Effects of landscape patterns on species density and abundance of trees in a tropical subdeciduous forest of the Yucatan Peninsula

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A B S T R A C T

Most studies of the effects of fragmentation and landscape patterns on plant communities focus on particular patches and on local species richness (α-diversity), while few studies examine different patch-types at the whole landscape level and address effects on abundance and composition of species or functional groups. The present study aims to identify and characterize relationships between patch-type metrics and species density and abundance of trees using four tropical subdeciduous forest landscapes in the Yucatan Peninsula considering the entire landscape as the unit of study. Species density and abundance of different groups of tree species resulting from hierarchical clustering were related to landscape patterns of patch-types (area, edge, shape, similarity and contrast) using regression analysis and Akaike Information Criterion (AIC). The abundance of tree species in the oldest stages of succession was associated with percentage of land of a patch-type. Total area may favor the establishment of shade-tolerant tree species in the study area because as the area of forest patches increases, the area of forest interior conditions also increases. Conversely, the abundance of species at early and intermediate stages was related to total edge contrast and edge density, respectively. Fragmentation increases the proportion of edge zones of a patch-type, creating contrasting microclimate conditions that could promote the establishment of pioneer and light-demanding species. Thus, the combined effect of total area and edge length of a patch-type may enhance total tree species richness in the study area by favoring species with different life-history strategies. The appearance of area, shape, edge and contrast in most of the regression models suggests that some generalization can be made about the effects of spatial geometry of patch-types on species composition and abundance of tropical trees. Understanding associations between landscape metrics and species density and abundance of objectively derived groups or guilds of species can provide important insights on the effects of fragmentation and landscape pattern on these guilds and on overall α-diversity, as well as guidelines for their conservation and management.

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1. Introduction

Habitat fragmentation is a dynamic process in which 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 (McGarigal et al., 2002). Habitat loss and fragmentation of a landscape alter the number and composition of species and contribute to the decline of several biological populations, as a result of a reduction of forest area, a change in forest edge and an increase in isolation of fragments (Fahrig, 2003; Hill and Curran, 2003). Although we are focusing on fragmentation of forest systems, these processes also occur in other ecosystems subject to natural and man-induced disturbances.

The amount of fragmentation that characterizes a given landscape can be described as a function of the size, shape, similarity, contrast of patches and other metrics of the geometry and structure of landscape patterns (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 et al., 2002). Evidence found over the past years suggests that spatial patterns of patches and patch characteristics may be good predictors of the abundance and composition of species (Atauri and de Lucio, 2001; Hernández-Stefanoni, 2005). Landscape patterns of forest patches influence plant communities due to

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their effects on ecological processes such as pollination, seed dispersal, seed predation and plant competition, and consequently they influence the number and composition of species in a landscape (Laurance et al., 2000; Hill and Curran, 2003). For example, Mazerolle and Villard (1999), examining 61 studies that analyzed the effects of both landscape and patch characteristics as predictors of species presence, found that patch variables were significant predictors of species abundance and composition in 93.4% of the cases.

In particular, forest fragmentation may enhance the abundance of shade-intolerant pioneer species in the landscape, since these species can rapidly colonize, grow and reproduce in open areas (Brokaw, 1987; Whitmore, 1989). In contrast, high levels of fragmentation may be detrimental to shade-tolerant species, which tend to germinate and get established almost entirely beneath the forest canopy, and may thus require forest interior conditions (Schupp et al., 1989; Alvarez-Buylla and Martinez-Ramos, 1992). Species with intermediate life-history strategies may benefit from a certain amount of canopy opening (Denslow, 1987), such as that created at or near the edge of a forest patch (Howe, 1990), and may therefore benefit from small levels of fragmentation in the landscape.

Most studies of the effects of fragmentation and landscape patterns on plant communities focus on particular patches and on local species richness (α-diversity), while few studies examine different patch-types at the whole landscape level and address effects on abundance and composition of species or functional groups (Metzger, 2000; Hill and Curran, 2003). Moreover, studies that focus on functional groups of tropical tree species often rely on incomplete and somewhat subjective classifications of species into guilds (e.g., pioneer, shade-tolerant, intermediate), sometimes based only on empirical information. In this study we assessed tree species density and abundance, and their response to landscape fragmentation, by relating metrics of patch-types (i.e., perimeter, shape, proximity, similarity, and contrast) distributed over the whole landscape with field measurements of species density and abundance of objectively derived groups of tree species showing different patterns of abundance along forest succession in the Yucatan Peninsula.

The Yucatan Peninsula has been recognized as one of the world's biodiversity "hotspots" with high levels of biological diversity (Myers et al., 2000). Nevertheless, forests of the area have been altered through time not only by natural disturbances such as hurricanes and forest fires (García et al., 1996) but also by human interventions, including subsistence slash and burn agriculture by indigenous Mayan farmers (Hernández-Xolocotzi et al., 1995) and conversion of forest to grasslands supporting livestock (Edwards, 1986). Depending on their intensity, frequency and extent, these disturbances produce a mosaic of secondary forests 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 abundance, diversity and composition of species in the region is unknown. The results of this study are important for understanding tree habitat associations, which can be used to assess tree species density and abundance in tropical forests of the Yucatan Peninsula as well as to find strategies to guide and evaluate management and conservation strategies.

2. Methods

2.1. Study area

The study was conducted in the southeastern portion of the Yucatan Peninsula, México, in four contiguous landscapes of 4 km × 4 km that were selected because they had similar environmental conditions, but different landscape configurations and degrees of fragmentation (Fig. 1). Most of the area is covered with tropical subdeciduous forests in different stages of secondary succession. This forest has 2 or 3 canopy layers consisting mostly of trees, shrubs and vines 3–25 m high. Four stages of succession
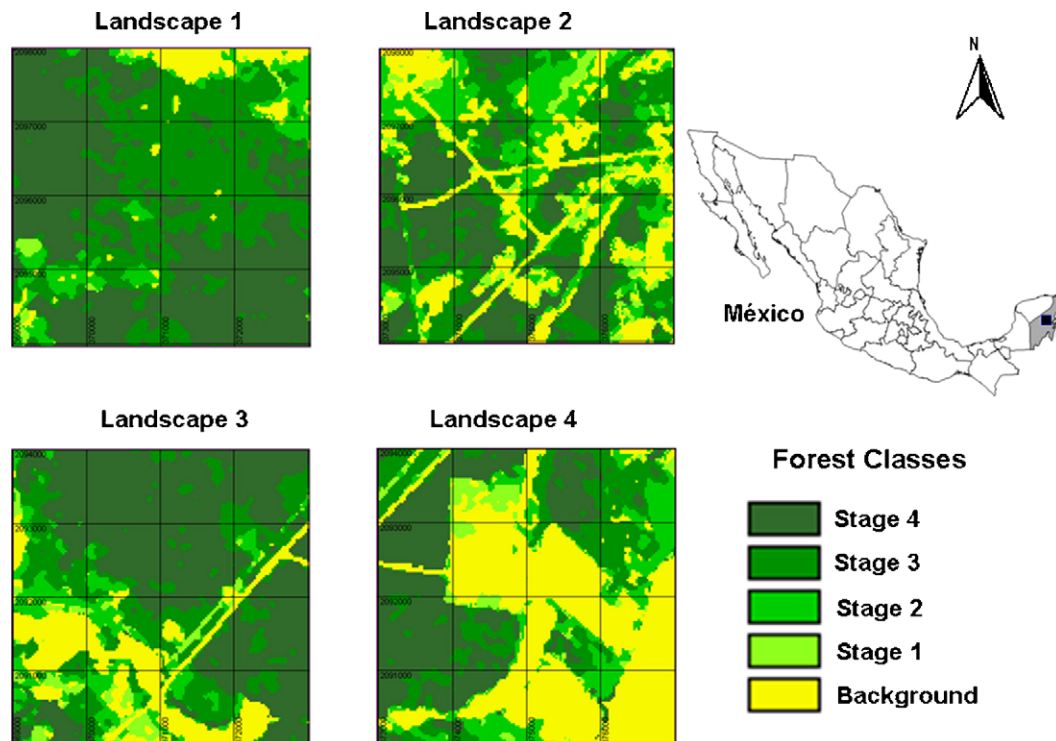

Fig. 1. Land cover map of the four landscapes obtained from a supervised classification. Background class represents deforested areas, grassland, crops, secondary associations and water bodies.

were identified: "Stage 1" refers to ≤3-y-old secondary vegetation; "Stage 2" corresponds to 4- to 10-y-old forests; "Stage 3" refers to 11- to 19-y-old forests and "Stage 4 to >20-y-old forests. There are also secondary plant associations found in flooded areas, including savanna forest, which have few sparse Trees 3–10 m tall, and low forest consisting of a shrub stratum (Cabrera et al., 1982). However, these associations were excluded from all analyses so that the relationship between landscape pattern metrics and species density and abundance of trees would not be confounded by different vegetation classes.

2.2. Land cover mapping and error assessment

A land cover map for the four contiguous landscapes was obtained from Landsat 7 Thematic Mapper (TM) imagery acquired on April 2000, after applying a supervised classification on bands 5 (mid 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 previously geo-referenced and radiometrically corrected. A false color image was used to perform a standard supervised classification of the Landsat 7 TM bands, using the Maximum Likelihood Algorithm as implemented by ER Mapper™ 6.1 (Earth Resource Mapping Ltd, 1998). Two measures of accuracy were used; overall accuracy and the Cohen's Kappa statistic (Jensen, 2000; see Hernández-Stefanoni and Ponce-Hernández, 2004 for details).

2.3. Abundance and species density data

Field data were recorded during two plant surveys conducted during the rainy season: June–July 2000, and July–August 2001. The surveys were based on a stratified random sampling design with a total of 116 sampling sites, which were located on the ground using a GPS unit in the four stages of forest succession. Each sampling site consisted of two quadrats. One 10 m × 10 m quadrat was used to sample trees taller than 3 m while a 5 m × 5 m quadrat was used for sampling young trees taller than 1 m. Of the total number of quadrats 25 fell in "Stage 1" class, 22 in "Stage 2", 27 in "Stage 3", and 42 in "Stage 4". A total of 16,322 sampled individuals were identified to species. Species accumulations curves were used to evaluate how representative the sample size was for the total species richness in every stage of succession as well as in the entire study area. Details of the sampling design and sample size are described in Hernández-Stefanoni and Ponce-Hernández (2004). In every quadrat we computed the number of tree species per unit area (species density) as a proxy for species richness as well as the abundance of each species.

Estimating tree species richness of tropical forests at the community level is difficult because most species have low local densities. It is therefore necessary to sample large areas in order to capture the rarity of most species. This can be achieved either by using very large sample units, or by placing a large number of small independent samples over a large area. We decided to use small sample plots (0.01 ha) because they are logistically more feasible, as well as more suitable to estimate and extrapolate plant diversity to a landscape scale (Clark et al., 1999; Plotkin et al., 2000), especially in patchy and fragmented landscapes. Besides, this is the scale at which individual plants can interact without substantial variation in geomorphology, hydrology, soil and climate variables (Palmer et al., 2000).

One hundred and eighteen tree species were registered in the studied area. We only considered the 35 most abundant species for the analysis of the abundance variable, comprising 12,499 individuals which represent 76.5% of the total number of tree individuals sampled (Table 1). Most researchers recognize the existence of a continuum of patterns in the life-history of the tropical

Table 1
List of 35 most abundant species in the studied area

Code	Scientific name	Common name
s8	*Tetramerium nervosum*	Baak soots
s9	*Lonchocarpus longistylus*	Balche che
s15	*Coccoloba spicata*	Boob
s21	*Chrysophyllum mexicanum*	Chi ke
s26	*Bursera simaruba*	Chaka
s27	*Metopium brownei*	Chechem negro
s30	*Manilkara zapota*	Sak ya
s38	*Protium copal*	Poom, Copal
s43	*Malmea depressa*	Elemuy
s46	*Cecropia obtusifolia*	Koochle, Guarumbo
s49	*Pisidia piscipula*	Ha'abin, Jabin
s51	*Nectandra salicifolia*	Hooch' oche
s56	*Lonchocarpus rugosus*	Kanasin
s57	*Pouteria campechiana*	Kanixte
s59	*Swartzia cubensis*	Katal ox
s67	*Hampea trilobata*	Majahua
s68	*Bauhinia erythrocalyx*	Mayvaca
s78	*Croton reflexifolius*	Pe'es Kuuts
s79	*Psidium sartorianum*	Pichi che
s89	*Coccoloba cozumelensis*	Sak boob
s90	*Dendropanax arboreus*	Sak chaka
s97	*Psidium guajava*	Sak pichi che
s100	*Eugenia mayana*	Saklob che
s103	*Guettarda gaumeri*	Siip che
s104	*Diospyros cuneata*	Siliil
s111	*Zuelania guidonia*	Tamay
s113	*Guettarda combsii*	Tas ta'ab
s116	*Ditaxis tinctoria*	Tinta
s123	*Exothea diphylla*	Wayam cox
s126	*Laetia thamnia*	Ximche
s130	*Coccoloba acapulcensis*	Xtoj yuub
s132	*Lonchocarpus yucatensis*	Ya'ax xu'ul, Sak xuul
s135	*Vitex gaumeri*	Ya'axnik
s136	*Piper psilorhache*	Yax pejel che
s139	*Lysiloma latisiliquum*	Zalam, Tsalam

forests tree species between the traditional pioneer and non-pioneer ends (Martinez-Ramos et al., 1989; Clark and Clark, 1992; Lieberman et al., 1995). Consequently, we used cluster analysis to characterize these 35 species into categories or functional groups, based on the abundance of each species in each of the four stages of succession. We implemented a hierarchical agglomerative clustering using Euclidean distance as dissimilarity measure and Ward's method (Ludwig and Reynolds, 1988) in the software PCORD version 4.34 (McCune and Mefford, 1999). This method uses an analysis of variance approach to evaluate the distance between clusters.

To test for significant differences between the groups determined by the hierarchical clustering, we employed multi-response permutation procedures (MRPP), a nonparametric analogue of multivariate analysis of variance that tests variability within and between groups, but is free of parametric assumptions of multivariate normality and homogeneity of variances (Zimmerman et al., 1985). We used MRPP to determine whether tree species composition was more similar within than between groups (stages of forest succession).

2.4. Calculation of landscape-pattern metrics

The ER Mapper™ raster files of the four landscape were exported to the GIS program IDRISI (Eastman, 2004), in order to calculate the patch-types metrics using the program software FRAGSTATS (McGarigal et al., 2002). The four stages of succession in the forest and a class named as "background" were considered for the calculations. The background class represents the two secondary associations and the remaining land cover classes considered in the classification (Fig. 1). Most of the metrics applied

to habitat classes can be interpreted as fragmentation indices, because they measure the configuration of a particular patch-type (McGarigal et al., 2002). Several indices at this level are calculated by FRAGSTATS and all of them were initially considered. The four landscapes in the study area were also considered for the computation of the indices per class (patch-type). The patch-type approach of this study requires calculation of individual metrics for each given patch-type, regardless of how many individual units (patches) make up that particular patch-type. In other words we calculated the different metrics for each stage of forest succession in every one of the four landscapes.

The four studied landscapes are large enough to encompass several forest patches with varying species density and abundance of trees. Gustafson (1998) used the range of influence, as depicted from the spatial auto-correlation of sample units, to define the maximum patch size of the variable of interest. Here, the range of influence of tree species density found in the semi-variance analysis is between 1.56 and 1.76 km^2 (Hernández-Stefanoni, 2005), which indicates that the four landscapes are sufficiently large to include independent patches of various sizes. Moreover, the size of the landscape maybe arbitrary but needs to be relevant to the process or organisms studied (McGarigal et al., 2002); in this case the four landscapes have the same size (16 km^2), and this size is relevant to define patches of tree species density and abundance.

Many patch-type metrics are redundant or represent an alternative formulation of the same information (Riitters et al., 1995; Hargis et al., 1998). Thus, only selected measurements were considered in this study. To choose the group of metrics, their correlations were analyzed. Pearson correlation coefficients between each pair of metrics, as well as the correlation of these metrics with tree species density and abundance values were computed. The selection of the indices also considered criteria including variables that quantify different aspects of the landscape configuration. The selection of the metrics was made considering how common such measurements are in landscape studies literature (Mazerolle and Villard, 1999), as well as the explanatory power that such metrics may have to describe tree species composition and abundance. On these bases, five indices belonging to four groups of metrics were selected to relate to tree species density and abundance in each patch-type in each landscape. These

groups and metrics are: area/edge (percentage of landscape—PLAND, and edge density—ED), shape (mean area weighted shape index—SHAPE_AM), isolation/proximity (mean area weighted similarity index—SIMI_AM) and contrast (total edge contrast index—TECI). A description of each metric is given in Table 2.

In order to calculate the similarity index, a search radius of 10 pixels (300 m) was considered. This radius is arbitrary but coincides with empirical evidence gathered in the field about an expected average size of a patch-type. In addition to the radius, this index requires for its calculation some similarity weights for each pair-wise comparison of patch-types. In this case, the weights were the mean values of 4 estimates of beta diversity between each pair of stages of succession (Table 3). These beta diversity estimates are similarity measures and are described by Magurran (1988) and they were calculated using cumulative values of the sampling quadrats for each vegetation class. Two of these diversity measures use presence and absence of species (i.e., Jaccard and Sørensen), while the other two require abundance data for their calculations (i.e., Sørensen-abundance and Morisita–Horn). Finally, the weighted edge contrast between stage classes required to compute total edge contrast index were calculated as the inverse values of the similarity weights.

2.5. Statistical analyses

Since the primary objective of this study is to relate tree species density and the number of individuals of trees species with landscape pattern metrics, a multiple regression analysis was performed. The dependent variables were the average values of species density (number of tree species per unit area) and the

Table 3
Values used to give a similarity weight between the different patch-types

	Stage 4	Stage 3	Stage 2	Stage 1
Stage 4	1.00			
Stage 3	0.73	1.00		
Stage 2	0.60	0.77	1.00	
Stage 1	0.39	0.47	0.52	1.00

Patch-types indicated in gray were not included in this study, and were only used to calculate the mean area similarity index metric (SIMI_AM).

Table 2
Description of metrics used to quantify patch-type metrics

Type of metric/code	Metric	Description
Area/edge		
PLAND	Percentage of landscape	This metric is a measure of landscape composition, specifically, how much of the landscape is comprised of a particular patch-type.
ED	Edge density	This index is a measure of total edge length of each patch-type on a per unit area basis that facilitates comparisons among patch-types of varying size.
Shape		
SHAPE_AM	Mean area-weighted shape index	This metric is calculated as the perimeter of a patch (m) divided by the square root of a patch area (m^2). Therefore, it is a measure of shape complexity of a patch compared to a standard shape (square) of the same size. Here it was measured as the weighted mean area of the shape indices of the patches corresponding to a patch-type.
Isolation/proximity		
SIMI_AM	Mean area-weighted similarity index	This index considers the size and proximity of all patches, regardless of class, whose edges are within a specified search radius of the focal patch. It quantifies the spatial context of a (habitat) patch in relation to its neighbors of the same or similar class; specifically, the index distinguishes sparse distributions of small and insular habitat patches from configurations where the habitat forms a complex cluster of larger, hospitable (i.e., similar) patches. Here it was measured as the mean of the similarity indices of the patches corresponding to a patch-type.
Contrast		
TECI	Total edge contrast index	This metric measures the edge contrast as a percentage of the maximum possible, applied to all edges of the corresponding patch-type. High values of this index mean that the edge present is of high contrast, and vice versa.

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

Table 4
Candidate models considered in the analyses of the relationship between patch-type metrics and species density and abundance of trees

Model	Model description
1	$DV^a = B_0 + B_1(PLAND) + B_2(ED) + B_3(SHAPE\_AM) + B_4(SIMI\_AM) + B_5(TECI)$
2	$DV^a = B_0 + B_1(PLAND) + B_2(ED) + B_3(SHAPE\_AM) + B_4(SIMI\_AM)$
3	$DV^a = B_0 + B_1(PLAND) + B_2(ED) + B_3(SHAPE\_AM) + B_4(TECI)$
4	$DV^a = B_0 + B_1(PLAND) + B_2(ED) + B_3(SIMI\_AM) + B_4(TECI)$
5	$DV^a = B_0 + B_1(SHAPE\_AM) + B_2(SIMI\_AM) + B_3(TECI)$
6	$DV^a = B_0 + B_1(PLAND) + B_2(ED) + B_3(SHAPE\_AM)$
7	$DV^a = B_0 + B_1(PLAND) + B_2(ED) + B_3(SIMI\_AM)$
8	$DV^a = B_0 + B_1(PLAND) + B_2(ED) + B_3(TECI)$
9	$DV^a = B_0 + B_1(SHAPE\_AM) + B_2(SIMI\_AM)$
10	$DV^a = B_0 + B_1(SHAPE\_AM) + B_2(TECI)$
11	$DV^a = B_0 + B_1(SIMI\_AM) + B_2(TECI)$
12	$DV^a = B_0 + B_1(PLAND) + B_2(ED)$
13	$DV^a = B_0 + B_1(SHAPE\_AM)$
14	$DV^a = B_0 + B_1(SIMI\_AM)$
15	$DV^a = B_0 + B_1(TECI)$

[a] Dependent variables are species density, abundance of group 1, abundance of group 2, and abundance of group 3.

average values of abundance of tree species of different groups, resulting from the hierarchical clustering. Multiple regression analyses assume that the observations are independent (i.e., not auto-correlated). To avoid auto-correlation we used as dependent variables the mean values of species density and abundance of trees for all quadrats within each successional stage, within each landscape. Dependent variables were formally tested for normality and homogeneity of variances in the residuals. The explanatory variables were a group of patch-type metrics (Table 2), which needed to be transformed with $1/x$, $\log 10(x)$, $\log 10(x + 1)$ and $\mathrm{sqrt}(x)$ as necessary to meet the assumptions of linearity. The sample size used in regression was 16 because we considered 4 landscapes and 4 stages of succession in each landscape. In order to avoid confounding the effects of patch-type metrics and land cover classes, we performed all analyses considering just the tropical subdeciduous forest class and we excluded from the analysis the other vegetation classes (low forest and savanna).

We evaluated a set of 15 models considering all possible combinations of the four main groups of metrics (Table 4). 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 $AIC = -2(\log \text{likelihood}) + 2K$, 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). A set of candidate models were then selected using both an approximate cutoff of $\Delta_i = 4$, and those models having $w_i > 0.1$ (Burnham and Anderson, 1998). Finally, we calculated model-averaged parameters and unconditional standard errors based on Akaike weights (Burnham and Anderson, 1998; Johnson and Omland, 2004).

3. Results

3.1. Land cover map

The land cover thematic map of the four landscapes produced by the supervised classification is shown in Fig. 1. The total area occupied by these landscapes is 6464.2 ha, 80.9% of which is covered by tropical subdeciduous forest in any of the four

successional stages. Deforested areas, grassland, crops, secondary associations and water bodies represented the remaining 19.1%. Stage 4 forest (20- to 60-y-old secondary forest) is the largest land cover type spanning over 36.8% of the total area with 2382.7 ha. Stage 3 (11- to 19-y-old secondary forest) represents 26.2% of the total area with 1698.0 ha. Stage 2 (4- to 10-y-old secondary forest) covers 11.9% of the total area with 771.6 ha whereas Stage 1 represents only 5.7% of the total area. The overall accuracy calculated for the map was 82.3%, while the kappa index was 0.78. The greatest misclassifications among the mapped classes occurred in the Stage 3 class (relative accuracy of this successional stage in the map was 76.0%). The latter error (14%) can be partly explained by the fact that this intermediate class is not clearly differentiated in terms of structure and species composition from its neighboring classes: Stage 4 and Stage 2, and because boundaries among these classes are fairly gradual and transitional.

3.2. Tree species density and abundance of species in forest classes

The mean values of tree species density in each successional stage for the four landscapes are presented in Table 5. These values showed a consistent pattern: Stage 1 class (i.e., the youngest stage of forest succession) has fewer species than the older successional stages. Average species density per sampling quadrat differed significantly among the four vegetation stages for each landscape considered: landscape 1 ($F_{[3,19]} = 8.18$, $p < 0.002$), landscape 2 ($F_{[3,37]} = 46.98$, $p < 0.001$), landscape 3 ($F_{[3,38]} = 49.37$, $p < 0.001$) and landscape 4 ($F_{[3,18]} = 17.485$, $p < 0.001$). Tukey HSD test revealed that Stage 1 differed significantly from the others (Table 5), which did not differ significantly among them (Table 5).

On the basis of a hierarchical cluster analysis of abundance of the 35 most abundant tree species in the different stages of succession, three different groups of species were recognized (Fig. 2, 5.59E+03 Euclidean distance). Group 1 included species that are more abundant in the oldest stage of succession (Stages 3 and 4). Group 2 consisted of species that are more abundant at intermediate stages of forest succession (Stages 2 and 3). Group 3 is formed by species

Table 5
Mean plant species density and abundance of trees and their standard error for the four studied landscapes

Stage of succession	Species density	Abundance		
		Group 1	Group 2	Group 3
Landscape 1				
Stage 4	26.70 ± 1.65	34.36 ± 6.33	28.18 ± 4.05	17.73 ± 3.13
Stage 3	26.00 ± 2.31	4.67 ± 1.20	41.67 ± 5.67	74.00 ± 3.06
Stage 2	19.00* ± 2.52	1.00 ± 0.58	29.00 ± 7.51	104.33 ± 36.18
Stage 1	12.00* ± 1.53	4.33 ± 2.96	4.00 ± 1.00	16.00 ± 3.51
Landscape 2				
Stage 4	27.57 ± 1.01	39.50 ± 8.68	28.07 ± 3.44	21.43 ± 2.65
Stage 3	25.66 ± 1.43	31.33 ± 6.60	57.67 ± 12.40	69.17 ± 11.39
Stage 2	22.50 ± 1.12	9.00 ± 3.87	33.00 ± 4.55	76.75 ± 11.81
Stage 1	10.90* ± 1.08	11.40 ± 6.02	13.40 ± 6.47	22.80 ± 4.71
Landscape 3				
Stage 4	28.08 ± 1.00	41.83 ± 6.64	33.50 ± 4.27	23.75 ± 5.76
Stage 3	23.45 ± 1.15	37.27 ± 6.74	38.27 ± 6.42	59.45 ± 7.45
Stage 2	21.57 ± 1.15	35.43 ± 9.99	43.57 ± 6.94	81.86 ± 13.92
Stage 1	9.77* ± 1.14	17.22 ± 4.97	7.00 ± 2.70	20.67 ± 5.84
Landscape 4				
Stage 4	28.00 ± 1.64	37.80 ± 8.87	33.40 ± 6.55	17.20 ± 5.70
Stage 3	24.85 ± 1.12	43.71 ± 10.75	32.71 ± 5.04	73.71 ± 7.75
Stage 2	20.25 ± 2.43	27.75 ± 13.11	39.25 ± 10.25	112.75 ± 42.13
Stage 1	10.67* ± 0.67	7.33 ± 5.84	12.67 ± 1.45	15.00 ± 6.03

* Significant differences were found among these groups and all others, using Tukey HSD test to compare the mean species density among successional classes in each landscape $p < 0.05$.
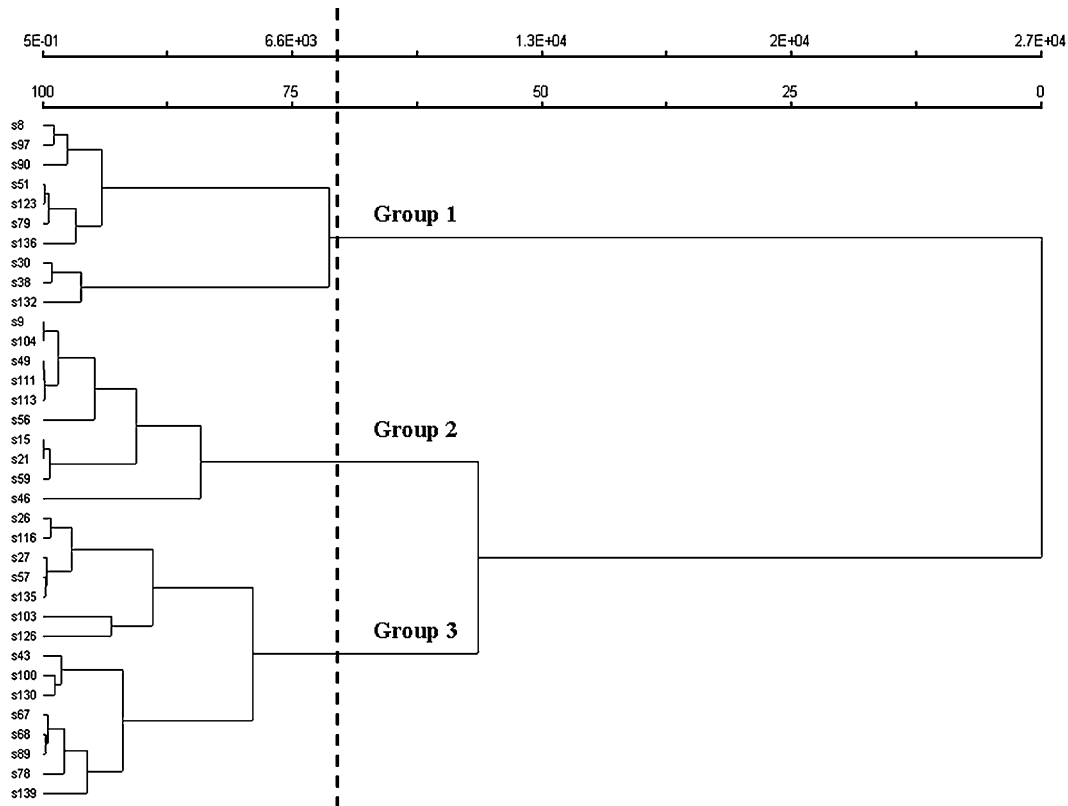
Fig. 2. Dendrogram of species dissimilarity based on the relative abundance of 35 tree species in each of four stages of tropical forest succession.

that are more abundant in the early stages of succession (Stages 1 and 2). The mean values of abundance of tree species in each patch-type for the four landscapes are presented in Table 5. The MRPP analysis of abundance of tree species indicated that the three groups of species obtained in the cluster analysis were significantly different from one another overall ($T = -16.72$, $p < 0.001$), as well as for each pair-wise comparison ($T \geq -11.51$, $p < 0.001$).

3.3. Relating landscape patterns with density and abundance of species

Model selection using an information-theoretical approach showed that four models were good predictors of species density,

while two or three models could predict the abundance of species of the different groups (Table 6). For species density, the most plausible model includes percentage of land (PLAND) and edge density (ED) as explanatory variables (Akaike weight = 0.63). Considering the abundance of the different groups of species, group 1 is best explained by a model including PLAND, ED and mean area weighted similarity index (SIMI_AM) with an Akaike weight of 0.30, group 2 by a model explained by PLAND, ED and total edge contrast index (TECI) has the highest Akaike weight (0.38) and finally for group 3, the model that includes mean area-weighed shape index (SHAPE_AM), TECI and SIMI_AM as explanatory variables (Akaike weight = 0.70). In all cases, other models had Akaike weights greater than 0.1, so we applied model

Table 6
Model selection statistics for the analyses of effects of patch-type metrics on species density and abundance of trees

Dependent Variable model[*]	Number of parameters	AIC	Δ_i	w_i
Species density				
$DV = B_0 + B_1(PLAND) + B_2(ED)$	3	90.3	0.00	0.63
$DV = B_0 + B_1(PLAND) + B_2(ED) + B_3(SIMI\_AM)$	4	92.2	3.50	0.11
$DV = B_0 + B_1(PLAND) + B_2(ED) + B_3(TECI)$	4	92.3	3.58	0.10
$DV = B_0 + B_1(PLAND) + B_2(ED) + B_3(SHAPE\_AM)$	4	92.3	3.62	0.10
Abundance of group 1				
$DV = B_0 + B_1(PLAND) + B_2(ED) + B_3(SIMI\_AM)$	4	127.8	0.00	0.30
$DV = B_0 + B_1(SIMI\_AM) + B_2(TECI)$	3	130.4	1.00	0.18
$DV = B_0 + B_1(TECI)$	2	131.7	1.25	0.16
Abundance of group 2				
$DV = B_0 + B_1(PLAND) + B_2(ED)$	3	119.7	0.00	0.38
$DV = B_0 + B_1(PLAND) + B_2(ED) + B_3(TECI)$	4	118.3	1.16	0.33
Abundance of group 3				
$DV = B_0 + B_1(SHAPE\_AM) + B_2(TECI)$	3	143.9	0.00	0.70
$DV = B_0 + B_1(SHAPE\_AM) + B_2(SIMI\_AM)$	4	145.8	3.50	0.12

AIC: Akaike Information Criterion; Δ_i: delta AIC values; w_i: Akaike weights.
[*] Only models with $w_i > 0.1$ and with $\Delta_i < 4$ are shown (see Section 2).

Table 7
Model-averaged parameter estimates and (unconditional standard error) for relating patch-type metrics with species density and abundance of trees of 3 groups selected by cluster analysis

Model terms	Species density	Abundance		
		Group 1	Group 2	Group 3
INTERCEPT	10.747 (2.69)[a]	27.290 (17.87)	−6.575 (13.94)	−108.026 (30.89)
PLAND	0.290 (0.07)[a]	2.380 (1.60)[b]	0.234 (0.21)	–
ED	0.090 (0.06)[b]	0.003 (0.05)	0.359 (0.15)[a]	–
SHAPE_AM	0.015 (0.12)	–	–	15.773 (5.05)[a]
SIMI_AM	0.000 (0.00)	−0.002 (0.001)	–	0.000 (0.00)
TECI	0.006 (0.03)	−0.461 (0.35)	0.348 (0.29)	3.768 (0.93)[a]

[a] Parameter estimates indicate that 95% confidence interval excludes 0.
[b] Parameter estimates indicate that 90% confidence interval excludes 0.

averaging to create a composite model for each dependent variable (Table 7).

Model-averaged results indicated statistically significant relationships between tree species density and percentage of land (PLAND) and edge density (ED) of habitat classes (Table 7). This means that tree species density of a patch-type increases when its area increases and when the perimeter of a patch-type also increases. On the other hand, the abundance of species that are most abundant in the oldest stage of succession (group 1) is best explained by PLAND (Table 7). Therefore, habitat classes that occupy a large proportion of the area of these landscapes favor the species density of trees and the abundance of species associated to the oldest stage of succession. In contrast, the abundance of species associated with early stages of succession (group 3) was positively related to TECI and SHAPE_AM, indicating that the abundance of those species increases as the contrast of the focal patch-type relative to other habitat classes increases, and as the shape of a patch-type is more irregular. Finally the group of species associated with the intermediate stages of succession (group 2) was significantly associated with ED, indicating that the abundance of these species increases as the habitat edge per unit area increases.

4. Discussion

The strong positive association between tree species density and percentage of land (PLAND) of a patch-type in a landscape, as well as between tree species density and edge density (ED) suggest that total area and edge length per unit area of a patch-type enhance tree species richness. Patch-type area and edge length may favor different life-history strategies, so their combined effect could increase total tree species richness in our forest-dominated landscape.

The three groups of tree species obtained in the Cluster analysis showed different patterns of association with patch-type metrics, and seem to correspond to different life-history strategies. Thus, cluster analysis, and multivariate techniques in general, provide a useful objective means of deriving functional groups that does not rely on *a priori*, often subjective, information. Tree species associated with the oldest stage of succession (group 1) were also positively associated with the percentage of land of a patch-type (Table 7). As the area of a patch-type increases, the proportion of interior conditions also increases (Turner, 1996). Since the oldest stages of forest succession occupied the largest patches and represented the largest proportion of the landscape, this increase in interior conditions would tend to favor the establishment and persistence of shade-tolerant species (Laurance, 1991; Turner, 1996; Metzger, 2000). The weak negative relationship between abundance of tree species of group 1 and Total Edge Contrast Index (TECI) is consistent with this interpretation. Several tree species associated to the oldest stage of forest succession (group 1) such as

Manilkara zapota, *Nectandra salicifolia* and *Protium copal* have been previously classified as shade-tolerant species, and are characterized by slow growth rates, long time spans to reach reproductive maturity, and production of few, large, animal-dispersed seeds that usually germinate and establish beneath the forest canopy (Schupp et al., 1989; Alvarez-Buylla and Martinez-Ramos, 1992), partly because their animal dispersors require or prefer forest interior conditions (Forman, 1995).

On the other hand, tree species in group 3 were most abundant in the youngest stages of succession (≤10-y-old forest), and were associated with patch-types with irregular shape, high edge density and high contrast with neighboring patch-types. Edge conditions generally facilitate the establishment and growth of pioneer and light-demanding species (Laurance et al., 1998). An irregular shape and a high contrast of patch-types indicate a high proportion of edge zones and a strong contrast of the perimeter of a patch-type with neighboring patches, which can alter microclimatic conditions, modify patterns of species colonization, growth and other ecological processes, and may favor light-demanding over shade-tolerant tree species (Laurance et al., 1998, 2000).

Several tree species in group 3, such as *Cecropia obtusifolia*, *Guettarda combsii* and *Hampea trilobata* can be classified as pioneer or shade-intolerant, which commonly produce numerous, small, well-dispersed seeds with a high probability of reaching newly formed patches. These pioneer species also grow and achieve reproductive maturity rapidly, which increases their capacity to occupy and dominate a patch, especially in open areas (Brokaw, 1987; Alvarez-Buylla and Martinez-Ramos, 1992). This might explain the significant relationship of this group of species with irregular patch shape indicated by a positive coefficient of the shape metric. However, the regeneration of this group of species also seems to be favored by the availability of nearby forest patches of older successional stages serving as sources of seeds and seed dispersers (Schupp et al., 1989), as suggested by the positive association of patch contrast with the abundance of this group of species. The latter result is consistent with recent findings underscoring the role of seed- and recruitment limitation in seedling dynamics, and in the maintenance of species diversity in tropical forests, including pioneer tree species (Nathan and Muller-Landau, 2000; Svenning and Wright, 2005; Norden et al., 2007).

Tree species in group 2 were associated with intermediate stages of forest succession (4- to 19-y-old forests), and were also positively associated with edge density. We also found a weak positive relationship between the abundance of tree species of this group and both PLAND and TECI, as indicated in the two models selected (Table 6), although neither parameter was significant in the model-averaged results (Table 7). These associations suggest that this group of species can survive under the shade as seedlings, but may require a certain amount of canopy opening to survive beyond the early stages of their life cycle, and could thus be considered as non-pioneer light-demanders (Hill and Curran, 2003).

Examples of tree species in this group are *Metopium brownei*, *Bursera simaruba* and *Malmea depressa*.

In summary, total area of a patch-type may favor the establishment of long-lived, shade-tolerant tree species in the study area because, as the area of forest patches increases, the area of forest interior conditions also increases (Laurance, 1991; Turner, 1996; Metzger, 2000). Conversely, fragmentation increases the proportion of edge zones of a patch-type, thereby creating contrasting microclimate conditions that tend to promote the establishment of pioneer and light-demanding species (Laurance et al., 2000). Thus, the combined effect of total area and edge length of a patch-type may promote total tree species richness in the study area by favoring species with different life-history strategies.

Most ecological studies of the effects of fragmentation on species diversity have focused on patches varying in area, edge length or degree of isolation (Laurance, 1991; Laurance et al., 2000; Hill and Curran, 2003). The results of this study indicate that it is possible to associate tree species density and abundance with landscape patterns of habitat types at the whole landscape level. Using the landscape instead of the forest patch as the analytical unit can be more informative of the patterns and processes involved in the observed associations, and provide results that can be more readily generalized to the whole landscape. Our results suggest that moderate levels of disturbance, such as those produced by natural disturbance, such as hurricanes (Vandermeer et al., 2000), or by human activities such as timber extraction and traditional "slash and burn" agriculture, may enhance tree species richness in a forest-dominated landscape, because they enhance habitat diversity by creating environmental conditions that are very different from those prevailing in the forest interior, thereby enabling the coexistence of tree species with different life-history strategies. Thus, habitat diversity at the landscape level may enhance species richness (Honnay et al., 2003), as indicated by the finding that several small habitat patches usually contain more plant species than a few large habitat patches (Margules et al., 1994; Honnay et al., 1999). However, high levels of disturbance resulting in a high degree of fragmentation can have a strong negative impact on tree species richness (Honnay et al., 1999), highlighting the importance of considering the landscape context, that is, the prevailing landscape matrix (e.g., natural forest *versus* urban or agricultural fields).

5. Management implications and conclusions

The appearance of area, shape, edge and contrast in most of the regression models suggests that some generalization can be made about the effects of spatial geometry of patch-types on species composition and abundance of trees, which may have important implications for forest management and conservation. Understanding associations between landscape metrics and species density and abundance of objectively derived groups or guilds of species can provide important insights on the effects of fragmentation and landscape pattern on these guilds and on overall α-diversity, as well as guidelines for their conservation and management. For example, in a forested landscape dominated by long-lived, shade-tolerant tree species, traditional "slash and burn" agriculture (Hernández-Xolocotzi et al., 1995), or small-scale monocyclic management systems, such as clear- or strip-cutting (Hartshorn, 1989; Guariguata, 2000) may enhance overall tree species richness by allowing the regeneration of pioneer species, while increasing the availability of resources at the edge of the patch-types, thereby providing favorable conditions for the regeneration of other light-demanding species. This is important not only for the conservation of biodiversity *per se*, but also because some light-demanding species are valuable timber species, such as

mahogany (*Swetenia macrophylla*) and Spanish cedar (*Cedrela odorata*), which appear to require large open areas for successful regeneration (Snook, 1996; Dickinson and Whigham, 1999). Large clearings may also be required for the successful regeneration of long-lived pioneer tree species that dominate the canopy of young and intermediate-aged secondary forests in lowland Costa Rica (Guariguata, 2000; Dupuy and Chazdon, 2006). Many of these species have economic value for timber, medicine and other uses (Chazdon and Coe, 1999). Pioneer and light-demanding species can also be useful for restoration purposes, since they are adapted to colonize open areas, have high intrinsic growth rates, and can rapidly achieve reproductive maturity.

On the other hand, in a highly fragmented landscape dominated by agriculture or pasture lands, conserving large patches of regular shapes can enhance overall tree species richness by promoting the establishment and persistence of long-lived, shade-tolerant tree species, a functional group that has been found to be particularly vulnerable to fragmentation (Metzger, 2000), and that also includes commercially valuable species such as *Manilkara zapota* and *Brosimum alicastrum*. Thus, our results highlight the importance of considering the landscape context, and the hitherto little explored potential of relating patterns and metrics of habitat types to species density and abundance of objectively defined groups of species at the whole landscape level.

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