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Modelling tree diversity in a highly fragmented tropical montane landscape

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ABSTRACT

Aim There is an urgent need for conservation in threatened tropical forest regions. We explain and predict the spatial variation of α (i.e. within plot) and β (i.e. between plot) tree diversity in a tropical montane landscape subjected to a high deforestation rate. A major aim is to demonstrate the potential of a method that combines data from multiple sources (field data, remote sensing imagery and GIS) to evaluate and monitor forest diversity on a broad scale over large unexplored areas.

Location The study covered an area of c. 3500 km² in the Highlands of Chiapas, southern Mexico.

Methods We identified all of the tree species within 204 field plots (1000 m² each) and measured different environmental, human disturbance-related, and spatial variables using remote sensing and GIS data. To obtain a predictive model of α tree diversity (Fisher's alpha) based on selected explanatory variables, we used a generalized linear model with a gamma error distribution. Mantel tests of matrix correspondence were used to determine whether similarities in floristic composition were correlated with similarities in the explanatory variables. Finally, we used a method that combines α and β tree diversity to define priority areas for conservation.

Results The model for α tree diversity explained 44% of the overall variability, of which most was mainly related to precipitation, temperature, NDVI, and canopy (all relationships were positive, and quadratic for temperature and NDVI). There were no spatially structured regional factors that were ignored. Similarity in tree composition was correlated positively with climate and NDVI.

Main conclusions The results were used to: (1) identify and assign conservation priority of unexplored areas that have high tree diversity, and (2) demonstrate the importance of several vegetation formations in the region's biodiversity. The method we present can be particularly useful in assessing regional needs and in developing local conservation strategies in poorly surveyed (and often at risk) tropical areas worldwide, where accessibility is usually limited.

Keywords

Beta diversity, Fisher's alpha, generalized linear model, Highlands of Chiapas, hotspot, Mantel test, spatial autocorrelation, tree diversity.

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INTRODUCTION

The current scale of deforestation and the large areas of degraded land in tropical regions underscore the urgent need for interventions to restore and protect biodiversity, ecological functioning, and the supply of goods and services used by poor rural communities (Lamb *et al.*, 2005). One of the main responses to this process of

degradation has been to create or expand networks of protected areas to help protect the remaining biodiversity. In large part, the response has focused on selecting candidate sites that are as representative and comprehensive as possible (Williams *et al.*, 1996; Araújo, 1999; Justus & Sarkar, 2002). The quantification of species–environment relationships has gained importance as a tool to assist in decision-making related to nature conservation

at the landscape level (Stockwell & Peterson, 2003). But this task is not simple because diversity can be measured in a variety of ways and at different scales. The factors that influence patterns of diversity are varied and can include phylogenetic, historical, biogeographical and environmental processes (Brown & Lomolino, 1998; Rey Benayas & Scheiner, 2002). In addition, human activities can influence the shape of geographical patterns of diversity in intensively managed regions (Lawton *et al.*, 1998). At large spatial scales, factors related to the entry of energy in the system (e.g. productivity and evapotranspiration) have emerged as primary predictors of species diversity (Wright *et al.*, 1993; Pausas & Austin, 2001; González-Espinosa *et al.*, 2004). At finer grained scales, however, it is the history and frequency of disturbance, land use, and heterogeneity of different landscape features (e.g. topography and habitats) that might be more important in explaining patterns of species diversity (Kerr & Packer, 1997; Wohlgemuth, 1998; Rahbek & Graves, 2001).

Geographic information systems (GIS) and remote sensing data are useful for extrapolating information from ground-based ecological studies to large and unexplored areas. The mapping of plant diversity can be accomplished by analysing the variation in a spectral signal (e.g. Normalized Difference Vegetation Index, NDVI) and correlating the variation with measures of landscape or taxa diversity (Rey Benayas & Pope, 1995; Jørgenson & Nøhr, 1996; Gould, 2000; Luoto *et al.*, 2002; Tuomisto *et al.*, 2003). Climatic, biophysical and land cover data, as well as factors related to human disturbance, can also predict and explain patterns of species diversity (Lobo & Martín-Piera, 2002).

Local diversity should not be the only valuable asset to be evaluated in conservation networks. A habitat might contain a relatively small number of species, but it can be ecologically important because of the presence of species or species assemblages that are not present in highly diverse habitats. Thus, it is desirable that conservation networks be representative of habitats (Araújo, 1999).

In this study, we present a procedure to predict the spatial variation of α (within-plot) and β (between-plot) tree diversity

in a tropical montane region. Our model includes information obtained at multiple spatial scales, including field sampling, satellite imagery and GIS. As an illustrative example of the use of our model, we present data from the Highlands of Chiapas, southern Mexico. That region is important because of its high biodiversity and environmental heterogeneity (Ceballos *et al.*, 1998; Wolf & Flamenco, 2003; González-Espinosa *et al.*, 2004). The chronic intensification of land use, particularly following a violent conflict in 1994 (the Zapatista riot), has caused much deforestation and forest disturbance, which may have had a negative impact on biodiversity (González-Espinosa, 2005).

The specific objectives of this study are: (1) to identify the determinants of the spatial variation of α tree diversity; (2) to develop a predictive model that permits the identification of less-surveyed areas of high α tree diversity; (3) to identify the factors that influence β diversity; and (4) to use α and β diversity as selection criteria in identifying priority areas for conservation. Our study makes no hypotheses about the mechanistic processes that shape the spatial patterns of tree diversity but, rather, it seeks to provide *post hoc* explanations for such processes. The model we propose can be the basis for identifying tracts of land worthy of conservation, establishing protected areas and facilitating forest restoration programmes. By identifying patterns of α and β tree diversity, this study will help to foster conservation and the use of land management tools in other tropical regions of the world (Lamb *et al.*, 2005).

MATERIALS AND METHODS

Study area

The Highlands of Chiapas (Fig. 1) is a biologically diverse region that covers 11,000 km² and is home to about a third of the approximately 9000 vascular plant species found in the state of Chiapas (Breedlove, 1981). In the Highlands, there is a variety of forest types, including oak, pine–oak, pine, and montane cloud forests (Miranda, 1952; Rzedowski, 1978; González-Espinosa

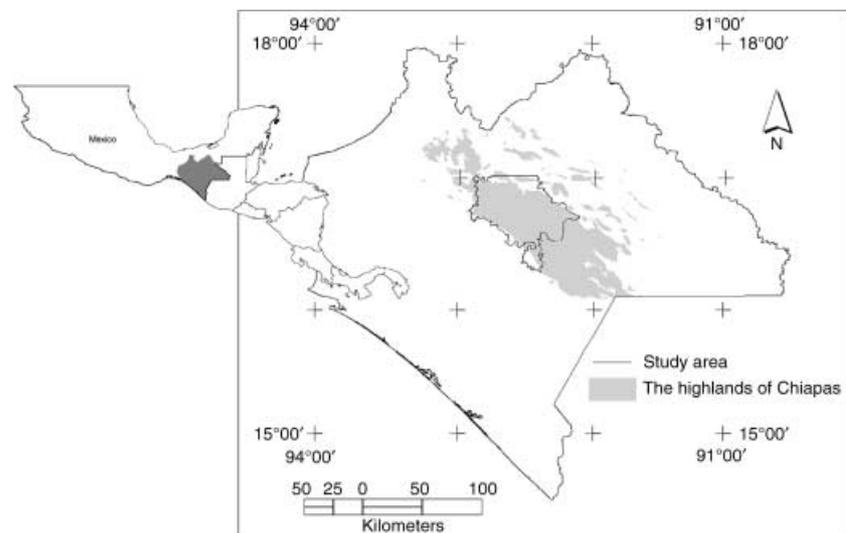


Figure 1 Location of the study area in the Highlands of Chiapas, southern Mexico.

et al., 1991). Our study area covers c. 3550 km² and ranges between 600 m and 2900 m a.s.l. (mostly above 1500 m). The topography is abrupt and slopes are moderately steep (mean = 14.8°, SD = 9.6°). The climate is cool (mean daily temperatures range between 14 and 17 °C) and humid (annual rainfall range between 1200 and 1800 mm) with a rainy summer and a 5–6 month dry season. The underlying geology of the area is carboniferous limestone with rocky outcrops. The soils are a mixture of thin lithic rendzinas, deeper humic Acrisols in forested areas and rather infertile Chromic Luvisols.

Mayan peasants, who have made clearings for shifting cultivation and extracted firewood and other forest resources since pre-Columbian times, densely populate the region. The main economic activities are traditional agriculture and non-commercial forestry. Slash-and-burn agriculture and the chronic use of forests for fuelwood have contributed to the expansion of relatively low diversity pine and mixed pine–oak stands, and a reduction in the extent of highly diverse oak and montane cloud forests (Ramírez-Marcial *et al.*, 2001; Galindo-Jaimes *et al.*, 2002).

Field sampling and estimation of α tree diversity

Floristic inventories were made in 204 1000-m² circular plots distributed among forest fragments. In 1998, data were collected from 36 plots (Galindo *et al.*, 2002; L. Galindo, unpublished data). Between January 2003 and May 2004, we sampled 168 additional plots. In each plot, all of the trees with a d.b.h. greater than 10 cm were identified to species and counted. Local residents did not always permit access to forests; yet, the forest fragments were evenly spaced across the broader landscape and they provided an accurate sample of the regional diversity. On average, plots contained 13.3 (\pm 5.2) tree species (range 2–28) and 97.2 (\pm 36.5) stems per plot (range 22–211). All of the locations were geo-referenced. The mean distance between plots was 25.2 km (\pm 15.3 km). In the study, we documented 230 native tree species (see Appendix S1 in Supplementary Material). Fisher's alpha, an

estimator of α diversity, was calculated for each sample. Fisher's alpha was highly correlated with the number of species observed ($r = 0.91$, $P < 0.0001$). Nevertheless, Fisher's alpha was preferred because it is independent of sample size and assumes a parametric distribution of relative abundances for the population from which the sample is drawn (Rosenzweig, 1995).

Explanatory variables

For practical reasons, those variables (e.g. slope, elevation, precipitation and soil type) used as surrogate measures of processes and factors that might have a direct effect on species diversity and composition (e.g. incoming radiation, water vapour deficit in the air, soil drought and available pool of nutrients) are referred to as 'explanatory'. The explanatory variables were chosen based on their potential to account for factors that might explain patterns of tree diversity at local and regional scales, and based on their availability and degree of coverage in the study area. The set used in the analysis contains 15 continuous variables, including two climatic variables, a soil fertility/quality index, two spectral variables, two measures of environmental heterogeneity, two topographical variables, four human disturbance-related variables, and two spatial variables (Table 1).

Values of climatic variables were generated for 1 \times 1 km cells using interpolation techniques (Golicher *et al.*, 2006). Daily measurements of maximum and minimum temperature, and precipitation, which date back to 1950, were available for 212 climate stations in the state of Chiapas. Monthly precipitation values were obtained using iterated universal kriging. The surfaces of monthly maximum and minimum temperatures were generated using linear models and by fitting the residuals by universal kriging after correcting for altitudinal effects (D. J. Golicher, unpublished data). After assessing the redundancy among closely correlated variables, we averaged the monthly measurements of precipitation and temperature and reduced the initial 36 climatic

Table 1 Variables used in the analysis of determinants of tree diversity in the Highlands of Chiapas, Mexico

Variable	Source of data
Normalized Difference Vegetation Index (NDVI)	2000 ETM+ images, bands 3 and 4
Normalized Difference Infrared Index (NDII)	2000 ETM+ images, bands 3 and 5
NDVI within-site heterogeneity	2000 ETM+ images, bands 3 and 4
NDII within-site heterogeneity	2000 ETM+ images, bands 3 and 5
Mean annual precipitation	Interpolated maps of meteorological data
Mean annual temperature	Interpolated maps of meteorological data
Elevation	1 : 50,000 digital elevation model
Slope	1 : 50,000 digital elevation model
Soil quality/fertility	1 : 250,000 digitized map
Road density	1 : 50,000 digitized road map
Canopy	Classified 2000 ETM+ images
Human population density	Digitized 2000 population censuses
Distance to forest edge	Classified 2000 ETM+ images
Latitude	UTM x -coordinates
Longitude	UTM y -coordinates

variables to two variables: mean monthly precipitation and temperature (using maximum and minimum values).

We generated an index of soil fertility/quality following González-Espinosa *et al.* (2004), which was based on an interpretation of the physical and chemical properties of the soil taxa as described in the legend of the FAO–UNESCO maps (Duchaufour, 1987) and information of soil texture and physical phases available from the maps.

The Normalized Difference Vegetation Index (NDVI) was calculated using the visible and near-infrared bands of Landsat Enhanced Thematic Mapper (ETM+) images recorded during the peak of the dry season in 2000 (path 21 row 48, path 21 row 49 and path 22 row 48). The NDVI is sensitive to photosynthetically active biomass and is correlated with leaf area index and net primary productivity (Cramer *et al.*, 1999). The Normalized Difference Infrared Index (NDII), which is related to the relative water content of leaves (Gao, 1996), was calculated using the near-infrared and middle-infrared bands of the ETM+ images. Each of the indices were averaged using a 3×3 pixel window centred over each pixel. Based on NDVI and NDII, we obtained measures of heterogeneity by applying a standard deviation filter with a 5×5 pixel window centred over each pixel. All of the calculations were performed using Idrisi 32 (Eastman, 2001).

Values of elevation and slope were extracted from a 1 : 50,000 digital elevation model. Four variables were used as measures of human disturbance (Table 1). Road density was calculated within a 500-m radius of the centre of each plot using relative weightings for paved and unpaved roads. Canopy was based on classified ETM+ Landsat imagery (Cayuela *et al.*, 2006a) and calculated as the proportion of forest cells within a 500-m radius of the centre of each plot. Estimates of human population density were obtained by partitioning the study area into a meaningful tessellation of Thiessen polygons and dividing the total population in each settlement by the area of its corresponding polygon. Distance to forest edge was calculated using the classified ETM+ Landsat imagery.

Modelling α tree diversity

To obtain a predictive model of α tree diversity based on selected explanatory variables (Pausas, 1994; Austin *et al.*, 1996) we used generalized linear models (GLM) (see Crawley, 1993). With respect to linear models, an advantage of GLM is that they can deal with a range of distributions in the error component. We assumed a gamma error distribution for α tree diversity related to the set of predictor variables via a logarithmic link function. Fisher's alpha index is a rather artificial measure and it is difficult to define a model that contains a hypothesis about the way in which randomness enters into the system. In those cases, the gamma distribution is very useful because of its flexibility.

Deviance is the measure of discrepancy used by GLM to assess the model's goodness of fit. Deviance reduction or explained deviance (D^2) is estimated as:

$$D^2 = (\text{null deviance} - \text{residual deviance})/\text{null deviance}.$$

We followed a step-by-step model-building procedure. To avoid multicollinearity, some of the explanatory variables that were highly correlated ($|r| > 0.8$) were excluded before building the model. NDVI and NDII ($r = 0.88$, $P < 0.0001$), and NDVI and NDII within-site heterogeneities ($r = 0.91$, $P < 0.0001$) were highly correlated. We selected NDVI because it is widely used and is more closely related to the diversity–productivity relationship, which is a subject of debate in the scientific community. Elevation was strongly correlated with mean temperature ($r = 0.87$, $P < 0.0001$). We used mean temperature because, unlike elevation, it has a direct physiological effect on species performance (Guisan & Zimmermann, 2000; Pausas & Austin, 2001).

In the first step of building the model, tree diversity was examined in relation to each of the explanatory variables separately. The relationships between species richness and environmental variables are often curvilinear (Austin, 1980); therefore, we explored the effects of the quadratic and cubic terms of the explanatory variables in tree diversity. Spatial coordinates were incorporated into the model by adding all of the terms for a cubic trend surface regression (Legendre, 1993; Legendre & Legendre, 1998), which ensures that complex features, such as patches and gaps, are correctly described. We selected either the linear, quadratic or cubic function of each explanatory variable by statistically testing their reduction in the Akaike Information Criterion (AIC) as compared to the null model (Akaike, 1973). AIC is a measure of model optimality that trades off complexity and the fit of the model to the data. The proportion of explained deviance was calculated for each model.

In the second step of the analysis, all of the selected terms of the variable that accounted for the most important change in deviance were entered into the model. To test the significance of all of the remaining variables, each was added to the model, one by one. After each new variable was included, the significance of the terms previously entered was tested using a backward stepwise selection procedure based on exact AIC. The procedure was repeated, iteratively, until no significant explanatory variables remained ($P \leq 0.05$). Finally, the spatial variables were included in the model and tested for statistical significance.

In each step of building the model, we examined the deviance, the significance of the coefficients, the normal probability plot, the Cook statistics and the leverages. To avoid the influence of outliers in the regression procedure, observations that exhibited simultaneously high leverage and large Cook statistic values were excluded from the analysis.

After the model was reduced for optimality, a spatial correlogram based on Moran's Index of autocorrelation was used to explore the autocorrelation of the raw diversity data and the residuals of the model at different geographical distances (Diniz-Filho *et al.*, 2003). If spatial autocorrelation was detected in a distance class, we assumed that there were spatially patterned variables not included in the model that contributed to explaining α tree diversity.

To validate the model, we used a leave-one-out, cross-validation procedure. Given a data set of size n , we recalculated the model $n - 1$ times, leaving out one datum in each turn. To produce a predicted Fisher's alpha score, each of the generalized linear models based on the $n - 1$ data was applied to the excluded

datum. We tested the predictive power of the model using the mean of the percentage absolute errors of prediction (E), given by

$$E = \frac{1}{n} \sum_{i=1}^n \frac{|y_i - \hat{y}_{(i)}|}{y_i} \times 100$$

where y_i is the observed species richness and $\hat{y}_{(i)}$ is the predicted value for y_i when the i th observation is excluded (Davidson & Hinkley, 1997).

Patterns of floristic similarity

β diversity was measured using the floristic similarities between pairs of plots. We ran Mantel tests of matrix correspondence to determine whether similarities in floristic composition were correlated with similarities in climatic variables, edaphic conditions, NDVI, spectral variability (NDVI within-site heterogeneity), topography, human disturbance-related variables and geographical distance. All of the numerical analyses explained below are based on resemblance matrices. The floristic resemblance matrix was calculated using the Sørensen Index. All of the other resemblance matrices were based on Euclidean distances. We used the standardized form of the Mantel test, which computes the Pearson correlation coefficient between the cell values of two resemblance matrices. To avoid problems associated with autocorrelation and non-normal distributions of the measured variables, the statistical significance of each correlation was determined using a Monte Carlo permutation test. To test for statistical significance at the $P < 0.001$ level, 1000 permutations were computed for each correlation.

To determine the subset of variables that had the maximum correlation with community dissimilarities, we selected the combinations of explanatory variables that contributed the most to explaining the variability in the floristic resemblance matrix (based on the work by Clarke & Ainsworth, 1993). Initially, all of the variables used in modelling α tree diversity were included. Then, the function found the best correlation between community dissimilarities and distance matrices based on different combinations of explanatory variables and, for each size of subsets, output the best result. In this study, we reported the correlation coefficients for the final models.

Selecting sites for conservation

Hierarchical clustering was performed using the matrix of dissimilarities for the best subset of explanatory variables selected to maximize correlations with floristic dissimilarities. We used Ward's method because it generates more compact and representative clusters. Using the height distances of the hierarchical clustering, we classified the plots in an increasing number of clusters, from three to 10. To select the number of clusters that maximize floristic differences between groups, we used analyses of similarities (ANOSIM), which operate directly on a dissimilarity matrix by using the rank order of dissimilarity values (Clarke, 1993). The ANOSIM statistic R is based on the differences of mean ranks between groups and within groups. R will be in the interval -1 to 1 , and a value of 0 indicates completely random grouping. The statistical significance of observed R was determined by permuting the grouping vector and obtaining the empirical distribution of R under the null-model (Oksanen *et al.*, 2005).

Finally, to predict plot membership in a cluster when the information in the explanatory variables (i.e. those selected to maximize correlations with floristic dissimilarities) is considered, we used classification and regression trees (CART). CART can perform univariate splits and examine the effects of predictors, one at a time. To classify all of the pixels in the study area, we used splitting rules, which allowed us to define unexplored areas of complementary floristic composition based on inference made using the best subset of explanatory variables, and to select sites of high predicted α tree diversity within each floristic region. All of the statistical analyses were performed with the R environment (R Development Core Team, 2004). Mantel tests, ANOSIM, and CART were run using the R 'vegan' package (Oksanen *et al.*, 2005).

RESULTS

Predicting spatial patterns of α tree diversity

With the exception of soil fertility/quality, all of the explanatory variables were statistically significant as linear, quadratic or cubic

Table 2 Explanatory variables (abbreviation in parentheses) recorded for 204 sample plots in the Highlands of Chiapas, Mexico. AIC = Akaike Information Criterion; d.f. = degrees of freedom; D^2 = deviance reduction; Sign = sign of the fitted parameter for each variable at $P = 0.01$

Variable	Selected terms	Deviance	AIC	d.f.	D^2	Sign
Null model		70.6	931.3	203		
Mean temperature (T)	T + T ² + T ³	63.3	914.0	200	0.10	++-
Mean precipitation (Pr)	Pr + Pr ³	63.2	911.5	201	0.10	+ -
Soil fertility/quality (SFQ)			934.3			
NDVI	NDVI ² + NDVI ³	59.9	900.1	201	0.15	++
NDVI within-site heterogeneity (Het)	Het	68.6	927.1	202	0.02	-
Slope (Sl)	Sl	66.2	919.6	202	0.06	+
Road density (RD)	RD ² + RD ³	67.8	926.7	201	0.04	+ -
Canopy (CC)	CC	69.0	928.4	202	0.02	+
Human population density (PD)	PD + PD ²	67.0	924.3	201	0.05	+ -
Distance to edge (DE)	DE + DE ²	69.0	930.4	201	0.02	+ -
Longitude (Lon)	Lat + Lat ³ + Lon × Lat ²	52.3	873.3	200	0.26	+ - -
Latitude (Lat)						

Table 3 Summary of the step-by-step GLM model selection for the prediction of α tree diversity in the Highlands of Chiapas, Mexico. AIC = Akaike Information Criterion; d.f. = degrees of freedom; and D^2 = deviance reduction

Variable	Terms	Deviance	d.f.	AIC	D^2	<i>t</i> -value	Coefficients	SE
Null model		67.8	199	911.0				
Intercept						23.17***	1.193	0.051
Mean precipitation	Pr	61.7	198	893.2	0.09	5.94***	0.236	0.040
Mean temperature	T ²	51.6	197	857.6	0.15	4.50***	0.180	0.040
NDVI	NDVI ³	48.2	196	845.3	0.05	2.34*	0.061	0.026
	NDVI ²	44.4	195	830.6	0.06	3.12**	0.144	0.046
Canopy	CC	41.1	194	816.6	0.05	3.59***	0.141	0.039
Slope	SI	40.1	193	813.3	0.02	2.12*	0.071	0.034
NDVI within-site heterogeneity	Het	38.7	192	808.0	0.02	1.97*	0.078	0.039
Spatial variables	Lon × Lat ²	37.9	191	805.6	0.01	-2.10***	-0.071	0.034
Final model		37.9	191	805.6	0.44			

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

functions when tested separately (Table 2). In addition, when latitude and longitude were included, variability in α tree diversity (Fisher's alpha) depended on the geographical position of the plot. A site's tree diversity tended to be more similar to those of sites close by, than to those of sites farther away. Alone, that model has little predictive value and, where possible, spatial coordinates should be replaced by explanatory variables that account for these spatial variations (e.g. climatic variables). Variables were entered into the model based on the extent to which they influenced the deviance; therefore, NDVI was entered first, the linear and cubic terms of mean precipitation were entered next, followed by all of the terms of mean temperature, and so on, until the model was iteratively fitted (Table 3). Finally, the spatial terms were added. The model accounted for 44% of the observed variability in α tree diversity, which was most strongly related to mean precipitation, mean temperature, NDVI and canopy (Table 3).

Spatial autocorrelations for the raw diversity data were significant for most lag distances, although the pattern was very erratic (Fig. 2a). The inclusion of spatially structured variables, such as mean annual precipitation, in the model reduced the spatial autocorrelation in most distance classes (Fig. 2b). The mean of the percentage absolute errors of prediction obtained in the cross-validation test was 45.6% and the residual analysis did not reveal aberrant features.

Correlations between distance matrices

Correlations between the floristic similarity matrix and the similarity matrices based on different sets of environmental, human disturbance-related, and spatial variables are shown in Table 4. Floristic composition was most strongly correlated with climatic variables, and correlations with matrices based on geographical distance and topographical features were high (Table 4). NDVI and species similarity were weakly, but significantly, correlated. Correlations with the similarity matrices of soil condition, spectral variability and human disturbance-related variables were close to zero. Statistical significance, however, should be interpreted with care because distance measurements were not independent.

Table 4 Mantel test correlations between floristic similarities and similarities in environmental, human disturbance-related and spatial variables in 204 sample plots in the Highlands of Chiapas, Mexico

Variable	Floristic similarities	
	<i>r</i>	95% CI
Climatic variables	0.50***	± 0.05
Soil fertility/quality	0.07*	± 0.03
NDVI	0.17***	± 0.03
NDVI within-site heterogeneity	-0.02	± 0.05
Topographical features	0.40***	± 0.04
Human disturbance	0.07*	± 0.05
Geographical distance	0.43***	± 0.04

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Table 5 Mantel tests for best possible subsets of explanatory variables (from 1 to 10) that maximize correlations with floristic dissimilarities among sample plots in the Highlands of Chiapas, Mexico. The number of variables that are selected to maximize correlations with floristic dissimilarities has been highlighted in bold. See Table 2 for explanations of abbreviations

Size	Best subsets of explanatory variables	<i>r</i>
1	T	0.50
2	Pr + T	0.51
3	Pr + T + NDVI	0.50
4	Pr + T + NDVI + SI	0.49
5	Pr + T + NDVI + SI + CC	0.47
6	Pr + T + NDVI + SI + RD + CC	0.43
7	Pr + T + SFQ + NDVI + SI + RD + CC	0.39
8	Pr + T + SFQ + NDVI + Het + SI + RD + CC	0.35
9	Pr + T + SFQ + NDVI + Het + SI + PD + RD + CC	0.30
10	Pr + T + SFQ + NDVI + Het + SI + PD + RD + DE + CC	0.27

The selection of subsets of explanatory variables that had the best correlations with community data indicated that a high proportion of the variation in floristic similarity could be explained by one to three variables (Table 5). As predicted by Mantel tests,

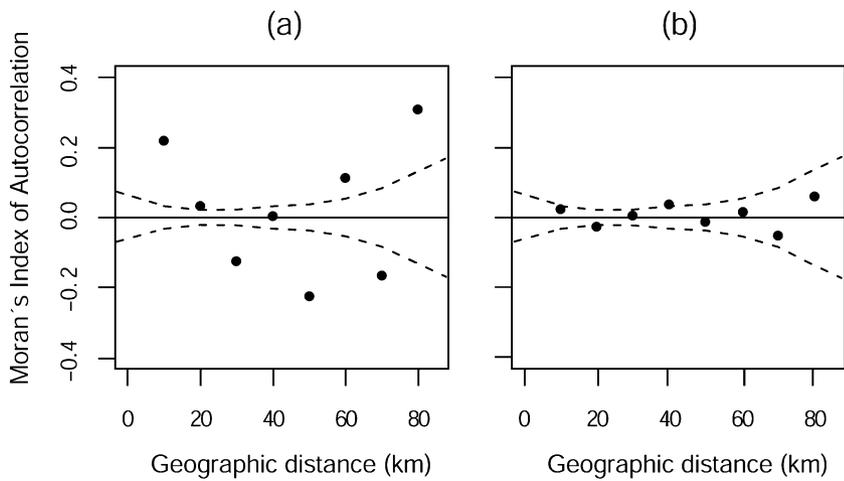


Figure 2 Spatial correlograms based on Moran's Index of spatial autocorrelation for (a) Fisher's alpha values, and (b) residuals after fitting the significant variables in the model shown in Table 3. Dashed lines represent 95% standard error intervals for Moran's test.

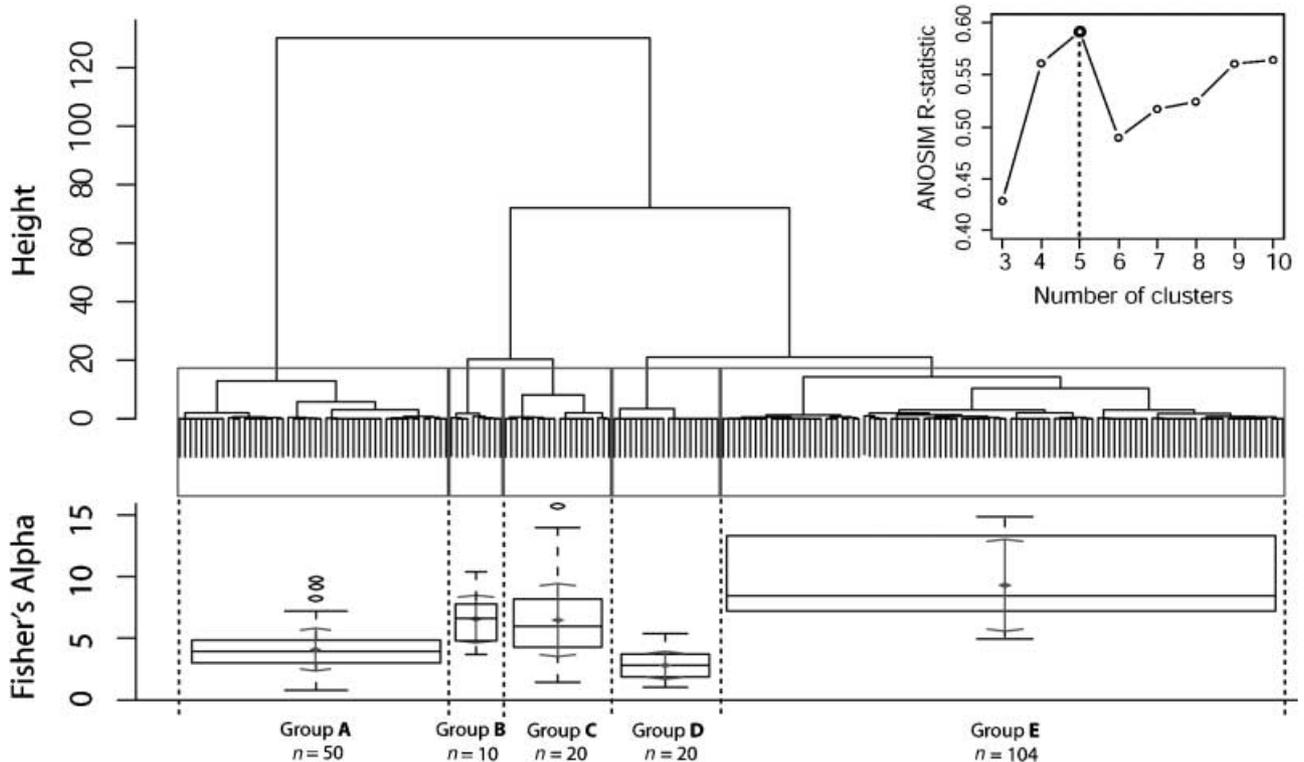


Figure 3 Dendrogram of sample plots created by a hierarchical clustering using Ward's method as the linkage rule and the squared Euclidean distance as the measure of similarity. The variables included in the analyses are mean precipitation and temperature. ANOSIM R-statistic (upper right) shows the relative floristic differences between groups for an increasing number of clusters (3–10). Five groups maximize the floristic differences between groups. These groups are represented in boxes. Box-plots of α diversity (Fisher's Alpha) are presented for each of the floristic groups, and arrows indicate the mean and standard deviation.

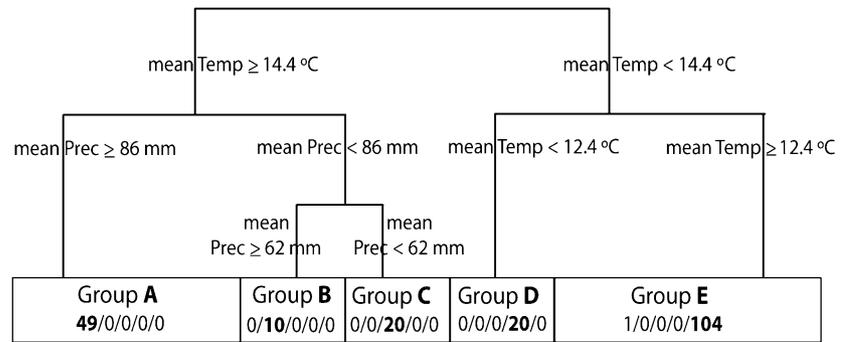
mean precipitation and temperature explained 51% of the variation in species composition. Models that included more than three variables progressively decreased their correlation with floristic similarity.

Prioritizing areas for conservation

We took a variable number of clusters (3–10) and compared floristic dissimilarities between the groups at each clustering.

Five clusters maximized the floristic differences among groups (ANOSIM R-statistic = 0.59, $P = 0.001$), and these floristic groups also exhibited differences in α tree diversity based on Euclidean distances (ANOSIM R-statistic = 0.26, $P = 0.001$) (Fig. 3). Those differences, however, were less than the floristic dissimilarities, which is a desirable property because we wanted to use a single model for predicting tree diversity across the landscape, rather than a model for each of the floristic groups.

Figure 4 Classification and regression tree (CART) for the five groups of vegetation using mean precipitation and temperature as predictor variables. Numbers under each of the group names indicate the number of sample plots belonging to each of the five floristic groups that have been allocated within that group.



Patterns of α tree diversity

Climatic variables had the strongest relationship with α tree diversity (Table 3). Typically, climate has been interpreted as a strong predictor of broad-scale patterns of diversity (Wright *et al.*, 1993; Austin *et al.*, 1996; Hawkins *et al.*, 2003). Our results might be dependent on the spatial scale of our analysis (Willis & Whittaker, 2002), but they show that, to some extent, climatic gradients can explain α diversity, which indicates that broad-scale patterns can be replicated across an altitudinal gradient at finer spatial scales. Precipitation and temperature contribute to define actual evapotranspiration, which possibly influences plant growth. Positive correlations between tree species richness in tropical lowlands and annual precipitation have been interpreted as support for the diversity–energy hypothesis (Gentry, 1982, 1988; Givnish, 1999), although the use of this variable independent of temperature has been criticized (Francis & Currie, 2003).

If the NDVI is interpreted as a surrogate for the amount of biologically available energy (Rosenzweig, 1995), we can assume that greater biomass increases biological heterogeneity, which, in turn, favours specialization and promotes the local coexistence of species (Wright *et al.*, 1993; Scheiner & Rey Benayas, 1994; Mittelbach *et al.*, 2001; González-Espinosa *et al.*, 2004; Seto *et al.*, 2004). Correlations between NDVI and species diversity, however, have been mostly emphasized in areas that have relatively structurally homogeneous vegetation (Jakubauskas & Price, 1997). In areas where vegetation structure is heterogeneous, structural, rather than species differences, might predominate in imagery (Nagendra, 2001), which makes it difficult to predict spatial patterns of tree diversity based solely on remote sensing data (see also Tuomisto *et al.*, 2003). Furthermore, NDVI should be interpreted with caution because it summarizes the energy used and stored (plant biological activity) over a particular period. Multi-temporal data might provide additional information on intra- and inter-annual shifts in vegetation and support more detailed models that incorporate time lags and temporal changes in productivity (Oindo & Skidmore, 2002).

Studies have demonstrated positive, negative and hump-shaped relationships between soil characteristics and plant diversity at meso- and landscape scales (e.g. Huston, 1980; Clinebell *et al.*, 1995; Clark *et al.*, 1999; Rey Benayas & Scheiner, 2002; González-Espinosa *et al.*, 2004). In our study, soil fertility/quality did not explain a significant amount of variability in α tree diversity, which might be, at least partially, a consequence of the low resolution of the regional soil maps from which our soil fertility/quality index was derived. Nevertheless, our results are consistent with those of Tuomisto *et al.* (2003), who found no correlation between plant species richness and soil characteristics, such as texture or cation content, when data were analysed at fine-grained scales.

In our study, within-site heterogeneity was positively related to α tree diversity (Table 3), but it accounted for a very small proportion of the variation, which might be because the effect of environmental heterogeneity is highly scale-dependent (Phillips *et al.*, 2003; Seto *et al.*, 2004). At large spatial scales, the presence of environmental or resource heterogeneity can create high niche

diversity (e.g. Pollock *et al.*, 1998; Gould, 2000; Pausas *et al.*, 2003); at the local scale, those factors might be secondary in importance to resources and conditions (Pausas & Austin, 2001).

Canopy (a surrogate measure of human disturbance) and slope were positively correlated with α tree diversity. Canopy might indicate a buffering effect of the surrounding forest on tree diversity through a reduction in edge effects. Other human disturbance-related variables were excluded from the final model; yet, they did not provide a direct measure of the type and intensity of human impact (e.g. number of stumps, logs). The relationship between α tree diversity and slope might be due to the lower accessibility of sloped areas and therefore less intensive human disturbance.

The reduction in spatial autocorrelation in the residuals compared to the raw diversity data (Fig. 2) reflected the collinearity of some of the environmental variables, particularly climatic variables, and space (Currie *et al.*, 1999). Diversity measurements are based on the relative abundance of species; therefore, local, non-spatially structured biotic factors, such as interspecific competition, might account for some of the unexplained variability in α tree diversity.

Patterns of floristic similarity

In the Highlands of Chiapas, similarity in tree composition was most strongly correlated with climatic variables and NDVI. Given the correlations between mean annual precipitation and temperature and elevation, and the spatially structured component of these variables, it is not surprising that both topographical features and geographical distance were also highly correlated with similarity in tree composition. Tuomisto *et al.* (2003) showed that reflectance patterns in satellite images could be used to predict landscape-scale patterns in Amazonian rain forests, which was not completely true in the Highlands of Chiapas. In our study area, there were pronounced altitudinal and climatic gradients and different vegetation types could be recognized (Cayuela *et al.*, 2006a); thus, compared to climatic variation, spectral variation in the satellite images was a poor predictor of floristic differences at the landscape scale.

Identifying priority areas for conservation

Mexico is a megadiverse country, but it has high rates of deforestation and ecological impoverishment (CONABIO, 1999). In recent decades, the Highlands of Chiapas have experienced one of the most rapid rates of deforestation in the world — average annual rates of 2–5% (Ochoa-Gaona & González-Espinosa, 2000; Cayuela *et al.*, 2006b) — which poses a severe threat to the conservation of forest habitats and a risk to local human welfare (Costanza *et al.*, 1997). Mapping of α and β diversity can contribute to the conservation of natural resources by helping to identify species-rich hotspots and areas that include as many of the species as possible (Myers, 1990; Gentry, 1992; Araújo, 1999; Rey Benayas & de la Montaña, 2004). Further research should be directed toward identifying patterns of species endemism (Gentry, 1992) and rarity (Williams *et al.*, 1996; Rey Benayas

et al., 1999; Rey Benayas & de la Montaña, 2004) because they are largely independent of patterns of α diversity.

Our model approximates the spatial configuration of α and β tree diversity in south-eastern Mexico. The predictions of floristic spatial patterns indicated that there are three main floristic regions (Fig. 5a) that correspond to major climatic trends. In the north-east, there is abundant precipitation and a mild winter season (group A); in the central region, there is a cold and dry winter season (group E); and, in the south-west, there is a dry and warm winter season (Group B). In the Highlands of Chiapas, biodiversity hotspots chiefly occur in ridge-top montane forests in the central and northern ranges, and in the transitional forests that lead towards the lower depression in the south-western range of the study area (Fig. 5b). In general, our study provides a first step toward identifying sites that maximize tree diversity. The prioritization of areas of high α diversity within each floristic region identified the location of tree diversity hotspots across the study area (Fig. 5c). Given the accelerated pace of habitat loss, at least a small portion of the priority areas we have identified should be reserved for the preservation of the original vegetation. Unfortunately, no environmental or conservation policy is currently being implemented in the region.

In conclusion, we found that: (1) climatic variation is a good predictor of α and β tree diversity at the landscape scale; (2) NDVI is a good descriptor of α tree diversity, but not of β diversity in the study area; and (3) both α and β tree diversity show different spatial patterns and therefore both are needed for effective conservation. Studies like the one that we have presented here will help to promote regional and local conservation strategies.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online from www.blackwell-synergy.com/loi/geb

Appendix S1 Tree species list from study area in the Highlands of Chiapas, Mexico