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Relationships between landscape patterns and species richness of trees, shrubs and vines in a tropical forest

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Abstract

The present study aims to identify and characterize the relationships among landscape structure and plant diversity in a tropical landscape forest in Quintana Roo, Mexico. Total species richness as well as that of trees, shrubs and vines species were identified from 141 sampling quadrats (16,543 individuals sampled). Based on vegetation classes obtained from multi-spectral satellite image classification, I constructed plant diversity maps of the landscape under study using stratified kriging. I calculated the mean number of species in individual patches as the average values of kriging estimates inside each patch. I then explored the relationships between landscape pattern metrics and the species richness of trees, shrubs and vines, as well as all groups combined using regression analysis. I employed Akaike Information Criterion (AIC) to select a set of candidate models. Based on akaike weights, I calculated model-averaged parameters. Results show that plant diversity of the patches depends on both the quality of the surrounding habitats and the proximity of surrounding patches (i.e., patch isolation).

Introduction

Habitat fragmentation occurs when a continuous habitat is subdivided as a result of either human activities (e.g., agricultural clearing, timber harvest) or natural events such as fires and hurricanes (Saunders et al. 1991; Dale and Pearson 1997). The degree of fragmentation that characterizes a landscape and the connectedness of ecosystem components may be two of the main determinants of biodiversity (Mazerolle and Villard 1999). For example, a habitat may be too fragmented for a particular species or an entire community to survive or to remain in equilibrium (Forman 1995; Frohn

1998). Habitat loss and the resulting fragmentation are two of the major factors contributing to the decline of several biological populations. Some species or populations at risk are dependent on the existence and extent of specific habitats, and the loss of these habitats can directly or indirectly impact such species (Dale et al. 1999).

Forests of the Yucatan peninsula, Mexico have been altered through time not only by natural disturbances such as hurricanes and forest fires (Whigham et al. 1991; Garcia et al. 1996) but also by human interventions, including subsistence slash and burn agriculture by indigenous Mayan farmers (Hernandez-Xolocotzi et al. 1995) and

conversion of forest to grasslands supporting livestock (Edwards 1986). Depending on their intensity, these disturbances produce a mosaic of secondary forest in different stages of succession or result in small forest remnants embedded in a matrix of agriculture and grasslands. The degree to which this fragmentation alters the biodiversity of the region is unknown.

The spatial heterogeneity of landscape mosaics can be studied in terms of patches and their characteristics through landscape metrics (O'Neill et al. 1988; Turner et al. 1991; Gustafson 1998; McGarigal et al. 2002). With the use of these metrics, the degree of fragmentation in a region can be compared between areas (Tinker et al. 1998). Landscape patterns can also be linked quantitatively with ecological and environmental processes, through the use of such metrics (Krummel et al. 1987; McGarigal and Marks 1995). Evidence found over the past years in the field of landscape ecology, suggests that spatial patterns of patches and patch characteristics may be good predictors of the presence of species (Miller et al. 1997; Mazerolle and Villard 1999; Atauri and de Lucio 2001). Therefore, patch characteristics including patch size, patch density, perimeter–area ratio, patch shape, and inter-patch distance may be also used to predict biodiversity.

There are two different groups of species in a tropical forest that play a role in the stages of succession (Swaine and Whitmore 1988): pioneer and non-pioneer species. Pioneer species commonly produces small well-dispersed seeds that increase the probability of reaching newly formed patches. These shade intolerant species also grow rapidly, which increases their capacity to occupy a patch, especially in open areas (Brokaw 1987; Whitmore 1989). However, the greatest likelihood of regeneration of this group of species occurs in the neighborhood of maturing patches due to seeds and seedlings being released from adjacent forested areas (Schupp et al. 1989). In contrast, non-pioneer species are characterized by having large animal-dispersed seeds that will germinate and get established almost entirely beneath the forest canopy, due to few seeds reaching a new-formed patch; most of the seeds that find such a patch are eaten by mammals (Schupp et al. 1989; Alvarez-Buylla and Martinez-Ramos 1992). These species require an open canopy for growth and reproduction (Denslow 1987). In other words,

non-pioneer species need a certain amount of canopy opening, such as that created at the edge of the patches (Howe 1990). Consequently, the area, shape, perimeter, distance and similarity or contrast of adjacent patches may play all an important role in generating within-patch diversity.

The main goal of this study was to examine the relationships between landscape patterns and plant diversity. This was done with a view of predicting plant species richness from landscape features easily observable/measurable from satellite images or maps. I assessed plant diversity and its response to landscape fragmentation, by relating landscape-pattern metrics (i.e., perimeter, shape, perimeter–area ratio, proximity, distance, similarity, and contrast) with estimates of plant diversity (number of species) using remote sensing and GIS techniques. The results of this study are important for understanding plant habitat associations, which can be used to assess plant diversity in the area as well as to find strategies for helping in the design of conservation plans.

Methods

Study area and plant diversity data

The study was conducted in the southeastern portion of the Yucatan peninsula, Mexico over an area of 64 km^2 (18°53′54″–18°58′14″ N latitude and 88°10′04″–88°14′37″ W longitude). Most of the area is covered with tropical sub-deciduous forests in different stages of succession characterized by age. This forest has 2 or 3 canopy levels consisting of trees, shrubs and vines 3–25 m high. Indigenous local farmers identified the stages of succession with Mayan names. 'Kanah kax' refers to a forest 20–60 years old; 'kelenche' is used for vegetation between 11 and 19 years of age; 'juche' is used for plant species between 4 and 10 years of age and 'saakab' with plants species of 3 years or less. There are also secondary plant associations in the area, including 'savanna', which have few sparse tree species between 3 and 10 m of height and 'akalche' (in local Mayan language) consisting of a shrub stratum. Both of these plant associations are found in flooded areas or areas with intermittent flooding (Cabrera et al. 1982).
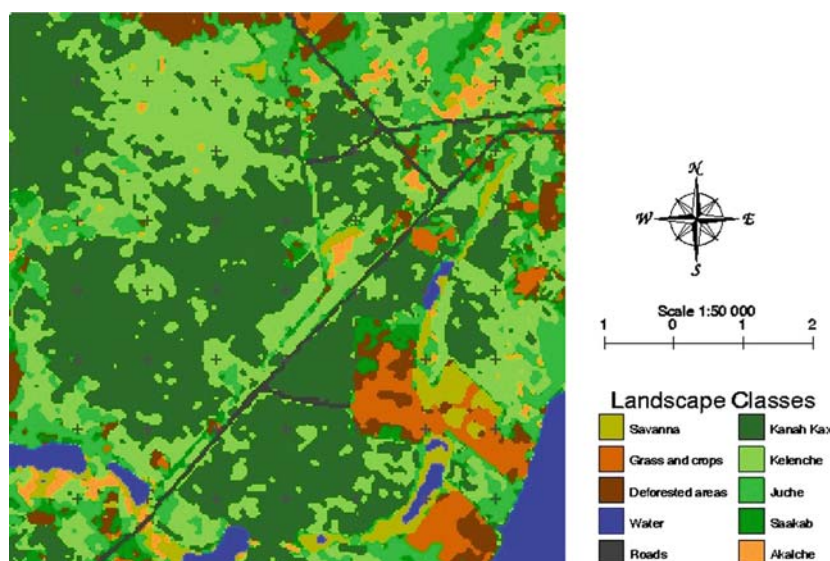
Figure 1. Land cover map of the study area obtained from a supervised classification.

Two plant surveys were conducted during two periods, the first between June and July of 2000 and the second in July and August of 2001. The surveys were based on a stratified random sampling design with a total of 141 sampling sites, which were located on the ground using a GPS unit in the six vegetation types. Each sampling site consisted of two quadrats. One 10×10 m quadrat was used to sample trees and vines higher than 3 m while a 5×5 m quadrat was used for sampling all shrubs taller than 1 m. Of the total number of quadrats 42 fell within the class 'kanah kak', 25 in 'kelenche', 20 in 'juche', 20 in 'saakab', 17 in 'ak-alche' and 17 in the 'savanna' vegetation class. A total of 16,543 sampled individuals were identified to species. In every quadrat, I computed total species richness and the number of species of trees, shrubs and vines (Hernandez-Stefanoni 2004).

Landscape mapping

The landscape mosaic was composed of four successional classes of forest; two secondary associations, deforested areas, grasslands and cropping areas. These land cover classes were designated as patch types. The land cover map was obtained from Landsat 7 Thematic Mapper (TM) imagery acquired on April 2000, after applying a supervised classification on bands 5 (short-wave infrared:

1.55–1.75 nm), 4 (near infrared: 0.76–0.90 nm) and 3 (red: 0.63–0.69 nm). Each band was geo-referenced and radiometrically corrected. The 'Maximum Likelihood Algorithm' implemented by the image analysis software ER Mapper[TM] 6.1 (Earth Resource Mapping Ltd 1998) was used to classify the image data. Based on the sampling quadrats, the classification method yielded an overall accuracy of 82.3%. The accuracy of the land cover classes was higher than 82.4% in most cases, with the exception of the 'kelenche' class, which had an accuracy of 76.0%. The final land cover map is shown in Figure 1. Details of the classification and the accuracy assessment procedures of the resulting land cover map are found in Hernandez-Stefanoni (2004) and Hernandez-Stefanoni and Ponce-Hernandez (2004).

Calculation of landscape-pattern metrics

The ER Mapper[TM] raster file of the landscape mosaic was exported to the GIS IDRISI (Eastman 1999), in order to calculate the landscape-pattern metrics using the program software FRAGSTATS 3.0 (McGarigal et al. 2002). The six vegetation types identified during the classification and the remaining of the land cover classes grouped as 'background' were considered for the calculations. The examination of the relationships between

Table 1. Description of metrics used to quantify landscape spatial patterns of individual patches.

Type of metric/Code	Metric	Description
Area/Edge		
Area	Patch area	The area of the patch.
Perim	Patch perimeter	The perimeter of the patch, including any internal holes in the patch.
Shape		
Para	Perimeter–area ratio	Measure of shape complexity, calculated as the ratio of the patch perimeter to area.
Shape	Shape index	Measure of shape complexity of a patch compared to a standard shape (square) of the same size.
Frac	Fractal dimention index	Measure of shape complexity, calculated as 2 times the logarithm of patch perimeter divided by the logarithm of patch area.
Isolation/Proximity		
Prox	Proximity index	The size and proximity of all patches whose edges are within a specified search radius of the focal patch.
Simi	Similarity index	The size and proximity of all patches, regardless of class, whose edges are within a specified search radius of the focal patch.
Enn	Euclidean nearest neighbor distance	The distance to the nearest neighboring patch of the same type, based on shortest edge-to-edge distance.
Contrast		
Econ	Edge contrast index	Measures of the degree of contrast between a patch and its immediate neighborhood.

See McGarigal et al. (2002) for a detailed description of each index.

Table 2. Values used to give a similarity weight between the different vegetation types.

	Kanah Kax	Kelenche	Juche	Saakab	Akalche	Savanna
Kanah Kax	1.00					
Kelenche	0.73	1.00				
Juche	0.60	0.77	1.00			
Saakab	0.39	0.47	0.52	1.00		
Akalche	0.08	0.09	0.10	0.11	1.00	
Savanna	0.01	0.02	0.02	0.02	0.08	1.00

landscape metrics and plant diversity was conducted for individual patches or fragments. The metrics of these patches were obtained from the classified image (Figure 1).

The individual patches were classified as clusters of vertical, horizontal or diagonal pixels as in other studies (Gustafson et al. 1994), producing a total 1181 patches (i.e., occurrences) of the six vegetation types. Considering the practical non-significance of small pixel clusters, all the fragments that have less than 0.45 ha (5 pixels in the image) were eliminated from the analysis, ending with 577 cases. The indices calculated for those patches are listed in Table 1, which correspond to 9 of the 10 metrics available in FRAGSTATS 3.0 at patch level. The selected measurements are factors of landscape metrics that might explain the plant diversity in the tropical forests of the area.

In order to calculate the proximity and similarity indices, a search radius of 10 pixels (300 m) was considered. This radius is arbitrary but coincides with empirical evidence gathered in the field for the average expected size of a patch. In addition to the radius, the similarity index requires for its calculations some similarity weights for each pair of patch types. In this case the mean values of 4 estimates of beta diversity between each pair of vegetation types were used as those weights (Table 2). These beta diversity estimates are similarity measures and are described by Magurran (1988). They were calculated using cumulative values of the sampling quadrats for each vegetation class. Two of these measures use presence and absence of species (i.e., Jaccard and Sorenson) while the other two require abundance data for their calculations (i.e., Sorenson-abundance and Morisita-Horn).

Finally, the weighted edge contrast between vegetation classes demanded to compute edge contrast index was calculated as the inverse values of the similarity weights.

The selection of the landscape metrics was made on the basis of the frequency of their use in the landscape ecology literature (Mazerolle and Villard 1999), and their importance as metrics influencing plant species composition. On these bases, four groups of metrics were selected to analyze the predictive capacity of plant diversity by landscape-patterns. Those metrics were: area/edge, shape, isolation/proximity and contrast (Table 1).

Estimation of number of species

To estimate the species richness (i.e., total, trees, shrubs and vines) for each of the 577 individual patches identified with FRAGSTATS, I used average values of kriging estimates within each patch. The objective of this technique is to create a continuous surface of interpolated values, taking advantage of the spatial structure of the phenomena (Isaaks and Srivastava 1989; Webster and Oliver 2001). Thus, I used the existing species richness data collected from the field and interpolated the data to unvisited sites of the study area, obtaining a map of plant diversity across the landscape. Here, the number of species was the average value in an area of 100 m^2. There were sharp changes in plant diversity between the six vegetation classes [i.e., total number of species ($F_{[5,140]} = 225.3$, $p < 0.00001$), number of tree-species ($F_{[5,140]} = 263.45$, $p < 0.00001$), number of shrub-species ($F_{[5,140]} = 21.89$, $p < 0.00001$) and number of vine-species ($F_{[5,140]} = 8.66$, $p < 0.00001$)], so kriging estimates where computed within each stratum to optimize the precision (Riemann Hershey 1996; Wallerman et al. 2002; Hernandez-Stefanoni 2004).

Because the number of samples was insufficient to fit reliable variograms in every vegetation type, data were pooled by grouping classes that made practical sense. Consequently, the six vegetation types were reclassified in three new classes: forest 1 (grouping kanah kax and kelenche), forest 2 (juche and saakab) and secondary associations (akalche and savanna). The semi-variogram models were fitted within each new class using the GS+ software (Robertson 2000).

Statistical analyses

As the primary objective of this paper is to find predictive models that best reflected the relationship between plant diversity and landscape metrics, a multiple regression analysis was performed. The dependent variables were mean number of species (total, trees, shrubs and vines) per unit area estimated at patch level. Such variables were formally tested for normality and homogeneity of variances. The explanatory variables were a group of landscape metrics (Table 1), which needed to be transformed with $1/x$, $\log10(x)$, $\log10(x+1)$ and $sqrt(x)$ as necessary to meet the assumptions of linearity (Tabachnick and Fidell 1996). The number of explanatory variables was reduced to 7, eliminating PERIM and FRAC because they had a correlation coefficient > 0.75 with other variables and they were less related to species richness.

I evaluated a set of 15 models considering all possible combinations of the four main groups of metrics (Table 1). The Akaike Information Criterion (AIC) was employed to select the best models. The AIC has its roots in Kullback–Leibler information and statistical maximum likelihood, which make possible to combine estimation and model selection under a single theoretical framework (Anderson et al. 2000; Anderson and Burnham 2002). This procedure is based on parsimony, a trade-off between model fit and the number of parameters in the model. The AIC values were calculated from the formula AIC $= -2 *(\log$ likelihood$) + 2K$, where K is the number of parameters. The models were ranked based on both delta AIC values (Δ_i) and a measure of the weight of evidence of being the best model or akaike weights (w_i) (Anderson et al. 2000; Johnson and Omland 2004). Then, a set of candidate models were selected using both an approximate cutoff of $\Delta_i = 4$, and those models having $w_i > 0.1$ (Burnham and Anderson 1998). Finally, I calculated model-averaged parameters and unconditional standard errors based on the akaike weights (Burnham and Anderson 1998; Johnson and Omland 2004).

The multiple regression analyses I conducted assume that the observations are independent (i.e., not auto-correlated). Deviations from this assumption can result in declaring significant effect when there are not (Legendre and Fortin 1989;

Table 3. Parameters and statistics of semi-variogram models fitted for number of species within each of the three vegetation classes.

Group of species / Vegetation type *	Model	Nugget variance	Total variance	Range	Relative structural variance (%)	r^2
Total						
Forest 1	Spherical	12.19	26.19	1836.0	53.5	0.97
Forest 2	Gaussian	33.50	67.31	1333.0	50.2	0.97
Secondary associations	Spherical	1.05	4.59	1334.0	77.1	0.97
Trees						
Forest 1	Spherical	6.12	14.13	1580.0	56.7	0.94
Forest 2	Spherical	14.20	49.39	1769.0	71.2	0.96
Secondary associations	Spherical	1.76	5.27	1871.0	66.6	0.84
Shrubs						
Forest 1	Spherical	0.48	2.09	2983.0	77.0	0.96
Forest 2	Spherical	1.56	3.82	1625.0	59.2	0.78
Secondary associations	Spherical	0.39	1.12	2515.0	65.0	0.97
Vines						
Forest 1	Spherical	1.10	3.68	870.0	70.0	0.74
Forest 2	Spherical	0.70	2.14	926.0	67.2	0.98
Secondary associations	Spherical	0.01	0.19	740.0	94.7	0.70

* Forest 1, kanah kax + kelenche; Forest 2, Juche + Saakab; Secondary associations, Akalche + Savanna.

Dale and Fortin 2002). I formally checked this assumption with Moran's I statistic (Legendre and Legendre 1998).

Results

Kriging estimates of number of species

The spatial variation depicted by the semi-variogram models revealed a spatial structure in the species richness of each group of species (total, trees, shrubs and vines) from every one of the three vegetation classes (Forest 1, forest 2 and secondary associations), as it is shown in Table 3. Spherical, and Gaussian models were found to fit well the experimental semi-variograms, and to explain the spatial autocorrelation present in the four groups of species, yielding r^2 ranging from 0.70 to 0.98. The structural variance, which determines the variance due to spatial dependence explained by the model and calculated as (total variance − nugget variance)/total variance*100, ranged from 50.2 to 94.1%. This result suggests that some of the models have a substantial unexplained variability of number of species and that this may vary over small distances. There was, however, a moderate fraction of variability attributable to the nugget variance in most of the models (Figure 2).

The range of influence showed values between 740.0 and 2983.0 m. This indicates that one would

reasonably expect that the number of species in places separated by distances as far as in between 0.74 and 2.9 km is still somewhat related. The derived contour maps of number of species (total, trees, shrubs and vines) obtained after kriging interpolation are presented in Figure 3. Details of the geostatistical analysis for estimating and mapping different diversity variables in the studied area are found in Hernandez-Stefanoni (2004).

Relating landscape-pattern metrics and species richness

Model selection using an information-theoretical approach showed that three or four models could predict species richness, depending on the group of species (Table 4). In the case of total number of species and that of trees and shrubs, the most plausible model includes metrics of area, isolation/proximity and contrast as explanatory variables (akaike weights = 0.54, 0.52 and 0.60, respectively). For the number of vine species, the model explained by isolation/proximity and contrast metrics had the highest akaike weight (0.42). However, in all cases other models had akaike weights greater than 0.1. Therefore, I applied model averaging to create a composed model for each group of species (Table 5).

Model-averaged results indicated statistically significant relationships between total number of
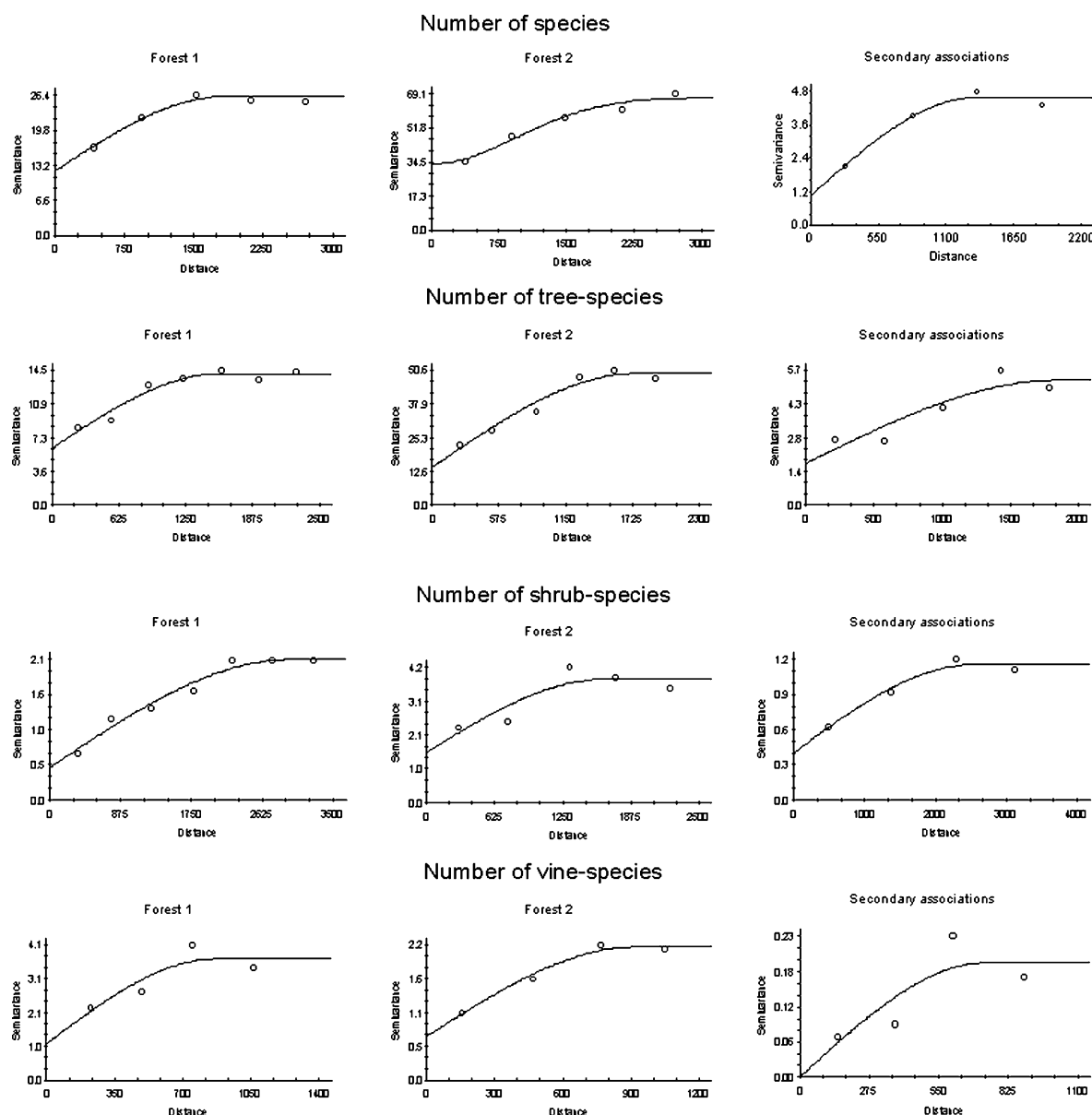
Figure 2. Experimental and model semivariograms of number of species (total, trees, shrubs and vines) for different vegetation classes.

species and proximity, similarity, nearest neighbor distance and edge contrast indices (Table 5). Considering the richness of trees, shrubs and vines separately, the results vary according to the group of species in question. The case of richness of trees and shrubs for instance, showed similar behavior to that observed by the total number of species. However, the number of species of vines is explained by three variables (PROX, SIMI and

ECON, Table 5). The species richness in all groups of species consistently respond negatively to edge contrast index (ECON), which means that the plant diversity increases as the perimeter of the focal patch decreases its contrast with other patches. This finding supports the intuitive notion of greater diversity in patches with smooth transitional and low contrasting edges. In addition, similarity, proximity and nearest neighbor distance
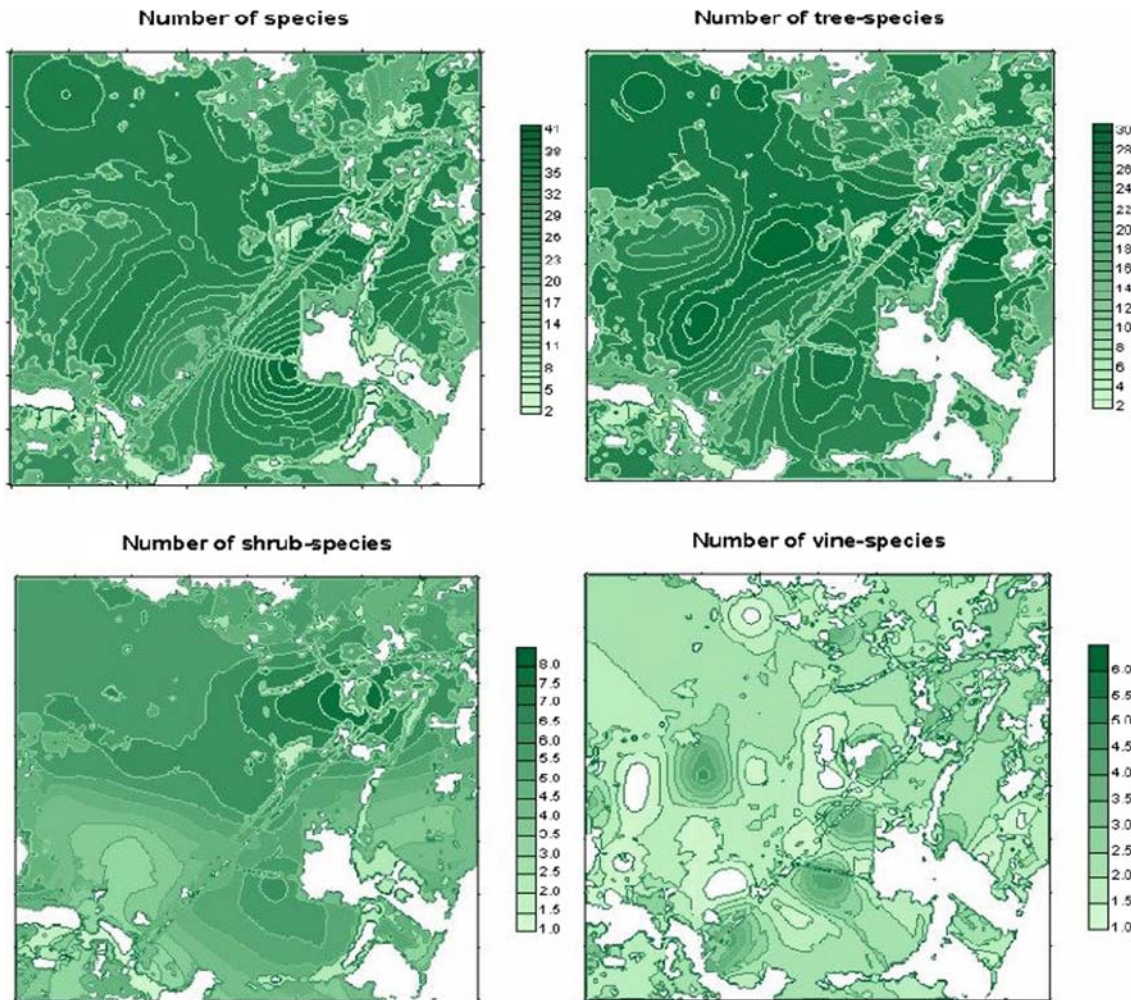
Figure 3. Contour maps of number of species (total, trees, shrubs and vines) created using stratified kriging.

indices responded positively to number of plant species.

Spatial autocorrelation test

The expected value of Moran's I statistic $= -1(n - 1)$, where n is the number of samples (Oden 1984). In this study, for the 577 individual patches an expected value for the absence of autocorrelation had a coefficient of -0.0017, the calculated values of autocorrelation for the total number of species was -0.0040, while the calculated values of autocorrelation for richness of trees, shrubs and vines were -0.0041, -0.0042 and -0.0041, respectively. To evaluate the significance of the Moran's coefficient, the z values of all plant diversity indices were computed. These values (-1.52, -1.54, -1.58 and -1.55) were lower than 1.96 and greater than -1.96, which means that the null hypothesis (i.e., Ho: spatial autocorrelation $= 0$) cannot be rejected at the 5% of significance level.

Additionally, the absence of spatial autocorrelation among the estimates of plant diversity indices within the individual patches can be appreciated at different separation distances in the correlograms calculated in GS+ software in Figure 4. These results indicated that spatial autocorrelation of number of species within individual patches is indeed absent and therefore, that the predictive multiple regression models computed using such data are statistically sound and valid.

Table 4. Model selection statistics for the analyses of effects of landscape patterns of individual patches on species richness.

Group of species / Model*	Number of parameters	AIC	Δ_i	w_i
Total				
Area, isolation/proximity, contrast	6	3765.1	0.00	0.54
Isolation/proximity, contrast	5	3766.8	1.72	0.23
Area, shape, isolation/proximity, contrast	8	3767.5	2.35	0.17
Trees				
Area, isolation/proximity, contrast	6	3607.4	0.00	0.52
Area, shape, isolation/proximity, contrast	8	3608.7	1.33	0.27
Isolation/proximity, contrast	5	3609.9	2.56	0.15
Shrubs				
Area, isolation/proximity, contrast	6	1678.2	0.00	0.60
Shape, isolation/proximity, contrast	7	1680.6	2.38	0.18
Area, shape, isolation/proximity, contrast	8	1681.6	3.38	0.11
Isolation/proximity, contrast	5	1681.8	3.58	0.10
Vines				
Isolation/proximity, contrast	5	1053.1	0.00	0.42
Shape, isolation/proximity, contrast	7	1054.1	1.07	0.25
Area, isolation/proximity, contrast	6	1054.2	1.16	0.24

* Only models with Akaike weights greater than 0.1 and with Δ_i smaller than 4 are shown.

Table 5. Model-averaged parameter estimates and (unconditional standard error) for predicting species richness from landscape patterns of individual patches.

Model terms	Total	Trees	Shrubs	Vines
Intercept	4.886 (3.25)	1.522 (1.99)	**2.596 (0.61)**	**1.444 (0.32)**
Area	0.708 (0.46)	0.885 (0.56)	1.586 (0.85)	0.008 (0.01)
Para	−0.001 (0.00)	−0.001 (0.00)	0.000 (0.00)	0.000 (0.00)
Shape	−0.319 (0.47)	−0.388 (0.62)	−0.026 (0.10)	−0.037 (0.05)
Prox	**2.930 (0.42)**	**2.858 (0.37)**	**0.299 (0.07)**	**0.108 (0.04)**
Simi	**4.614 (0.44)**	**3.969 (0.36)**	**0.660 (0.10)**	**0.258 (0.04)**
Enn	**6.312 (1.35)**	**5.941 (1.19)**	**0.688 (0.23)**	0.052 (0.12)
Econ	**−1.759 (0.20)**	**−1.251 (0.16)**	**−0.285 (0.03)**	**−0.137 (0.02)**

Parameter estimates in bold indicate that 95% confidence interval excludes 0.

Discussion

The main result shows a strong association between number of species and landscape metrics such as contrast and isolation. The degree of contrast between a fragment and its neighboring patches was one of the metric most strongly related to species richness. This result may explain the fact that resource availability of a patch is determined by the quality of the surrounding areas (Alvarez-Buylla and Garcia-Barros 1991). For example, Gomez-Pompa et al. (1972) found that non-pioneer species lack the means for long-distance seed dispersal and long-lasting seed banks that facilitate the re-colonization of deforested areas. Moreover, Alvarez-Buylla and Martinez-

Ramos (1992) found that some pioneer species (e.g., *Cecropia obtusifolia*) do not possess long-lasting seed bank as it was supposed to have. Instead, these species depend mostly on the constant influx of new seeds for regeneration. These observations suggest that most of the regeneration of the forest patches depends on the seeds available in adjacent areas.

Another example of resource availability created by the contrast between the focal patch and its neighbors is the intensity of light. Denslow (1987) indicated that seedling establishment and sapling growth of tropical rain forest trees and shrubs appear to be limited by the total incident radiation. Further, not only the center of a new patch and the oldest patches received different intensity
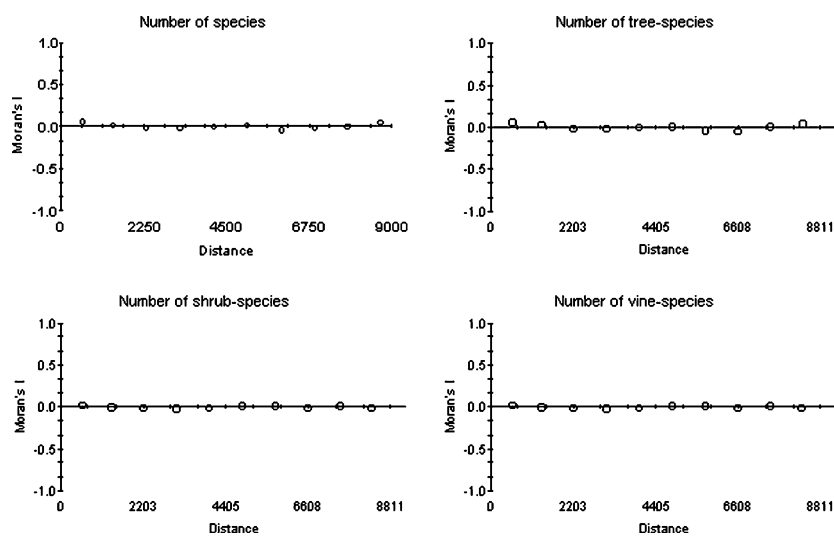
Figure 4. All-directional spatial correlograms using Moran's I Statistic, calculated from the centroid of 577 individual patches for mean estimates of number of species (total, trees, shrubs and vines).

of sunlight, but also the various light conditions created at the edges by the contrast between the focal patch and its neighbors. Therefore, the establishment and growth of some species will be favored or disfavored by the different incident light level, affecting the species composition within patches.

Plant species richness also depended strongly on patch similarity and patch proximity indices, as they appeared in all models. The type of disturbance created in the forest, which may favor habitat diversity, could explain this association. When a forest is cut in a 'slash and burn' agricultural pattern, in which cleared patches remain intermingled with forest patches (Hernandez-Xolocotzi 1985), the artificial cleared patch would be equivalent to large tree-fall gap (Alvarez-Buylla and Garcia-Barros 1991). However, when the forest is cut for land use conversion (e.g., to agriculture or to grassland areas), most of the cleared areas remain isolated from the undisturbed forest. These cleared areas are out of the normal dispersal range of species and received low seed depositions (Alvarez-Buylla and Garcia-Barros 1991).

A greater degree of contrast between a fragment and its neighbors reflects a landscape that is more fragmented, in the same way a greater distance between a patch and its neighbors suggest a patch that is more isolated. On the contrary, as the proximity and similarity indices increase their values, it is expected that configurations where

patches form clusters of similar fragments or patches with less contrast among them can be found. This indicates that the focal fragment is less isolated and the landscape is less fragmented (McGarigal et al. 2002). Therefore, the results of this study suggest that when a landscape is more fragmented and a patch is more isolated, it has a community with fewer species. This provides a reasonable match with the theoretical expectations. Similar results have been found in several other studies (Metzger 1997; Debinski and Holt 2000).

The results also concur with several other works (Turner et al. 1994; Holt et al. 1995; Fukamachi et al. 1996; Metzger 1997; Whitmore 1997; Haig et al. 1999) in finding a weak relationship between species richness and area of the fragment. Patch area was not always part of the best candidate models. In addition, area of the fragment had no significant relationship with species richness in model-averaged results. The surrounding vegetation, as well as the frequency and intensity of disturbances play a mayor role in determining the species composition within a patch (Martinez-Ramos et al. 1989; Turner et al. 1994). For example, Turner and Corlett (1996), pointed out that the fragments of forest between 0.5 and 10 ha in Manaus, Brazil were separated from large areas of continuous forest by very short distances (sometimes less than 300 m). Such distance allowed the development of secondary forest in

cleared areas and thus, the creation of a continuous canopy, linking the fragments to the entire forest.

The relationship between plant diversity and patch area could also be masked by the use of community level variables (i.e., number of species). Because each individual species has its own pattern of dispersal and is affected in a different way by the reduction of its habitat area (Bastin and Thomas 1999; Haig et al. 1999). The low association between patch area and number of species may be explained by life history of these tropical plants. The majority of tree species can survive beneath the forest canopy. However, most of these species are gap dependant during their lives (Hubbell and Foster 1986). This means, they can be established or reached maturity in the moderate light environments of the gap edges. Thus, the quality of surrounding patches is more important for their grow than patch area. Vines rely on large plants for support and grow (Putz 1984) and their establishment is expected in patches where they can find such support regardless the size of the fragment.

These results, however, should be considered with caution. As was indicated before, small disturbances distributed in the forest promote spatial variation of patches that create several physical environments for plants within a patch (Denslow 1987; Martinez-Ramos et al. 1988). This allows the increase of habitat diversity that may elevate species composition of a particular fragment (Honnay et al. 2003). However, large and more frequent disturbances increase the contrast of a patch and its neighbors, indicating a major degree of fragmentation that negatively impacts plant species diversity. This suggests the need for a certain threshold of the number and degree of disturbances that influences plant diversity (Honnay et al. 1999).

The design of conservation areas or maintenance of particular groups of species represents a difficult task due to several factors. First, as noted above, each individual species is affected in a different way by fragmentation (Bastin and Thomas 1999; Haig et al. 1999; McGarigal et al. 2002). Second, there is a continuum of patterns in the life history of the tropical forests species instead of having simply pioneer and non-pioneer species (Brokaw 1985; Martinez-Ramos et al. 1989; Whitmore 1989). Finally, there is a lack of understanding of the detailed life history of several tropical species (Alvarez-Buylla and Martinez-

Ramos 1992). However, some generalizations can be made based on the results of this investigation. For instance, the maintenance of the 'slash and burn' agricultural activities (Hernandez-Xolocotzi et al. 1995) or the promotion of small clear-cutting areas distributed in the forest (Hartshorn 1989). Both activities may lead to a high level of diversity in the landscape, by allowing the establishment of pioneer species (e.g., pioneer species in the shrub community). In the same way, such activities could increase the availability of resources at the limits of the patches, thus providing conditions for the regeneration and establishment of other group of species (e.g., shade-tolerant that would require light to their development).

In conclusion, there are two main factors that explain the patterns of distribution of plant species in a tropical forest of the Yucatan peninsula. The first factor is the quality of the surrounding habitats, which reflects the degree of fragmentation between the focal patch and its neighbors. The other important factor was the proximity and distance to the nearest patch of the same vegetation class, suggesting that plant diversity is also affected by the degree of isolation of the patches. Consequently, the number of species of trees, shrubs and vines would decrease in patches that are isolated and located in landscapes undergoing high fragmentation. Models allowing for the quantitative prediction of the three plant diversity indices studied, as a function of selected landscape fragmentation metrics were developed successfully. These empirical models can be used for prediction of plant diversity based on landscape and habitat characteristics of similar areas of the tropical sub-deciduous forests of the Yucatan peninsula, Mexico. Such models can be incorporated into a framework for assessing the status of plant diversity of such forests, to guide management and conservation efforts.

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