

Capítulo 6

Predicción de la diversidad de árboles y priorización de sitios para la conservación

Este capítulo reproduce el texto del siguiente manuscrito, a excepción de la sección de Métodos, que aparece resumida:

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Resumen

Los bosques tropicales están desapareciendo en muchas regiones del mundo debido a la deforestación y al uso no sostenible de los recursos forestales. Ello exige la implementación de estrategias de conservación que persigan la conservación de la biodiversidad forestal. Los Altos de Chiapas, en el sureste mexicano, tiene una de las tasas de deforestación más altas descritas hasta el momento a nivel mundial. En este estudio se intenta explicar y predecir la diversidad local de árboles y la complementariedad de los distintos tipos de vegetación existentes en la zona. Uno de los principales objetivos que se persigue es ilustrar la potencialidad de un método que combine información procedente de distintas fuentes (datos de campo, imágenes de satélite, SIG) para evaluar y monitorear la diversidad forestal a nivel de paisaje.

Para ello registramos la composición de especies arbóreas en 204 inventarios forestales (de 1000 m² cada uno) y medimos distintas variables ambientales, espaciales y relacionadas con la perturbación humana a partir de información contenida en SIG e imágenes de satélite. Se utilizaron los siguientes procedimientos analíticos: (1) modelos generalizados lineales (GLM) para predecir la diversidad local de árboles (alpha de Fisher); (2) tests de Mantel para averiguar si las similitudes en composición florística entre pares de inventarios se correlacionan con las similitudes en las distintas variables explicativas; y (3) un método que combina la diversidad local y la complementariedad para definir áreas prioritarias para la conservación.

El modelo final explicaba el 44% de la variabilidad total en diversidad local, que estaba relacionada principalmente con la precipitación, la temperatura, el NDVI, y la apertura del dosel arbóreo (todas las relaciones fueron positivas, y cuadráticas para la temperatura y el NDVI). La similitud en composición florística estaba positivamente correlacionada con las variables climáticas y el NDVI.

Estos resultados fueron usados para: (1) localizar y priorizar áreas que no han sido exploradas con valores altos de diversidad de árboles para su conservación; y (2) mostrar la contribución de diversas formaciones vegetales en la configuración de la biodiversidad regional. Este método puede ser de gran utilidad para evaluar estrategias de conservación a nivel regional y local en áreas tropicales amenazadas y de difícil acceso en cualquier parte del mundo.

Modelling tree diversity in a highly fragmented tropical montane landscape for conservation prioritisation

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Abstract

Aim There is an urgent need for conservation interventions in threatened tropical forest regions. We explain and predict the spatial variation of local tree diversity and complementarity in a tropical montane landscape under a high deforestation rate. A major goal was to illustrate the potentiality of a method that combines data from different sources (field data, remote sensing imagery, and GIS) for evaluating and monitoring forest diversity over broad scales in large unexplored areas.

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

Methods We field inventoried tree species composition in 204 field plots (1000 m² each) and measured different environmental, human disturbance-related, and spatial variables based on remote sensing data and GIS. We used: (1) GLM with a gamma error distribution to obtain a predictive model of local tree diversity (Fisher's alpha) based on selected explanatory variables; (2) Mantel tests of matrix correspondence to find out whether similarities in floristic composition correlated with similarities in the explanatory variables; and (3) an approach that combines local tree diversity and complementarity to define priority areas for conservation.

Results The final model for local tree diversity explained 44% of the total variability, which was mainly related to precipitation, temperature, NDVI, and canopy openness (all relationships were positive, and quadratic for T and NDVI). There were not spatially structured regional factors that had been ignored. Similarity in tree composition correlated positively with climate and NDVI.

Main conclusions These results were used to: (1) locate and prioritise non-explored areas with high values of tree diversity for their conservation; and (2) show the importance of several vegetation formations in the configuration of the region's biodiversity. This method can be particularly useful to assess regional and local conservation strategies in poorly surveyed and often at risk tropical areas anywhere in the world, where accessibility is usually limited.

Keywords: complementarity; conservation prioritisation; Fisher's alpha; generalised linear model; Highlands of Chiapas; hotspot; Mantel test; spatial autocorrelation; tree diversity.

1. Introduction

The current scale of deforestation in tropical regions and the large areas of degraded lands now present underscore the urgent need for interventions to restore and protect biodiversity, ecological functioning, and the supply of goods and ecological services previously 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 this response, the focus has largely been on making selection of candidate sites as representative and comprehensive as possible (Williams *et al.* 1996, Araújo 1999, Justus & Sarkar 2002). The quantification of species-environment relationships has recently gained importance as a tool to assist decision-making related to nature conservation at the landscape level (Stockwell & Peterson 2003). This task is not simple because diversity can be measured in a variety of ways and at different scales. The processes that determine patterns of diversity can be also varied, including phylogenetic, historical, biogeographic, and environmental processes (Brown & Lomolino 1998, Rey Benayas & Scheiner 2002). Human activities may also play a role in shaping 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 habitat types) that may become more relevant for explaining patterns of species diversity (Kerr & Packer 1997, Wohlgemuth 1998, Rahbek & Graves 2001).

Geographic Information Systems (GIS) and remotely sensed data are useful to extrapolate information from ground-based ecological studies to large and non-explored areas. Mapping of plant diversity estimates can be accomplished by analysing variation of some spectral signals (e.g. the Normalized Difference Vegetation Index, NDVI), and correlating

this 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). Climate, biophysical, land cover data, as well as factors related to human disturbance, can be also used to predict and explain patterns of species diversity (Lobo & Martín-Piera 2002).

Point diversity, however, is not the solely valuable property to be evaluated for conservation purposes. Some habitats may contain a low number of species but being still relevant due to the presence of species or species assemblages that are not found in highly diverse habitats. Representativeness of habitats is therefore also a desirable property of conservation networks (Araújo 1999).

In this study we propose a methodology that is applied to predict the spatial variation of local tree diversity and complementarity in a tropical montane region. Our models include information obtained at different spatial scales from field sampling, satellite imagery, and GIS. As an illustrative example, we studied the Highlands of Chiapas, southern Mexico. This region is notable because of its high biodiversity and environmental heterogeneity (Ceballos *et al.* 1998, Wolf & Flamenco 2003, González-Espinosa *et al.* 2004). Chronic intensification of land use, particularly after occurrence of a violent conflict in 1994 (the Zapatista riot), has caused much deforestation and forest disturbance and hence may have a negative impact on biodiversity (González-Espinosa 2005).

The specific objectives of this study are: (i) to ascertain the determinants of the spatial variation of local tree diversity; (ii) to propose a predictive model which enables us to identify less surveyed areas of high local tree diversity; (iii) to explore the factors that determine complementarity among floristic groups; and (iv) to prioritise areas for conservation using both diversity and complementarity criteria and information from different sources. Our study makes no mechanistic hypotheses about the processes that shape the spatial patterns of tree diversity and complementarity, but seeks to provide post hoc explanations of such processes. The models we propose can be the basis for detecting tracts of land worthy for

conservation, establishing protected areas and conduct forest restoration programs. By identifying patterns of tree diversity and complementarity, and understanding the effect of their possible determinants at this scale, this study may contribute to foster conservation and land management tools and actions in other tropical regions of the world (Lamb *et al.* 2005).

2. Material and methods

Study area

The study area covers the Highlands of Chiapas, Mexico (**Figure 4.1**). A detailed description can be found in **chapter 4**.

Field sampling and tree diversity estimation

Floristic inventories were accomplished for 204 circular plots of 1000 m² each distributed in different forest fragments (**Figure 2.2, chapter 2**); 168 plots were sampled by us from January 2003 to May 2004. Extra data from 36 plots collected in 1998 following the same sampling protocol (Galindo *et al.* 2002, L. Galindo, unpublished data) were also analysed in this study. In each plot, all trees with dbh larger than 10 cm were identified to species and counted. Access to forests required permission from local inhabitants, which was not always given. Despite this fact, the study fragments were well spaced over the broader landscape and provide a valuable description of the regional diversity. The number of observed tree species per plot ranged between 2 and 28 and averaged 13.3 ± 5.2 . The number of stems per plot ranged between 22 and 211 and averaged 97.2 ± 36.5 . All locations were geo-referenced. Mean distance between plots was 25.2 km (SD = ± 15.3 km). The final database included 230 native tree species (see **Appendix 6.1**). Fisher's alpha was calculated for each sample. This estimator of diversity was highly correlated with the observed number of species ($r = 0.91$, p -value < 0.0001). Nonetheless Fisher's alpha was selected 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, we will use the term 'explanatory' to refer to those variables (e.g. slope, elevation, precipitation, soil type) used as surrogates of processes and factors that may have a direct effect on species diversity and composition (e.g. incoming radiation, water vapour deficit in the air, soil drought, available pool of nutrients). The explanatory variables were selected to take into account relevant information to explain patterns of tree diversity at both local and regional scales, but also with regard to their availability and degree of coverage for the study area. The selected set included 15 continuous variables (**Table 6.1**): two climatic variables (mean temperature and precipitation); a soil fertility/quality index; two spectral variables (Normalized Difference Vegetation Index (NDVI) and Normalized Difference Infrared Index (NDII)); two variables of environmental heterogeneity (NDVI and NDII in-site heterogeneity); two topographical variables (elevation and slope); four variables related to human disturbance (road density, canopy openness, human population density, and distance to forest edge); and two spatial variables (latitude and longitude).

Climatic variables were generated for 1x1 km cells using interpolation techniques (Golicher *et al.* 2006). Measurements of maximum and minimum temperature, and precipitation were available on a daily basis since 1950 for 212 climate stations in the state of Chiapas. Monthly precipitation values were obtained using a method that involves iterated universal kriging. Surfaces of monthly maximum and minimum temperature were generated by using linear models and fitting the residuals by universal kriging after accounting for altitudinal effects (D.J. Golicher, unpublished data). Mean precipitation and temperature were then calculated by averaging monthly data.

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

Table 6.1. Variables used for the analysis of determinants of local tree diversity.

Variable	Origin of data
Normalised Difference Vegetation Index (NDVI)	2000 ETM+ images, bands 3 and 4
Normalised Difference Infrared Index (NDII)	2000 ETM+ images, bands 3 and 5
NDVI in-site heterogeneity	2000 ETM+ images, bands 3 and 4
NDII in-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 digitised map
Road density	1:50,000 digitised road map
Canopy openness	Classified 2000 ETM+ images
Human population density	Digitised 2000 population censuses
Distance to forest edge	Classified 2000 ETM+ images
Latitude	UTM x-coordinates
Longitude	UTM y-coordinates

The Normalized Difference Vegetation Index (NDVI) was calculated from the visible and near-infrared bands of Landsat Enhanced Thematic Mapper (ETM+) images acquired in 2000, during the peak of the dry season (path 21 row 48, path 21 row 49, path 22 row 48). NDVI is sensitive to photosynthetically active biomass, correlated with leaf area index, and related to net primary productivity (Cramer *et al.* 1999). The Normalized Difference Infrared Index (NDII) was calculated from the near-infrared and middle-infrared bands of the ETM+ images. This index is related to the relative water content of leaves (Gao 1996). Both indices were averaged using a 3x3 pixel size window centred over each pixel. Based on NDVI and NDII, we obtained measures of heterogeneity around the plots sampled for trees by applying a standard deviation filter with a 5x5 pixel size window centred over each pixel. All calculations were performed with Idrisi 32 (Eastman 2001).

Elevation and slope were extracted from a 1:50000 digital elevation model. Four variables were used as measures of human disturbance (**Table 6.1**). Road

density was calculated in a 500 m radius from each plot using relative weights for paved and unpaved roads. Canopy openness was calculated as the proportion of forest cells in a 500 m-radius circle centred on each plot based on classified ETM+ Landsat imagery. Human population density was obtained by dividing up the study area according to the location of human settlements into a meaningful tessellation of Thiessen polygons. Population density was then calculated by dividing total population in each settlement by the area of its corresponding polygon. Distance to forest edge was computed based on the classified ETM+ Landsat imagery.

Modelling local tree diversity

We used generalized linear models (GLM, see Crawley 1993) to obtain a predictive model of local tree diversity based on selected explanatory variables (Pausas 1994, Austin *et al.* 1996). An advantage of GLM with respect to linear models is that they can deal with a range of distributions for the error component. We assumed a gamma error distribution for

local tree diversity related to the set of predictor variables via a logarithmic link function. Because the Fisher's alpha index is a rather artificial tool, it is difficult to define an appropriate model that contains a hypothesis about the way in which randomness enters into the system. The gamma distribution is very useful in these cases due to its flexibility.

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

$$D^2 = \frac{\text{Null deviance} - \text{Residual deviance}}{\text{Null deviance}}$$

We followed a step-by-step model building procedure. Before starting building the model, some explanatory variables that were highly correlated ($|r| > 0.8$) were discarded for further analyses to avoid multicollinearity. NDVI and NDII were highly correlated ($r = 0.88$, p -value < 0.0001), as well as NDVI and NDII in-site heterogeneity ($r = 0.91$, p -value < 0.0001). We selected NDVI because it is universally used and because it is more closely related to a gradient that arises debate in the scientific literature (the diversity-productivity relationship). Elevation also showed a high correlation with mean temperature ($r = 0.87$, p -value < 0.0001). We selected mean temperature because it has a direct physiological effect whereas elevation has no direct relevance for species' performance (Guisan & Zimmermann 2000, Pausas & Austin 2001).

In the first step of model building, tree diversity was related separately with each of the explanatory variables. Because the relationships between species richness and environmental variables are often curvilinear (Austin 1980), we explored the effects of quadratic and cubic terms of the explanatory variables in tree diversity. Spatial coordinates were incorporated to the model by adding all terms for a cubic trend surface regression (Legendre 1993, Legendre & Legendre 1998). This ensures that complex features like patches or 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 represents a measure of model optimality, trading off complexity and fit to the data. The percentage of explained deviance was also calculated for each model.

In a second step of the analysis, all selected terms of the variable that accounted for the most important change in deviance were entered into the model. Next, all remaining variables were tested for significance by adding them one by one. After each new variable inclusion, the significance of the terms previously selected was tested by a backward stepwise selection procedure, using exact AIC, to avoid multicollinearity with other variables. The procedure was repeated iteratively until no more significant explanatory variables remained (p -value = 0.05). Finally, the selected terms of spatial variables were included in the model and tested for statistical significance.

In each of the steps of model building, we examined the reduction in the corrected deviance from the null model, the significance of coefficients, the probability plot of the standardised residuals, the Cook statistic and the standardised leverage. Those observations displaying simultaneously large values for the Cook statistic and the standardised leverage were discarded from the analysis to avoid over-influence of outliers in the regression procedure.

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 geographic distances (Diniz-Filho *et al.* 2003). We used the Moran's test for statistical significance of spatial autocorrelation (Cliff & Ord 1981). If detectable spatial autocorrelation existed in a distance class, then we can assume that there are still some spatially patterned variables not included in the model that were contributing to the patterns of local tree diversity.

To validate the model we applied a leave-one-out cross-validation procedure. Given a data set of size n , we recalculated the model $n-1$ times, leaving out one data in turn. Each one of the generalised linear

models based on the $n-1$ data was then applied to that excluded data in order to produce a predicted Fisher's alpha score. We checked the predictive power of the model by

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

where E is the mean of the percentage absolute errors of prediction, y_i is the observed species richness, and \hat{y}_i the predicted value for y_i when the i th observation is excluded (Davidson & Hinkley 1997).

Patterns of floristic similarity

Mantel tests of matrix correspondence were run to find out whether similarities in floristic composition correlated with similarities in climatic variables, edaphic conditions, NDVI, spectral variability (NDVI in-site heterogeneity), topography, human disturbance-related variables, and geographic distance. We used the standardized form of the Mantel test, which computes the Pearson correlation coefficient between the cell values of two resemblance matrices. The statistical significance of each correlation was determined by a Monte Carlo permutation test to avoid problems related to autocorrelation and non-normal distributions of the measured variables. In all cases, 1000 permutations were used, which allows testing of the statistical significance at p -values < 0.001 for each individual correlation.

In order to find the subset of variables with the maximum correlation with community dissimilarities, we selected the combinations of explanatory variables that contributed most to explain the variability in the floristic resemblance matrix. Initially, all the variables used for modelling local tree diversity were included. Then the function finds the best correlation between community dissimilarities and distance matrices based on different combinations of explanatory variables, and for each size of subsets, outputs the best result. We reported the correlation coefficients for the final models. These analyses were run with the R vegan package (Oksanen *et al.* 2005) based on the work by Clarke & Ainsworth (1993).

Selecting sites for conservation

Hierarchical clustering was performed using the matrix of dissimilarity distances for the best subset of explanatory variables selected to maximize correlation with floristic dissimilarities. We used Ward's method because it makes more compact and representative clusters. Based on the height distances of the hierarchical clustering we classified the plots in an increasing number of clusters, from three to ten. We then used analyses of similarities (ANOSIM) to select the number of clusters that maximize floristic differences between groups. ANOSIM operates 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, value 0 indicating completely random grouping. The statistical significance of observed R was assessed by permuting the grouping vector to obtain the empirical distribution of R under null-model (Oksanen *et al.* 2005).

Finally, classification and regression trees (CART) were used to predict membership of plots in the selected clusters from their measurements on the explanatory variables (i.e. those selected to maximize correlation with floristic dissimilarities). CART has the ability to perform univariate splits, examining the effects of predictors one at a time. Splitting rules were further used to classify all pixels in the study area. This allowed us to define non-explored areas of complementary floristic composition based on inference made from the best subset of explanatory variables, and select sites of high predicted tree diversity within each floristic region. All statistical analyses were performed with the R environment (R Development Core Team 2004).

3. Results

Predicting spatial patterns of local tree diversity

All explanatory variables, with the exception of soil fertility/quality, were significant when tested separately as either linear, quadratic, or cubic functions (**Table 6.2**). Variability in local tree diversity (Fisher's

Table 6.2. Explanatory variables (abbreviation in parentheses) considered in the 204 sampled plots in the Highlands of Chiapas. 'df' are the degrees of freedom, 'D²' is the deviance reduction, 'AIC' is the Akaike Information Criterion, and 'Sign' represents the sign of the significant terms of each function (p -value = 0.01).

Variable	Selected terms	Deviance	AIC	df	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 in-site heterogeneity (Het)	Het	68.6	927.1	202	0.02	-
Slope (SI)	SI	66.2	919.6	202	0.06	+
Road density (RD)	RD ² +RD ³	67.8	926.7	201	0.04	+ -
Canopy openness (CO)	CO	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)						
Latitude (Lat)	Lat+Lat ³ +Lon*Lat ²	52.3	873.3	200	0.26	+ - -

alpha) depended on the geographical position of the plot. Sites close together in the space tend to be more similar in their diversity than those that are further away, but this model on its own has little predictive utility. NDVI, mean precipitation, and mean temperature were the non-spatial variables that accounted for the most important change of deviance. NDVI was consequently the first variable to be included in the model; next, the linear and cubic terms of mean precipitation; then all the terms of mean temperature and so on until the model was iteratively fitted and all the selected variables were statistically tested for significance (**Table 6.3**). Finally, significant spatial terms were added. The final model accounted for 44% of the observed variability in local tree diversity, which was mainly related to mean precipitation, mean temperature, NDVI, and canopy openness (**Table 6.3**).

Spatial autocorrelation for the raw diversity data was significant for most lag distances, though the pattern revealed very erratic (**Figure 6.1a**). The inclusion of spatially structured variables in the model such as mean annual precipitation reduced the spatial autocorrelation in most distance classes (**Figure 6.1b**).

The mean of the percentage absolute errors of prediction obtained in the cross-validation test was 45.6%, and the examination of the residuals did not show 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 6.4**. Climatic variables showed the highest correlation with floristic composition. Correlations between the floristic similarity matrix and matrices based on geographical distance and topographical features were also high. NDVI showed a low significant correlation with species similarity. Correlations between the floristic similarity matrix and the similarity matrices of soil conditions, spectral variability and human disturbance-related variables were generally close to zero, despite some of them were statistically significant. Statistical significance, however, must be interpreted with caution, as correlations were based on a large number of data (i.e. all the possible combinations of sample pairs).

Table 6.3. Summary of the step-by-step model selection for prediction of local tree diversity.

Variable	Terms	Deviance	df	AIC	D^2	t value	Coefficient	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 openness	CO	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 in-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			

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

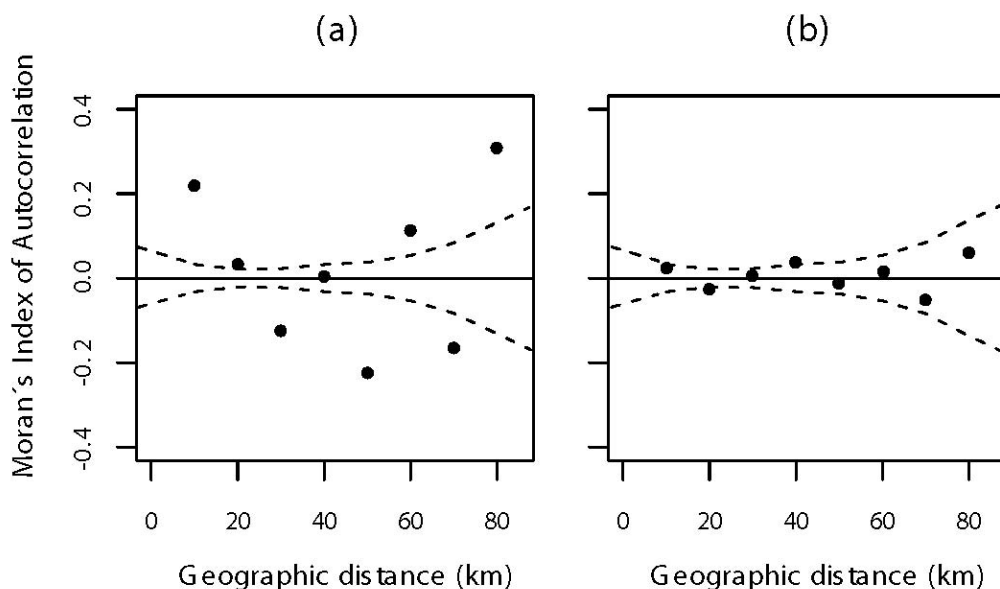


Figure 6.1. Spatial correlograms based on Moran's index of spatial autocorrelation for Fisher's alpha values (a), and for residuals after fitting the significant variables in the model shown in Table 3. Dashed lines represent 95% standard error intervals for Moran's test.

The selection of different subsets of explanatory variables with best correlation to community data indicated that a high proportion of the variation in floristic similarity could be explained by 1-3 variables (Table 6.5). As predicted by Mantel tests, mean pre-

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

Table 6.4. Mantel test correlations of floristic similarities with similarities in environmental, human disturbance-related, and spatial variables.

Variable	Floristic similarities	
	r^1	95% CI
Climatic variables	0.50 ^{***}	± 0.05
Soil fertility/quality	0.07 [*]	± 0.03
NDVI	0.17 ^{***}	± 0.03
NDVI in-site heterogeneity	-0.02	± 0.05
Topographical features	0.40 ^{***}	± 0.04
Human disturbance	0.07 [*]	± 0.05
Geographical distance	0.43 ^{***}	± 0.04

¹ *** $p < 0.001$, ** $0.001 < p < 0.01$, * $0.01 < p < 0.05$.

Table 6.5. Mantel tests for best possible subsets of explanatory variables (from one to ten) that maximize correlation to floristic dissimilarities.

Size	Best subsets of explanatory variables	r
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 + CO	0.47
6	Pr + T + NDVI + SI + RD + CO	0.43
7	Pr + T + SFQ + NDVI + SI + RD + CO	0.39
8	Pr + T + SFQ + NDVI + Het + SI + RD + CO	0.35
9	Pr + T + SFQ + NDVI + Het + SI + PD + RD + CO	0.30
10	Pr + T + SFQ + NDVI + Het + SI + PD + RD + DE + CO	0.27

Prioritising areas for conservation

We took a varying number of clusters, from three to ten, and compared floristic dissimilarities between the groups at each clustering. The results revealed that five clusters maximized floristic differences between groups (ANOSIM R -statistic = 0.59, p -value < 0.001). These floristic groups showed also some differences regarding local tree diversity (ANOSIM R -statistic = 0.26, p -value < 0.001) (**Figure 6.2**). However, these differences were lower than floristic

dissimilarities. This is a desirable property as we want to use a single model for predicting tree diversity across the landscape and not one model for each of the floristic groups.

Figure 6.3 shows the classification and regression tree (CART) developed for the five groups defined in the hierarchical clustering. Variables in CART models are selected to create splits that maximize the resulting node homogeneity, and the variables used in early splits can be considered as more important.

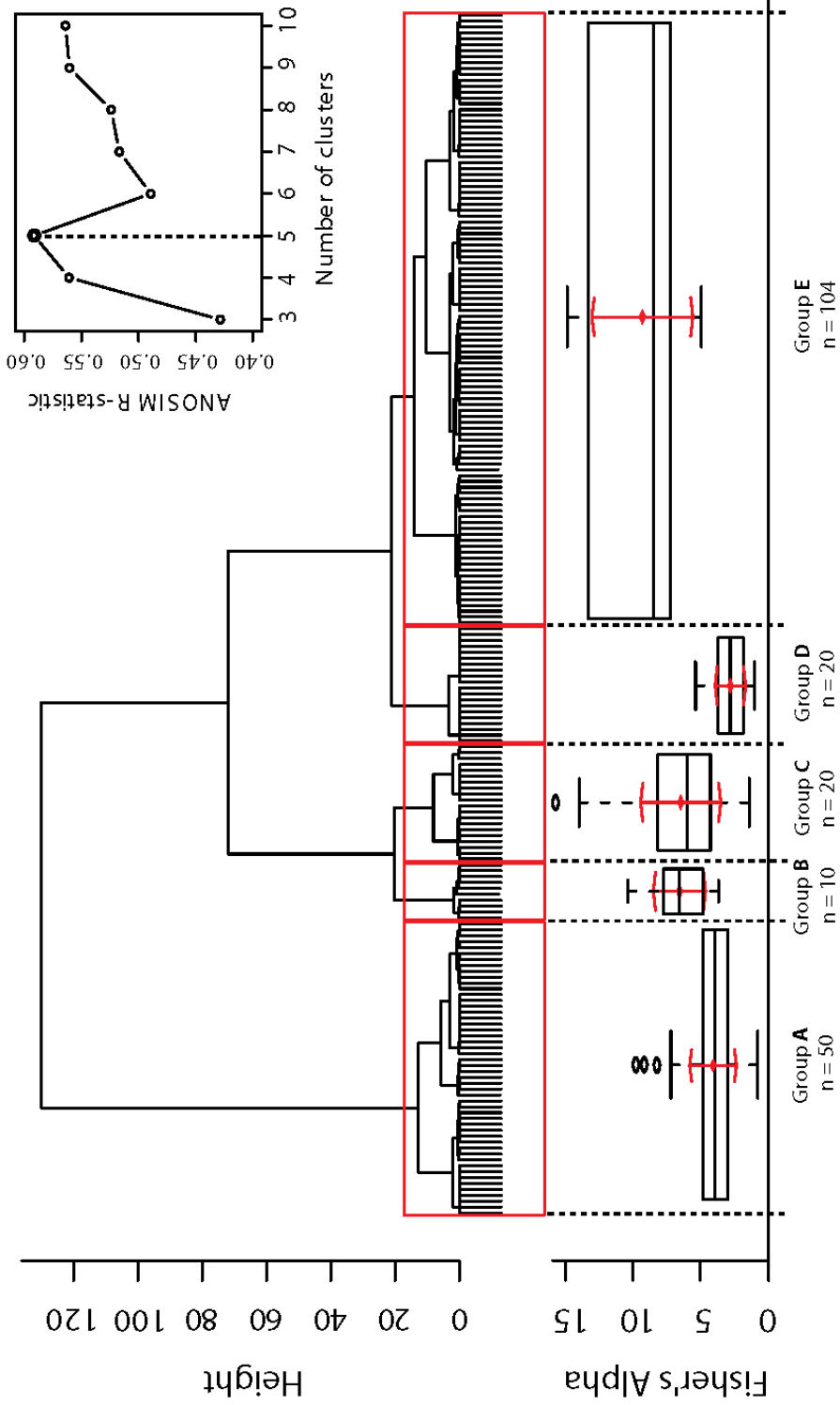


Figure 6.2. Dendrogram of sampled plots produced by a hierarchical clustering with Ward's method as the linkage rule and the squared Euclidean distance as the measure of similarity. The variables considered in the analyses are mean precipitation and temperature. ANOSIM R-statistic (upper right) shows the relative floristic differences between groups for an increasing number of clusters, from three to ten. A number of five groups maximizes floristic differences between groups. Boxplots of alpha diversity are displayed for the different floristic groups, with arrows indicating the mean and standard deviation.

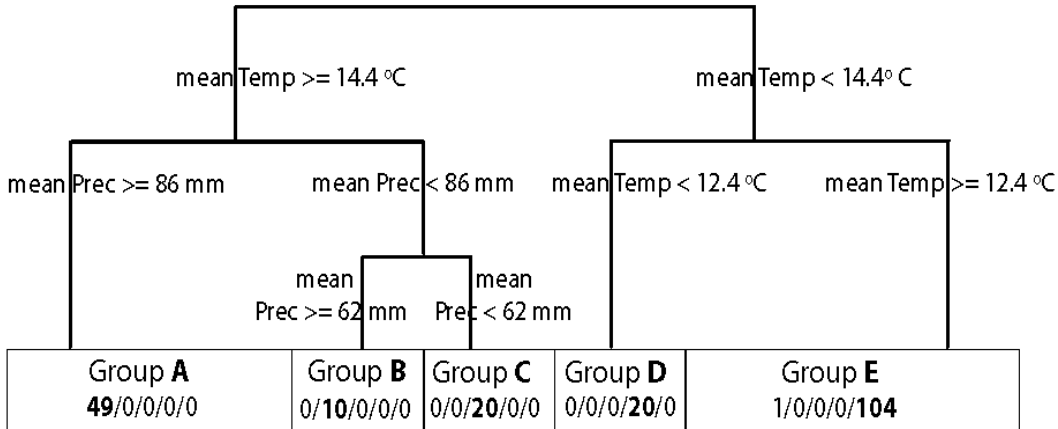


Figure 6.3. Classification and regression tree (CART) for the five groups of vegetation defined in the hierarchical clustering using mean precipitation and temperature as predictor variables.

Mean temperature was selected in the first split. This variable was also used to define the membership to groups labelled D and E in **Figure 6.2**, whereas mean precipitation was used in splitting groups A, B and C. All plots but one (belonging to group A but misclassified in group E) were correctly classified.

Using these simple classification rules, all pixels within our study area were assigned to one of the five floristic groups (**Figure 6.4a**). Local tree diversity was forecasted by applying the final reduced GLM (**Figure 6.4b**). In the last step, pixels within each floristic region were ranked from higher to lower local diversity, and reclassified into five groups of decreasing diversity (all covering an area equivalent to 5000 ha except for the last group that was formed by all the remaining pixels, **Figure 6.4c**). Because groups C and D were much smaller than the others, all their pixels were classified as having the highest priority for conservation. This exercise exemplifies the manner in which our results may be used to prioritise sites for conservation.

4. Discussion

The assessment of biodiversity in managed landscapes poses several methodological difficulties for different reasons: 1) Diversity measures strongly depend on the chosen spatio-temporal scale, and the

scaling functions applicable to transfer results from one scale to another are not completely satisfactory (Waldhardt 2003); 2) It is impracticable to consider all the different ecological, historical and human-related factors that may contribute to patterns of species diversity (Lobo & Martín-Piera 2002); 3) Field data are often scarce, particularly in tropical regions, due to limited accessibility to the forests (Stockwell & Peterson 2003). Although our study suffers of these caveats, we obtained models of the determinants of local tree diversity and complementarity that were satisfactory. The results of the GLM-diagnostic methods and the lack of autocorrelation in the residuals suggest that the model assumptions are reasonable. The analyses show that variation in tree diversity was mostly related to climatic variables and the NDVI. Climatic variables were also responsible for the main differences in floristic composition. This allowed to divide the study area into five major floristic regions and prioritise areas of high local tree diversity within each of them.

Patterns of local tree diversity

Climatic variables showed the strongest relationship with local tree diversity (**Table 6.3**). Climate has been typically defined as a strong descriptor of broad-scale diversity patterns (Wright *et al.* 1993, Austin *et al.* 1996, Hawkins *et al.* 2003). Our findings may be

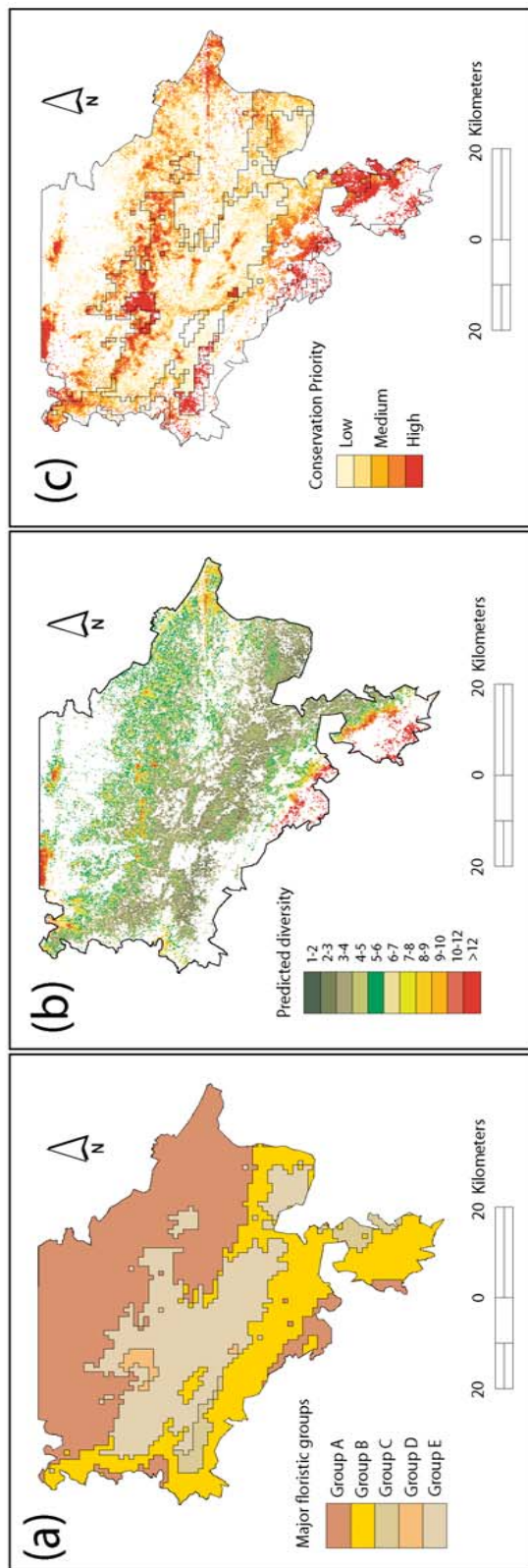


Figure 6.4. (a) Major floristic regions defined through hierarchical clustering and extrapolated to the entire study area by means of a classification and regression tree (CART) with mean temperature and precipitation as input variables; (b) Predicted values of local tree diversity in the Highlands of Chiapas. Fisher's alpha scores were forecasted by applying the final reduced GLM; (c) Prioritisation of areas for conservation based on diversity values and complementarity of floristic composition.

dependent on the spatial scale of analysis (Willis & Whittaker 2002), but they show that local diversity can be explained to some extent by climatic gradients. This 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 may be related to plant growth. Positive correlations between tropical lowland tree species richness and annual precipitation have been interpreted as supporting the diversity-energy hypothesis (Gentry 1982, 1988, Givnish 1999). Yet, using this variable separately from temperature has been recently criticized (Francis & Currie 2003).

If the NDVI is interpreted as a surrogate of the amount of biologically available energy (Rosenzweig 1995), we can assume that greater biomass increases biological heterogeneity which, in turn, favours specialisation 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 highlighted in areas with vegetation that is relatively structurally homogeneous (Jakubauskas & Price 1997). In areas where vegetation structure is heterogeneous, structural rather than species differences may predominate in imagery (Nagendra 2001). Thus the difficulty to predict spatial patterns of tree diversity based solely on remotely sensed data (see also Tuomisto *et al.* 2003). Further, NDVI must be interpreted with caution as it summarises the energy use and storage (plant biological activity) in a particular period of time. Multi-temporal data might thus provide further information on intra- and inter-annual shifts in vegetation and support more detailed models with the incorporation of time lags and temporal changes in productivity (Oindo & Skidmore 2002).

Soil fertility/quality did not explain a significant amount of variability of local tree diversity. Other studies have highlighted different relationships (positive, negative, hump-shaped) 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). The lack of relationship in our study may 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 at finer grained scales between plant species richness and different soil characteristics such as texture or cation content.

In-site heterogeneity is positively related to local tree diversity (**Table 6.3**) but it accounts for a very small percentage of its variation. This 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 existence of environmental or resource heterogeneity may create high niche diversity (e.g. Pollock *et al.* 1998, Gould 2000, Pausas *et al.* 2003); at the local scale it may be secondary in importance to resources and conditions (Pausas & Austin 2001).

Canopy openness, a surrogate of human disturbance, and slope were also positively associated with tree diversity. Canopy openness may indicate a buffering effect of the surrounding forest on local tree diversity through a reduction of 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 impacts (e.g. number of stumps, logs, etc.). The relationship with slope may reflect the consequence of lower accessibility to these areas and, thereby, to less intensive human disturbance regimes.

The reduction of spatial autocorrelation in the residuals as compared to the raw diversity data (**Figure 6.1**) indicates that correlations of diversity with metrics of space were reflecting the collinearity of other variables with space (Currie *et al.* 1999). Climatic variables were mostly responsible for this reduction. Because diversity measurements are based on the distribution of the abundance and/or the number of species, local non-spatially structured biotic factors such as interspecific competition may be accounting for part of the unexplained variability of tree diversity.

Patterns of floristic similarity

Similarity in tree composition correlated mainly with climatic variables and NDVI (**Table 6.4**). Given the existing correlation of mean annual precipitation and temperature with elevation, and the spatially structured component of these variables, it is not rare that both topographical features and geographical distance were also highly correlated with similarity in tree composition. Tuomisto *et al.* (2003) found that reflectance patterns in satellite images could be efficiently used to predict landscape-scale patterns in Amazonian rain forests. Our results do not fully support their results. In our study area there was a strong altitudinal and climatic gradient and different vegetation types could be recognized (Cayuela *et al.* 2006a); thus, spectral variation in the satellite images was a poor predictor of floristic differences at the landscape scale as compared to climatic variation.

Identifying priority areas for conservation

Mexico is a megadiverse country but has high rates of deforestation and ecological impoverishment (CONABIO 1999). In recent decades, the Highlands of Chiapas have undergone one of the most rapid processes of deforestation worldwide, at average rates of 2-5% per year (Ochoa-Gaona & González-Espinosa 2000; Cayuela *et al.* 2006c). This poses severe threats to conservation of forest habitats and a risk to local welfare (Costanza *et al.* 1997). Mapping of diversity and complementarity can aid conservation of natural resources by helping 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 made on 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 non-coincident with patterns of point diversity.

Our modelling represents an approximation to the spatial configuration of local tree diversity and complementarity in south-eastern Mexico. Spatial prediction of floristic patterns indicated that there are three dominant floristic regions (**Figure 6.4a**) matching major climatic trends: a north-eastern one with abun-

dant precipitation and a mild winter season (group A), a central one with a cold and dry winter season (group E), and a south-western one with a dry but warm winter season (Group B). Hotspots chiefly occur on ridge-top montane forests in the central and northern ranges, and in transitional forests towards the lower depression in the south-western range of the study area (**Figure 6.4b**). Overall, our study provides a first step towards identification of sites that maximise the representation of tree diversity. Prioritisation of areas of high diversity within each floristic region identified the location of tree diversity hotspots across the study region (**Figure 6.4c**). Given the accelerated pace of habitat loss, at least a small portion of the prioritised areas should be reserved for some maintenance of the original vegetation. Unfortunately, no environmental policy is being implemented in the region at the moment.

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

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References

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood. Second International Symposium on Information theory. Akademiai Kiadó Budapest.
- Araújo, M.B. 1999. Distribution patterns of biodiversity and the design of a representative reserve network in Portugal. *Diversity and Distributions* 5: 151-163.
- Austin, M.P. 1980. Searching for a model for use in vegetation analysis. *Vegetatio* 42: 11-21.
- Austin, M.P., Pausas, J.G. & Nicholls, A.O. 1996. Patterns of tree species richness in relation to environment in southeastern New South Wales, Australia. *Australian Journal of Ecology* 21: 154-164.
- Brown, J.H. & Lomolino, M.V. 1998. *Biogeography*. Sinauer Associates, Sunderland.
- Cayuela, L., Golicher, D.J., Salas Rey, J. & Rey Benayas, J.M. 2006a. Classification of a complex landscape using Dempster-Shafer theory of evidence. *International Journal of Remote Sensing*, in press.
- Cayuela, L., Rey Benayas, J.M. & Echeverría, C. 2006c. Clearance and fragmentation of tropical montane forests in the Highlands of Chiapas, Mexico (1975-2000). *Forest Ecology and Management*, under review.
- Ceballos, G., Rodríguez, P. & Medellín, R.A. 1998. Assessing conservation priorities in megadiverse Mexico: mammalian diversity, endemism, and endangerment. *Ecological Applications* 8: 8-17.
- Clark, D.B., Palmer, M.W. & Clark, D.A. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* 80: 2662-2675.
- Clarke, K.R. 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18: 117-143.
- Clarke, K.R. & Ainsworth, M. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, 92, 205-219.
- Cliff, A.D. & Ord, J.K. 1981. *Spatial processes: models and applications*. Pion.
- Clinebell, R.R.II, Phillips, O., Gentry, A.H., Stark, N. & Zuuring, H. 1995. Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation* 4: 56-90.
- CONABIO 1999. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. URL: <http://www.conabio.gob.mx>
- Costanza, R., Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. & van den Belt, M. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253-260.
- Cramer, W., Kicklighter, D.W., Bondeau, A., Moore, B., Churkina, C., Nemry, B., Ruimy, A. & Schloss, A.L. 1999. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biology* 5: 1-15.
- Crawley, M.J. 1993. *GLIM for ecologists*. Blackwell Scientific, Oxford.
- Currie, D.J., Francis, A.P. & Kerr, J.T. 1999. Some general propositions about the study of spatial patterns of species richness. *Ecoscience* 6(3): 392-399.
- Davidson, A.C. & Hinkley, D.V. 1997. *Bootstrap Methods and Their Application*. Cambridge University Press, Cambridge.
- Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. 2003. Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography* 12: 53-64.
- Duchaufour, P. 1987. *Manual de Edafología*. Masson, Barcelona.
- Eastman, J.R. 2001. *Idrisi 32. release 2. Guide to GIS and image processing*. Clark Labs, Clark University, Massachusetts.
- Galindo-Jaimes, L., González-Espinosa, M., Quintana-Ascencio, P. & García-Barríos, L. 2002. Tree composition and structure in disturbed stands with varying dominance by *Pinus* spp. in the Highlands of Chiapas, Mexico. *Plant Ecology*: 162: 259-272.
- Gao, B.C. 1996. NDWI-A normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sensing of Environment* 58: 257-266.
- Gentry, A.H. 1982. Patterns of Neotropical plant species diversity. *Evolutionary Biology* 15: 1-84.

- Gentry, A.H. 1988. Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Science USA* 85: 156-159.
- Gentry, A.H. 1992. Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos* 63: 19-28.
- Givnish, T.J. 1999. On the causes of gradients in tropical tree diversity. *Journal of Ecology* 87: 193-210.
- Golicher, D.J., Ramírez-Marcial, N. & Levey-Tacher, S. 2006. Correlations between precipitation patterns in the state of Chiapas and the El Niño sea surface temperature index. *Interciencia*, in press.
- González-Espinosa, M. 2005. Forest use and conservation implications of the Zapatista rebellion. In: Kaimowitz, D. (ed.). *Chiapas, Mexico. Forests and Conflicts*. ETRN News No. 43-44 (European Tropical Forest Research Network), Wageningen, The Netherlands. pp 74-76.
- González-Espinosa, M., Rey-Benayas, J.M., Ramírez-Marcial, N., Huston, M.A. & Golicher, D. 2004. Tree diversity in the northern Neotropics: regional patterns in highly diverse Chiapas, Mexico. *Ecography* 27: 741-756.
- Gould, W. 2000. Remote sensing of vegetation, plant species richness, and regional biodiversity hotspots. *Ecological Applications* 10(6): 1861-1870.
- Guisan, A. & Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147-186.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84(12): 3105-3117.
- Huston, M.A. 1980. A general hypothesis of species diversity. *American Naturalist* 113: 81-101.
- Kerr, J.T. & Packer, L. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 285: 252-254.
- Jakubauskas, M.E. & Price, K.P. 1997. Empirical relationships between structural and spectral factors of Yellowstone Lodgepole Pine forests. *Photogrammetric Engineering and Remote Sensing* 63: 1375-1381.
- Justus, J. & Sarkar, S. 2002. The principle of complementarity in the design of reserve networks to conserve biodiversity: A preliminary history. *Journal of Biosciences* 27: 421-435.
- Jørgenson, A.F. & Nøhr, H. 1996. The use of satellite images for mapping of landscape and biological diversity in Sahel. *International Journal of Remote Sensing* 17: 91-109.
- Lamb, D., Erskine, P.D. & Parrotta, J.A. 2005. Restoration of degraded tropical forest landscapes. *Science* 310: 1628-1632.
- Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S. & Watt, A.D. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391: 72-76.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74(6): 1659-1673.
- Legendre, P. & Legendre, L. 1998. *Numerical Ecology*. 2nd edn. Elsevier, Amsterdam.
- Lobo, J.M. & Martín-Piera, F. 2002. Searching for a predictive model for species richness of Iberian dung beetle based on spatial and environmental variables. *Conservation Biology* 16(1): 158-173.
- Luoto, M., Toivonen, T. & Heikkinen, R. 2002. Prediction of total and rare plant species richness in agricultural landscapes from satellite images and topographic data. *Landscape Ecology* 17: 195-217.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82(9): 2381-2396.
- Myers, N. 1990. The biodiversity challenge: expanded hot-spots analyses. *The Environmentalist* 10: 243-256.
- Nagendra, H. 2001. Using remote sensing to assess biodiversity. *International Journal of Remote Sensing* 22(12): 2377-2400.
- Oindo, B.O. & Skidmore, A.K. 2002. Interannual variability of NDVI and species richness in Kenya. *International Journal of Remote Sensing* 23: 285-298.
- Oksanen, J., Kindt, R. & O'Hara, R.B. 2005. *Vegan: Community Ecology Package* version 1. URL:

- <http://cc.oulu.fi/~jarioksa/>
- Pausas, J.G. & Austin, M.P. 2001. Patterns of plant species richness in relation to different environments: an appraisal. *Journal of Vegetation Science* 12: 153-166.
- Pausas, J.G., Carreras, J., Ferré, A. & Font, X. 2003. Coarse-scale plant species richness in relation to environmental heterogeneity. *Journal of Vegetation Science* 14: 661-668.
- Phillips, O.L., Nuñez Vargas, P., Monteagudo, A.L., Peña Cruz, A., Chuspe Zans, M.E., Sánchez, W.G., Li-Halla, M. & Rose, S. 2003. Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology* 91: 757-775.
- Pollock, M.M., Naiman, R.J. & Hanley, T.A. 1998. Plant species richness in riparian wetlands—a test of biodiversity theory. *Ecology* 79: 94-105.
- R Development Core Team. 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-00-3, URL: <http://www.R-project.org>.
- Rahbek, C. & Graves, G.R. 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences USA* 98: 4534-4539.
- Rey Benayas, J.M. & de la Montaña, E. 2004. Identifying area of high-value vertebrate diversity for strengthening conservation. *Biological Conservation* 114: 357-370.
- Rey Benayas, J.M. & Pope, K.O. 1995. Landscape ecology and diversity patterns in the seasonal tropics from Landsat TM imagery. *Ecological Applications* 5: 386-394.
- Rey Benayas, J.M., Scheiner, S.M., García Sánchez-Colomer, M. & Levassor, C. 1999. Commonness and rarity: theory and application of a new model to Mediterranean montane grasslands. *Conservation Ecology* (online) 3(1), 5. Available from <http://www.consecol.org/vol3/iss1/art5>.
- Rey Benayas, J.M. & Scheiner, S.M. 2002. Plant diversity, biogeography and environment in Iberia: Patterns and possible causal factors. *Journal of Vegetation Science* 13: 245-258.
- Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.
- Scheiner, S.M. & Rey Benayas, J.M. 1994. Global patterns of plant diversity. *Evolutionary Ecology* 8: 331-347.
- Seto, K.C., Fleishman, E., Fay, J.P. & Betrus, C.J. 2004. Linking spatial patterns of bird and butterfly species richness with Landsat TM derived NDVI. *International Journal of Remote Sensing* 25(20): 4309-4324.
- Stockwell, D. & Peterson, A.T. 2003. Comparison of resolution of methods used in mapping biodiversity patterns from point-occurrence data. *Ecological Indicators* 3: 231-221.
- Tuomisto, H., Poulsen, A.D., Ruokolainen, K., Moran, R.C., Quintana, C., Celi, J. & Cañas, G. 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecological Applications* 13(2): 352-371.
- Waldhardt, R. 2003. Biodiversity and landscape—summary, conclusions and perspectives. *Agriculture, Ecosystems and Environment* 98: 305-309.
- Williams, P., Gibbons, D., Margules, C., Rebelo, A., Humphries, C. & Pressey, R. 1996. A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biology* 10: 155-174.
- Willis, K.J. & Whittaker, R.J. 2002. Species diversity - Scale matters. *Science* 295: 1245-1247.
- Wohlgemuth, T. 1998. Modelling floristic species richness on a regional scale: a case study in Switzerland. *Biodiversity and Conservation* 7: 159-177.
- Wolf, J.H.D. & Flamenco, A. 2003. Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography* 30: 1689-1707.
- Wright, D.H., Currie, D.J. & Maurer, B.A. 1993. Energy supply and patterns of species richness on local and regional scales. In: Ricklefs, R.E. & Schluter, D. (eds.) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. Chicago University Press, Chicago. pp 66-74.

Appendix 6.1

Species included in the present analysis. Nomenclature follows the Index Kewensis, except for those cases in which no record was found, for which the Gray Herbarium Card Index (*) (<http://www.ipni.org>) and the Missouri Botanical Garden Databases (†) (www.mobot.org) were used.

Family	Species
Actinidiaceae	<i>Saurauia oreophila</i> Hemsl. † <i>S. scabrida</i> Buscal.*
Anacardiaceae	<i>Pistaceae mexicana</i> H.B. & K. <i>Rhus schiedeana</i> Schtdl. <i>Tapirira mexicana</i> Marchand
Annonaceae	<i>Malmea depressa</i> (Baill.) R.E.Fr. Undetermined sp1
Aquifoliaceae	<i>Ilex macfadyenii</i> Rehder <i>I. sp1</i> <i>I. vomitoria</i> Aiton
Araliaceae	<i>Dendropanax populifolius</i> (Marchal) A.C. Sm. <i>D. arboreus</i> (L.) Decne. & Planch. <i>Oreopanax arcanus</i> A.C. Sm. <i>O. capitatus</i> Steyerm. <i>O. liebmannii</i> Marchal <i>O. peltatum</i> Linden <i>O. xalapense</i> Decne. & Planch.
Asteraceae	<i>Lasianthaea</i> aff. <i>fruticosa</i> (L.) K.M. Becker
Betulaceae	<i>Alnus acuminata</i> H.B. & K.
Bignoniaceae	<i>Tecoma stans</i> (L.) H.B. & K.
Boraginaceae	<i>Ehretia luxiana</i> Donn. Sm. <i>E. tinifolia</i> L. <i>Tournefortia acutifolia</i> Willd. ex Roem. & Schult.
Brunelliaceae	<i>Brunellia mexicana</i> Standl.
Buddlejaceae	<i>Buddleja cordata</i> H.B. & K. <i>B. nítida</i> Benth. <i>B. skutchii</i> Morton
Burseraceae	<i>Bursera simaruba</i> Sarg.
Caprifoliaceae	<i>Sambucus canadensis</i> L. <i>S. mexicana</i> Presl ex DC. <i>Viburnum acutifolium</i> Benth. <i>V. aff. lautum</i> Morton <i>V. discolor</i> Benth. <i>V. elatum</i> Benth. <i>V. hartwegii</i> Benth. <i>V. jucundum</i> Morton
Celastraceae	<i>Crossopetalum parviflorum</i> (Hemsl.) Lundell <i>C. sp1</i> <i>Perrottetia ovata</i> Hemsl. <i>Quetzalia contracta</i> (Lundell) Lundell <i>Rhacoma standleyi</i> (Lundell) Standl. & Steyerm. <i>R. tonduzii</i> (Loes.) Standl. & Steyerm. Undetermined sp1 Undetermined sp2 <i>Zinowiewia rubra</i> Lundell
Clethraceae	<i>Clethra macrophylla</i> M.Martens & Galeotti <i>C. oleoides</i> L.O.Williams <i>C. sp1</i> <i>C. suaveolens</i> Turcz.
Chloranthaceae	<i>Hedyosmum mexicanum</i> Cordem. Ex Baill.

Appendix 6.1. Continued.

Family	Species
Compositae	<i>Baccharis vaccinoides</i> H.B. & K. <i>Eupatorium areolare</i> DC. <i>E. ligustrinum</i> DC. <i>E. nubigenum</i> Benth. <i>E. pittieri</i> Klatt* <i>Montanoa leucantha</i> S.F.Blake <i>M. leucantha</i> var. <i>arborescens</i> (DC.) B.L.Turner <i>Perymenium grande</i> Hemsl. <i>Roldana</i> sp1 <i>Telanthophora cobanensis</i> (Coulter) H.Rob. & Brettell <i>T. grandiflora</i> (Less.) H.Rob & Brettell Undetermined sp1 <i>Verbesina perymenioides</i> Sch.Bip. ex Klatt <i>Vernonia canescens</i> Sch.Bip <i>V. leiocarpa</i> DC. <i>V. scorpioides</i> Pers.
Cornaceae	<i>Cornus disciflora</i> Moc. & Sessé ex DC. <i>C. excelsa</i> H.B. & K. <i>Nyssa sylvatica</i> Marsh.
Corylaceae	<i>Carpinus caroliniana</i> Walter
Cupressaceae	<i>Cupressus lusitanica</i> Mill.
Cupuliferae	<i>Ostrya virginiana</i> K.Koch
Cyatheaceae	<i>Cyathea fulva</i> Fée
Ericaceae	<i>Arbutus xalapensis</i> H.B. & K. <i>Comarostaphylis discolor</i> (Hooker) G.M.Diggs <i>Vaccinium breedlovei</i> L.O. Williams
Euphorbiaceae	<i>Croton</i> aff. <i>fragilis</i> Schltld. <i>C.</i> aff. <i>glabellus</i> Heyne ex Wall. <i>C. guatemalensis</i> Lotsy <i>Sebastiania cruenta</i> (Standl. & Steyerem.) Miranda <i>Stillingia zelayensis</i> Müll.Arg.
Fagaceae	<i>Quercus acatenangensis</i> Trel. <i>Q. benthami</i> A.DC. <i>Q. candicans</i> Nee <i>Q. crassifolia</i> Benth. <i>Q. crispipilis</i> Trel. <i>Q. lancifolia</i> Liebm. ex A.DC. <i>Q. laurina</i> Liebm. Ex. A.DC. <i>Q. peduncularis</i> Nee <i>Q. polymorpha</i> Schlecht. & Cham. <i>Q. rugosa</i> Nee <i>Q. sapotaefolia</i> Liebm. <i>Q. segoviensis</i> Liebm. <i>Q. skutchii</i> Trel. <i>Q.</i> sp1
Flacourtiaceae	<i>Xylosma flexuosum</i> Hemsl.
Garryaceae	<i>Garrya laurifolia</i> Benth.
Guttiferae	<i>Clusia mexicana</i> Vesque <i>C. rosea</i> Jacq.
Hamamelidaceae	<i>Liquidambar styraciflua</i> L.
Lamiaceae	<i>Cornutia grandiflora</i> Steud.
Lauraceae	<i>Cinnamomum zapatae</i> F.G.Lorea-Hernández <i>C.</i> sp1 <i>Licaria campechiana</i> (Standl.) Kosterm.

Appendix 6.1. Continued.

Family	Species
Lauraceae	<i>Litsea glaucescens</i> H.B. & K. <i>Nectandra longicaudata</i> (Lundell) C.K.Allen <i>N. salicifolia</i> Nees <i>N. sp1</i> <i>Ocotea efusa</i> Hemsl. <i>O. helicterifolia</i> Hemsl. <i>O. sp1</i> <i>Persea americana</i> Mill. <i>P. liebmannii</i> Mez*
Leguminosae	Undetermined sp1 <i>Acacia angustissima</i> Kuntze <i>Calliandra houstoniana</i> Standl. <i>Cojoba arborea</i> Britton & Rose <i>Dalbergia glomerata</i> Hemsl. <i>D. sp1</i> <i>Diphysa americana</i> (Miller) M.Sousa S. <i>Erythrina chiapasana</i> Krukoff <i>Inga oerstediana</i> Benth. <i>I. sp1</i> <i>Lonchocarpus rugosus</i> Benth. <i>Lysiloma divaricata</i> MacBride Undetermined sp1 Undetermined sp2
Magnoliaceae	<i>Magnolia sharpii</i> Miranda
Malpighiaceae	<i>Bunchosia lanceolata</i> Turcz.
Melastomataceae	<i>Miconia glaberrima</i> Naud. <i>M. minutiflora</i> DC.
Meliaceae	<i>Cedrela odorata</i> L.
Meliosmaceae	<i>Meliosma dentata</i> Urban <i>M. dives</i> Standl. & Steyerl. <i>M. sp1</i> Undetermined sp1
Moraceae	<i>Trophis chiapensis</i> Brandegees <i>T. chorizantha</i> Standl.
Myricaceae	<i>Myrica cerifera</i> Bigelow
Myrsinaceae	<i>Ardisia densiflora</i> Krug & Urb. <i>A. sp1</i> <i>Parathesis belizensis</i> Lundell <i>P. chiapensis</i> Fernald <i>P. leptopa</i> Lundell <i>Rapanea juergensenii</i> Mez <i>R. myricoides</i> (Schltdl.) Lundell ¹ <i>Synardisia venosa</i> (Mast. ex Donn.Sm.) Lundell
Myrtaceae	<i>Calyptanthes pallens</i> Griseb. <i>Eugenia acapulcensis</i> Steud. <i>E. capuli</i> Schlecht. <i>E. capuloides</i> Lundell*
Olacaceae	Undetermined sp1
Oleaceae	<i>Ximения americana</i> L. <i>Forestiera reticulata</i> Torr.* <i>Fraxinus uhdei</i> (Wenzig) Lingelsh. <i>F. vellerea</i> Standl. & Steyerl.
Onagraceae	<i>Fuchsia paniculata</i> Lindl. <i>Hauya elegans</i> ex DC.

Appendix 6.1. Continued.

Family	Species
Palmae	<i>Brahea edulis</i> H.Wendl. ex S.Wats.
Papaveraceae	<i>Bocconia arborea</i> S.Watson
Pinaceae	<i>Juniperus gamboana</i> Martinez <i>Pinus ayacahuite</i> Ehrenb. ex Schlecht. <i>P. chiapensis</i> (Martinez) Andresen <i>P. devoniana</i> Lindl. <i>P. maximinoi</i> H.E.Moore <i>P. montezumae</i> Lamb. <i>P. oocarpa</i> Schiede <i>P. pseudostrobis</i> Lindl. <i>P. tecunumanii</i> T.Eguiluz Piedra & J.P.Perry
Piperaceae	<i>Piper psilorhachis</i> C.DC.
Podocarpaceae	<i>Podocarpus matudae</i> Laub. & Silba
Polygalaceae	<i>Monnina xalapensis</i> H.B. & K.
Rhamnaceae	<i>Ceanothus caeruleus</i> Lag. <i>Colubrina</i> aff. <i>arborescens</i> Sargent <i>Rhamnus capreaefolia</i> Schlecht. <i>R. sharpii</i> M.C.Johnst. & L.A.Johnston
Rosaceae	<i>Amelanchier nervosa</i> Standl. <i>Crataegus pubescens</i> Steud. <i>Holodiscus argenteus</i> Maxim. <i>Photinia microcarpa</i> Standl. <i>Prunus brachybotrya</i> Zucc. <i>P. lundelliana</i> Standl. <i>P. rhamnoides</i> Koehne <i>P. serotina</i> Poir.
Rubiaceae	<i>Chiococca</i> aff. <i>alba</i> (L.) Hitchc. <i>Deppea grandiflora</i> Schlecht. <i>Psychotria</i> aff. <i>minarum</i> Standl. & Steyerm. <i>P. costivenia</i> Griseb. <i>P. marginata</i> Schlecht. <i>Randia aculeata</i> L. <i>Rondeletia cordata</i> Benth. <i>R. stenosphon</i> Hemsl.
Rutaceae	<i>Zanthoxylum melanostictum</i> Schlecht. & Cham.
Sapindaceae	<i>Cupania dentata</i> Moc. & Sessé <i>Dodonaea viscosa</i> Jacq. <i>Turpinia occidentalis</i> G.Don
Sapotaceae	<i>Pouteria lundellii</i> (Standl.) L.O.Williams
Saxifragaceae	<i>Phyllonoma laticuspis</i> Engl. <i>Weinmannia pinnata</i> Ruiz ex. Engl.
Simaroubaceae	<i>Picramnia quaternaria</i> Donn.Sm.
Solanaceae	<i>Cestrum aurantiacum</i> Lindl. <i>C. guatemalense</i> Francey <i>Solanum hispidum</i> Pers. <i>S. nigricans</i> M.Martens & Galeotti <i>S. nudum</i> Humb. & Bonpl. ex Dun.
Sterculiaceae	<i>Chiranthodendron pentadactylon</i> Larreat
Styracaceae	<i>Styrax argenteus</i> var. <i>ramirezii</i> (Greenm.) Gonsoulin <i>Symplocos limoncillo</i> Humb. & Bonpl. <i>S. longipes</i> Lundell <i>S. sp1</i>
Tiliaceae	<i>Trichospermum mexicanum</i> Baill.
Theaceae	<i>Cleyera theoides</i> Choisy

Appendix 6.1. Continued.

Family	Species
Theaceae	<i>Symplococarpon purpusii</i> (Brandegee) Kobuski <i>Ternstroemia lineata</i> DC. <i>T. oocarpa</i> Melch.
Thymelaeaceae	<i>Daphnopsis selerorum</i> Gilg.
Turneracea	<i>Erblichia odorata</i> Seem.
Urticaceae	<i>Morus celtidifolia</i> H.B. & K. <i>Myriocarpa longipes</i> Liebm. <i>Olmediella betschleriana</i> Loes. Undetermined sp1
Verbenaceae	<i>Urera</i> aff. <i>caracasana</i> Griseb. <i>Citharexylum donnell-smithii</i> Greenm. <i>C. mocinnii</i> var. <i>longibracteolatum</i> Moldenke <i>C.</i> sp1 <i>Lippia substrigosa</i> Turcz.
Winteraceae	<i>Drimys granadensis</i> var. <i>mexicana</i> (DC.) A.C. Sm.
Undetermined	Undetermined sp1 Undetermined sp2 Undetermined sp3