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# Small-Scale Environmental Drivers of Plant Community Structure and Diversity in Neotropical Montane Cloud Forests Harboring Threatened *Magnolia dealbata* in Southern Mexico

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**Abstract:** Gradient analysis was used to determine factors driving small-scale variation of cloud forest communities harboring *Magnolia dealbata*, a threatened species and bioculturally relevant tree for the Chinantecan, Mazatecan, Nahuatl, and Zapotecan ethnicities in southern Mexico. Particularly, we aimed to: (a) determine factors explaining major community gradients at different heterogeneity scales along a small-scale elevational gradient, (b) test the Decreasing and the Continuum hypotheses along elevation, and (c) classify vegetation to assist in identifying conservation priorities. We used a stratified random sampling scheme for 21 woody stands along a small-scale (352 m) elevational transect. Four main data matrices were used (presence-absence, density, basal area, and guild data). Through Non-metric Multidimensional Scaling (NMS), Principal Coordinates Analysis (PCoA), and distance-based Redundancy Analysis (db-RDA), we found that major community variation was explained by soil pH, displaying an outstanding vegetation discontinuity, separating the species-rich relic *Oreomunnea-Ticodendron*-stands from stands with higher importance values for *M. dealbata*. The high species richness observed was explained by a combination of the windward effect of dry-seasonal maximum cloud condensation gain and habitat differentiation-specialization, a phenomenon that may also explain the mid-peak hypothesis and ensure the survival of relic species. Sampling-truncation and conservation status also played a role in this. Our results do not support the Decreasing and Continuum hypotheses along elevation.

**Keywords:** alpha diversity; beta diversity; *Magnolia* section *Macrophylla*; *Oreomunnea*; *Ticodendron*; cloud forest; Sierra de Juárez; Oaxaca; habitat specialization; continuum hypothesis

## 1. Introduction

Neotropical montane cloud forests (CF) are known to display high gamma, beta, and alpha species diversity, environmental heterogeneity, endemism, and a high number of species of conservation concern. They form a continental pattern of island-like fragmented habitats resembling archipelagos [1–8]. Despite their biological relevance, these complex ecosystems are being replaced or

negatively impacted by coffee plantations, logging, induced grasslands [9], and more recently, the land conversion for production of avocado: the “butter fruit” or “green gold” is causing havoc to plant communities, diminishing plant diversity, depleting soil and water resources, and increasing runoff volume rates [10,11]. In Southern Mexico, in the state of Oaxaca, CF occurs in six physiographic provinces [12] in close interaction with a complex and long biocultural gradient of high ethnic and language turnover, including Chinantecos, Cuicatlecos, Mazatecos, Mixtecos, Nahuas, Triquis, Zapotecos, and Zoques [13]. Gradient analyses of these forests have focused on La Chinantla [14], Tiltepec [15], Huautla de Jiménez [16], Sierra de Juárez [17], Sierra Mazateca [18], and Santa Cruz Tepetotutla [19]. However, only those from the Sierra de Juárez de Oaxaca (Ixtlán de Juárez, Villa Alta) and Sierra Mazateca are confirmed to harbor the narrowly endemic, bioculturally relevant and threatened CF tree *Magnolia dealbata* Zucc. [20–22].

Neotropical *Magnolia* L. includes 170 extant species and four sections: section (sect.) *Macrophylla* Figlar & Noot. in the southeastern USA, and eastern Mexico, sect. *Magnolia* in North America and Central America, sect. *Talauma* (Juss.) Baill. from western and eastern Mexico to Paraná, Brazil, and sect. *Splendentes* Dandy ex A. Vázquez in the Caribbean [23–25], and all sections display a remarkable pattern of allopatric speciation [23,24,26]. *Magnolia dealbata* belongs to section *Macrophylla* which includes *M. macrophylla* and *M. ashei* Weath. from southeastern USA, *M. nuevoleonensis* A. Vázquez-Domínguez-Yescas from Nuevo León, *M. alejandrae* García-Mor & Iamónico from Tamaulipas, *M. rzedowskiana* A. Vázquez, Domínguez-Yescas & Pedraza-Ruiz from Querétaro, San Luis Potosí, and Hidalgo, and *M. vovidesii* A. Vázquez, Domínguez-Yescas & L. Carvajal from Veracruz [27–30]. *Magnolia dealbata* is a mid-successional, short-lived, and fast-growing tree species with gigantic (40–50 cm in diameter) fragrant flowers, enormous leaves (40–70 × 20–35 cm), and an outstanding biocultural relevance in the Zapotec, Mazatec, and Nahua cultures, where it is known as “Yaj saá” (“sublime flower” in Zapotec) and Eloxóchitl (“flower of corn husk” in Náhuatl). Flowers are harvested yearly on Easter for ornamental, medicinal, and ceremonial purposes (the flowers are locally sold at 0.5 USD each) [28,29,31]. This species is endemic to Oaxaca with an elevational niche breadth ranging from 1380 to 2145 m and confined to the upper central zone of Río Papaloapan watershed [32]. It is listed as Near Threatened in the International Union for Conservation of Nature IUCN red list of Magnoliaceae [21], and as Endangered in the Mexican Endangered Species Act [22]. Understanding the community organization of forest stands harboring *M. dealbata* and generating hypotheses about its major environmental drivers constitute an essential step for guiding the design of conservation strategies of highly relevant forest species.

Vegetation science relies on both gradient analysis and niche theories. Gradient analysis sensu lato involves indirect, direct, bivariate, and multivariate analyses [33–37], the latter includes classification [38], ordination [39,40], and constrained ordination [41]. Gradient analysis is a valuable approach in assisting the interpretation of forest community patterns and species ecological niches in terms of their species responses to environmental variables [40–43]. Classification is particularly effective in searching for patterns when data show major discontinuities [44], however, continuity vs. discontinuity is mostly a scale-dependent issue [45,46]. A combination of regression, ordination, constrained ordinations, and classification can be used as complementary analyses to assess small-scale CF community variation; in turn, this can guide management decisions for sustainability, including in situ conservation of endangered species and highly threatened CF communities.

Many large-scale gradient analyses in CF have assessed community trends along various ecological gradients including latitude [1,8,17], precipitation [1,47], soil conditions [1,48–51], and elevation [1,8,17,47,52–61]. For tropical lowland forests, successional time [62] and rate of tree mortality [63] have also been studied. However, few studies use the full spectrum of gradient analysis, including bivariate and multivariate gradient analyses (ordination, constrained ordination, and classification), as complementary approaches to interpreting community patterns in CF [64,65]. Even fewer studies explore community patterns on various scales or deal with extreme acidity in forest soil conditions, and none of the studies examine guild trends among forest sites with a floristic

affinity to the Miocene flora of Chiapas [66], sharing an endemic tree species of conservation concern, *Magnolia dealbata*, with broad elevational niche, and outstanding biocultural relevance [31].

Quantitative classifications of CF heterogeneity have been usually assessed at a single scale, using different community attributes, and resulting clusters have been explained by different environmental variables: (I) At the Neotropical scale, Vázquez-García [8] distinguished four regional CF: (1) Northern-Neotropical, (2) Mesoamerican, (3) The Caribbean, and (4) Northern-South American, explained by latitude and geographical location. (II) At a country scale (within Mexico), four provincial CF: (1) Atlantic, (2) Pacific southwest, (3) Interior highlands, and (4) northern Mesoamerican [8], corresponding to groups IV, I, V, and II of Ramírez-Marcial [5], who also reports one additional type of CF, South Pacific. Similarly, the groups A, F, D, and B of Jiménez et al. [6] correspond to those four groups previously mentioned, and they described eight additional CF types for Mexico, including one cluster (groups H, I, and J) for the Sierra Madre of Oaxaca. (III) At the mountain range scale: Puig et al. [67], using similarity index, report three CF types for the Sierra de Gómez-Farías: the groups share many dominant species by the following species (1) *Randia laetevirens* Standl., (2) *Carya ovata* (Mill.) K. Koch, and (3) none of the previous species. Using Non-metric Multidimensional Scaling NMS, Vázquez-García [8] reports six types of CF for the Sierra de Manantlán: (1) *Matudaea-Podocarpus*, (2) *Ternstroemia-Quercus*, (3) *Abies-Persea*, (4) *Carpinus-Cornus*, (5) *Magnolia-Acer*, and (6) *Ficus-Sapium-Dipholis* [*Sideroxylon*]. (IV) At the elevational transect scale, several studies report two community types: upper and lower CF [52,58,61,68], few studies report three or more types of CF along elevation [69], and over three types of CF are rarely reported [8].

The overall purpose was to examine small-scale vegetation patterns along a short (352 m long) elevational gradient (1608–1960 m), within a small area (1.6 km of radius) and at different heterogeneity scales (gradient lengths) to guide the design of conservation strategies for CF harboring the bioculturally relevant and threatened *Magnolia dealbata*.

We aimed to: (1) determine what environmental variables explain major community gradients at four different heterogeneity scales, gradient lengths (species composition, density, basal area, and guilds data matrices), expecting topographic and edaphic variables to be more influential for community organization than climatic variables, given the short length of the studied elevational gradient. (2) Test the Continuum hypothesis and high overlap and absence of family turnover among communities along short environmental gradients through classifying vegetation of four different data matrices, relating them to environmental variables and identifying indicator species for community clusters. (3) Test the Decreasing hypothesis [70], the most common outcome for woody species, stating that alpha diversity (species richness) decreases with increasing elevation. (4) Assess beta diversity as a measure of heterogeneity (gradient length) for each of the four community datasets presence/absence P/A, density, basal area, and guild data, expecting this to fall within the range of field studies [71,72], and use this measure to test the continuum hypothesis through assessing the magnitude of community discontinuities, and (5) determine conservation priorities in these CF.

## 2. Materials and Methods

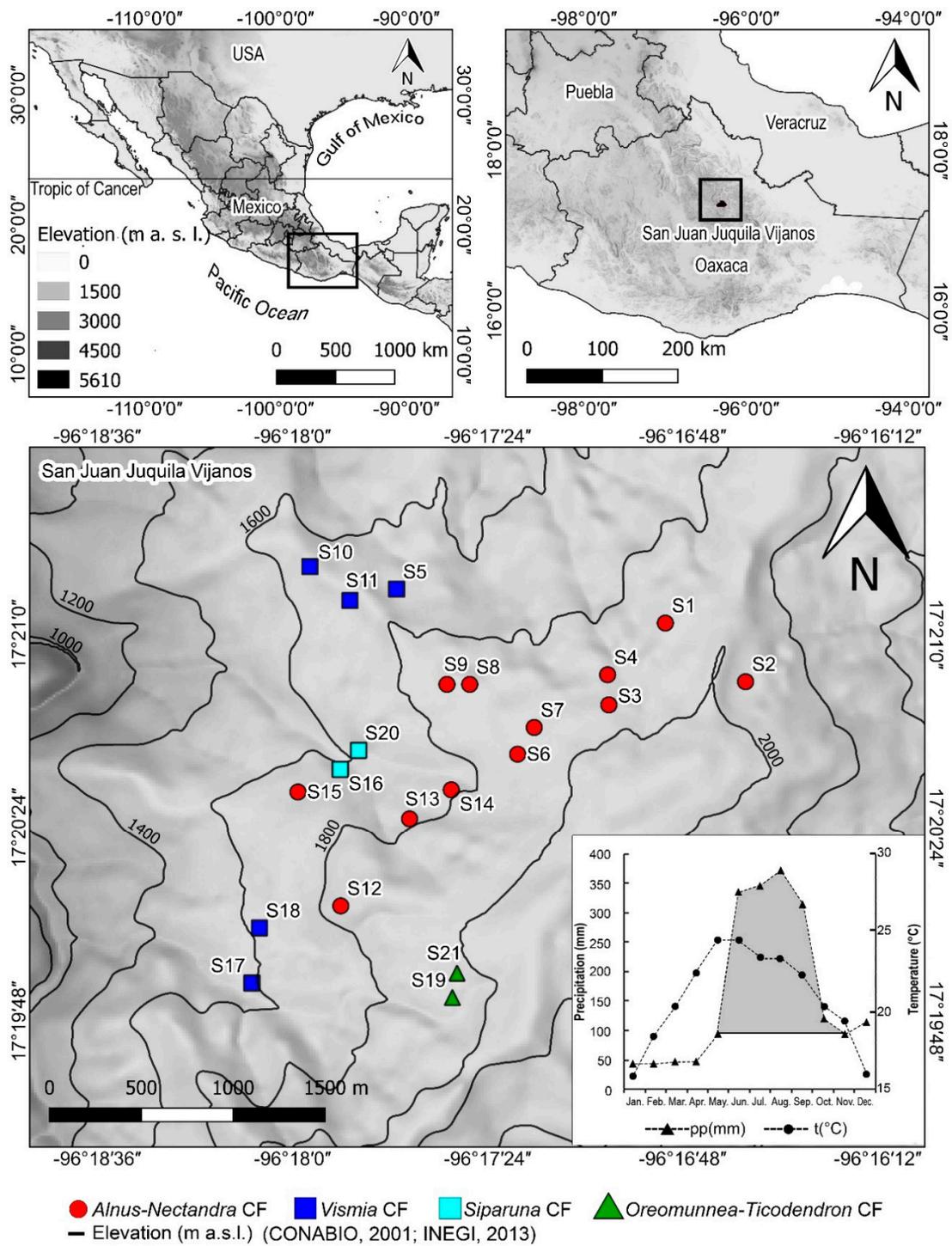
### 2.1. Study Area

Field research was conducted in CF of lands of the Zapotec (the “cloud people”, “Be’ena’ Za’a” in Zapotec) San Juan Juquila Vijanos community, in Villa Alta District, Sierra de Juárez (Sierra Norte), Oaxaca, southern Mexico, 17°18′–17°23′ N, 96°14′–96°20′ W [73] (Figure 1). Juquila Vijanos is part of the Juárez terrain, consisting of early Cretaceous volcano-sedimentary marine rocks [74], including basaltic spills, tuffs, volcanoclastic, and limestone [75]. The most important geological event in Oaxaca occurred in the Tertiary period, starting mid-Miocene (14 Mya), with the formation of the Sierra de Juárez (including de Sierra de Zongolica, Sierra Cuicateca, and Sierra Mazateca) lifting at least 2100 m above the central valley [74]. This lift was caused by the Oaxacan Fault and changed the climate of many regions of the state, increasing mountain moisture from trade winds (easterlies) and creating a rain shadow effect in the central valleys [74]. The study area is located

in the central orographic axis of the physiographic sub-province Sierra Madre de Oaxaca [12], particularly characterized by steep topography (15–100%) [76]. Major rocks in Juquila Oaxaca include igneous intrusive: monzonite (12.52%), sedimentary: lutita-sandstone (2.73%), metamorphic slate (44.67%), and shale (40.08%) [73]. Soils include luvisol (85.35%) and cambisol (14.65%) and are mostly acidic [77–79]. Juquila Vijanos includes the Juquila and Río Blanco rivers, the two drain into the Cajonos River, and finally reach the Papaloapan River. Climate is semi-warm humid with mean annual temperatures ranging from 16 to 22 °C, with abundant mean annual rainfall of 2600 mm (San Juan Yae, 1900 m a.s.l.), with 69.34% of rainfall occurring during the summer [73]. Due to the abundance of temperate elements and diagnostic families such as Actinidiaceae, Clethraceae, Chloranthaceae, Hamamelidaceae, Symplocaceae, Theaceae, and Winteraceae [76], the original vegetation is considered an upper Tropical Montane (TM)-CF [80]. Cloud forests in the Sierra Norte de Oaxaca occur between 1300 and 2300 m a.s.l., mostly on the Atlantic windward side of the mountains [14], on hilly sides with pine-oak forest and “acahuales” (secondary successional vegetation) of different ages resulting from the abandonment of agricultural lands [81]. However, much of the original vegetation has been converted to coffee plantations, agriculture (including polycultures), and some pasturelands [78,81]. Oaxaca is an important center of domestication of Mesoamerican plants, including currently complex agroforestry systems like those in Sierra de Juárez (Chinantla), where useful species are tolerated within field crops or rustic coffee plantations involving up to 34 native tree species, including threatened species of *Magnolia*, which serve as nurse plants. This type of forest management with high beta diversity has important implications for biodiversity conservation and sustainable development [13]. In the area prevail allogenic disturbances such as logging, slash and burn agriculture, firewood, and non-timber product extraction; meanwhile, autogenic disturbances, such as landslides, fires, and natural tree falls, occur to a lesser extent [78,81,82]. In contrast with other successional processes in humid forest areas, soil becomes progressively more acidic along succession, despite a decrease in pine dominance [78,82].

## 2.2. Community Sampling

A stratified random sampling including 21 0.1 ha forest stands (sites) within the habitat of *Magnolia dealbata* was carried out from December 2016 to August 2017, in San Juan Juquila Vijanos, on areas with minimum disturbance and excluded from cattle grazing. A 60 × 48 m rectangular universe was defined, divided into a 4 × 5 grid (each cell 12 × 12 m). At the center of each cell, a circle was delimited to include an area of 100 m<sup>2</sup> per quadrat (subplot). The centers of the possible circular quadrats (11.28 m in diameter) were separated by 12 m, to avoid any overlap between the adjacent quadrats. Ten circular quadrats per site were chosen in a stratified random sampling design [56]. In each circle, the diameters of all woody species ≥2.5 cm in diameter at breast height (dbh, at 1.3 m) were measured and recorded. A triplicate collection of voucher plant specimens was obtained: they were mostly identified by the authors, and difficult taxa were determined by specialists. For accepted names of species, we used Tropicos.org [83], and for plant distributions, we consulted Plants of the World Online (POWO) [84]: their nomenclature and author abbreviations follow the International Plant Name Index [85]. The main voucher collection was deposited in the herbarium of the Instituto de Botánica de la Universidad de Guadalajara (IBUG) herbarium at the University of Guadalajara and sets of duplicates were deposited at Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional (CIDIR) and the herbarium Sociedad para el Estudio de los Recursos Bióticos de Oaxaca, A. C. (SERO).



**Figure 1.** Location of sampling sites in San Juan Juquila Vijanos, Villa Alta, Oaxaca.

### 2.3. Environmental Sampling

At each site, a total of 31 environmental variables were recorded in five subsets: Climatic (5), topographic (4), edaphic (14), canopy structure (5), and disturbance (5) (Table 1). Highly correlated variables ( $r > 0.8$ ) of each subset were excluded from the analysis to avoid collinearity. Climatic data were extracted from the WorldClim database [86] and an index of the heat load was estimated [87]. Topographic variables were directly measured in the field and elevation was recorded by a Global Positioning System GPS Garmin 60CSx. Edaphic variables were obtained from soil analyses. One mixed

soil sample (500 gr) per site, was taken from five quadrats of 30 × 30 cm each, and 30 cm deep (one quadrat in each site's corner and one in the center) [88]. The samples were analyzed in the Agroecology Laboratory of the Centro Universitario de Ciencias Biológicas y Agropecuarias, University of Guadalajara. Soil density was determined through the test tube method, and sand, silt, and clay texture were determined by Bouyoucos. Usable water was determined by the difference between the soil field's capacity and permanent wilt point. Organic matter was estimated through the Walkley and Black [89] (1934) method; for interchangeable cations (Ca), we used the volumetric method. Mg was inferred from the volumetric method, Na and K were assessed by flammometry, and soil pH was measured by a potentiometer; for electrical conductivity, we used a conductometer, and for soil macronutrients, phosphorus (P), and percentage of nitrogen (N), we used the Kjeldahl method [90]. Canopy structure variables were obtained from hemispheric photographs at each site, using a Nikon D7100 digital camera and a hemispherical (fisheye) Canon lens. To reduce the effects due to the slope, in each site, the camera was mounted on a tripod at a height of 1.20 m [91] and a level device was used to ensure horizontal alignment of the camera. Each photograph was taken at the center of each site and oriented to match the top of the photograph with the north [91,92]. Photos were taken on cloudy days, to prevent the sun's rays from directly affecting the camera lens. Each canopy photograph was taken from a leveled camera [93]. Images obtained were analyzed through the Gap Light Analyzer software (GAP free version 2.0, 1999), to correct the distortion inherent in this type of photographs. The disturbance was assessed, assigning a score from 0 to 10 to each variable, depending on the intensity of the disturbance: a score of 0 was considered as insignificant, 1 as low, 5 as intermediate, and 10 as high. A disturbance index was calculated following Mir et al. [94].

**Table 1.** Environmental variables and methods used.

Variable Name	Acronym	Method/Database/ Software	Measured Units and/or Categories
		Climatic	
1. Mean Annual Temperature	MAT *	WorldClim v.1.4	°C
2. Precipitation of Wettest Month	PWEM	WorldClim v.1.4	mm
3. Precipitation of Driest Month	PDM	WorldClim v.1.4	mm
4. Precipitation of Driest Quarter	PDQ	WorldClim v.1.4	mm
5. Precipitation of Coldest Quarter	PCQ	WorldClim v.1.4	mm
		Topographic	
6. Elevation	ELE *	GPS	m
7. Potential Annual Direct Incident Radiation	RAD	McCune and Keon 2002 [87]	MJ cm <sup>-2</sup> yr <sup>-1</sup>
8. Head Load Index	HLI	McCune and Keon 2002 [87]	
9. Topographic Position	TP		1—Valley; 2—Low slope; 3—Mid slope
		Edaphic	
10. Apparent Density	APD	Test tube	g/cm <sup>3</sup>
11. Sand	SAND	Bouyoucos	%
12. Silt	SILT	Bouyoucos	%
13. Clay	CLAY	Bouyoucos	%
14. Usable Water	USWT		%
15. Organic Matter Content	OMC	Walkley and Black	%
16. Nitrogen	N	Kjeldahl	%
17. Calcium	Ca	Volumetry	Meq/100 g
18. Magnesium	Mg	Calculated	Meq/100 g
19. Sodium	Na*	Flamometry	Meq/100 g
20. Potassium	K*	Flamometry	Meq/100 g
21. Phosphorus	P	Kjeldahl	Mg/k
22. pH	pH*	Potentiometer	Logarithmic units (0–14)
23. Electric Conductivity	EC	Conductimeter	Mili-mhos/cm at 25 °C
		Canopy Structure	
24. Mask Area	MASKA	Gap Light Analyzer software	%
25. Canopy Openness	CANOP	Gap Light Analyzer software	%
26. Leaf Area Index	LAI5	Gap Light Analyzer software	Angle 0–75°
		Disturbance	
27. Wood Extraction	WEXT	Disturbance index	Scores 0 to 10
28. Firewood Extraction	FEXT*	Disturbance index	Scores 0 to 10

Table 1. Cont.

Variable Name	Acronym	Method/Database/ Software	Measured Units and/or Categories
29. Collection of Non-Timber Forest Products	NTFP	Disturbance index	Scores 0 to 10
30. Grazing	GRA	Disturbance index	Scores 0 to 10
31. Fire	FIRE	Disturbance index	Scores 0 to 10

Abbreviations: Meq (milliequivalents). \* Those only included in the constrained ordination analysis.

#### 2.4. Data Matrices

From summary statistics obtained in PC-ORD 7 (MjM Software, Gleneden Beach, OR, USA) [85], we generated four data matrices, three of them consisting of 21 sites  $\times$  77 species. for (1) P/A (Supplementary Tables S1 and S2), (2) density, and (3) basal area data, and (4) a matrix for guilds, consisting of 21 sites and 60 guilds, grouped in ten categories: biogeographical affinities (8), geographic distribution (6), life forms (4), leaf morphology (15), reproductive (3), phenological (3), successional (3), dispersal (9), antiherbivore defenses (2), and pollination (5). Guild categories were designated using Tropicos.org and POWO for biogeographical and distributional data, and morphological and functional guilds were determined by consulting numerous taxonomic monographs and regional floras. These guilds are summarized for only 76 species since one species (morphospecies) was excluded (Supplementary Table S3).

#### 2.5. Ordination

We used Non-metric multidimensional scaling (NMS), a distance-based ordination considered superior to currently available model-based methods [95], to map the location of sample units from the high-dimensional space of the distance matrices, to positions along community dissimilarity gradients in a low-dimensional space. In NMS, species similarity between samples represent their environmental similarities but in a highly coalescent configuration, including similarities in intra- (density-dependent mortality, resource competition) and inter-specific interactions (herbivory, dispersal, predation, pollination) and biogeographical events [42]. Four main raw matrices (P/A, density, basal area, and guild data) were used, each consisting of 21 sites and 31 environmental variables. We used the Sørensen (Bray-Curtis) distance measure, having a monotonic relationship to environmental distance, and considered as a robust measure of ecological distance [42,43,96]. The secondary matrix consisted of 21 sites  $\times$  31 variables (Table 2). NMS is considered among the most effective methods for the ordination of ecological data because it does not require the assumption of a linear relationship among the variables and because it determines the dimensionality of the data [89]. Preliminary runs were performed to determine the appropriate dimensionality using the autopilot mode, choosing the slow and thorough option, the Sørensen distance, an instability criterion of 0.00001, with 50 runs with real data, and 500 iterations to evaluate instability. We used Pearson's correlation coefficients to evaluate the relationship between the identified axes of the ordination and the environmental variables. Principal Coordinates Analysis (PCoA) was performed only for guild data, since these data showed the lowest gradient length (low heterogeneity), making it appropriate for this metric multidimensional technique. We used a Sørensen distance matrix of 21 sites  $\times$  60 guilds for this ordination method, in which the distances among sites in the ordination diagram are maximally correlated with the ecological distances [97]. Additionally, we used distance-based Redundancy Analysis (db-RDA), a reliable constrained ordination technique, to assess the influence of environmental variables [98,99]. The db-RDA allows for the flexible selection of many resemblance functions; again, we used Sørensen dissimilarity in each of the four matrices: P/A, density, basal area, and guild data. The variables most associated (with highest  $r$  values) with the NMS axes were selected as input for a standard RDA. NMS, PCoA, and db-RDA were performed using the program PC-ORD 7 [97].

**Table 2.** Environmental variables used in ordination analyses.

Variable Name	SITES																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
ELE (m a.s.l.)	1835	1939	1944	1899	1730	1898	1950	1911	1873	1744	1726	1855	1798	1792	1688	1659	1608	1645	1951	1613	1960
MAT (°C)	15.2	15.2	15.7	15.7	17.3	15.7	15.7	15.7	15.7	17.3	17.3	16	16	16	16	16	17	17	15.2	16	15.2
PWEM (mm)	151	151	151	148	148	144	144	144	144	144	144	143	143	141	141	141	141	141	141	140	140
PDM (mm)	28	28	27.1	27.1	28.6	27.1	27.1	27.1	27.1	28.6	28.6	26.1	26.1	26.1	26.1	26.1	26.3	26.3	27	26.1	27
PDQ (mm)	7.5	7.5	7.3	7.3	8.3	7.3	7.3	7.3	7.3	8.3	8.3	7.2	7.2	7.2	7.2	7.2	7.5	7.5	7.1	7.2	7.1
PCQ (mm)	15.2	15.2	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.7	14.1	14.1	14.1	14.1	14.1	13.2	13.2	14.3	14.1	14.3
RAD (MJ cm <sup>-2</sup> yr <sup>-1</sup> )	0.8	0.75	0.74	0.83	1.05	1.14	1.14	0.81	0.91	1.06	1.11	1.08	0.86	0.83	1	0.72	0.89	1.07	0.94	0.89	0.78
HLI	0.65	0.6	0.59	0.69	0.89	1.07	1.08	0.93	1.06	0.97	1.04	1	0.71	0.69	1.1	0.56	0.75	0.94	0.82	0.75	0.62
TP	2	3	3	3	2	2	2	2	2	3	2	3	2	3	1	1	3	3	1	3	3
SAND (%)	54.3	56.3	39.3	50.3	51.3	59.3	53.3	52.3	57.3	49.3	48.3	48.3	59.9	50.9	64.9	61.9	58.9	48.9	46.9	49.9	66.9
SILT (%)	32.6	30.6	37.6	33.6	30.6	24.6	31.6	30.6	24.6	25.6	28.6	31	19	28	22	27	27	31	29	35	26
CLAY (%)	13.1	13.1	23.1	16.1	18.1	16.1	15.1	17.1	18.1	25.1	23.1	20.1	21.1	21.1	13.1	11.1	14.1	20.1	24.1	15.1	7.08
USWT (%)	15	14	21	16	17	15	16	16	16	20	19	18	17	18	13	13	14	19	20	16	10
OMC (%)	9.64	11.8	5.03	10.7	9.7	8.85	6.43	6.61	11.3	6.36	13	9.64	12.9	10.9	13.2	12.5	13.1	8.73	8	10	7.27
N (%)	0.17	0.26	0.15	0.25	0.16	0.23	0.18	0.15	0.2	0.15	0.14	0.2	0.28	0.23	0.28	0.27	0.22	0.22	0.2	0.26	0.22
Ca (Meq/100 g)	0.83	0.83	0.83	0.41	1.24	0.83	0.41	0.41	0.41	0.83	0.41	0.42	0.83	0.42	0.41	0.83	0.41	0.42	0.83	0.83	0.83
Mg (Meq/100 g)	1.24	1.66	1.66	2.08	0.83	0.41	0.41	0.83	0.83	0.83	0.83	0.42	0.41	0.42	0.83	0.77	0.83	0.42	0.41	0.41	0.41
Na (Meq/100 g)	0.19	0.19	0.16	0.16	0.19	0.16	0.16	0.16	0.19	0.19	0.23	0.19	0.19	0.27	0.23	0.31	0.19	0.31	0.19	0.23	0.19
K (Meq/100 g)	0.22	0.2	0.15	0.2	0.22	0.2	0.17	0.17	0.2	0.17	0.22	0.17	0.22	0.25	0.31	0.31	0.17	0.22	0.17	0.22	0.22
P (Mg/k)	5.3	5.87	6.92	3.01	3.96	4.05	3.58	4.82	5.3	2.62	7.58	3.48	5.01	3.29	8.73	5.39	0.01	5.68	5.3	5.58	12.3
pH (Logarithmic units, 0–14)	5.07	4.86	4.94	4.88	4.86	4.84	4.8	4.93	5.14	4.99	5.02	4.64	4.8	4.47	4.48	4.3	4.4	4.32	4.2	4.35	4
EC (Mili-mhos/cm at 25 °C)	0.07	0.08	0.07	0.08	0.09	0.07	0.08	0.07	0.07	0.09	0.08	0.04	0.05	0.06	0.05	0.1	0.06	0.04	0.06	0.06	0.07
MASKA (%)	0.1	0.1	0.1	0.11	0.12	0.11	0.12	0.09	0.11	0.12	0.11	0.12	0.12	0.11	0.1	0.12	0.12	0.09	0.11	0.11	0.11
CANOP (%)	9.51	12.9	16.3	11.4	15.2	16	15.5	11.4	22.5	26.8	18.7	10.5	5.24	6.69	18.7	12	8.1	17	6.02	7.95	9.45
LAI 5 (angle 0–75°)	2.52	2.14	1.89	2.28	2.01	1.9	1.91	2.37	1.62	1.4	1.8	2.47	3.33	2.89	1.79	2.26	2.72	1.9	3.09	2.73	2.53
WEXT (Scores, 0–10)	0	0	5	5	5	1	0	5	5	5	5	0	5	0	5	0	0	10	5	0	0
FEXT (Scores, 0–10)	5	5	0	5	5	1	1	5	5	5	10	5	1	10	1	1	10	10	5	5	10
NTFP (Scores, 0–10)	1	2	1	5	5	1	1	1	5	5	10	10	0	10	0	0	1	0	5	0	0
GRA (Scores, 0–10)	0	0	0	0	5	0	0	0	0	0	0	0	0	0	1	0	0	5	0	0	0
FIRE (Scores, 0–10)	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0

Climate data: MAT (Mean Annual Temperature), PWEM (Precipitation of Wettest Month), PDM (Precipitation of Driest Month), PDQ (Precipitation of Driest Quarter), PCQ (Precipitation of Coldest Quarter); soil data: APD (apparent density), Sand, Silt, Clay, Usable water (USWT), Organic matter content (OMC), Nitrogen (N), Calcium (Ca), Magnesium (Mg), Sodium (Na), Potassium (K), Phosphorus (P), pH, electric conductivity (EC); topographic data: ELE (Elevation), (RAD) Potential annual direct incident Radiation, HLI (Headload index), (TP) Topographic position; anthropogenic disturbance data: WEXT (Wood extraction), FEXT (Firewood extraction), NTFP (Collection of non-timber forest products), GRA (Grazing), Fire; canopy data: MASKA (Mask Area), CANOP (Canopy Openness), and LAI 5 (Leaf Area Index).

## 2.6. Classification

A hierarchical cluster analysis, was performed using PC-ORD 7 [97], with the flexible beta algorithm, was performed to determine community groups, using a Sørensen distance matrix of 21 sites  $\times$  77 species. We used a restriction criterion ( $\beta = -0.25$ ) as a linkage method to obtain a dendrogram [95]. Compositional differences among groups, generated by cluster analysis, were assessed using a multi-response permutation procedure (MRPP), a technique not requiring distributional assumptions (multivariate normality and homogeneity of variance) [95]. This technique provides a statistical test (T) describing the separation among groups, a  $p$ -value evaluating the likelihood that an observed difference is due to chance, and the agreement statistic A, describing within-group homogeneity compared to that expected by chance. When all the items within groups are identical, the weighted mean within-group distance ( $\delta$ ) = 0 and  $A = 1$ , the highest possible value for A. A neutral value ( $A = 0$ ) is obtained when heterogeneity matches that expected by chance. If there is less agreement within groups than expected by chance, then  $A < 0$  [95]. We run MRPP available on the PC ORD 7 software [97] using the Sørensen distance measure, the same one used in both the ordination and classification. Indicator Species Analysis (ISA) was used to determine the most representative and exclusive tree species in each of the groups detected in the cluster analysis [89], using the relative frequency and relative abundance of the species in each selected group. Indicator values were tested through 1000 Monte Carlo randomizations [95]. ISA was also used to objectively define the optimum number of groups, selecting the hierarchical cluster step with both the smallest average  $p$ -value and the highest number of significant indicator species [95,100]. ISA was performed for P/A data, using the Tichý and Chytrý [101] method; for abundance data (density, structure, and guilds), we used Dufrêne and Legendre [100], with the Sørensen distance measure. We used the software package PC-ORD 7 for all multivariate analyses [95].

## 2.7. Diversity and Structure

A regression analysis was carried out using species richness ( $\alpha$ -diversity) as the dependent variable and elevation as the independent variable. The resulting pattern for the 21 sites of this study was compared against data of alpha diversity for 146 sites from previous studies using the same sampling scheme with circular quadrats [47]. The relative species-richness of families was examined along the elevational gradient: the 21 sites were grouped and averaged by elevation into four classes: 1600–1699 m a.s.l. (sites 15–17, 18, 20), 1700–1799 m a.s.l. (sites 5, 10–11, 13–4), 1800–1899 (sites 1, 4, 6, 9, 12), and 1900–1999 m a.s.l. (sites 2–3, 7–8, 19, 21). Species turnover ( $\beta$ -diversity) was assessed through detrended correspondence analysis (DCA), performed with PC ORD 7 [97] to quantify the heterogeneity, as gradient length, for each of the four data matrices (P/A, density, basal area, and guilds). This measure is ecologically meaningful, and it was also used to assess the magnitude of discontinuities along the primary gradient in ordination and among clusters in vegetation classification. The total amount of the species found ( $\gamma$ -diversity) was obtained from the 21 sites along the 350 m elevational gradient. Structure data were obtained from summary statistics of individual tree species (frequency, density, and dominance) in the 21 sites, using the PC-ORD software package version 7.0.

## 2.8. Endemism and Conservation

We used Tropicos.org and POWO to assess the geographic distribution and endemism of each species. The risk status and endemism of all species were determined using various criteria: The International Union for Conservation of Nature and Natural Resources Red List [102], the Mexican endangered species act NOM-059 [22], and the Red List of Mexican Cloud Forest Trees [20].

### 3. Results

#### 3.1. Ordination

NMS suggested three dimensions for P/A data, and two and one for density and basal area, respectively. Axis 1 accounted for a greater proportion of variance for basal area data, followed by density and P/A data (Table 3), axis 1 was consistently explained by pH (Table 4) in all three datasets (P/A, density, and basal area). Axis 2 was explained by elevation and MAT for P/A data and by Na for density data, and none of the measured variables explained axis 3 (Table 4). The lowest “stress” value was achieved with P/A data and with fewer iterations, followed by basal area and density data (Table 3). Groups overlays (convex hulls), showed no overlap in all three datasets (Figure 2A–C), except for P/A data, where the *Siparuna*-CF overlapped with the *Vismia*-CF in axis 1–2. *Oreomunnea-Ticodendron*-CF were consistently separated in all three datasets along axis 1 and explained by soil acidity. For P/A data, the *Vismia*-CF was separated from the *Siparuna*-CF along axis 2 and explained by elevation. For density data, the *Zinowewia*-CF was separated from the *Oreomunnea-Ticodendron*-CF along axis 2 and explained by Na and K. For basal area data, all three groups were separated along axis 1 by pH. For guild data, PcoA showed high eigenvalues and accounted for a high total variance, inertia (76.22%) (68.01%, corrected), suggesting the existence of strong environmental gradients in the Juquila river watershed. Axis 1 explained 69.74% and axis 2 explained 6.48% (Figure 3A). Groups overlays (convex hulls) showed no overlap among all four groups, with three of them separated along elevation in lower (lw-CF), mid-elevation (me-CF), and upper CF, with the latter subdivided and separated by soil acidity into low acidity (up-la-CF) and high acidity (*O-T*-CF) (Figure 3B).

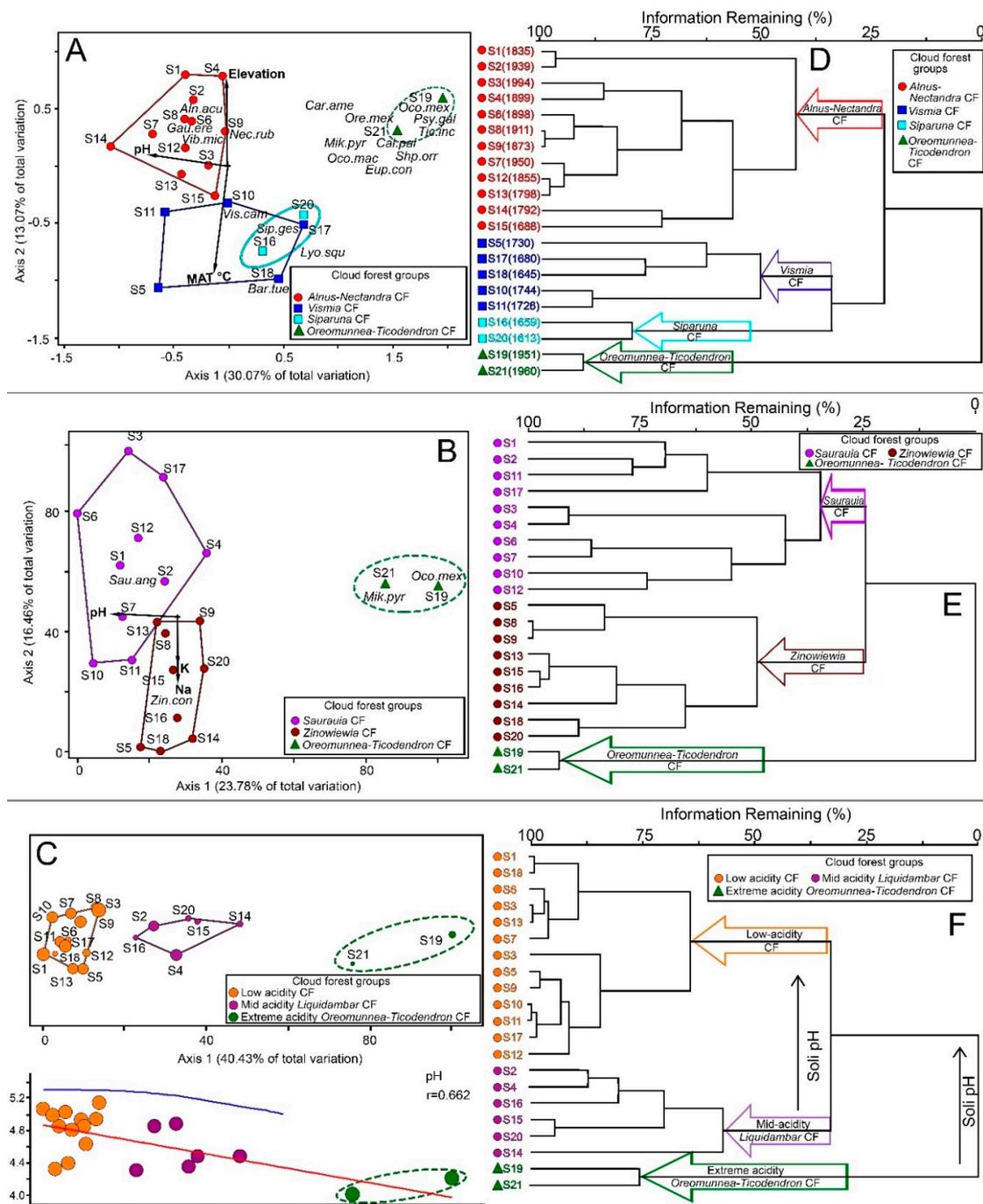
**Table 3.** Proportion of variance (NMS) for three different data matrices (P/A, density, and basal area).

Distance Matrix	Dimensions	<i>p</i>	Stress	Final Instability	Iterations	Proportion of Variance Accounted		
						Axis 1	Axis 2	Axis 3
Presence Absence	3	0.004	10.26	$<1 \times 10^{-6}$	151	0.608	0.181	0.107
Density	2	0.004	14.50	$<1 \times 10^{-6}$	375	0.672	0.123	0
Basal Area	1	0.004	11.97	$<1 \times 10^{-6}$	281	0.81	0	0

**Table 4.** Pearson (*r*) correlation of environmental variables and ordination axes of Bray and Curtis for presence-absence, density, and basal area to NMS.

Distance Matrix	Variables	Axis 1	Axis 2
Presence Absence	pH	−0.694	0.255
	Elevation	−0.012	−0.806
	MAT	−0.204	−0.805
Density	pH	0.658	−0.184
	Na	0.046	0.699
Basal Area	pH	−0.609	0

The db-RDA showed that the canonical axis 1 was explained by pH in three different datasets (P/A, density, and basal area), except for guild data, which was explained by MAT. Canonical axis 2 was explained by MAT in two datasets (P/A and basal area), by elevation for P/A data, by Na and K for density data, and by pH for guild data. Guild data accounted for a greater proportion of both cumulative explained variance from total variation (Table 5, Figure 4A–D). In summary, the db-RDA confirmed that vegetation change was best explained by pH, MAT, and elevation, and the guild dataset was the most efficient.



**Figure 2.** NMS ordinations of the vegetation for presence-absence (A), density (B), and basal area (C) data. The fitted vectors (full-line arrows in black) show the direction and strength of the linear correlations of environmental variables. Cloud forest groups, determined by Flexible clustering for presence-absence (D), density (E), and basal area (F) data, are color-coded, indicated by convex hulls or ellipses, and typified by indicator taxa or associated environmental conditions. Values in brackets are proportions of variation represented by the axes. Stress was 10.26%, 14.50%, and 11.97%, for A, B, and C, respectively.

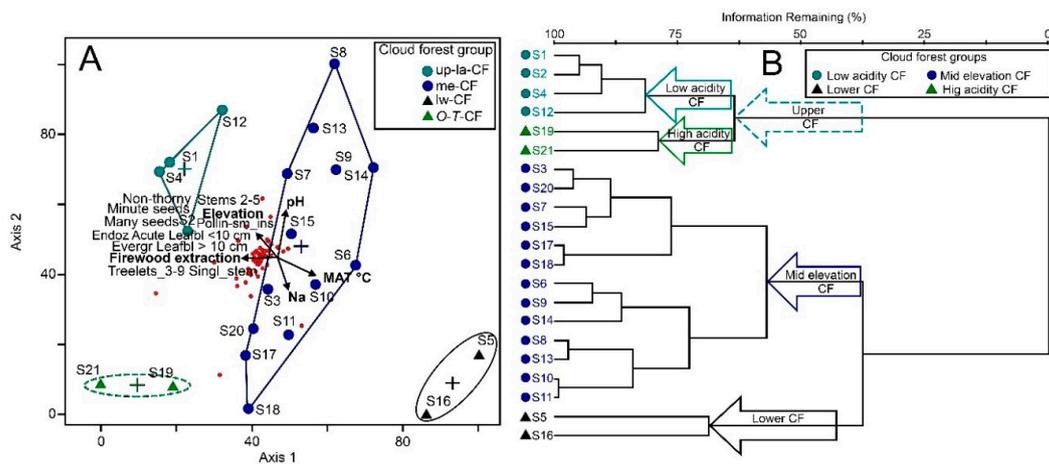


Figure 3. (A) Principal coordinate analysis (PCoA) on guild data. (B) Flexible-Beta cluster analysis.

Table 5. Explained variation (db-RDA) for presence-absence, density, basal area, and guilds data for ecological guild data.

Distance Matrix	Cumulative Explained Variance (%)	Explained from Total Variation (%)	Strongest Inter-Set with Correlations (r)	
			Canonical Axis 1 Predictor/r/Biplot Scores	Canonical Axis 2 Predictor/r/Biplot Scores
Presence-Absence	32.9	15.5	pH (0.845), 0.1820	Elevation (0.818), 0.1705 MAT (−0.886), −0.2000
Density	28.5	14.6	pH (−0.613), −0.0499	Na (−0.788), −0.0542 K (0.554), −0.0501
Basal Area	30.1	24.6	pH (−0.709), 0.2562	MAT (0.516), 0.1637
Guilds	36.6	28.6	MAT (0.525), 0.0586	pH (0.680), 0.0983

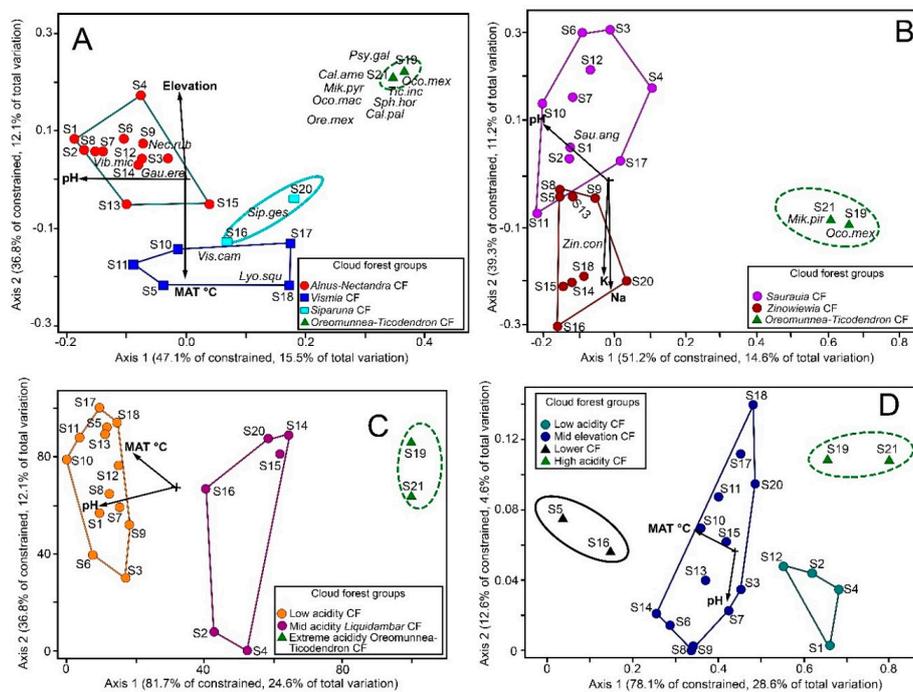


Figure 4. Constrained ordination triplots (db-RDA) relating the plant species presence-absence (A), density (B), and basal area (C) or (PCoA) guilds data (D) to the selected environmental variables (full-line arrows). Species names represent positions of the significant ( $p < 0.05$ ) indicator species with indicator values (IV)  $\text{IndVal} \geq 43.07\%$  and  $28.58\%$ . The first three letters are for the generic name and the last three letters are for the specific epithet. The cloud forest groups are indicated by convex hulls or ellipses.

3.2. Classification

ISA, applied to every hierarchical step of the flexible-clustering, determined where to prune each dendrogram, suggesting four groups for P/A data (Table 6, Figure 2D), 3 groups for density data (Table 6, Figure 2E), four groups for the basal area (Table 6, Figure 2F), and 4 groups for guild data (Table 6 and Figure 3B). P/A and density data were the only ones that resulted in having species with significant indicator values, while for basal area and guild data, the analysis failed to highlight species with significant indicator values (Tables 6 and 7). The *Oreomunnea-Ticodendron*-CF had an outstanding number of species with significant IV's. The MRPP showed homogeneity within groups for P/A, density, basal area, and guild data (Table 6).

**Table 6.** Summary for Indicator Species Analysis (ISA) and Multi-Response Permutation Procedures (MRPP).

Distance Matrix	Spp. or Guild # with Significant IV	Lowest Average p-Value	Suggested Group Number	Cloud Forest Group Names	MRPP T/p/A
Presence-Absence	16	0.4307	4	(1) <i>Alnus-Nectandra</i> (A-N-CF), (2) <i>Vismia</i> (V-CF), (3) <i>Siparuna</i> (Si-CF), (4) <i>Oreomunnea-Ticodendron</i> (OT-CF)	-8.14/7.4 × 10 <sup>-7</sup> /0.21
Density	4	0.2258	4, three interpretable	(1) <i>Saurauia</i> (Sa-CF), (2) <i>Zinowiewia</i> (Z-CF), (3) <i>Oreomunnea-Ticodendron</i> (OT-CF).	-9.87/2.01 × 10 <sup>-6</sup> /0.18
Basal Area	0	0.1822	5, three interpretable	(1) Low acidity (la-CF), (2) Mid acidity (ma-CF), and (3) extreme acidity (O-T-CF)	-10.25/3 × 10 <sup>-8</sup> /0.34.
Guilds	0	0.0325	5, four interpretable	(1) Upper, low acidity (up-la-CF), (2) Upper, high acidity (O-T-CF), (3) Mid elevation (me-CF), and (4) Low (lw-CF)	-8.12/6.8 × 10 <sup>-7</sup> /0.34

**Table 7.** Indicator species of the groups determined for the presence-absence and density data.

Distance Matrix	Species	Group	(IV)	p-Value
Presence-Absence	<i>Viburnum microcarpum</i>	1	0.683	0.001
	<i>Alnus acuminata</i>	1	0.775	0.002
	<i>Gaultheria erecta</i>	1	0.615	0.002
	<i>Nectandra rubriflora</i>	1	0.556	0.033
	<i>Vismia camparaguey</i>	2	0.798	0.001
	<i>Lyonia squamulosa</i>	2	0.577	0.061
	<i>Siparuna gesnerioides</i>	3	1	0.008
	<i>Ocotea mexicana var. diminuta</i>	4	1	0.009
	<i>Psychotria galeottiana</i>	4	1	0.009
	<i>Ticodendronincognitum</i>	4	1	0.009
	<i>Oreomunnea mexicana</i>	4	0.905	0.03
	<i>Calyptanthes pallens</i>	4	0.905	0.033
	<i>Sphaeropteris horrida</i>	4	0.905	0.033
	<i>Cartrema americana</i>	4	0.825	0.048
	<i>Eupatorium constipatiflorum</i>	4	0.825	0.055
	Density	<i>Mikania pyramidata</i>	4	0.825
<i>Saurauia angustifolia</i>		1	50	0.042
<i>Zinowiewia concinna</i>		2	44.4	0.049
<i>Ocotea mexicana var. diminuta</i>		3	100	0.008
<i>Mikania pyramidata</i>		3	75	0.033

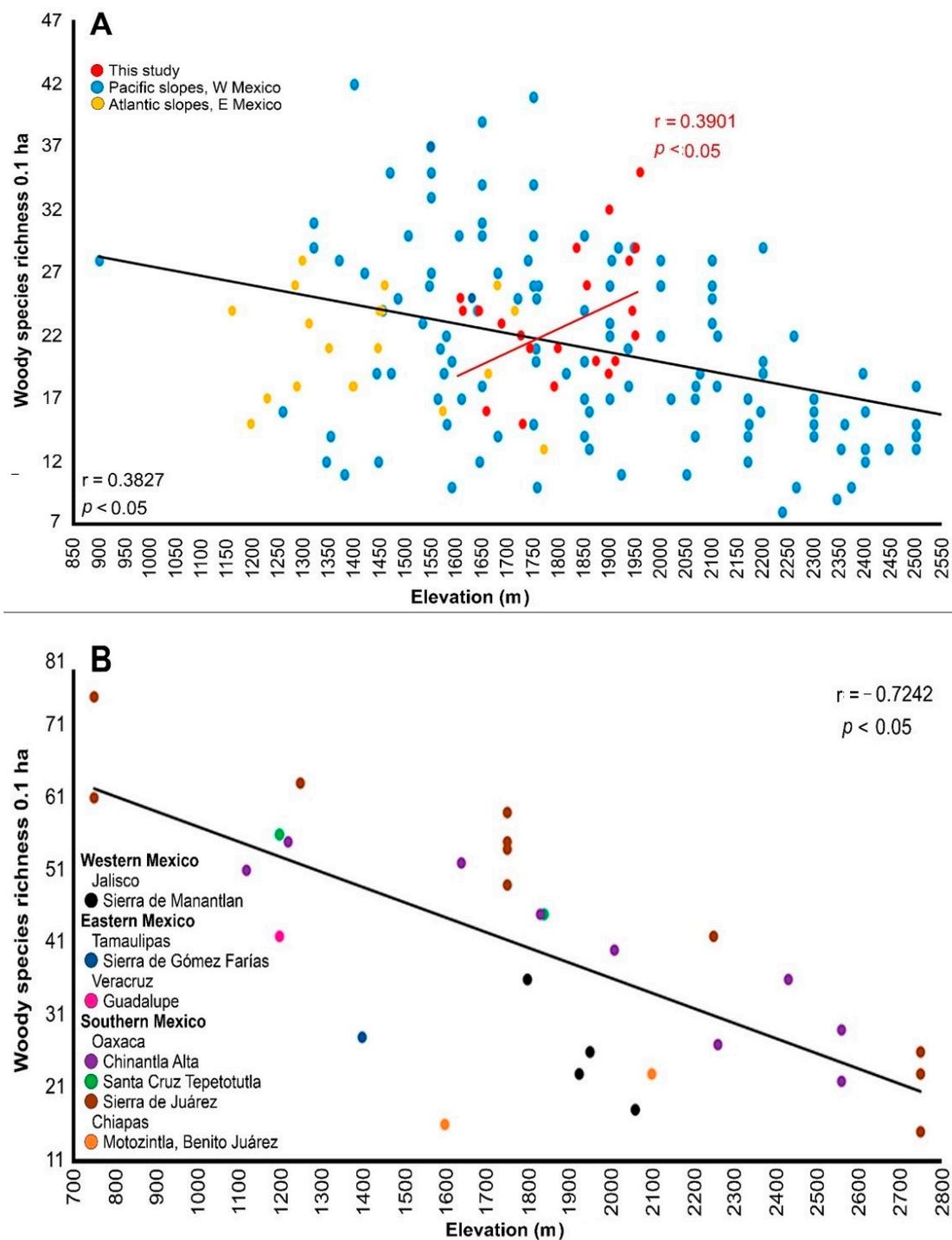
IV (Indicator values).

### 3.3. Diversity

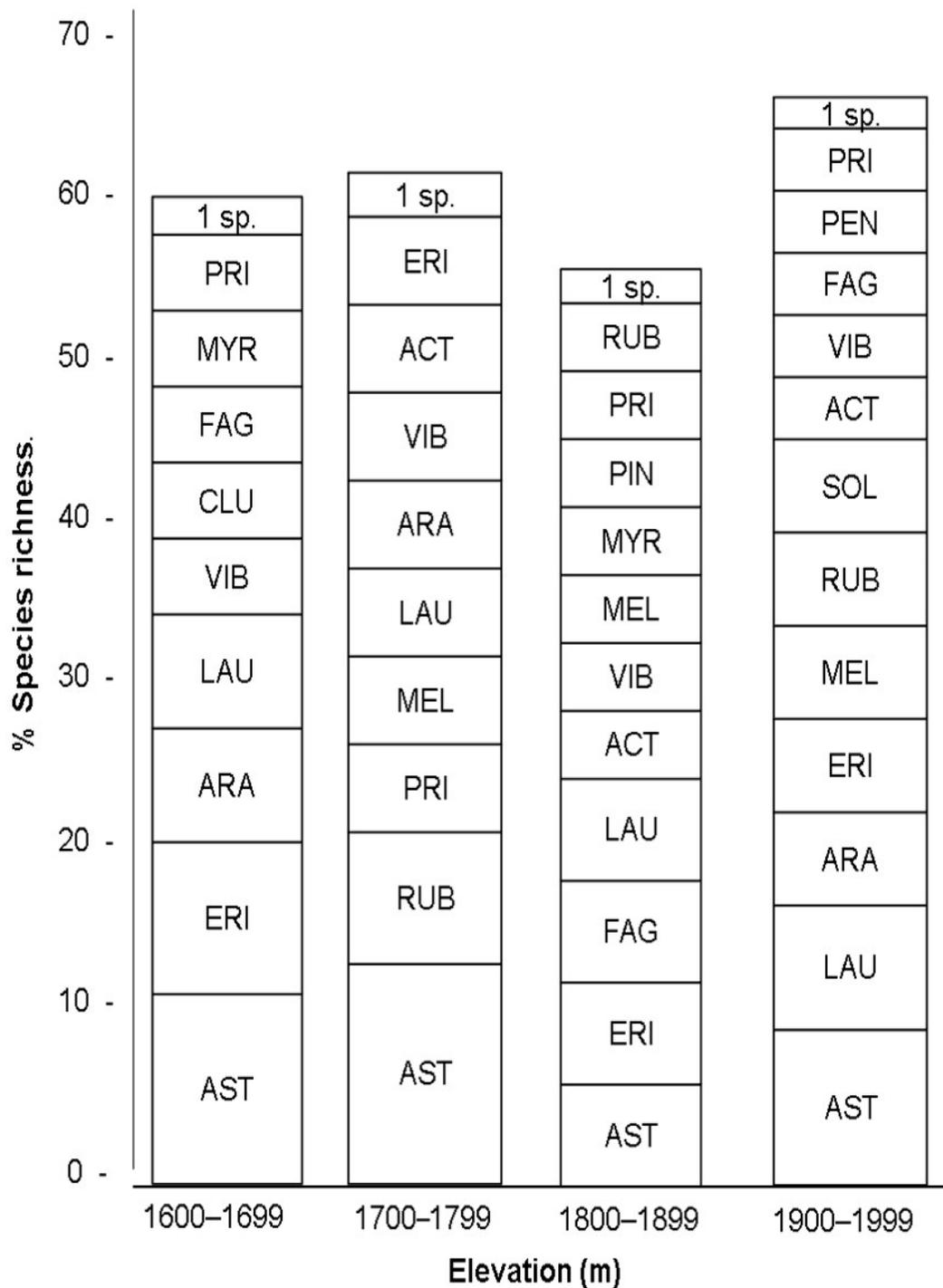
Species richness increased with increasing elevation ( $r = 0.39$ , degrees of freedom (d.f.) GL 19,  $p < 0.05$ ) (Figure 5A), inversely to the expected pattern observed for 167 Mexican CF sites ( $r = -0.38$ , GL 165,  $p < 0.005$ ) (Figure 5A), with the same sampling scheme. The elevation gradient of CF sites in Mexico with transect sampling of 0.1 ha with the Gentry method was 750 to 2750 m a.s.l., and the richness gradient was 15 to 75 species per 0.1 ha (average of 40 species). Transect richness, in general, for 30 Mexican CF sites tended to decrease with increasing elevation ( $r = -0.7242$ , d.f.L 28;  $p < 0.005$ ) (Figure 5B). Species turnover or gradient length for ecological guild data for the first axis, as determined by DCA, had an eigenvalue of 0.01, and the shortest gradient length of 0.39 of standard deviation SD, representing a low beta diversity. For the P/A data, the eigenvalue of axis 1 was 0.3 and a gradient length of 2.2 SD, using importance value data the eigenvalue of axis 1 was 0.5, and the gradient length was 2.8 SD, using density data the eigenvalue of axis 1 was 0.6, and the gradient length was 2.9 SD, and using basal area data the eigenvalue of axis 1 was 0.7, and had the largest gradient length was 3.9 SD, representing a high beta diversity or high species turnover with almost no species in common between the endpoints of axis 1. Total species diversity of the woody vascular flora (>2.5 cm in dbh) in the 21 sites (2.1 ha) was represented by 77 species (including one morphospecies), corresponding to 61 genera and 41 families. Three species occurred along the entire elevational gradient and had high importance values: *Pinus chiapensis* (Martínez) Andresen, *Magnolia dealbata*, and *Hedyosmum mexicanum* C. Cordem. The most frequent species (>80%) were *Hedyosmum mexicanum*, *Palicourea padifolia* (Humb. & Bonpl. ex Schult.) C.M. Taylor & Lorence, *Phyllonoma laticuspis* (Turcz.) Engl., *Clethra mexicana* DC., *Magnolia dealbata*, *Miconia glaberrima* (Schltdl.) Naudin, *Pinus chiapensis*, *Liquidambar styraciflua* L., *Vaccinium leucanthum* Schltdl., *Viburnum acutifolium* Benth., and *Myrsine juergensenii* (Mez) Ricketson & Pipoly. Asteraceae was the most species-rich family in most elevation ranges, except at 1800–1899 m a.s.l., where it was matched by Lauraceae, Ericaceae, and Fagaceae. Families showed greater equitability at this elevational range. Ericaceae unexpectedly increased toward lower elevations and Lauraceae increased toward higher elevations (1900–1999 m a.s.l.) (Figure 6). The family richness in terms of species/genera were Asteraceae (9/6), Ericaceae and Rubiaceae (4/4), Lauraceae and Pentaphylacaceae (4/3).

### 3.4. Structure

Total density was 6223 woody individuals ( $\geq 2.5$  cm dbh) in the 21 sites, representing an average of 141 trees/0.1 ha. Species with large densities (trees/0.1 ha) were *Hedyosmum mexicanum* (482), *Phyllonoma laticuspis* (389), *Magnolia dealbata* (249), *Clethra mexicana* (177), *Liquidambar styraciflua* (162), *Palicourea padifolia* (156), *Pinus chiapensis* (144), *Miconia glaberrima* (131), and *Vaccinium leucanthum* (105). The rest of the species had <100 trees/0.1 ha. The total basal area was 86.73 in the 21 sites, averaging 4.13 m<sup>2</sup>/0.1 ha, ranging from 1.7 to 6.5 m<sup>2</sup>/0.1 ha (sites 18 and 14, respectively). Site 18, the one with the maximum basal area, was densely populated by *P. chiapensis*, with this species occupying 5.04 m<sup>2</sup>/0.1 ha, followed by *L. styraciflua* with 0.43 m<sup>2</sup>/0.1 ha. Site 14, the one with the minimum basal area, had *H. mexicanum* as the dominant tree, occupying 0.58 m<sup>2</sup>/0.1 ha of the total basal area for the site. Dominant species, in terms of the basal area along the entire gradient (m<sup>2</sup>/2.1 ha), included *P. chiapensis* (53%), and *L. styraciflua* (7%), *H. mexicanum* (7%), and *Magnolia dealbata* (6%). The rest of the species had <5% dominance. A-O-CF averaged 4.1 m<sup>2</sup>/0.1 ha, ranging from 1.7 to 6.2 m<sup>2</sup>/0.1 ha (sites 14 and 1, respectively). V-CF averaged 4.4 m<sup>2</sup>/0.1 ha, ranging from 3.7 to 6.5 m<sup>2</sup>/0.1 ha (sites 10 and 18, respectively). O-T-CF average was 4.4 m<sup>2</sup>/0.1 ha, ranging from 3.8 to 5.01 m<sup>2</sup>/0.1 ha (sites 19 and 21, respectively). S-CF average was 3.4 m<sup>2</sup>/0.1 ha ranging from 2.8 to 4.0 m<sup>2</sup>/0.1 ha (sites 20 and 16, respectively). The highest importance value index at the entire gradient (2.1 ha) was maximum for *P. chiapensis* (36%), followed by *H. mexicanum* (25%), *Liquidambar styraciflua* (24%), *Magnolia dealbata* and *P. laticuspis* (tied at 16%), *P. padifolia* (14%), and *C. mexicana* (12%).



**Figure 5.** Alpha diversity in relation to elevation in 0.1 ha Mexican cloud forests (CF) sites. The central trend line in is black. (A) 167 Mexican CF sites, using circular quadrats, with a fixed sampling universe [56]. Pacific slopes (dots in light blue), Atlantic slopes (dots in yellow), this study (dots in yellow) and central trend line in red). (B) Thirty Mexican CF sites, using transects: with undefined sample universe (19 sites) [1] and within a defined sampling universe (11 sites, brown circles) [17].



**Figure 6.** Percentage of woody species in the most diverse plant families (with more than two species) at each elevation in the cloud forest of San Juan Juquila Vijanos, Oaxaca. Family names consist of their initial three letters: ACT, Actinadiaceae; ARA, Araliaceae; AST, Asteraceae; CLU, Clusiaceae; ERI, Ericaceae; FAG, Fagaceae; LAU, Lauraceae; MEL, Melastomataceae; MYR, Myricaceae; PEN, Pentaphylacaceae; PIN, Pinaceae; PRI, Primulaceae; RUB, Rubiaceae; SOL, Solanaceae; VIB, Viburnaceae.

### 3.5. Endemism and Conservation

All 76 species are new world endemics: 70 species were Neotropical endemics, 59 spp. were Mesoamerican endemics, including *Oreomunnea mexicana* (Standl.) J.-F. Leroy and *Ticodendron incognitum* Gómez-Laur. & L.D. Gómez. Twenty-five spp. were northern Mesoamerican endemics,

including *Pinus chiapensis*. Twenty-five spp. were central and southern Mexican endemics, including *Pinus patula* and *Quercus trinitatis* Trel. Five spp. were southeastern Mexican endemics, including *Cleyera cernua* and *Ternstroemia oocarpa* (Rose) Melch., and only one species was an Oaxacan endemic, *Magnolia dealbata*. Only four spp. occurred in North, Central, and South America, and only one species, *Liquidambar styraciflua*, occurred in both North and Central America. The IUCN Red List includes one third (31 spp.) of the 77 species found in the Juquila, Oaxaca gradient: Vulnerable 5% (4 spp.), including *Arachnothryx buddleioides* (Benth.) Planch., *Cornus disciflora* Moc. & Sessé ex DC., *Hedyosmum mexicanum*, and *Saurauia angustifolia* Turcz, Near Threatened 4% (3 spp.), including *Magnolia dealbata*, *Quercus skinneri* Benth., and *Ticodendron incognitum*, Endangered 3% (2 spp.), including *Dendropanax populifolius* (Marchal) A.C. Sm. and *Zinowiewia concinna* Lundell, and under Least Concern 29% (22 spp.). In contrast, the Red List of Mexican cloud forest trees includes over two thirds (52 spp.) listed for the Juquila gradient. Critically Endangered 4% (3 spp.): *Dendropanax populifolius*, *Cleyera cernua* (Tul.) Kobuski, and *Quercus skinneri*, Endangered 12% (9 spp.): *Magnolia dealbata*, *Cleyera velutina* B. M. Barthol., *Viburnum acutifolium*, *Vaccinium leucanthum*, *Zinowiewia concinna*, *Clusia guatemalensis* Hemsl., *Symplocos pycnantha* Hemsl., and *Quercus trinitatis*, Vulnerable 16% (12 spp.), including, among others: *Pinus chiapensis*, *Ternstroemia oocarpa*, and *Quercus sapotifolia* Liebm., Near Threatened 12% (9 spp.), including, among others: *Ticodendron incognitum*, *Weinmannia pinnata* L., and *Saurauia scabrida* Hemsl., and under Least Concern 25% (19 spp.). (Supplementary Table S3).

## 4. Discussion

### 4.1. Environmental Community Drivers

Community composition and structure of CF with *Magnolia dealbata* in the Sierra Norte de Oaxaca may be explained by habitat specialization to soil gradients and altitude. On short elevational gradients, edaphic variables are often more relevant than climatic variables in explaining the strongest community gradients [51,103]. For instance, moisture and topography can change within small scales, impacting species composition, while soil nutrients across topography gradients may result in fertility gradients affecting species dominance. Spatial environmental variation in temperature, light, soil pH, moisture, nitrogen, and altitude at any scale may drive to the occurrence of habitat-specialized plant species [104,105], which leads to changes in species composition even on small scales.

Soil acidity (pH) along the short (352 m) elevational gradient was more relevant than any other measured climatic variables in explaining the variance in each of the three strongest community gradients recovered by NMS (compositional, structural, and dominance). In contrast to other studies in *Fagus*-CF, out of all the analyzed microenvironmental factors, pH was the only one not correlated with community variation [106]. Studies in the study area report soils with a pH below 5, so they are considered acidic and easily leached [77,78]. Despite the fact that conifers tend to increase the acidity of the soil [77,107–109] and that conifer needles provide lower amounts of Ca, K, and Mg than deciduous species [110], the dominance of *Pinus chiapensis* was inversely correlated to the acidity gradient. The acidity gradient was instead correlated with precipitation of the driest month ( $r = 0.59$ ,  $p < 0.01$ ) and inversely correlated with N ( $r = -0.48$ ,  $p < 0.05$ ). It is well known that acidity is also attributed to soil leaching [56,111], which is enhanced under high rainfall and steep slopes, like those reported for our sites, generating a higher concentration of aluminum and displacement of cations [78,112]. A significant number of species that prefer acidic soils grow in high-altitude areas because soil pH is negatively correlated with elevation (higher tendency to acidification at higher altitudes), since at higher altitude, the decomposition of organic matter is slower, and the acidification process is more intense due to higher precipitation [113].

However, elevation was not correlated with the strongest gradient (axis 1) on any of the three ordinations. Soil acidity is common in CF [114]; in Mexico, it has been recorded in both the Atlantic slopes of Veracruz and Oaxaca [58,78,115], and the Pacific slopes of Guerrero and Jalisco [116,117] from

early to the late-successional stage and under different conservation and extraction regimes, as shown for Juquila Vijanos in the Sierra Norte de Oaxaca [78,79,110].

However, this is the first time that an acidity gradient explains the strongest CF gradients along a short elevational range. The outstanding discontinuity along the acidity gradient (axis 1), separating two major groups of CF does not support the Continuum hypothesis [118]. The great majority of CF stands (19 sites) occur in acidic soils (pH 4.3–5.15), while the other group includes only two sites occurring in strongly acidic soils (pH 4.4–4.0); site 19 (1951 m a.s.l.), mono-dominated by *Oreomunnea mexicana* (relative dominance, 18%), and the site 21 (1960 m a.s.l.), co-dominated by *Persea liebmannii* Mez (14%), *Ticodendrum incognitum* and *Dendropanax populifolius* (11% each), and *Oreomunnea mexicana* (10%). However, the acidity level is not as extreme as shown in other *Oreomunnea* populations in Oaxaca, with pH values from 3.7 to 3.5 [119]. Monodominance of *Oreomunnea mexicana* has also been registered from La Esperanza (1600 and 1800 m a.s.l.), Santiago Comaltepec, Oaxaca [14], other nearby areas in the same region [120], and in Santa Cruz Tepetotutla, south of San Felipe de Usila, Oaxaca at 1840 m a.s.l. [121]. It has also been inferred from density data, in one single site east of Cofre de Perote, Veracruz [58]. Codominance of this species has been reported in La Esperanza, in coexistence with different taxa (mostly *Quercus* spp.), between 1800 and 2050 m a.s.l. [14]. Meave et al. [121] recorded for the first time a forest dominated by *O. mexicana* and *T. incognitum* in Santa Cruz Tepetotutla at 1840 m a.s.l. After twenty-one years, the present study is the second record for the Sierra Norte of Oaxaca, where the two biogeographic relicts, *O. mexicana* and *T. incognitum*, are reported as codominant in a 0.1 ha site, among the other few dominant tree species. *Ticodendron incognitum* has been found at high densities (39 trees/0.1 ha) in La Esperanza, Oaxaca (1750 m), Mexico [17], while in Santa Cruz Tepetotutla, the highest density (10 trees/0.1 ha) was recorded at 1840 m in elevation [121]. In San Miguel Tiltepec (418 trees/0.1 ha), it was recorded at 1640 m [15], and in lower densities at the Barva volcano, Costa Rica (14–27 trees/ha), at 1750–2000 m [54].

Elevation was of secondary importance in shaping vegetation structure, and composition also changes with altitude. Environmental variables such as temperature, precipitation, potential evapotranspiration, and radiation can play a vital role in determining the distribution of species along the altitudinal gradient [65,122–124]. One of the first patterns observed in nature was the change of species richness in an altitudinal gradient, which was widely accepted to decrease as elevation increased [70,125]. In elevation gradients, depending on the type of vegetation, species richness may be associated with different climatic variables [65]. The fact that elevation explained a secondary gradient and not the first may have to do with the range of the elevation of the gradient. The longer the gradient elevation, the more expected to be the overriding variable, suggesting that for each elevational mountain gradient, there must be a gradient range threshold below which edaphic or topographic variables become more important than elevation to explain community structure [51].

#### 4.2. Cloud Forest Types and Relationships

In general, the CF studied in the present work correspond environmentally to the warm-temperate lower-montane moist forests [126]. The high woody species turnover and heterogeneity found in Juquila Vijanos has been documented frequently for CF transects in different biogeographic provinces with contrasting floristic composition, for instance, the three cloud forest communities reported from the calcareous Cerro Grande Manantlán Massif in the Sierra de Manantlán [69]: evergreen CF (2400–2500 m), mesophyll CF (2100–2300 m), and *Myrcianthes* CF (1900–2000 m). Other authors have identified only two types of CF along elevation, for instance, Williams-Linera et al. [58] distinguished lower (1250–1630 m) and upper montane forests (1483–2550 m), Rodríguez-González [61] found upper montane CF (1600–2200 m) and lower montane CF (1300–1600 m), Cruz-Peña [68], for the southern windward slopes of Nevado de Colima Volcano, describes upper montane CF (1935–2656 m) and lower montane CF (1290–1860 m), and Guerrero et al. [52] described lower montane CF (1500–2020 m) and upper montane CF (1920–2450 m). Cloud forests thriving at very high elevations such as those found in Nevado de Colima, Cofre de Perote, Cerro Grande Massif, and Cerro La Bufa, may be explained by

the Massenerhebung effect [127]. We found no records of CF inhabiting soils with low pH values such as those observed in *O-T-CF* in Juquila Vijanos, Oaxaca. Concerning ISA, indicator species for *O-T-CF* are associated with low acidity, while indicator species for *A-O-CF* are associated with high elevation. The absence of indicator species in *V-CF* suggests that their species have a wide distribution range and could be shared with other neighboring CF.

### 4.3. Diversity

#### 4.3.1. Alpha Diversity

The effect of elevation on species richness is not universal but rather scale- and context-dependent. Some studies report that species richness depends on the life form considered [56,128]. Four major patterns of species diversity along elevation are described among different organisms [70]: (1) Midpeak is the most common pattern in plants [34,37,101,102], (2) decreasing richness with increasing elevation is the most common for woody plants in tropical montane forest [1,23,28–30,32,34,43,57,110,111], and less common patterns are: (3) low plateau and (4) low plateau with a mid-peak [70]. Our study, showing increasing richness with increasing elevation in CF transects, does not conform to any of the major trends, however, to some extent, our result is related to studies showing the increasing pattern from the lowlands to some mid-elevation peak [129–132]. Thus, the observed increasing pattern for CF could be considered a sampling artifact. Sampling truncation at the upper portion of an assumed unimodal CF species richness pattern could result in a short gradient displaying a positive relationship. Alternatively, it could be explained in part by a combination of (a) habitat specialization to edaphic conditions along a gradient of high soil heterogeneity, where forests develop on soils ranging from low to high acidity, as evidenced in this study (see below), (b) a higher rainfall and fog from eastern trade winds out of the Gulf of México toward higher elevations, which is expected to influence species richness [1,70], (c) biogeographic refugia, including paleoendemic relics, which may also contribute to the high diversity. For instance, among the sites with to the richest and highest elevation group: the *O-T-CF*, which are considered Oligocene-Miocene relics [14], and (d) better conservation status on steep slopes that are farther away from towns, e.g., disturbance or successional gradients [77,78,82], which in turn may be correlated to altitude [70]. The resulting diversity values for the Juquila Vijanos gradient increased two-fold (15–35) along the elevational gradient, and every value fell within the expected species richness ranges for Mexican CF: 8–42 spp. ha<sup>-1</sup> using circular quadrats (Figure 5A) and 15–75 spp. ha<sup>-1</sup> using transects (Figure 5B). Only two sites (19 and 21) showed unusually high values (32 and 35 spp., respectively) for their elevational zone, being greater than that reported for Neotropical CF [1,17,27]. These two sites correspond to the richest and highest elevation group, the *O-T-CF*.

#### 4.3.2. Family Shifts Along Elevation

The top five species-richest families at the Juquila, Oaxaca gradient, were Asteraceae, Ericaceae, Fagaceae, Lauraceae, and Rubiaceae. The latter two are also among the top five families at similar elevation range in the Andes, in Antioquia, Colombia, however, in the latter, Melastomataceae is also among the top families [133]. The family Asteraceae dominated at most elevations in congruence with studies in western México: the karstic Cerro Grande massif, Sierra de Manantlán [56], the volcanic and plutonic Sierra de Cacoma, Talpa de Allende, Jalisco, from 1600 to 2200 m a.s.l., with its greatest contribution being from 1750–2000 m a.s.l. [61]. Geographic isolation and optimal growth conditions led to the evolution of a particularly large number of Asteraceae in the montane regions of Guatemala and Mexico [134]. High species richness of Asteraceae along most of the Juquila gradient could be attributed to the high dispersal efficiency of the family through their anemochorous and ectozoochorous mechanisms, but also to their antiherbivore defenses through the production of secondary metabolites [135]. However, this family showed the lowest values at the middle portion of the CF gradient (1800–1899 m a.s.l.), this may be explained by the fact that Asteraceae do better

in dryer habitats and this elevation range is associated to the highest moisture regime observed between 1835 and 1944 m a.s.l., possibly corresponding to a unimodal distribution of precipitation and or an area of high condensation of moisture from trade winds [136] out of the Gulf of Mexico, as evidenced by the 102% gain from fog through water collectors during the dry season, peaking at 1898 m a.s.l. in Altotonga, Veracruz, also in the windward side of the Gulf of México, in the neighboring Sierra Madre Oriental [137]. Other CF with low diversity of Asteraceae include the mesic CF in the Cerro Grande Sierra de Manantlán, in western Mexico, where Orchidaceae and Aspleniaceae out-number the Asteraceae only from 2300 to 2400 m a.s.l. [56]. The observed decrease of Asteraceae at 1800–1900 m a.s.l. in the Juquila gradient could be explained by high moisture. For instance, along an elevational gradient in Cerro Grande, Manantlán [56], Asteraceae shows its lowest richness value at 2300 m a.s.l. in moist CF with higher fog incidence, where umbrophilic ferns (Aspleniaceae), orchids, and Lamiaceae outcompete heliophytes like Asteraceae due to greater efficiency in using understory diffuse light [56,138]. In the same Manantlán gradient, at 2400 m, again, orchids out-number Asteraceae as the leading family. Similarly, but in a contrasting ecosystem, wet grasslands in Uganda have less diversity of Asteraceae than dry grasslands [139]. Higher moisture or rainfall could also make pappus and bristles wet, interfering with wind-dispersed species, except for those with ectozoochory.

#### 4.3.3. $\beta$ -Diversity

Gradient length estimates, except for guild data (0.39), match the expected outcome, ranging from 1.36 to 11.98 for field studies [71,72], and the length observed on structural vs. P/A data tends to be higher, representing their high structural heterogeneity, complexity, and turnover. Comparison of distance estimates between datasets should, however, be restricted to situations with the same abundance scale, range of the abundance scale, and species deletion level [71].

#### 4.3.4. $\gamma$ -Diversity

Gamma diversity values are not directly comparable among CF studies, due to different sampling schemes, elevational range, and area size covered, among many other factors. For instance, a 1300 m elevational CF gradient in Cofre de Perote, eastern Mexico, had 128 tree species  $\geq 5$  cm dbh [58], while for Juquila Vijanos, after excluding species with dbh  $< 5$  cm and  $\geq 2.5$  cm, we reported 64 woody species  $\geq 5$  cm dbh. Thus, gamma species richness of the Juquila gradient is half of that of the more northern Cofre de Perote (Veracruz), however, the altitudinal range of the Juquila gradient is only 26% of that of Cofre de Perote. This suggests that the gamma diversity in the southern Juquila gradient is proportionally greater than that in the Cofre de Perote gradient, in agreement with the globally known pattern of increasing species richness with the decrease in latitude [140].

#### 4.3.5. Floristic Affinities

Floristic affinities of these CF, in terms of species composition, are similar to that of other CF in the Sierra Madre de Oaxaca and the Chimalapas, including La Chinantla, Sierra Mazateca, and Cerro Salomón, Chimalapas [6]. It is worth noting that the generic composition of the Juquila gradient is highly similar (ca. 50%) to that of the Miocene flora of northern Chiapas [64]. This Sierra de Juárez gradient also has affinities to the Cretaceous formations: Tarahumara (Sonora) and Cerro del Pueblo (Coahuila), which include *Alnus*, Betulaceae; *Hedyosmum*, Chloranthaceae; *Quercus*, Fagaceae; Juglandaceae (possibly), *Magnolia*, Magnoliaceae; Myrtaceae; *Pinus*, Pinaceae [141], while floristic affinities with Early Eocene floras of the formations La Carroza, La Trinidad (Chiapas), and Jackson (Tamaulipas) include *Alnus*; *Ilex*, Aquifoliaceae; *Liquidambar*, Altingiaceae; *Oreomunnea*, Juglandaceae; Myrica, Myricaceae; *Eugenia*, Myrtaceae, and the families Asteraceae, Caryophyllaceae, Fabaceae, and Poaceae [139]. The presence of additional boreal elements such as *Pinus*, *Quercus*, and *Ilex* represent the effect of decreasing temperatures before the Pleistocene, which allowed colonization to southern latitudes, as evidenced in Veracruz (Paraje Solo) of Mid-Pliocene [141,142].

#### 4.4. Endemism and Conservation

Temperate semi-humid zones have higher endemism at the species level than warm humid zones [143]. The high endemism of these CF is explained by various factors: (a) the long permanence of the topographic relief of the Sierra de Juárez since the Miocene ca. 16 Ma, (b) the constant volcanic activity in eastern Oaxaca during the Miocene [144] contributed to the modification of environments, climates, and niches, as well as the formation of geographical barriers, inducing vicariance and allopatric speciation, (c) the effective ecological isolation of these CF archipelagos [8] that have resulted from the decrease of the space matrix with the increase in elevation, and (d) the high physiographic, geological, and edaphic heterogeneity [143]. However, some taxa managed to overcome barriers, and some constitute major disjunctions: Eastern Mexican and eastern North American disjunction, separated by northern Mexico and the southern Texas gap [145], Transisthmian disjunctions, separated by the Tehuantepec Isthmus, and northern vs. southern Mesoamerican disjunctions, separated by the Nicaraguan depression [146].

The proportion of Critically Endangered species in Juquila, Oaxaca (4%), were similar to that reported for the ecological reserve El Cielo, in Tamaulipas (4%) [67], and in Cofre de Perote National Park, Veracruz (3%) [58] and Sierra de Cacoma, Jalisco (3%) [57,61]. Endangered species in Juquila, Oaxaca (9%), represented a lower fraction than in Cofre de Perote, Veracruz (16%) and El Cielo, Tamaulipas (11%), and it was similar to Sierra de Cacoma, Jalisco (8%). Near Threatened species had a higher proportion in Juquila, Oaxaca (12%), than in Sierra de Cacoma, Jalisco (1%), Cofre de Perote, Veracruz (9%), and El Cielo, Tamaulipas (7%). The proportion of Vulnerable species in Juquila, Oaxaca (18%), was lower than in Cofre de Perote, Veracruz (21%), and higher than in El Cielo, Tamaulipas (11%) and Sierra de Cacoma, Jalisco (9%). In Juquila Vijanos, the high proportion of species under a risk category (31%) [20] suggests that this area may have been functioning as a biodiversity refuge [14,64]. This result confirms that the Sierra Madre de Oaxaca is one of the major biodiversity hotspots in Mexico [147] and the area with the largest number of threatened taxa reported for the Sierra Norte of Oaxaca (Ixtlán, Villa Alta y Mixe districts) [148]. However, the conservation status of many tree species is poorly documented, and many species are yet to be included in the Red List of Mexican cloud forest trees [20].

A considerable number of floristic elements along this gradient indicate disturbance, for instance, the dominant shade-intolerant woody Asteraceae and several other gap-phase regeneration species such as *Hedyosmum mexicanum*, *Phyllonoma laticuspis*, *Magnolia dealbata*, *Clethra mexicana*, *Liquidambar styraciflua*, *Palicourea padifolia*, *Pinus chiapensis*, *Miconia glaberrima*, and *Vaccinium leucanthum*. This disturbance aspect is acknowledged as a limitation in this research.

## 5. Conclusions

Major small-scale CF community variation was explained by soil pH, while elevation, K, Na, and firewood extraction were environmental variables of secondary importance. This supports the habitat specialization hypothesis as the major driver of small-scale community organization of CF stands harboring *M. dealbata* in Juquila, Oaxaca.

The high discontinuity separating the *Oreomunnea-Ticodendron* forest stands do not support the Continuum hypothesis. This relic *Oreomunnea-Ticodendron*-CF resulted isolated at the high acidity end of the gradient, and there, species richness reached its maximum, where *Magnolia dealbata* had its lowest density and basal area. In contrast, *Magnolia dealbata* presented the highest density values in the *Vismia*-CF and the highest basal area in the *Alnus-Ocotea*-CF and *Siparuna*-CF.

The increasing species richness with increasing elevation does not support the Decreasing hypothesis, but this may be due to a sampling artifact, sampling truncation at the top of an assumed unimodal (mid peak) pattern, or may be explained in part by a combination of habitat specialization, contributions from biogeographic refuges, and from sites with good conservation status. The high species richness observed was associated with the sea windward dry-seasonal maximum cloud condensation gain and habitat differentiation-specialization. We hypothesize that a combination of these

factors may also explain the hypothesis of mid-peak species richness and may have allowed long-term survival of relict species such as *Oreomunnea Mexicana* and *Ticodendron incognitum*. Future studies may consider testing the unimodal (mid-peak) hypothesis for species-rich and mist-loving vascular families such as Aspleniaceae, Grammitidaceae, Orchidaceae, and Bromeliaceae, on longer altitudinal transects, a wider range of edaphic and topographic variables, using different scales, and incorporating land-use change, among additional factors.

The species-richest *Oreomunnea-Ticodendrum*-CF, considered an Oligocene-Miocene relict, must be legally protected urgently, and since it is isolated and specialized to the acidic end of the gradient, it requires specific maintenance of soil conditions. The generated or tested hypotheses about major environmental variables influencing community organization as well as the relationships among various CF groups should be used to guide conservation and sustainable development strategies for these communities harboring the bioculturally relevant *Magnolia dealbata*.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/1424-2818/12/12/444/s1>, Table S1: List presence-absence of tree species from 21 sampling sites (acidity gradient) in San Juan Juquila Vijanos, Oaxaca, México, Table S2: List presence-absence of tree species from 21 sampling sites (altitude gradient) in San Juan Juquila Vijanos, Oaxaca, México, Table S3: Ecological guilds identified at each sampling site.

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