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Structure and Floristic Composition in a Successional Gradient in a Cloud Forest in Chiapas, Southern Mexico

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1. Introduction

Southern Mexico is well known for its high biodiversity (CONABIO, 2008). This biodiversity is a result of several factors like its geographic position, geographic diversity, and physiographic richness (Ferrusquilla-Villafranca, 1998). In particular, Chiapas, Mexico's southernmost state holds seven physiographic zones, including valleys, mountain chains, plateaus, and coastal plains (Müllerried, 1957). Most of this biological richness is to be found in the eastern moist forest, northern mountains, central plateau, and Sierra Madre (Breedlove, 1981). The Sierra Madre mountain chain harbors some of the very last patches of Cloud Forest, which is one of the most endangered ecosystems both in Mexico and at a global scale (Challenger, 1998; Toledo-Aceves et al., 2010). Fortunately, three existing biosphere reserves namely El Triunfo, La Sepultura and Volcán Tacaná, aim to protect and maintain this highly threatened ecosystem.

As elsewhere, natural areas compete for land with human activities such as agriculture and cattle ranching, recently, climate change has added up to the list of threats. Only at El Triunfo reserve between 1983 and 1993 were lost 8,946 ha, including 5,084 ha of Cloud Forest (March & Flamenco, 1996). As a region, the Sierra Madre de Chiapas, was between 1998 and 2005, the region that suffered the greatest impact related to climate change in the form of massive landslides. For example, more than 15,000 ha of Cloud Forest were affected in Chiapas by Hurricane Isis (Richter, 2000), while this phenomenon has also occurred in other parts of the Americas (Restrepo & Alvarez, 2006).

The loss of forest cover in the upper parts of the mountain chain generates a reduction of water retention and filtering capability which results in soil loss and consequently in river sedimentation. This also has occasioned an increment of water flow volume which augments flood risk. One way to help to reduce flood risk is through the ecological restoration of forest systems in the upper basin, and subsequent recovery of the ecological services associated to forest. Hence, information on the structure of natural plant communities, including structure and floristic composition, is central to establish sound ecological restoration strategies and policies. Our research objective, was thus, to evaluate and analyze the natural successional process in a cloud forest along a successional gradient

(20-25 years old, 30-35 years old, and mature forest), and to determine the floristic composition, vegetation structure, and species replacement along this gradient.

2. Methods

Our study took place at El Triunfo Biosphere Reserve (ETBR) in Chiapas, Mexico. El Triunfo lays on the Sierra Madre de Chiapas Mountain range (Figure 1), which runs parallel to the Pacific coast. ETBR has an extension of 119,177 ha and its altitudinal range goes from 450 to 3000 meters above sea level (Arreola-Muñoz et al., 2004). Along this range, several climates occur; from hot humid in the low parts to temperate humid in the high lands (García, 2004). Several vegetation types are present, but upper parts are dominated by Cloud Forest (Rzedowski, 1978).

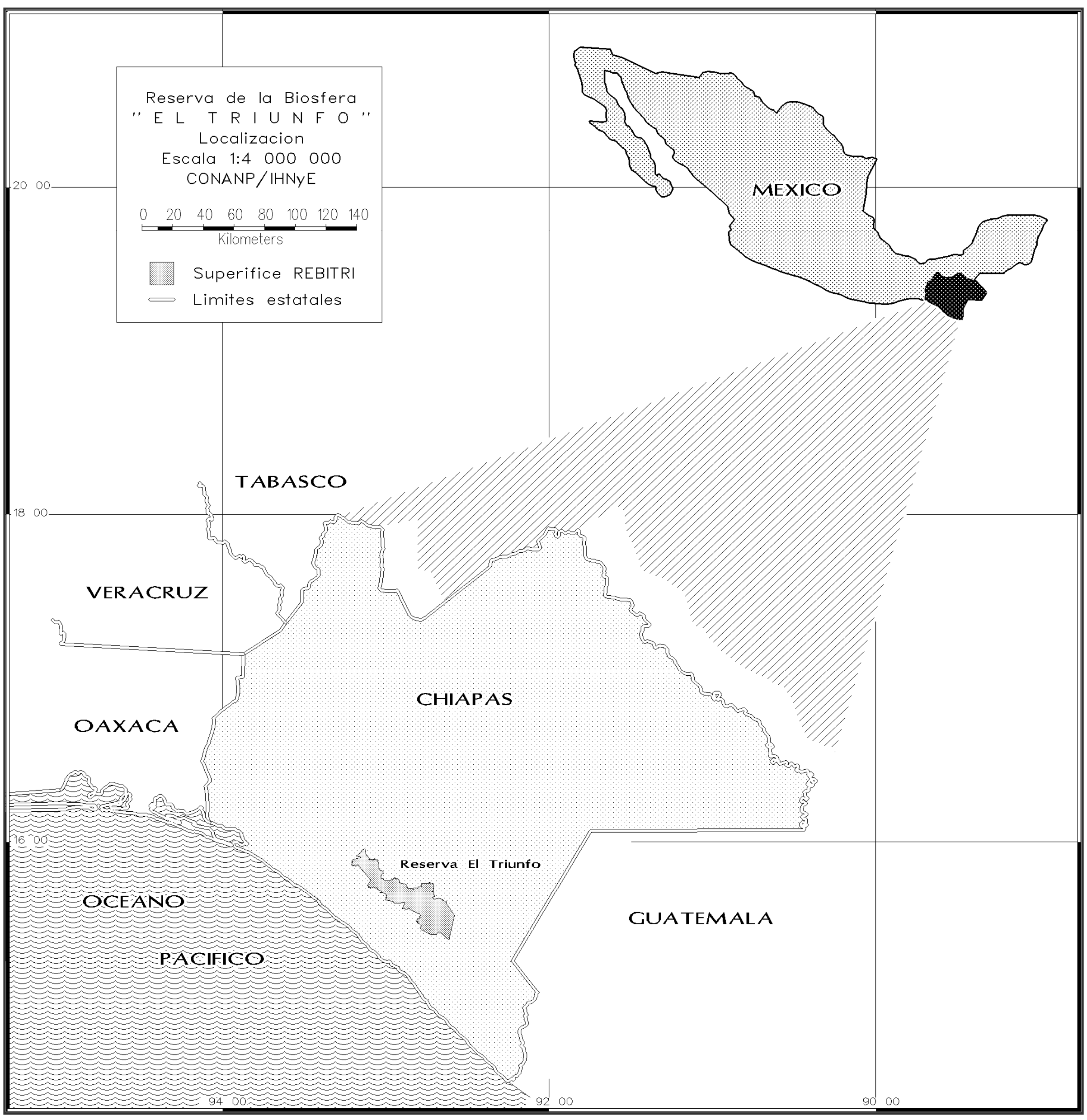

Fig. 1. Map showing El Triunfo Biosphere Reserve boundaries in Chiapas, southern Mexico.

We selected three study sites at ETBR, all localized in the core zone I, based on accessibility and disturbance history. We established sampling plots in three different successional stages according to the time elapsed since disturbance: 1.- Early growth, 20-25 years old (n = 10); 2.- old growth 30-35 years old (n = 7); and 3.- Mature forest (n = 10).

We modified the method proposed by Ramírez-Marcial et al. (2001) to describe the physiognomy and structure of plant communities. We used 0.1 ha circular plots, with a radius of 17.8 m. Inside each circular plot we set smaller circular sub-plots (Figure 2). To avoid border effect, plots were placed at least 50 meters from the border. We randomly selected a point to be used as the center of the plot, and then we placed four straight lines 17.8 m long to each cardinal direction with marks at 5.6, 12.6 y 17.8 m. Then, beginning from the plot center, we traced a circle at the 5.6 m mark (circle "A"), another at the 12.6 m mark (circle "B"), and finally one at the 17.8 mark (circle "C"). Then we measured different vegetation features in each circle. Circle A: all trees with DBH ≥5 cm and ≤ 10 cm; circle B: all trees with a DBH >10 cm and ≤ 30 cm; circle C: all trees with a DBH > 30 cm.

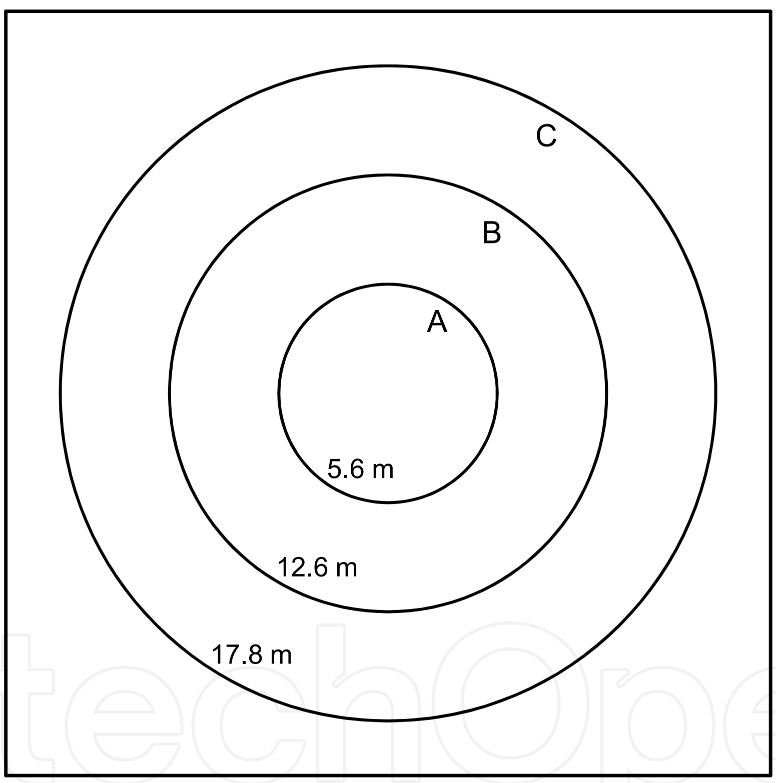

Fig. 2. Plot sampling layout (modified from Ramírez-Marcial et al., 2001)

2.1 Data analysis

Dominance (D): Due to the difficulty of measuring horizontal crown projection to estimate dominance (Lamprecht, 1990), we used basal area, expressed in m², for each species to estimate Absolute Dominance (AD):

$$\mathbf{AD} = (\pi/4) \times dbh^2$$

Where:
π = 3.1416, dbh = diameter at breast height

Relative dominance (DR): Is the percentage of the contribution of each species to the total basal area:

$$\boldsymbol{DR} = \frac{Absolut\ Dominance}{Total\ Absolut\ Dominance} \times 100 \tag{1}$$

Absolut Density (De): Is a parameter that allow us to know the density of each species or family

$$\boldsymbol{De} = \frac{N}{a} \tag{2}$$

Where:
N = Number of individuals of each species or family
a = a given area
Relative Density (Der): Is the percentage of the contribution of each species or family to the total number of individuals per hectare:

$$\boldsymbol{Der} = \frac{Density\ of\ a\ given\ species}{Sum\ of\ the\ density\ of\ all\ species} \times 100 \tag{3}$$

Frecuency (FA): Is the distribution regularity of each species in a given area. It is measured as the percentage of the number of sub-plots where a given species occurs in relation to the total of sampled sub-plots

$$\boldsymbol{FA} = \frac{number\ of\ sub-plots\ where\ the\ species\ occurs}{total\ number\ of\ sub-plots} \tag{4}$$

Relative frequency (FR): Is the percentage of the absolute frequency of a given species in relation to the sum of the frequencies of all present species

$$\boldsymbol{FR} = \frac{absolut\ frequency\ of\ a\ given\ species}{total\ absolut\ frequency} \times 100 \tag{5}$$

Importance Value Index (IVI): Is the arithmetic sum of the relative relative abundance (AR), relative frequency (FR), and relative dominance (DR). Being the sum of these three parameters for an ecosystem equal to 300, we divide the result by three. This value could be used for species or families:

$$\textbf{IVI (F)} = (AR + FR + DR) / 3 \tag{6}$$

Floristic diversity: For each parcel we measured the Shannon-Wiener index, Fisher's α, and Jaccard's equitability. Floristic similarity was estimated using binary coefficients Krebs (1999) based in the presence/absence of families, expressed as:

$$CC_i = \frac{c}{s_1 + s_2 - c} \tag{7}$$

Where:
CC_i= Jaccard's coefficient
s_1 y s_2= NUmber of species in community 1 and 2
c = number of species for both communities
This index is designed to equal 1 when similarity is total and 0 when no species are shared (Magurran, 1988). We then constructed a dendrogram to show using the UPGMA method. Floristic groups from the dendrogram were then compared using the Hutcheson t test (P *(P<0.05)* (Magurran, 1988), as described by the equation:

$$t = \frac{H'_1 - H'_2}{(Var\ H'_1 + Var\ H'_2)^{1/2}} \tag{8}$$

And with the degrees of freedom defined by the equation:

$$t = \frac{(Var\ H'_1 + Var\ H'_2)^2}{[(Var\ H'_1)^2/N_1] + [(Var\ H'_2)^2/N_2]} \tag{9}$$

Where:
Hi = Shannon-Wiener index for area i.
Var Hi = Shannon-Wiener index variance for area i.
Ni = Total number of individuals in area i.

3. Results

We found a total of 1416 individuals belonging to 105 species, 74 genera and 48 families. The old growth was the successional stage that presented the highest number of species, genera and families (Table 1). The families with the greatest number of species in all successional stages were Lauraceae, Asteraceae and Rubiaceae (Table 2). The Genera better represented were *Quercus, Clethra, Eugenia, Saurauia*, and *Cyathea*.

Successional stage	**Species**	**Genera**	**Families**
Old growth (30-35 years)	56	45	31
Early growth (20-25 years)	43	39	30
Mature forest	54	40	29
Total	105	74	48

Table 1. Number of species, genera and families in a Cloud Forest successional gradient at El Triunfo, Chiapas, Mexico

Families	Mature Forest		Old growth		Early growth		G	S
	G	S	G	S	G	S		
Lauraceae	4	7	4	5	2	2	5	10
Fagaceae	1	6	1	3	0	0	1	7
Asteraceae	0	0	5	5	3	3	6	6
Myrtaceae	1	6	1	3	0	0	1	6
Rubiaceae	5	5	2	2	2	2	5	5
Clethraceae	1	2	1	2	1	2	1	5
Fabaceae	2	2	0	0	2	2	4	4
Myrsinaceae	2	3	2	3	1	1	2	4
Araliaceae	2	2	2	3	2	2	2	4
Melastomataceae	1	1	1	2	1	2	2	3
Rest of families	21	20	26	28	25	27	45	51

Table 2. Wood plant families with a DBH >5 cm families in a Cloud Forest successional gradient at El Triunfo, Chiapas, Mexico. Species is denoted by (S) and Genera by (G).

3.1 Mature forest

We found 54 species in the mature forest, which also presented the greatest basal area (46.88 ±280.86 cm). Five species contributed with 175% of the IVI: *Matudaea trinervia, Symplococarpon flavifolium, Glossostipula concinna, Amphitecna montana,* and *Licaria excelsa* in order of importance (Table 3). Total tree density was 7.65 ± 13.65 ind/ha.

Mature forest presented a well-developed tree stratum, defined by trees with a DBH > 400 cm, dominated by *Matudaea trinervia, Symplococarpon flavifolium, Quercus laurina, Quercus benthamii, Glossostipula concinna, Licaria excelsa, Quercus peduncularis* and *Amphitecna montana*. While the understory is defined by a great variety of wooded plants with small DBH (> 10 cm) like *Geonoma undulata, Piper subsessilifolium* and *Psychotria galeottiana*.

SPECIE	Relative Frequency	Relative Density	Relative Basal Area	IVI
Mature Forest				
Matudaea trinervia	6.43	18.4	81.50	106.33
Symplococarpon flavifolium	7.14	14.53	6.82	28.49
Glossostipula concinna	7.14	6.54	1.71	15.39
Old Growth				
Quercus benthamii	4.42	11.09	27.50	43.01
Asteraceae sp2.	0.88	6.33	25.40	32.62
Matudaea trinervia	4.42	5.66	21.45	31.53
Early Growth				
Saurauia madrensis	6.25	13.55	41.24	61.04
Crossopetalum parviflorum	5.56	12.12	11.70	29.38
Hedyosmum mexicanum	6.25	10.87	10.93	28.05

Table 3. The three most important species for each stage in a Cloud Forest successional gradient at El Triunfo, Chiapas, Mexico.

3.2 Old growth

We found 56 species in the 30-35 years old successional stage, accounting for more than 50% of the total number of species. This stage presented the lowest total, basal area, while tree density was 10.85 ± 18.22 ind/ha. The more important tree species were *Quercus benthamii, Matudaea trinervia, Ardisia compressa, Ocotea acuminatissima,* and *Clethra nicaraguensis*, which accounted for an IVI of 113% (Table 3). Arboreal elements with a DBH between 100 and 400 cm were: *Fuchsia paniculata, Crossopetalum parviflorum, Glossostipula concinna, Cyathea myosuroides, Styrax glabrescens, Desmopsis lanceolata, Rhamnus capraeifolia, Nectandra sinuata, Symplococarpon flavifolium, Saurauia kegeliana, Quercus conspersa, Clethra mexicana, Trophis cuspidata,* and *Nectandra globosa*. While species with a DBH < 10 cm were dominated by *Turpinia paniculata, Eugenia* aff. *uliginosa, Meliosma matudae, Malvaviscus arboreus,* and *Cestrum elegantissimum*. Total tree density was 11.28 ± 10.72 ind/ha.

3.3 Early growth

A total of 43 species and above 50% of the total genera were found in the 20-25 years old successional stage. This stage presented the lowest basal area and a tree density of 16.96±50.75 ind/ha. The species with the highest importance values were *Saurauia madrensis, Crossopetalum parviflorum, Hedyosmum mexicanum, Heliocarpus donnellsmithii,* and *Cestrum elegantissimum*, which account for an added IVI of 162% (Table 3). Trees with a DBH > 400 cm were represented by *Saurauia madrensis, Crossopetalum parviflorum, Hedyosmum mexicanum, Heliocarpus donnellsmithii, Cestrum elegantissimum, Rhamnus capraeifolia, Saurauia* aff. *oreophila,* and *Liquidambar styraciflua;* arboreal elements with a DBH between 100 and 400 were *Saurauia kegeliana, Fuchsia paniculata, Verbesina apleura, Lepidaploa polypleura, Clethra lanata, Brunellia mexicana, Arachnothryx buddleioides, Wigandia urens* and *Comarostaphylis arbutoides*; finally, species with a DBH < 100 cm included *Pinus oocarpa, Ocotea acuminatissima, Citharexylum mocinoi, Clethra hondurensis, Clusia flava, Piper pseudo-lindenii, Trichillia havanensis, Matudaea trinervia, Prunus annularis, Myriocarpa longipes, Licaria excelsa, Cyathea sp, Conostegia volcanalis, Ardisia compressa, Pterocarpus* aff. *rohrii, Glossostipula concinna, Ostrya virginiana,* and *Dendropanax arboreus* (Table 3). Total tree density was 13.05 ± 19.61 ind/ha.

3.4 Diversity patterns

The greates richnness and diversity were found in the intermediate successional stage (30-35 years growth). This stage presented species that are characteristic both of the mature forest and the early growth (Table 4). The nature of this intermediate state is supported by statistical differences in diversity between the early growth and mature forest (Δ = - 0.21 p = 0.01), while there were no differences between early growth and old growth (Δ = -0.56 p > 0.05), nor between old growth and mature forest (Δ = 0.35 p > 0.05).

Successional stage	Mature forest	Old growth	Early growth
# Plots	10	7	10
Area (ha)	1	0.70	1
Density	413	442	561
Species	54	56	43
H'	3.127	3.48	2.92
α	16.59	16.98	10.86
D	13.48	23.79	13.71

Table 4. Number of plots, total sampled area (ha), plant density and estimated values for species richness(S), Shannon-Wiener diversity index (H'), Simpson's diversity index (D) and Fisher's alpha (α) for each successional stage.

In all three successional stages there was a high abundance of plants in early development stages and a low abundance of bigger sizes, so, according to Peter (1996), the class of structure found in the system is Type I (Figure 3). In all three successional stages, short size individuals are predominant, while in the early successional stage, no individual reaches a DBH of 200 cm.

Similarity analysis results showed that mature forest has a higher similarity with the old growth (26%). Figure 4 shows dominant species of each successional stage and shared species between habitats. Eight species were found in all three stages, while mature forest presented the highest number of exclusive species.

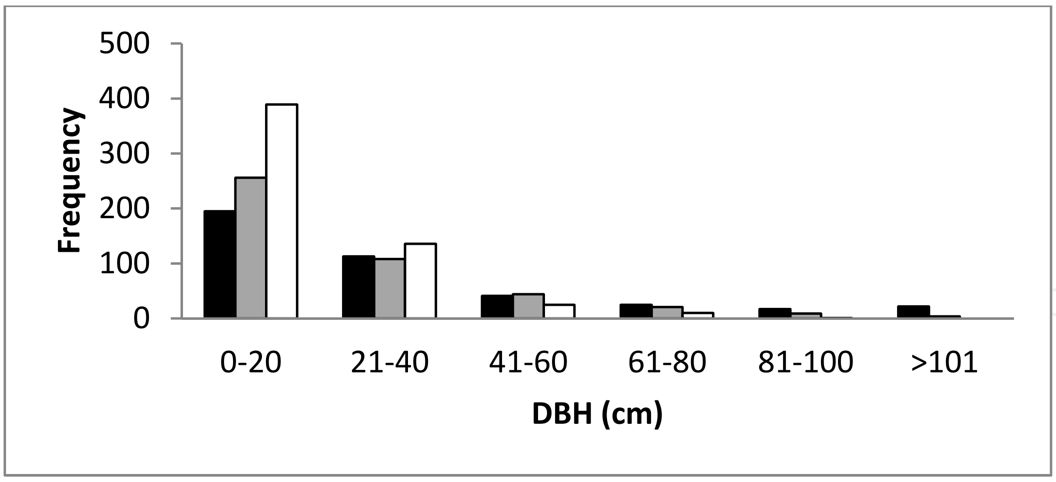

Fig. 3. Diametric class structure in three successional stages in El Triunfo, Chiapas, Mexico. Black columns denote Mature Forest, gray columns Old Growth and blank columns Early Growth.

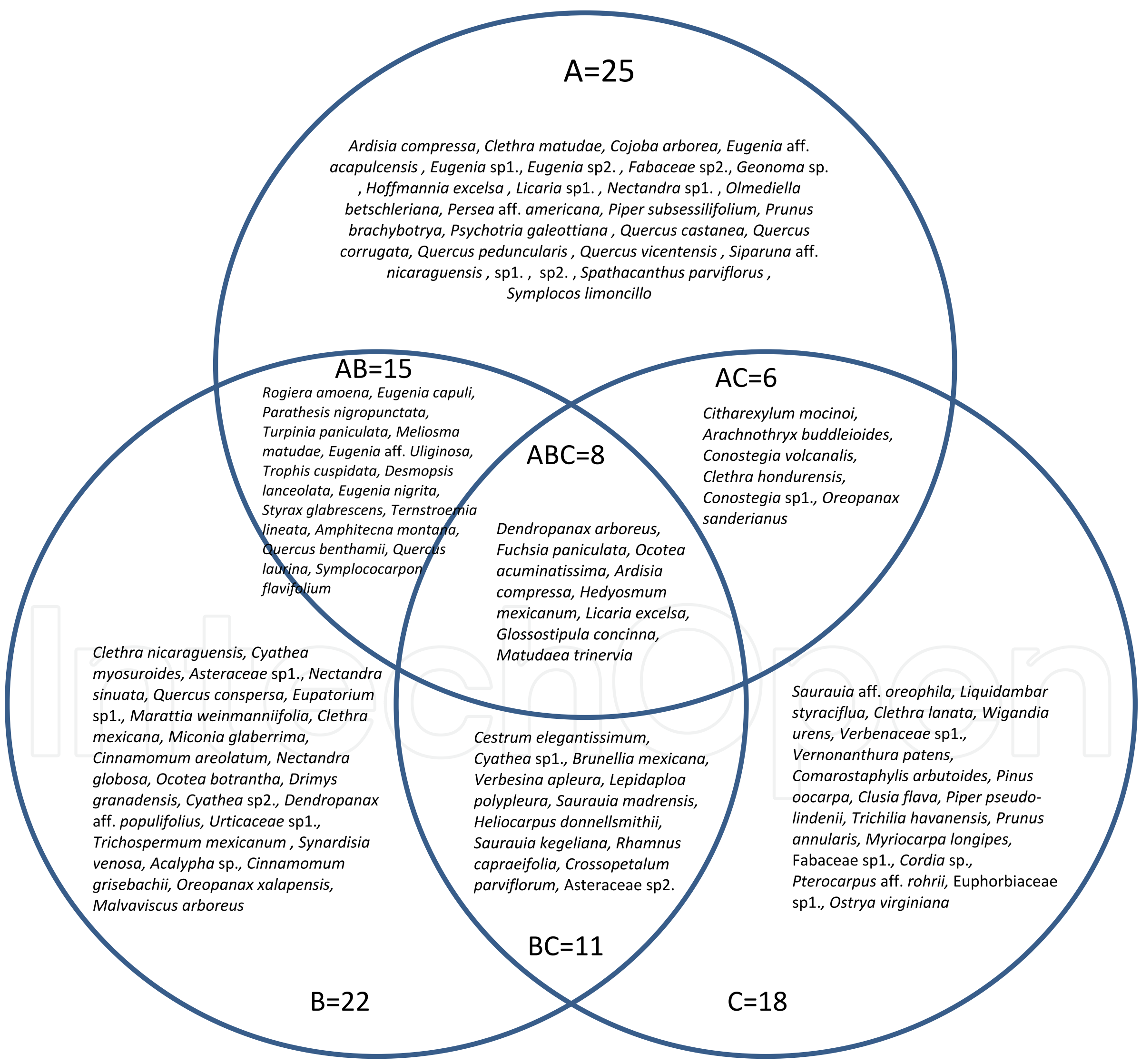

Fig. 4. Unique and shared species for each successional stage and their transitional phases between them. A=Mature forest, B=Old Growth, C=Early growth.

In contrast with Kappelle (1996) who found the highest richness and diversity in early successional stages, our results indicate that intermediate stage (old growth) has the highest richness and diversity. Nowadays, the old idea that the highest diversity is to be found in mature undisturbed systems has been challenged. The intermediate disturbance hypothesis, originally presented by Connell (1978) states that at intermediate levels of disturbance, diversity is maximized because both competitive and opportunistic species can coexist. The highest diversity at intermediate levels of disturbance that we found may support this notion. It is probable that our intermediate successional stage has spatial and temporal heterogeneity within the system, favoring the coexistence of numerous species. Denslow (1980) suggests that alpha diversity in successional stages in tropical forests is due to the high number of plantules of disturbance adapted species. According to Bazzaz (1975) the high species diversity in secondary forests may be explained by the high degree of horizontal and vertical micro-environmental complexity in early successional stages.

Williams-Linera (1991) found for mature Cloud Forest IVI values very similar to what we report in this study for *Matudaea trinervia, Quercus peduncularis,* and *Hedyosmum mexicanum* in a study done in the same area. Old growth had a 20% similarity with early growth, which suggests a high rate of species substitution. Availability, dispersion and germination of these species may play a key role in forest recovery and restauration in early phases after a disturbance (Guariguata & Kattan, 2002; Ten Hoopen & Kappelle, 2006; Wilms & Kappelle, 2006).

We may consider our system to be healthy because all class structures in all habitats had a DBH between 0-20 cm in more than 40% of individuals. This, according to Peter (1996) suggests that these structures are more stable and are considered healthy.

Finally, we compared our results with several other studies on successional gradients elsewhere in the neotropics (table 5). Some Costa Rica mature forest has twice the number of species than El Triunfo. However, secondary forest in Costa Rica showed similar numbers to

Forest stage	Country	Age (years)	Plot size (ha)	Average altitude	Species richness	Shannon Index	Reference
Tropical subalpine forest							
Primary	Peru	Mature	0.10	3400	9	-	Young, 1992
Tropical upper montane forest							
Primary	Ecuador	Mature	1	3280	32	-	Valencia & Jørgensen, 1993
Primary	Colombia	Mature	0.80	2850	33	-	Bazuin et al 1993
Primary	Costa Rica	Mature	0.1	2975	20	3.31	Kappelle et al 1996
Secundary	Costa Rica	15	0.10	2975	21	3.39	Kappelle et al 1996
Secundary	Costa Rica	30	0.10	2975	20	3.14	Kappelle et al 1996
Tropical montane cloud forest							
Primary	Mexico	Mature	1	1920	54	3.13	This study
Secundary	Mexico	30-35	0.7	1860	56	3.48	This study
Secundary	Mexico	20-25	1	1820	43	2.92	This study
Tropical lower montane forest							
Primary	Costa Rica	Mature	0.18	1050	105	4.06	Kuzee et al, 1994
Secundary	Costa Rica	11	0.19	1030	54	2.84	Kuzee et al, 1994
Secundary	Costa Rica	35	0.10	950	69	3.51	Kuzee et al, 1994

Table 5. Comparison of species richness and diversity between some primary and secondary forests in the Neotropics.

what we found in El Triunfo. These results suggest that secondary forest at El Triunfo could be more diverse than primary forest.

The patterns on species diversity and species replacement along a successional gradient we obtained from this study would be of great help to design sound strategies for Cloud Forest restoration. This is very important since little is known on Cloud Forest dynamics and because this habitat is considered one of the most endangered all over the world.

5. Acknowledgement

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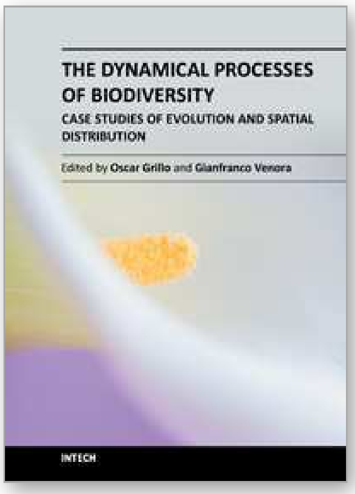

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Driven by the increasing necessity to define the biological diversity frame of widespread, endemic and threatened species, as well as by the stimulating chance to describe new species, the study of the evolutive and spatial dynamics is in constant execution. Systematic overviews, biogeographic and phylogenic backgrounds, species composition and distribution in restricted areas are focal topics of the 15 interesting independent chapters collected in this book, chosen to offer to the reader an overall view of the present condition in which our planet is.

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