



Species dynamics in a montane cloud forest: Identifying factors involved in changes in tree diversity and functional characteristics

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ABSTRACT

Tropical montane cloud forests constitute a rare and fragile ecosystem, which is threatened in many of the areas in which it is found due to the pressure of human-originated disturbances. Cloud forests have been identified as a forest type with high levels of species endemism and biodiversity. The aim of this study, which focuses on a patch of cloud forest located in the Piura region of the Peruvian Andes, is to assess the changes in species composition and to identify the factors involved in the loss of biodiversity using data from a single inventory.

Random sampling plots were established throughout the forest area. An index of the difference in species richness between recruitment and older trees (Tree Diversity Change index, *TDC* index) was calculated for each plot. A Tree Diversity Change Index (*TDC*) and an index of species replacement based on the second order properties of the diameter distribution (*RE*) were defined to assess changes in species richness and to characterize the change in the functional groups of tree species within the plot. The factors involved in these processes were also identified by means of a Universal Kriging model.

The negative correlation between the *TDC* and the distance to the nearest track indicates that species richness is decreasing close to these tracks and that it is only maintained in the inner areas. The negative correlation of the *RE* index with altitude and deeper zones indicates that dynamic replacement of humid-condition species by dry-condition species is occurring at lower elevations. A loss in diversity along with a change towards species adapted to dryer conditions was observed throughout the forest. Zones at lower altitudes, on spurs or at the edges of the forest are more prone to these processes. This suggests that a change in the functions of the ecosystem has been taking place and that a minimum extension of cloud forest is required to maintain the ecological processes necessary for the continued existence of the cloud forest.

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1. Introduction

Tropical montane cloud forest is an unusual and unique ecosystem, comprising just 1.6% of the total area of tropical mountain forest in the world (Kapos et al., 2000), often forming 'islands' of vegetation (Howard, 1970) which evolve differently. Cloud forests are characterized by the presence of persistent or frequent wind-driven clouds (Hamilton, 1995) and many species in these forests show a high degree of specialisation (Gentry, 1992a), having developed adaptation mechanisms related to the cloud formation regime (Brujinzeel and Proctor, 1995; Still et al., 1999). Consequently, this type of forest exhibits high levels of species endemism and biodiversity (Fjeldså and Hjarsen, 1999; Luna-Vega et al., 2001), in fact, Andean cloud forest ecosystems display one of the highest levels of biodiversity in the world (Gentry, 1992b;

Churchill et al., 1995). Unfortunately, they are also currently considered among the most threatened ecosystems in the world (Stadtmüller, 1987; Hamilton, 1995; Brown and Kappelle, 2001). In the northern Andean region, 90% of the cloud forest has been lost (Hamilton et al., 1993). Human pressure, manifested in activities such as the conversion of forested land to agricultural land, fuel-extraction (Sarmiento, 1993) or illegal logging (Aubad et al., 2008), has probably played a major role in the disappearance and fragmentation of cloud forest (Young and León, 1993). However, human pressure is not the only factor which threatens the continued existence of cloud forest. Climate change is also having an important impact on these forest systems; changing the pattern and frequency of dry-season mist (which has declined dramatically since the mid-1970s [Pounds et al., 1999]), supporting the hypothesis that the cloud base in tropical montane forests has risen over the last few decades (Still et al., 1999). These changes would appear to be occurring rapidly (Foster, 2001) whereas paleo-ecological evidence suggests that the process of establishment in montane tree line migration is slow (taking around 200 years

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[Körner, 1994]), which may bring about the complete disappearance of mountaintop cloud forests located on lower mountains, since these are not able to 'migration' to higher altitudes (Lawton et al., 2001).

Habitat fragmentation and changes in environmental conditions have led to a reduction in plant diversity in natural ecosystems (Chapin et al., 1997; Mooney et al., 1996). Determining the factors which bring about changes in the biodiversity of fragments of tropical montane cloud forests is essential to the development of conservation strategies (Williams-Linera, 2002). Biodiversity encompasses not only species diversity but also the structure and function of the ecosystem (Franklin et al., 1981), so it may be possible to detect changes in biodiversity through analysing either of these three aspects. The most widely used diversity indices reflect the richness and evenness or dominance of species assuming that all the species are included in the inventory (Magurran, 1988). However, due to the great species diversity found in cloud forest (Hamilton, 1995), the latter assumption is unlikely to be fulfilled in a single forest inventory. For this reason, it would be preferable to use non-parametric species richness indices to assess changes in species composition (Colwell and Coddington, 1994). A simple diversity index value often provides little information, although the space-time variation in this value may reflect important processes or changes in the species composition taking place in the ecosystem. Moreover, such changes in the diversity indices over time have served to assess the effect of anthropogenic disturbances in forests (Battles et al., 2001; Polyakov et al., 2008), although it is often not possible to carry out such analyses since the necessary species composition data, which must be consistently recorded over long periods of time, are rarely available. Indicator species that are sensitive to some ecological processes can be used for monitoring environmental impacts on biodiversity (Noss, 1990). The use of indicator groups of species or species assemblages, which include species covering a broader sociological range (for example, understory and overstory species) should provide more detailed information about the response of the ecosystem to environmental changes than the use of a single species (Kremen, 1992). However, when plant species are used as indicators, it should be borne in mind that a given indicator species (associated with determined functional traits) may persist even after a change to less favourable conditions due to its longevity (Cousins and Lindborg, 2004). Therefore, in addition to the data relating to the abundance of indicator groups of species, other population parameters should be taken into account in order to identify possible changes in the composition of the ecosystem in the short term (Carignan and Villard, 2001). In the present study, a new method is proposed for characterizing the age (or, since tree age data is not usually available, size distribution) distribution of two species or groups of species based on the second order properties of the diameter distribution. Although second order analysis is usually associated with the distribution of individual objects in space (Legendre, 1993), it is straightforward to apply second order moment measures to the distribution of points on the axis of a measurable variable (Ripley, 1981).

By analysing the spatial distribution of species diversity it is possible to identify the environmental factors involved in species dynamics at larger scales as well as to determine the zones of the forest that have suffered detrimental processes. With regards to the spatial dynamics of species, autocorrelation is a very general property of ecological variables because of shared biotic characteristics such as genetic fluxes, reproduction, growth, mortality or migration (Legendre, 1993). Moreover, ecological factors tend to vary smoothly within the biotope (Borcard et al., 1992; Dimov et al., 2005). Spatial autocorrelation typically leads to a violation of the assumption of independence of observations in a classical test of hypothesis based on the variance analysis (Zas, 2006a), therefore

increasing the test error (Legendre et al., 2002, 2004). Several approaches have been proposed to account for spatial autocorrelation in the model used for the analysis of variance (Dutilleul, 1993; Dutkowski et al., 2002; Zas, 2006b). However, there is no all-embracing recipe for dealing with spatial autocorrelation in field experiments (Dutilleul, 1993; Gilmour et al., 1997), and determining the extent to which the variation is induced by the environment or as a result of intrinsic ecological processes is not always easy. Geostatistical techniques such as Universal Kriging allow us to account for the spatial autocorrelation in the variance-covariance matrix, identifying the relationship between the spatial structure of biodiversity indicators and the environmental variables or spatial features related to such processes (Torres et al., 2006).

The aim of this study is to provide evidence for the following hypotheses: (i) minor habitat disturbance may be a critical factor affecting tropical montane cloud forest species diversity and (ii) modification of the micro-environment brings about changes in species distribution within the forest, implying a variation in functional characteristics. For that purpose spatial analyses techniques were used to identify the factors involved in these processes in order to understand the current species dynamics in one of the last montane cloud forest patches in the Peruvian Tropical Andean Region.

2. Materials and methods

2.1. Study site

The study site is known as *Monte de Neblina de Cuyas*, which is in the western Andean range of northern Peru. The forest is situated in *Cerro Chacas*, in the *Ayabaca* province of the *Piura* region and the area chosen for the study covers 171 ha in the upper altitudinal zone of the forest. The UTM area coordinates vary from 642700 to 644300W and 9493300 to 9490499N, in the 17S zone, Datum WGS84. The area of forest studied is delimited by two tracks marking the upper and lower limits. The lower track is newer and in better condition than the upper track, allowing access for small vehicles during the dry season. The forest is surrounded by shrubs, cultivated fields and secondary vegetation. It once formed part of a larger cloud forest that occupied an extensive area of the mountain range, but this has gradually shrunk so that today, only small patches of forest remain (Gentry, 1995; Vellinga et al., 2004). The nearest similar patches of cloud forest are 20 km away and occupy relatively small areas. Elevation ranges from 2259 to 3012 a.s.l. and the average slope is 39%, although it often exceeds 90%. The main part of the study area is situated on south-westerly facing slopes. The location has a cold temperate climate with a dry winter according to Köpen (1936). The mean temperature is 15 °C and variations in the temperature are low; varying between 8.5 °C and 18 °C. Mean annual precipitation is around 1200 mm (AECI, 2004), generally being very intense during the summer. In years when the ENSO (*El Niño* Southern Oscillation) phenomenon occurs, the precipitation increases substantially (Romero et al., 2007).

The area is included in the neotropical region according to Takhtajan (1986) and has one of the highest levels of endemism in the world (Gentry, 1992b). The area is not a protected area; it has only been classified as an 'Important Bird Area', the IBA PE 005 (Freile and Santander, 2005).

2.2. Inventory

The inventory was carried out between January and March of 2006. The positions of the 38 sampling plots were selected by generating random XY coordinates throughout the study area during the planning stage. The plots were square shaped of



Fig. 1. View of the forest.

20 m × 20 m, and located in the field using a GPS receptor. Two diameters at breast height (DBH) (in orthogonal directions) and total height of all trees higher than 1.3 m were recorded for all the woody plants in each plot, along with species and any special characteristics. Trees with a DBH less than or equal to 2.5 cm were considered recruitment and all trees with a diameter greater than 7.5 were considered older trees. The stand has a multilayer distribution, as can be seen in Fig. 1, a mean number of trees per hectare of 1246.7 (standard deviation: 476.06 trees per ha) and a mean basal area of 45.27 m²/ha (standard deviation: 7.33 m²/ha). A total of 120 species of woody plants were found in the forest.

To identify species, samples of the woody plants were collected during the fieldwork and compared to catalogued specimens in the Trujillo Herbarium Truxillense, HUT and the Herbarium de la Universidad de Piura UPADI, consulting with specialists in particular taxa when necessary.

2.3. Tree Diversity Change Index (TDC)

To quantify the loss or gain in diversity of the stand, a tree diversity change index based on the richness index designed by Kempton (1979) was proposed:

$$TDC = \left(\frac{S}{N} \right)_{\text{recruitment}} - \left(\frac{S}{N} \right)_{\text{older trees}}$$

where S is the number of species and N is the number of trees.

This index shows the difference in species richness values between older trees and recruitment in each plot, and can indicate the different levels of diversity between the trees that form the current stand and the regeneration that will form the stand in the future. Negative values for the index may imply that a loss in tree diversity is occurring in the stand, whereas positive values reveal that species diversity is greater in the recruitment than in the older trees. Values near 0 indicate no change in species richness.

2.4. Species Replacement Index (RE)

To evaluate changes in the functioning of the ecosystem, two functional groups of indicator species were selected: (a) species with high-humidity requirements and (b) species with lower humidity requirements. Only 'process-limited' species (*sensu* Carignan and Villard, 2001) sensitive to the level of humidity were included as indicator species for these functional groups. The species selected for the analysis were those with documented humidity requirements. The rest of the species present in the forest were not included in this analysis. For each functional group,

species characterized as "pioneer species" (*sensu* Whitmore, 1989) and canopy-emergent species were selected. The first functional group was composed of species with high-humidity requirements. From this group the species *Vallea stipularis* L.F., two species of the *Meliosma* genus and *Oreopanax raimondii* Harms. were selected as indicator species. These species are characteristic of remnant cloud forest and are unable to survive outside the forest since they require high levels of humidity to develop and thrive (Gentry, 1992b,c; Mostacero León et al., 1996; León, 2006). Consequently, they are good indicators of the humidity conditions. The second functional group was composed of species with lower humidity requirements, the indicator species selected being: one species of the genus *Solanum* and another of the genus *Persea*. The *Solanum* species is characteristic of cloud forests, but is generally found in those with lower levels of humidity (Gentry, 1992b). *Persea* is another genus which is characteristic of cloud forest and is frequently found near the upper or lower limits of the forest because, like *Solanum*, it is less demanding as regards strict cloud forest micro-environmental conditions (Gentry, 1992b; Mostacero León et al., 1996). These species were used to evaluate changes in the abundance of the different indicator groups, since these species are characteristic of this type of forest and are representative of the different diameter classes and successional stages within the stand. Moreover, they are widespread throughout the whole forest area. All the above species were correctly differentiated in the field, although in some cases, no catalogued samples were available to adequately identify the plants at species level. Hence, where identification at species level is in doubt, the scientific name for the genus is used in this study.

To evaluate the dynamics between the two functional or indicator groups it was necessary to develop a method capable of reflecting the progressive changes in functional group dominance. A new second order O-ring type function was developed which is based on the distribution of diameter differences among pairs of trees in both indicator groups. This technique is analogue to the K_{12} function proposed by Lotwick and Silvermann (1982) for identifying the underlying processes of interaction between two types of plant using fully mapped data (Goreaud and Pélissier, 2003). If we make the assumption that for each of the analysed species, the size of a tree is related to its age, this technique may provide a tool for characterizing the species interactions over time using data from a single inventory:

$$r(\Delta) = \frac{\sum_{i=1}^n \sum_{j=1}^n f(i, j) I_{ij}(\Delta - \delta, \Delta + \delta)}{\sum_{i=1}^n \sum_{j=1}^n I_{ij}(\Delta - \delta, \Delta + \delta)}$$

where n is the number of trees in the plot, Δ is the diameter difference, $f(i, j)$ gives -1 if i and j individuals are included in the same functional group (either higher humidity-requirement species or lower humidity-requirement species), or 1 if the i species group does not coincide with j , 2δ is the width of the diameter difference lags and the O-ring function $I_{ij}(\Delta - \delta, \Delta + \delta)$ gives 1 if the diameter difference between tree i and j is within the $(\Delta - \delta, \Delta + \delta)$ interval or 0 if not, so for a pair included in the interval $f(i, j) \cdot I_{ij}(\Delta - \delta, \Delta + \delta)$ gives -1 if species are included in the same functional group or 1 if the two species are included in the other functional group. The function was calculated including only the abovementioned species representative of each functional group.

In other words, the value of the $r(\Delta)$ function is close to -1 when, for a diameter difference Δ , there are no changes in the relative abundance of indicator species in both functional groups, and is close to 1 when, for a diameter difference Δ , individuals belong to different functional groups. An increasing function

indicates that there is a gradual shift in functional group dominance from the larger diameter classes to the smaller ones (replacement).

The O-ring is calculated for discrete lags centred on each diameter difference Δ_i , and to achieve an index of the change in functional groups in each plot, the sum of the $r(\Delta_i)$ function weighted by the diameter difference Δ_i was calculated for $i = 1, 2, \dots$

The Replacement Species Index (RE) defined was:

$$RE = \sum_{i=1}^t \Delta_i r(\Delta_i)$$

where Δ_i is the greatest diameter difference in the plot. Both the $r(\Delta)$ function and RE were evaluated for diameter difference lags of 5 cm.

This index analyses whether a shift in the dominance of one group of indicator species over another is taking place in the stand. Positive values of the index indicate a shift from the current composition to the dominance of a different group of species, and negative values imply an increase in the dominance of the group of species currently most representative; the absolute value of the index increasing with the width of the diameter range in the plot.

2.5. Assessment of the current indicator species group dominance

To evaluate the change in species composition, a preliminary analysis of the current group of dominant species was performed. To obtain the current distribution and level of dominance between functional groups, the ratio of high-humidity-requirement older trees to low-humidity-requirement older trees was calculated.

Ordinary kriging of this variable indicates the likelihood of dominance of the higher humidity-requirement species. The kriging prediction of the value of the variable $Z(s_0)$ (Z is the ratio of high-humidity-requirement older trees to low-humidity-requirement older trees) at an unsampled location s_0 is given by:

$$p(Z, s_0) = \sum_{i=1}^n \lambda_i \cdot Z(s_i)$$

and the unbiasedness condition is given by: $\sum_{i=1}^n \lambda_i = 1$ where $Z(s_i)$ is

the value of the variable at a sampled location and λ_i is determined by minimizing the prediction error and depends on the variogram $\hat{\gamma}(d)$ (Cressie, 1993):

$$\hat{\gamma}(d) = \frac{1}{2 \cdot N(d)} \sum_{i=1}^{N(d)} [Z(s_i) - Z(s_i + d)]^2$$

where $N(d)$ is the number of pairs of observations d distant.

2.6. Spatial analysis of species diversity change and replacement

In order to analyse the spatial dynamics of the changes in species diversity and in the spatial arrangement of functional groups (given that both TDC and RE were expected to be related to environmental variables that can be expressed as a function of the spatial location, as well as the fact that the species distribution is expected to be spatially auto-correlated) the Universal Kriging system was used to find the spatial covariance structure of TDC and RE and to predict the behaviour of the indices over the whole study area.

A multiple-regression analysis was carried out to determine the most significant variables in this process, selecting those which showed the strongest correlation (higher r^2 and admissible p -value). The explanatory variables considered were those related to either stand structure (basal area, number of trees per ha, canopy

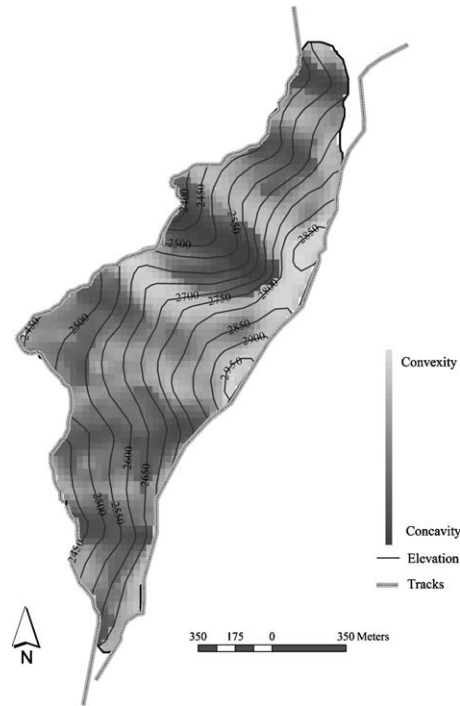


Fig. 2. Map of the tracks, elevation and concavity of the terrain in the studied forest.

cover, quadratic mean diameter, dominant height) or to environmental factors (altitude, slope, orientation, micro-topography, distance to nearest track). The variables finally selected for inclusion in the TDC index model were: elevation and concavity of the terrain (calculated as the second derivative of the Digital Elevation Model) and minimum distance from each point to the nearest access track (calculated using ARCGIS[®]). In the case of the RE index, the variables chosen were the concavity of the terrain and the altitude. The tracks, elevation and concavity of the terrain in the studied forest are shown in Fig. 2.

Universal Kriging of a regionalized variable $Z(s)$ (where $Z(s)$ in this case, is values of TDC and RE indices) involves applying the following model:

$$Z(s) = \sum_{j=1}^{p+1} f_{j-1}(s) \beta_{j-1} + \delta(s)$$

where $f_{j-1}(s)$ are the $p + 1$ explanatory variables whose value is a function of location s , β is an unknown vector of parameters, and $\delta(s)$ is a zero-mean intrinsically stationary random process with variogram $2\gamma(\cdot)$ which describes the variance of the variable as a function of the distance between sample plots (Cressie, 1993):

$$\hat{\gamma}(d) = \frac{1}{2 \cdot N(d)} \sum_{i=1}^{N(d)} [\delta(s_i) - \delta(s_i + d)]^2$$

The parameters of the variogram for Universal Kriging, and the β regression coefficients of the explanatory variables were estimated using the Restricted Maximum Likelihood (REML) method (Kitadinis, 1985; Harville, 1977).

The prediction $Z^*(s_0)$ of the variable at each point s_0 estimated from the value of Z in the measured sampled plots s_i is expressed as:

$$Z^*(s_0) = \sum_{i=1}^n \lambda_i \cdot Z(s_i)$$

$$\sum_{i=1}^n \lambda_i \cdot f_{j-1}(s_i) = f_{j-1}(s_0) \quad j = 1, \dots, p + 1$$

To obtain the optimal linear estimator, the sum of the squared errors was minimized, adding the Lagrange parameter to ensure global unbiasedness, which necessarily implies that $f_0(s) \equiv 1$.

The variance of the prediction was calculated as:

$$\sigma_{UK}^2 = \sum_{i=1}^n \lambda_i \gamma(s_0 - s_i) + \sum_{j=1}^{p+1} m_{j-1} f_{j-1}(s_0)$$

The values for the ratio of high-humidity-requirement trees to low-humidity-requirement trees, as well as both the *TDC* and *RE* indices, were considered punctual estimates referenced to the centre point of the plot. A grid spacing of 10×10 m was used to obtain the kriging prediction for these variables (current high-humidity-indicator older trees fraction, *TDC* and *RE*) throughout the forest.

2.7. Cross-validation

Cross-validation was used to compare the performance of the different methods. The sum of the estimation errors (SEE) was used to check for bias (SEE must be close to 0):

$$SEE = \frac{\sum_{i=1}^n (Z^*(s_i) - Z(s_i))}{n}$$

where n is the number of observations.

The variance of the standardised estimation errors (that must approximate to 1) was used to check the validity of the prediction error given by the kriging variance:

$$VSEE = \frac{\sum_{i=1}^n ((Z^*(s_i) - Z(s_i))^2) / \sigma_k^2(s_i)}{n}$$

Table 1

REML estimates of the variogram parameters (θ) and the β coefficients for the Universal Kriging (UK) model of the Tree Diversity Change index (*TDC*) and the Replacement Species index (*RE*) and the Ordinary kriging (OK) model of the high-humidity-requirement species dominance fraction.

Variable	Model	θ			β			
		Nugget	Sill	Range	Elevation	Concavity	Proximity to roads	Intercept
<i>TDC</i>	UK	0.034	0.062	726.49	–	–19,8982	–0.0006	–0.0473
High requirement fraction	OK	0.01125	0.0544	377.64	–	–	–	–
<i>RE</i>	UK	1610.5	10,497.4	220.9	–0.361	–9614	–	920.6

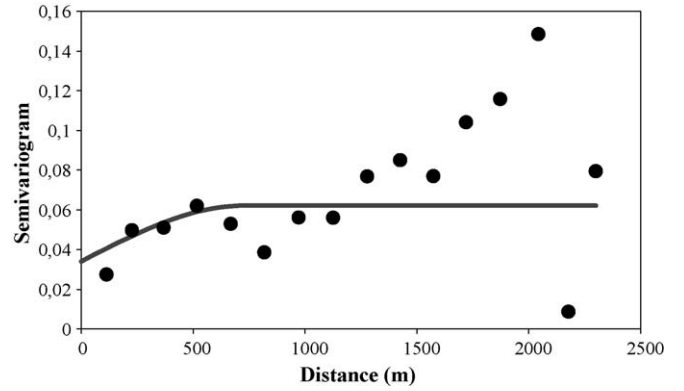


Fig. 3. Empirical variogram of the δ residuals of the Universal Kriging model for the Tree Diversity Change Index (*TDC*) and spherical model fitted using REML. The values of semivariance were calculated for each distance lag using more than 30 pairs of observations.

3. Results

3.1. Tree Diversity Change Index

The average value of the *TDC* for all the inventory plots was 0.04, ranging from –0.37 to 0.75. The exploratory analysis indicates that the *TDC* displays spatial autocorrelation, which means that the index values are similar in neighbouring plots. The Universal

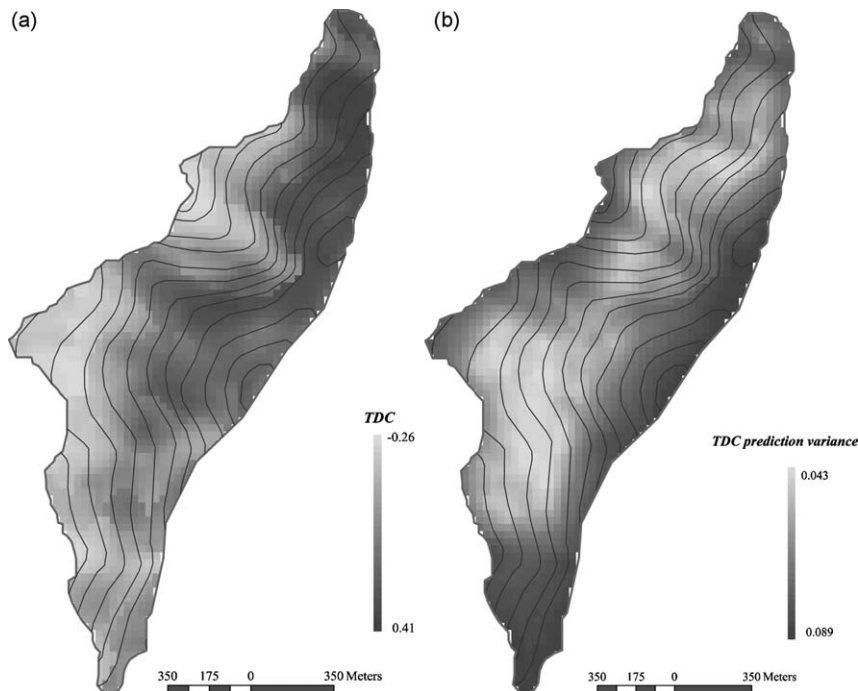


Fig. 4. (a) Universal Kriging prediction of Tree Diversity Change index (*TDC*) and (b) map of prediction variance.

Kriging model was constructed using the concavity of the terrain and distances to nearest track as explanatory variables. The REML estimates of the variogram parameters, as well as the β coefficient estimates for the explanatory variables are shown in Table 1. The results of the cross-validation described above; a SEE of -0.000441 (1.1% of the mean) and VSEE: 1.023441, indicate the suitability of the model in terms of bias and prediction variance. The range of spatial autocorrelation for the tree diversity change index is around 700 m. The nugget effect is about 55% of the sill (Fig. 3), so 45% of the TDC variability is explained by the spatial autocorrelation of the variable, probably due to ecological processes such as seed dispersion or mortality.

Fig. 3 shows the fitted variogram and the δ residuals.

The resultant TDC prediction map and that for prediction variance are shown in Fig. 4a and b. The dark zones correspond to the areas in which species richness has been enhanced and the light zones imply a loss in diversity. As was expected from the index trend analysis using the β coefficients, the inner zones are those where the species richness remains constant, as reflected in the positive TDC values.

The negative correlation between the TDC and the distance to the nearest track indicates that species richness is decreasing close to these tracks and that it is only maintained in the inner areas. The TDC also reveals higher values on spurs than in gullies, probably because the poorer conditions for growth associated with the former lead to a decrease in the diversity of canopy species.

3.2. Current dominant species

The variogram of the fraction corresponding to high-humidity species presents a range of autocorrelation around 380 m with the nugget effect beginning at approximately 20% of the sill (Table 1), indicating a strong spatial continuity in species composition.

As can be seen in Fig. 6, the ordinary kriging prediction for the ratio of high-humidity-requirement indicator species to low-humidity-requirement ones shows a dominance of species with high-humidity requirements in most of the forest (about 99.05% of the total forest area was dominated by species with high-humidity requirements).

3.3. The $r(\Delta)$ function analysis

The values and shapes of the $r(\Delta)$ function are related to the dynamics of the species replacement process. The values of $r(\Delta)$ can fluctuate between 1 and -1 . Based on the $r(\Delta)$ function, three different types of species dynamics can be identified: (1) When the relative abundance of indicator species is not changing, the value of the $r(\Delta)$ function is negative and fairly constant (Fig. 5a). If the stand is composed of species within the same functional group, the value of $r(\Delta)$ is -1 . (2) The $r(\Delta)$ function of plots included in Fig. 5b shows the continuous replacement of one group of indicator species by another. In this case the curve will show an upward trend; from negative values for the first diameter difference lags to positive values for large diameter differences. This behaviour, found in 34% of the plots, implies that individuals with similar diameters belong to the same functional group, and that the larger trees belong to a different functional group from that of the smaller trees. (3) In the plots presented in Fig. 5c, this ‘replacement’ of both indicator groups takes place in ‘phases’ rather than being a continuous process. Approximately 34% of the plots present a fluctuating $r(\Delta)$ function.

3.4. Species Replacement Index (RE)

In the studied forest, high-humidity species currently dominate the older trees strata, so the increase in the $r(\Delta)$ function from negative values to positive values indicates a change in the

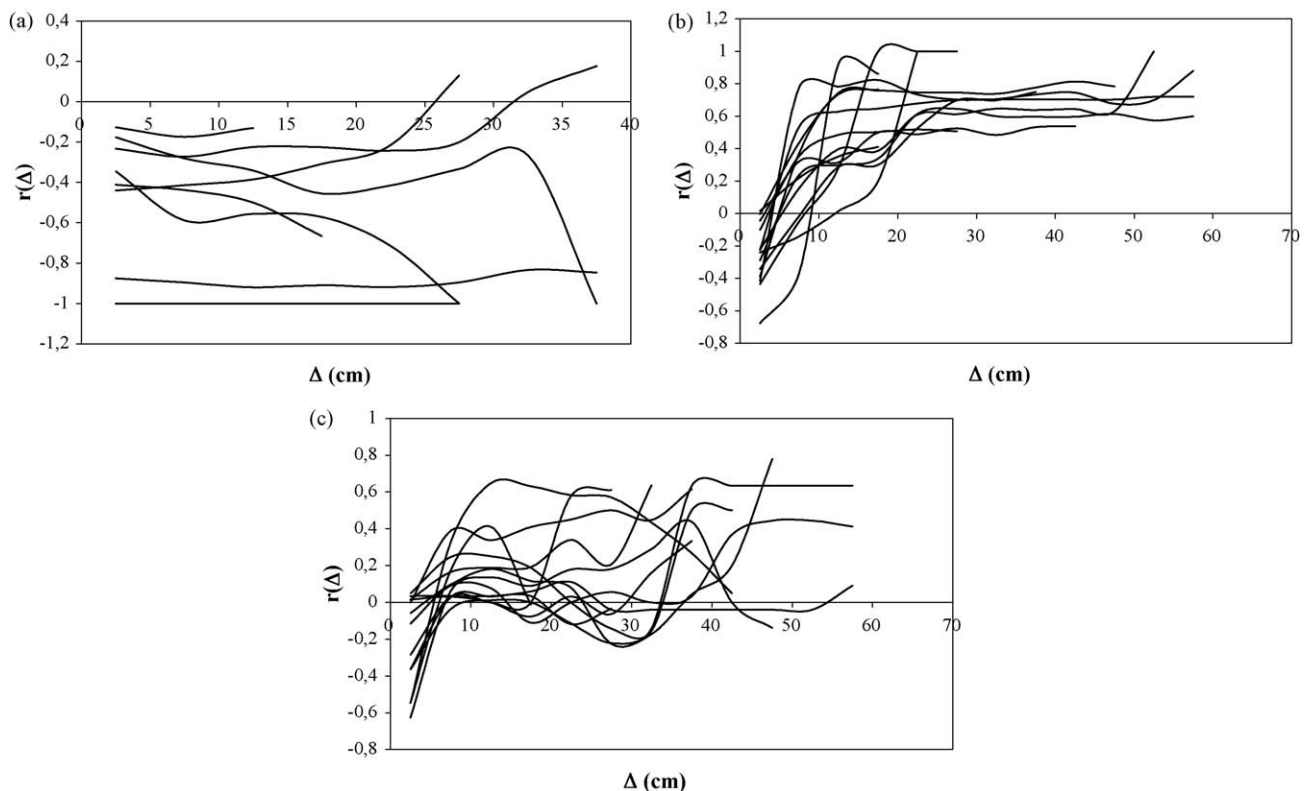


Fig. 5. $r(\Delta)$ function (a) for those plots which mainly contains species of one functional group (b) for those plots which show a gradual change from one group of species to another group and (c) for those plots which shows fluctuating values.

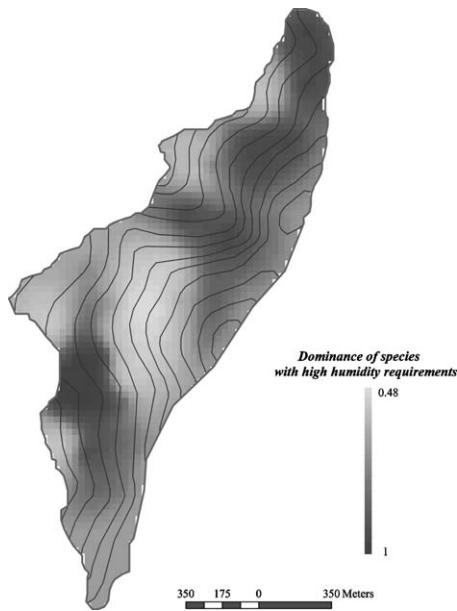


Fig. 6. Ordinary kriging prediction of the ratio between humidity-indicator species and species with low-humidity requirements.

dominance of species from humid-condition species to dry-condition species. The weighted sum in the *RE* index shows the trend of the $r(\Delta)$ function as the DBH difference increases (over time), characterizing the dynamics between two functional groups with a single variable which is continuous in space, allowing the spatial distribution to be analysed at landscape scale. The average value of the *RE* for all the inventory plots was 11.52, ranging from 259 to –360.

On the basis of the multiple-regression analysis, the convexity of the terrain and the elevation were selected as explanatory variables for the Universal Kriging. The REML variogram and the δ residuals are shown in Fig. 7. The residuals of the cross-validation present a SEE of –1.428417 (0.13% of the mean) and VSEE: VSEE:

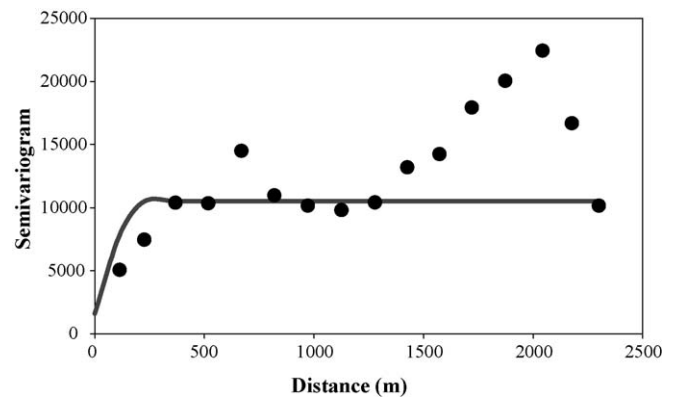


Fig. 7. Empirical variogram of the δ residuals of the Universal Kriging model for the Species Replacement index (*RE*) and spherical model fitted using REML. The values of semivariance were calculated for each distance lag using more than 30 pairs of observations.

1.074500. The variogram parameters indicate that spatial correlation exists up to 221 m, and the small nugget effect (16%) implies that there is considerable spatial continuity. The different values for the range of correlation in species richness decrease and indicator species replacement reveals that the processes driving these phenomena are different. The sign of the β parameters show that a negative relationship exists between the likelihood of the current group of indicator species and the elevation, as well as the concavity of the terrain (Table 1).

As can be seen from the prediction map, a change in relative abundance of indicator species has been occurring in much of the forest (Fig. 8a). In the upper zones and gullies, the populations of the current group of indicator species are either stable or increasing, whereas in the lower zones or on the spurs there is a change in indicator species abundance. The negative correlation between the *RE* index and the altitude indicates that there is a dynamic replacement of humid-condition species by dry-condition species at lower elevations, where the temperature is slightly higher. The negative correlation between the *RE* index and the concavity of the

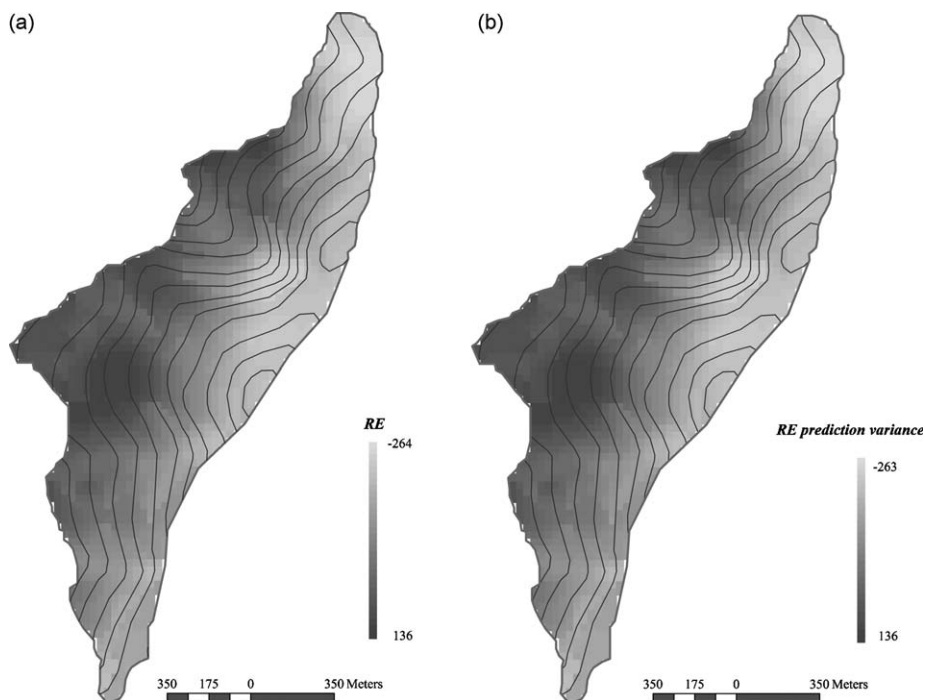


Fig. 8. (a) Universal Kriging prediction of the Species Replacement index (*RE*) and (b) map of prediction variance.

land indicates that the process of replacement between the two groups of indicator species seems to depend on the presence of suitably humid micro-ambient conditions. Such conditions are necessary for the development of species with high-humidity requirements and tend to be found at the bottom of the gullies.

4. Discussion

Several studies have highlighted the high rate at which montane cloud forests are disappearing (Zadroga, 1981; Stadtmüller, 1987; Hamilton et al., 1993; Brown and Kappelle, 2001). However, despite the high biodiversity value of these ecosystems, they are among the least known in the world (Stadtmüller, 1987; Aubad et al., 2008). A detailed assessment of species dynamics is required in order to understand the processes that take place in forest ecosystems and to design biodiversity conservation strategies. In this paper, an approach for assessing species dynamics in the forest stand was proposed; using the information derived from the species diameter distribution and extending the value to the whole study area by Universal Kriging. The abundance of individuals of a determined species in the smallest size classes may indicate suitable conditions for regeneration, whereas dominance of the largest classes may indicate that the conditions had previously been favourable for the development of the species. Therefore, when noticeable differences in the relative abundance of two functional groups exist between small and large trees, the $r(d)$ analysis is capable of detecting a trend towards a change in the species dynamics if the indicator species considered in each group include pioneer and canopy species, even in the case of weak correlation between the size and the age of the tree. The analyses of the prediction variance maps (Figs. 4b and 8b) reveal the suitability of the proposed techniques for identifying the spatial arrangement of species dynamics using data from a single forest inventory.

The *TDC* analysis shows a trend towards loss of diversity throughout most of the studied forest (Fig. 4a). The values for species richness have remained constant at higher elevations where species are able to regenerate as well as in the north, where there is greater continuity of vegetation beyond the forest. The findings of this study agree with those of others which highlight the sensitivity of these forests to disturbances. According to previous studies (Pounds et al., 1999), these cloud forests are strongly affected by the proximity of roads or tracks, as reflected by the correlation between *TDC* and distance to the tracks. Moreover, these roads or tracks may act as 'vectors' of human-originated perturbations and may be partly responsible for the serious loss of biodiversity. Furthermore, the loss of species diversity in montane cloud forest appears also to be related to the negative impact of fragmentation (Arango-Vélez and Kattan, 1997). The *TDC* gradient from high values in the inner part of the forest to low values near the forest boundaries may indicate that fragmentation also affects the micro-environmental conditions, the existence of which, in large forest areas, is necessary for the dispersion process and establishment of many species.

Leuschner (2000) found that the greater degree of scleromorphy present in tropical alpine plants was linked to the humidity conditions rather than to low temperature or high levels of radiation as was previously thought. The strong influence of humidity in tropical Andean mountains is evidenced by the results of the *RE* index calculated in the present study, which indicate that species with lower humidity requirements are increasing their presence on the mountain and species with greater humidity requirements (the recruitment of which is limited to zones with higher humidity levels) are having their habitat reduced (Fig. 8a). However, species dynamics in this type of forest are extremely complex, as reflected by the different trends exhibited by the $r(\Delta)$ functions. An aspect which should be highlighted is that many of the species with lower humidity requirements are generally

characteristic of the inferior vertical strata whereas most of the species with greater humidity requirements are those which form part of the upper strata. Consequently, a change in the dominant group of species may also lead to a change in the stand structure; the latter being very important to the maintenance of habitat biodiversity (Fjeldså and Krabbe, 1990).

Some authors have suggested that rising sea-surface temperatures have altered the climate of tropical mountains (Pounds et al., 1999) and may bring about a shift in the cloud base, threatening the very existence of cloud forests since the presence of clouds is indispensable for their formation (Still et al., 1999). The increase in area occupied by tree species with lower humidity requirements would appear to support these hypotheses. In order to evaluate the effects of climate change on montane cloud forest, Still et al. (1999) proposed the use of biogeographic models to predict the locations of cloud forest, using cutoffs in temperature sums and moisture balance calculations. Vegetation indicators, such as the techniques proposed in this study, may provide evidence of these changes since it has been demonstrated that the composition of tree species and regeneration patterns are climate sensitive and can also be affected by changes in microclimate conditions. Pounds et al. (1999) proposed that the invasion of montane forests by premontane species should be analysed to determine the effect of climate change on montane vegetation. However, since this invasion by premontane species may be a symptom of irreversible damage, the use of *RE* analysis to study changes in the current species composition may allow us to detect potential species changes prior to invasion by premontane or alien species.

The results of this study indicate that the primary cloud forest is being reduced and restricted to the most suitable inner areas. Moreover, the *TDC* and *RE* reflect changes in the composition and relative abundance of functional groups which are currently taking place in parallel throughout most of the forest. These changes may increase the rate of extinction of some cloud forest species (Ray et al., 2006). The fact that these changes are detected from data that describe the current species composition and diameter distribution means that the effect of these processes may be appreciable during the life cycle the trees. Felling or change to agricultural use are the main factors behind the loss of montane cloud forest (Sarmiento, 1993; Young and León, 1993), although according to the results of the present study, the situation is worsened by the fragmentation of the forest into small patches which may not offer the necessary conditions for life and the level of biodiversity falls significantly in the remaining patches of forest (Fjeldså and Krabbe, 1990). Consequently, the forest ecosystem becomes impoverished.

In spite of the fact that these results were obtained using data from a single inventory conducted at one single cloud forest and although more research is needed both to assess species dynamics in other cloud forests as well as to monitor these changes over time, this study highlights the fragility of this ecosystem, which may disappear from the Andean region over the course of the coming years if the current trend is maintained. Urgent action is needed to conserve these mountain forests.

5. Conclusions

The proposed Species Replacement Index (*RE*) shows that species with greater humidity requirements are having their habitat reduced to upper and inner zones with higher humidity levels. Furthermore, the analysis of Tree Diversity Change Index (*TDC*) suggests the existence of a minimum forest area necessary to ensure the continuity of the cloud forest. The species with greater humidity requirements, which according to the analysis of the current dominant species were once able to live throughout the forest area, are now restricted to the gullies and higher elevations. Therefore, it is probable that the high-humidity conditions required by these

species may once have existed over the whole area, but are now restricted to the gullies and higher elevations. If this trend continues, the findings of this study suggest that the future may bring the disappearance of montane cloud forest in its original form.

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References

- AECI, 2004. Caracterización hídrica y adecuación entre la oferta y la demanda en el ámbito de la cuenca binacional Catamayo-Chira. Consorcio ATA-UNP-UNL, Resumen ejecutivo, 82 pp.
- Arango-Vélez, N., Kattan, G., 1997. Effects of forest fragmentation on experimental nest predation in Andean Cloud Forest. *Biological Conservation* 81, 137–143.
- Aubad, J., Aragón, P., Olalla-Tárraga, M.A., Rodríguez, M.A., 2008. Illegal logging, landscape structure and the variation of tree species richness across North Andean forest remnants. *Forest Ecology and Management* 255, 1892–1899.
- Battles, J.J., Shliskya, A.J., Reginald, H., Barretta, R.H., Heald, R.C., Allen-Diaz, B.H., 2001. The effects of forest management on plant species diversity in a Sierran conifer forest. *Forest Ecology and Management* 146, 211–222.
- Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055.
- Brown, A.D., Kappelle, M., 2001. Bosques nublados del Neotrópico. Instituto Nacional de biodiversidad (INBio), Costa Rica, 240 pp.
- Brujnzeel, L.A., Proctor, J., 1995. Hydrology and biogeochemistry of tropical montane “cloud forests”: what do we really know? In: Hamilton, L.S., Juvik, J.O., Scatena, F.N. (Eds.), *Tropical Montane Cloud Forests*. Ecological Studies no. 110. Springer, New York, pp. 38–78.
- Carignan, V., Villard, M.A., 2001. Selecting indicator species to monitor ecological integrity: a review. *Environmental Monitoring and Assessment* 78, 45–61.
- Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., Tilman, D., 1997. Biotic control over the functioning of ecosystems. *Science* 277, 500–504.
- Churchill, S.P., Balslev, H., Forero, E., Luteyn, J.L., 1995. Biodiversity and conservation of Neotropical montane forest. In: *Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium*. The New Botanical Garden, New York, p. 720.
- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society Series B* 345, 101–118.
- Cousins, S.A.O., Lindborg, R., 2004. Assessing changes in plant distribution patterns—indicator species versus plant functional types. *Ecological Indicators* 4, 17–27.
- Cressie, N.A.C., 1993. *Statistics for Spatial Data*. Wiley, New York.
- Dimov, D.L., Chambers, J.L., Lockhart, B.R., 2005. Spatial continuity of tree attributes in bottomland hardwood forests in the southeastern United States. *Forest Science* 51, 532–540.
- Dutilleul, P., 1993. Spatial heterogeneity and the design of ecological field experiments. *Ecology* 74, 1646–1658.
- Dutkowski, G.W., Costa-Silva, J., Gilmour, A., Lopez, G.A., 2002. Spatial analysis methods for forest genetic trials. *Canadian Journal of Forest Research* 32, 2201–2214.
- Fjeldsá, J., Hjarsen, T., 1999. Needs for sustainable land management in biological unique areas in the andean highland. In: *Símpoio internacional del desarrollo sustentable de montañas: entiendo las interfaces ecológicas para la gestión de los paisajes culturales en los Andes*, Quito.
- Fjeldsá, J., Krabbe, N., 1990. *Birds of the High Andes*. Zoological Museum, University of Copenhagen, 876 pp.
- Foster, P., 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth Science Reviews* 55, 73–106.
- Franklin, J.F., Cromack, K., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F., Juday, G., 1981. Ecological characters of old-growth Douglas-fir forests. USDA Forest Service Technical Report PNW-118. Pacific North-west Forest and Range Experimental Station, Portland, Oregon.
- Freile, J.F., Santander, T., 2005. Áreas Importantes para la Conservación de las Aves en Ecuador. In: *BirdLife International and Conservation International. Áreas Importantes para la Conservación de las Aves en los Andes Tropicales: sitios prioritarios para la conservación de la biodiversidad*, Serie de Conservación de BirdLife No. 14. BirdLife International, Quito, pp. 283–470.
- Gentry, A.H., 1992a. Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos* 63, 19–28.
- Gentry, A.H., 1992b. Diversity and floristic composition of Andean forest of Peru and adjacent countries: implication for their conservation. In: Young, K.R., Valencia, N. (Eds.), *Biogeografía, ecología y conservación del bosque montano en el Perú*. *Memorias Museo de Historia Natural, UNMSM* 21, pp. 11–29.
- Gentry, A.H., 1992c. Four new species of *Meliosma* (Sabiaceae) from Perú. *Novon* 2, 155–158.
- Gentry, A.H., 1995. Patterns of diversity and floristic composition in Neotropical montane forest. In: Churchill, S.P., Balslev, H., Forero, E., Luteyn, J.L. (Eds.), *Biodiversity and Conservation of Neotropical Montane Forest*. The New York Botanical Garden Press, New York, pp. 103–126.
- Gilmour, A.R., Cullis, B.R., Verbyla, A.P., 1997. Accounting for natural and extraneous variation in the analysis of field experiments. *Journal of Agricultural, Biological and Environmental Statistics* 2, 269–293.
- Goreaud, F., Pélissier, R., 2003. Avoiding misinterpretation of biotic interactions with the intertype K_{12} -function: population independence vs. random labelling hypothesis. *Journal of Vegetation Science* 14, 681–692.
- Hamilton, L.S., 1995. Mountain cloud forest conservation and research: a synopsis. *Mountain Research and Development* 15, 259–266.
- Hamilton, L.S., Juvik, J.O., Scatena, F., 1993. The Puerto Rico Tropical Cloud Forest Symposium: introduction and workshop synthesis. In: Hamilton, L., Juvik, J., Scatena, F. (Eds.), *Tropical Montane Cloud Forests*. The East West Center, Honolulu, pp. 1–12.
- Harville, D.A., 1977. Maximum likelihood approaches to variance component estimation and related problems. *Journal of the American Statistical Association* 72, 320–338.
- Howard, K., 1970. The summit forest of Pico del Oeste, Puerto Rico. In: Odum, H.T., Pidgeon, R.F. (Eds.), *A Tropical Rain Forest. A Study of Irradiation and Ecology at El Verde, Puerto Rico*. U.S. Atomic Energy Commission, Oak Ridge, pp. B-325–B-328.
- Kapos, V., Rhind, J., Edwards, M., Price, M.F., Ravilious, C., 2000. Developing a map of the world's mountain forests. In: Price, M.F., Butt, N. (Eds.), *Forests in Sustainable Mountain Development—A State of Knowledge Report for 2000*. IUFRO Research Series No. 5. CAB International, Oxford, pp. 4–9.
- Kempton, R.A., 1979. The structure of species abundance and measurement of diversity. *Biometrics* 35, 307–321.
- Kitadinis, P.K., 1985. Minimum variance unbiased quadratic estimation of covariances of regionalized variables. *Journal of the International Association for Mathematical Geology* 7, 195–208.
- Köpen, W., 1936. *Der geographische System der Klimate*. *Handbuch der Klimatologie*, vol. 1(C). Borntraeger, Berlin, 44 pp.
- Körner, Ch., 1994. Impact of atmospheric changes on high mountain vegetation. In: Beniston, M. (Ed.), *Mountain Environments in Changing Climates*. Routledge, London, pp. 155–166.
- Kremen, C., 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 2, 203–217.
- Lawton, R.O., Nair, U.S., Pielke Sr., R.A., Welch, R.M., 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. *Science* 19, 584–587.
- Legendre, P., Dale, M.R.T., Fortin, M.J., Casgrain, P., Gurevitch, J., 2004. Effects of spatial structure on the results of field experiments. *Ecology* 85, 3202–3214.
- Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M., Myers, D., 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25, 601–615.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 34, 659–673.
- León, B., 2006. *Sabiaceae endémicas de Perú*. *Revista peruana de biología. Número especial* 13 (2), 602.
- Leuschner, C., 2000. Are high elevations in tropical mountains arid environments for plants? *Ecology* 81, 1425–1436.
- Lotwick, H.W., Silverman, B.W., 1982. Methods for analysing spatial processes of several types of points. *Journal of the Royal Statistical Society Series B* 44 (3), 406–413.
- Luna-Vega, I., Alcantara, O., Espinosa, D., 2001. Biogeographical affinities among neotropical cloud forest. *Plant Systematics and Evolution* 228, 229–239.
- Magurran, A.E., 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, New Jersey, p. 175.
- Mooney, H.A., Cushman, J.H., Medina, E., Sala, O.E., Schulze, E.D., 1996. *Functional Roles of Biodiversity: A Global Perspective*. John Wiley & Sons, New York.
- Mostacero León, J., Mejía, F., Pelaez, F., 1996. *Fitogeografía del norte del Perú*. Serie ciencias Concytec-Perú, 406 pp.
- Noss, R.F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4, 355–364.
- Polyakov, M., Majumdar, I., Lawrence Teeter, L., 2008. Spatial and temporal analysis of the anthropogenic effects on local diversity of forest trees. *Forest Ecology and Management* 255, 1379–1387.
- Pounds, A., Michael, J., Fogden, P.L., Campbell, J.H., 1999. Biological response to climate change on a tropical mountain. *Nature* 398, 611–615.
- Ray, D.K., Nair, U.S., Lawton, R.O., Welch, R.M., Pielke Sr., R.A., 2006. Impact of land use on Costa Rican tropical montane cloud forests: sensitivity of orographic cloud formation to deforestation in the plains. *Journal of Geophysical Research* 111, D02108. doi:10.1029/2005JD006096.
- Ripley, B.D., 1981. *Spatial Statistics*. John Wiley & Sons, New York, p. 252.
- Romero, C.C., Baigorria, G.A., Stroosnijder, L., 2007. Changes of erosive rainfall for El Niño and La Niña years in the northern Andean highlands of Peru. *Climatic Change* 85, 343–356.

- Sarmiento, F.O., 1993. Human impacts on the cloud forests of the upper Guayllabamba river basin, Ecuador, and suggested management responses. In: Hamilton, L., Juvik, J., Scatena, F. (Eds.), *Tropical Montane Cloud Forests*. The East West Center, Honolulu, pp. 183–190.
- Stadtmüller, T., 1987. Cloud forest in the humid tropics. In: *A Bibliographic Review*, United Nations University, Tokio and CATIE, Turrialba, Costa Rica, 82 pp.
- Still, C.J., Foster, P.N., Schneider, S.H., 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* 398, 608–610.
- Takhtajan, A.L., 1986. *Floristic Regions of the World*. University of California Press, Berkeley, p. 522.
- Torres, I., Pérez, B., Fernández-González, F., Moreno, J.M., 2006. Spatial structure of an early post-fire plant community changes with time and scale. *Forest Ecology and Management* 234 (Suppl. 1), S204.
- Vellinga, W.-P., Flanagan, J.N.M., Mark, T.R., 2004. New and interesting records of birds from Ayabaca province, Piura, north-west Peru. *Bulletin of the British Ornithologists's Club* 124, 124–142.
- Williams-Linera, G., 2002. Tree species richness complementarity, disturbance and fragmentation in a Mexican tropical montane cloud forest. *Biodiversity and Conservation* 11, 1825–1843.
- Whitmore, T.C., 1989. Canopy gaps and the two major groups of forest trees. *Ecology* 70, 536–538.
- Young, K.R., León, B., 1993. Distribution and conservation of Perú's montane forest: interactions between the biota and human society. In: Hamilton, L., Juvik, J., Scatena, F. (Eds.), *Tropical Montane Cloud Forests*. The East West Center, Honolulu, pp. 237–246.
- Zadroga, F., 1981. The hydrological importance of a montane cloud forest area of Costa Rica. In: Lal, R., Russell, E.W. (Eds.), *Tropical Agricultural Hydrology*. John Wiley & Sons, New York, pp. 59–73.
- Zas, R., 2006a. Iterative kriging for removing spatial autocorrelation in analysis of forest genetic trials. *Tree Genetics & Genomics* 2, 177–185.
- Zas, R., 2006b. Consecuencias de la estructura espacial de los datos en el diseño y análisis de experimentos en campo. *Ecosistemas* 15, 107–114.