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Patterns of vegetation along contrasting elevation gradients in Oaxaca and Veracruz, Mexico

Patrones de vegetación en gradientes altitudinales contrastantes en Oaxaca y Veracruz, México

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Abstract

Elevation gradients have been widely documented, but few studies have compared patterns of variation between contrasting transects. Our objective was to compare vegetation structure and tree species composition of forest communities on 2 extended gradients located along the Pacific coast (Oaxaca, 0-3,600 m), and the Gulf of Mexico coast (Veracruz, 70-4,000 m), Mexico. We established 21 one-ha plots on each gradient. A total of 4,229 trees were measured and identified. Results showed that with increased elevation, basal area decreased unimodally in Oaxaca, and increased monotonically in Veracruz, whereas taxa richness decreased non-linearly in both gradients. Oaxaca was warmer and drier than Veracruz, however, richness was higher in Oaxaca (260 species) than in Veracruz (210 species). A multinomial classification model identified 58 species as Oaxaca specialist and 41 as Veracruz specialists, but only 12 species were generalist in both gradients. Canonical correspondence analyses for species, genus, and family consistently separated dry forests related to temperature and potential evapotranspiration from high elevation conifer forests. Mid-elevation montane forest differed between gradients. We conclude that climate is differentially important in vegetation structure and taxa distribution, but geographical location and disturbance history should be discussed for each gradient.

Keywords: Disturbance history; Multinomial classification model; Oaxaca; Precipitation; Species richness; Temperature; Vegetation structure; Veracruz

Resumen

Los gradientes altitudinales han sido ampliamente documentados, pero pocos estudios han comparado patrones de variación entre transectos contrastantes. El objetivo fue comparar la estructura de la vegetación y diversidad de especies de árboles en 2 gradientes extensos ubicados en las costas del Pacífico (Oaxaca, 0-3,600 m) y golfo de México (Veracruz, 70-4,000 m). Se establecieron 21 parcelas de 1 ha en cada gradiente y se midieron e identificaron

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un total de 4,229 árboles. Al aumentar la elevación, el área basal disminuyó unimodalmente en Oaxaca y aumentó monotónicamente en Veracruz, mientras que la riqueza disminuyó en ambos gradientes. Oaxaca es más cálido y seco que Veracruz, sin embargo, la riqueza es mayor en Oaxaca (260 especies) que en Veracruz (210 especies). El modelo de clasificación multinomial reveló 58 especies como especialistas de Oaxaca y 41 como especialistas de Veracruz, pero solo 12 generalistas para ambos gradientes. Los análisis de correspondencia canónica separaron consistentemente selvas secas relacionadas con temperatura y evapotranspiración potencial de bosques de coníferas, pero los bosques mesófilos difieren entre gradientes. En conclusión, el clima es diferencialmente importante en la estructura vegetal y distribución de taxones, pero debe discutirse la ubicación geográfica y la historia de perturbación de los gradientes.

Palabras clave: Historia de perturbación; Modelo de clasificación multinomial; Oaxaca; Precipitación; Riqueza de especies; Temperatura; Estructura de la vegetación; Veracruz

Introduction

One of the fundamental challenges of ecology is to determine which factors influence the distribution of organisms on Earth (Sanders & Rahbek, 2012). Gradients are the most commonly utilized tool for analyzing the response of the biota to environmental change, and elevation gradients are well-studied systems, since there are diverse life zones along these gradients, with particular and diverse collections of organisms, where different types of vegetation can be observed. Due to strong climatic variation over short distances, biotic zones and vegetation types are both compressed into a small area (Liao et al., 2014).

Biodiversity along elevation gradients shows variation in patterns depending on the group under study and the geographic location of the gradient itself (Grytnes & Beaman, 2006). Among the diverse patterns of elevation variation, the unimodal pattern is the most common (Rahbek, 1995) although there are many diverse responses of the biota to environmental changes over elevation gradients. For example, in a study on Mt. Rinjani, Lombok, Indonesia, it was determined that the alpha diversity of understory, low-canopy and canopy plants decreases with increasing elevation, while that of the creeping plants shows a unimodal pattern (Dossa et al., 2013). Along a 2,700 m elevation transect in Costa Rica, the maximum diversity of woody species was found at 400-600 m elevation (Clark et al., 2015) whereas in Nepal, maximum diversity of tropical genera was found below the midpoint of the elevation gradient, and the diversity of temperate genera presented a unimodal pattern (Li & Feng, 2015).

The range of patterns of elevation variation challenges to propose a general model; the variation has been attributed to the use of different sampling methods (Nogués-Bravo et al., 2008), analysis of incomplete elevation gradients (Grytnes & Vetaas, 2002) and the effect of scale (Rahbek, 2005). To obtain a general explanation of the underlying causes of the patterns of elevation variation, it is advisable to adopt similar sampling methods, standardize both the area sampled and the monitoring of environmental data and include complete elevation gradients (Lomolino, 2001). Studies based on only part of a gradient face an important limitation and, their results can only apply to that part of the gradient (Grytnes & Vetaas, 2002). Frequently, the lowest and highest parts of mountains have been severely disturbed by human activities (Nogués-Bravo et al., 2008), such that the native vegetation has largely been altered and replaced by other land uses (Arévalo et al., 2010; Da et al., 2009; González-Abraham et al., 2015; Piperno, 2006).

Diverse studies have documented patterns of elevation variation of species richness, diversity and environmental factors (e.g., Salas-Morales & Meave, 2012; Sanders & Rahbek, 2012; Toledo-Garibaldi & Williams-Linera, 2014). Several hypotheses have been proposed to explain which factors underlie the elevation variation of organisms. The hypotheses include area, biogeographic interpretations, climate, environmental heterogeneity, geological and climatic history, geometric restrictions, productivity, and soil characteristics (Colwell & Lees, 2000; Hawkins et al., 2003; Kitayama & Aiba, 2002; Latham & Ricklefs, 1993; Li & Feng, 2015; Rowe, 2009; Sanders, 2002; Wang et al., 2009). More recently, elevation gradients are central to study plant and animal responses in the face of global climate change since some species could potentially migrate upslope, but others will go extinct under most projections of global temperature increases (Clark et al., 2015; Colwell et al., 2008; Feeley et al., 2013).

Few studies have compared patterns of change over several elevation transects. Sanders (2002) analyzed ant species richness along elevation transects in 3 states in the USA: Colorado, Nevada and Utah. Grytnes (2003) compared 7 transects in Norway in order to determine patterns of elevation richness variation in vascular plants. Rowe (2009) studied patterns of richness of non-flying mammals over 4 elevation gradients located close together in North America. In northeast China, Wang et al. (2009) analyzed regional patterns of forest plant species on 6 elevation gradients, and Kessler et al. (2011) determined patterns of elevation variation in ferns over 20 gradients located at diverse sites around the world. To the best of our knowledge, there is no study yet comparing extended gradients facing 2 different oceans.

Mexico is a land of mountains flanked by the Pacific and Atlantic Oceans on the western and eastern sides, respectively, and thus offers a great opportunity to compare gradients in the Neotropics. The objective of this study was to contrast the variation in vegetation structure and characteristics of the arboreal component of 2 extended and environmentally distinct elevation gradients. We hypothesized that if precipitation, air temperature and potential evapotranspiration (PET) vary over elevation gradients then differential patterns in vegetation structure and tree species composition would relate to different climatic variables. Alternative explanations would be related to mountain range location and disturbance history.

Materials and methods

We studied a Pacific coast elevation gradient in the state of Oaxaca, and a Gulf of Mexico coast gradient in the state of Veracruz, both in Mexico (Fig. 1). In both gradients, selected sites were distributed along the entire elevation gradients, had relatively little disturbance, and field work was conducted during the same years, 2010 and 2011. The Oaxaca elevation gradient is located on the southern slope of the Sierra Madre del Sur and vegetation is well conserved; 21 sites were located from 70 to 3,600 m elevation at the summit. The climate is sub-humid with a marked rainy season in the summer months. Mean annual temperature decreases from 27 °C at the lowest to 9 °C at the highest sites, total annual precipitation varies from 437 mm at the lowest site to 1,632 mm at mid-elevations

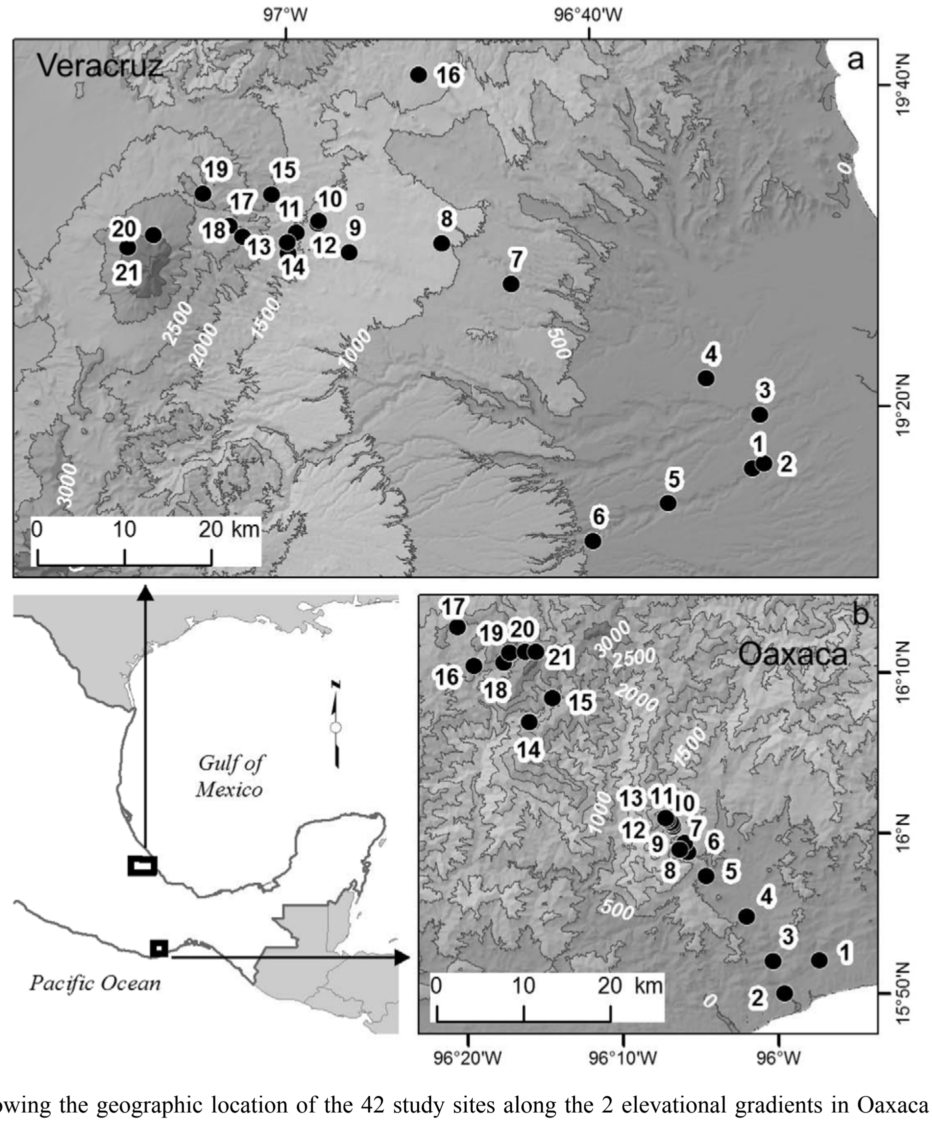

Figure 1. Map showing the geographic location of the 42 study sites along the 2 elevational gradients in Oaxaca (below right) and Veracruz (above), México.

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(Salas-Morales & Meave, 2012). The Veracruz elevation gradient is located in the central part of the state; 21 sites were located from 97 m to 4,000 m elevation at the tree line on the Cofre de Perote Volcano. The vegetation along the gradient has historically been disturbed, but well-preserved sites are scattered throughout the landscape. Mean annual temperature decreases from 25 °C at the lowest to 8 °C at the highest sites, total annual precipitation ranges from 932 mm at lower elevations, to ca. 2,000 mm at mid-elevations (Toledo-Garibaldi & Williams-Linera, 2014). Hereafter, the Oaxaca and the Veracruz elevation gradients will be referred as Oaxaca and Veracruz, respectively.

Meteorological stations are scarce along the elevation gradients; however, we used the few that are available to corroborate data obtained from WorldClim (Hijmans et al., 2005) for each study site. We analyzed 8 variables extracted from WorldClim at a 1-km spatial resolution (mean temperature of the warmest and coldest quarter, annual mean temperature, precipitation of the warmest and coldest quarter, precipitation of the wettest and driest quarter and annual precipitation). In addition, we estimated PET as an indicator of dryness where the annual PET exceeds annual precipitation (Harris et al., 2013).

At each site, a 0.1 ha plot was established. In each plot, we counted the number of individuals and identified the species of all trees ≥ 5 cm diameter at 1.3 m in height (dbh). Vouchers were deposited at the SERO herbarium of the Sociedad para el Estudio de los Recursos Bióticos de Oaxaca, and the XAL herbarium of the Instituto de Ecología, A.C.

To identify groups of taxa that are specialists in each gradient, we used a classification model (CLAM; Chazdon et al., 2011). This is a multinomial statistical method that uses the relative abundance of taxa to classify specialists and generalists (Chazdon et al., 2011). We used a K-level of 0.5 for the simple-majority rule or liberal threshold, with a P-level of 0.005 as has been suggested when the objective is whole community analysis (Chao & Lin, 2011; Chazdon et al., 2011). We excluded morphospecies from the classification analysis; for analysis of the species and genera, we also excluded individuals identified to family level.

For each site, we calculated basal area (m^2/ha), density (individuals/ha), species, genus, and family richness, and the Shannon diversity index (H´). Differences in climate variables between the gradients were analyzed using analyses of variance. To determine patterns of distribution, vegetation structure, taxa richness, diversity and climatic data, we fitted each variable to linear and polynomial models using generalized linear models. The best model was selected with the Akaike Information Criterion for small sample size, AICc (Burnham & Anderson, 2002). For the number of taxa (counts), we used a Poisson distribution and log link function. Data were analyzed using R project software version 3.4.2 (R Core Team, 2017).

Canonical correspondence analysis (CCA) was used to examine the relationship between plant taxa and climate variables along environmental gradients. The species, genus and family matrices consisted of the number of individuals of each taxa recorded in each of the 42 sites. The environmental data matrix included elevation and 8 climatic variables. Monte Carlo permutation tests were performed to determine whether the observed patterns differed from a random relationship. The forward selection procedure was used to determine the statistical significance of each environmental variable. Analyses were performed with CANOCO software version 4.5 (ter Braak & Šmilauer, 2002).

Results

Mean annual temperature decreased linearly with increasing elevation in both Oaxaca and Veracruz (Fig. 2a, b). However, in Oaxaca, the mean temperature values in both the warmest and coldest quarters were higher than those in Veracruz. The temperature difference between the coldest and the warmest quarters was smaller along the Oaxaca gradient (1.1 to 2.7 °C) than in Veracruz (3.2 to 5.7 °C; $F_{7, 34} = 207.10$, $p < 0.0001$). Mean rainfall presented a unimodal relationship with elevation (Fig. 2c, d). A slight peak was observed between 500 and 1,200 m asl in Oaxaca and between 1,500 and 1,800 m asl in Veracruz. Climatic differences between the gradients were clear for PET below 2,000 m asl in elevation (Fig. 2e, f). These values indicated that Oaxaca is drier than Veracruz.

A total of 4,229 individuals were recorded belonging to 435 species, 212 genera, 85 families and 19 morphospecies on the 2 gradients. Along the Oaxaca gradient, 1,678 individuals were measured and 260 species, 146 genera and 66 families were identified (Appendix). Along the Veracruz gradient, 2,551 trees were measured and 210 species, 124 genera and 63 families were identified (Appendix). The families represented by the highest number of individuals and species were Leguminosae (53 species), Fagaceae (22 species), Euphorbiaceae (21 species), Rubiaceae (21 species), Malvaceae (19 species), Burseraceae (11 species) and Pinaceae (11 species). The genera with the highest number of species were *Quercus* (21 species), *Bursera* (10 species) and *Pinus* (10 species) (Appendix).

Classification of 388 species into groups of gradient specialization by CLAM indicated that, from 31 shared species, only 12 presented a relatively similar abundance in both gradients for classification as generalist (Appendix). The CLAM identified 58 species as Oaxaca specialists, while 41 were identified as Veracruz specialists (Appendix). Classification of 212 genera showed that, from 58 shared genera, 19 were generalist; 43 genera were Oaxaca specialists (e.g., *Amphyterygium*, *Arbutus*, *Jacquinia*, *Phenax*, *Poeppigia*) whereas 24 genera were Veracruz specialists (e.g., *Fagus*, *Hedyosmum*, *Liquidambar*, *Savia*, *Turpinia*). The classification of 85 families indicated that 16 families were generalists; 22 were Oaxaca specialists and 14 were Veracruz specialists (Table 1).

Basal area showed a unimodal pattern in Oaxaca and a monotonic pattern in Veracruz (Fig. 3a; Table 2). Density of trees showed inverse linear patterns on the studied gradients; in Oaxaca, density decreased with increasing elevation, while in Veracruz density increased with elevation (Fig. 3b; Table 2).

Overall, species, genus and family richness and Shannon diversity index tended to decrease with increasing elevation along Oaxaca and Veracruz (Fig. 3c-f; Table 2). Richness and diversity were higher in Oaxaca than in Veracruz; however, above 1,800-2,000 m elevation, these parameters were similar on both gradients (Fig. 3c-f).

Ordination by CCA of the 42 sites for species, genus and family abundance was significant for the first axis (Monte Carlo test, F = 1.74, 2.52, 5.29, respectively, p = 0.002) and all canonical axes (Monte Carlo test, F = 1.56, 1.95, 2.66, respectively, p = 0.002), showing that the observed patterns differed from a random relationship. For species, the first 2 axes accounted for 12.9 and 12.4% of the cumulative variance, respectively (Fig. 4a). For genus, axis 1 and axis 2 accounted for 18.6% and 16.3%, respectively (Fig. 4b). For family, axis 1 and axis 2 described 30.3% and 24.6% of the cumulative variance, respectively (Fig. 4c). For species, genus and family, the first axis may be interpreted by temperature gradients whereas the second axis was related to precipitation and PET (Fig. 4). The retained significant variables in each CCA are shown in table 3.

In general, the CCA for species, genus and family, consistently separated 3 groups of sites (Fig. 4). The biplots indicated that, on axis 1, pine-oak and coniferous forests in Oaxaca and Veracruz had positive scores while dry forest sites had negative scores. On axis 2, all montane cloud forests of Veracruz had positive scores; however, montane

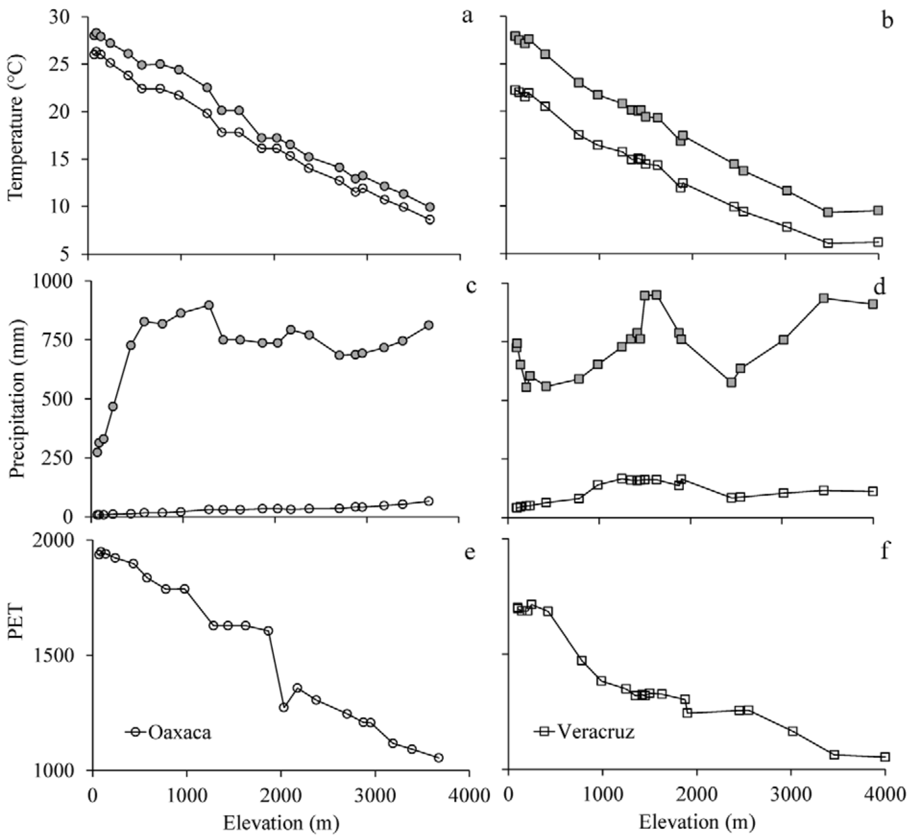

Figure 2. Climatic variables along elevation gradients in Oaxaca (left panels) and Veracruz (right panels), Mexico. a and b) mean temperature of the warmest (gray symbols) and coldest (open symbols) quarters; c and d) precipitation of the wettest (gray symbols) and driest (open symbols) quarters, and PET in e) Oaxaca (circle) and f) Veracruz (square). Labels on the far-left y-axes apply to both panels within a row.

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Table 1

Families in the elevational gradients of Oaxaca and Veracruz, Mexico, classified as generalists to both gradients, Oaxaca specialists and Veracruz specialists according to the CLAM analysis. Values are number of individuals recorded along each gradient. Superscripts indicate biogeographical distribution of each family: [1], tropical; [2], temperate; [3], cosmopolitan.

Generalist			Oaxaca Specialist			Veracruz Specialist		
Family	Oax	Ver	Family	Oax	Ver	Family	Oax	Ver
Actinidiaceae[3]	12	28	Anacardiaceae[3]	62	21	Betulaceae[2]	26	127
Burseraceae[1]	61	111	Annonaceae[1]	20	6	Celastraceae[1]	1	11
Caricaceae[1]	5	15	Apocynaceae[1]	31	13	Chloranthaceae[1]	0	40
Lauraceae[1]	11	30	Araliaceae[1]	24	15	Clethraceae[3]	13	60
Malvaceae[1]	101	84	Bignoniaceae[1]	30	20	Convolvulaceae[3]	0	15
Moraceae[1]	9	16	Boraginaceae[3]	14	3	Fagaceae[2]	48	392
Myrsinaceae[1]	5	10	Clusiaceae[1]	14	0	Hamamelidaceae[2]	0	84
Myrtaceae[3]	37	51	Combretaceae[1]	14	0	Melastomataceae[1]	0	19
Nyctaginaceae[1]	9	2	Ericaceae[3]	48	8	Pinaceae[2]	267	632
Polygonaceae[3]	8	12	Euphorbiaceae[3]	124	101	Sapindaceae[1]	1	16
Rhamnaceae[3]	2	11	Hernandiaceae[1]	17	4	Staphyleaceae[2]	0	75
Rosaceae[2]	10	15	Julianiaceae[1]	14	0	Styracaceae[2]	0	27
Rubiaceae[1]	66	70	Leguminosae[3]	207	134	Symplocaceae[1]	0	11
Rutaceae[1]	4	13	Meliaceae[1]	33	6	Theaceae[1]	0	26
Ulmaceae[3]	9	7	Myricaceae[3]	16	0			
Verbenaceae[1]	8	15	Oleaceae[3]	17	0			
			Proteaceae[1]	9	0			
			Salicaceae[3]	33	6			
			Sapotaceae[1]	18	0			
			Simaroubaceae[1]	12	1			
			Theophrastaceae[1]	13	0			
			Urticaceae[1]	37	0			

forest sites on Oaxaca gradient had negative scores for species and were separated from the Veracruz group.

Discussion

Differences in climate along the gradients of both, Oaxaca and Veracruz, are related to their geographic location and the meteorological phenomena affecting them (Espinosa et al., 2008). On Veracruz gradient, the frequent presence of mist is attributed to the dominant warm marine current of the Gulf of Mexico, whereas the Oaxaca gradient on the Pacific side is influenced by dry wind and cold marine currents (Espinosa et al., 2008). Moreover, from November to March, cold northerly winds across the Gulf of Mexico, contribute to the lower temperatures reported for the Veracruz gradient, and bring rains and fog during the relative dry season (Holwerda et al., 2010). PET plays an important role in determining community types since same amount of rainfall manifests different in warm than in cold environments. PET values clearly indicated that Oaxaca is drier than Veracruz, but only below 2,000 m elevation.

The CCA results evidenced the relationship between vegetation and climate on these 2 gradients. Several authors have emphasized the importance of climate, not only in large-scale patterns, but also at the local level (Francis & Currie, 2003; Hawkins et al., 2003). The groups of forest types were differentially related to precipitation or temperature variables (Toledo-Garibaldi & Williams-Linera, 2014). On the Oaxaca gradient, temperature was

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the most important environmental factor (Salas-Morales et al., 2015). In Oaxaca, groups of sites were related to low and high temperatures, separating tropical from temperate vegetation (Salas-Morales & Meave, 2012). Temperature is a variable that is highly associated with altitude and with elevation patterns in floristic and vegetation variation (Grubb, 1977; Sang, 2009). On the Veracruz gradient, 3 groups of sites were distinguished: lowland dry forests and highland temperate forests related to high and low temperatures, respectively, and montane cloud forests related to humidity. These forests are found in particular sites on the mountains of Mexico, in an elevation belt where there is a frequent influence of fog (Holwerda et al., 2010).

Forests on the Oaxaca gradient display lower basal area and density of trees than on Veracruz. Differences become complicated because along the whole gradients, BA and density tend to increase in Veracruz whereas in Oaxaca tend to decrease with elevation. Differences are greater in vegetation structure in the temperate forests of higher elevations, and may be related to humidity, since during the warmest, coldest, and driest quarters, the Veracruz gradient receives twice the precipitation in the highest-altitude sites than Oaxaca. Different patterns of vegetation structure along gradients have been observed in a number of studies, and generality is not expected when comparing tropical elevation transects (Clark et al., 2015). For example, on Mount Kinabalu in Borneo, stem density increased with elevation, and basal area in non-ultrabasic soils increased monotonically, while in the ultrabasic soils presented a unimodal pattern (Aiba & Kitayama, 1999). However, on an elevation gradient on the Barba Volcano in Costa Rica, there were 2 peaks in tree density, at 400 m and 2,800 m elevation, while the basal area varied little along the gradient and was the highest in the 2,800 m plot (Clark et al., 2015).

Variation in elevation patterns is not limited to vegetation structure. Elevation gradients display variation in richness, diversity and taxa composition. For both gradients, richness and diversity decrease with increasing elevation; however, the patterns differ from each other. On the Oaxaca gradient above 1,800 - 2,000 m occurs a rapid decreasing trend in species, genera and family richness and diversity related to the low tolerance of some tropical taxa to relatively cold temperatures (Salas-Morales et al., 2015). While in Oaxaca the elevation pattern seems to be related to a critical elevation, the richness pattern in Veracruz decreased smoothly related to the mixture of temperate and tropical taxa and more humid conditions (Challenger & Soberón, 2008). Likewise, in Eastern Asia forests with tropical and temperate genera are found in similar elevation gradients (Li & Feng, 2015; Liao et al., 2014). Li and Feng (2015) reported that tropical genera are found below and temperate genera above mid-point in Nepal.

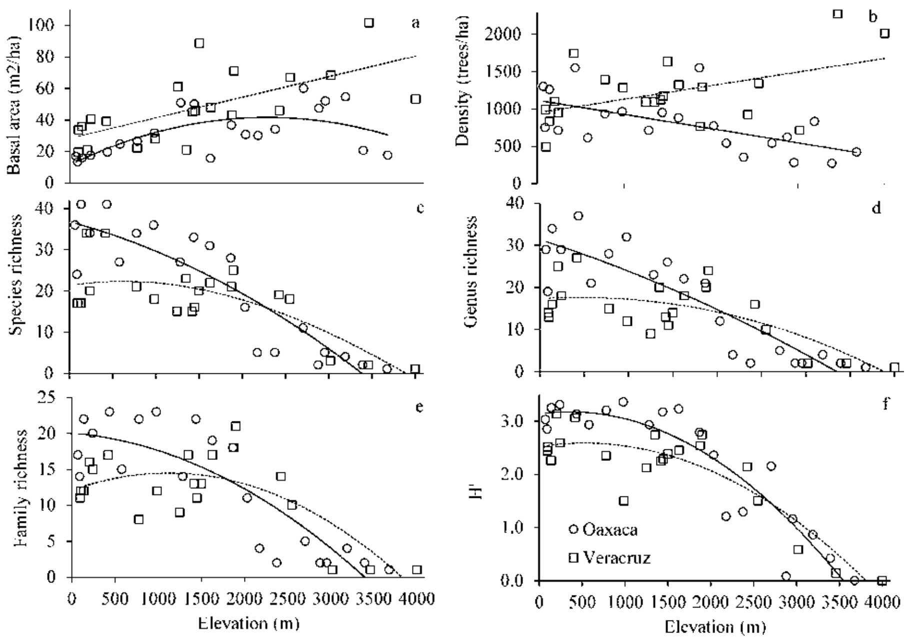

Figure 3. Fitted models of vegetation structure, richness and diversity changes along the elevation gradients of Oaxaca and Veracruz, Mexico. a) basal area, b) density, c) species richness, d) genus richness, e) family richness, and f) Shannon diversity. In each panel, circles are sites on Oaxaca, and squares are sites on Veracruz.

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Table 2

Model fitting of species, genus and family richness, Shannon's diversity index, basal area and density in relation to elevation in Oaxaca and Veracruz, Mexico. Results shown are residual deviance, deviance explained (%), X^2 and *P*. AICc is corrected Akaike information criterion and Δi is the AICc difference between the AICc of the best model and that of the model i. Note that models having ΔAICc within 2 of the best model have substantial support and receive consideration (Burnham & Anderson, 2002). Boldface indicates the best model. Model 1 is linear; Model 2 is quadratic, Model 3 is cubic. $*p$ is < 0.05, ** is < 0.01, *** is < 0.001.

	Oaxaca					Veracruz				
Model	Residual deviance	Percentage deviance explained	X^2	AICc	Δi	Residual deviance	Percentage deviance explained	X^2	AICc	Δi
Species richness										
1	74.9	69.84	173.45***	173.2	41.1	61.61	38.76	38.99***	161.1	25.4
2	31.12	87.47	217.24***	132.1	0	36.57	63.65	64.03***	138.8	3.1
3	31.07	87.49	217.28***	135.2	3.1	30.32	69.86	70.27***	135.7	0
Genus richness										
1	63.91	71.56	160.81***	156.7	33.2	55.72	36	31.34***	150.4	19.2
2	27.99	87.54	196.73***	123.5	0	37	57.5	50.06***	134.4	3.2
3	26.43	88.24	198.28***	125.1	1.6	30.67	64.77	56.40***	131.2	0
Family richness										
1	50.89	62.92	86.36***	139.6	26.4	53.02	24.17	16.90***	143.5	27.8
2	21.75	84.15	115.50***	113.2	0	28.08	59.84	41.84***	121.3	5.6
3	20.62	84.98	116.63***	115.2	2	19.4	72.25	50.52***	115.7	0
H'										
1	6.44	76.38	30.31***	42.2	7.3	5.45	64	21.45***	38.7	7.78
2	3.93	85.59	40.69***	34.9	0	3.25	78.53	32.32***	30.9	0
3	3.41	87.5	43.69***	35.4	0.5	3.25	78.53	32.32***	34.4	3.5
Basal area										
1	3413.5	24.66	5.95*	173.9	3	5508.1	44.19	12.25**	183	0
2	2549.2	43.74	12.08**	170.9	0	5348.6	45.81	12.86**	186.4	3.4
3	2375.1	47.58	13.56**	172.9	2	4965.2	49.69	14.43**	188.4	5.4
Density										
1	1762528	36.61	9.57**	305.1	0	2805447	23.33	5.58*	314.9	0.6
2	1735128	37.59	9.90**	307.9	2.8	2655046	27.44	6.74*	316.8	2.5
3	1728317	37.84	9.98*	311.3	6.2	1997907	45.4	12.71**	314.3	0

Oaxaca was more diverse (260 species) than Veracruz (210 species), which was contrary to expected given that the Veracruz gradient is more humid. In the Neotropics, plant species richness is strongly correlated with total annual precipitation (Gentry, 1988), but the most diverse dry forest are not the wettest ones, but rather the western Mexico dry forests (Gentry, 1995). Thus, the dry forest is more diverse in the Pacific coast than in the Gulf of Mexico, contributing greatly to the high diversity of Oaxaca.

The family with the highest number of individuals for both, Oaxaca and Veracruz, was Pinaceae. In elevations above 2,200 and 2,450 m on the Oaxaca and Veracruz gradients, respectively, the forests are dominated by the genus *Pinus*, which shares dominance with *Quercus* in these elevation belts. This result is consistent throughout the mountains of Mexico where forests are dominated by pine-oak and pine forests, and although Mexico has more than 150 species of oaks and more than 40 species of pines

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(Gernandt & Pérez-de la Rosa, 2014; Valencia, 2004), in each particular site they were represented by a few species (Challenger & Soberón, 2008). Gentry (1988) indicated that Neotropical plant communities are together in nonrandom ways. In Oaxaca and Veracruz, families classified by CLAM as generalists (e.g., Lauraceae, Rubiaceae) were the families that contributed most to species richness in the Neotropics according to Gentry (1988). Oaxaca specialist families identified by CLAM were mainly of tropical affinity (e.g., Euphorbiaceae, Leguminosae), whereas in Veracruz, several of the indicator families were of temperate affinity (e.g., Betulaceae, Fagaceae, Pinaceae; Table 1).

It is likely that difference in temperature and precipitation was not the only factor to affect forest development and composition. Other variables, such as soil characteristics and land use history or legacy play a role, and they are alternative explanations as has been shown in previous studies (Aiba & Kitayama, 1999; Arévalo et al., 2010; Da et al., 2009; Kitayama & Aiba, 2002; Piperno, 2006). Fragmentation and worldwide forest disappearance are mostly due to a long history of human activities (Da et al., 2009; González-Abraham et al., 2015; Piperno, 2006). Veracruz has a long history of land use before and after the arrival of the Spaniards, and the center of Veracruz was intensively used and deforested, since this gradient is located along a major route to Mexico City (González-Abraham et al., 2015). In contrast, up until 50 years ago, the Oaxaca gradient lacked paved roads and the human impact on the vegetation is therefore more recent and confined to lower altitudes (Salas-Morales & Meave, 2012).

Our results support the hypothesis that climate is one of the main underlying factors related to differential patterns in vegetation structure and taxa distribution along elevation gradients. However, climate influence depends on other local factors such as mountain range location, physiography, slope, and disturbance. The results strongly indicate differential influence of climate, since humidity is apparently an important environmental factor for the vegetation of the Gulf of Mexico, while temperature is the determining factor on the Pacific coast. The Oaxaca gradient displayed higher taxa richness than Veracruz gradient, particularly in the lower elevations. In both gradients richness decreases with increased elevation, but in Veracruz there is a smooth transition from tropical to temperate vegetation whereas in Oaxaca richness at mid-elevation shows an abrupt decreased related to temperature.

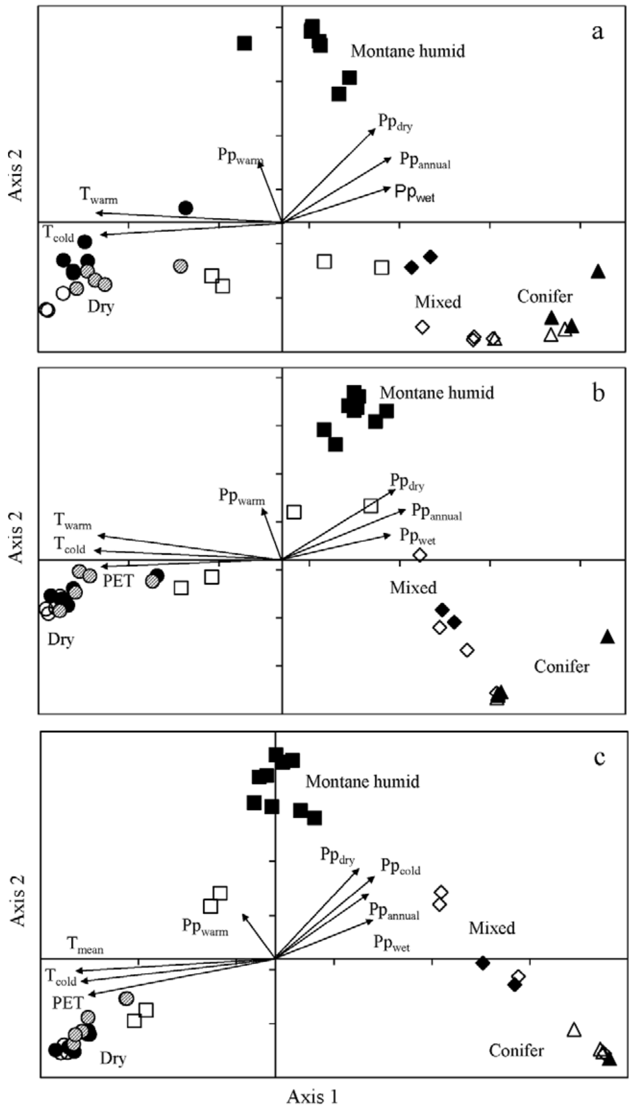

Figure 4. Canonical correspondence analysis biplots for 42 sites located along elevation gradients in Oaxaca (open and dashed symbols) and Veracruz (black symbols), Mexico. a) species, b) genus, and c) family abundance in sites along the 2 elevation gradients. In each panel, squares represent montane humid forests, circles are dry forest, diamonds are mixed forests, and triangles are conifer forests. Vectors are significant explanatory variables (Table 3), annual mean temperature (T_{mean}), temperature of warmest quarter (T_{warm}), temperature of coldest quarter (T_{cold}), annual precipitation (Pp_{annual}), precipitation of wettest quarter (Pp_{wet}), precipitation of driest quarter (Pp_{dry}), precipitation of warmest quarter (Pp_{warm}), precipitation of coldest quarter (Pp_{cold}), potential evapotranspiration (PET).

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Table 3

Results of the forward selection procedure to choose climate explanatory variables for CCA analyses of species, genera and family along the elevation gradients of Oaxaca and Veracruz, Mexico. Boldface indicates significant *p* values.

	Species			Genus			Family		
Variable	λA	*F*	*p*	λA	*F*	*p*	λA	*F*	*p*
Elevation	0.65	1.41	0.058	0.33	1.37	0.128	0.06	0.63	0.900
Annual mean temperature	0.46	1.02	0.434	0.26	1.1	0.326	0.85	6.75	0.002
Temperature of warmest quarter	0.97	1.95	0.002	0.92	3.27	0.002	0.12	1.12	0.292
Temperature of coldest quarter	0.79	1.66	0.002	0.34	1.38	0.044	0.15	1.55	0.040
Annual precipitation	0.75	1.58	0.002	0.52	1.98	0.002	0.27	2.42	0.002
Precipitation of wettest quarter	0.63	1.39	0.016	0.46	1.8	0.006	0.24	2.21	0.002
Precipitation of driest quarter	0.93	1.89	0.002	0.72	2.65	0.002	0.55	4.74	0.002
Precipitation of warmest quarter	0.69	1.47	0.010	0.44	1.72	0.008	0.19	1.83	0.008
Precipitation of coldest quarter	0.51	1.14	0.288	0.35	1.43	0.102	0.17	1.68	0.048
Potential evapotranspiration	0.62	1.36	0.064	0.39	1.59	0.048	0.19	1.87	0.028

Appendix. Tree species and family recorded along the elevation gradients of Oaxaca (OAX) and Veracruz (VER), Mexico. The numbers are species abundance in 21 sites in each gradient. Classification is based on CLAM analysis as OAX specialist, VER specialist, generalist or too rare to classify. Bold type indicates the specialist species in each elevation gradient. Individuals identified to family level and morphospecies were excluded. When more than 1 species was not identified within a genus, they were numbered.

Species	OAX	VER	Classification
ACTINIDIACEAE			
Saurauia leucocarpa Schltdl.	0	22	VER specialist
Saurauia pedunculata Hook.	0	6	Too rare to classify
Saurauia pringlei Rose	12	0	OAX specialist
ADOXACEAE			
Sambucus nigra L.	0	3	Too rare to classify
Viburnum tiliifolium (Oerst.) Hemsl.	0	2	Too rare to classify
ALTINGIACEAE			
Liquidambar styraciflua L.	0	84	VER specialist
ANACARDIACEAE			
Amphipterygium adstringens (Schltdl.) Standl.	14	0	OAX specialist
Astronium graveolens Jacq.	13	0	OAX specialist
Comocladia engleriana Loes.	45	16	OAX specialist

Continued			
Spondias mombin L.	0	2	Too rare to classify
Spondias purpurea L.	4	0	Too rare to classify
Spondias sp.	0	2	Too rare to classify
Tapirira mexicana Marchand	0	1	Too rare to classify
ANNONACEAE			
Annona cherimola Mill.	0	4	Too rare to classify
Annona squamosa L.	2	0	Too rare to classify
Annona sp.	6	0	Too rare to classify
Sapranthus microcarpus (Donn. Sm.) R.E. Fr.	0	1	Too rare to classify
APOCYNACEAE			
Tonduzia longifolia (A. DC.) Markgr.	9	0	OAX specialist
Plumeria rubra L.	8	1	OAX specialist

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Stemmadenia obovata K. Schum.	2	11	Generalist
Tabernaemontana litoralis Kunth	2	0	Too rare to classify
Thevetia ovata (Cav.) A. DC.	10	0	OAX specialist
Thevetia sp.	0	1	Too rare to classify
AQUIFOLIACEAE			
Ilex discolor Hemsl.	0	9	Too rare to classify
Ilex sp.	0	1	Too rare to classify
ARALIACEAE			
Dendropanax arboreus (L.) Decne. & Planch.	1	0	Too rare to classify
Dendropanax sp.	0	2	Too rare to classify
Oreopanax xalapensis (Kunth) Decne. & Planch.	15	13	Generalist
ARECACEAE			
Acrocomia aculeata (Jacq.) Lodd. ex Mart.	3	0	Too rare to classify
ASPARAGACEAE			
Nolina longifolia (Karw. ex Schult. f.) Hemsl.	3	0	Too rare to classify
Yucca elephantipes Regel	0	2	Too rare to classify
ASTERACEAE			
Critonia sp.	1	0	Too rare to classify
Koanophyllon pittieri (Klatt) R.M. King & H. Rob.	0	3	Too rare to classify
Verbesina olivacea Klatt	0	1	Too rare to classify
Verbesina sp.	0	1	Too rare to classify
Vernonia sp.	3	0	Too rare to classify
BETULACEAE			
Alnus acuminata Kunth	0	1	Too rare to classify
Alnus jorullensis Kunth	26	0	OAX specialist
Carpinus tropicalis (Donn. Sm.) Lundell	0	126	VER specialist

Continued

BIGNONIACEAE			
Parmentiera aculeata (Kunth) Seem.	1	0	Too rare to classify
Handroanthus chrysanthus (Jacq.) S.O. Grose	6	20	Generalist
Handroanthus impetiginosus (Mart. ex DC.) Mattos	19	0	OAX specialist
Tecoma stans (L.) Juss. ex Kunth	4	0	Too rare to classify
BIXACEAE			
Cochlospermum vitifolium (Willd.) Spreng.	4	6	Too rare to classify
BORAGINACEAE			
Bourreria aff. *purpusii* Brandegee	4	0	Too rare to classify
Cordia alliodora (Ruiz & Pav.) Oken	7	3	Generalist
Cordia tinifolia Willd. ex Roem. & Schult.	3	0	Too rare to classify
BRUNELLIACEAE			
Brunellia mexicana Standl.	0	1	Too rare to classify
BUDDLEJACEAE			
Buddleja sp.	1	0	Too rare to classify
BURSERACEAE			
Bursera aff. *cinerea* Engl.	1	0	Too rare to classify
Bursera aff. ***grandifolia*** (Schltdl.) Engl.	8	0	OAX specialist
Bursera aff. *simaruba* (L.) Sarg.	3	0	Too rare to classify
Bursera cinerea Engl.	0	28	VER specialist
Bursera excelsa (Kunth) Engl.	8	0	OAX specialist
Bursera fagaroides (Kunth) Engl.	0	14	VER specialist
Bursera graveolens (Kunth) Triana & Planch.	6	10	Generalist
Bursera heteresthes Bullock	7	0	Too rare to classify
Bursera simaruba (L.) Sarg.	27	58	Generalist
Bursera sp.	1	0	Too rare to classify

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Protium copal (Schltdl. & Cham.) Engl.	0	1	Too rare to classify
CANNABACEAE			
Celtis caudata Planch.	1	5	Too rare to classify
Trema micrantha (L.) Blume	0	2	Too rare to classify
CAPPARACEAE			
Quadrella incana (Kunth) Iltis & Cornejo	1	1	Too rare to classify
Quadrella indica (L.) Iltis & Cornejo	2	0	Too rare to classify
CARICACEAE			
Jacaratia mexicana A. DC.	5	15	Generalist
CELASTRACEAE			
Euonymus mexicanus Benth.	0	1	Too rare to classify
CHLORANTHACEAE			
Hedyosmum mexicanum C. Cordem.	0	40	VER specialist
CLETHRACEAE			
Clethra lanata M. Martens & Galeotti	13	0	OAX specialist
Clethra macrophylla M. Martens & Galeotti	0	60	VER specialist
CLUSIACEAE			
Clusia salvinii Donn. Sm.	14	0	OAX specialist
COMBRETACEAE			
Bucida macrostachya Standl.	14	0	OAX specialist
CONVOLVULACEAE			
Ipomoea wolcottiana Rose	0	15	VER specialist
CORNACEAE			
Cornus excelsa Kunth	0	2	Too rare to classify
CUNONIACEAE			
Weinmannia pinnata L.	0	6	Too rare to classify
CUPRESSACEAE			
Cupressus lusitanica Mill.	0	5	Too rare to classify
DIPENTODONTACEAE			
Perrottetia ovata Hemsl.	0	1	Too rare to classify

Continued

Wimmeria sp.	1	0	Too rare to classify
Zinowiewia sp. 1	0	2	Too rare to classify
Zinowiewia sp. 2	0	7	Too rare to classify
EBENACEAE			
Diospyros salicifolia Humb. & Bonpl. ex Willd.	1	0	Too rare to classify
ERICACEAE			
Arbutus sp.	1	0	Too rare to classify
Arbutus xalapensis Kunth	47	0	OAX specialist
Gaultheria acuminata Schltdl. & Cham.	0	1	Too rare to classify
Vaccinium leucanthum Schltdl.	0	8	Too rare to classify
ERYTHROXYLACEAE			
Erythroxylum havanense Jacq.	3	0	Too rare to classify
Erythroxylum pallidum Rose	1	0	Too rare to classify
EUPHORBIACEAE			
Acalypha adenostachya Müll. Arg.	0	7	Too rare to classify
Alchornea latifolia Sw.	0	7	Too rare to classify
Bernardia mexicana (Hook. & Arn.) Müll. Arg.	0	4	Too rare to classify
Cnidoscolus spinosus Lundell	0	16	VER specialist
Cnidoscolus tubulosus (Müll. Arg.) I.M. Johnst.	37	0	OAX specialist
Cnidoscolus multilobus (Pax) I.M. Johnst.	0	3	Too rare to classify
Cnidoscolus sp.	0	2	Too rare to classify
Croton cortesianus Kunth	0	4	Too rare to classify
Croton draco Schltdl. & Cham.	2	0	Too rare to classify
Croton reflexifolius Kunth	0	15	VER specialist
Croton septemnervius McVaugh	41	0	OAX specialist
Croton sp.	1	0	Too rare to classify

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Continued			
Drypetes sp.	6	0	Too rare to classify
Euphorbia calcarata (Schltdl.) V.W. Steinm.	1	3	Too rare to classify
Euphorbia pulcherrima Willd. ex Klotzsch	2	0	Too rare to classify
Euphorbia schlechtendalii Boiss.	0	5	Too rare to classify
Gymnanthes longipes Müll. Arg.	0	4	Too rare to classify
Gymnanthes sp.	0	1	Too rare to classify
Jatropha malacophylla Standl.	12	0	OAX specialist
Jatropha sympetala S.F. Blake & Standl.	2	0	Too rare to classify
Sapium glandulosum (L.) Morong	16	0	OAX specialist
Sebastiania pavonia (Müll. Arg.) Müll. Arg.	4	0	Too rare to classify
FAGACEAE			
Fagus grandifolia Ehrh.	0	52	VER specialist
Quercus acherdophylla Trel.	0	1	Too rare to classify
Quercus acutifolia Née	0	4	Too rare to classify
Quercus candicans Née	8	0	OAX specialist
Quercus corrugata Hook.	0	15	VER specialist
Quercus cortesii Liebm.	0	17	VER specialist
Quercus crassifolia Bonpl.	0	5	Too rare to classify
Quercus delgadoana S. Valencia, Nixon & L.M. Kelly	0	43	VER specialist
Quercus germana Schltdl. & Cham.	0	29	VER specialist
Quercus glabrescens Benth.	0	12	VER specialist
Quercus lancifolia Schltdl. & Cham.	0	61	VER specialist
Quercus laurina Bonpl.	11	0	OAX specialist

Continued			
Quercus peduncularis Née	2	0	Too rare to classify
Quercus pinnativenulosa C.H. Mull.	0	2	Too rare to classify
Quercus rugosa Née	14	0	OAX specialist
Quercus sapotifolia Liebm.	0	84	VER specialist
Quercus sartorii Liebm.	0	17	VER specialist
Quercus xalapensis Bonpl.	0	48	VER specialist
Quercus sp. 1	8	0	OAX specialist
Quercus sp. 2	0	2	Too rare to classify
Quercus sp. 3	4	0	Too rare to classify
Quercus sp. 4	1	0	Too rare to classify
HERNANDIACEAE			
Gyrocarpus americanus Jacq.	0	4	Too rare to classify
Gyrocarpus mocinnoi Espejo	17	0	OAX specialist
LAMIACEAE			
Vitex hemsleyi Briq.	8	0	OAX specialist
LAURACEAE			
Beilschmiedia mexicana (Mez) Kosterm.	0	3	Too rare to classify
Cinnamomun effusum (Meisn.) Kosterm.	0	12	VER specialist
Cinnamomum triplinerve (Ruiz & Pav.) Kosterm.	1	0	Too rare to classify
Licaria misantlae (Brandegee) Kosterm.	0	5	Too rare to classify
Litsea glaucescens Kunth	2	1	Too rare to classify
Nectandra salicifolia (Kunth) Nees	4	1	Too rare to classify
Ocotea effusa (Meisn.) Hemsl.	1	0	Too rare to classify
*Ocotea psychotrioide*s Kunth	0	5	Too rare to classify
Persea americana Mill.	3	3	Too rare to classify

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LEGUMINOSAE			
Acaciella angustissima (Mill.) Britton & Rose	1	0	Too rare to classify
Apoplanesia paniculata C. Presl	1	0	Too rare to classify
Bauhinia sp.	0	10	Too rare to classify
Caesalpinia eriostachys Benth.	11	0	OAX specialist
Caesalpinia sp.	0	1	Too rare to classify
Calliandra houstoniana (Mill.) Standl.	1	0	Too rare to classify
Calliandra rubescens (M. Martens & Galeotti) Standl.	0	1	Too rare to classify
Chloroleucon mangense (Jacq.) Britton & Rose	1	0	Too rare to classify
Cojoba arborea (L.) Britton & Rose	5	1	Too rare to classify
Coulteria platyloba S. Watson	1	0	Too rare to classify
Coulteria velutina (Britton & Rose) Standl.	4	0	Too rare to classify
Dalbergia granadillo Pittier	5	0	Too rare to classify
Diphysa carthagenensis Jacq.	0	9	Too rare to classify
Erythrina lanata Rose	5	0	Too rare to classify
Erythrina sp.	0	1	Too rare to classify
Gliricidia sepium (Jacq.) Kunth ex Walp.	9	12	Generalist
Inga oerstediana Benth. ex Seem.	3	0	Too rare to classify
Inga paterno Harms	5	0	Too rare to classify
Inga punctata Willd.	16	0	OAX specialist
Leucaena lanceolata S. Watson	6	20	Generalist
Leucaena leucocephala (Lam.) de Wit	0	3	Too rare to classify
Lonchocarpus aff. ***magallanesii*** M. Sousa	9	0	OAX specialist
Lonchocarpus constrictus Pittier	13	0	OAX specialist

Continued

Lonchocarpus emarginatus Pittier	8	0	OAX specialist
Lonchocarpus lanceolatus Benth.	6	0	Too rare to classify
Lonchocarpus molinae Standl. & L.O. Williams	4	0	Too rare to classify
Lonchocarpus sp.	2	0	Too rare to classify
Lysiloma acapulcense (Kunth) Benth.	0	22	VER specialist
Lysiloma auritum (Schltdl.) Benth.	0	4	Too rare to classify
Lysiloma divaricatum (Jacq.) J.F. Macbr.	0	6	Too rare to classify
Lysiloma microphyllum Benth.	27	0	OAX specialist
Machaerium biovulatum Micheli	2	0	Too rare to classify
Myrospermum frutescens Jacq.	7	0	Too rare to classify
Piptadenia obliqua (Pers.) J.F. Macbr.	3	0	Too rare to classify
Piscidia piscipula (L.) Sarg.	0	16	VER specialist
Poeppigia procera C. Presl	17	0	OAX specialist
Pterocarpus rohrii Vahl	16	0	OAX specialist
Pterocarpus sp.	1	0	Too rare to classify
Senegalia polyphylla DC.	6	0	Too rare to classify
Senna atomaria (L.) H.S. Irwin & Barneby	0	6	Too rare to classify
Senna pendula (Humb. & Bonpl. ex Willd.) H.S. Irwin &Barneby	0	1	Too rare to classify
Senna pallida (Vahl) H.S. Irwin & Barneby	0	1	Too rare to classify
Senna skinneri (Benth.) H.S. Irwin & Barneby	1	0	Too rare to classify
Senna sp. 1	0	2	Too rare to classify
Senna sp. 2	0	5	Too rare to classify
Styphnolobium conzattii (Standl.) M. Sousa & Rudd	3	0	Too rare to classify

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Continued			
Tara cacalaco (Bonpl.) Molinari & Sánchez Och.	0	3	Too rare to classify
Vachellia collinsii Saff.	1	0	Too rare to classify
Vachellia cornigera (L.) Willd.	0	1	Too rare to classify
Vachellia farnesiana (L.) Willd.	0	2	Too rare to classify
Vachellia hindsii Benth.	5	0	Too rare to classify
Vachellia pennatula (Schltdl. & Cham.) Benth.	0	7	Too rare to classify
Zapoteca sp.	2	0	Too rare to classify
LYTHRACEAE			
Ginoria nudiflora (Hemsl.) Koehne	2	0	Too rare to classify
MAGNOLIACEAE			
Magnolia schiedeana Schltdl.	0	2	Too rare to classify
MALPIGHIACEAE			
Bunchosia aff. *gracilis* Nied.	3	0	Too rare to classify
Malpighia glabra L.	0	1	Too rare to classify
MALVACEAE			
Bernoullia flammea Oliv.	6	0	Too rare to classify
Ceiba aesculifolia (Kunth) Britten & Baker f.	3	9	Generalist
Gossypium aridum (Rose & Standl.) Skovst.	1	0	Too rare to classify
Guazuma ulmifolia Lam.	10	6	Generalist
Hampea mexicana Fryxell	2	0	Too rare to classify
Heliocarpus americanus L.	0	3	Too rare to classify
Heliocarpus donnellsmithii Rose	0	43	VER specialist
Heliocarpus terebinthinaceus (DC.) Hochr.	8	0	OAX specialist
Heliocarpus sp. 1	9	0	OAX specialist
Heliocarpus sp. 2	11	0	OAX specialist
Heliocarpus sp. 3	6	0	Too rare to classify

Continued			
Hibiscus purpusii Brandegee	2	0	Too rare to classify
Luehea candida (DC.) Mart.	8	22	Generalist
Luehea speciosa Willd.	0	1	Too rare to classify
Malvaviscus arboreus Cav.	2	0	Too rare to classify
Melochia oaxacana Dorr & L.C. Barnett	3	0	Too rare to classify
Pseudobombax ellipticum (Kunth) Dugand	16	0	OAX specialist
Robinsonella speciosa Fryxell	1	0	Too rare to classify
Tilia americana L.	13	0	OAX specialist
MELASTOMATACEAE			
Conostegia arborea Steud.	0	2	Too rare to classify
Miconia glaberrima (Schltdl.) Naudin	0	13	VER specialist
Miconia mexicana (Bonpl.) Naudin	0	3	Too rare to classify
Miconia oligotricha (DC.) Naudin	0	1	Too rare to classify
MELIACEAE			
Cedrela oaxacensis C. DC. & Rose	2	0	Too rare to classify
Cedrela salvadorensis Standl.	2	0	Too rare to classify
Guarea sp. 1	1	0	Too rare to classify
Guarea sp. 2	1	0	Too rare to classify
Swietenia humilis Zucc.	8	0	OAX specialist
Trichilia havanensis Jacq.	17	0	OAX specialist
Trichilia hirta L.	2	0	Too rare to classify
Trichilia trifolia L.	0	6	Too rare to classify
MENISPERMACEAE			
Hyperbaena jalcomulcensis E. Pérez & Cast.-Campos	0	1	Too rare to classify
Hyperbaena mexicana Miers	1	0	Too rare to classify
Hyperbaena sp.	1	0	Too rare to classify

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Continued			
MONIMIACEAE			
Mollinedia viridiflora Tul.	0	2	Too rare to classify
Siparuna andina (Tul.) A. DC.	2	0	Too rare to classify
MORACEAE			
Brosimum alicastrum Sw.	1	14	VER specialist
Ficus citrifolia Mill.	1	0	Too rare to classify
Ficus pertusa L. f.	1	0	Too rare to classify
Ficus sp.	0	1	Too rare to classify
Maclura tinctoria (L.) D. Don ex Steud.	3	1	Too rare to classify
Trophis mexicana (Liebm.) Bureau	3	0	Too rare to classify
MYRICACEAE			
Myrica lindeniana C. DC.	16	0	OAX specialist
MYRSINACEAE			
Ardisia compressa Kunth	2	0	Too rare to classify
Ardisia revoluta Kunth	1	0	Too rare to classify
Ardisia sp.	2	0	Too rare to classify
MYRTACEAE			
Calyptranthes schiedeana O. Berg	0	26	VER specialist
Eugenia liebmannii Standl.	0	18	VER specialist
Eugenia mexicana Steud.	0	5	Too rare to classify
Eugenia xalapensis (Kunth) DC.	0	2	Too rare to classify
Eugenia sp. 1	6	0	Too rare to classify
Eugenia sp. 2	31	0	OAX specialist
NYCTAGINACEAE			
Neea tenuis Standl.	0	1	Too rare to classify
Neea sp.	2	0	Too rare to classify
Pisonia sp.	0	1	Too rare to classify
Torrubia macrocarpa Miranda	7	0	Too rare to classify
OLEACEAE			
Fraxinus uhdei (Wenz.) Lingelsh.	17	0	OAX specialist
ONAGRACEAE			
Hauya elegans DC.	2	0	Too rare to classify
OPILIACEAE			
Agonandra obtusifolia Standl.	2	0	Too rare to classify
Agonandra racemosa (DC.) Standl.	3	0	Too rare to classify
PAPAVERACEAE			
Bocconia frutescens L.	3	0	Too rare to classify
PENTAPHYLACACEAE			
Cleyera integrifolia (Benth.) Choisy	0	14	VER specialist
Ternstroemia sylvatica Schltdl. & Cham.	0	12	VER specialist
PHYLLANTHACEAE			
Phyllanthus sp.	0	3	Too rare to classify
Savia sessiliflora (Sw.) Willd.	0	29	VER specialist
PICRAMNIACEAE			
Alvaradoa amorphoides Liebm.	12	0	OAX specialist
Picramnia mexicana Brandegee	0	1	Too rare to classify
PINACEAE			
Abies religiosa (Kunth) Schltdl. & Cham.	0	222	VER specialist
Pinus ayacahuite C. Ehrenb. ex Schltdl.	8	40	VER specialist
Pinus douglasiana Martínez	1	0	Too rare to classify
Pinus hartwegii Lindl.	112	265	VER specialist
Pinus herrerae Martínez	11	0	OAX specialist
Pinus maximinoi H.E. Moore	23	0	OAX specialist

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Appendix.

Continued			
Pinus montezumae Lamb.	8	0	OAX specialist
Pinus patula Schltdl. & Cham.	0	100	VER specialist
Pinus pseudostrobus Brongn.	101	5	OAX specialist
Pinus sp. 1	1	0	Too rare to classify
Pinus sp. 2	2	0	Too rare to classify
PIPERACEAE			
Piper umbricola C. DC.	1	0	Too rare to classify
PODOCARPACEAE			
Podocarpus matudae Lundell	0	5	Too rare to classify
POLYGONACEAE			
Coccoloba liebmannii Lindau	1	0	Too rare to classify
Coccoloba schiedeana Lindau	4	0	Too rare to classify
Coccoloba sp.	0	7	Too rare to classify
Podopterus mexicanus Bonpl.	0	1	Too rare to classify
Ruprechtia fusca Fernald	3	0	Too rare to classify
Ruprechtia pallida Standl.	0	1	Too rare to classify
Ruprechtia sp.	0	3	Too rare to classify
PRIMULACEAE			
Bonellia nervosa (C. Presl) B. Ståhl & Källersjö	13	0	OAX specialist
Myrsine coriacea (Sw.) R. Br. ex Roem. & Schult.	0	10	Too rare to classify
PROTEACEAE			
Roupala montana Aubl.	9	0	OAX specialist
RESEDACEAE			
Forchhammeria pallida Liebm.	3	0	Too rare to classify
RHAMNACEAE			
Colubrina triflora Brongn. ex G. Don	1	6	Too rare to classify
Rhamnus capreifolia Schltdl.	0	3	Too rare to classify

Continued			
Rhamnus longistyla C.B. Wolf	0	1	Too rare to classify
Rhamnus mcvaughii L.A. Johnst. & M.C. Johnst.	0	1	Too rare to classify
Rhamnus sp.	1	0	Too rare to classify
ROSACEAE			
Cercocarpus macrophyllus C.K. Schneid.	2	0	Too rare to classify
Prunus brachybotrya Zucc.	6	3	Too rare to classify
Prunus rhamnoides Koehne	0	7	Too rare to classify
Prunus samydoides Schltdl.	0	3	Too rare to classify
Prunus tetradenia Koehne	2	0	Too rare to classify
Prunus sp. 1	0	1	Too rare to classify
Prunus sp. 2	0	1	Too rare to classify
RUBIACEAE			
Arachnothryx capitellata (Hemsl.) Borhidi	0	34	VER specialist
Calycophyllum candidissimum (Vahl) DC.	4	0	Too rare to classify
Chiococca pachyphylla Wernham	3	8	Too rare to classify
Chiococca sp.	1	0	Too rare to classify
Chomelia crassifolia Borhidi	1	0	Too rare to classify
Deppea grandiflora Schltdl.	0	2	Too rare to classify
Deppea sp.	1	0	Too rare to classify
Exostema caribaeum (Jacq.) Schult.	2	0	Too rare to classify
Guettarda sp.	3	0	Too rare to classify
Hamelia patens Jacq.	10	0	OAX specialist
Hintonia latiflora (DC.) Bullock	2	0	Too rare to classify
Palicourea padifolia (Humb. & Bonpl. ex Schult.) C.M. Taylor & Lorence	0	4	Too rare to classify

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Appendix.

Continued			
Psychotria galeottiana (M. Martens) C.M. Taylor & Lorence	0	1	Too rare to classify
Randia aculeata L.	0	7	Too rare to classify
Randia armata (Sw.) DC.	3	0	Too rare to classify
Randia monantha Benth.	0	14	VER specialist
Randia nelsonii Greenm.	3	0	Too rare to classify
Randia oaxacana Standl.	1	0	Too rare to classify
Randia tetracantha (Cav.) DC.	3	0	Too rare to classify
Rogiera langlassei (Standl.) Borhidi	24	0	OAX specialist
Solenandra mexicana (A. Gray) Borhidi	5	0	Too rare to classify
RUTACEAE			
Esenbeckia berlandieri Baill.	4	0	Too rare to classify
Ptelea sp.	0	1	Too rare to classify
Zanthoxylum melanostictum Schltdl. & Cham.	0	10	Too rare to classify
Zanthoxylum sp.	0	2	Too rare to classify
SABIACEAE			
Meliosma alba (Schltdl.) Walp.	0	1	Too rare to classify
Meliosma dentata (Liebm.) Urb.	0	3	Too rare to classify
SALICACEAE			
Bartholomaea sessiliflora (Standl.) Standl. & Steyerm.	3	0	Too rare to classify
Casearia nitida Jacq.	7	1	Too rare to classify
Casearia obovata Schltdl.	1	0	Too rare to classify
Casearia sylvestris Sw.	0	5	Too rare to classify
Casearia tremula (Griseb.) Griseb. ex C. Wright	8	0	OAX specialist
Casearia sp. 1	1	0	Too rare to classify
Casearia sp. 2	3	0	Too rare to classify

Continued			
Prockia crucis P. Browne ex L.	1	0	Too rare to classify
Samyda mexicana Rose	1	0	Too rare to classify
Xylosma sp. 1	1	0	Too rare to classify
Xylosma sp. 2	1	0	Too rare to classify
Xylosma sp. 3	4	0	Too rare to classify
Xylosma sp. 4	1	0	Too rare to classify
Xylosma sp. 5	1	0	Too rare to classify
SAPINDACEAE			
Matayba oppositifolia (A. Rich.) Britton	0	1	Too rare to classify
Sapindus saponaria L.	0	1	Too rare to classify
Thouinidium decandrum (Bonpl.) Radlk.	0	14	VER specialist
Thouinia villosa DC.	1	0	Too rare to classify
SAPOTACEAE			
Chrysophyllum mexicanum Brandegee ex Standl.	10	0	OAX specialist
Sideroxylon capiri (A. DC.) Pittier	6	0	Too rare to classify
Sideroxylon salicifolium (L.) Lam.	1	0	Too rare to classify
Sideroxylon sp.	1	0	Too rare to classify
SOLANACEAE			
Cestrum sp.	2	0	Too rare to classify
Solanum nigricans M. Martens & Galeotti	0	2	Too rare to classify
STAPHYLEACEAE			
Turpinia insignis (Kunth) Tul.	0	75	VER specialist
STYRACACEAE			
Styrax glabrescens Benth.	0	27	VER specialist
SYMPLOCACEAE			
Symplocos limoncillo Bonpl.	0	11	VER specialist
TAXACEAE			

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Appendix.

Continued			
Taxus globosa Schltdl.	0	5	Too rare to classify
THYMELAEACEAE			
Daphnopsis sp.	2	0	Too rare to classify
ULMACEAE			
Aphananthe monoica (Hemsl.) J.-F. Leroy	8	0	OAX specialist
URTICACEAE			
Cecropia obtusifolia Bertol.	2	0	Too rare to classify
Gyrotaenia microcarpa (Wedd.) Fawc. & Rendle	10	0	OAX specialist
Phenax mexicanus Wedd.	17	0	OAX specialist
Urera pacifica V.W. Steinm.	10	0	OAX specialist
VERBENACEAE			
Citharexylum berlandieri B.L. Rob.	0	2	Too rare to classify
Citharexylum caudatum L.	0	4	Too rare to classify
Citharexylum ligustrinum Van Houtte	0	3	Too rare to classify
Citharexylum mocinnoi D. Don	0	6	Too rare to classify
WINTERACEAE			
Drimys granadensis L. f.	0	2	Too rare to classify

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