

## Habitat patchiness and plant species richness

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### Abstract

The pattern of woody species richness decline with a decrease in woody vegetation cover was studied within a tallgrass prairie. The decline in species richness is highly non-linear, with a well-defined threshold below which species richness collapses. This relationship can be understood after considering information on how landscape structure changes with woody vegetation cover, and how species richness is related to landscape structure.

### Keywords

Biodiversity, habitat heterogeneity, habitat loss, patchiness, species richness.

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### INTRODUCTION

Understanding the mechanisms relating species richness variation to habitat heterogeneity is an important issue in ecology and conservation biology. Continuous areas of habitat have been progressively transformed into a patchy mosaic of isolated “islands” of available habitat as a result of human alterations (Holt *et al.* 1995; Hanski 1999). Despite the ubiquity of these highly fragmented habitats and their implications for biodiversity, a lack of knowledge still exists on how community diversity varies from sites within large, contiguous habitat areas to those within smaller, fragmented areas.

Recent theoretical work has shown that the decline of species richness with habitat loss is a non-linear process, with species extinctions becoming more and more frequent as habitat continues to disappear (Tilman *et al.* 1994; Stone 1995). However, these studies did not use spatially explicit models, making it difficult to infer relationships between spatial patterns of habitat arrangement and species richness.

In this letter, we explore data on woody vegetation patchiness to address two questions. First, what is the rate of species richness decline as woody vegetation cover decreases? Second, which landscape parameters are more related to the observed pattern of species reduction?

### MATERIALS AND METHODS

We analysed data on a detailed sampling of woody species distribution carried out in the southern part of Konza Prairie Research Natural Area (KPRNA). A total of 33 woody plant species were found in the sampled area. The data were obtained by J. M. Briggs and colleagues (Gibson 1988; Briggs & Gibson 1992), and are stored in the PWV01–DATA–1986 file of the KONZA–LTER Database (<http://www.konza.ksu.edu>). The sampling involved walking the area in parallel lines, approximately 15–20 m apart, to note the location, approximate diameter and shape of woody plant patches, as well as the height of the trees. These data were marked on a Mylar overlay placed on a large-scale aerial photograph (see Gibson 1988 and Briggs & Gibson 1992 for details). We rearranged the data into 164 maps of 160 m × 160 m, and sampled them at two scales: one that considered a quadrat of 80 m × 80 m per map, and the other entire maps. We obtained identical results at both scales; for brevity, we present here only the results of the small quadrats.

For each quadrat, we estimated woody species richness ( $S$ ), and four variables describing aspects of woody vegetation spatial structure, namely the number of patches, largest patch size, mean patch size and patch size heterogeneity, that is, the coefficient of variation of patch size. Patch sizes were estimated by counting the number of 0.5 m × 0.5 m cells covered by each patch. We also

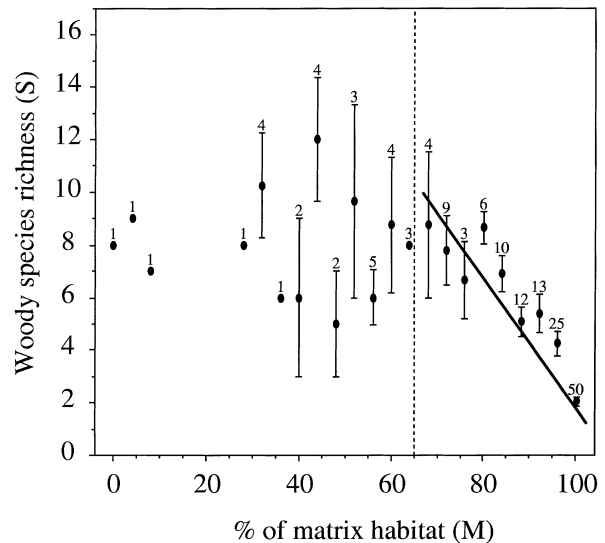
estimated the percentage of quadrat area without woody vegetation (prairie), a variable we called the percentage of matrix habitat ( $M$ ). This variable was used instead of woody vegetation cover (its reciprocal) to allow direct comparisons with studies dealing with habitat loss. Although deforestation is not currently important in the study area (it occurred in ancient times, probably favoured by Indian-induced fires and grazing by native ungulates; Kucera 1960; Bragg & Hulbert 1976; Abrams 1986; Knight *et al.* 1994), our results may be relevant to studies of habitat loss.

The variable mean patch size was logarithmically transformed before analysis to achieve homoscedasticity of its variance. The Pearson correlation, partial correlation and split-line regression methods were used. In the latter case, we first visually examined bivariate plots to find possible shifts in the relationships. Provided that a shift was apparent, we used split-line regression to establish the approximate threshold value of the explanatory variable under analysis marking the change of the response variable. Three breakpoint split-line regression routines were compared: Quasi-Newton, Simplex and Jooke-Jeeves (see StatSoft Inc. 1995). Once the breakpoint value had been established for a particular case, the data were divided into two groups: one including the quadrats with values below the breakpoint, and the other including the rest of the quadrats. The Pearson correlations between the variables being analysed for each group of data were then calculated.

## RESULTS

Woody species richness is plotted in Fig. 1 as a function of the percentage of matrix habitat. As observed, the relationship is highly non-linear with a well-defined threshold (split-line regression: breakpoint  $M = 65\%$ , variance explained = 81.4%). Species richness does not vary with matrix habitat below this critical point ( $r = -0.14$ ,  $N = 34$ ,  $P = 0.445$ ), but decays quickly beyond it ( $r = -0.73$ ,  $N = 130$ ,  $P \ll 0.0001$ ).

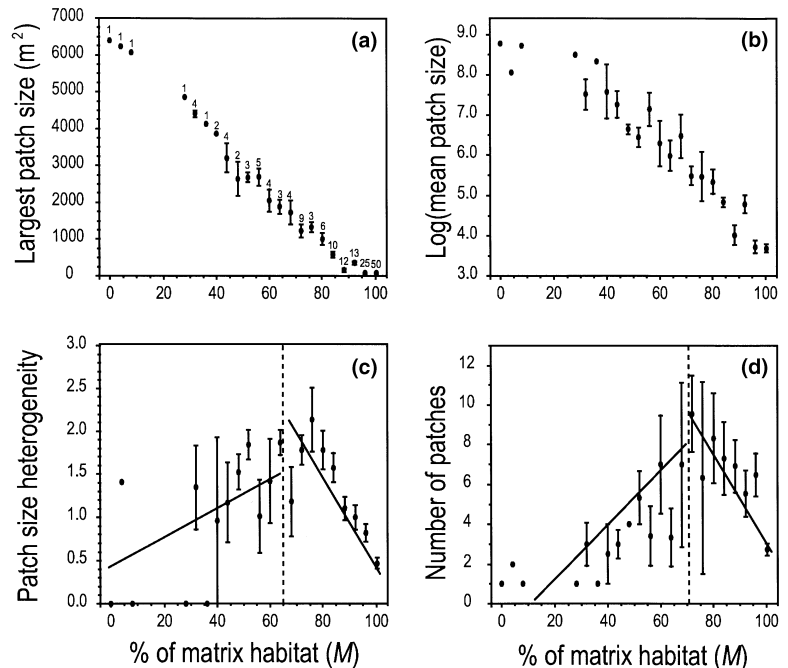
Which landscape variables are more related to this decay in species richness? Null models in landscape ecology have shown that, as the fraction of habitat is reduced, the number of patches, the size of the largest patch and other landscape variables change in a non-linear way (Gardner *et al.* 1987; Turner *et al.* 1989; Gustafson & Parker 1992; Bascompte & Solé 1996; Pearson & Gardner 1997). These relationships can be observed in Fig. 2 for the data of this study. The size of the largest patch, as well as the mean patch size, significantly decreases as the percentage of the matrix habitat increases ( $r = -0.97$ ,  $P \ll 0.0001$  and  $r = -0.85$ ,  $P \ll 0.0001$ , respectively). In contrast, patch size heterogeneity and the number of patches show a unimodal variation with matrix habitat: they first increase until the matrix habitat reaches a critical value ( $r = 0.32$ ,  $N = 34$ ,



**Figure 1** Woody species richness ( $S$ ) plotted as a function of the percentage of matrix habitat ( $M$ ). The broken line indicates the critical value of  $M$  (65%) beyond which species richness starts to decrease. This critical point was obtained with split-line regression routines (see text). The line fitted to the data on the right of the critical point was obtained with linear regression. There is no significant relationship between  $S$  and  $M$  to the left of this point ( $P = 0.45$ ). For representation purposes, the data were divided into 26 categories of percentage of matrix habitat (namely 0, >0–4, >4–8, >8–12, ..., >96–100). The average species richness values ( $\pm 1$  SE) in each category are presented. Numbers at the top of the error bars are the numbers of quadrats included in each category.

$P = 0.06$  and  $r = 0.52$ ,  $N = 43$ ,  $P = 0.0004$ , respectively) and then sharply decrease ( $r = -0.70$ ,  $N = 130$ ,  $P < 0.0001$  and  $r = -0.37$ ,  $N = 121$ ,  $P \ll 0.0001$ , respectively). Noticeably, the critical value of the matrix habitat is very similar for both patch size heterogeneity and the number of patches (split-line regression: breakpoint  $M = 65\%$ , variance explained = 81.8% and breakpoint  $M = 71\%$ , variance explained = 79.5%, respectively), and also coincides with that previously obtained for species richness (65%). Interestingly enough, the threshold observed in Fig. 2(d) is exactly as predicted from the theory of landscape ecology (e.g. Gustafson & Parker 1992; Bascompte & Solé 1996; Pearson & Gardner 1997).

The second step of our study involves the analysis of the relationships between woody species richness and the variables describing aspects of woody vegetation spatial structure. We wish to determine the effects of each of these variables on woody species richness after controlling for the effects of the others. Thus, we used partial correlation analysis with the number of patches, largest patch size and patch size heterogeneity as the explanatory variables and woody species richness as the response variable. We have not included the mean patch size in the analysis because it is highly correlated



**Figure 2** Largest patch size, mean patch size, patch size heterogeneity and number of patches plotted against the proportion of matrix habitat ( $M$ ). Critical points in the relationships of patch size heterogeneity and number of patches with matrix habitat (split-line regression results) are indicated with broken lines. In each case, the lines fitted to the data to the left and to the right of this point were obtained with linear regression. Conventions as in Fig. 1.

**Table 1** Pearson and partial correlation coefficients of woody species richness with three variables describing aspects of woody vegetation spatial structure.

	Woody species richness	
	Pearson correlation ( $N = 164$ )	Partial correlation ( $N = 164$ )
Largest patch size	0.48 (<0.0001)	0.57 (<0.0001)
Patch size heterogeneity	0.57 (<0.0001)	0.39 (<0.0001)
Number of patches	0.42 (<0.0001)	0.43 (<0.0001)

Each partial correlation index is calculated after controlling for the effects of the other listed variables. Mean patch size is not included in this analysis because it is highly correlated with the largest patch size. Probabilities are given in parentheses.

with the size of the largest patch ( $r = 0.86$ ,  $P \ll 0.0001$ ). We find positive independent effects of all of these variables on species richness (Table 1). With this information, we can understand the threshold-like behaviour in species richness decline with matrix habitat shown in Fig. 1.

## DISCUSSION

We have shown that the species richness decline with an increase in matrix habitat cover is not a simple linear process. As the fraction of matrix habitat increases, the size of the largest patch decreases, which has a negative influence on species richness. On the other hand, increases in the number and heterogeneity of patches have a positive

influence on species richness. Thus, for low to intermediate values of matrix habitat, there is a balance between opposing trends, and species richness does not change. However, above a critical amount of increase in matrix habitat, both the number of patches and their heterogeneity start to decline. Now all the landscape variables change in the same direction and species richness decreases very rapidly. This explains the threshold in species decline.

Two points should be emphasized here. First, one has to bear in mind that the location of the threshold is likely to vary among communities. This is due to the fact that extinction processes will be affected by the biology of the species. Species with long dispersal distances, for example, would perceive their habitat as fragmented for higher values of matrix habitat than species with short dispersal distances. Second, all our results are based on correlations, which do not provide information on the mechanisms leading to the observed patterns of species loss. Thus, this approach should be complemented by other sorts of approximations, such as theoretical models, which can give an insight into the relationship between processes and patterns.

The existence of critical habitat destruction thresholds for accelerated species richness loss has been inferred from relationships emerging in species–area curves (Harris & Silva-Lopez 1992). However, in patchy environments, both the amount of habitat and its spatial structure may be relevant for species richness (see Saunders *et al.* 1991). Our results suggest that patterns of landscape structure have a strong explanatory power on the observed loss of species richness. This supports the claim that landscape patterns are

important in understanding ecological processes (Turner 1989).

Previous studies have looked at the relationship between species richness and specific properties of the landscape structure, such as isolation of fragments (Kruess & Tscharntke 1994) or patch size (Holt *et al.* 1995). Our synthetic approach has considered the simultaneous influence of different factors, which has provided us with a good understanding of the pattern of species richness variation with habitat abundance. The number of habitats becoming fragmented is rising rapidly at present, and our results may be useful for the management of many natural areas.

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## BIOSKETCH

Jordi Bascompte works on the spatial dimension of population and community dynamics.

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