	1–4	≈
Brose (2003b)	Ground beetles	Agriculture	1–2	+
Ceballos *et al.* (1999)	Mammals	Grassland	3	+
Celada & Bogliani (1993)	birds	Wetland	2–3	+
Colunga-Garcia *et al.* (1997)	Beetles	Agriculture	3	+
Cramer & Willig (2002)	Rodents	Shrubland	2	+
Davidowitz & Rosenzweig (1998)	Grasshoppers	Multiple types	4	+
Debinski & Brussard (1994)	Birds, butterflies	Mountain habitats	3	+
Dean *et al.* (1999)	Birds, mammals	Savanna	3	+
Dennis *et al.* (1998)	Small insects, spiders	Grassland	2	+
Docherty & Leather (1997)	Spiders	Forest	2	+
Ecke *et al.* (2002)	Small mammals	Forest	3	+
Estades (1997)	Birds	Forest, steppe, scrub	3	+
Estrada *et al.* (1994)	Mammals	Forest	3	+
Farley *et al.* (1994)	Birds	Forest	3–4	+
Feller & Mathis (1997)	Insects	Mangrove	2	≈
Finch (1989)	Birds	Mountain habitat	3	+
Fletcher & Koford (2002)	Birds	Prairie	3	+
French & Picozzi (2002)	Birds	Multiple types	4	+
Froneman *et al.* (2001)	Birds	Agriculture	2–3	+
Ganzhorn *et al.* (1997)	Lemurs	Forest	4	+
Greenstone (1984)	Spiders	Mountain habitats	1	+
Halaj *et al.* (2000)	Arboreal arthropods	Forest	1	+
Hamer *et al.* (2003)	Butterflies	Forest	4	≈
Hanowski *et al.* (1997)	Birds	Forest	3	+
Haslett (1997)	Arthropods	Mountain habitats	3	+
Heaney (2001)	Small mammals	Mountain habitats	4	≈
Henderson & Harper (1992)	Birds	Wetland	3	+
Horvath *et al.* (2001)	Rodents	Agriculture, forest	3	+
Hill *et al.* (1995)	Butterflies	Forest	3	−
Hurd & Fagan (1992)	Spiders	Agriculture	2–3	+
Johnsingh & Joshua (1994)	Birds	Forest	4	≈
Kerley (1992)	Small mammals	Semi-desert	4	+
Kerr & Packer (1997)	Mammals	Multiple types	4	+
Kerr (2001)	Butterflies	Multiple types	4	+
King & DeGraaf (2000)	Birds	Forest	3	+
Kruess & Tscharntke (2002)	Insects	Grassland	2	+
MacArthur & MacArthur (1961)	Birds	Forest	4	+
McNett & Rypstra (2000)	Spiders	Agriculture	3	+
Medellin & Equihua (1998)	Mammals	Forest, agriculture	2–3	+
Milton & Dean (1995)	Birds, mammals	Savanna	3	+
Moser *et al.* (2002)	Small mammals	Forest	3	+
Murdoch *et al.* (1972)	Insects	Agriculture	2	+
Novotny (1993)	Insects	Forest	2	+
Perfecto & Snelling (1995)	Ants	Agriculture	3	+
Pianka (1967)	Reptiles	Desert	4	+

Table 1 *continued.*

Reference	Species group	Ecosystem	Spatial scale	Effect
Poulsen (2002)	Birds	Forest	3	+
Ralph (1985)	Birds	Forest, steppe	3	–
Recher (1969)	Birds	Multiple types	4	+
Riffel *et al.* (2001)	Birds	Wetland	2–3	+
Romero-Alcaraz & Avila (2000)	Epigaeic beetles	Mountain habitats	4	+
Roth (1976)	Birds	Shrubland, forest	3	+
Schiegg (2000)	Saproxylic insects	Forest	2–3	+/≈
Schwarzkopf & Rylands (1989)	Primates	Forest	4	+
Shochat *et al.* (2001)	Birds	Forest, scrubland	3	+
Southwell *et al.* (1999)	Macropods	Forest	4	+
Southwood *et al.* (1979)	Insects	Agriculture	2	+
Spitzer *et al.* (1997)	Butterflies	Forest	2	+
Sullivan *et al.* (2000)	Small mammals	Forest	3	–
Sullivan & Sullivan (2001)	Small mammals	Forest	3	–
Tanabe *et al.* (2001)	Drosophilids	Forest	2	+
Terborgh (1977)	Birds	Mountain habitats	3–4	+
Thiollay (1990)	Birds	Forest	3	+
Tockner *et al.* (1999)	Dragonflies, amphibians	Wetland	4	+
Tomoff (1974)	Birds	Scrubland	4	+
Uetz (1975)	Spiders	Forest	1–2	+
Vallan (2002)	Amphibians	Forest	3	+
van Rensburg *et al.* (2002)	Birds	Multiple types	3–4	+
Verschoor & Krebs (1995)	Arthropods	Salt-marsh	1	+
Walter (1992)	Mites	Forest	1	+
Weibull *et al.* (2000)	Butterflies	Agriculture	3–4	+/≈
Whitmore *et al.* (2002)	Spiders	Savanna	2	+
Wiens & Rotenberry (1981)	Birds	Shrubsteppe	4	+
Williams & Marsh (1998)	Small mammals	Forest	4	–
Williams *et al.* (2002)	Small mammals	Forest	4	+
Willson (1974)	Birds	Forest	3	+
Zerm *et al.* (2001)	Beetles	Forest	4	+

The overall effects: heterogeneity or fragmentation?

Negative effects of habitat heterogeneity may occur as a consequence of fragmentation, causing the disruption of key biological processes such as dispersal and resource acquisition (Saunders *et al.*, 1991). However, there is general consensus that not all species in an ecosystem are equally affected by spatial structures, depending on whether they cause heterogeneity or fragmentation (Andrén, 1994; Steffan-Dewenter & Tscharntke, 2000). For example, while forest gaps increase habitat heterogeneity for butterflies (Spitzer *et al.*, 1997) and birds (Greenberg & Lanham, 2001), they may fragment the habitats of ground beetles (Rainio & Niemela, 2003). In a butterfly community study of fragmented woodlots Baz & Garcia-Boyero (1995) showed that species diversity increased with increasing patchiness of forest fragments. However, increase in patchiness of relict forests may decrease the diversity of beetle assemblages (Didham *et al.*, 1998; Barbosa & Marquet, 2002). From the organism perspective the remaining question is, at what point does internal habitat heterogeneity become fragmentation, i.e. how can we distinguish the difference between within-habitat and between-habitat vegetation structure? To avoid this question one can ask whether either positive or negative effects of heterogeneity (or fragmentation) dominate in their influence on overall species diversity. For example, in traditionally heavily used cultural landscapes of central Europe increase in forest patchiness likely increases species diversity as more potential habitat is added (e.g. Böhning-Gaese, 1997). Whereas in tropical areas disruption of formerly closed-canopy forests likely decreases diversity as a result of habitat fragmentation (Turner, 1996; Didham *et al.*, 1998; for a comparison of tropical vs. temperate forest bird communities see also Báldi, 1996).

Measuring species diversity

The resulting effect of habitat heterogeneity/diversity on species diversity is subject to the measurement of species diversity. In general, species diversity is a measure of the number of component species and their abundance at a defined point in space and time (Rosenzweig, 1995). On the smallest spatial scale the diversity of animal species measured is the result of individual behaviour, i.e. habitat selection, and of course sampling chance. Here, rarefaction is one widely used method to scale down to the same number of individuals between habitats (see Sanders, 1968; Hurlbert, 1971). On larger spatial scales species diversity depends on, e.g. the size of the regional species pool and evolutionary history. Considering these aspects, the measurement of species diversity is always a snapshot and results may vary even for similar habitats. Furthermore, correlations between species diversity and habitat heterogeneity in different locations are subject to equilibrium and non-equilibrium dynamics. For example, if species diversity patterns show year-to-year variations this will have great implications for across-study comparison (see e.g. Wiens, 1994).

The identity of the structural variable

The response of species diversity to habitat heterogeneity may also vary, depending on the group of species considered and the type of structural variable that is chosen (Atauri & Lucio, 2001). What is considered as an important structural variable may vary between studies, dependent on, e.g. habitat requirements of the species group, home range, and the scientific perspective. This has been nicely illustrated by Huston (1994) who claimed that a lawn is a green salad for a sheep and a complex universe for an insect. In other words, one would obviously not expect species diversity of large herbivorous mammals to be correlated with the architectural complexity of single plants. However, even in one species group structural variables may vary between studies, depending on the type of habitat and the spatial resolution.

A questionable choice of the structural variable in some studies may explain the failure to confirm an initially hypothesized relationship. For example, in a study on forest structure, Sullivan & Sullivan (2001) showed that, contrary to their initial hypothesis, mean species diversity of ground-dwelling mammals was lowest in uncut forests with high structural diversity (measured as an index of basal area, density and percentage cover of trees and woody debris and crown volume), but similarly high in four treatments of tree harvest with low structural diversity (Table 1). Even the clear-cut forest site showed significantly higher diversity than the uncut site, as some species tend to prefer successional habitats with abundance of herbs and grasses. Choosing a structural variable in this study that considers forest floor heterogeneity as a measure of shelter availability might have altered the perception of high and low habitat heterogeneity resulting in low values for uncut forests and high values for tree harvest sites.

Similar variable-biased results were obtained in a study of Ralph (1985) for *Nothofagus* beech forests of Patagonia where habitat heterogeneity was measured as an index of foliage height diversity (Table 1). He found that bird species were more diverse in the lower stature shrub communities than in structurally diverse forest. Based on a subsequent study on the same forest type in Chile, Estades (1997) then suggested that this inverse relationship compared with the classical theory, might be attributed to the fact that for *Nothofagus* forests, particular species composition rather than the vegetation structure itself might better explain the diversity of bird species. So in this case, a variable correlated with particular species could have been attributed to higher bird species diversity. These facts highlight the need to select biologically meaningful variables in studies of habitat heterogeneity effects.

Measuring habitat heterogeneity

In general, the quantification of vegetation-shaped habitat heterogeneity is not a straightforward task as the measurement depends on the definition of the structural variable. As a consequence, only few attempts have been made to propose general and widely applicable methods, and most studies have used different approaches. Here we introduce a classification of heterogeneity measurements that is based on the type of the structural variables, discrete or continuous, and the number of study sites, single or multiple (Table 2). On single study sites, heterogeneity might be measured as a count for discrete variables (structural richness) or as the extent for continuous variables (structural extent). The most often used type of heterogeneity based on multiple study sites is 'structural diversity' that uses Shannon's or similar indices of diversity that are well known from biodiversity studies (Magurran, 1988). This leads to compound measurements of the number and evenness of the discrete structural elements. Measuring structural qualities on multiple study sites, a 'structural gradient' can be calculated by Euclidian distances (see Brose, 2003 for details).

Which measurement is most appropriate? If the study area contains subareas that (1) differ substantially in their structure

Table 2 Measurement of habitat heterogeneity.

	Discrete variables (structural elements)		Continuous variables (structural qualities)	
Study sites	Single	Multiple	Single	Multiple
Definition	Number of structural elements	Number and evenness of structural elements	Extent of structural qualities	Structural difference between various sites
Name	Structural richness	Structural diversity	Structural extent	Structural gradient
Measurement	Count of the elements	Shannon's index of diversity	Measured structural quality	Gradient length, Euclidian distances
Example	Number of habitat types in a landscape	Diversity of habitat types in a landscape	Vegetation height or coverage	Difference in vegetation structure between sites

and (2) subsequently in their species communities, the 'structural richness' count will most likely yield accurate insight in the habitat heterogeneity–species diversity relationship. For instance the number of habitat types in a landscape is most likely highly correlated with its species diversity when the habitat types are sufficiently distinct. A measurement of 'structural diversity' will lead to superior results if the species need subareas of different structural groups in an even distribution to persist in the study area as, e.g. many bird species that have different breeding and feeding habitats or taxonomic groups with species that use different habitat types in different life stages. Continuous structural variables are related to gradients that continuously affect the species distribution in the study area. In these cases, the gradient length will be correlated with the number of coexisting species. The 'structural extent' can be used when the gradient is characterized by a single variable, whereas 'structural gradients' apply to multivariate gradients. For instance, the structural complexity of the vegetation depends on a variety of parameters like height, coverage and vegetation types. While correlating carabid beetle diversity in a field study to gradients of any one of these variables did not yield significant results, the correlation with the multivariate structural gradient was highly significant (Brose, 2003b).

Accordingly, the measurement of habitat heterogeneity depends on the structural variables used and the taxonomic group studied. Although we cannot come to a general recommendation of a single variable, empirical measurements should be discussed in the framework developed here. Furthermore, in many studies the comparative analysis of multiple types of measurements and their influence on species diversity might be more interesting than the presentation of just a single significant habitat heterogeneity–species diversity correlation.

The time of observation

Another important issue concerns the time of observation. Possible correlations between habitat heterogeneity/diversity and species diversity are most likely unstable, as they are valid only for a certain time slot that has been studied. This pattern was shown, e.g. for habitat succession from fallow fields to birch woodland in a study by Southwood *et al.* (1979) (Table 1). They showed that the relative importance of habitat heterogeneity changed in the course of succession: while in early successional stages insect diversity rose with plant taxonomic diversity, it was determined by habitat heterogeneity in the later stages. This pattern was also confirmed for carabid diversity during succession in an embanked salt-marsh area (Verschoor & Krebs, 1995). Brose (2003b), however, found that for temporary wetlands, habitat heterogeneity was always the best indicator for carabid beetle diversity, independent of successional stage. While in some habitat types (such as fallow fields in the study of Southwood *et al.*, 1979) habitat heterogeneity increases slowly along the successional trajectory, its amount in other habitat types depends less on the successional stage and is generally more variable (Brose, 2003b).

The spatial scale

Eventually, the spatial scale on which measurements are taken is crucial. First, based on the species group, the spatial scale determines the type of structural variable that has to be chosen as different scales require different appropriate variables (Grimm & Wissel, 1997). Secondly, the effect of habitat heterogeneity relative to the structural variable measured may vary depending on the spatial scale (Fig. 2a,b). To illustrate this, Brose (2003a) showed that effects of habitat heterogeneity for ground beetle assemblages were positive on the micro- and meso-scale (0.25 and 500–1000 m^2, respectively), while they were non-significant on a macro-scale of 10 km^2 (Brose, 2003a). For butterflies in tropical forests, effects of habitat heterogeneity have been reported to be positive on the gap scale (Spitzer *et al.*, 1997), while being negative for large-scale disturbances such as moderate levels of logging (Hill *et al.*, 1995). Schiegg (2000) studied saproxylic insect diversity in relation to volume and connectivity of coarse woody debris of mixed beech-spruce forest. She reported that a positive habitat heterogeneity–species diversity relationship was only significant for a 150-m scale, measured as a radius around the plots where the insects were collected. Remarkably, the relationship was non-significant for all other spatial scales, as this range could be attributed to the mean home range of these species.

Generally, species diversity of each animal group is linked with structural characteristics that occur on a specific scale reflecting important habitat requirements such as escape from

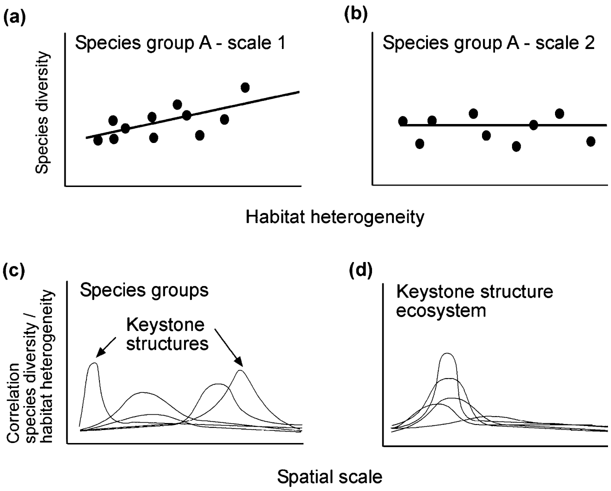

Figure 2 (a, b) Correlation between habitat heterogeneity of the vegetation and species diversity of a species group for two spatial scales: scale 1 (a) shows a positive correlation, scale 2 (graph b) shows no significant trend. (c) Latter relationships for a given ecosystem for all spatial scales and taxonomic groups. If one moves from small to large spatial scales, taxonomic groups have varying operational scales where increase in habitat heterogeneity results in high species diversity. (d) A keystone structure ecosystem with a unimodal pattern. One keystone structure detectable on a specific spatial scale provides ecological conditions that are relevant for a large proportion of the species groups.

predation, foraging efficiency or reproduction requirements. The presence or quality of this specific structure may then determine species diversity of the respective group. Interestingly, some studies showed that species diversity of even different groups may be facilitated simultaneously by the same structural element of the vegetation. For example for savannas, Milton & Dean (1995) reported that sites with large, solitary trees where characterized by a higher diversity of birds, mammals and plants, as opposed to sites where they were lacking or where population structure was different (Table 1). Therefore, the 'green salad' principle may not be generally true, despite its appealing simplicity.

THE 'KEYSTONE STRUCTURE CONCEPT'

Our literature survey indicated that measuring structural variables at specific spatial scales is critically important for the habitat heterogeneity–species diversity relationship. Most patterns are specific for the habitat type, the taxonomic group and the spatial scale of the study. This scale-dependence is caused by the species operational scales as defined by their home ranges, dispersal abilities and other habitat-specific spatial processes. The type of correlation between species diversity and habitat heterogeneity will vary according to the species group and the spatial scale where habitat heterogeneity is measured. In other words, each species group depends on a specific structural aspect of the vegetation which presence or quality can be detected on a certain spatial scale. For example, if the spatial scale is too large even a high value of habitat heterogeneity measured for a certain area will not indicate the quality or presence of a structural aspect occurring on a smaller scale (e.g. deadwood). As a consequence, species groups show distinct peaks of high habitat heterogeneity effects at specific spatial scales (Fig. 2c). We infer that these peaks indicate a 'keystone structure' of the vegetation.

In this context, we define a 'keystone structure' as a distinct spatial structure providing resources, shelter or 'goods and services' crucial for other species. A 'keystone structure' thus should not be confounded with the concept of 'keystone species' (see Paine, 1969; Mills *et al.*, 1993). For example, dead wood in mixed beech-spruce forests may be a keystone structure, as the removal of this structure (through e.g. forest management) would significantly reduce saproxylic insect diversity (see Schiegg, 2000). In addition, 'keystone structure' should be clearly distinguished from the term 'keystone habitat', as the meaning of habitat is usually associated with a broad vegetation type (e.g. Davidar *et al.*, 2001).

A keystone structure may not only affect a single species group: our literature survey revealed a few studies showing a positive habitat heterogeneity/diversity–species diversity relationship for multiple species groups on one spatial scale (e.g. Milton & Dean, 1995; Dean *et al.*, 1999). Here, an ecosystem may be dominated by a single keystone structure, which homogenizes the operational scales and determines species diversity of several species groups (Fig. 2d). In other words, several species groups may depend on one important structural aspect, which quality may be detected on a certain spatial scale. We suggest that biological diversity in these 'keystone structure ecosystems' may be more vulnerable than in multi-structured systems, as reduction in quality or the loss of this structure implicit severe consequences for a high proportion of taxonomic groups. To emphasize our hypothesis, we will present South African savannas as an example of a keystone structure ecosystem and temporary wetlands in agricultural fields as an example of a keystone structure relevant for one species group. Subsequently, we will discuss applications of this concept.

Example of a 'keystone structure': temporary wetlands in agricultural fields

The agricultural landscape of north-east Germany is dominated by large-size conventional fields. Temporary wetlands are 'ephemeral puddles', which occur in conventionally ploughed hollows in these fields after heavy precipitation in winter or spring. Due to these flooding events the vegetation differs substantially from other parts of the fields. The physical structure varies between tall and dense vegetation dominated either by forbs (e.g. *Matricaria maritima* ssp. *inodora*, *Bidens tripartita*) or by grasses (*Elytrigia repens*) and sparsely vegetated dwarf-rush communities (*Peplis portula*, *Juncus tenagaeia*). The carabid beetle diversity of the temporary wetlands is strongly correlated with the within-habitat heterogeneity of the vegetation structures that constitute a continuous structural gradient (Brose, 2003b). On a larger spatial scale of the entire fields, some of these temporary wetlands are keystone structures that determine species diversity, which is shown by an example of one agricultural field with three temporary wetlands (Fig. 3). The keystone structure characteristic is indicated by abrupt discontinuities in the species–accumulation curves when a sampling transect enters the temporary wetland. This increase in

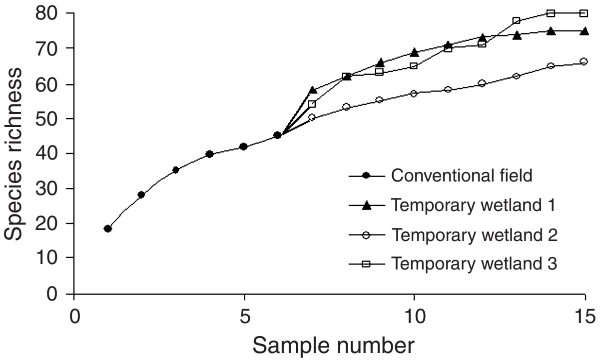

Figure 3 Temporary wetlands as keystone structures for carabid beetles in a conventional field – indicated by discontinuities in species–accumulation curves. We combined data from six traps that were randomly placed on the dry (conventional) part of the field with transect data from three temporary wetlands within the same field. The data points for the dry part show mean species richness values of 10 replications with randomized sampling order. The data points from the temporary wetlands represent pitfall transects from the field edges to the centres of the wetlands.

species diversity is not only caused by the presence of some obligate wetland species, but also by an increase in the number of rare field species that depend on specific vegetation structures (Brose, 2003b). The discontinuous species–accumulation curves qualify the first and third temporary wetland in Fig. 3 as keystone structures within this field, whereas the transect of the second temporary wetland merely seems to continue the accumulation of the field community. This habitat heterogeneity effect is scale-specific as correlations between carabid beetle diversity and the density of temporary wetlands or any other measurement of habitat heterogeneity at a landscape scale of 10 km^2 are not significant (Brose, 2003a). Together, these results qualify the temporary wetlands as keystone structures for carabid beetles in agricultural fields.

Example of a 'keystone structure ecosystem': South African savanna

Whereas temporary wetlands represent a keystone structure relevant for one specific species group, trees in arid and semi-arid savannas of southern Africa provide an example of a keystone structure ecosystem. Here, one predominant vegetation structure creates structural diversity essential for a wide array of species groups (see Fig. 4). Large solitary trees, scattered in a grassy matrix are focal points for animal activity because they supply nest sites, shade and scarce food resources (Barnes *et al.*, 1997; Dean *et al.*, 1999). They provide, e.g. shade for ungulates resting in the subcanopy of adult trees (Milton & Dean, 1995), nests for arboreal rodents (Eccard & Meyer, 2001), perches and nesting sites for raptors, owls and vultures (MacLean, 1970), or nest sites for different bird species in the crowns of the trees (Milton & Dean, 1995). Faeces, fallen nest material and carcass remains left below trees elevate levels of nutrients available to plants in the otherwise poor soil (Dean *et al.*, 1999). Some of the dominant woody plants that provide these 'goods and services' are *Acacia haematoxylon*, *Boscia albitrunca* and *Acacia erioloba* in arid savanna and the latter co-occurring with *Terminalia sericea* and *Peltophorum africanum* under more mesic conditions (Milton & Dean, 1995). It is noticeable that positive effects on species diversity have been reported for multiple tree species. Furthermore, these effects are mainly mediated by the architectural structure of large trees but not thickets or saplings. As this does not indicate a species effect *per se*, we believe that our keystone structure concept describes this system more adequately than a previously used keystone species concept (Milton & Dean, 1995).

Applications of the 'keystone structure concept'

With the aid of the keystone structure concept we are able to abandon the discussion of 'keystone vs. non-keystone species' (see Hurlbert, 1997) and focus on spatial structures that are provided by specific species: for ecosystem function and species diversity a given structure itself is important, independent of whether it is made up of one or several ecologically similar species. Then, the presence or quality of structure-based variables may function as biodiversity indicators (Lindenmayer *et al.*, 2000). In terms of biodiversity management this means that conservation of a keystone structure will maintain a high level of biodiversity whereas its removal will most likely lead to a breakdown in species diversity.

The two examples of keystone structures given here show several similarities. First, they contain a keystone element that increases species diversity by its presence. Secondly, the remaining ecosystems have a comparatively homogeneous vegetation structure. Using these characteristics it appears reasonable that the diversity of many similar ecosystems might be influenced by keystone structures. For instance, gaps in forests (e.g. Belsky & Canham, 1994) are likely to be a further example of keystone structures important for animal species diversity. As indicated by our temporary wetland example, keystone structures may be detected by abrupt discontinuities in the species–accumulation curves when sampling transects enter the structure.

In both ecological systems described above, the keystone elements are seriously affected by changes in anthropogenic

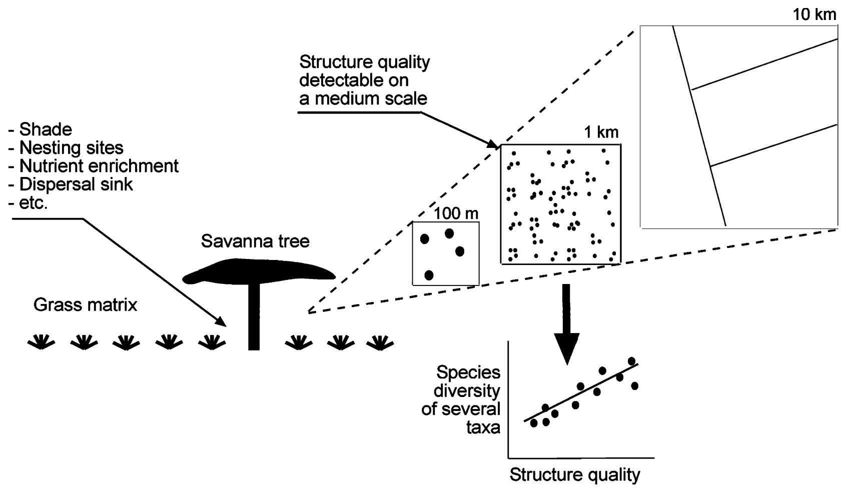

Figure 4 Tree savannas are a typical keystone structure ecosystem. A wide array of species groups (e.g. arthropods, birds or mammals) depend on trees as a food resource, shelter or nesting site. Consequently, overall species diversity is strongly linked to the quality of this structure. The quality, e.g. the proportion of large, solitary trees is detectable on a medium spatial scale: if the scale is too small distinction between degraded savanna sites and intact savanna with high structural diversity is difficult to quantify, if the scale is too large, large-scale landscape components such as land-use patterns may yield biased results.

land use. In many areas of southern Africa, the typical vegetation structure of the savanna has been altered by shrub encroachment (i.e. thickening of shrub cover due to overgrazing and fire reduction) (e.g. Roques *et al.*, 2001) and wood harvesting of large trees (e.g. Carr, 1974; Anderson & Anderson, 2001). Such changes in the density and demographic distribution of keystone elements should be prevented in order to maintain biological diversity. As temporary wetlands reduce the agricultural crop yield, they were drained in many cases, and consequently, disappeared from many agricultural landscapes. The keystone structure concept, however, offers an opportunity for the integration of biodiversity conservation in conventional land use. For instance, protecting the temporary wetlands as segregated nature conservancy elements in otherwise intensively used fields stabilized species diversity of these ecosystems at a high level while having a minimized impact on the agricultural land use (Berger *et al.*, 2003). Similar approaches of concentrating conservation efforts on keystone elements may be applied to other ecosystems with important keystone structures.

CONCLUSIONS AND FUTURE PERSPECTIVES

Although much research has been carried out in the field of habitat heterogeneity and species diversity patterns, empirical support is almost restricted to studies of vertebrate communities and habitats under anthropogenic influence. In addition, the measurement of habitat heterogeneity is very inconsistent making across-study comparisons difficult. For example, across-study comparison may include the relative effect of habitat heterogeneity between species groups (and thus spatial scales). The use of the measuring framework developed here will enable researchers to embed their studies in a larger perspective.

Furthermore, there is a significant lack of studies that consider multiple spatial scales and species groups within one ecosystem. This approach, however, is particularly important, as it enables detection of keystone structures that are crucial for maintaining species diversity. Examples from temporary wetlands in agricultural fields and solitary trees in South African savannas have demonstrated that keystone structures may simplify biodiversity conservation by protecting a wide array of species and functional mechanisms at the same time. However, until now empirical evidence is scarce. Therefore, we call for studies testing the keystone structure concept as it may have profound implications for nature conservation and biodiversity management.

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