Taxonomic diversity as complementary information to assess plant species diversity in secondary vegetation and primary tropical deciduous forest

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Abstract

Question: Species diversity is commonly expressed as the number of species present in an area, but this unique value assumes that all species contribute equally to the area's biodiversity. Can taxonomic diversity be used as a complementary measure for species richness in order to assess plant biodiversity in remnants of primary forest and patches of secondary vegetation?

Location: Veracruz, Mexico.

Methods: Using data from six sampling transects of each vegetation type in an elevation gradient (400-900 m a.s.l.), we compare the point, mean and cumulative floristic diversity of primary forest and secondary vegetation in a tropical deciduous landscape, using species richness and two measures of taxonomic diversity: average taxonomic distinctness ($\Delta+$) and variation in taxonomic distinctness ($\Lambda+$). We performed a randomization test to detect differences in the observed taxonomic diversity, from the expected values derived from the species pool of each vegetation type.

Results: We found that the species of secondary vegetation are more closely related at low taxonomic levels (lower $\Delta+$ value) than the species of primary forest remnants. Also, in secondary vegetation the distribution of species is uneven among the taxonomic levels and units (high $\Lambda+$ value). These patterns are consistent for point, mean and cumulative taxonomic diversity. Families Asteraceae, Euphorbiaceae, Fabaceae and Poaceae are over-represented, while families Bromeliaceae, Cactaceae, Orchidaceae and Pteridaceae are under-represented in secondary vegetation.

Conclusions: Although in a previous paper we concluded that secondary vegetation is more alpha-diverse than primary forest (in terms of both cumulative and mean species richness), and beta-diversity between vegetation types is notoriously high, we now provide a wider view by highlighting the importance of taxonomic diversity in primary forest remnants. Our data indicate that to measure biodiversity accurately, we should seek to capture its different facets. This will allow us to make conservation recommendations based on a broader view, and not on a single dimension.

Keywords: Alpha-diversity; Distinctness; Mexico; Relatedness; Taxonomy; Veracruz.

Nomenclature: Cronquist (1988).

Introduction

Biodiversity at the species level is the most meaningful expression of spatial and temporal variability in species richness, composition and structure. Spatial variation is a particularly key factor when species diversity is assessed over landscapes or large heterogeneous regions. For this purpose, a very practical approach has been to partition the diversity of the entire landscape (gamma) into the species richness of each particular community (alpha) and the degree of replacement of species among the different communities in the landscape (beta, *sensu* Whittaker 1972). Within a particular community, alpha-diversity can be measured and conceptually defined in different ways (Halffter & Moreno 2005), i.e. as the number of species at a specific sample (*point alpha-diversity*), as the mean of point values corresponding to several samples (*mean alpha-diversity*) or as the total number of species of a set of samples or points of a community type during a certain period of time (*cumulative alpha-diversity*).

At the alpha level, species diversity can be quantitatively measured by counting the number of species present in each habitat, although this unique value assumes that all species contribute

equally to the habitat's biodiversity (Harper & Hawksworth 1995; Gaston 1996; Magurran 2004). To reduce this bias, ideally, complementary measures of biodiversity should be used in order to capture its different facets (Purvis & Hector 2000). From an ecological point of view, species richness is complemented with information on the community structure in terms of species abundances (number of individuals, biomass, coverage, etc.). In this way, a community with a more even distribution of abundances among the species is more diverse than a community that is clearly dominated by a few species and has many species that are only represented by very few individuals (see Magurran 2004, for a review of approaches for measuring this ecological diversity).

From another point of view, the degree of species relatedness is an additional feature that can be used in analysis of species diversity. A set of closely related species is more difficult to distinguish, thus such a community should be considered as having low phylogenetic diversity. Some approaches have been proposed to measure distinctness amongst species, by taking into account the topology of their phylogenetic tree (May 1990; Vane-Wright et al. 1991; Humphries et al. 1995; Posadas et al. 2001), the cumulative branch length of the tree if all branch lengths are known (Faith 1992, 1996), or considering only the taxonomical arrangement of species as a crude approximation to their evolutionary distinctness (Faith 1994; Warwick & Clarke 1995; Clarke & Warwick 1998). This last approach, which only requires the taxonomical arrangement of species, allows for measures of taxonomic diversity, and like the other approaches, is based on the idea that a community with closely related species is less biodiverse, in a phylogenetic sense, than a community with low relatedness among species.

Taxonomic diversity has great potential as a complementary measure of diversity in environmental impact studies (Warwick & Clarke 1998). For example, such measurements have been used to assess different perturbation scenarios for fish assemblages (Rogers et al. 1999; Bhat & Magurran 2006), the impact of anthropogenic activities on aquatic communities (Abellán et al. 2006; Salas et al. 2006; Heino et al. 2007; Marchant 2007), for marine environmental assessment in the UK (Leonard et al. 2006) and on litter ant assemblages on different forest types (Anu & Sabu 2007), as well as the impact of a hydroelectric dam impoundment on odonates in Mexico (Campbell & Novelo-Gutierrez 2007). For plants, da Silva & Batalha (2006) used taxonomic distinctness to assess the influence of waterlogging on the phylogenetic structure of a savannah in central Brazil, and recently Bacaro et al. (2007) proposed a novel way to measure taxonomic beta-diversity by incorporating the degree of higher order taxonomic structure between plots of heath plant communities.

The purpose of this paper is to use taxonomic diversity as a complementary measure of species richness in order to assess plant biodiversity in remnants of primary forest and patches of secondary vegetation within a landscape of tropical deciduous forests (TDF) on a volcanic substrate. We compare both communities by separately analysing their point, mean and cumulative alpha taxonomic diversity. From a previous study (Castillo-Campos et al. 2008) we know that, in terms of the number of species, secondary vegetation is more alpha-diverse than primary forest, for both mean and cumulative species richness. But we have also noticed that, even when both vegetation types have a similar number of plant families, in primary forest each family is represented by one to 35 species, while in secondary vegetation each family is represented by one to 66 species. Also, there are one to 21 genera per family in primary forest, while each family in secondary vegetation is represented by one to 34 genera. This higher number of species and genera per family indicates that in a taxonomic classification the mean distance between two species from secondary vegetation would be lower than the mean distance between two species from primary forest. In other words, the degree of taxonomic diversity among the species of secondary vegetation would be lower than the taxonomic diversity of primary forest. We test this prediction and discuss the usefulness of taxonomic measurements as complementary information for a more complete representation of biodiversity.

Methods

Study area and plant diversity of the landscape

Located in the Actopan River basin in central Veracruz, Mexico, the study landscape is 17-km long, with a variable width of 0.5-2.7 km, and covers an area of 3976 ha. Altitude ranges from 400 to 900 m a.s.l. The area is comprised of volcanic rock of chaotic basalt deposited during different periods. The largest lava flow was deposited during the most recent period (Holocene), approximately 10 000 years ago (Negendank et al. 1985). Mean annual temperature is 24°C and mean annual precipitation is 893.8 mm (García 1981).

This landscape was originally covered by TDF, but it has been fragmented along a substantial area.

The present landscape is a mosaic that includes remnant patches of primary vegetation (canopy height from 3 to 8 m) and secondary vegetation. These two communities represent ca. 45% of the landscape area, while the other 55% is covered by induced or introduced pastureland, and crops such as sugar cane (*Saccharum officinarum*), chayote (*Sechium edule*), mango (*Mangifera indica*) and coffee (*Coffea arabica*) (see Castillo-Campos et al. 2007, for a description of proportion and distribution of the landscape elements). Depending on when crop fields or pastures were abandoned (1 to 12-20 years), secondary vegetation is observed at different regenerative stages. Despite this spatial heterogeneity, all the fragments are imbedded in the same landscape. The floristic structure of secondary vegetation that was abandoned over 10 years ago has from one to three strata, with an arboreal layer 3-7-m high.

In a previous study, we evaluated the way in which both primary forest remnants and secondary vegetation patches contribute to the floristic diversity of this landscape (Castillo-Campos et al. 2008). Sampling was carried out along transects located at six altitudinal levels, 400, 500, 600, 700, 800 and 900 m a.s.l. For each altitudinal transect, 100 m^2 plots (10×10 m) were used for arboreal and shrub layer surveys. In each transect, plots were separated by 50 m intervals along the transect. For herbaceous vegetation inventory, we sampled three subplots of 4 m^2 inside each 100-m^2 plot. For this paper, our analyses are based only on species presence-absence data. The number of plots varied with the width of the study area and the size of the original and human-induced plant cover fragments, but for each vegetation type (primary forest and secondary vegetation) we sampled ca. 1000 m^2 at each altitudinal level (from 800 to 1500 m^2 per altitudinal transect). Even though there were variations in the number of sampling plots, the number of plant species recorded was not significantly correlated with sample size (Castillo-Campos et al. 2008). Sampling was carried out during the rainy season and during consecutive 4-month periods over 2 years (August-November of 1999 and 2000). Botanical material was identified using dichotomous keys from the *Flora de Veracruz* (fascicles 1-141, 1978-2006) and by comparison with material identified by specialists. Voucher specimens of all the species recorded are deposited in the XAL herbarium of the Instituto de Ecología, A.C.

For this landscape, we recorded 682 plant species (see Castillo-Campos et al. 2008, for a detailed description of plant biodiversity results). In order to assess the completeness of inventories, we compared the observed species richness for each vegetation type with the expected maximum number of species predicted by a nonlinear regression model and a non-parametric estimator. According to these procedures, species inventories for both vegetation types are about 80% complete (Castillo-Campos et al. 2008).

Data analysis

Here we compare primary forest remnants and secondary vegetation patches using three measures of plant diversity: species richness (number of species) and two taxonomic measures: average taxonomic distinctness ($\Delta+$) and variation in taxonomic distinctness ($\Lambda+$) (*sensu* Clarke & Warwick 1998, 2001). The database includes all the embryophytes collected in the area, classified in seven hierarchical taxonomical categories: 682 species, 398 genera, 105 families, 68 orders, 39 superorders, 13 subclasses and five classes (Liliopsida, Lycopodiopsida, Magnoliopsida, Polypodiopsida and Psilotopsida).

Average taxonomic distinctness ($\Delta+$) is calculated as $\bar{\omega}$:

$$\bar{\omega} = \frac{2 \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} \omega_{ij}}{S(S-1)}$$

where S is the number of species present and ω_{ij} is the "distinctness weight" given to the path length linking species i and j in the taxonomy (Warwick & Clarke 1995, 1998; Clarke & Warwick 1998, 2001). We used a simple linear scaling whereby the largest number of steps in the tree is set to $\omega = 100$. Average taxonomic distinctness takes into account the taxonomic level at which any two species are related and can be thought of as the average length between any two randomly chosen species present in the sample (Warwick & Clarke 1995). Thus, $\Delta+$ is a direct measure of taxonomic diversity: a high value of $\Delta+$ reflects high taxonomic diversity (low relatedness among species).

$\Lambda+$ is the variation in taxonomic distinctness and reflects the degree to which certain taxa are over- or under-represented in samples. It is calculated as:

$$\Lambda+ = \frac{2 \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} \left(\omega_{ij} - \bar{\omega}\right)^2}{S(S-1)}$$

This measure can help us to distinguish between two taxonomical trees that might have the same number of species, and even an identical value of $\Delta+$, but for which one tree has a more uneven structure across taxonomic units than the other. The presence of some genera with many species would tend to increase $\Lambda+$, but this would be counterbalanced by the presence of families represented by only one (or very few) species (Clarke & Warwick 2001). Therefore, $\Lambda+$

measures the unevenness in the taxonomic tree, and is thus contrary to the concept of taxonomic biodiversity: high taxonomic diversity would be expected for a community with an even distribution of species among the taxonomic levels and units, a situation that would result in a low value of $\Lambda+$. Both $\Delta+$ and $\Lambda+$ measures are independent of the sampling effort and of the species richness at each site (Clarke & Warwick 1998; Abellán et al. 2006; Bhat & Magurran 2006; Leonard et al. 2006).

In a similar way to that proposed for species richness, here we define *point taxonomic diversity* as the taxonomic distinctness at a specific sampling point, *mean taxonomic diversity* as the mean of point distinctness values of all the samples within a community type, and *cumulative taxonomic diversity* as the overall measure of distinctness that can be calculated considering all the species found in the set of samples of a community type during sampling.

For both primary forest and secondary vegetation, we calculated the point taxonomic diversity (measured as $\Delta+$ and $\Lambda+$) for each of the six sampling transects of a vegetation type that were located at different altitudinal levels. Then, we performed a randomization test to detect differences in the taxonomic distinctness at each observed sample transect, from the expected values derived from the species pool derived from the combined species list for both vegetation types, taking into account the m number of species of the sample transect (Clarke & Warwick 1998). This test uses the theoretical mean and variance of $\Delta m+$ and $\Lambda m+$, the values of which are obtained by taking 1000 random samples of m species from the pool. The null hypothesis assumes that each sample contains species randomly selected from the pool and that it should therefore fall within the 95% confidence interval. Since the theoretical mean remains constant while the variance decreases as m increases, the 95% confidence interval takes the form of a "funnel".

In a strict sense, a randomization test is a statistical resampling technique that is used to generate a reference distribution from the same data obtained by sampling (Manly 1977). Randomization testing provides an efficient approach when the data do not conform to the distributional assumptions of traditional statistical methods for hypothesis testing, and is also applicable to very small samples (Legendre & Legendre 1998). Although Clarke & Warwick (1998) use randomization testing to deal with the data limitations cited above, we feel that as a statistical tool this technique has more to offer. It indicates what the pattern would be in the absence of an ecological effect, and so is actually a null model, and we have

applied it as such. According to Gotelli & Graves (1996) a null model is "a pattern-generating model that is based on randomization of ecological data or random sampling from a known or imagined distribution ... The randomization is designed to produce a pattern that would be expected in the absence of a particular ecological mechanism." In our case, resampling allowed us to construct null models on the statistical distributions of the taxonomic diversity values expected for randomly assembled species from the pool. Departures from these expected values could indicate a non-random process.

Then, to compare the mean taxonomic diversity ($\Delta+$ and $\Lambda+$) and species richness between primary forest and secondary vegetation, we performed paired *t*-tests using Statistica (version 6, StatSoft, http://www.statsoft.com), taking into account that the six sampling transects are dependent samples according to the altitudinal level. Finally, to assess the cumulative taxonomic diversity, we followed the same randomization test described above for the point taxonomic diversity. For the cumulative data of each vegetation type, the test detects differences between the observed and the expected values derived from randomly assembled communities from the landscape species pool (taking into account the specific richness: $m = 389$ for primary forest and $m = 461$ for secondary vegetation). We compared the observed values of $\Delta+$ and $\Lambda+$ with the 1000 expected values of $\Delta m+$ and $\Lambda m+$ represented by frequency histograms. All the analyses of taxonomic diversity measures and randomization tests were performed using PRIMER (version 5.2.8, PRIMER-E, Plymouth, UK).

Results

Point taxonomic diversity

The six transects of primary forest sampled had higher values of average taxonomic distinctness ($\Delta+$) than the six transects of secondary vegetation (Fig. 1). Also, five of the transects in primary forest had values of $\Delta+$ within the 95% confidence interval of the randomization model, while the sixth had a value of $\Delta+$ above that expected for a sample of its richness (202 species). In contrast, average taxonomic distinctness in the six transects of secondary vegetation was lower than expected (Fig. 1).

The opposite trend was detected for the variation in taxonomic distinctness ($\Lambda+$): the six transects in secondary vegetation had higher values of $\Lambda+$ than those of primary forest (Fig. 2). Five transects in
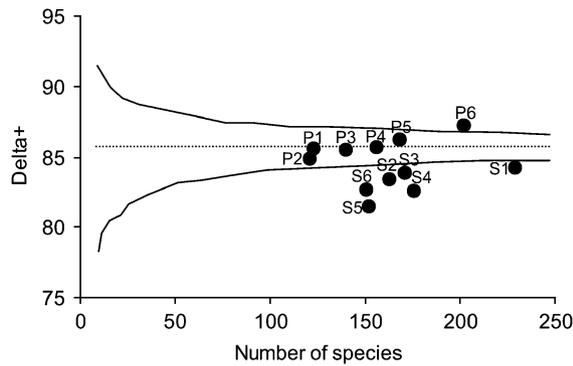
Fig. 1. Taxonomic distinctness Δ+ for study transects plotted with theoretical mean taxonomic distinctness (dotted line) and 95% confidence funnel obtained from the global species list. P1-P6 are primary forest transects, and S1-S6 are secondary vegetation transects.
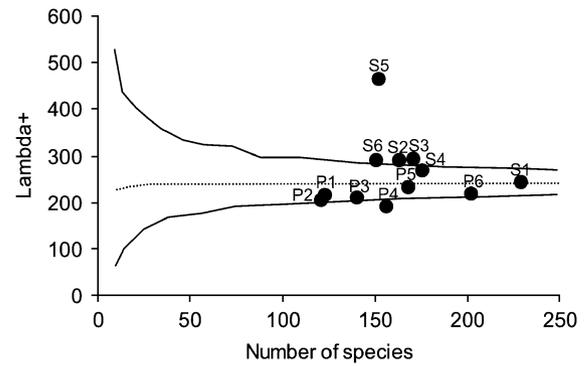

Fig. 2. Variation in taxonomic distinctness Λ+ for study transects plotted with theoretical mean Λ+ (dotted line) and 95% confidence funnel obtained from the global species list. P1-P6 are primary forest transects, and S-S6 are secondary vegetation transects.

primary forest had values within the 95% confidence interval of the random expected values, while one transect had a value of Λ+ below that expected by chance for a sample of its richness (156 species). Two transects in secondary vegetation had values within the 95% confidence interval of the randomization model, while the other four transects (with 151, 152, 163 and 171 species) had higher values of Λ+ than expected (Fig. 2).

Mean taxonomic diversity

Although there is no statistical difference in the mean alpha-diversity (number of species) of primary forest and secondary vegetation ($P = 0.36$), mean taxonomic diversity revealed clear differences that followed the patterns observed for point taxonomic diversity: the mean average taxonomic distinctness (Δ+) of primary forest is higher than that of secondary vegetation ($P < 0.01$), while the mean variation in taxonomic distinctness (Λ+) of secondary vegetation is higher than that of primary forest ($P = 0.02$) (Table 1).

Cumulative taxonomic diversity

In spite of their similarity in mean species richness, the cumulative richness of primary forest is lower than the cumulative richness of the secondary vegetation (Table 1). We observed that the same pattern in cumulative taxonomic diversity occurs for the point and mean values: the cumulative average taxonomic distinctness (Δ+) of primary forest is higher than that of secondary vegetation, with both values clearly different from the values expected by chance (Table 1). In contrast, the cumulative varia-

tion in taxonomic distinctness (Λ+) of secondary vegetation is higher than that of primary forest, and both values are again statistically different from randomly expected values (Table 1).

Discussion

The low value of average taxonomic distinctness (Δ+) in secondary vegetation means that the species are more closely related at low taxonomic levels (e.g. several species belonging to the same genus or to the same family), while its high value of variation in taxonomic distinctness (Λ+) is related to an over- or under-representation of some taxonomic groups (unevenness in the taxonomic tree). Both in primary and secondary vegetation, families Asteraceae, Euphorbiaceae, Fabaceae and Poaceae are the richest in species. In primary forest these four families include 28.28% of all species, while in secondary vegetation they are far more dominant, including up to 42.30% of the total number of species. Also, in the primary forest, 30.95% of the families are represented by only one species, while in secondary vegetation 46.59% of the families have a single species. Some families can clearly be recognized as under-represented in secondary vegetation. For example, in Bromeliaceae, Cactaceae, Orchidaceae and Pteridaceae there are 18, 13, 14, and nine species in the primary forest, respectively, while in secondary vegetation they are represented by only five, five, one and one species, respectively. If we consider the successional changes of vegetation, the availability of niches in different vertical layers (within the arboreal cover) increases as the forest matures. This succession especially favours epiphytic plants, such as Bromeliaceae, Orchidaceae, and several Cactaceae and

Table 1. Comparison of mean and cumulative values of species richness and measures of taxonomic diversity between primary forest and secondary vegetation. For mean values, degrees of freedom = 5 for all. Cumulative values were calculated using all the species recorded in the set of transects for each community type, and P-values correspond to the null model.

	Primary forest (mean $\pm$ SD)	Secondary vegetation (mean $\pm$ SD)	Paired t-test value	P
Mean alpha				
Species richness	151.67 $\pm$ 30.72	173.67 $\pm$ 28.88	-1.01	0.3601
$\Delta+$	85.86 $\pm$ 0.81	83.05 $\pm$ 0.99	4.49	0.0064
$\Lambda+$	211.29 $\pm$ 13.51	307.95 $\pm$ 79.36	-3.36	0.0202
Cumulative alpha				
Species richness	389	461		
$\Delta+$	86.7 ($P = 0.002$)	83.61 ($P < 0.002$)		
$\Lambda+$	210.74 ($P = 0.002$)	265.33 ($P = 0.004$)		

Pteridaceae. For example, in the premontane forests of Costa Rica, there is a positive relationship between the richness of bromeliad communities and the maturity of the forest (Cascante-Marín et al. 2006). So, in secondary vegetation there are fewer trees and fewer niches available for those species that need the support of trees. Hence, the number of species in secondary vegetation may increase, for example, by packing new species into the niche space already occupied by original species, thus creating species-rich communities that maintain constant the overall niche size of the community (Ricklefs & Schluter 1993). In contrast, trees in primary vegetation provide diverse niches for epiphytic plants, thereby creating a more taxonomically diverse vegetation system.

Given the low relatedness among species and the uniformity of their distribution across the classification, we interpret the composition of primary forest remnants to be more diverse in terms of taxonomic diversity than secondary vegetation. Although we focus on taxonomy, if we assume that it is a rudimentary approximation of phylogeny (Warwick & Clarke 1995; Clarke & Warwick 1998), we could say that the primary forest remnants include more evolutionary diversity because their flora is more diversified; while secondary vegetation could be said to have lower phylogenetic diversification. Fortunately, for many plant groups there are some recent phylogenetic tools that allow us to construct reliable phylogenetic trees (Webb & Donoghue 2005; http://www.phylodiversity.net/phylocom). But frequently, for many other groups such as invertebrates, the information available for the analysis of biodiversity is insufficient to construct phylogenetic cladograms and therefore we do not know the pattern of organismal evolutionary divergence. As such, the only available information on possible phylogenetic relationships among the organisms is simple taxonomy, but even when the taxonomy is the only information available, it can be interpreted as representative of the phylogenetic relationships (Faith 1994; Martín-Piera 1997).

The analysis of taxonomic and/or phylogenetic diversity may improve our understanding of the processes that regulate species coexistence in landscape and community ecology (Ricotta et al. 2008). Recently, phylogenies and community ecology have been integrated predominantly in studies examining the phylogenetic structure of community assemblages, in attempts to explore the phylogenetic basis of community niche structure, and in efforts to add a community context to studies of trait evolution and biogeography (see Webb et al. 2002 for a review). The theoretical model of Webb and colleagues proposes that a phylogenetic low diverse community (with "phylogenetic attraction") indicates that habitat use is a conserved trait within the pool of species, while a phylogenetic diverse community can result either when closely related taxa with the most similar niche use are being locally excluded (phenotypically repulsed), or when distantly related taxa have converged on similar niche use and are phenotypically attracted (Webb et al. 2002). Following this, we can say that the differences in taxonomic diversity between vegetation types might suggest differences in community assembly rules driven by ecological interactions or other natural selection forces. A group of species that is more evenly dispersed across a taxonomical classification and with low relatedness among them (with phylogenetic overdispersion *sensu* Webb et al. 2002), like the species of the primary forest, might indicate the presence of mechanisms that determine which species of the regional pool may compose local communities. In this sense, local communities such as primary forest are structured according to a model of limited membership (Elton 1933), reflected in their low number of species. Habitat selection filters a set of the regional pool of species that may be part of the community, and exclusion processes (such as competition) reduce the number of species that may coexist locally. According to the competitive exclusion principle, if two competing species are not differentiated on their realized niches, or if one is precluded by the habitat, then one competing species will eliminate or exclude the other

(Begon et al. 2006). These processes do not seem to occur in secondary vegetation, probably because of an evolutionary process such as conservatism of habitat use as a trait, or an ecological process such as the instability of the environment. For example, fire has been proposed to be a strong assembly force driving phylogenetic community structure in instable communities subject to high fire frequency, while competitive interactions may be the main assembly mechanisms where fires are rare (Verdú & Pausas 2007).

In a previous analysis of this dataset (Castillo-Campos et al. 2008), we found that species presence-absence clearly separates sampling transects into two groups corresponding to primary and secondary vegetation, and within each major group, the grouping sequence reflects a gradient of species turnover along altitudinal transects. Despite the differences in species composition similarity among transects (point alpha) nested within vegetation types (cumulative alpha), in this paper our results indicate that the shape of the taxonomic tree has essentially the same structure at point, mean and cumulative levels. Also, point taxonomic diversity in primary forest fits the pattern expected in the absence of any process that could generate a non-random structure. But in secondary vegetation, species composition produces a lower than expected taxonomical diversity, so there might be some mechanism influencing the assembly of species. This contrasts with the pattern that seems to be emerging from marine animal communities, where successional communities appear to comprise a random selection of species from the regional species pool and therefore have similar taxonomic distinctness to more mature communities (R. Warwick, pers. comm.). Further research should focus on the relationships between ecological mechanisms for species coexistence and phylogenetic (taxonomic) diversity in communities. An important issue to consider is that patches of secondary vegetation cover different stages of regeneration depending on when the crop fields or pastures were abandoned (high temporal heterogeneity), while remnants of primary TDF are genuine representatives of the original vegetation in the area. The temporal heterogeneity that results from including different successional stages as part of a single community might account for the increase species richness and the reduction in taxonomic diversity. However, we lack complete data on field abandonment and our sampling design was not planned to assess the influence of temporal heterogeneity on plant diversity.

Interestingly, taxonomic diversity gives just the opposite perspective when comparing the alpha-diversity of primary forest and secondary vegetation based on species richness: it is more important to conserve primary forest remnants because of their high taxonomic diversity. In a previous paper (Castillo-Campos et al. 2008), we concluded that secondary vegetation is more alpha-diverse than primary forest, both in terms of cumulative and mean species richness. Also, we found outstandingly high beta-diversity between vegetation types (75% of complementarity, 91.60% of mean dissimilarity). Based on this information, we suggested that it would not be possible to protect the flora of this land mosaic by focusing on primary forest remnants alone. Now, we provide a wider view by highlighting the importance of taxonomic diversity in primary forest remnants. Indeed, the information provided by the two measures of taxonomic diversity used ($\Delta+$ and $\Lambda+$) is not repetitive: each reflects a different aspect of a hierarchical classification. Our data support the idea that to measure biodiversity accurately we cannot focus on a single dimension (Whittaker 1972; Purvis & Hector 2000; Merigot et al. 2007). Rather, a concept that is fundamentally multidimensional should be quantified by including its different facets. Even though policy-makers often want a single number, this would allow us to make conservation and management recommendations based on a broader and therefore more representative view. Species richness is the usual measure of biodiversity considered in conservation decisions, but in this study we found that the degree of species taxonomic relatedness may follow a different trend than species richness for plant communities.

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