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# FLORISTIC DIFFERENTIATION IN LIMESTONE OUTCROPS OF SOUTHERN MEXICO AND CENTRAL BRAZIL: A BETA DIVERSITY APPROACH

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**Abstract:** We studied the spatial arrangement of floristic diversity in two systems of limestone outcrops, located in two distant Neotropical sites: the region of Nizanda (S Mexico) and the Paranã Valley (Central Brazil). We addressed the question whether their vegetation could display a similar zonation, and we explored the relative effects of distance and an environmental gradient on α-, β- and γ-diversities. The limestone outcrops at both sites are similar in size and in elevation, but strongly differ in between-outcrop distance by an order of magnitude. At each study site three individual limestone outcrops were selected; in each of them three plant communities along the edaphic gradient were distinguished (a xerophytic scrub and two tropical dry forests types, one of which had a more xeric character than the other), and sampled for structural variables and floristic composition in 100-m$^2$ plots. At both study sites, structural variables responded similarly to the edaphic gradient. Species density was larger in Nizanda for both α- and γ-diversity, but the largest value of β-diversity was obtained in Paranã. The edaphic gradient produced larger mean β-diversity values than the simple distance effect, with the interaction of both factors resulting in an even larger β-diversity. Classification analyses by site showed larger floristic similarities between the two xerophytic communities than those existing between them and the more mesic forests. The spatial arrangement of diversity showed that both α- and γ-diversity were smaller for the xerophytic communities. As hypothesized, the more extreme changes in community physiognomy were associated with larger β-diversity values.

**Key words:** Alpha diversity, gamma diversity, rupicolous plants, seasonally dry tropical forest, species turnover, xerophytic scrub.

**Resumen:** Estudiamos el arreglo espacial de la diversidad florística en dos sistemas de afloramientos de roca caliza localizados en dos sitios neotropicales distantes entre sí: la región de Nizanda (sur de México) y el valle del río Paranã (centro de Brasil). Los objetivos fueron analizar si la zonificación de la vegetación de estos dos sistemas era similar y explorar los efectos relativos de la distancia y de un gradiente ambiental sobre las diversidades α, β y γ. Los afloramientos calcáreos en ambos sitios son similares en tamaño y altitud, pero las distancias entre ellos difieren fuertemente entre las dos regiones por un orden de magnitud. En cada sitio seleccionamos tres afloramientos distintos y en cada uno de ellos distinguimos tres comunidades vegetales ubicadas a lo largo de un gradiente edáfico (un matorral xerófilo y dos tipos de bosque tropical, uno de ellos con un carácter más xérico que el otro), y las muestreamos usando parcelas de 100 m$^2$ para estimar variables estructurales y conocer su composición florística. En ambos sitios las variables estructurales respondieron de manera similar al gradiente edáfico. La densidad de especies fue mayor en Nizanda tanto para la diversidad α como para la γ, pero la diversidad β más grande se obtuvo en Paranã. El gradiente edáfico produjo valores promedio de diversidad β mayores que los asociados al simple efecto de distancia, pero la interacción de ambas variables generó una diversidad β aún mayor. Los análisis de clasificación por sitio mostraron que la similitud florística es mayor entre las comunidades xerófilas que entre éstas y los bosques más mésicos. El arreglo espacial de la diversidad mostró que tanto la diversidad α como la γ fueron menores en las comunidades xerófilas. Los resultados apoyan nuestra hipótesis de que los cambios más extremos en la fisonomía de estas comunidades están asociados con los valores más grandes de diversidad β.

**Palabras clave:** Diversidad alfa, diversidad gamma, matorral xerófilo, plantas litófitas, recambio de especies, bosque tropical estacionalmente seco.

A major goal in conservation biology is the protection of the largest possible number of species in areas that sometimes are relatively small. To this aim, knowing the spatial arrangement of biodiversity may be crucial (Whittaker, 1960; Arita and Rodríguez, 2001; Halffter *et al*., 2005), since a large gamma (γ)-diversity (*i.e.* total species richness in a region or in a set of individual study units, totaling a given area) may result from different combinations of alpha

($\alpha$)-diversity (*i.e.* number of species in a locality or in one individual study unit forming part of a set of many similar units, each representing a fraction of the total area), and beta ($\beta$)-diversity (a measure of the difference between sites in a region or between study units) (Whittaker, 1960; Felfili and Felfili, 2001; Magurran, 2004; Pérez-García *et al.*, 2005). This issue is particularly important in the dry tropics because of their large vegetational heterogeneity observed at various spatial scales, usually associated to a sizeable floristic variability (Pérez-García *et al.*, 2005).

In the tropical dry regions of the world, mainly characterized by a climate of the $A_W$ type, two major plant formations have been recognized (Walter, 1973; Murphy and Lugo, 1986; Mooney *et al.*, 1995; Cox, 2001; Trejo and Dirzo, 2002; Pennington *et al.*, 2004; Prance, 2006). These plant formations are called tropical grasslands (variously known as savanna, *cerrado*, *llanos*, *vegetación sabanoide*), and tropical dry forest (seasonally dry tropical forest, tropical deciduous forest, *selva baja caducifolia*, or *caatinga*, among other names). Also, within each region dominated by either one of these formations, it is possible to distinguish a gamut of plant communities (usually recognized as vegetation types, plant associations, phyto-physiognomies, etc.), which are linked to environmental factors like topography, surface lithology, soil depth, water and nutrient availability, and disturbance regimes (Walter, 1973; Silva *et al.*, 1996; Balvanera *et al.*, 2002; Durán *et al.*, 2006; Gallardo-Cruz *et al.*, in press.). Actually, much of the variation of these factors is perceived by plants as differences in water availability (Martínez-Yrízar *et al.*, 2000). Consequently, landscapes located in regions dominated by tropical dry forest or savannas tend to be more heterogeneous than those located in tropical rain forest regions (see compilation by Oliveira and Marquis, 2002).

The prevailing plant communities in the forested tropical region have been encompassed under the term tropical dry forest (TDF, Murphy and Lugo, 1986). TDF is usually applied to forests of low elevation (< 1,400 m a.s.l.) from intertropical regions with a well defined dry season (Mooney *et al.*, 1995; Gentry, 1995). The length of the dry season is highly variable, although it normally lasts for between four and six months. In TDFs total annual precipitation generally ranges from 500 to 1,800 mm (Gentry, 1995; Trejo, 1996, 1998), sub-zero temperatures are lacking, and their minimum mean annual biotemperature ranges between 18 and 26°C (Murphy and Lugo, 1995; Trejo, 1996, 2005). Despite these generalities, it must be acknowledged that the circumscription of TDFs is not easy. For example, establishing its boundaries in terms of the presence of foliage in plants during the dry season is troublesome, as the limits between varying degrees of deciduousness are arbitrary and difficult to assess in the field (Martínez and Galindo-Leal, 2002; Scariot and Sevilha, 2005). A further complication in setting the limits to the concept of TDF is the gradually increasing climatic seasonality of a tropical region as one moves away from the equator. However, even for the most equatorial tropical systems it is generally possible to distinguish between a humid (moist/rain) forest and a dry (deciduous) forest. Such differentiation is based on the lower stature of the canopy trees (< 30 m, but usually much less) and the degree of deciduousness of the dry forests (> 75%), along with other characteristics, such as the lower diversity and abundance of epiphytes in the TDF.

In addition to TDF, the world's tropical dry regions are notorious for encompassing various vegetation types (Menaut *et al.*, 2005; Lott and Atkinson, 2006), even in small areas, due to local variations in water and nutrient availability (Sampaio, 1995; Pérez-García *et al.*, 2001). Such variability involves a complex array of plant communities, some of which are equally elusive of a simple definition (Eiten, 1986; Furley, 2006), ranging from dense, large biomass and relatively tall riparian forests, through several types of savanna and deciduous scrub, to open, sparse, xerophytic vegetation typical of rock outcrops. Among the latter, the floristic composition of the vegetation occurring on limestone outcrops is of special interest, as it contains a considerable share of endemic species that are absent from the surrounding areas (Borhidi, 1996; Silva and Scariot, 2003, 2004a, b; Pérez-García and Meave, 2004).

Despite the biological importance and the particular ecological conditions in systems of limestone outcrops, few studies have examined their characteristics in detail. An example is found in the work of Borhidi (1996), who described seven plant associations on limestone outcrops (*mogotes*) in Cuba. He distinguished two different *mogote* forest types: one typical of the deeper soils of piedmonts, and the other growing on bare rock. Besides, among non-forest vegetation types he recognized monocot-dominated (with Bromeliaceae and *Agave*), and shrub-dominated communities. The presence of succulent plants, such as *Agave* and columnar or liana-like cacti, epiphytes, and water-storing trees with barrel-shaped trunks are characteristic of the extremely dry and hot habitats of these limestone outcrops. A similar differentiation in vegetation type was found by Pérez-García and Meave (2004) in limestone outcrop systems of the Isthmus of Tehuantepec region (S Mexico). They described three different plant communities based on their physiognomy; two of them corresponded to different types of forest communities possessing a continuous canopy, and a xerophytic scrub with a discontinuous plant cover. The differentiation between the two forest communities was based on the fact that each is associated to a different substrate; one of them grows on the exposed limestone bedrock, and the other develops on continuous and deeper soils. Preliminary field observations conducted in the Paranã River basin showed an analogous spatial structure of the vegetation.

Restrictions for plant growth, together with the consequent ecological specialization of the rock outcrop flora, are well documented phenomena (Silva *et al.*, 1996; Pavletić and Trinajstić , 1997; Porembski *et al.*, 1998; Barthlott and Porembski, 2000; Seine *et al.*, 2000). These constraints on plant growth are related to a discontinuous soil cover and a small soil volume, a combination that causes lower water and nutrient availability. Additionally, the scarce plant cover allows more solar radiation to reach the ground, increasing soil temperature and evaporation rates. Overall, moving from lower topographic positions to the hilltops of limestone outcrops strong decreasing gradients of soil humidity and fertility are found.

A further feature that makes TDF of the Americas of particular interest is that, unlike those forests typical of the almost continuous humid areas that span from Amazonia to the Mexican Atlantic watershed (Hartshorn, 2002), TDF regions are more discontinuous (figure 1), and the largest areas of this vegetation type are geographically very distant (Miles *et al.*, 2006). Habitat continuity allows species to disperse across large distances of biogeographic scale (Cox, 2001). This is relevant because it appears that Mesoamerican tropical rain forests represent a relatively recently evolved floristic subset derived from the Amazonian species pool (Wendt, 1998), although for the TDF this does not appear to be the case, as this forest type may have a diverging evolutionary history (Gentry, 1995; Cevallos-Ferriz and Ramírez, 2004; Becerra, 2005).

Due to the biogeographic discontinuity of the TDF region throughout the Americas, plant communities located at opposite ends of its geographical range hardly share any species; this differentiation is particularly evident for mature forest species (Lott and Atkinson, 2006). Given such transcontinental floristic differentiation, it is unclear whether systems of limestone outcrops located far-apart within this region display similar floristic ensembles, and by analogy, if the spatial distribution of species and community attributes results in an equivalent vegetation zonation. The study of such patterns may be useful in exploring the existing hypotheses about β-diversity. Therefore, having identified two distant systems of limestone outcrops in the Americas (southern Mexico and central Brazil), our goal was to make a comparison between them in order to answer the following questions: What is the contribution of α- and β-diversities to γ-diversity in these limestone outcrops, and which factor, *i.e.* the edaphic gradient or the spatial separation (distance), is more strongly associated with a larger floristic differentiation?

Based on the environmental structure typical of limestone outcrops described above, we hypothesized that, in comparing sets of vegetation samples, larger differences in physiognomy would be associated to a large floristic turnover (β-diversity). In turn, due to the limitations of dispersal over large distances, it was reasonable to expect that floristic turnover would be even greater with increasing between-sample distances.

## Material and methods

*Study areas*. The study was conducted in two Neotropical localities of the seasonally dry forest region located more than 6,000 km apart (figure 1). In both localities a conspicuous terrain feature is the presence of limestone outcrops (LO), which are nearly half a kilometer long and usually no less than 200 m wide.

Nizanda (Oaxaca), Mexico.- The site is located on the Pacific slope of the Isthmus of Tehuantepec (figure 1). The regional climate is highly seasonal, warm and sub-humid, with a mean annual temperature of 26°C. Annual precipitation (mean *ca.* 1,000 mm) concentrates from August to November (Pérez-García and Meave, 2004). A published vascular plant checklist for this region includes 746 species (Pérez-García *et al.*, 2001), although an updated inventory comprises over 920 species. The prevailing vegetation type is a low stature, tropical dry forest (*selva baja caducifolia*, after Miranda and Hernández-X., 1963), with a mean cano-

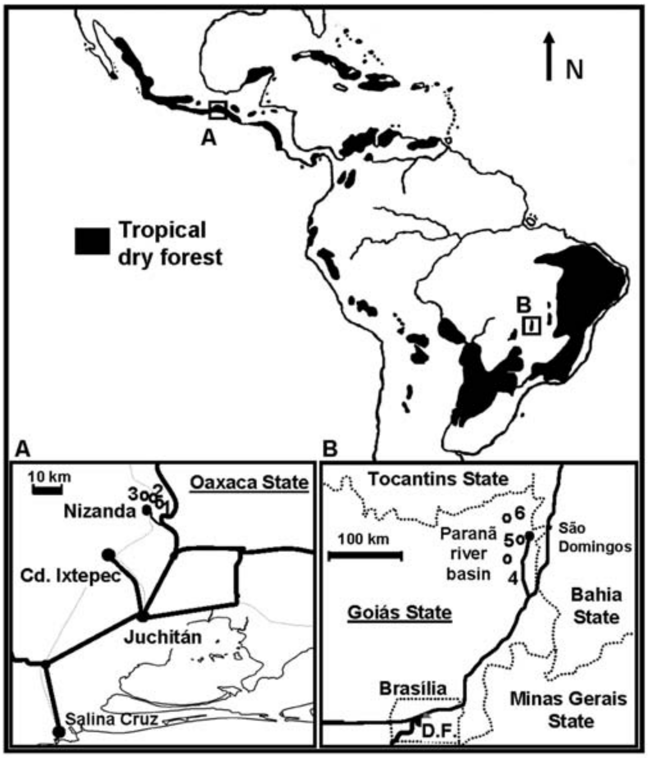

**Figure 1.** Distribution of tropical dry forest region in the Americas (map modified from the Pennington *et al.*, 2000), and location of the study areas in Mexico and Brazil. (A) Nizanda, Isthmus of Tehuantepec (Oaxaca state), southern Mexico, and (B) Paranã River basin (Goiás State), central Brazil. Note the differences in scales between the local maps from Mexico and Brazil, and the fact that predominantly non forest communities of seasonally dry regions are excluded (see Pennington *et al.*, 2004). 1 = Cerro de la Piedra Azul, 2 = Pedrera de la Vía, 3 = Birmaniano, 4 = Fazenda São José, 5 = Fazenda São Vicente, 6 = Fazenda Canadá.

py height of *ca*. 7 m. Maximum elevation at the three studied LO ranges between 250 and 350 m a.s.l., and they are separated from each other by narrow ravines cut by seasonal streams (Pérez-García and Meave, 2004).

Paranã River basin, Brazil.- The location of this site is central Brazil, Goiás state (figure 1). The Paranã River basin (hereafter Paranã only) has a S to N orientation, and its elevation ranges from 400 to 600 m a.s.l. Regional climate is warm, with a mean annual temperature of 24°C, and an average total annual precipitation of 1,500 mm (Silva and Scariot, 2003, 2004a, b). Rainy season concentrates between spring and summer (October to March) (Scariot and Sevilha, 2005).

Seasonally dry tropical forest (*floresta estacional decídua* or *mata seca*) is the predominant natural vegetation type, with a canopy height of around 20 m; this community may thus be classified as medium-height tropical deciduous forest *sensu* Miranda and Hernández-X. (1963).

The three LO studied at Paranã form part of São Domingos municipality (Goiás State), and are located in different cattle farms: Fazenda São José (Silva and Scariot, 2004a), Fazenda São Vicente (Silva and Scariot, 2004b), and Fazenda Canadá (Silva and Scariot, 2003).

All studied LO are well conserved, which is certainly due to their rocky nature and to their very irregular topography. In contrast, there is one major difference between the two systems regarding the spatial separation between the LO. The largest between-limestone outcrop distance in the Mexican locality is *ca*. 2 km, whereas outcrops in Brazil are separated by distances as large as 84 km. For the two systems previous plant surveys are available (Silva and Scariot, 2003, 2004a, b; Pérez-García and Meave, 2004), but for the Brazilian LOs the floristic checklists include trees only. In the LO of Brazil, all plant with DBH > 5 cm were recorded in 400-m$^2$ plots. For the LO of Fazenda Canadá 924 trees were found, and they belong to 24 families, 38 genera and 48 species (Silva and Scariot, 2003). In Fazenda São Vicente the survey produced a total of 860 living and 36 dead trees, and they represented 51 families, 41 genera and 51 species (Silva and Scariot, 2004b). Finally, for Fazenda São José,

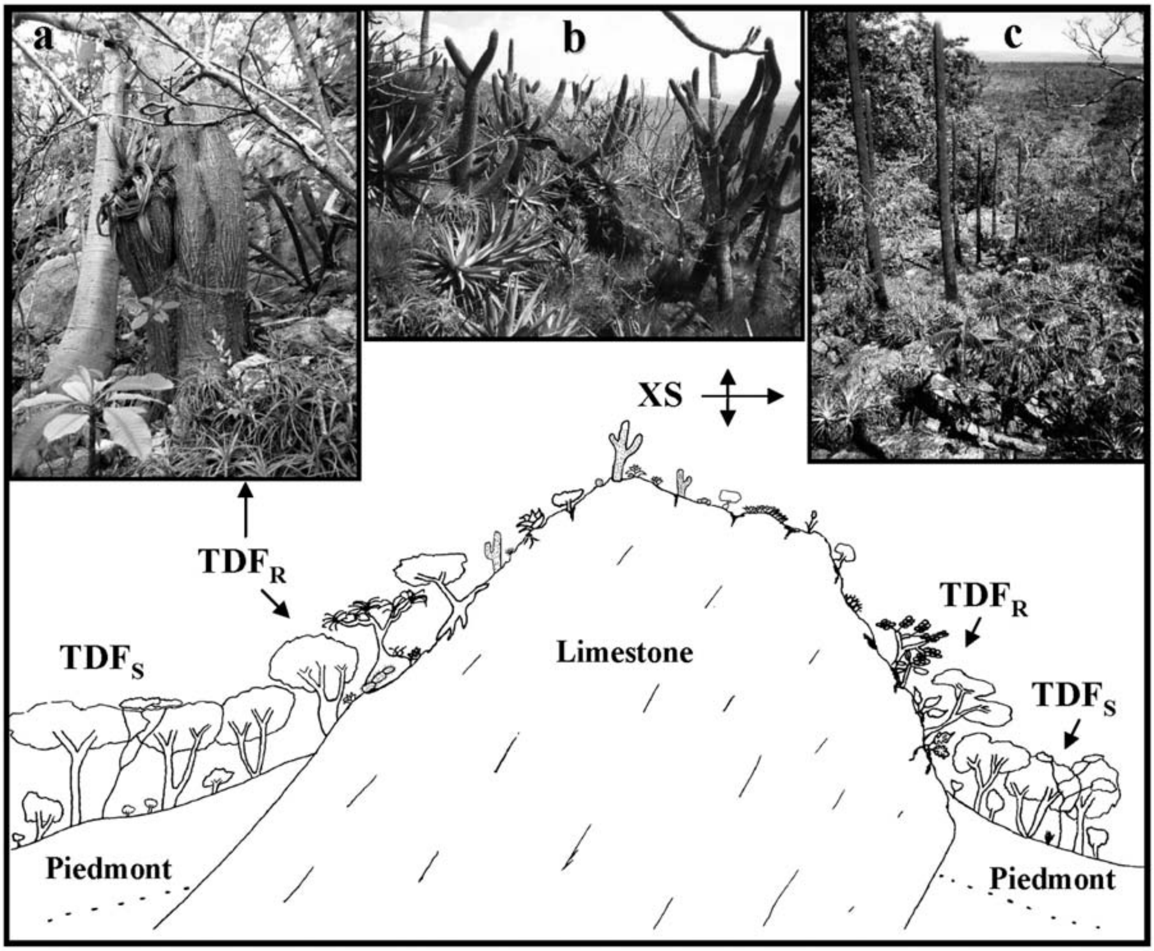

**Figure 2.** Schematic diagram and photographs illustrating the vegetation in a limestone outcrop (not to scale). XS = xerophytic scrub; TDFR = tropical dry forest on bare rock; TDFS = tropical dry forest on deeper and continuous soil; a = TDFR, and b = XS of Nizanda, Mexico; c = XS of Paranã, Brazil.

a total of 536 living and 52 dead trees were recorded, and the trees belonged to 36 species, 31 genera and 21 families (Silva and Scariot, 2004a).

*Vegetation sampling*. In each individual limestone outcrop at both localities we distinguished and sampled three plant communities. The first one occurs on the piedmonts where soil is continuous and relatively deep (> 50 cm), and was referred to as tropical dry forest on soil (TDFs). Moving up along the topographic gradient a second forest type is found, which is established on the exposed limestone matrix; it was named tropical dry forest on bare rock (TDFr). According to Pérez-García and Meave (2004), these two forests are not only floristically different (the TDFs being richer in species), but they also differ in their physiognomy, such as a larger occurrence of trees with water-accumulating stems in the TDFr. The third community, restricted to outcrop tops and escarpments with exposed limestone, was classified as xerophytic scrub (XS) due to its discontinuous canopy and the low stature (< 4 m) of the woody stratum (figure 2).

In terms of environmental harshness, there are indications of the existence of an increasing gradient of xerophytic conditions in these plant communities as: TDFs < TDFr < XS. For concision, the TDFr and XS will be hereafter referred to together as xerophytic communities, whereas TDFr and TDFs will be referred to as forest communities. This means that TDFr is included in both the xerophytic and the forest communities (Pérez-García and Meave, 2004). In the studied limestone outcrops the two forest communities covered larger and more continuous areas, while the xerophytic scrub had a patchier and limited distribution. The small extent of this latter community determined the use of small-sized sampling units.

Vegetation was sampled in 10 × 10 m plots, in which we recorded all individuals ≥ 1 cm DBH rooted within the plot; this set was referred to as upper stratum. A lower stratum was sampled in five 2 × 2 m subplots placed at each corner and in the centre of the plot; this stratum included woody plants and herbs ≥ 30 cm tall, but < 1 cm DBH, globose cacti ≥ 5 cm in diameter, and terrestrial rosettes and colonial plants (individual or colonial cover ≥ 20 cm in diameter). In Paranã, only one plot per vegetation type was taken from each limestone outcrop, which resulted in a total of nine plots (1 plot by community × 3 communities × 3 limestone outcrops), whereas in Nizanda three plots were taken by community, giving 27 plots in total (3 plots by community × 3 communities × 3 limestone outcrops). Within these plots, the height and two perpendicular diameters (from which cover was calculated later) of each individual plant were measured, and its identity recorded; for the upper stratum plant's DBH was also measured. The high frequency of clonal plants in the lower stratum prevented the counting of individuals and therefore density values were calculated for the upper stratum only.

Based on the most frequent species per community and per site, we identified potential ecologically equivalent species. To this end we considered both species actually encountered in our samples and those reported in the published checklists (Pérez-García et al., 2001; Silva and Scariot, 2003, 2004a, b; Scariot and Sevilha, 2005). Ecological equivalence was assessed according to similar habitat preferences, taxonomic identities, and morphological attributes. Among the latter, we took into consideration the natural variability in the vegetation of the two study systems, as trees in Paranã may be twice as big as those at Nizanda. In addition, we used morphological criteria such as plant height, leaf morphology, presence of spines, and occurrence of succulent stems.

*Data analyses*. A binary (presence/absence) data matrix of species distribution for each of the two studied sites was constructed. With these matrices we were able to arrange the samples in several ways in order to evaluate the effect of plot location on species density and the β-diversity in these systems. Because vegetation sampling at each site involved three different communities and three separate LO, samples were taken in groups of three plots (which we named triplets). Each triplet included one of three possible combinations. The first combination included three samples from the same community, but from different LO; this combination minimized environmental effects, but maximized the effect of distance. Next, a different combination included one sample from each community, but all from the same LO; this combination maximized the effect of environmental heterogeneity, but minimized the effect of distance. The third combination consisted of one sample from each community, each from a different LO; unlike the previous combinations, this one maximized both the effects of environmental heterogeneity and of distance. These combinations were selected to test the hypothesis that β-diversity would increase from the first to the third triplet combination.

For each triplet we calculated Whittaker's β-diversity index ($\beta_w$, Whittaker, 1960; Wilson and Shmida, 1984), as follows:

$$\beta_w = \gamma/\alpha$$

where $\gamma$ is total number of species for the triplet, and $\alpha$ is mean species density per plot. Indices were calculated only for plots located in the same site, but not for groups involving both Mexican and Brazilian plots.

In order to evaluate a distance-related effect on $\beta_w$, we calculated this value for each triplet of plots from the same community (either TDFs, TDFr or XS), but with each plot coming from a separate limestone outcrop, *i.e.* first triplet combination described above (figure 3, exemplified by plots labeled with number 1). Because of the limited sampling intensity in Paranã (only three plots per community), we were able to calculate $\beta_w$ only once for each community. In contrast, the larger number of plots per community in

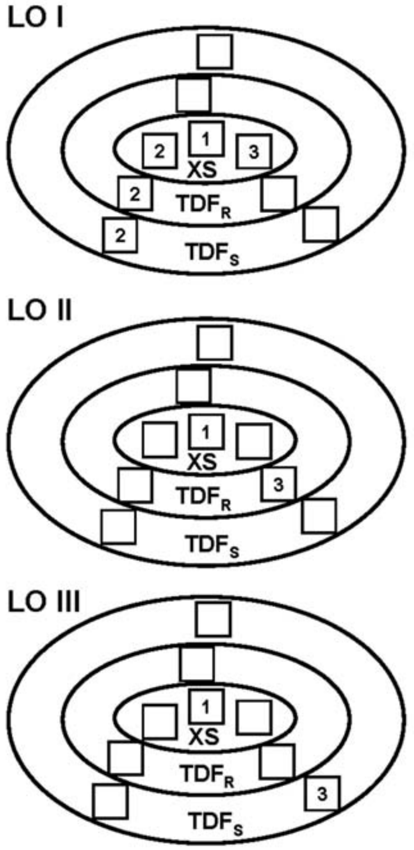

**Figure 3.** Schematic representation of the sampling and data analysis design for limestone outcrops (LO) of Nizanda. Plots labelled with number 1 are examples of a triplet of plots from the same community type (in this case XS), but from separate LO. Plots number 2 exemplify a triplet of plots situated in different communities but from the same limestone outcrop. Plots number 3 belong to a triplet conformed by plots situated in different communities and in separate limestone outcrops. XS = xerophytic scrub; TDFR = tropical dry forest on bare rock; TDFS = tropical dry forest on deeper and continuous soil.

Nizanda enabled us to obtain several values for $\beta_W$, which allowed calculating a mean (± 1 S.E.) value (in the tables of Results the number of triplets used for its calculation is indicated). In all cases, each plot was used only once in calculating each value of this index.

Similarly, to evaluate the effect of the environmental gradient on $\beta_W$ we used triplets of plots each from a different community, but all from the same LO, *i.e.* second triplet combination described above (figure 3, exemplified by plots labeled number 2). In addition, we assessed the combined effect of distance and environmental gradient on $\beta_W$, which required using triplets of plots both from different communities and different LO, *i.e.* the third above-described combination (figure 3, exemplified by plots labeled number 3). Again, plots were used only once in each calculation. The smaller number of plots in Brazil prevented us from comparing the spatial configuration of diversity within the same community and the same LO.

**Table 1.** Sampling plot sequences for triplet construction. For these triplets we calculated β- and γ-diversity for different plant communities located in separate limestone outcrops (LO); the mean species diversity for each plot included in the triplet was α-diversity. Shown are the arrangements performed for plots labelled number 1; in Paranã, Brazil, these represent the totality of plots, while for Nizanda, Mexico, the same sequence was reproduced for plots labelled number 2 and number 3. XS = xerophytic scrub; TDFR = tropical dry forest on bare rock; TDFS = tropical dry forest on deeper and continuous soil.

| Triplet 1 | Triplet 2 | Triplet 3 |
|---|---|---|
| LO1 XS1 | LO2 XS1 | LO3 XS1 |
| LO2 TDFR1 | LO3 TDFR1 | LO1 TDFR1 |
| LO3 TDFS1 | LO1 TDFS1 | LO2 TDFS1 |

The sampling plots of Nizanda were numbered 1 to 3 for each community. In the comparisons between LO or between communities, only plots bearing the same number were compared. The basic scheme of triplet construction is illustrated in table 1; the arrangement shown includes all of the Paranã samples, while it exemplifies the set of triplets containing all plots numbered 1 for Nizanda. For this latter site, subsequent calculations of $\beta_W$ were done by using the same numerical sequence of plots, but changing the plot number.

Discrimination of the magnitude of the effects of distance and the environmental gradient in limestone outcrops required examining the between-site differences of mean $\beta_W$ values calculated for different sets of triplets. Because absolute differences may not be comparable as they would reflect the magnitude of the original $\beta_W$ values rather than that of their difference, we chose to express these differences as percentages, as follows:

$$\% \text{ difference} = [1 ( (\beta_{WS} / \beta_{WL})] \times 100$$

where $\beta_{WS}$ is the smaller and $\beta_{WL}$ is the larger of the values being compared. According to this procedure, estimated percent differences were always either positive or zero when the two compared values of $\beta_W$ were identical.

We performed numerical classifications of the samples of each site using Ward's (minimum variance) clustering method, with Euclidean distances as measure of dissimilarity for the binary data matrix (Kent and Coker, 2003), using the STATISTICA software (StatSoft Inc., 1995).

## Results

*Quantitative structure*. Total number of recorded species in the twenty seven 100-m$^2$ plots from Nizanda was 211, whereas in the nine equal-sized plots from Paranã total richness was 78. At both study sites, TDFS had the largest mean species density, and this was always followed by TDFR, with the lowest values corresponding to XS (table 2). Over-

**Table 2.** Summary of structural variables for each of the three communities in the studied limestone outcrops, assessed in nine 100 $m^2$ plots in the Nizanda region (Oaxaca State), Mexico, and for three 100-$m^2$ plots in the Paranã River basin (Goiás State), Brazil. Figures are mean values (± 1 S.E.). XS = xerophytic scrub; TDFR = tropical dry forest on bare rock; TDFS = tropical dry forest on deeper and continuous soil.

| Structural value | Nizanda | | | Paranã | | |
|---|---|---|---|---|---|---|
| | XS | TDFR | TDFS | XS | TDFR | TDFS |
| **Species (S/100 $m^2$)** | | | | | | |
| Upper stratum | 4.0 (0.82) | 16.6 (2.46) | 24.6 (1.13) | 4.3 (0.3) | 10.0 (1.5) | 12.3 (0.9) |
| Lower stratum | 9.6 (0.5) | 12.6 (1.9) | 18.1 (1.9) | 4.0 (0.6) | 4.0 (1.5) | 18.3 (3.3) |
| *Total* | *11.6 (0.9)* | *25.3 (3.3)* | *36.9 (1.5)* | *6.7 (0.3)* | *12.0 (2.0)* | *25.3 (2.4)* |
| **Plant cover (%)** | | | | | | |
| Upper stratum | 37.6 (12.9) | 264.4 (50.8) | 312.8 (11.4) | 36.5 (13.5) | 291.4 (17.8) | 358.5 (52.7) |
| Lower stratum | 65.7 (6.1) | 57.0 (9.6) | 87.3 (23.4) | 27.4 (4.4) | 13.0 (5.5) | 48.4 (9.1) |
| *Total* | *103.3 (11.4)* | *322.8 (48.2)* | *404.7 (30.2)* | *63.9 (17.2)* | *304.4 (16.5)* | *406.9 (51.1)* |
| **Basal area ($m^2$/100 $m^2$)** | | | | | | |
| Upper stratum | 0.06 (0.02) | 0.66 (0.2) | 0.32 (0.04) | 0.13 (0.03) | 0.28 (0.03) | 0.47 (0.17) |
| **Density (ind./100 $m^2$)** | | | | | | |
| Upper stratum | 9.9 (3.5) | 44.8 (4.9) | 55.1 (3.2) | 15.0 (3.1) | 36.0 (8.6) | 33.0 (4.2) |

all, plots from Nizanda were more diverse than those from Paranã, but this was particularly noticeable for the two xerophytic communities (*i.e.* the TDFR and the XS). In contrast, the partitioning of species density values by stratum (upper and lower) did not produce any clear pattern, neither between sites nor between communities. Mean contribution of the upper stratum to total species density by plot was 60%, while the contribution of the lower stratum was 57%. These percentages mean that on average each stratum harbors exclusively *ca*. 40% of the total species density, implying a strong between-strata complementarity (*sensu* Vane-Wright *et al*., 1991).

Total plant cover was lowest in XS. This result is consistent with the initial physiognomic distinction between communities. According to such distinction, which is based on the occurrence (or lack thereof) of a continuous tree cover, no clear differences were expected between the two forest types. However, percent cover in TDFS was in both sites 25-33% larger than that of TDFR, implying that in absolute terms in the TDFS there is virtually an additional layer of foliage (100% extra of plant cover; table 2). As expected, in both forest types and at both sites, the upper stratum made the largest contribution to total cover. The similarity between total cover of TDFS in the two sites was remarkable (405% and 407% for Nizanda and Paranã, respectively), which was not the case for XS, as the value obtained for Nizanda was 1.6 times that obtained for Paranã (table 2). Similar decreasing trends from TDFS to XS were observed for basal area and density, with two important exceptions: a much larger basal area (0.66 $m^2$/100 $m^2$) for the TDFR of Nizanda and a low density for the TDFS of Paranã. In fact, density values for both forests types in Paranã were considerably smaller than their Nizanda counterparts (table 2).

*Floristic differences between the two studied systems*. Due in part to environmental differences, but mainly to the large geographical separation between the two sites, there are practically no coincidences between the two systems at the species level (table 3). *Tabebuia impetiginosa* (Mart. ex DC.) Standl., is a noteworthy exception; this species is important in Paranã according to its frequency and structural contribution (Silva and Scariot, 2004a, b), and it is also a common tree in the TDFS of Nizanda (Pérez-García and Meave, 2004; Gallardo *et al*., 2005). Some taxa were found in the outcrops of Paranã but not in those of Nizanda, although in the latter region they also occur but restricted to moister communities, such as riparian forests or higher-elevation moist forests. This is the case of the species *Guazuma ulmifolia* Lam., *Celtis iguanaea* (Jacq.) Sarg., and *Ficus insipida* Willd., and of the genera *Aspidosperma*, *Astronium*, *Cecropia*, and *Sapium*. In fewer cases some shared genera were frequent in the TDF of Nizanda, either on limestone outcrops or in other habitats: *Casearia*, *Cordia*, and *Heliocarpus*. No species were shared between the xerophytic communities of the two localities, although several genera were common to both, *e.g. Hechtia*, *Cnidoscolus*, *Ficus*, *Jatropha*, and *Pseudobombax*. Their corresponding species were taken as potential ecological equivalents, given the uniqueness of the habitats where they grow, as well as their morphological convergences (table 3).

*Spatial arrangement of limestone outcrop diversity*. Same community, different limestone outcrop.- At the two sites, when triplets of plots located in the same community but in different LO were analyzed, XS plots had the lowest $\gamma$-diversity (average for Nizanda: 21 species; total for Paranã: 15 species). Gamma diversity by triplet was intermediate in

**Table 3.** Potential ecological equivalents between Nizanda (Mexico) and Paranã (Brazil) based on taxomic relatedness, habitat distributions, and vegetative attributes. The species list is based on vegetation sampling. Underlined species were not found in the plots of one locality but were recorded in other floristic surveys for the site. The Paranã's species in bold were found in Nizanda only at moister places. TDFs = Tropical dry forest on deeper and continuous soil.

| Nizanda | Paranã |
|---|---|
| **Xerophytic scrub** | |
| *Hechtia caudata* L.B.Sm. (Bromeliaceae) | *Hechtia* sp. (Bromeliaceae) |
| *Cnidoscolus aconitifolius* (Mill.) I.M.Johnst. (Euphorbiaceae) | *Cnidoscolus* sp. 1 (Euphorbiaceae) |
| *Bursera schlechtendalii* Engl. (Burseraceae) | *Commiphora leptophloeos* (Mart.) J.B.Guillet (Burseraceae) |
| *Cephalocereus nizandensis* (Bravo et MacDoug.) Buxb. (Cactaceae) | *Cereus* sp. 1 (Cactaceae) |
| *Pseudosmodingium multifolium* Rose (Anacardiaceae)*[1] | *Cabralea canjerana* (Vell.) Mart. (Meliaceae)*[1] |
| **Tropical dry forest on bare rock** | |
| *Bursera excelsa* (Kunth) Engl. (Burseraceae) | *Commiphora leptophloeos* (Mart.) J.B.Guillet (Burseraceae) |
| *Ficus pertusa* L.f. (Moraceae) | *Ficus pertusa* L.f. (Moraceae) |
| *Ficus petiolaris* Kunth (Moraceae) | ***Ficus insipida*** Willd. (Moraceae) |
| *Randia thurberi* S.Watson (Rubiaceae) | ***Randia armata*** (Sw.) DC. (Rubiaceae) |
| *Pseudobombax ellipticum* (Kunth) Dugand (Bombacaceae) | *Pseudobombax tomentosum* (Mart. et Zucc.) A.Robyns (Bombacaceae) |
| *Pilosocereus collinsii* (Britton et Rose) Byles et G.D.Rowley (Cactaceae) | *Cereus* sp. 2 (Cactaceae) |
| *Comocladia enlgeriana* Loes (Anacardiaceae) | *Astronium fraxinifolium* Schott (Anacardiaceae) |
| *Spondias purpurea* L. (Anacardiaceae) | *Myracrodruon urundeuva* Fr.All. (Anacardiaceae) |
| *Bursera simaruba* (L.) Sarg. (Burseraceae) | *Commiphora* sp.nov. (Burseraceae) |
| **Tropical dry forest on deeper and continuous soil** | |
| *Tabebuia impetiginosa* (Mart.) Standl. (Bignoniaceae) | *Tabebuia impetiginosa* (Mart.) Standl. (Bignoniaceae) |
| *Ceiba grandiflora* Bartlett (Bombacaceae) | *Chorisia pubiflora* (A.St.-Hil.) G.Dawson (Bombacaceae) |
| *Cnidoscolus megacanthus* Ined. (Euphorbiaceae) | *Cnidoscolus* sp. 2 (Euphorbiaceae) |
| *Bauhinia divaricata* L. (Caesalpinaceae) | *Bauhinia ungulata* L. (Caesalpinaceae) |
| *Cordia dentata* Poir. (Boraginaceae) | *Cordia glabrata* (Mart.) DC. (Boraginaceae) |
| *Lysiloma divaricatum* (Jacq.) J.F.Macbr. (Mimosaceae) | *Anadenanthera peregrina* (L.) Speg. (Mimosaceae) |
| *Apoplanesia paniculata* C.Presl (Fabaceae) | *Luetzelburgia* sp. (Fabaceae) |
| *Thouinia villosa* DC. (Sapindaceae) | *Dilodendron bipinnatum* Radlk. (Sapindaceae) |
| *Plumeria rubra* L. (Apocynaceae) | *Aspidosperma subincanum* Mart. (Apocynaceae) |
| *Jacaratia mexicana* A.DC. (Caricaceae) *[2] | *Cecropia saxatilis* Snethl. (Cecropiaceae) *[2] |
| *Ximenia americana* L. (Olacaceae) | *Ximenia americana* L. (Olacaceae) |
| **Other habitats** | |
| *Alibertia edulis* (Rich.) A.Rich. ex DC. (Rubiaceae) in moist forest | *Alibertia edulis* (Rich.) A.Rich. ex DC. (Rubiaceae) in TDFs |
| *Celtis iguanaea* (Jacq.) Sarg. (Ulmaceae) in riparian forest | *Celtis iguanaea* (Jacq.) Sarg. (Ulmaceae) in TDFs |
| *Guazuma ulmifolia* Lam. (Sterculiaceae) in riparian secondary vegetation | *Guazuma ulmifolia* Lam. (Sterculiaceae) in TDFs |

* Species belonging to different families but with a similar distribution and similar morphological attributes. [1] Small trees with compound leaves. [2] Tall trees with soft wood and large lobate leaves.

TDFr (average for Nizanda = 55.0; total for Paranã = 36), and highest in TDFs (average for Nizanda = 87.3; total for Paranã = 51). The same pattern was also true for $\alpha$-diversity values in the three communities at the two sites (table 4).

*Between communities*.- At the two study sites, mean $\gamma$-diversity by triplet for plots located in different communities (62.9 and 39.3 species in Nizanda and Paranã, respectively) was larger than the corresponding mean value for plot triplets sharing community (Nizanda = 54.4 and Paranã = 34 species). Particularly, $\gamma$-diversity for triplets of plots located in different communities was slightly larger for plots coming from separate LO than for those located in the same one (table 4).

The analysis of plot triplets located in different communities (*i.e.* along the edaphic gradient) and in separate LO produced larger mean $\beta$-diversity values (Nizanda = 2.60; Paranã = 2.73), than the corresponding ones for plots differing in community but not in LO (Nizanda = 2.54; Paranã = 2.63). All these values, including their averages, were larger than mean $\beta$-diversity obtained for triplets sharing community but differing in LO (Nizanda = 2.12; Paranã = 2.42; table 4).

Comparison of $\beta_w$ of triplets located in the same community with those located in a different one (but always from separate LO) allowed assessing the effect of environmental gradient upon this index. As expected, this comparison produced very large differences: for Nizanda the percent difference was 18.5% ($\beta_w = 2.60$ for triplets differing in community vs. $\beta_w = 2.12$ for triplets located within the same community), while in Paranã the percent difference was 11.4% (between the corresponding $\beta_w = 2.73$ and $\beta_w = 2.42$). These percent differences contrasted strongly with those obtained from the comparison of triplets always differing in community, but located either in the same or in

**Table 4.** Floristic diversity obtained for several spatial arrangements of plots (in triplets) in the limestone outcrops (LO) at Nizanda region (Oaxaca State), Mexico, and the Paranã River basin (Goiás State), Brazil. The total value or the mean (± 1 S.E.), when the latter could be obtained, are shown. N = number of triplets used for calculating the means; XS = xerophytic scrub; TDFr = tropical dry forest on bare rock; TDFs = tropical dry forest on deeper and continuous soil.

| **Plot arrangement** | **Nizanda** | | | | **Paranã** | | | |
|---|---|---|---|---|---|---|---|---|
| | **Gamma** | **Alpha** | **Beta** | N | **Gamma** | **Alpha** | **Beta** | N |
| **Same community, different LO** | | | | | | | | |
| XS | 21.0 (0.6) | 11.6 (0.3) | 1.82 (0.0) | 3 | 15 | 6.6 (0.3) | 2.25 | 1 |
| TDFr | 55.0 (9.6) | 25.3 (4.0) | 2.16 (0.1) | 3 | 36 | 12.0 (2.0) | 3.00 | 1 |
| TDFs | 87.3 (1.7) | 36.9 (0.1) | 2.37 (0.0) | 3 | 51 | 25.3 (2.4) | 2.01 | 1 |
| *Mean* | *54.4 (9.9)* | *24.6 (3.8)* | *2.12 (0.1)* | *9* | *34.0 (10.4)* | *14.7 (5.5)* | *2.42 (0.3)* | *3* |
| **Different community** | | | | | | | | |
| Different community, same LO | 62.1 (3.1) | 24.6 (1.5) | 2.54 (0.0) | 9 | 38.7 (2.8) | 14.7 (1.0) | 2.63 (0.0) | 3 |
| Different community, different LO | 63.8 (2.5) | 24.6 (1.1) | 2.60 (0.0) | 9 | 40.0 (3.6) | 14.7 (1.3) | 2.73 (0.0) | 3 |
| *Mean* | *62.9 (1.9)* | *24.6 (0.9)* | *2.57 (0.0)* | *18* | *39.3 (2.1)* | *14.7 (0.7)* | *2.68 (0.0)* | *6* |

a different LO. For Nizanda this percent difference was 2.31% (between respective values of $\beta_W = 2.60$ and $\beta_W = 2.54$ for triplets located in different and the same LO), and 3.7% for Paranã (between the corresponding $\beta_W$ values of 2.63 and 2.42). These results indicate that the effects of spatial separation are relatively small and of the same order of magnitude at both sites (< 1 percent points), whereas the effect of the edaphic gradient, despite being also of the same order of magnitude, was larger in Nizanda than in Paranã (> 7 percent points).

*Classification analysis*. The dendrograms resulting from the classification of plots based on their floristic composition showed two clearly distinct groups in the two study sites, at a linkage distance of 12 for Nizanda (figure 4), and of 7 for Paranã (figure 5). In both cases, one of these groups comprised all TDFs plots, and the other included all plots from the two xerophytic communities. The separation of the TDFs group is in full agreement with the original vegetation categorization; however, in neither case was it a very homogeneous group, as between-sample similarity was rather low (figures 4 and 5). In contrast, XS samples displayed larger similarities between them, and therefore they grouped at smaller linkage distances. For Nizanda, a partial differentia-

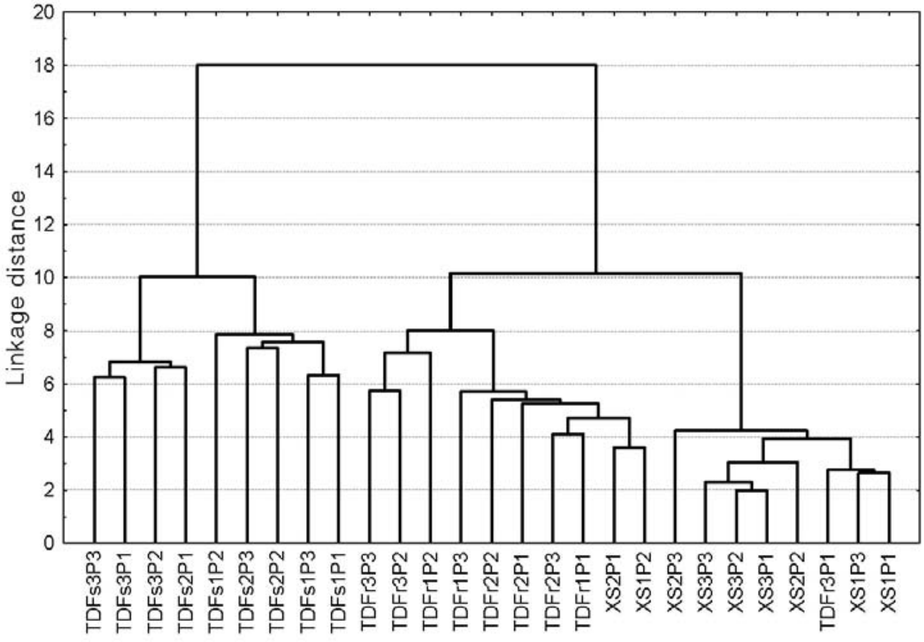

**Figure 4.** Classification analysis performed with Ward's clustering method and Euclidean distances for presence/absence data of species distributions in limestone outcrops at Nizanda (Oaxaca State), southern Mexico. XS = xerophytic scrub; TDFr = tropical dry forest on bare rock; TDFs = tropical dry forest on deeper and continuous soil. The numbers following vegetation type acronyms and the letter P indicate the number of the LO and plot, respectively.

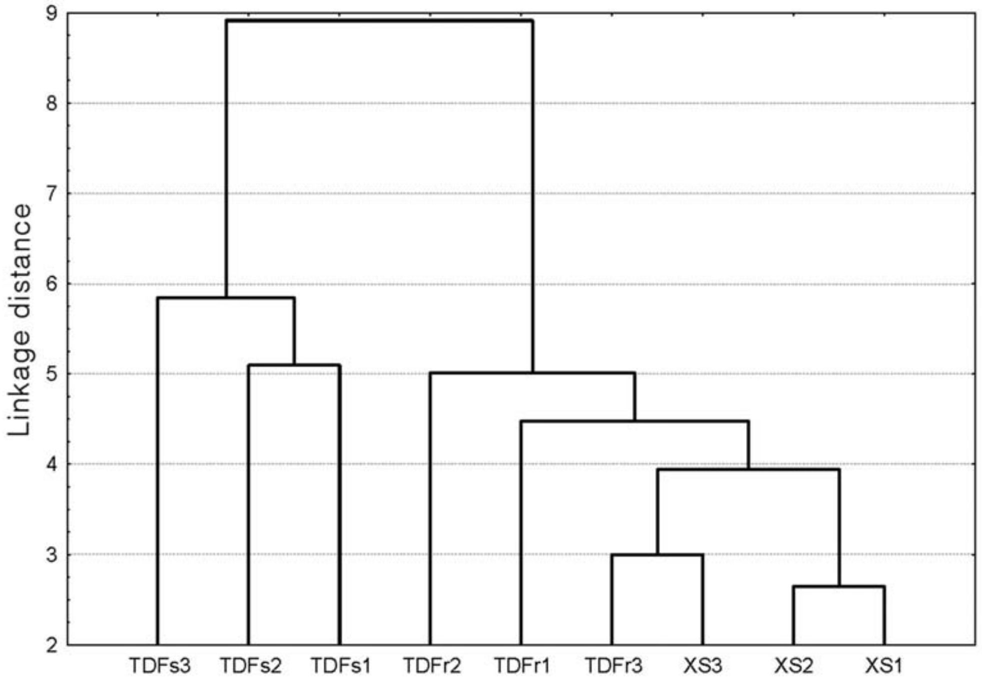

**Figure 5.** Classification analysis performed with Ward's clustering method and Euclidean distances for presence/absence data of species distributions in limestone outcrops at Paranã River basin (Goiás State), central Brazil. XS = xerophytic scrub; TDFr = tropical dry forest on bare rock; TDFs = tropical dry forest on deeper and continuous soil.

tion between TDFR and XS samples was observed (figure 4), a situation which was not true in the case of Paranã (figure 5).

## Discussion

*Quantitative structure*. The LO of Nizanda are characterized by a larger species density than those of Paranã, since they had not only a higher mean α-diversity, but also a larger mean γ-diversity. The fact that diversity is larger at Nizanda is not surprising, because the Mexican TDF biome is recognized to include many highly diverse communities (Gentry, 1995; Trejo and Dirzo, 2002; Gallardo-Cruz *et al*., 2005). However, it was difficult to make an equally clear prediction for species density of XS and TDFR, given the scarce knowledge available for these two xerophytic communities. For Nizanda's XS we were able to estimate its total richness (74 species, including those shared with other communities; unpublished data). Also, for XS both a large diversity and a high structural importance of monocotyledons have been reported (Pérez-García and Meave, 2004); unfortunately we lack information to attempt similar comparisons with other localities.

For the TDF of Paranã a complete regional species survey is not yet available, although there are indications that this region also harbors a large floristic diversity (total richness *ca*. 496; A. Scariot and A. Sevilha, unpublished data). In fact, the TDF that occurs on flat areas in the same region is more diverse than that growing on LO (Ivanauskas and Rodrigues, 2000; Scariot and Sevilha, 2005). The existing information on species richness for Paranã's LO refers basically to canopy trees (DBH ≥ 5 cm; Silva and Scariot 2003, 2004a, b; Scariot and Sevilha, 2005). Therefore, we cannot estimate precisely the total species richness of this system, a limitation that is particularly true for xerophytic communities.

Some factors may explain the lower species densities of Paranã with respect to Nizanda. The first one is the much shorter distance from Nizanda to the sea, both to the Gulf of Mexico and the Pacific Ocean, a circumstance that results in a frequent exposure to humid winds at this locality (Romero-Centeno and Zavala-Hidalgo, 2003). This may be the reason for the profuse growth of soil-drought resistant plants, despite their vulnerability to atmospheric drought (*e.g*. some Bromeliaceae and Orchidaceae). The presence of such plants is frequent in LO of Cuba, which are relatively closer to the sea (Borhidi, 1996). Nevertheless, the proximity to the coast alone does not explain the abundance of epiphytes in the LO of Nizanda, as illustrated in the surrounding TDF beyond LO, or further west on the Oaxaca coast, near Huatulco, where a considerably taller TDF also hosts a very low epiphyte density and diversity (Salas-Morales *et al*., 2003).

A second explanation may be related to the fact that species richness is a function of the number of sampled individuals (Magurran, 2004), leading to the argument that the lower density observed in the TDFs of Paranã is responsible for its low richness relative to Nizanda. However, this explanation is not supported by our results, given that the TDFr of Paranã had more individuals but less species than the TDFs in the same locality (table 2); in fact, a pattern of low species density in this forest type was reported for TDF all over the Paranã valley (Scariot and Sevilha, 2005).

A third possible explanation may be related to the geographic location of Nizanda and its relative proximity to the large arid regions of central Mexico. This situation could be responsible for an abnormal increase in the number of xerophytic species occurring on the outcrops, a phenomenon also observed in some granite outcrops or inselbergs (Porembski *et al*., 1995). There is some evidence supporting this possibility, as illustrated by some xerophytic species such as *Jatropha oaxacana* J.Jiménez-Ram. et R.Torres, and *Echeveria acutifolia* Lindl., which are shared between the LO of Nizanda and the arid Tehuacán Valley in central Mexico. Nonetheless, the unequal floristic knowledge available for our study sites in Mexico and Brazil precludes drawing a definite conclusion about this factor.

The structural values calculated for all forest communities at both sites fall within the reported range for other TDF localities (Gentry, 1995; Trejo and Dirzo, 2002; Gallardo-Cruz *et al*., 2005). The largest basal area was found in the TDFr of Nizanda, but this figure could have been strongly influenced by plants capable of storing water in their stems (succulents), and thus it may not represent proper wood (Pérez-García and Meave, 2004). Therefore, the largest woody basal area may actually be that observed for the TDFs of Paranã, where the biggest trees were present. The recorded basal area in this study was larger than the value previously reported for these limestone outcrops as a whole, without distinction between communities (Silva and Scariot, 2003, 2004a, b), but the large value of Paranã recorded here was accounted for to some extent by a single individual of *Cavanillesia arborea* (Willd.) K.Schum., having a DBH of 89 cm. This exemplifies the extent to which the presence of a succulent plant may result in a magnification of basal area.

*Spatial arrangement of floristic diversity*. Overall, a larger average β-diversity was observed along the edaphic gradient at both sites, but in association with longer between-outcrop distances (*i.e*. in Paranã), species turnover was even larger. Moreover, the more extreme physiognomy (from the tallest vegetation to the most open xerophytic scrub) observed in Paranã coincided with the largest mean β-diversity ($\beta_W = 2.73$). Nevertheless, it is noteworthy that the largest individual β-diversity value for a single triplet was found for the TDFr of Paranã ($\beta_W = 3.00$). In Nizanda, this community is very heterogeneous in species composition (*e.g*. its mean β-diversity has the largest standard error). This variability encompasses dense thickets of the columnar cactus *Neobuxbaumia scoparia* (Poselg.) Backeb., patches of *Plumeria rubra* L., or of the lithophytic *Ficus* trees (Moraceae). Also, the associated arrays of understorey plants are very different, including mats of clonal monocots like *Anthurium nizandense* Matuda (Araceae), *Agave nizandensis* Cutak (Agavaceae), *Cyrtopodium macrobulbum* (La Llave et Lex.) G.A.Romero (Orchidaceae). Unfortunately, we lack sufficient information to draw stronger conclusions about the very high β-diversity in the TDFr of Paranã.

At the two sites, both α- and γ diversity were smaller for the xerophytic communities, particularly for XS. Consequently, a clear pattern may be generalized of species reduction towards the more stressing environments. Contrastingly, we did not find an equally clear pattern for β-diversity: only in Nizanda was there a reduction in β-diversity in the xerophytic communities, unlike the case of Paranã. Moreover, the observed values of α- and β-diversity were not clearly related with each other. Again, both in Nizanda and Paranã the percent differences in β-diversity associated to the distance effect were relatively small. This is particularly relevant because between-outcrop distances in Paranã were one order of magnitude larger than those at Nizanda. Apparently, small $\beta_W$ values related to geographical distance are common; for example, in the Brazilian "*cerrado*" β-diversity between adjacent communities is usually very low, and it is necessary to travel across huge distances before observing a significant floristic differentiation, except when soil differences exist (Felfili and Felfili, 2001). Nonetheless, in a TDF of western Mexico, Balvanera *et al*. (2002) found contrasting evidence as distance out-weighed the edaphic gradient. We may thus argue for the possibility of a trade-off between distance and magnitude of the environmental gradient as determinants of β-diversity, although further information on the relative effects of both factors on between-community floristic differentiation is needed before drawing sounder conclusions.

*Implications for conservation*. The exclusive component of the xerophytic communities stands out given their particular morphological attributes and their high level of endemism (Torres-Colín, 1989; Burke, 2003; Pérez-García and Meave, 2004; Silva and Scariot, 2004a). The high level of endemism observed in the LO matches known patterns for Mexican arid zones (Rzedowski, 1962, 1991). For the LO of Nizanda several endemic species have been recorded, such as *Agave nizandensis*, *Barkeria whartoniana* (C.Schweinf.) Soto Arenas, *Cephalocereus nizandensis* (Bravo et T.MacDoug.) Buxb., *Encyclia nizandensis* Pérez-García et Hágsater, and *Solandra nizandensis* Matuda (Pérez-García *et al*., 2001). Similarly, new species of *Aspidosperma*, *Commiphora* and *Luetzelburgia* were discovered recently in the LO of Paranã (Scariot and Sevilha, 2005). In the two dendrograms resulting from the classifications performed for both sites (figures 4 and 5), those mixed groups that include both samples from TDFr and XS demonstrate that these communities have more species in common than those shared by them with TDFs, despite the intermediate structural character of the TDFr. Therefore, we may conclude that, rather than being an impoverished species subset of TDFs, the xerophytic component of the LO has it own identity.

An important conclusion derived from this study is that for LO systems, or for other systems with similar spatial configurations of their diversity, species density may not necessarily be the best criterion to establish a protected area. Among the three communities studied by us, TDFs had the largest mean $\alpha$- and $\gamma$-diversity values regardless the site, but these quantities were not matched by the largest $\beta_W$ value. In contrast, the mean larger $\beta$-diversity values were obtained from the comparison of communities with most dissimilar physiognomies. One implication of this finding, underlying the concept of $\beta$-diversity, is that the larger is $\beta$-diversity, the greater is the overall biological differentiation. Very limiting habitats sites are often poorer in species and thus make a smaller contribution to total $\gamma$-diversity of a region. However, the most specialized adaptations tend to concentrate in them, and they sometimes represent the only habitats for relictual species. Consequently, the incorporation of habitats into conservation schemes generally results in an increased diversity of life- and growth-form patterns, leaf morphology, ecological dispersal mechanisms, and ultimately, of evolutionary lineages (Chain-Guadarrama, 2005; López-Olvera, 2005; Pérez-García and Meave, 2006). Therefore, a conservation strategy uniquely aimed at maximizing species richness while disregarding species identities may be detrimental for the conservation of sets of species with an important biological value.

More studies providing detailed evaluations of the floristic similarities and differences between Neotropical LO are required. Particular interest should be paid to assess the role of these systems as seed sources, either for the regeneration of disturbed communities at present (Silva and Scariot, 2004b), or before a scenario of longer-term climatic change (see Pennington *et al*., 2000; Prance, 2006). In any case, the conservation of LO will rely upon the amount of knowledge that we can gather for these systems, since important attributes for their conservation, such as their large share of endemic species, may not be perceived at a first glance.

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