

Patterns of Tree Diversity in the Tropical
Dry Forests of Pacific Coast Mexico

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For Big Al and Ann

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Abstract

The tropical dry forest (TDF) is characterized by both extreme seasonality of rainfall and rich biological diversity. Nowhere is that diversity richer than along the Pacific coast of Mexico. In this region, tree species in particular display tremendous diversity, representing a substantial fraction of the angiosperm evolutionary tree. Of particular interest is how this diversity comes together in individual communities and how that changes across an elevation gradient. In this dissertation, I look at the tree diversity of the TDF at two different sites—Oaxaca and Jalisco—from three angles. First, I took an ecological perspective, looking at how movement along an elevation gradient affects community composition, species richness, associations, and turnover (beta diversity) from one site to the next. Second, I examined diversity from a biogeographic perspective, looking at how geographic range size and center of range relate to abundance and presence in different communities. Third, I take a phylogenetic perspective, looking at how the relatedness of species in a given community changes with elevation and climate variables.

The most notable findings were as follows. In the first study, I found that the two regions, showed considerable similarity in species, higher taxonomic composition and importance values in tree communities across the broad geographic area. More than half of the species were common among the two sampling regions. Family dominance was also similar, with Fabaceae and Euphorbiaceae as the most important families in both regions. The dominant genera were also comparable between Oaxaca and Jalisco, though less so. The most notable differences between sampling regions were (1) Oaxaca exhibited greater overall diversity at all taxon levels, and that diversity increased with elevation—a trend not visible in Jalisco; and (2) the Jalisco samples showed greater per hectare basal area, due largely to higher stem densities in the < 15 cm DBH range. Of the species found in only one region, Jalisco had most taxa

occurring below 300m, whereas the majority of unique taxa in Oaxaca were found above 300 m—an important finding given that Oaxaca lacks protection for forest above 200 m.

In the second study, there was no significant correlation between abundance and range size. Overall, many more locally abundant species had small ranges than large ones. Most species occupied the majority of the TDF range north of the Panama Canal, and those species present in South America occupied the majority of that continent's TDF range as well. This pattern was independent of local abundance. Also, there was no relationship between range size and local niche breadth as measured by elevation, or between local abundance and distance to range center. I hypothesized that the absence of abundant species with large ranges was due to opposing environmental constraints that prevent a species from thriving in multiple ecosystems (e.g., in both tropical wet and dry forests).

In the final study, I hypothesized that there would be a phylogenetic signal showing community composition change across the elevation and climatic gradients. This was in fact the case, however, the relationship observed was the opposite of what was expected. Phylogenetic relatedness was negatively correlated with elevation at both the genus and species levels for both sites. Spatial analysis using ~1 km climatic data confirmed the pattern, showing a strong correlation between annual precipitation and NRI. Phylogenetic diversity, but not species richness, was also inversely related to elevation. These results contradict expectations that higher temperatures, less rainfall and greater seasonality at low elevations act as abiotic constraints that lead to phylogenetic clustering relative to upland sites. I hypothesized that climate fluctuations in the Quaternary made low elevation sites close to the ocean milder and more stable over intermediate time scales that would favor biotic regulation of community assembly

relative to higher elevation inland sites that would be mediated by abiotic climate-related factors.

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Chapter 1

A Comparison of Community Structure and Tree Diversity in Two Parts of the Mexican Tropical Dry Forest

Authors: John N. Williams, Irma Trejo, Mark W. Schwartz

Abstract

We measured tree diversity and relative abundance at northern (Jalisco) and southern (Oaxaca) sites in the tropical dry forest of Pacific coast Mexico. The goal of this study was to evaluate how community composition varies along an elevation gradient and at two locations separated by 1000 km and 4° of latitude. The two regions, each sampled by over 40 transects across an area of approximately 2000 km², show considerable similarity in species, higher taxonomic composition and importance values in tree communities across the broad geographic area. More than half of the species were common among the two sampling regions. Family dominance was also similar, with Leguminosae and Euphorbiaceae as the most important families in both regions. The dominant genera were also comparable between Oaxaca and Jalisco, though less so. The most notable differences between sampling regions were (1) Oaxaca exhibited greater overall diversity at all taxon levels, and that diversity increased with elevation—a trend not visible in Jalisco; and (2) the Jalisco samples showed greater per hectare basal area, due largely to higher stem densities in the < 15 cm DBH range. Of the species found in only one region, Jalisco had most taxa occurring below 300m, whereas the majority of unique taxa in Oaxaca were found above 300 m—an important finding given that Oaxaca lacks protection for forest above 200 m.

Key words: elevation gradient; Jalisco; Oaxaca; relative abundance; tree community; tropical deciduous forest.

Introduction

The tropical dry forest (TDF) of Mesoamerica is defined by latitude, a pronounced dry season from December to May, and a closed canopy of low stature compared to tropical humid forests (Murphy and Lugo 1986, Bullock 1995, Pennington et al. 2000). The TDF biome is diverse and heterogeneous across its broad range, with patches of semi-deciduous medium-stature forest (*selva mediana sub-caducifolia* or *sub-perennifolia*), savanna, and thorn forest adding varying degrees of complexity to the floristic composition of local communities (Rzedowski 1981, Perez-Garcia and Meave 2006). As an originally widespread ecosystem, it is also severely threatened (Janzen 1988, Miles et al. 2006). In an effort to understand how community floristic patterns change with geography and environmental gradients, we examined tree species composition at a northern and southern site in Mexico's Pacific coastal TDF—the most extensive and rich in plant species diversity and endemism of the Neotropical dry forests (Gentry 1995, Reichenbacher 1998, Lott 2006).

In each region we collected data on tree species composition, relative abundance and productivity across an elevation gradient using a suite of over 40 belt transects. The two regions, though 1000 linear kilometers apart, have good habitat connectivity and are comparable in climate, soils and topography (Ferrusquia-Villafranca 1993, Cotler 2002, Garcia-Oliva 2002, Trejo and Dirzo 2002, Salas-Morales et al. 2003)—conditions that make them appropriate for an analytical comparison of how tree species populate local communities in different parts of their range (Mouquet et al. 2003, Currie et al. 2004, Kolb and Diekmann 2004). In addition, the two regions

are of recognized conservation significance in that they include the Chamela-Cuixmala Reserve in Jalisco and Huatulco National Park in Oaxaca, two of Mexico's most important TDF protected areas.

Tree species lists for the two regions indicate a large, shared species pool and increasing overlap at the generic and family levels (Lott 2002, Salas-Morales et al. 2003). Species differences between the two regions offer clues to ways in which (a) the ecosystem is heterogeneous, (b) geographic ranges of species are limited or discontinuous, and (c) patterns of species richness and endemism vary spatially—all of which have important implications for understanding and conserving this ecosystem and its constituent species.

This study focuses on the relative abundance and elevation breadth of species within and between regions to describe community similarities and differences across a large part of the TDF range (Cornell and Lawton 1992, Caley and Schluter 1997, Cornell 1999, Stevens 2006). Specifically, we test the following hypotheses:

- 1) Patterns of taxonomic importance are conserved across regions and suggest a common species pool that assorts into communities in similar ways (Wright et al. 1998).
- 2) Species turnover across an elevation gradient does not differ appreciably across regions (Gaston 1996).
- 3) Species diversity and accumulation rates with sampling intensity are consistent across the TDF (Gotelli and Colwell 2001) as estimated using two regions, and the regions exhibit similar patterns of rarity and abundance among species, genera and families (Brown 1984, He and Gaston 2000, Kolb et al. 2006).

Empirical examination of the above hypotheses should help clarify the degree to which patterns in species pool assortment into local communities are consistent across the regional breadth of an ecosystem. While numerous mechanisms may

determine the likelihood that two or more species coexist at a local scale (Snyder and Chesson 2004), examining community composition at a regional level may reveal patterns that transcend local determinants of diversity and abundance (Lennon et al. 2004, Becerra 2005). That is, by looking at species composition at a local scale through repeated sampling, one may expect to see patterns emerge that are indicative of species traits, biogeographic affinities, or other variables that are more sensitive to regional processes than local ones. Alternatively, if the above hypotheses can be rejected, one can argue that local processes and environmental factors are more important in determining the profile of diversity and abundance at the community level. This is not to say that local diversity is independent of regional factors, such as species pools, but rather that the environmental filters operating locally overpower the signals coming from larger scales (Zobel 1997).

Methods

We selected southern and northern research regions (Huatulco, Oaxaca and Chamela, Jalisco, respectively) based on distance apart, extent of intact forest, access, and topographic comparability (Fig. 1). The geology and soils of the Oaxaca study area are characterized by a mixture of Paleozoic-aged metamorphic complex and Jurassic-aged gneisses. Scattered throughout are Pre-Cambrian aged gneissic units, and the northwestern part of the study area contains granitic units of Jurassic-Cretaceous origin, as well as areas of limestone from the lower Cretaceous. Quaternary-aged sedimentary units can be found in the lower-elevation plains and in drainages (INEGI 1988, Salas-Morales et al. 2003). Edaphically, the soils are primarily well-drained chromic cambisols with weathered regosols and lithosols in the northern part of the study area. Flood plains and drainages are characterized by alluvial soils higher in organic matter (INEGI 1989). The average annual temperature is 26.5° C and the wet

month to dry month ratio (>100 mm/month vs. <60 mm/month) is 4.4: 6.8 with approximately 800 mm of precipitation falling per year (Trejo and Dirzo 2002).

Geologically, Chamela is on the southern edge of the Jalisco Block, a unit associated with Holocene volcanics and the Trans-Mexican Volcanic Belt. Chamela also straddles the Colima Graben, a seismically active zone defined by granitic and granodioritic bodies of the Jurassic and early Cretaceous, as well as gabbro intrusions from the late Cretaceous. Soil conditions are characterized by granitic haplic lixisols, regosols, conglomerates composed of alluvial and colluvial regosols, and cambisols with interspersed phaeozems and fluvisols (Schaaf 2002). Annual precipitation averages 788 mm per year, and temperature averages 24.6° C. There is a 4:7 wet to dry month ratio.

The Oaxaca and Jalisco data were collected from September to December 2005 and 2006, respectively. In each region we located transects haphazardly stratified along an elevation gradient with the criteria of being in closed-canopy primary forest with no obvious signs of human influence (e.g., introduced species, grazing, or species extraction). Transects were located a minimum of 1000m apart, and covered a range of aspects and elevations from 24 to 547 m above sea level. A transect was a 2 m-wide strip along a contour line (i.e., constant elevation, perpendicular to the slope) measuring the species name and diameter of the first 100 trees or woody vines (lianas) encountered. Trees were defined as woody individuals \geq 2 m tall, \geq 2.5 cm diameter at breast height (DBH = 1.3 m), and single stemmed or unbranched below that height. Lianas had to originate within the transect and had to be \geq 2.5 cm in diameter above the root node. Transect length was recorded to calculate a tree density per area. Geographic position and elevation of each transect were recorded with a handheld GPS unit, and average slope and aspect were taken with a clinometer and compass. Because access to primary forest and different elevations varied by site (i.e., there was

more high elevation terrain in Oaxaca than in Jalisco), the number of transects in each 100 m elevation band is not exactly the same at each site.

The area surveyed in Oaxaca was roughly 50 x 40 km, while that of Jalisco was 80 x 30 km. The larger extent in Jalisco was due to greater conversion of forest to agriculture and tourism development, and thus the need to travel greater distances to find undisturbed sites. In total, we conducted 42 transects in Oaxaca and 41 in Jalisco. In total, the transects covered 2.23 hectares, and recorded 8296 individual trees.

Individual trees were identified to species in the field, and voucher specimens were collected when fruit or flowers were present and/or when identity was uncertain. Collected specimens were deposited at the national herbarium (MEXU) or the National Polytechnic Institute herbarium in Oaxaca for identification, and were then contributed to the respective permanent collections. Where species collection was not allowed or unfeasible, photographs were used for comparison to herbarium specimens for identification. Those few species that could not be identified with the available plant material were classified to the nearest taxon.

Transect locations were entered into a geographic information system (ESRI 2006) to facilitate comparisons and to add data from web-based and remotely sensed databases. A digital elevation map of each region was used to supplement elevation, slope and aspect data, which were sometimes recorded on-site with low confidence (minimal satellite reception).

Vegetation sampling to measure species richness in the tropics presents challenges for capturing a complete picture of diversity because many species are sufficiently rare as to elude detection. Species accumulation curves are a useful tool to assess the degree to which diversity is fully sampled and to approximate the percentage of species missed. We used a Monte Carlo single-omission jack-knife simulation (Heltshe and Forrester 1983) in which 1000 runs generated species

accumulation curves for each site. We analyzed saturation rates using Estimate-S (Colwell 2005) and WS2M (Turner *et al.* 2003) software. We compared community diversity using the Shannon, Simpson, and Fisher's alpha diversity indices, evenness (Ludwig and Reynolds 1988) and Sorensen Similarity index for beta diversity (Jost 2006) using PC Ord 4.2 (McCune and Mefford 1999). We ranked species by overall abundance and prevalence across transects. Families and genera were also ranked by number of sub-taxa, individuals and presence across transects. We constructed species presence profiles across the sampled elevation gradient and compared them across sites. We used Bray-Curtis ordination, detrended correspondence analysis (DCA) and non-metric multidimensional scaling (NMS) to look for similarities in spatial responses to underlying gradients across sites (McCune and Mefford 1999).

Results

A comparison of the density and size distribution of trees and woody vines (Fig. 2) shows that the Jalisco TDF had significantly more trees per hectare overall than the Oaxaca TDF (4476 stems/ha compared to 3532 stems/ha, $p < 0.001$), most of which is explained by differences in the lower size classes (< 15 cm diameter at breast height—DBH). Average basal area per transect was also greater for the Jalisco samples ($37.3 \text{ m}^2/\text{ha}$ compared to $31.2 \text{ m}^2/\text{ha}$, $p = 0.099$). In Oaxaca, basal area increased significantly with elevation (Fig. 3), whereas no similar relationship was observed between basal area and elevation at Jalisco.

In both regions the distribution of taxa by abundance showed strong inverse J curves, with few dominants and many uncommon to rare groups at a given taxonomic level. The dominant families in terms of (a) overall abundance of stems and (b) presence in the greatest number of transects were mostly the same at both sites (Table 1), although the families were not uniformly dominant across elevations. The

three most dominant families in both sites were Leguminosae, Euphorbiaceae and Rubiaceae, in that order. The other families in the top 10 lists for both sites were similar, with important differences in the greater dominance in Jalisco of Nyctaginaceae and Sapindaceae compared to Oaxaca; and the greater dominance of Bignoniaceae and Combretaceae in Oaxaca compared to Jalisco.

The ranking of genera and species by abundance and prevalence was more site-specific than for families, although *Lonchocarpus* (Leguminosae) and *Croton* (Euphorbiaceae) were the most abundant genera at both locales, and 11 of the top 20 genera were shared among regions. Three species (*Caesalpinia eriostachys*, *Bursera instabilis* and *Apoplanesia paniculata*) ranked in the top 10 for importance value (IV) in both regions, but the majority of the remaining highest ranked species were site-specific (Table 2). Although multiple species ranked high for IV in more than one elevation band in a given region, this trend was 50% more prevalent in Oaxaca than Jalisco.

Of the 388 total species identified, 154 (40%) were found in both regions, and 140 of 218 genera (64%) were shared. For each of these shared taxonomic groups, we divided them into three equal-sized classes (rare, moderate, common) according to their importance values at each site and performed chi-square contingency tests to see if a taxon at one site was more or less likely than would be expected by chance to be in the same IV class at the other site. We found both tests to be significant ($p=0.003$ for species; $p<0.001$ for genera), with many more taxa sharing the same abundance classification across regions than expected.

Species accumulation curves show that Oaxaca's greater diversity is evident at low levels of sampling, and that the two sites show signs of flattening out at similar levels of sampling (Fig. 4). Table 3 shows species diversity and evenness and describes taxonomic richness for the two regions.

A look at the relationship between species richness and elevation shows that the Oaxaca TDF has a non-significant positive correlation, while the Jalisco TDF shows a negative trend (Fig. 5a). The results are similar when richness is decomposed into its site- and elevation-specific species components (Figs. 5b and 5c).

Within the same elevation band, transects at a given site show consistent species similarity when compared to one another using the Sorensen similarity index (Fig. 6). Oaxaca shows a gradual decrease in within-band similarity as elevation increases, most visible at the highest elevation band, which has significantly lower levels of internal similarity compared to other bands. The Jalisco bands do not reveal any elevation-related trend in within-band similarity.

We compared between-elevation band similarity of species composition within regions and found similar rates of species turnover (Table 4). For both regions, similarity declines with increasing elevation difference between bands. There is also a trend of greater species turnover ($1 - \text{similarity}$, a proxy for beta diversity) for higher elevation comparisons. These results suggest that the two regions are comparable in terms of beta diversity, and that beta diversity explains some of the increased species richness found at higher elevations, at least in Oaxaca.

Discussion

The premise of this study was that the 1000 kilometers and four degrees of latitude that separate the tropical dry forests of Jalisco and Oaxaca would provide sufficient distance to evaluate whether change in location across the geographic range of the dry forest ecosystem results in predictable changes in plant family representation, species composition and importance values, and whether such variables are sensitive to an elevation gradient. The similar physical environments at

both sites, such as soil type, average temperature, rainfall and duration of dry season facilitated these comparisons.

We found that these forests are similar in many ways—a finding that is indicative of their inclusion in a broadly defined and broadly distributed tropical dry forest biome. The results of the contingency tables for importance values of the shared taxa demonstrate that these groups play more similar roles in their respective communities than we would expect by chance. Furthermore, even in cases where the dominant species and genera differ among sites, both sites are dominated by members of the Leguminosae and Euphorbiaceae in terms of species diversity and within-stand abundance. Similarly, plots across these two regions are almost indistinguishable in terms of simple descriptive metrics of within-plot diversity and dominance. Sorenson similarity indices comparing plots within elevation bands are also generally alike, as are the indices comparing plots across elevation bands, suggesting similar rates of species turnover in the two regions. These findings led us to accept our first hypothesis, which posits taxonomic similarity and a common species pool.

The species overlap is substantial given the distance between the two sites and reported differences across the Mexican TDF. We note that 44% of the shared species occur in both regions at roughly the same frequency (see Table 2 for examples of differences in rankings). While this value is higher than that reported by Trejo and Dirzo (2002), it is important to put the numbers in context. Trejo and Dirzo (2002) compared 0.1 hectare plots at two locations in coastal Oaxaca and included shrubs, trees and lianas down to 1 cm DBH, whereas our individual plots sampled smaller areas at each site, did not include shrubs and only sampled down to 2.5 cm DBH. Our study, however, sampled more than 4000 trees in 40 transects in each region spread out across a 500 m elevation range and 2000 km², thus presenting a more robust estimate of similarity at the landscape level, though perhaps not as strong an estimate of alpha

diversity at the individual site level. This nuance is of interest for plant geographers considering range-abundance relationships (Murray and Lepsch 2004, Mills and Schwartz 2005), but is perhaps more important for its conservation implications. Specifically, the observation that species abundance patterns are conserved means that there is a large suite that remains rare at all elevations and over a broad latitudinal span. These species observed as rare in our study may comprise a suite of suffusively rare tree taxa. Suffusive rarity is defined as a species that is broadly distributed, but everywhere uncommon (Schoener 1987a). Tropical trees may be prone to suffusive rarity, as suggested by our data. Suffusively rare taxa pose a particular conservation problem as it may be very difficult to predict how many of what kinds of occurrences would represent an adequate population to protect the conservation of these biotic resources.

We tentatively accepted our second hypothesis, which states that species turnover within a region or across an elevation gradient would not vary across regions. We say "tentatively" because while turnover across elevation bands did not differ appreciably across regions, the greater diversity in Oaxaca above 300m suggests an elevation-diversity relationship. While there is an effect due to changes in climate and vegetation type—we estimate that roughly 20% of the species encountered in the highest elevation class in Oaxaca are more characteristic of the more mesic semi-deciduous forest (*selva mediana*) than of the TDF, compared to about 10% of the Jalisco species—we would need to sample well into the semi-deciduous forest range to say for sure which species prefer that vegetation type.

Despite the similarities, two fundamental differences emerge in the floristic composition of these regions. First, stand density and basal area were higher in the Jalisco TDF. This observation does not concord with the general trends for latitude and productivity (Scheiner and Reybenayas 1994), however, it is also not without precedent

(Partel *et al.* 2007). Given the trend does not hold for trees greater than 15cm DBH, the differences may also be an artifact of recent climate or differential biotic changes within the two regions (e.g., herbivore load).

The other major difference we observed between the regions was that family, generic and species diversity were higher in the Oaxaca site. Although we rejected our hypothesis that the sites are similar in species richness, this result is not altogether unexpected. Closer to the equator, warmer and wetter, Oaxaca can be expected to have greater diversity (Gentry 1982, Mittelbach *et al.* 2007), although evidence suggests this pattern may not hold for the Mexican TDF (Trejo and Dirzo 2002). Oaxaca also has a larger potential species pool, due to its biogeographic position at the nexus of the North American and Caribbean/Central American floristic provinces, and to its relative proximity to South America (Graham 1993, Wallace 1997).

Oaxaca's greater diversity is most striking at higher elevations. This may be (a) where the southern TDF diversity is concentrated, (b) a sampling effect (i.e., had we been able to sample more at higher elevations in Jalisco, we would have encountered additional species), or (c) a result of Oaxaca's elevation gradient continuing into semi-deciduous and then montane forests up to 2000m or more, and a degree of species spillover from these forest types into the TDF. In this last scenario, the increased number of species may be due less to a richer TDF, and more to a porous lower-bound in species associated with different forest types. In contrast, around Chamela, Jalisco, 550m really is an altitudinal upper bound, as there is both a plateau that separates the coastal forest from the higher-elevation inland forests, and a human-dominated landscape in the form of grazed and cultivated lands separating those forests.

The Oaxaca TDF also exhibits most of its "unique" species (those not encountered in the Jalisco transects) above 300m elevation. This finding may have important conservation implications because the only protected area in the Oaxaca

TDF is Huatulco National Park, a narrow strip of coastal forest and mangroves with only moderate topographic variation and a maximum elevation of 200m (CONANP 2003). By contrast, Jalisco has the Chamela-Cuixmala Reserve, which protects TDF habitat from 40 to 500m above sea level—essentially the entire altitudinal range of the coastal TDF. Thus, if we can show that the greater diversity and species uniqueness of the higher elevations in Oaxaca is as it appears—high alpha diversity and endemism rather than an increase in the presence of broadly tolerant and/or satellite species (*sensu* (Hanski 1982)—then TDF at this elevation band should receive conservation prioritization, especially given the pace of development in the Oaxaca study area.

Previous studies (Lott et al. 1987, Trejo and Dirzo 2002, Salas-Morales et al. 2003) have identified the areas around Chamela, Jalisco and Huatulco, Oaxaca as two of the most plant species-rich in the greater tropical deciduous forest ecosystem of Mexico—a core zone that contains the greatest plant diversity of the TDF ecosystem in Mesoamerica (Gentry 1995). This study has described patterns of floristic diversity in this species-rich TDF habitat, comparing and contrasting the two regions and detailing where taxonomic uniqueness and overlap occur. It is our hope that the results from this study can be used (1) in an ecological context to guide thinking about the processes and evolutionary history that have shaped this flora, and (2) in a conservation context to help environmental managers develop strategies to safeguard the impressive diversity that occurs within this threatened ecosystem.

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Figures



Figure 1. Location of the two tropical dry forest regions sampled in this study (circles).

The northern region encompasses roughly 2400 km² and is centered around Chamela, Jalisco (19°31'N; 105°04'W); the southern region encompasses roughly 2000 km² and is centered around Huatulco, Oaxaca (15°45'N, 96°08'W).

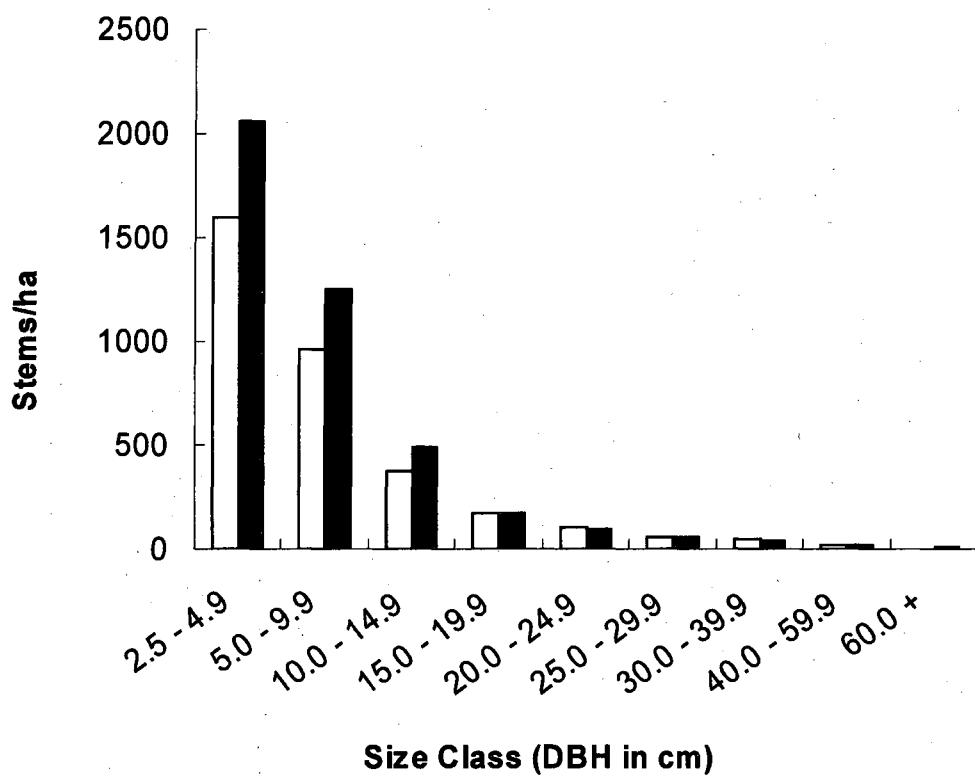


Figure 2. Distribution of trees and woody vines by size class as sampled from two regions of the tropical dry forest in Pacific Coast Mexico (Oaxaca = white bars; Jalisco = black bars). Size classes are defined by tree diameter at breast height (DBH).

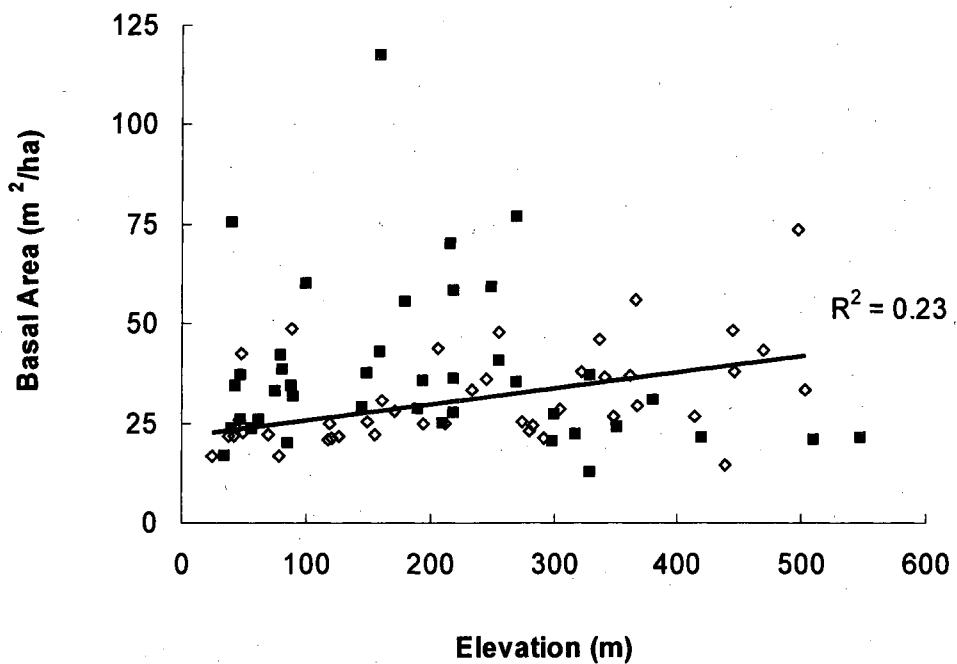
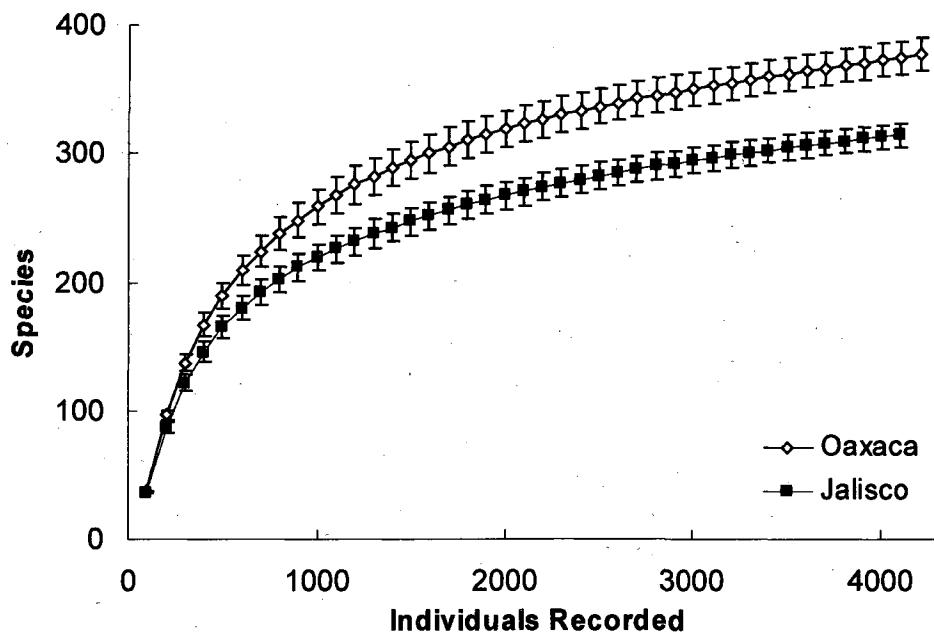


Figure 3. Basal area of tropical dry forest trees $\geq 2.5\text{cm DBH}$ for each transect of 100 trees and plotted by elevation. Open diamonds represent Oaxaca transects; closed squares represent those in Jalisco. The R^2 value shown is for Oaxaca and is the only significant one ($P = 0.001$).



* Error bars are +/- one standard deviation.

Figure 4. Species accumulation curves for sampling of trees and woody vines ≥ 2.5 cm DBH in two regions in the tropical dry forest of Pacific Coast Mexico.

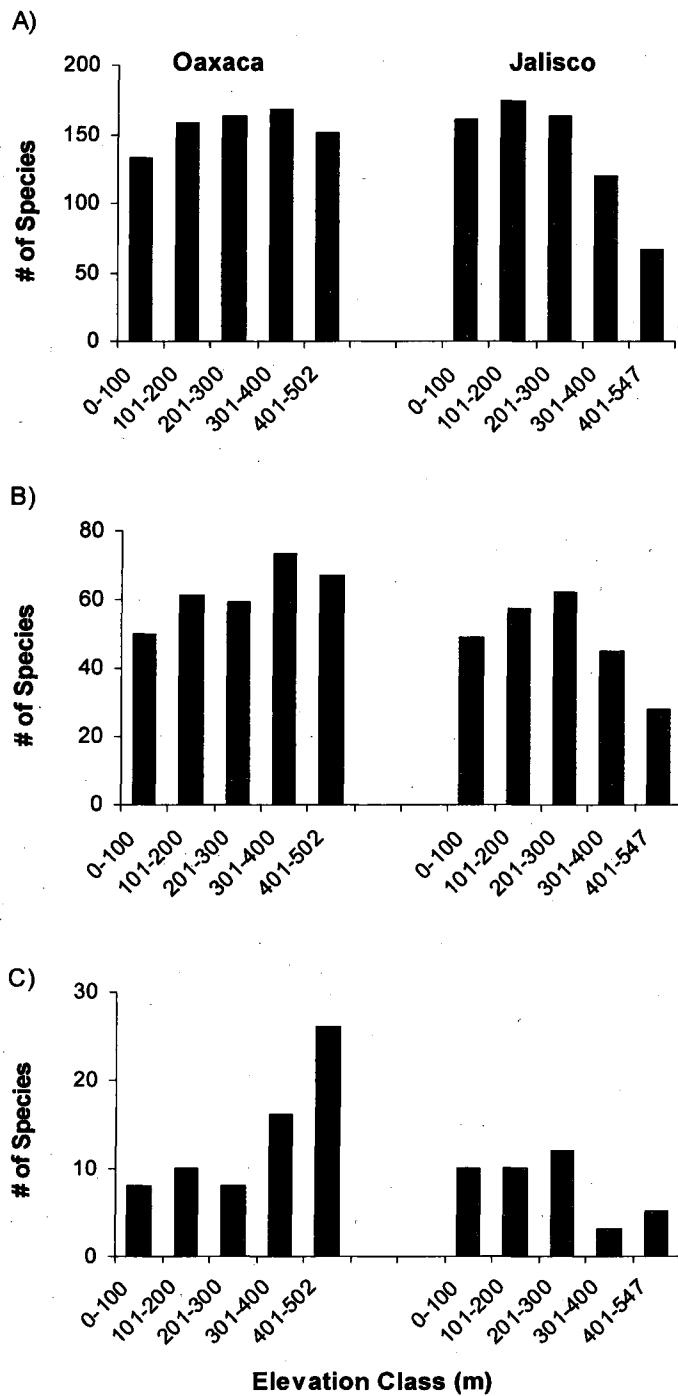


Figure 5. Comparison of tree species diversity by elevation band at two regions in the tropical dry forest of Pacific Coast Mexico. Graphic (A) compares all species found at each elevation band; (B) compares species that are unique to each site; and (C) compares those species that are unique to both their site and elevation class.

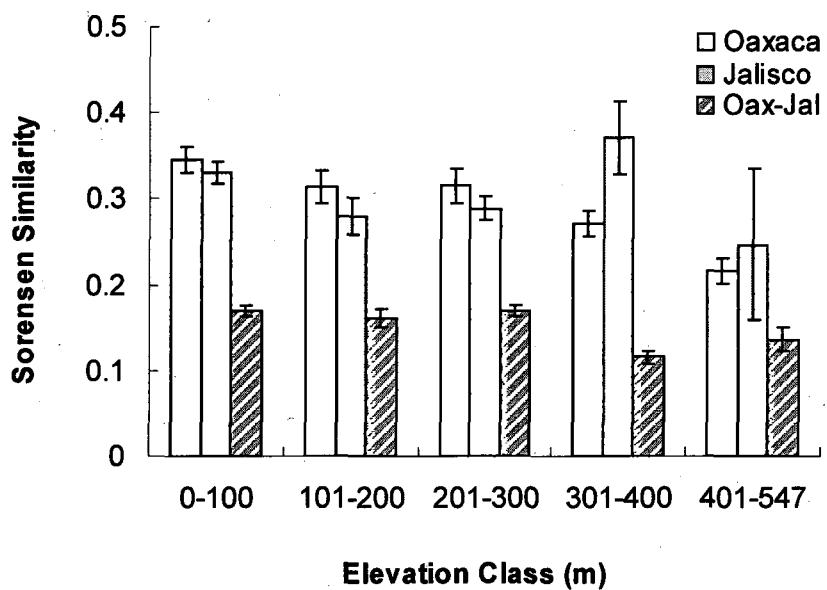


Figure 6. Species similarity within elevation bands within and across northern (Jalisco) and southern (Oaxaca) tropical dry forest regions of Pacific Coast Mexico. Values are based on averages of Sorenson Similarity Index for all pair-wise comparisons of species composition of transects within the same elevation class. Error bars represent the standard error of the mean.

Tables

Family	Oaxaca Abundance Ranking	Oaxaca Prevalence Ranking	Jalisco Abundance Ranking	Jalisco Prevalence Ranking
Leguminosae *	1	1	1	1
Euphorbiaceae*	2	5	2	2
Rubiaceae*	3	3	3	4
Anacardiaceae**	4	8	7	5
Burseraceae**	5	2	9	6
Bignoniaceae	6	6	11	11
Flacourtiaceae**	7	4	10	8
Tiliaceae	8	17	8	10
Combretaceae	9	16	21	24
Boraginaceae**	10	10	5	7
Apocynaceae	11	7	13	12
Sapindaceae	12	9	6	9
Cactaceae	13	14	26	23
Nyctaginaceae	14	12	4	3
Capparaceae	15	20	12	13

Table 1. Ranking of tree families by abundance and prevalence at two locales in the Mexican Pacific Coast tropical dry forest. Abundance refers to the total number of stems of a tree species in a given family and prevalence refers to the number of transects in which the species occurs. One asterisk families rank in the top five in all categories; two asterisk families rank in the top ten in all categories.

Species (Family)	Overall Rank		Rank by Elevation Band (m)				
	J	O	0-100	101-200	201-300	301-400	401-547
<i>Amphipterygium adstringens (Juli)</i>	40	4	3-O		2-O		
<i>Apoplanesia paniculata (Legu)</i>	3	10	2-J				
<i>Astronium graveolens (Anac)</i>	21	15	5-J				5-O
<i>Bursera excelsa (Burs)</i>	132	8	4-O				
<i>Bursera instabilis (Burs)</i>	7	3			2-J;1-O		2-O
<i>Caesalpinia eriostachys (Legu)</i>	1	6	1-J;5-O	2-O	5-O		
<i>Cnidoscolus tubulosus (Euph)</i>	x	2	1-O	3-O			
<i>Comocladia engleriana (Euph)</i>	42	7			4-O		
<i>Cordia alliodora (Bora)</i>	8	22		3-J		3-O	
<i>Croton septemnervius (Euph)</i>	x	1	2-O	1-O	1-O		
<i>Gliricidia sepium (Legu)</i>	11	46					1-J
<i>Guapira macrocarpa (Nyct)</i>	2	24	3-J	4-J	5-J	4-J	
<i>Helicarpus pallidus (Tili)</i>	4	x		5-J	4-J		
<i>Lonchocarpus constrictus (Legu)</i>	44	9		5-O			
<i>L. emarginatus (Legu)</i>	6	21			1-J		
<i>L. magallanesii (Legu)</i>	14	44		2-J			
<i>Lysioma microphyllum (Legu)</i>	15	5		4-O	3-O		
<i>Piptadenia obliqua (Legu)</i>	5	19				3-J	4-J
<i>Poeppigia procera (Legu)</i>	9	99				1-J	2-J
<i>Thouinia paucidentata (Sapi)</i>	10	66	4-J				

Table 2. Ranking of top twenty tree species by region (Jalisco = J; Oaxaca = O) and elevation according to importance value (IV = relative basal area + relative frequency + relative density) in the tropical dry forest of Pacific Coast Mexico. Rankings by elevation class are only for the top 5 from that class. Species in bold are ranked in the top 10 of both sites; "x" means the species does not occur at that site. The first four letters of the family name are in parentheses, e.g., "Legu" refers to Leguminosae.

	Oaxaca	O-s.d.	Jalisco	J-s.d.
Number of Families	65		61	
Number of Genera	189		168	
Number of Species	294		248	
Species per Transect	37.5	6.67	35.4	7.13
Fisher's Alpha	22.9	8.60	20.6	7.43
Shannon Diversity (H)	3.15	0.31	3.13	0.38
Simpson Diversity (D')	0.925	0.043	0.929	0.052
Evenness	0.871	0.054	0.881	0.064

Table 3. Comparison of community taxon diversity and structure of tree species in 4197 and 4099 trees sampled from two tropical dry forest regions of Pacific Coast Mexico. Diversity indices and evenness are per transect averages with standard deviations (s.d.).

Elev (m)	101-200		201-300		301-400		401-520	
	Oax	Jal	Oax	Jal	Oax	Jal	Oax	Jal
0-100	0.83	0.78	0.72	0.68	0.51	0.59	0.32	0.35
101-200			0.80	0.79	0.58	0.66	0.40	0.41
201-300					0.70	0.74	0.50	0.48
301-400							0.69	0.64

Table 4. Sorenson similarities of tree species composition between elevation classes within each of two tropical dry forest regions (Oaxaca, Jalisco) of Pacific Coast Mexico.

Chapter 2

Tropical Dry Forest Trees and the Relationship between Local Abundance and Geographic Range

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Abstract

Data from two sites in the tropical dry forest (TDF) of Pacific Coast Mexico suggest that the majority of tree species do not conform to the macroecological theory that posits a positive correlation between local abundance and geographic range size. We compared field data from primary forest in Oaxaca and Jalisco to occurrence data from national and online databases to examine how local patterns relate to putative geographic range areas and latitudinal breadth. Results showed no significant correlation between abundance and range size. Overall, many more locally abundant species had small ranges than large ones. We found that most species occupy the majority of the TDF range north of the Panama Canal, and those species present in South America occupy the majority of that continent's TDF range as well. This pattern was independent of local abundance. We also found no relationship between range size and local niche breadth as measured by elevation, or between local abundance and distance to range center. We hypothesize that the absence of abundant species with large ranges is due to opposing environmental constraints that prevent a species from thriving everywhere.

Key Words: biogeography; community; elevation; Jalisco; latitude; macroecology; niche breadth; Oaxaca.

Introduction

A central tenet of macroecology argues that within large assemblages of species, one should see a positive relationship between abundance and geographic range size (Brown 1984, Brown 1995, Gaston 2003). A corollary to this theory is that niche breadth and range size are also positively correlated (Pyron 1999, Thompson et al. 1999, McPherson and Jetz 2007). Given the attention to these relationships in the ecological literature (Holt et al. 2002), there have been surprisingly few attempts to examine its robustness in plant communities. For those studies that have looked at plants, some have found a positive relationship between abundance and incidence at selected spatial scales (Gotelli and Simberloff 1987, Collins and Glenn 1990, Boeken and Shachak 1998, Russell et al. 2005), but not at the scale of the entire geographic range. Still others have found contradicting evidence that uncommon species are widespread and abundant species have narrowly defined ranges (Pitman et al. 1999, Kenfack et al. 2007).

That a positive abundance-range correlation exists at the local and landscape scales makes intuitive sense, as spatial autocorrelation in density, dispersal, and environmental conditions is a general feature of forest ecosystems (Miller et al. 2002, Schwarz et al. 2003), just as it in other systems. One can expect to see a pattern whereby organisms in homogeneous habitats disperse from a high density zone into a less populated surrounding matrix of similar or only marginally inferior quality (Bahn et al. 2008). The scale for which this explanation is viable, however, is generally limited to distances that are relevant to individual organisms over the course of their lifespan, which is usually much smaller than the species' geographic range.

At the geographic range scale, which is much larger than the dispersal distance for most organisms, the correlation of movement and environmental homogeneity breaks down, and one must look for other mechanisms to explain correlation between

local abundance and range size. Of the mechanisms offered by (Gaston et al. 1997) to explain why locally abundant species might be expected to have large ranges, the resource breadth and resource availability hypotheses—species that use a wide breadth of resources or that depend on resources that are widespread have the largest ranges—are the most compelling for plants. Yet for plants and some animal species, these resource characteristics explain distribution much better than abundance (Hughes 2000). While there are certainly examples of generalist plant species that thrive across a broad range (Page 2002), or specialists that exist at low densities in small ranges (Rabinowitz et al. 1986), it remains to be seen whether an assemblage of plant species supports the relationship that some have claimed to be virtually universal (Hanski et al. 1993).

A number of studies have looked for, but not found, the abundance-range relationship in forest tree communities (Pitman et al. 2001, Kolb et al. 2006, Kenfack et al. 2007). This lack of evidence does not negate the possibility that the relationship exists. If tree communities do exhibit the pattern on a range scale that many faunal communities have shown (Holt et al. 2002), then it would be of broad interest to investigate whether the underlying mechanisms were the same (Kotze et al. 2003). Conversely, if there is consistently no pattern or a different one, then it is worth examining whether local abundance is linked more to local biotic or abiotic factors, (e.g. competition, precipitation gradients), or whether there are broadly applicable ecological or evolutionary explanations, such as spatial or temporal niche partitioning, neutrality, phylogenetic clustering/dispersion or combinations thereof (Bell 2001, Chase and Leibold 2003, Cavender-Bares et al. 2004, Volkov et al. 2007, Kelly et al. 2008).

From a conservation perspective, it would be useful to know how tightly local abundance is linked to distribution, and distance to range center so that the extent of rarity and endemism might be more accurately assessed. For example, while not

conforming to the positive abundance-range relationship on the community level, the findings of (Pitman et al. 2001)—that large expanses of lowland neotropical rainforest are dominated by small oligarchies of tree species and that the rarest species are not widespread—hint at macroecological patterns that could help direct conservation efforts.

In this study, we test the applicability of the abundance-range and niche breadth-range relationships at the ecosystem level. The study system, the tropical dry forest (TDF) of Pacific Coast Mexico, has a species-rich flora subject to strong biotic interactive forces (Kelly and Bowler 2002, Becerra 2007) and abiotic constraints (Cuevas-Reyes et al. 2004), particularly the marked seasonality of rainfall (Andresen 2005). These characteristics lend themselves to probing for both macroecological relationships and some of the above-mentioned alternatives. Additionally, the Mexican TDF (Figure 1) is of interest for its high biodiversity, endemism and broad recognition as a threatened ecosystem (Gentry 1995, Brooks et al. 2006, Miles et al. 2006).

Methods

We selected southern and northern research sites on the Pacific coast of Mexico (Huatulco, Oaxaca and Chame, Jalisco, respectively, Figure 1) based on the extent of intact primary forest, high diversity (Trejo and Dirzo 2002, Lott 2006), access, topographic comparability and for their widely-spaced positions in the Mexican TDF. Although 1000 km apart, the two sites examined in this study are part of contiguous biome (Olson and Dinerstein 2002).

At each site we collected data on tree species composition, size and relative abundance using 2m – wide belt transects laid along contour lines (constant elevation). We haphazardly stratified transects along an elevation gradient from 24 – 547 m.a.s.l. with the criteria of being in closed-canopy primary forest with no obvious signs of

human influence A transect was a 2 m-wide strip along a contour line (i.e., constant elevation, perpendicular to the slope), the length of which was determined by distance needed to encounter 100 viable trees or woody vines (lianas). A viable tree was defined as a woody individual \geq 2.5 cm diameter at breast height (DBH = 1.3 m), single stemmed or unbranched below that height. Lianas had to emerge from the ground within the transect and had to be \geq 2.5 cm in diameter above the root node. The identity of each individual was recorded and transect length was measured to calculate tree density. Geographic position and elevation of each transect were recorded with a handheld GPS. Average slope and aspect were measured using a clinometer and compass.

We conducted a total of 83 transects, measuring 8297 trees representing 387 species or morpho-species. Of those, 319 species were both unambiguously identified to species level and had open source global distribution data available that we could use to estimate geographic range from (CONABIO 2006, MBG 2008). Species were identified using diagnostic fruit and flowers, photos, comparison to herbarium specimens and/or collected and sent to herbaria for identification as conditions allowed. All voucher specimens were deposited in the permanent collections of either the national herbarium (MEXU) at the National Autonomous University (UNAM) in Mexico City or the National Polytechnic Institute herbarium in Oaxaca.

To define geographic distributions for species, we tabulated and transferred point distribution records into a geographic information system (ESRI 2007). We did not include records outside the Western Hemisphere or that appeared as isolated occurrences in latitudes suggesting cultivation (e.g., many species were recorded as occurring in the Missouri Botanical Gardens in Saint Louis, Missouri, USA). From the remaining records, we created putative geographic distributions by drawing the minimum convex polygon (MCP) around the occurrences for each species and clipping

out any ocean area. Because CONABIO's occurrence data for Mexico was more extensive, we used it to extend range size and latitudinal breadth where appropriate. We used JMP statistical software (SAS 2007a) to compare abundance, elevation breadth and other occurrence data on geographic range size.

Results

The abundances for the 320 species considered here show the reverse "J" curve typical of species-rich tropical communities (Figure 2). The distribution for latitudinal breadth of range for those species according to published occurrences shows a bimodal distribution with a larger hump of species having ranges from 5-20° and a second smaller hump with ranges from 45-55°, attenuating to very few species with ranges greater than 60° (Figure 3). As New World TDF occurs predominantly between 6° and 27° north and south of the equator, this bimodal distribution suggests that a large number of species are restricted to, but are found throughout, the northern TDF. Those species that made it across the narrow land bridge into the southern TDF, or from south to north, are also able to inhabit the majority of that biome's latitudinal breadth.

We found a strong positive correlation between total stem number and the number of transects in which a species occurred, indicating that abundance is a good predictor of occupancy (Figure 4). We saw no relationship, however, between species' abundance at a site and geographic range size using the MCP metric. We tested the relationship between abundance and range size independently by site and using the combined abundances of species present in both sites; we used both linear and logarithmic scales with no change in results (Figure 5).

Because the TDF is a relatively understudied system, we expect many species have not been detected in parts of their range. As a result, an approximation of range

using existing herbarium records and databases may underestimate range size in some cases. The use of the MCP to approximate range size may introduce its own biases into range estimation, potentially including large areas of inappropriate habitat. The polygons are generated by connecting one occurrence to another with a line that may cross habitat where that species is never found. Also, species with part of their distribution in South America may have much larger range sizes because South America contains much more area per degree of latitude than does Central America. Thus the relatively larger ranges of species found in South America might be an artifact of geography and not an indicator of any increased ecological tolerance or evolutionary adaptability of those species.

To examine the characteristics of geographic range without using MCP area or using complex habitat suitability models that require data on many environmental variables, we used latitudinal range breadth based on recorded occurrences as a second range metric. We tested the Jalisco and Oaxaca data sets for a correlation between the latitudinal breadth and local abundance. We found no correlation at either study site ($p=0.49$ Jalisco; $p=0.28$ Oaxaca). Examining this data further, we divided the species list into quartiles according to abundance to see if the least abundant and most abundant quartiles might reveal correlations with small and large ranges, respectively. Instead we found similar distributions as shown in Figure 3 (Figure 6). Analyzing a species' abundance at a site as a function of the linear distance in km from the putative center of its range (using the centroid of the MCP) we also found no correlation ($R^2 < 0.01$ for both Jalisco and Oaxaca).

In addition to testing for a correlation between abundance and geographic range, we wanted to test for a relationship between niche breadth and range. We used the elevation breadth across which a species was detected at a given site as a surrogate for niche breadth. Because species that occur more often will have a higher

probability of being detected at more elevations, we did a regression of abundance on elevation breadth and used the residuals to remove the effect of abundance. We then plotted these residuals against latitudinal range breadth, but found correlation ($R^2 < 0.001$).

Discussion

The purpose of this study was to examine how local demographic characteristics of a community of tree and liana species at two sites in the TDF reflect or predict geographic range. By having two sites that are widely separated yet share a large fraction (>40%) of their species and a similar climate, we were able to compare how species' local abundance, occupancy and elevation breadth across a site change or stay the same as a function of range size, breadth and distance to center of range. Based on relationships between abundance and geographic range found for other taxa (Blackburn et al. 1997, Gaston 2003), our working hypothesis was that local abundance and geographic range would be positively correlated, whether taken together or by individual site. We found that local abundance predicted number of transects occupied at a site—a finding that, while perhaps not of much ecological interest (Wright 1991), corroborates results reported by other investigators (Gaston et al. 2000, Holt et al. 2002, Soininen and Heino 2005). We found no evidence, however, that the abundance-breadth relationship could be extrapolated to the scale of geographic range. Moreover, we can think of no *a priori* reason that such an extrapolation should hold for plants, given that the general processes thought to determine patch occupancy, such as dispersal and recruitment success, depend on local conditions and are heterogeneous at the scale of geographic range. That is, factors such as soil conditions, micro-climate, competition and herbivory are not expected to be spatially autocorrelated at large scales.

Are rare species are common where you find them? When the number of exceptions to a theory reaches a critical mass, a competing theory generally emerges. Such is the case with the abundance-range size relationship and the finding that globally rare species are often common in the few places where they are found—sometimes even more abundant than co-occurring widespread species (Lesica et al. 2006). Figure 5A suggests that not only are there no species that are abundant and widespread, but also there are numerous restricted-range species that are locally abundant. A chi-square contingency test did not, however, find that there were more locally common species with large ranges than expected by chance. The test also found that the number of locally common small-breadth species was almost exactly what was expected.

Numerous study species that were locally uncommon were found to have large ranges. Of the species shared among both sites, the least abundant quartile had a larger mean range size than the most abundant quartile (although not significantly so) and 61.7% of the least abundant quartile species had ranges larger than the median range size for all shared species. This pattern is suggestive but not indicative of widespread uncommonness or suffusive rarity (*sensu* (Schoener 1987b). Since data on relative abundance is itself scarce, it is difficult to know whether these species are truly suffusively rare. In examining rare species of North America, (Mills and Schwartz 2005) found very few species that would be classified as such. (Rabinowitz et al. 1986) also found this type of rarity to be uncommon to absent (depending on the strictness of the definition used) in their classification of the flora of the British Isles. Although saying nothing about geographic range size, Pitman et al. (2001) found that while the majority of individuals found at two widely-separated sites in the humid tropics of the western Amazon were from common species, the majority of species represented in both sites were uncommon where found. As more abundance data becomes available, it will be

interesting to see if a large number of species are widespread and everywhere uncommon in both the TDF and tropic humid forests.

Although there are a number of ways to improve upon our estimation of range boundaries for the study species—either with more extensive data collection or using tools like habitat suitability or species distribution models ((Guisan and Thuiller 2005, Phillips et al. 2006)—there is little to suggest that such effort would yield significant correlations for these species. Just as others have found links between local abundance and habitat parameters such as niche and range size to be weak despite limitations in their approach (Macnally 1989, Kenfack et al. 2007), so too do we feel confident that the absence of a pattern is not due to methodological shortcomings.

The confidence in our findings aside, it is important to point out the mitigating factors that could change our values for range size and elevation breadth. First, the MCP is a crude estimate of range area and exaggerates range in some cases (e.g., a species that occurs only in coastal areas of Peru, Venezuela and Brazil will include the majority of the Amazon in its range). Second, there is a high likelihood that many of the uncommon species have larger ranges than currently thought because they have gone undetected because of rarity and sparse sampling in many parts of the TDF. Third, the estimate of niche breadth using local elevation breadth depends on detecting the species where it occurs. However, if a species is sufficiently rare as to only be detected once, it has an elevation breadth of zero meters, even though it may exist at other elevations in the survey area. Thus, the less likely we are to detect a species within transects, the narrower its recorded niche breadth will be. Furthermore, many species have ranges that go beyond the elevation limits imposed by this study and will therefore register only their truncated ranges stopping at 550m. This limit was selected because there is a rainfall gradient that increases with elevation, resulting in a wetter and less draught-regulated habitat containing a different suite of species that is more

apparent above the 550m elevation mark. These species are more characteristic of semi-deciduous or semi-evergreen forests (*bosque sub-caducifolia* or *sub-perrenifolia*, JNW, personal observation).

The above caveats aside, there was not a hint of the abundance-range size correlation discussed in macroecology literature (Brown 1995, Gaston 2003). The only pattern we saw that begs an ecological explanation was the absence of any species above the dashed line in Figure 4. We hypothesize that two factors may be responsible for the absence of species that are both widespread and abundant. First, the TDF is a much harsher environment than the tropical rain forest, and species that thrive there must be well-adapted to draught. However, a species with a geographic range that spans the neotropical dry forests on both sides of the equator would likely have to spill over into rainforest areas. Such a species would need to split the environmental difference between the requirements of the TDF and the rainforest, making it unlikely to thrive in either. Alternatively, species spanning multiple habitat types occur in disjunct populations, suggesting that they are able to occupy this breadth of range only because the TDF was historically contiguous when range expansion occurred (Caetano et al. 2008).

The second factor limiting TDF species from being both widespread and abundant may be dispersal. Rainforest trees depend more on animal dispersal, while TDF species tend to be more wind dispersed. Would-be animal dispersers, such as birds, are largely absent or dormant in the TDF during the dry season when many of the trees flower and fruit. Conversely, wind dispersal is largely ineffective in the dense conditions of the rain forest. Additionally, much of the neotropical TDF tends to be along the edge of mountain ranges. These mountains may act as barriers to broad dispersal for many species, and conversely may favor the evolutionary importance of endemics in community structure (Gordon et al. 2004). Although a sizeable percentage

of the species considered here were present in both sites, many of them are still restricted-range species, endemic to Mexico. Their shared presence is probably due at least in part to the fact that both sites are on the western side of Sierra Madre Occidental mountain range. It would be interesting to test whether there were fewer shared species and different range patterns at TDF sites in Veracruz or the Yucatan that are comparable distances away, but separated by more substantial geographic barriers. Likewise one could test these patterns elsewhere in the TDF where topographic features such as the inter-Andean valleys have been shown to harbor high levels of endemism (Lewis et al. 2006, Linares-Palomino 2006).

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Figures

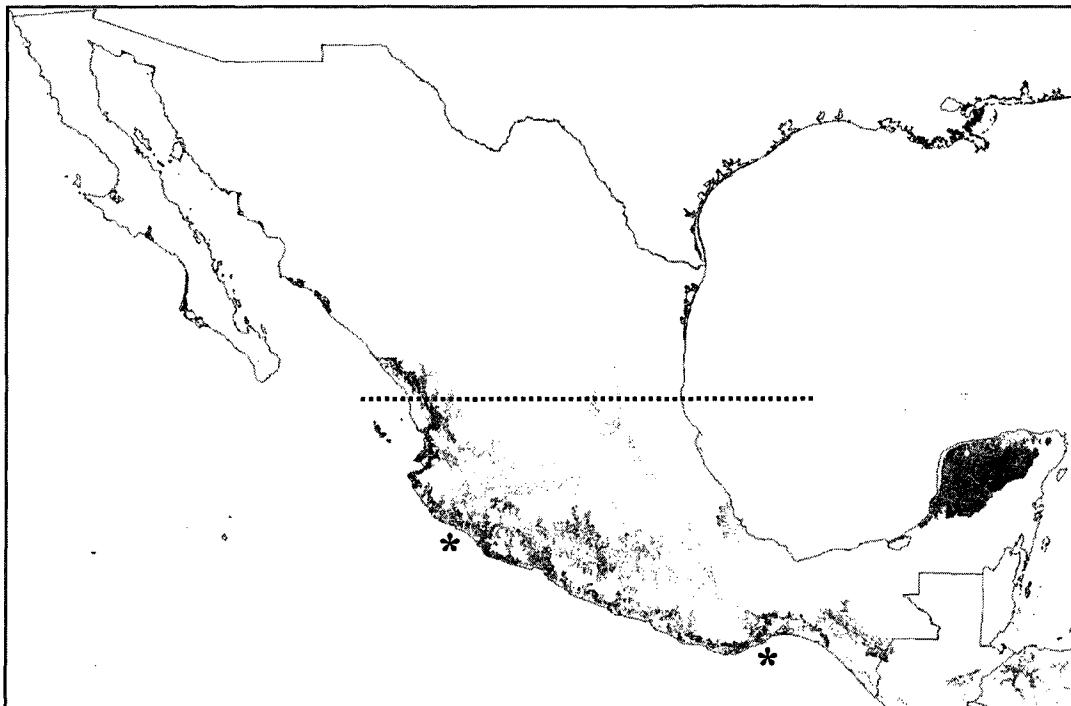


Figure 1. Distribution of closed canopy tropical dry forest (TDF) in the tropical latitudes (below the dashed line) of Mexico (reproduced with permission from (Miles et al. 2006). Mexico has the largest remaining area of this ecosystem in Mesoamerica. Formerly, the TDF was contiguous along the Pacific slope from Sonora to Panama. Asterisks show the northern (Jalisco) and southern (Oaxaca) field sites.

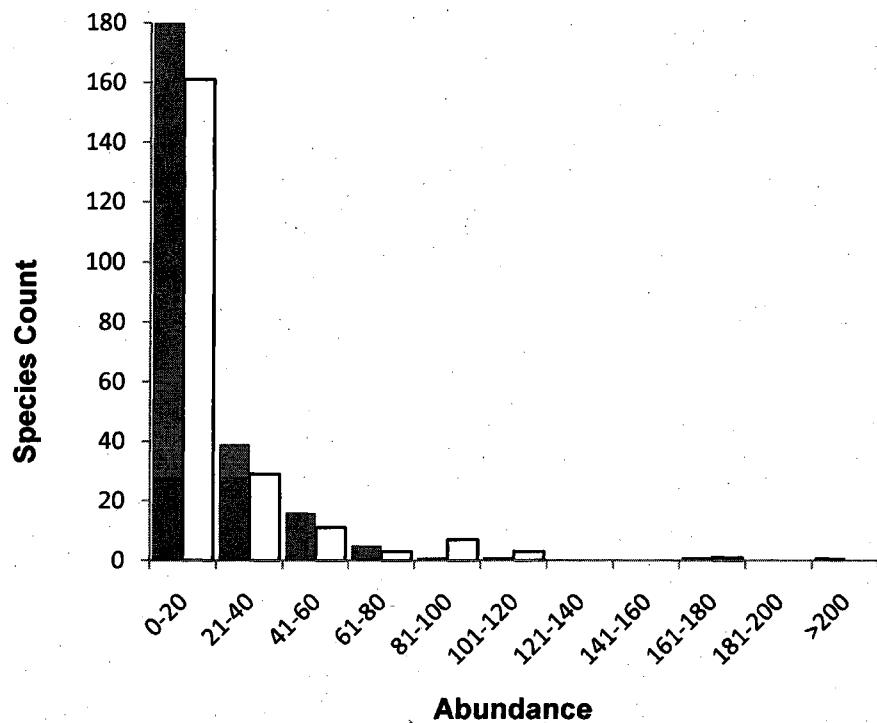


Figure 2. The graphs show the distribution of the study species ($n=318$) by abundance (A) and latitudinal range (B). Data on abundance was collected for this study; latitudinal range data comes from open source online records (see text).

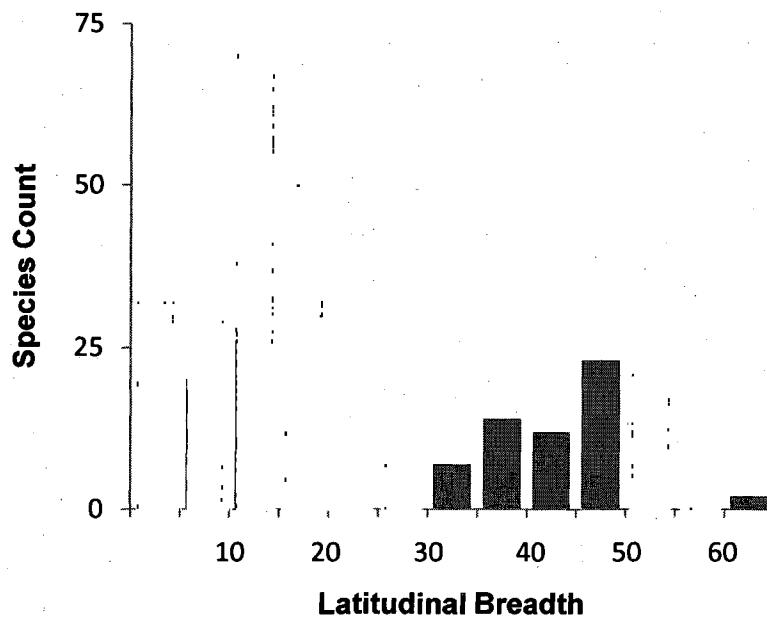


Figure 3. Distribution of latitudinal range breadth for tree species ($n=320$) recorded at two sites in the tropical dry forests of Mexico. The distributions for the sites taken separately show the same bimodal pattern.

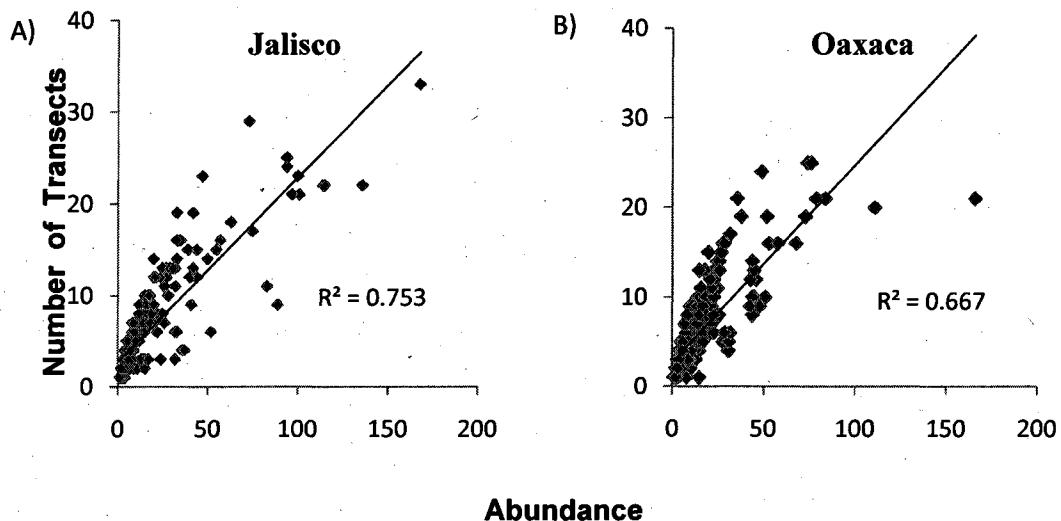


Figure 4. Species abundance from plots regressed against the number of transects in which it occurs for Jalisco ($n=210$) and Oaxaca ($n=238$) field sites. Both regression lines are highly significant ($p < 0.001$).

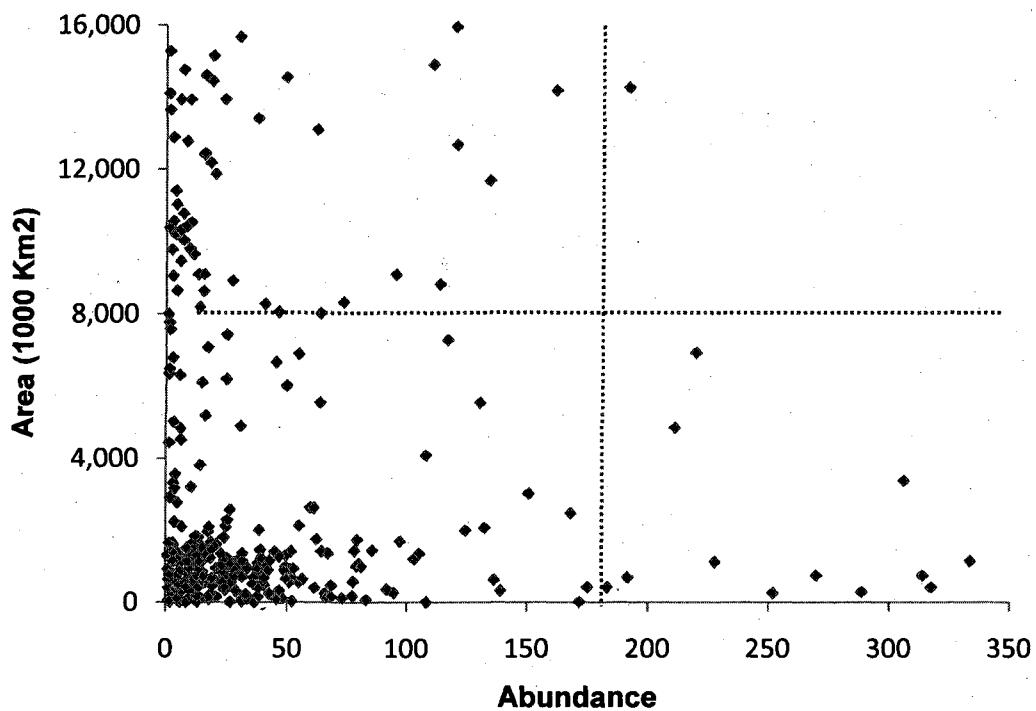


Figure 5. Species abundance normalized by area surveyed at two field sites plotted against geographic range area (using minimum convex polygons around occurrences—see text) for 318 tree and liana species with published occurrence records (Conabio 2006; MBG 2007). Note that most abundant species are narrowly distributed and almost no species are both abundant and have large ranges (upper right quadrant). There is no correlation between abundance and range size ($r^2 < 0.01$).

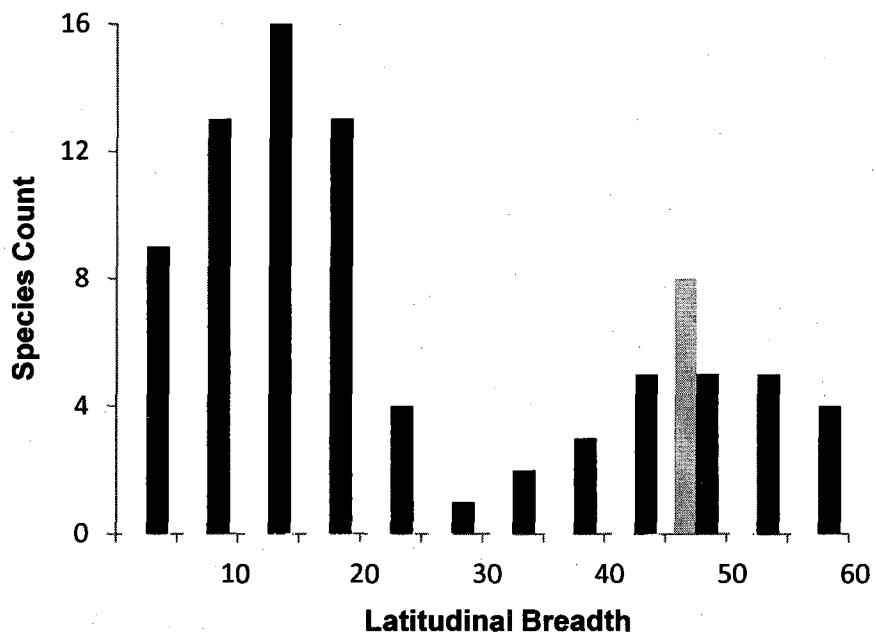


Figure 6. Latitudinal breadth of range compared to local abundance for the least abundant (grey) and most abundant (black) quartiles of tree and liana species found at two sites in the tropical dry forest of Mexico.

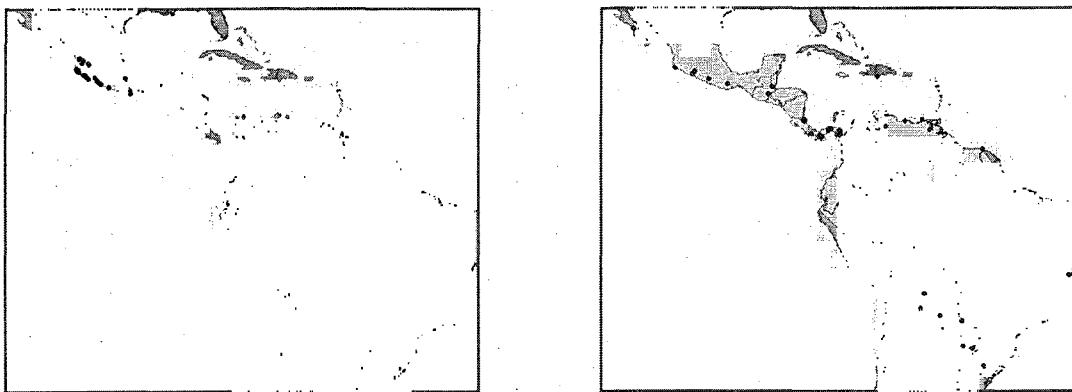


Figure 7. Illustration of the reverse relationship between local abundance and range size. Shown on the left is the minimum convex polygon (MCP – light area) and recorded presences (dark diamonds) for *Bursera instabilis* (Burseraceae), one of the most abundant tree species in both the Oaxaca and Jalisco sites, occurring a total of 149 times and accounting for 1.8% of all trees sampled, but with a global distribution limited to a small area within the Mexican dry forest. In contrast, the map on the right shows the MCP and records for *Cordia curassavica* (Boraginaceae), a tree that occurs only twice (once at each site) among the more than 8000 individuals recorded, yet has one of the largest putative geographic ranges of any species encountered in this study.

Chapter 3

Patterns of Phylogenetic Dispersion in Tropical Dry Forest Trees and Implications for Community Assembly

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Abstract

The tropical dry forests of Mexico exhibit both high floristic diversity and strong seasonality, inviting an analysis of the relative roles of biotic and abiotic factors in community assembly. I sampled tree diversity in plots across an elevation gradient at two widely-separated sites on the Pacific slope and compared the phylogenetic diversity in each sample with that of the site species pool. Because rainfall correlates positively with elevation, I hypothesized that there would be a phylogenetic signal showing community composition change across this gradient. For each site I used the species list to construct a phylogenetic supertree based on published relationships and the Angiosperm Phylogeny Group's backbone tree. I then made pruned phylogenetic trees composed of the species found in each transect as sample communities. All trees were agnostic about branch length, using simple unity between nodes. I used Phylocom software to analyze the trends in the net relatedness index (NRI) and phylogenetic diversity of sample communities with respect to the supertree across the elevation gradient. Phylogenetic dispersion was negatively correlated with elevation at both the genus and species levels for both sites. In a spatial analysis using ~1 km climatic data, I confirmed the strong correlation between annual precipitation and NRI. Phylogenetic diversity, but not species richness, was also inversely related to elevation. These results contradicted expectations that higher temperatures, less

rainfall and greater seasonality at low elevations would lead to phylogenetic clustering relative to upland sites. I hypothesize that climate fluctuations in the Quaternary made low elevation sites close to the ocean milder and more stable over intermediate time scales that would favor biotic regulation of community assembly relative to higher elevation inland sites that would be mediated by abiotic climate-related factors.

Key Words: abiotic filtering; clustering; competition; elevation gradient; Jalisco; Oaxaca; over-dispersion; phylogeny; Quaternary; species distribution.

Introduction

Biotic (competition, predation) and abiotic (environment) constraints are generally seen as opposing forces in regards to their respective roles in shaping community species structure (Elton 1946, Macarthur and Levins 1967, Menge and Sutherland 1987, Chesson and Huntly 1997), with the former driving communities toward dissimilarity among the component species, and the latter selecting for similarity. That is, for species to coexist in a community shaped by biotic constraints, they must assemble or evolve in a way that allows them to partition resources and minimize direct competition (*sensu* (Schoener 1965). By contrast, environmental constraints, such as climate or soil type, act as filters that select for a set of traits that the member species must possess in order to persist (Keddy 1992). One can think of these constraints as forming two ends of a continuum, along which communities can be situated depending on the relative strength of each.

Clearly, community assembly is more complex, with factors like time, disturbance and spatial scale figuring prominently into this complexity (Belyea and Lancaster 1999, Leibold et al. 2004), but there is a value in this simplification in that it offers a first filter for considering the major axes of community organization (e.g.,

(Cardillo et al. 2008). The addition of phylogenetic topographies into the analysis of community structure and assembly (a) permits a more nuanced understanding of how constituent species respond to biotic and abiotic constraints (Ackerly 2003, Webb et al. 2006), and (b) makes a more compelling case for situating a community at a given point along the biotic-abiotic continuum in terms of the forces that shaped that community (Cavender-Bares et al. 2004, Cooper et al. 2008).

The origins of ecological theories about what causes communities to be composed of similar or dissimilar organisms come from observations of species traits (e.g., (Darwin 1859). Each of those traits has an evolutionary expression in the genome of the species that possess it. Shared traits in a species assemblage can occur either by being conserved in evolutionary lineages that undergo speciation events or by being derived, as multiple lineages converge on a similar trait in response to the same constraint. Alternatively, communities will assemble or lineages will diverge based on differences that promote coexistence. These types of patterns are frequently visible in the examination of community phylogenies (Winemiller 1991, Losos et al. 2003).

The community phylogenetic tree has a wide range of ecological applications and can frequently be constructed using published phylogenies and minimal or no time in a genetics laboratory. The two-way nature of trees allows them to be used as backbones on which to map specific traits, or as exploratory tools that can be used to look for phenotypic responses across gradients (Webb et al. 2002, Johnson and Stinchcombe 2007). At the community level, phylogenies can be used to elucidate how evolutionary processes shape assemblages, niche structure and trait distribution and either support or contrast with present ecological processes (Webb et al. 2002). Phylogenetic analyses of plant communities or specific clades have been used to test for over-dispersion or clustering with respect to specific traits, environmental gradients,

or to test the role that competition plays in determining community composition (Kembel and Hubbell 2006, Verdu and Pausas 2007, Prinzing et al. 2008). Likewise, the strength or weakness of a phylogenetic signal has been used to assess the spatial and taxonomic scales at which processes such as competition and niche partitioning are taking place (Cavender-Bares et al. 2006, Swenson et al. 2007, Kelly et al. 2008). In this study, I used the phylogenetic relatedness of tree communities relative to local species pools in the tropical dry forests of Mexico to examine how environmental gradients shape community assembly. I assessed the somewhat counterintuitive results in the spatial and taxonomic scales across which these signals appear and reconsider what the underlying drivers of phylogenetic clustering and over-dispersion might be in this case.

Methods

I selected two study sites in the Mexican TDF: a southern site near Huatulco, Oaxaca; and a northern site near Chamela, Jalisco (Figure 1). Both sites are part of a contiguous dry forest ecosystem and share a similar climate with considerable overlap in species lists (Noguera et al. 2002, Trejo and Dirzo 2002, Salas-Morales et al. 2003). The roughly 1000 km that separate the sites ensure that the two sites are independent of one another in terms of all the biotic and abiotic variables that shape community assembly (e.g., dispersal, disturbance, weather, etc.) except for those that operate on regional or continental scales (e.g., timing and length of dry season).

The Oaxaca and Jalisco data were collected from September to December 2005 and 2006, respectively. In each region I located transects haphazardly stratified along an elevation gradient with the criteria of being in closed-canopy primary forest with no obvious signs of human influence (e.g., introduced species, grazing, or species extraction). Transects were located a minimum of 500m apart, and covered a range of

aspects and elevations from 24 to 578 m above sea level. Each transect consisted of a 2 m-wide strip along a contour line (i.e., constant elevation, perpendicular to the slope) whose length was determined by the distance necessary to include the first 100 trees or woody vines (lianas) encountered. Trees were defined as woody individuals \geq 2 m tall, \geq 2.5 cm diameter at breast height (DBH = 1.3 m), and single stemmed or unbranched below that height. Lianas had to break ground within the 2 m-wide transect and had to be \geq 2.5 cm in diameter above the root node. Transect length was recorded to calculate tree density per unit area. Geographic position and elevation of each transect were recorded with a handheld GPS unit. Because access to primary forest and different elevations varied by site (i.e., there was more high elevation terrain in Oaxaca than in Jalisco), the number of transects in each 100 m elevation band is not exactly the same at each site.

The area surveyed in Oaxaca was roughly 50 x 40 km, while that of Jalisco was 80 x 30 km. The larger extent in Jalisco was due to greater conversion of forest to agriculture and tourism development, and thus the need to travel greater distances to find undisturbed sites. In total, I conducted 43 transects in Oaxaca and 41 in Jalisco, covering 2.23 hectares, and recorded 8396 individual trees.

Trees were identified to species in the field, and voucher specimens were collected when fruit or flowers were present and/or when identity was uncertain. Collected specimens were deposited at the national herbarium (MEXU) or the National Polytechnic Institute herbarium in Oaxaca for identification, and were then contributed to the respective permanent collections. Where species collection was not allowed or unfeasible, photographs were used for comparison to herbarium specimens for identification. Species that could not be identified with the available plant material were classified to the nearest taxon. For purposes of constructing a phylogenetic tree for

each site, only species that could be positively identified to the genus level were included in the analysis (Appendix 1).

For each site I constructed a parent phylogenetic tree consisting of all the species identified in the transects. To do this, I took the species lists of trees identified to genus or better and classified them according to family. I then constructed a backbone tree with branches for each family represented using the tree structure adopted by the Angiosperm Phylogeny Group (Stevens 2008). I extended the tree to sub-family and genus where possible using (Soltis et al. 2000) and (Mabberley 2008). I then used specific publications on individual families or clades to resolve the relationships down to the species level where possible, otherwise I left the grouping as a polytomy (see Appendix 2 for parent trees and references used).

Each phylogenetic tree was prepared using Mesquite (Maddison and Maddison 2008) or CAIC software (Purvis and Rambaut 1995), and pruned according to the specific analysis (e.g., individuals \geq 5 cm DBH, genus level, family level). Because availability of information about branch length was extremely variable, I made the trees agnostic with respect to branch length, choosing simple unity at the species level as the basis for all branches (default setting). I used Phylocom software (Webb et al. 2008) to generate a net relatedness index (NRI) and phylogenetic diversity (D_p, (Faith 1992) of the transects (sample communities) at a site with respect to the parent tree for that site using the *construct* function. In general terms, the software creates a null model for a sample community of size x by randomly drawing x individuals from the parent (site) phylogeny a specified number of times (10,000). It then generates an NRI and D_p value for each sample relative to the null model. There is an option to weight the null model for each sample according to the abundances of the component taxa, which I included in the analyses. Using an R script (Gentleman et al. 2006) that maps sample phylogenies onto a parent phylogeny (B. Anacker, *pers. com.*), I examined how

movement along the elevation gradient was expressed in the phylogenetic topology in terms of which branches or clades appeared or disappeared in a sample community.

Transect locations were entered into a geographic information system (ESRI 2007) and overlaid onto a climate surface (www.worldclim.org) with 30 arc-second (~1 km) resolution (Hijmans et al. 2005) to generate climate variables for each transect. I performed exploratory regression and principal components analyses (SAS 2007b) to determine which climate variables were significantly correlated with NRI and Dp, and how those variable correlated with one another.

Results

For both the Oaxaca and Jalisco transect data, NRI had a significantly negative correlation with elevation at the genus and species level (Figure 2). The correlations were also a negative for restricted species lists of individuals \geq 5 cm DBH (a proxy for reproducing adults; Oaxaca: n=228, p<0.001; Jalisco: n=190, p=0.017), and species from Fabaceae (compared to a site legume phylogeny; Oaxaca only, p=0.033). When taxon abundance in each transect was incorporated into the regression of NRI on elevation, the significance levels and R² values increased for all Oaxaca analyses, but decreased for the Jalisco analyses, with only the genus-level regression remaining significant (p=0.025) and species-level regression becoming marginally significant (p=0.059). There was no significant relationship between elevation and NRI at the family level for either site.

Species to genus and genus to family ratios were calculated for each sample community and regressed against elevation to assess whether the phylogenetic patterns found were due to the simple addition or removal of taxa from one or more clades across the gradient. There were no significant trends with respect to either of these ratios and elevation. I then examined the elevation distributions of the site taxa to

see if there were any consistent patterns with respect to the upper and lower limits of those ranges that would explain the NRI pattern found. There were families that were limited to lower elevation transects (e.g., Achatocarpaceae \leq 200 m; Cucurbitaceae: \leq 340 m; Zygophyllaceae \leq 130 m) and upper elevation transects (e.g., Dilleniaceae \geq 330 m; Fagaceae \geq 330 m; Lauraceae \geq 270 m). The number of individuals they represented was small, however, and thus it is uncertain whether the elevation restrictions observed are real or an artifact of small sample sizes. The effect of these families on the overall phylogenetic signal was minimal.

An analysis of genera by elevation range was more informative. I considered only genera represented by \geq 10 individuals at a given site and calculated an elevation range for each, defined by the mean elevation at which it occurred (weighted by the number of individuals recorded at a given elevation) plus and minus one standard deviation. I then took the upper and lower elevation quartiles of genera for each site (Table 1) and analyzed their phylogenetic relatedness relative to the site genus tree in the same way that I analyzed the original sample communities using Phylocom (Table 2). Although only the low-elevation genera in Oaxaca were significantly different (over-dispersed) relative to the null distribution, all categories exhibited the same trends as the overall NRI analysis presented in Figure 1. Namely, there was relative clustering at upper elevations and greater dispersion at lower elevations. This analysis held constant the number of genera compared at lower and upper elevations at a site. Additionally, I divided the elevation range at Oaxaca into two equal bands (0-289 m and 290-578 m) and compared the genera whose range (mean \pm 1 s.d.) fell entirely within the lower band to genera from the upper band. The lower band contained 30 genera from 19 families compared to 21 genera from 14 families for the upper band, showing greater taxon richness and phylogenetic diversity at the lower elevations (this comparison was not valid for the Jalisco site due to the lack of upper elevation sample

communities). An analysis of sample community phylogenetic diversity (D_p) corroborated this finding, with significant negative correlations between phylogenetic diversity and elevation at both sites (Figure 3).

Results from the analysis of climate data showed significant correlations between NRI and the bioclimatic variables examined (Table 3a). Because there are correlations among climate variables I performed a principal components analysis to identify the magnitude and direction of variable overlap (Table 3b). The first principal component, which explains 67.7% and 77.0% of the variation in Jalisco and Oaxaca, respectively, correlates strongly with elevation ($R^2 = 0.755$ Jalisco; $R^2 = 0.872$ Oaxaca). I then added the first two principal components to the list of bioclimatic variables and elevation and used an automated stepwise regression, with 0.30 probability to enter and 0.10 to leave, to make the best model for each site with the species-level NRI weighted by abundance as the dependent variable (Table 4).

Discussion

Climate in the Mexican TDF imposes strong environmental constraints on species in the form of a long (5 – 7 month), hot dry season. At the same time, tree species diversity is high, approaching the diversity of tropical wet forests in places. In the Mexican TDF rainfall tends to increase and temperatures tend to decrease with elevation. Given the general trend of increasing floristic diversity with rainfall in the tropics (Gentry 1988), I expected to see phylogenetic clustering at low elevations in response to abiotic cues, moving to over-dispersion at higher elevations where biotic interactions were presumably the primary organizing force on community assembly—the opposite of what I found. While the elevation range explored here is confined to the TDF itself and is much smaller than that explored by Gentry, the trend I found was nevertheless significant and robust at the species and genus levels in two widely-

separated sites (though not at the family level—see Kelly et al. (2008) for evidence that niche partitioning in the TDF occurs at or below the level of genus).

Precipitation, temperature and length of dry season were the major environmental variables occurring across the elevation gradients that I considered in the analysis. Their importance was reflected in the two stepwise models I made (Table 4), where total annual precipitation was the most important predictor variable for both sites, and temperature annual range was included in both (precipitation seasonality regressed significantly with NRI at both sites, but temperature seasonality did not at the Jalisco site; neither of these two variables, however, is a direct measure of length of dry/wet season). Regression analysis showed that most of the bioclimatic variables gave significant to highly significant regressions with NRI. Likewise, the principal components analysis (Table 3a) demonstrated that the variables load fairly evenly on the first two components (more so for PC1 than PC2). Without further information to separate causation from correlation, I do not have much in the way of clues as to why one or more of these variables would produce the surprising patterns I found.

There is no a priori reason to suspect that the general phylogenetic pattern associated with community assembly along the biotic-abiotic continuum should be reversed for the dry forest, *per se*. Without a compelling ecological explanation—there is no evidence of a counter-current variable, such as increased herbivory (Becerra 2007, Dirzo and Boege 2008) operating preferentially at low elevations, that would produce the over-dispersion signal I found—it seems probable that an historical or evolutionary explanation may be more compelling. History, or the lack thereof (i.e., insufficient time to come to equilibrium), can mask or counteract the kinds of phylogenetic signals one might otherwise expect from a given system, e.g., (Lowenberg-Neto et al. 2008). In another example, Losos et al. (Losos et al. 2003),

gave compelling evidence as to why evolution in island communities of anoles precludes a phylogenetic signal of niche conservatism under conditions of sympatry.

The majority of the common dry forest genera are also found in the tropical wet forests (TWF), leading to the characterization of the TDF flora as a "depauperate subset" of the TWF (Gentry 1995). At least part of this reduction in floral diversity (as well as some of its endemism) may be explained by the combination of harsher climate of the TDF and its history during the Cenozoic era (Graham and Dilcher 1995). There is evidence that there were as many as 20 major glacial/interglacial periods lasting on the order of 100,000 and 10,000 – 20,000 years, respectively, over the course of the Quaternary (Johnson 1982). The longer-lasting glacial periods are presumed to have been cooler and drier and may have caused major vegetation shifts (Ortega-Rosas et al. 2008), as well as extinctions to occur, especially among taxa more adapted to the TWF (van der Hammen and Hooghiemstra 2000).

There is broad support for the hypothesis that Quaternary climate fluctuations were responsible for enriching landscape-level biodiversity by mixing previously disjunct species and allopatric populations through the creation of refugia (Haffer 1969, Whitmore and Prance 1987, Richardson et al. 2001). The primary response of taxa to climate change, however, was most likely migration rather than speciation, especially considering the relatively short time scales involved (Huntley and Webb 1989). Extinctions undoubtedly also occurred on a large scale for those species that either could not make it to refugia or were not tolerant of the changing conditions.

Taking a place-based perspective rather than a taxon-based perspective then, one may predict that the effect of frequent climate fluctuations outside of refugia would have been a loss of diversity and a simplifying of community structure that was more pronounced at high latitudes and high elevations than in the tropics or at low elevations. Such changes with respect to latitude have been documented in the

analysis of continental phylogenies. Hewitt (Hewitt 2000, Hewitt 2004) reviewed and analyzed phylogenetic data from the arctic, temperate Europe and North America and the tropics to show that climatic cycling in the Quaternary had a restricting effect on phylogenies—making them shallower with increasing latitude.

Temperature seasonality in the tropics is less pronounced than it is in the temperate and polar regions, although rainfall can be quite seasonal (especially in the sub-tropical latitudes—home to some of the world's most arid places). Just as it is in temperate climes, however, fluctuations in temperature and rainfall in the tropics, whether seasonal or diurnal, tend to be more dramatic with increases in elevation. It is because of the diminished level of seasonality in the tropics that mountains and topographic relief are thought to produce tighter species packing along elevation gradients and greater barriers to species movement and range expansion relative to temperate latitudes (Janzen 1967).

The Sierra Madre Occidental mountain range, which delineates the eastern edge of the TDF of Pacific Coast Mexico, was formed 34 – 15 Mya when conditions are thought to have been warmer and wetter up until the beginning of the Quaternary glaciations than they are today (Moran-Zenteno 1994, Graham and Dilcher 1995). Relative to the mountains, the coastal areas would have been drier and warmer, and were probably defined by a smaller dry forest biome than is present today. The longer glacial periods, relative to the interglacials, are generally thought to have brought cooler, drier conditions that would have allowed for the expansion of the dry forest biome ((Pennington et al. 2000) although see (Colinvaux et al. 1996)) up the western slope of the Sierra Madre and with it, the retreat of vegetation adapted to wetter conditions. The comparatively brief returns of warmer, wetter conditions may not have been sufficient for the more hydrophilic species to return, whereas more of the dry forest taxa of the day, the majority of which were of wet forest origin, could most likely

have persisted during those wet periods. The low elevation areas closest to the coast probably remained relatively dry even during the interglacials because (a) the wet periods are thought to be similar to today's climate and thus still fairly dry (Graham and Dilcher 1995), and (b) proximity to the ocean must have had a buffering effect on climate change relative to the mountainous interior.

I take these reconstructions together with the phylogenetic signals from the study sites—especially at the Oaxaca site where the more heavily sampled upper elevations produce stronger patterns at all levels and a similar signal within the legume phylogeny—to hypothesize that oscillating climatic conditions over the roughly 2.5 Mya of the Quaternary would create conditions for species assembly that were more stable at lower elevations and closer to the coast. On the western slopes of the Sierra Madre where the deciduous dry forest grades into semi-deciduous montane forest today (300–600 m), the fluctuating climate would have caused divergent selection (Saint-Laurent et al. 2003)—alternatively favoring taxa adapted to warm, wet conditions during the interglacial periods, and those adapted to cool, dry conditions during the glacial periods—ultimately selecting for subset of taxa tolerant of a broad climatic range. In terms of species richness, the upper elevation communities might have just as many if not more species than the lower elevation communities because of the greater mixing of wet and dry forest taxa (although I saw no trend one way or the other). By contrast, the lower elevations would be expected to have phylogenetically deeper lineages because the milder, more stable climate would have provided more time for speciation within lineages and produced fewer extinctions.

Reconstruction of ecological communities on geologic time scales is particularly challenging for the tropical dry forest because lakes and other mesic environments that accumulate fossil evidence are scarce. Lacking such an evolutionary smoking gun, one can turn to the phylogenetic record that is increasingly yielding rich insights on past

events and present patterns (Becerra 2005). One should be vigilant, however, for new evidence either in the fossil record or elsewhere that may corroborate or contradict current hypotheses, as drawing conclusions about a poorly understood biome like the TDF from a small number of sites or taxa may lead to erroneous conclusions (Dick and Wright 2005). While far from being a foregone conclusion, the hypothesis presented here nevertheless resonates as a plausible synthesis of the phylogenetic data constructed from the study sites, what is known about current climate, as well as the generally accepted understanding of what climate was like during the Quaternary. It is my hope that this threatened ecosystem will be increasingly valued and protected, both for its diversity and for the ecological and evolutionary secrets it has yet to reveal.

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Figures



Figure 1. Location of the two tropical dry forest regions sampled in this study (circles). The northern region encompasses roughly 2400 km² and is centered around Chamela, Jalisco (19°31'N; 105°04'W); the southern region encompasses roughly 2000 km² and is centered around Huatulco, Oaxaca (15°45'N, 96°08'W).

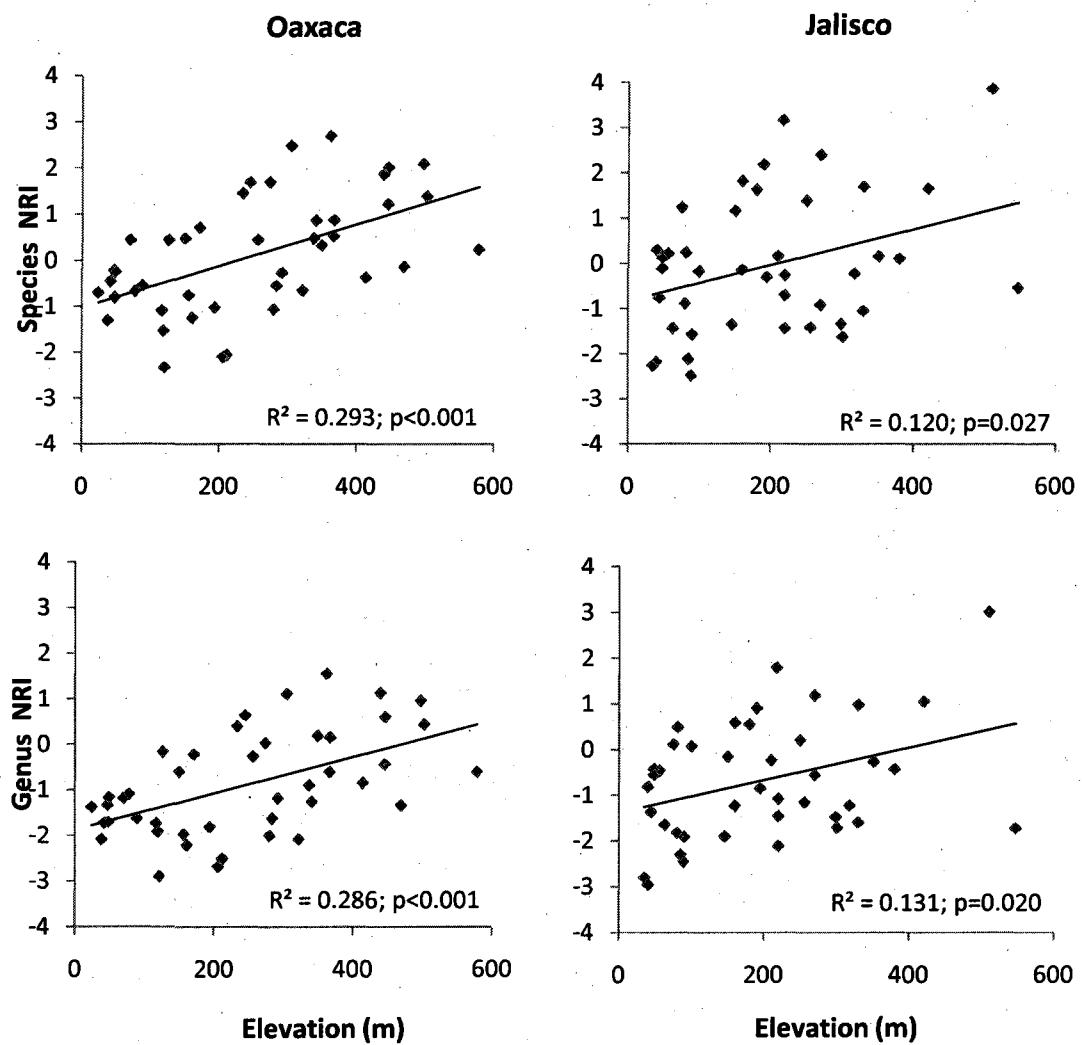


Figure 2. The net relatedness index (NRI) of tree taxa found in each transect at the Oaxaca and Jalisco field sites is plotted against the elevation of that transect. The NRI is a measure of how the taxa occurring in that transect are phylogenetically clustered (positive values) or over-dispersed (negative values) relative to the phylogenetic super tree for that site.

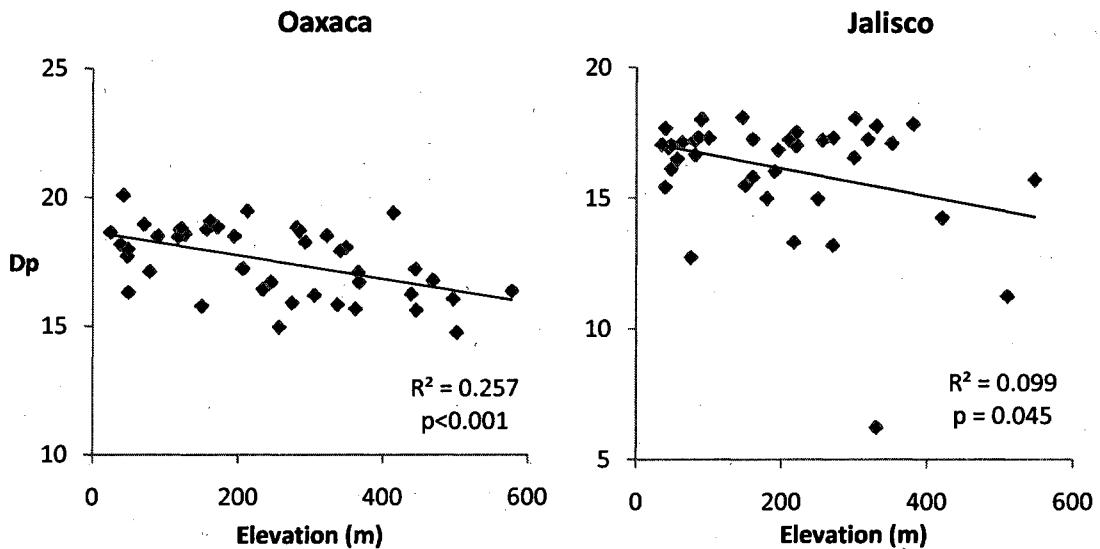


Figure 3. Phylogenetic diversity (Dp) of tree species found in each transect is plotted against elevation of that transect for Oaxaca and Jalisco sites. The Jalisco graphic remains significant with or without the outlier in the bottom middle of the graph.

Lower Quartile Genera				Upper Quartile Genera					
Genus	Family	m-sd	mean	m-sd	Genus	Family	m-sd		
							mean		
Thevetia	Apocynaceae	29	129	229	Astronium	Anacardiaceae	362	445	529
<u>Talpebuia</u>	Bignoniaceae	46	123	201	<u>Godmania</u>	Bignoniaceae	367	367	367
Hylocereus	Cactaceae	0	82	187	Tecoma	Bignoniaceae	254	322	391
Pachycereus	Cactaceae	78	170	263	<u>Pseudobombax</u>	Bombacaceae	332	413	494
Pilosocereus	Cactaceae	18	63	107	<u>Combretum</u>	Combretaceae	294	379	465
Forchhammeria	Capparaceae	69	166	264	Bauhinia	Fabaceae	350	412	475
Quadrella	Capparaceae	92	163	234	Dalbergia	Fabaceae	320	417	515
Bucida	Combretaceae	42	121	199	Entada	Fabaceae	270	384	498
Ibervillea	Cucurbitaceae	34	126	218	Gilrigidia	Fabaceae	317	377	437
Erythroxylum	Erythroxylaceae	78	164	249	Hymenaea	Hymenaeaceae	466	487	507
Cnidoscolus	Euphorbiaceae	22	88	154	Machaerium	Fabaceae	338	400	461
Croton	Euphorbiaceae	77	148	220	Poepigia	Fabaceae	336	418	500
Jatropha	Euphorbiaceae	15	67	120	Homalium	Fabaceae	373	439	505
Manihot	Euphorbiaceae	95	186	277	Xylosma	Fabaceae	275	374	473
Caesalpinia	Fabaceae	47	144	242	Licaria	Lauraceae	371	464	558
Calliandra	Fabaceae	95	167	239	Nectandra	Lauraceae	402	428	455
Havardia	Fabaceae	36	81	125	<u>Brosimum</u>	Moraceae	450	527	603
Piptadenia	Fabaceae	46	141	236	<u>Calycoiphyllum</u>	Rubiaceae	369	441	513
Senegalia	Fabaceae	2	55	109	Genipa	Rubiaceae	249	377	505
Bunchosia	Malpighiaceae	76	150	223	Cupania	Sapindaceae	379	415	452
Gossypium	Malvaceae	84	172	260	<u>Thouinidium</u>	Sapindaceae	356	497	638
Trichilia	Meliaceae	12	80	148	Guazuma	Sterculiaceae	296	381	467
Karwinskia	Rhamnaceae	21	69	117	Trema	Ulmaceae	400	449	497
Hintonia	Rubiaceae	95	176	257	<u>Urtrea</u>	Urticaceae	326	391	457
Esenbeckia	Rutaceae	118	145	173	Vitex	Verbenaceae	321	402	482

Table 1a. Elevation range (mean +/- 1 standard deviation in meters) for lower and upper quartiles of Oaxaca tree genera with ≥ 10 individuals. Taxa in bold are shared with the corresponding quartile in Jalisco; underlined taxa are shared with the opposite quartile.

Lower Quartile Genera				Upper Quartile Genera					
Genus	Family	m-sd	mean	m+sd	Genus	Family	m-sd	mean	m+sd
Achatocarpus	Achatocarpaceae	59	107	155	Comocladia	Anacardiaceae	207	290	373
<u>Astronium</u>	Anacardiaceae	24	88	151	Cylosophila	Arecaceae	241	291	341
Prestonia	Apocynaceae	28	81	134	Sabal	Arecaceae	236	262	288
Cydista	Bignoniaceae	39	49	59	Pithecoctenium	Bignoniaceae	148	230	312
Cynophalla	Capparaceae	25	90	155	<u>Tabebuia</u>	Bignoniaceae	183	296	410
Forchhammeria	Capparaceae	74	145	216	Cochlospermum	Cochlospermaceae	164	287	409
Quadrella	Capparaceae	41	133	225	Curatella	Dilleniaceae	383	446	509
Jacaratia	Caricaceae	103	170	238	Enriquebeltrania	Euphorbiaceae	249	350	450
Jatropha	Euphorbiaceae	44	121	198	Sapium	Euphorbiaceae	140	302	464
Caesalpinia	Fabaceae	33	129	225	Bauhinia	Fabaceae	252	360	468
Mariosousa	Fabaceae	46	62	79	Dalbergia	Fabaceae	136	251	366
Trichilia	Malpighiaceae	82	152	223	Girardinia	Fabaceae	246	379	512
Brosimum	Moraceae	24	98	171	Poepigia	Fabaceae	279	358	438
Ruprechtia	Polygonaceae	50	135	220	Xyloma	Flacourtiaceae	167	285	402
Gouania	Rhamnaceae	46	102	159	Gyrocarpus	Hernandiaceae	147	223	300
Randia	Rubiaceae	36	126	215	Psidium	Myrtaceae	137	236	336
Thouinia	Sapindaceae	41	115	190	Colubrina	Rhamnaceae	253	302	351
<u>Thouinidium</u>	Sapindaceae	40	70	101	Ayenia	Sterculiaceae	226	296	365
Recchia	Sapotaceae	59	143	226	Luehea	Tiliaceae	195	336	478
Urtica	Urticaceae	83	157	232	Turnera	Turneraceae	142	220	299

Table 1b. Elevation range (mean +/- one standard deviation in meters) for lower and upper quartiles of Jalisco tree genera with ≥ 10 individuals. Taxa in bold are shared with the corresponding quartile in Oaxaca; underlined taxa are shared with the opposite quartile.

Quartile	NRI	P - Value
Low Elevation - Oaxaca	-1.6555	0.044*
Low Elevation - Jalisco	0.4799	0.309
High Elevation - Oaxaca	0.0193	0.483
High Elevation - Jalisco	1.3264	0.095

Table 2. Net relatedness indices (NRI) for the upper and lower elevation quartiles of genera listed in tables 1a and 1b relative to the respective site phylogenies (Appendix 1). Positive NRI values indicate phylogenetic clustering, while negative number indicate overdispersion relative to null distributions based on 10,000 runs. * Indicates NRI is significantly different from null ($p=0.05$).

Climate Variable	Jalisco			Oaxaca		
	S	R ²	P	S	R ²	P
B1 Annual Mean Temperature	-	0.111	0.0336	0.279	0.0003	
B2 Mean Diurnal Temperature Range	+	0.280	0.0004	0.259	0.0005	
B3 Isothermality (B2/B7) (* 100)	-	0.219	0.0020	0.120	0.0227	
B4 Temperature Seasonality (standard deviation *100)	+	0.092	0.0534	0.129	0.018	
B5 Max Temperature of Warmest Month	+	0.080	0.0734	0.237	0.0009	
B6 Min Temperature of Coldest Month	-	0.240	0.0012	0.287	0.0002	
B7 Temperature Annual Range (B5-B6)	+	0.311	0.0002	0.316	0.0001	
B8 Total Annual Precipitation	+	0.431	0.0001	0.249	0.0007	
B9 Precipitation of Wettest Month	+	0.406	0.0001	0.244	0.0008	
B10 Precipitation Seasonality (Coefficient of Variation)	+	0.273	0.0005	-0.132	0.0166	

Table 3a. Slope (S), R² and significance (P) of regressions of the species-level net relatedness index (NRI) for sample tree communities on ten bioclimatic variables (Hijmans et al. 2005) for the Jalisco and Oaxaca field sites. Numbers in bold are not significant at the p=0.05 level. The slope of the Oaxaca regressions are the same as those for Jalisco unless otherwise indicated.

Variable	Jalisco	Oaxaca		
	PC1 (67.7%)	PC2 (24.8%)	PC1 (77.0%)	PC2 (19.7%)
B1 Annual Mean Temperature	-0.32	0.34	0.36	0.04
B2 Mean Diurnal Temperature Range	0.34	0.26	-0.32	0.28
B3 Isothermality (B2/B7) (* 100)	-0.33	0.04	0.20	0.59
B4 Temperature Seasonality (standard deviation *100)	0.04	0.60	-0.18	-0.61
B5 Max Temperature of Warmest Month	0.07	0.60	0.35	-0.02
B6 Min Temperature of Coldest Month	-0.38	0.09	0.36	0.08
B7 Temperature Annual Range (B5-B6)	0.37	0.18	-0.34	-0.18
B8 Total Annual Precipitation	0.37	0.05	-0.34	0.23
B9 Precipitation of Wettest Month	0.38	-0.01	-0.33	0.26
<u>B10 Precipitation Seasonality (Coefficient of Variation)</u>	0.32	-0.23	0.32	-0.22

Table 3b. Principal components analysis for bioclimatic variables included in Table 3a, showing the loading of eigenvectors on the first two principal components for each site and percent variation explained by component.

Oaxaca $R^2 = 0.544$		AIC = -12.429	
Step	Parameter	Seq SS	R^2
1	B8 Total Annual Precipitation	28.877	0.493
	B7 Temperature. Annual		
2	Range	0.819	0.507
3	PC1 (see Table 3b)	2.187	0.544

Jalisco $R^2 = 0.639$		AIC = -4.107	
Step	Parameter	Seq SS	R^2
1	B8 Total Annual Precipitation	28.355	0.370
2	Elevation	8.425	0.480
	B2 Mean Diurnal Temp.		
3	Range	5.160	0.547
	B7 Temperature. Annual		
4	Range	5.205	0.615
5	B6 Min. Temp. Coldest Month	1.812	0.639

Table 4. Site-specific best fit models for predicting species-level phylogenetic net relatedness (NRI) of sampled tree communities with elevation and bioclimatic variables using stepwise regression (see text for details).

Appendices

Appendix 1a – Tree species list from 43 transects Huatulco, Oaxaca State, Mexico, Fall 2005

Species (274)	Related Family (58)
1 Achatocarpus oaxacanus	Achatocarpaceae
2 Aeschynomene sp1	Fabaceae
3 Agonandra obtusifolia	Opiliaceae
4 Agonandra racemosa	Opiliaceae
5 Albizia adinocephala	Fabaceae
6 Albizia niopoides	Fabaceae
7 Albizia occidentalis	Fabaceae
8 Alibertia edulis	Rubiaceae
9 Alvaradoa amorphoides	Simaroubaceae
10 Amphiptygium adstringens	Julianiaceae
11 Amyris sp1	Rutaceae
12 Andira inermis	Fabaceae
13 Aphananthe monoica	Ulmaceae
14 Aphelandra scabra	Acanthaceae
15 Apoplanesia paniculata	Fabaceae
16 Astronium graveolens	Anacardiaceae
17 Bauhinia cookii	Fabaceae
18 Bauhinia divaricata	Fabaceae
19 Bauhinia ungulata	Fabaceae
20 Bourreria purpusii	Boraginaceae
21 Brosimum alicastrum	Moraceae
22 Bucida macrostachya	Combretaceae
23 Bucida wigginsiana	Combretaceae
24 Bumelia celastrina	Sapotaceae
25 Bumelia sp1	Sapotaceae
26 Bunchosia discolor	Malpighiaceae
27 Bunchosia montana	Malpighiaceae
28 Bursera cinerea	Burseraceae
29 Bursera excelsa	Burseraceae
30 Bursera fagaroides	Burseraceae
31 Bursera grandifolia	Burseraceae
32 Bursera heteresthes	Burseraceae
33 Bursera instabilis	Burseraceae
34 Bursera laurihuertae	Burseraceae
35 Bursera schlechtendalii	Burseraceae
36 Bursera simaruba	Burseraceae
37 Bursera sp1	Burseraceae
38 Byrsinima crassifolia	Malpighiaceae
39 Byttneria aculeata	Sterculiaceae
40 Caesalpinia coccinea	Fabaceae
41 Caesalpinia coriaria	Fabaceae
42 Caesalpinia eriostachys	Fabaceae
43 Caesalpinia platyloba	Fabaceae
44 Caesalpinia pulcherrima	Fabaceae

45	<i>Caesalpinia sclerocarpa</i>	Fabaceae
46	<i>Caesalpinia velutina</i>	Fabaceae
47	<i>Calliandra houstoniana</i>	Fabaceae
48	<i>Calliandra sp1</i>	Fabaceae
49	<i>Calycophyllum candidissimum</i>	Rubiaceae
50	<i>Canavalia acuminata</i>	Fabaceae
51	<i>Capparis baducca</i>	Capparaceae
52	<i>Casearia nitida</i>	Flacourtiaceae
53	<i>Casearia tremula</i>	Flacourtiaceae
54	<i>Cecropia obtusifolia</i>	Cecropiaceae
55	<i>Cedrela salvadorensis</i>	Meliaceae
56	<i>Ceiba aesculifolia</i>	Bombacaceae
57	<i>Celtis caudata</i>	Ulmaceae
58	<i>Celtis iguanaea</i>	Ulmaceae
59	<i>Chiococca alba</i>	Rubiaceae
60	<i>Chloroleucon mangense</i>	Fabaceae
61	<i>Cissus sicyoides</i>	Vitaceae
62	<i>Cnidoscolus tubulosus</i>	Euphorbiaceae
63	<i>Coccocloba barbadensis</i>	Polygonaceae
64	<i>Coccocloba liebmennii</i>	Polygonaceae
65	<i>Cochlospermum vitifolium</i>	Cochlospermaceae
66	<i>Cojoba arborea</i>	Fabaceae
67	<i>Combretum fruticosum</i>	Combretaceae
68	<i>Combretum laxum</i>	Combretaceae
69	<i>Bursera sarcopoda</i>	Burseraceae
70	<i>Comocladia engleriana</i>	Anacardiaceae
71	<i>Cordia alliodora</i>	Boraginaceae
72	<i>Cordia curassavica</i>	Boraginaceae
73	<i>Cordia dentata</i>	Boraginaceae
74	<i>Cordia elaeagnoides</i>	Boraginaceae
75	<i>Cordia sonorae</i>	Boraginaceae
76	<i>Cordia tinifolia</i>	Boraginaceae
77	<i>Cordia truncatifolia</i>	Boraginaceae
78	<i>Coursetia glandulosa</i>	Fabaceae
79	<i>Crataeva tapia</i>	Capparaceae
80	<i>Croton axillaris</i>	Euphorbiaceae
81	<i>Croton fragilis</i>	Euphorbiaceae
82	<i>Croton niveus</i>	Euphorbiaceae
83	<i>Croton septemnervius</i>	Euphorbiaceae
84	<i>Croton suberosus</i>	Euphorbiaceae
85	<i>Cryosophila nana</i>	Arecaceae
86	<i>Cupania dentata</i>	Sapindaceae
87	<i>Curatella americana</i>	Dilleniaceae
88	<i>Cydistia diversifolia</i>	Bignoniaceae
89	<i>Cynophalla flexuosa</i>	Capparaceae
90	<i>Dalbergia congestiflora</i>	Fabaceae
91	<i>Dalbergia granadillo</i>	Fabaceae
92	<i>Dalea sp1</i>	Fabaceae
93	<i>Dendropanax arboreus</i>	Araliaceae
94	<i>Diospyros aequoris</i>	Ebenaceae

95	<i>Diospyros digna</i>	Ebenaceae
96	<i>Diospyros salicifolia</i>	Ebenaceae
97	<i>Diphyesa humilis</i>	Fabaceae
98	<i>Entada polystachya</i>	Fabaceae
99	<i>Erythrina lanata</i>	Fabaceae
100	<i>Erythroxylum havanense</i>	Erythroxylaceae
101	<i>Esenbeckia berlandieri</i>	Rutaceae
102	<i>Esenbeckia collina</i>	Rutaceae
103	<i>Euphorbia segoviensis</i>	Euphorbiaceae
104	<i>Euphorbia sp1</i>	Euphorbiaceae
105	<i>Ficus cotinifolia</i>	Moraceae
106	<i>Ficus pertusa</i>	Moraceae
107	<i>Forchhammeria pallida</i>	Capparaceae
108	<i>Garcia nutans</i>	Euphorbiaceae
109	<i>Genipa americana</i>	Rubiaceae
110	<i>Gliricidia sepium</i>	Fabaceae
111	<i>Godmania aesculifolia</i>	Bignoniaceae
112	<i>Gossypium aridum</i>	Malvaceae
113	<i>Gouania eurycarpa</i>	Rhamnaceae
114	<i>Gouania polygama</i>	Rhamnaceae
115	<i>Gouania sp1</i>	Rhamnaceae
116	<i>Guaiacum coulteri</i>	Zygophyllaceae
117	<i>Guapira petenensis</i>	Nyctaginaceae
118	<i>Guarea glabra</i>	Meliaceae
119	<i>Guazuma ulmifolia</i>	Sterculiaceae
120	<i>Guettarda elliptica</i>	Rubiaceae
121	<i>Gyrocarpus americanus</i>	Hernandiaceae
122	<i>Gyrocarpus mocinoi</i>	Hernandiaceae
123	<i>Hamelia patens</i>	Rubiaceae
124	<i>Hamelia versicolor</i>	Rubiaceae
125	<i>Hauya elegans</i>	Onagraceae
126	<i>Havardia campylacantha</i>	Fabaceae
127	<i>Helicteres guazumifolia</i>	Sterculiaceae
128	<i>Heliocarpus appendiculatus</i>	Tiliaceae
129	<i>Heliocarpus mexicanus</i>	Tiliaceae
130	<i>Heliocarpus terebinthinaceus</i>	Tiliaceae
131	<i>Heteroflorum sp1</i>	Fabaceae
132	<i>Hintonia latiflora</i>	Rubiaceae
133	<i>Hippocratea celastroides</i>	Hippocrateaceae
134	<i>Hippocratea excelsa</i>	Hippocrateaceae
135	<i>Homalium trichostemon</i>	Flacourtiaceae
136	<i>Hylocereus undatus</i>	Cactaceae
137	<i>Hymenaea courbaril</i>	Fabaceae
138	<i>Hyperbaena mexicana</i>	Menispermaceae
139	<i>Ibervillea hypoleuca</i>	Cucurbitaceae
140	<i>Indigofera sp1</i>	Fabaceae
141	<i>Inga jinicuil</i>	Fabaceae
142	<i>Inga paterno</i>	Fabaceae
143	<i>Inga punctata</i>	Fabaceae
144	<i>Ipomoea arborescens</i>	Convolvulaceae

145	<i>Ipomoea wolcottiana</i>	Convolvulaceae
146	<i>Jacaratia mexicana</i>	Caricaceae
147	<i>Jacquinia donnell-smithii</i>	Theophrastaceae
148	<i>Jacquinia macrocarpa</i>	Theophrastaceae
149	<i>Jacquinia sp1</i>	Theophrastaceae
150	<i>Jatropha malacophylla</i>	Euphorbiaceae
151	<i>Jatropha sympetala</i>	Euphorbiaceae
152	<i>Karwinskia humboldtiana</i>	Rhamnaceae
153	<i>Lagrezia monosperma</i>	Amaranthaceae
154	<i>Leucaena lanceolata</i>	Fabaceae
155	<i>Leucaena macrophylla</i>	Fabaceae
156	<i>Licaria capitata</i>	Lauraceae
157	<i>Lonchocarpus constrictus</i>	Fabaceae
158	<i>Lonchocarpus emarginatus</i>	Fabaceae
159	<i>Lonchocarpus eriocarinalis</i>	Fabaceae
160	<i>Lonchocarpus guatemalensis</i>	Fabaceae
161	<i>Lonchocarpus magallanesii</i>	Fabaceae
162	<i>Lonchocarpus moliniae</i>	Fabaceae
163	<i>Lonchocarpus phaseolifolius</i>	Fabaceae
164	<i>Luehea candida</i>	Tiliaceae
165	<i>Luehea speciosa</i>	Tiliaceae
166	<i>Lysiloma acapulcensis</i>	Fabaceae
167	<i>Lysiloma microphyllum</i>	Fabaceae
168	<i>Machaerium acuminatum</i>	Fabaceae
169	<i>Machaerium biovulatum</i>	Fabaceae
170	<i>Machaerium salvadorense</i>	Fabaceae
171	<i>Maclura tinctoria</i>	Moraceae
172	<i>Malpighia mexicana</i>	Malpighiaceae
173	<i>Manihot oaxacana</i>	Euphorbiaceae
174	<i>Mariosousa acatlensis</i>	Fabaceae
175	<i>Marsdenia propinqua</i>	Asclepiadaceae
176	<i>Mimosa acantholoba</i>	Fabaceae
177	<i>Mimosa antioquensis</i>	Fabaceae
178	<i>Mimosa arenosa</i>	Fabaceae
179	<i>Mimosa pigra</i>	Fabaceae
180	<i>Mimosa sp1</i>	Fabaceae
181	<i>Mimosa sp2</i>	Fabaceae
182	<i>Momordica charantia</i>	Cucurbitaceae
183	<i>Morisonia americana</i>	Capparaceae
184	<i>Mosannonia depressa</i>	Annonaceae
185	<i>Muntingia calabura</i>	Elaeocarpaceae
186	<i>Myrospermum frutescens</i>	Fabaceae
187	<i>Nectandra ambingens</i>	Lauraceae
188	<i>Neea stenophylla</i>	Nyctaginaceae
189	<i>Neobuxbaumia tetetzo</i>	Cactaceae
190	<i>Nopalea auberi</i>	Cactaceae
191	<i>Opuntia decumbens</i>	Cactaceae
192	<i>Opuntia tomentosa</i>	Cactaceae
193	<i>Pachycereus pecten-aboriginum</i>	Cactaceae
194	<i>Paullinia cururu</i>	Sapindaceae

195	<i>Petria volubilis</i>	Verbenaceae
196	<i>Pilosocereus collinsii</i>	Cactaceae
197	<i>Piptadenia flava</i>	Fabaceae
198	<i>Piptadenia obliqua</i>	Fabaceae
199	<i>Piscidia carthagrenensis</i>	Fabaceae
200	<i>Pisonia aculeata</i>	Nyctaginaceae
201	<i>Pisonia macranthocarpa</i>	Nyctaginaceae
202	<i>Pithecellobium lanceolatum</i>	Fabaceae
203	<i>Pithecellobium oblongum</i>	Fabaceae
204	<i>Pithecellobium unguis-cati</i>	Fabaceae
205	<i>Pithecoctenium crucigerum</i>	Bignoniaceae
206	<i>Plumeria rubra</i>	Apocynaceae
207	<i>Podopterus cordifolius</i>	Polygonaceae
208	<i>Poeppigia procera</i>	Fabaceae
209	<i>Pseudobombax ellipticum</i>	Bombacaceae
210	<i>Psidium guineense</i>	Myrtaceae
211	<i>Pterocarpus acapulcensis</i>	Fabaceae
212	<i>Pterocarpus rohrii</i>	Fabaceae
213	<i>Quadrella incana</i>	Capparaceae
214	<i>Quadrella indica</i>	Capparaceae
215	<i>Randia laevigata</i>	Rubiaceae
216	<i>Randia nelsonii</i>	Rubiaceae
217	<i>Randia sp1</i>	Rubiaceae
218	<i>Randia tetracantha</i>	Rubiaceae
219	<i>Recchia mexicana</i>	Simaroubaceae
220	<i>Ruprechtia fusca</i>	Polygonaceae
221	<i>Sapindus saponaria</i>	Sapindaceae
222	<i>Sapium macrocarpum</i>	Euphorbiaceae
223	<i>Sapranthus violaceus</i>	Annonaceae
224	<i>Sebastiania pavoniana</i>	Euphorbiaceae
225	<i>Senegalia picachensis</i>	Fabaceae
226	<i>Senna atomaria</i>	Fabaceae
227	<i>Senna hirsuta</i>	Fabaceae
228	<i>Senna holwayana</i>	Fabaceae
229	<i>Senna sp1</i>	Fabaceae
230	<i>Serjania triquetra</i>	Sapindaceae
231	<i>Sideroxylon capiri</i>	Sapotaceae
232	<i>Simira rhodoclada</i>	Rubiaceae
233	<i>Solanum sp1</i>	Solanaceae
234	<i>Spondias mombin</i>	Anacardiaceae
235	<i>Spondias purpurea</i>	Anacardiaceae
236	<i>Stemmadenia donnell-smithii</i>	Apocynaceae
237	<i>Stemmadenia obovata</i>	Apocynaceae
238	<i>Stenocereus chacalapensis</i>	Cactaceae
239	<i>Swartzia simplex</i>	Fabaceae
240	<i>Swietenia humilis</i>	Meliaceae
241	<i>Synardisia venosa</i>	Myrsinaceae
242	<i>Syzygium jambos</i>	Myrtaceae
243	<i>Syzygium sp1</i>	Myrtaceae
244	<i>Tabebuia chrysanthia</i>	Bignoniaceae

245	<i>Tabebuia impetiginosa</i>	Bignoniaceae
246	<i>Tabebuia rosea</i>	Bignoniaceae
247	<i>Tabernaemontana amygdalifolia</i>	Apocynaceae
248	<i>Tecoma stans</i>	Bignoniaceae
249	<i>Tephrosia cinerea</i>	Fabaceae
250	<i>Tephrosia sp1</i>	Fabaceae
251	<i>Thevetia ovata</i>	Apocynaceae
252	<i>Thevetia thevetioides</i>	Apocynaceae
253	<i>Thouinia paucidentata</i>	Sapindaceae
254	<i>Thouinia villosa</i>	Sapindaceae
255	<i>Thouinidium decandrum</i>	Sapindaceae
256	<i>Trema micrantha</i>	Ulmaceae
257	<i>Trichilia multifoliola</i>	Meliaceae
258	<i>Trichilia trifolia</i>	Meliaceae
259	<i>Trichospermum mexicanum</i>	Tiliaceae
260	<i>Trophis racemosa</i>	Moraceae
261	<i>Urera caracasana</i>	Urticaceae
262	<i>Vachellia campechiana</i>	Fabaceae
263	<i>Vachellia collinsii</i>	Fabaceae
264	<i>Vachellia cornigera</i>	Fabaceae
265	<i>Vachellia hindsii</i>	Fabaceae
266	<i>Vitex gaumeri</i>	Verbenaceae
267	<i>Vitex mollis</i>	Verbenaceae
268	<i>Vitex sp1</i>	Verbenaceae
269	<i>Waltheria indica</i>	Sterculiaceae
270	<i>Xylosma sp1</i>	Flacourtiaceae
271	<i>Xylosma velutina</i>	Flacourtiaceae
272	<i>Zanthoxylum riedelianum</i>	Rutaceae
273	<i>Calliandra formosa</i>	Fabaceae
274	<i>Ziziphus amole</i>	Rhamnaceae

Appendix 1b - Tree species list from 41 transects
 Chamela, Jalisco State, Mexico, Fall 2006

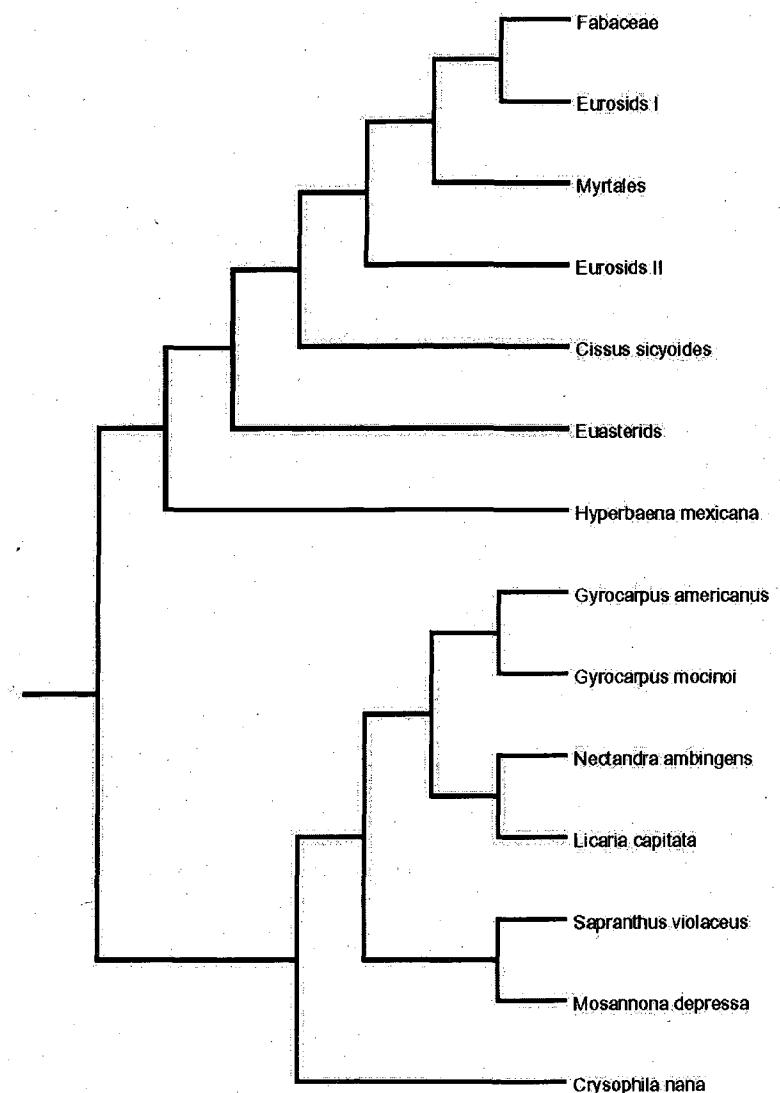
Species (229)	Related Family (57)
1 <i>Achatocarpus gracilis</i>	Achatocarpaceae
2 <i>Acrocomia aculeata</i>	Arecaceae
3 <i>Aeschynomene amorphoides</i>	Fabaceae
4 <i>Ageratum houstonianum</i>	Asteraceae
5 <i>Agonandra racemosa</i>	Opiliaceae
6 <i>Albizia occidentalis</i>	Fabaceae
7 <i>Alvaradoa amorphoides</i>	Simaroubaceae
8 <i>Amphipterygium adstringens</i>	Julianiaceae
9 <i>Amyris cf.madrensis</i>	Rutaceae
10 <i>Apoplanesia paniculata</i>	Fabaceae
11 <i>Aristolochia foetida</i>	Aristolochiaceae
12 <i>Astronium graveolens</i>	Anacardiaceae
13 <i>Attalea cohune</i>	Arecaceae
14 <i>Ayenia micrantha</i>	Sterculiaceae
15 <i>Bauhinia divaricata</i>	Fabaceae
16 <i>Bourreria cf.purpusii</i>	Boraginaceae
17 <i>Brosimum alicastrum</i>	Moraceae
18 <i>Bumelia celastrina</i>	Sapotaceae
19 <i>Bunchosia mcvaughii</i>	Malpighiaceae
20 <i>Bunchosia palmeri</i>	Malpighiaceae
21 <i>Bursera arborea</i>	Burseraceae
22 <i>Bursera excelsa</i>	Burseraceae
23 <i>Bursera fagaroides</i>	Burseraceae
24 <i>Bursera grandifolia</i>	Burseraceae
25 <i>Bursera heteresthes</i>	Burseraceae
26 <i>Bursera instabilis</i>	Burseraceae
27 <i>Bursera simaruba</i>	Burseraceae
28 <i>Bursera sp1</i>	Burseraceae
29 <i>Bursera sp2</i>	Burseraceae
30 <i>Byrsonima crassifolia</i>	Malpighiaceae
31 <i>Byttneria sp1</i>	Sterculiaceae
32 <i>Caesalpinia cacalaco</i>	Fabaceae
33 <i>Caesalpinia coriaria</i>	Fabaceae
34 <i>Caesalpinia eriostachys</i>	Fabaceae
35 <i>Caesalpinia platyloba</i>	Fabaceae
36 <i>Caesalpinia pulcherrima</i>	Fabaceae
37 <i>Caesalpinia sclerocarpa</i>	Fabaceae
38 <i>Calliandra emarginata</i>	Fabaceae
39 <i>Calliandra formosa</i>	Fabaceae
40 <i>Canavalia acuminata</i>	Fabaceae
41 <i>Canavalia rosea</i>	Fabaceae
42 <i>Casearia corymbosa</i>	Flacourtiaceae
43 <i>Casearia sylvestris</i>	Flacourtiaceae
44 <i>Casearia tremula</i>	Flacourtiaceae
45 <i>Cedrela salvadorensis</i>	Meliaceae
46 <i>Ceiba aesculifolia</i>	Bombacaceae

47	<i>Celtis iguanaea</i>	Ulmaceae
48	<i>Cephalocereus purpusii</i>	Cactaceae
49	<i>Chiococca alba</i>	Rubiaceae
50	<i>Chloroleucon mangense</i>	Fabaceae
51	<i>Cissus sicyoides</i>	Vitaceae
52	<i>Cnidoscolus spinosus</i>	Euphorbiaceae
53	<i>Coccoloba barbadensis</i>	Polygonaceae
54	<i>Coccoloba liebmannii</i>	Polygonaceae
55	<i>Cochlospermum vitifolium</i>	Cochlospermaceae
56	<i>Colubrina heteroneura</i>	Rhamnaceae
57	<i>Colubrina triflora</i>	Rhamnaceae
58	<i>Combretum fruticosum</i>	Combretaceae
59	<i>Combretum laxum</i>	Combretaceae
60	<i>Comocladia engleriana</i>	Anacardiaceae
61	<i>Cordia alliodora</i>	Boraginaceae
62	<i>Cordia curassavica</i>	Boraginaceae
63	<i>Cordia elaeagnoides</i>	Boraginaceae
64	<i>Cordia gerascanthus</i>	Boraginaceae
65	<i>Cordia tinifolia</i>	Boraginaceae
66	<i>Couepia polyandra</i>	Chrysobalanaceae
67	<i>Coursetia glandulosa</i>	Fabaceae
68	<i>Crataeva tapia</i>	Capparaceae
69	<i>Croton alamosanus</i>	Euphorbiaceae
70	<i>Croton axillaris</i>	Euphorbiaceae
71	<i>Croton fragilis</i>	Euphorbiaceae
72	<i>Croton niveus</i>	Euphorbiaceae
73	<i>Croton pseudoniveus</i>	Euphorbiaceae
74	<i>Croton suberosus</i>	Euphorbiaceae
75	<i>Cryosophila nana</i>	Arecaceae
76	<i>Cupania dentata</i>	Sapindaceae
77	<i>Curatella americana</i>	Dilleniaceae
78	<i>Cydista aequinoctialis</i>	Bignoniaceae
79	<i>Cydista diversifolia</i>	Bignoniaceae
80	<i>Cynophalla flexuosa</i>	Capparaceae
81	<i>Cynophalla verrucosa</i>	Capparaceae
82	<i>Dalbergia congestiflora</i>	Fabaceae
83	<i>Dendropanax arboreus</i>	Araliaceae
84	<i>Diospyros aequoris</i>	Ebenaceae
85	<i>Diospyros aff.rosei</i>	Ebenaceae
86	<i>Diphysa humilis</i>	Fabaceae
87	<i>Diphysa occidentalis</i>	Fabaceae
88	<i>Enriquebeltrania crenatifolia</i>	Euphorbiaceae
89	<i>Entada polystachya</i>	Fabaceae
90	<i>Erythrina lanata</i>	Fabaceae
91	<i>Erythroxylum havanense</i>	Erythroxylaceae
92	<i>Erythroxylum mexicanum</i>	Erythroxylaceae
93	<i>Esenbeckia berlandieri</i>	Rutaceae
94	<i>Esenbeckia collina</i>	Rutaceae
95	<i>Esenbeckia nesiotica</i>	Rutaceae
96	<i>Euphorbia calyculata</i>	Euphorbiaceae

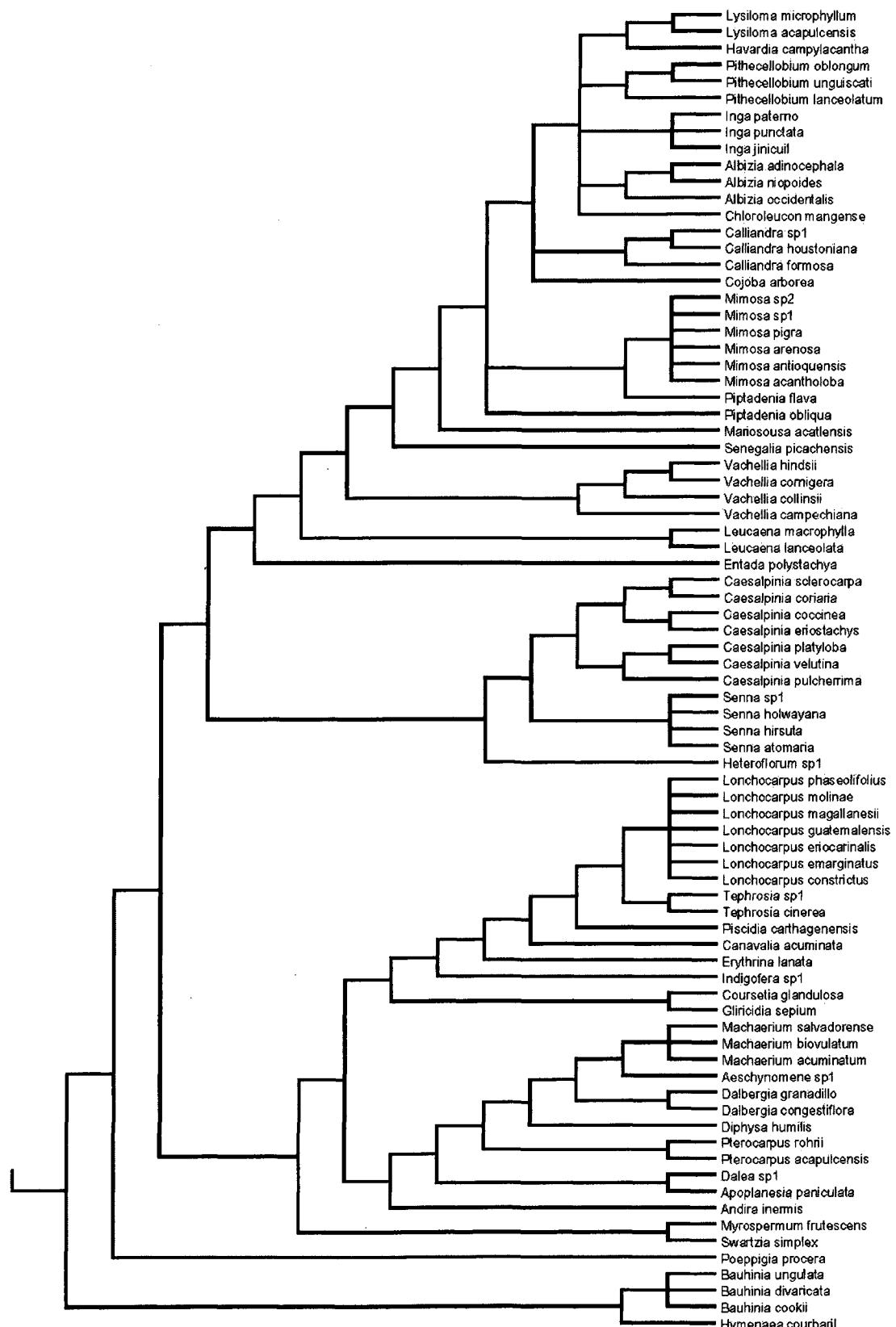
97	Euphorbia sp1	Euphorbiaceae
98	Euphorbia tanquahuete	Euphorbiaceae
99	Ficus cotinifolia	Moraceae
100	Ficus insipida	Moraceae
101	Ficus pertusa	Moraceae
102	Forchhammeria pallida	Capparaceae
103	Gliricidia sepium	Fabaceae
104	Godmania aesculifolia	Bignoniaceae
105	Gossypium aridum	Malvaceae
106	Gouania eurycarpa	Rhamnaceae
107	Gouania rosei	Rhamnaceae
108	Guaiacum coulteri	Zygophyllaceae
109	Guapira petenensis	Nyctaginaceae
110	Guazuma ulmifolia	Sterculiaceae
111	Guettarda elliptica	Rubiaceae
112	Gyrocarpus jatrophifolius	Hernandiaceae
113	Haematoxylum brasiletto	Fabaceae
114	Hamelia versicolor	Rubiaceae
115	Hauya elegans	Onagraceae
116	Heliocarpus pallidus	Tiliaceae
117	Hemiangium excelsum	Hippocrateaceae
118	Heteroflorum sclerocarpum	Fabaceae
119	Hintonia latiflora	Rubiaceae
120	Homalium senarium	Flacourtiaceae
121	Hura polyandra	Euphorbiaceae
122	Hylocereus ocamponis	Cactaceae
123	Ibervillea hypoleuca	Cucurbitaceae
124	Ipomoea ampullacea	Convolvulaceae
125	Ipomoea arborescens	Convolvulaceae
126	Ipomoea wolcottiana	Convolvulaceae
127	Jacaratia mexicana	Caricaceae
128	Jacquinia pungens	Theophrastaceae
129	Jatropha chamelensis	Euphorbiaceae
130	Jatropha malacophylla	Euphorbiaceae
131	Jatropha platyphylla	Euphorbiaceae
132	Jatropha sympetala	Euphorbiaceae
133	Karwinskia humboldtiana	Rhamnaceae
134	Lagrezia monosperma	Amaranthaceae
135	Leucaena lanceolata	Fabaceae
136	Leucaena leucocephala	Fabaceae
137	Licania arborea	Chrysobalanaceae
138	Lonchocarpus constrictus	Fabaceae
139	Lonchocarpus emarginatus	Fabaceae
140	Lonchocarpus eriocarinalis	Fabaceae
141	Lonchocarpus guatemalensis	Fabaceae
142	Lonchocarpus magallanesii	Fabaceae
143	Luehea candida	Tiliaceae
144	Lysiloma microphyllum	Fabaceae
145	Machaerium salvadorense	Fabaceae
146	Maclura tinctoria	Moraceae

147	<i>Malpighia mexicana</i>	Malpighiaceae
148	<i>Manihot chlorosticta</i>	Euphorbiaceae
149	<i>Mariosousa acatlensis</i>	Fabaceae
150	<i>Marsdenia lanata</i>	Asclepiadaceae
151	<i>Mimosa acantholoba</i>	Fabaceae
152	<i>Mimosa antioquensis</i>	Fabaceae
153	<i>Mimosa arenosa</i>	Fabaceae
154	<i>Mimosa sp1</i>	Fabaceae
155	<i>Morisonia americana</i>	Capparaceae
156	<i>Mosannona depressa</i>	Annonaceae
157	<i>Myrospermum balsamiferum</i>	Fabaceae
158	<i>Myrospermum sp1</i>	Fabaceae
159	<i>Nectandra martinicensis</i>	Lauraceae
160	<i>Opuntia excelsa</i>	Cactaceae
161	<i>Pachycereus pecten-aboriginum</i>	Cactaceae
162	<i>Paullinia cururu</i>	Sapindaceae
163	<i>Peniocereus rosei</i>	Cactaceae
164	<i>Pilosocereus aff. collinsii</i>	Cactaceae
165	<i>Piptadenia obliqua</i>	Fabaceae
166	<i>Piranhea mexicana</i>	Euphorbiaceae
167	<i>Piscidia carthagrenensis</i>	Fabaceae
168	<i>Pisonia aculeata</i>	Nyctaginaceae
169	<i>Pisonia macranthocarpa</i>	Nyctaginaceae
170	<i>Pithecellobium dulce</i>	Fabaceae
171	<i>Pithecellobium lanceolatum</i>	Fabaceae
172	<i>Pithecoctenium crucigerum</i>	Bignoniaceae
173	<i>Plumeria rubra</i>	Apocynaceae
174	<i>Poepigia procera</i>	Fabaceae
175	<i>Prestonia mexicana</i>	Apocynaceae
176	<i>Psidium sartorianum</i>	Myrtaceae
177	<i>Psychotria erythrocarpa</i>	Rubiaceae
178	<i>Pterocarpus orbiculatus</i>	Fabaceae
179	<i>Quadrella indica</i>	Capparaceae
180	<i>Quercus magnoliifolia</i>	Fagaceae
181	<i>Randia aculeata</i>	Rubiaceae
182	<i>Randia armata</i>	Rubiaceae
183	<i>Randia laevigata</i>	Rubiaceae
184	<i>Randia sp1</i>	Rubiaceae
185	<i>Randia tetracantha</i>	Rubiaceae
186	<i>Recchia mexicana</i>	Simaroubaceae
187	<i>Ruprechtia fusca</i>	Polygonaceae
188	<i>Sabal mexicana</i>	Arecaceae
189	<i>Sapindus saponaria</i>	Sapindaceae
190	<i>Sapium macrocarpum</i>	Euphorbiaceae
191	<i>Sapium pedicellatum</i>	Euphorbiaceae
192	<i>Sapranthus violaceus</i>	Annonaceae
193	<i>Sciadodendron excelsum</i>	Araliaceae
194	<i>Sebastiania pavoniana</i>	Euphorbiaceae
195	<i>Senna atomaria</i>	Fabaceae
196	<i>Senna mollissima</i>	Fabaceae

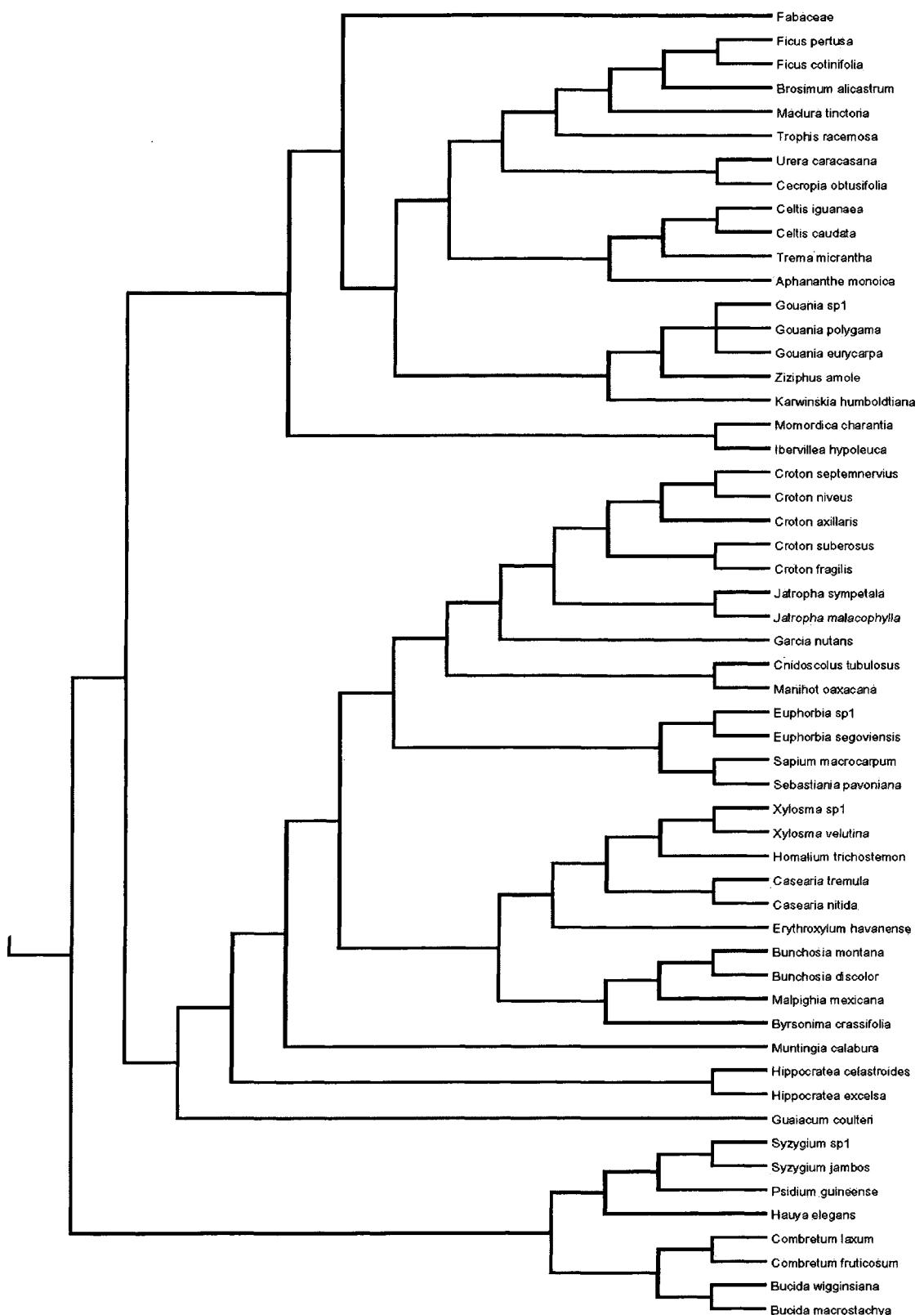
197	<i>Serjania brachycarpa</i>	Sapindaceae
198	<i>Serjania triquetra</i>	Sapindaceae
199	<i>Sideroxylon capiri</i>	Sapotaceae
200	<i>Simira</i> sp1	Rubiaceae
201	<i>Spondias mombin</i>	Anacardiaceae
202	<i>Spondias purpurea</i>	Anacardiaceae
203	<i>Stemmadenia donnell-smithii</i>	Apocynaceae
204	<i>Stemmadenia obovata</i>	Apocynaceae
205	<i>Stenocereus chrysocarpus</i>	Cactaceae
206	<i>Swartzia</i> sp1	Fabaceae
207	<i>Swietenia humilis</i>	Meliaceae
208	<i>Tabebuia chrysantha</i>	Bignoniaceae
209	<i>Tabebuia donnell-smithii</i>	Bignoniaceae
210	<i>Tabebuia impetiginosa</i>	Bignoniaceae
211	<i>Tabebuia rosea</i>	Bignoniaceae
212	<i>Tabernaemontana amygdalifolia</i>	Apocynaceae
213	<i>Thevetia ovata</i>	Apocynaceae
214	<i>Thouinia paucidentata</i>	Sapindaceae
215	<i>Thouinidium decandrum</i>	Sapindaceae
216	<i>Trichilia americana</i>	Meliaceae
217	<i>Trichilia trifolia</i>	Meliaceae
218	<i>Trophis racemosa</i>	Moraceae
219	<i>Turnera diffusa</i>	Turneraceae
220	<i>Urera caracasana</i>	Urticaceae
221	<i>Vachellia campechiana</i>	Fabaceae
222	<i>Vachellia hindsii</i>	Fabaceae
223	<i>Vitex gaumeri</i>	Verbenaceae
224	<i>Vitex mollis</i>	Verbenaceae
225	<i>Waltheria indica</i>	Sterculiaceae
226	<i>Xylosma intermedium</i>	Flacourtiaceae
227	<i>Xylosma velutina</i>	Flacourtiaceae
228	<i>Zanthoxylum arborescens</i>	Rutaceae
229	<i>Zanthoxylum fagara</i>	Rutaceae

Appendix 2a. Oaxaca Site Phylogeny – Backbone

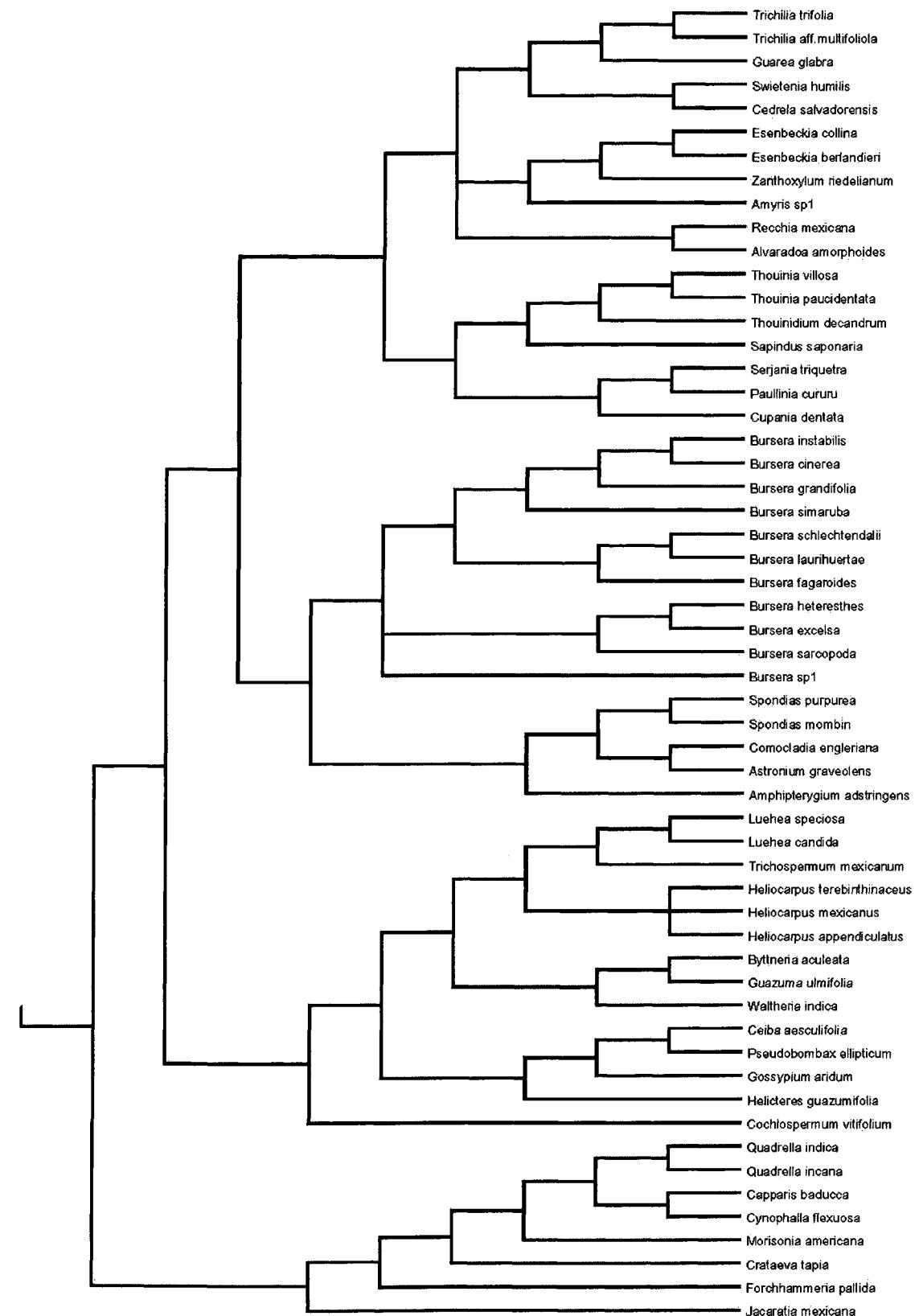
Oaxaca Site Phylogeny - Fabaceae



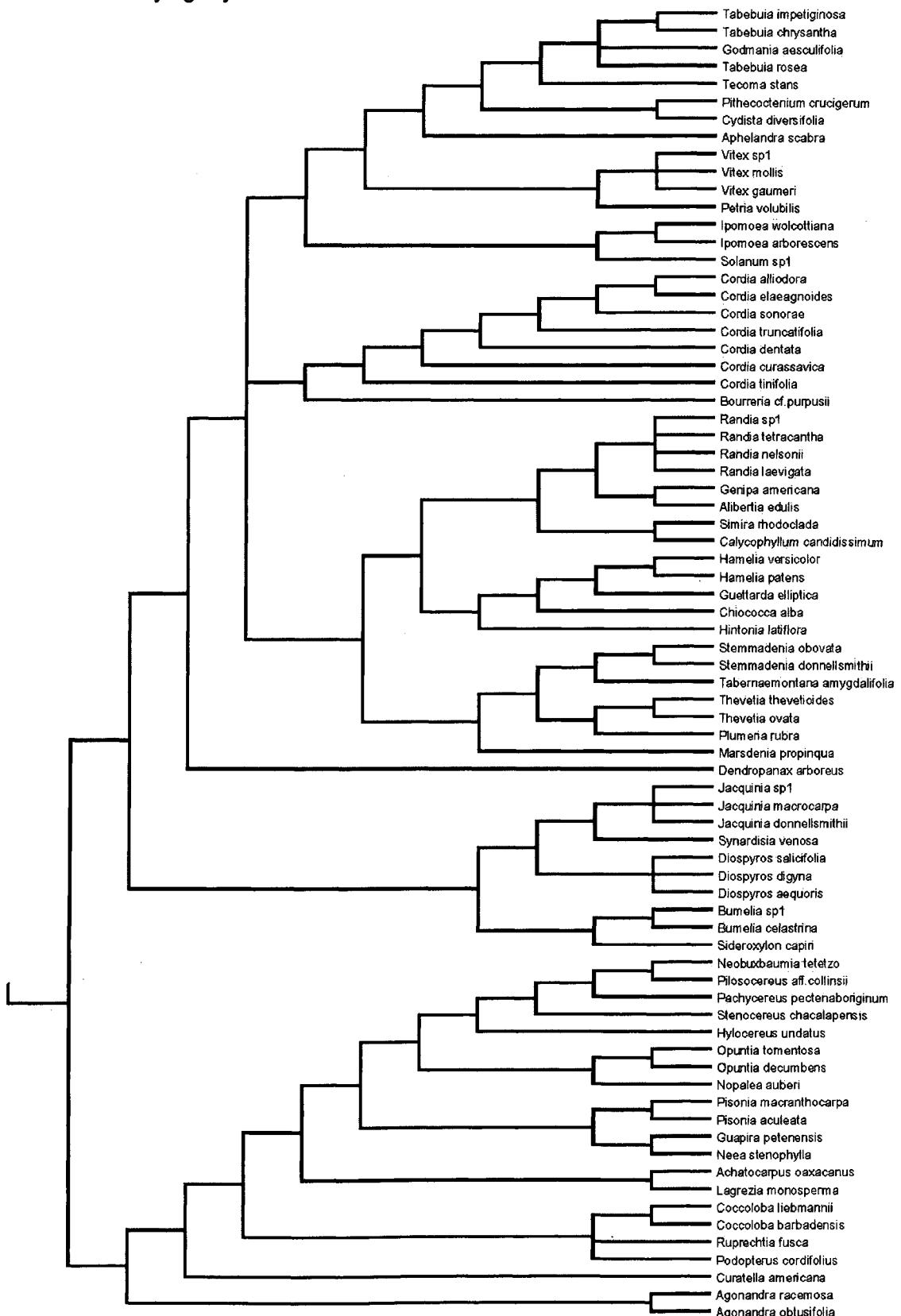
Oaxaca Site Phylogeny – Eurosids I and Myrtales without Fabaceae



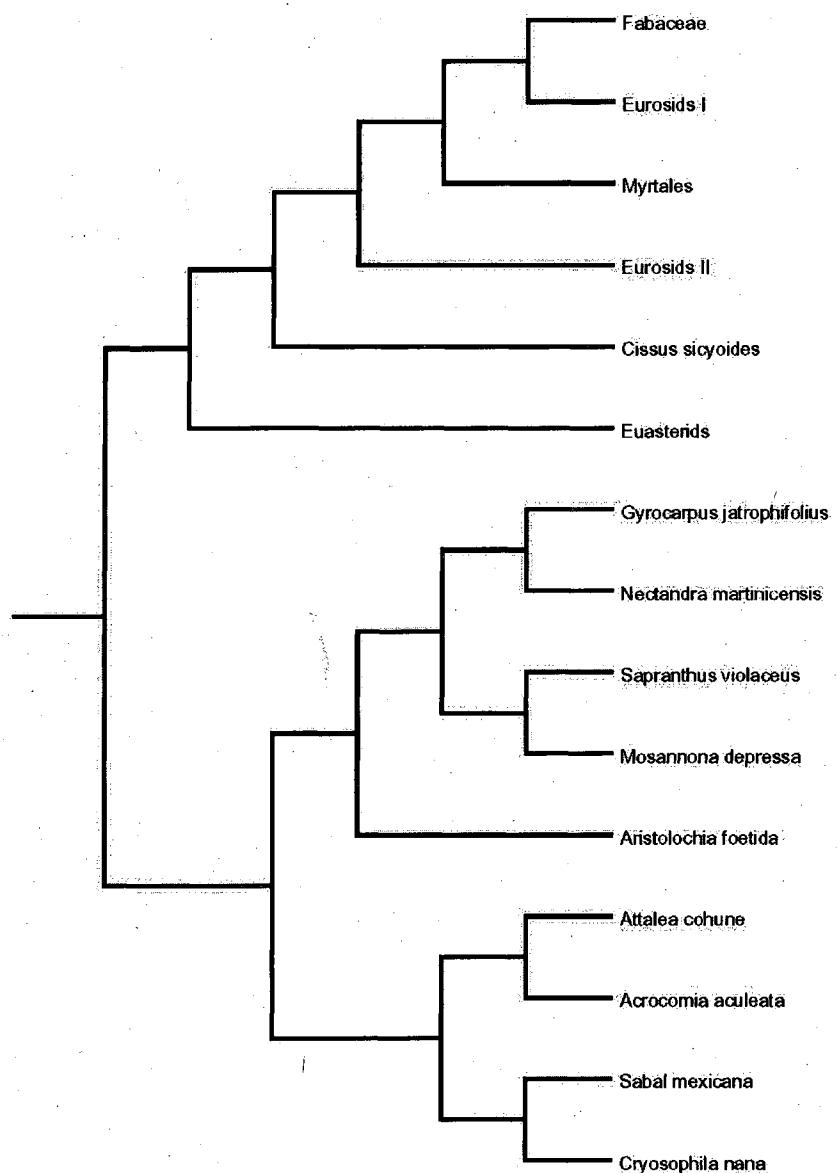
Oaxaca Site Phylogeny – Eurosids II



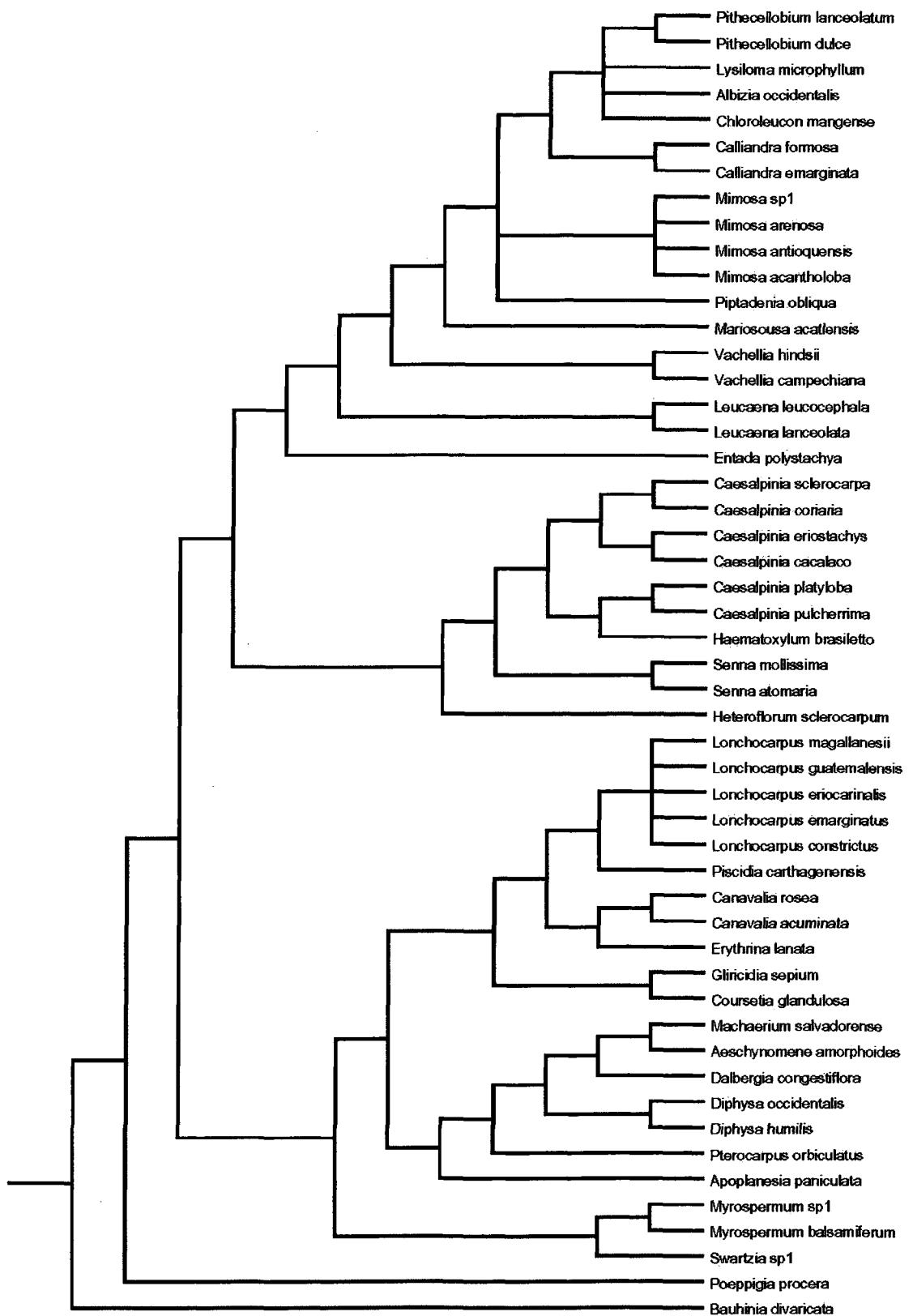
Oaxaca Site Phylogeny – Euasterids



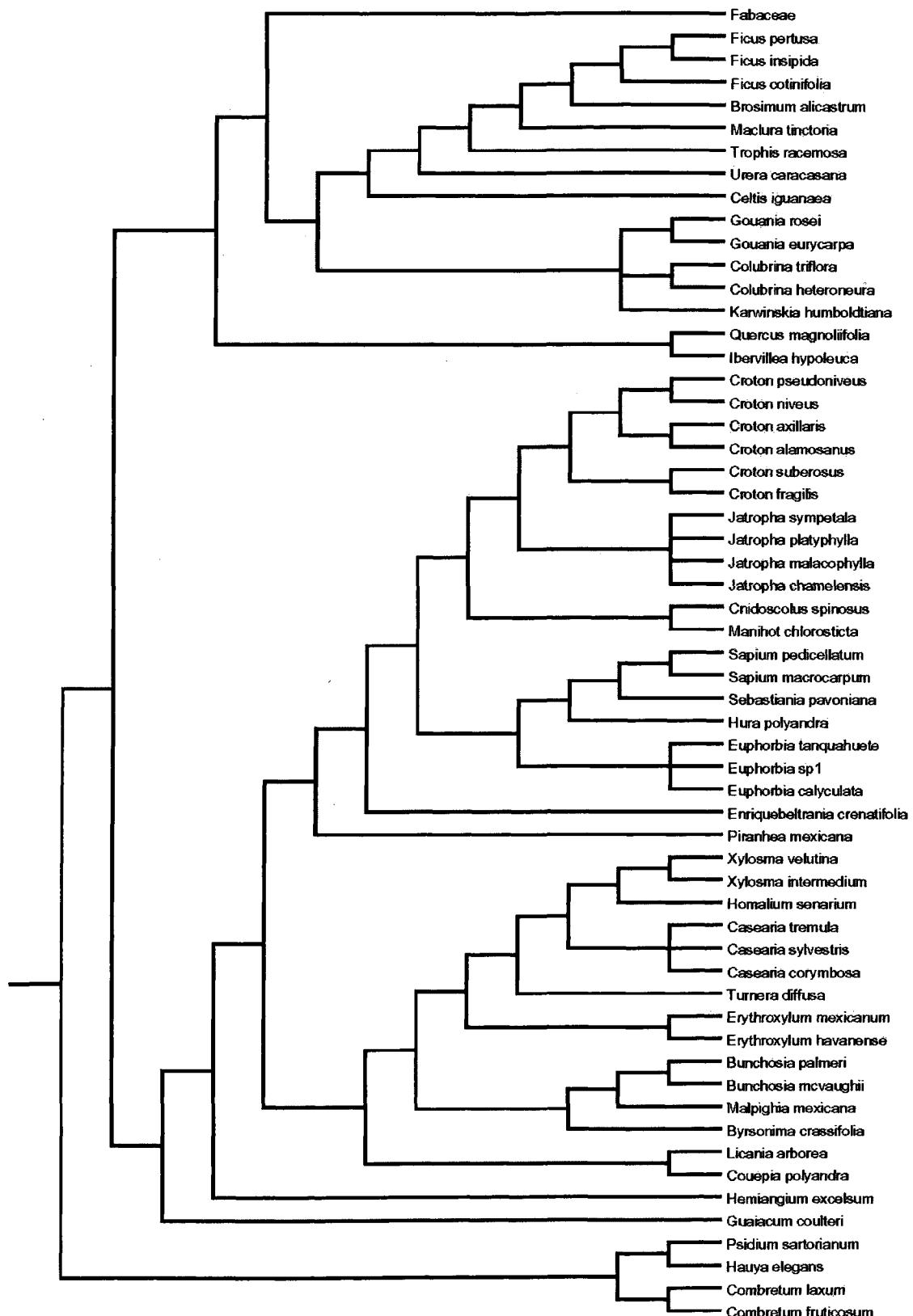
Appendix 2b. Jalisco Site Phylogeny – Backbone



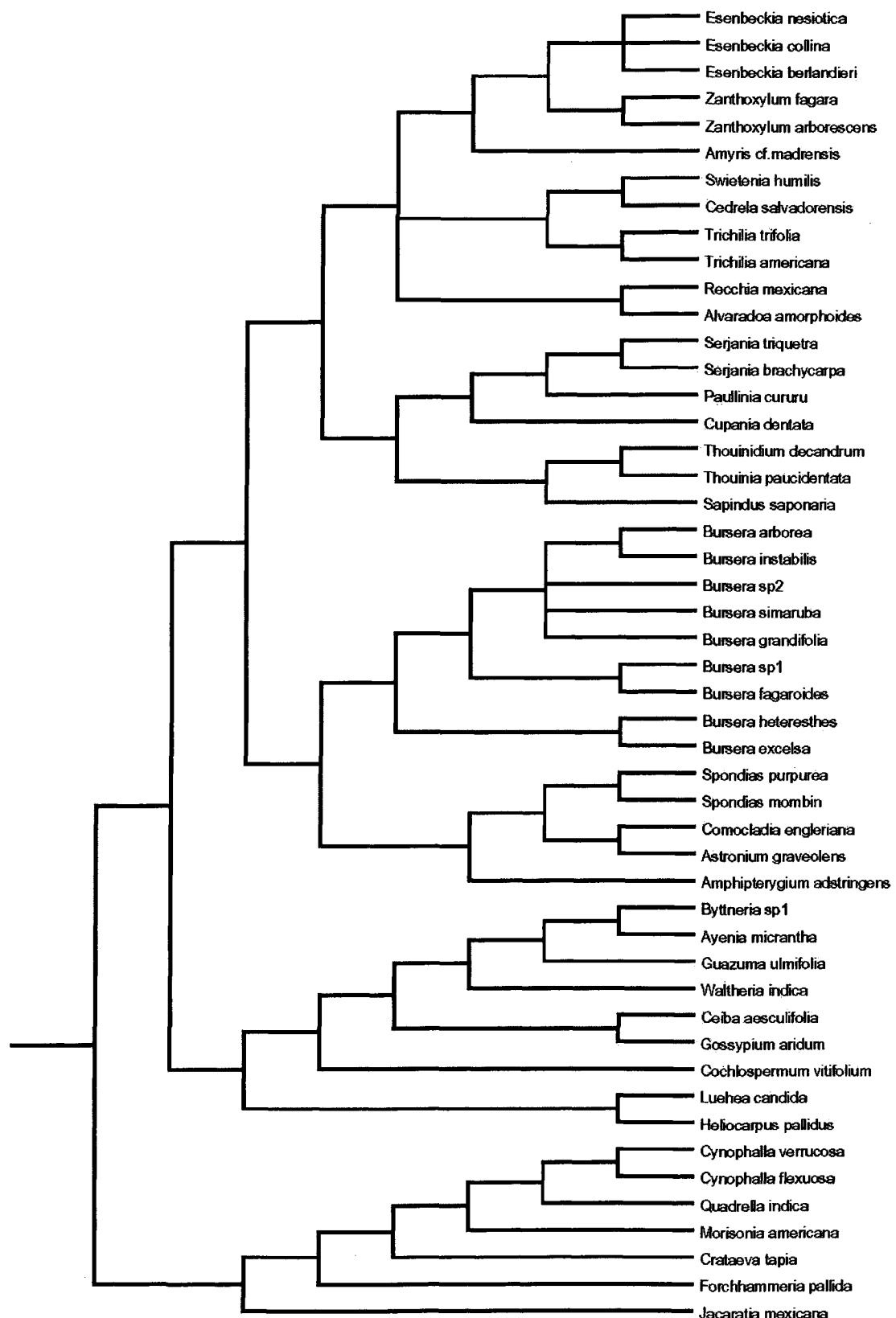
Jalisco Site Phylogeny - Fabaceae



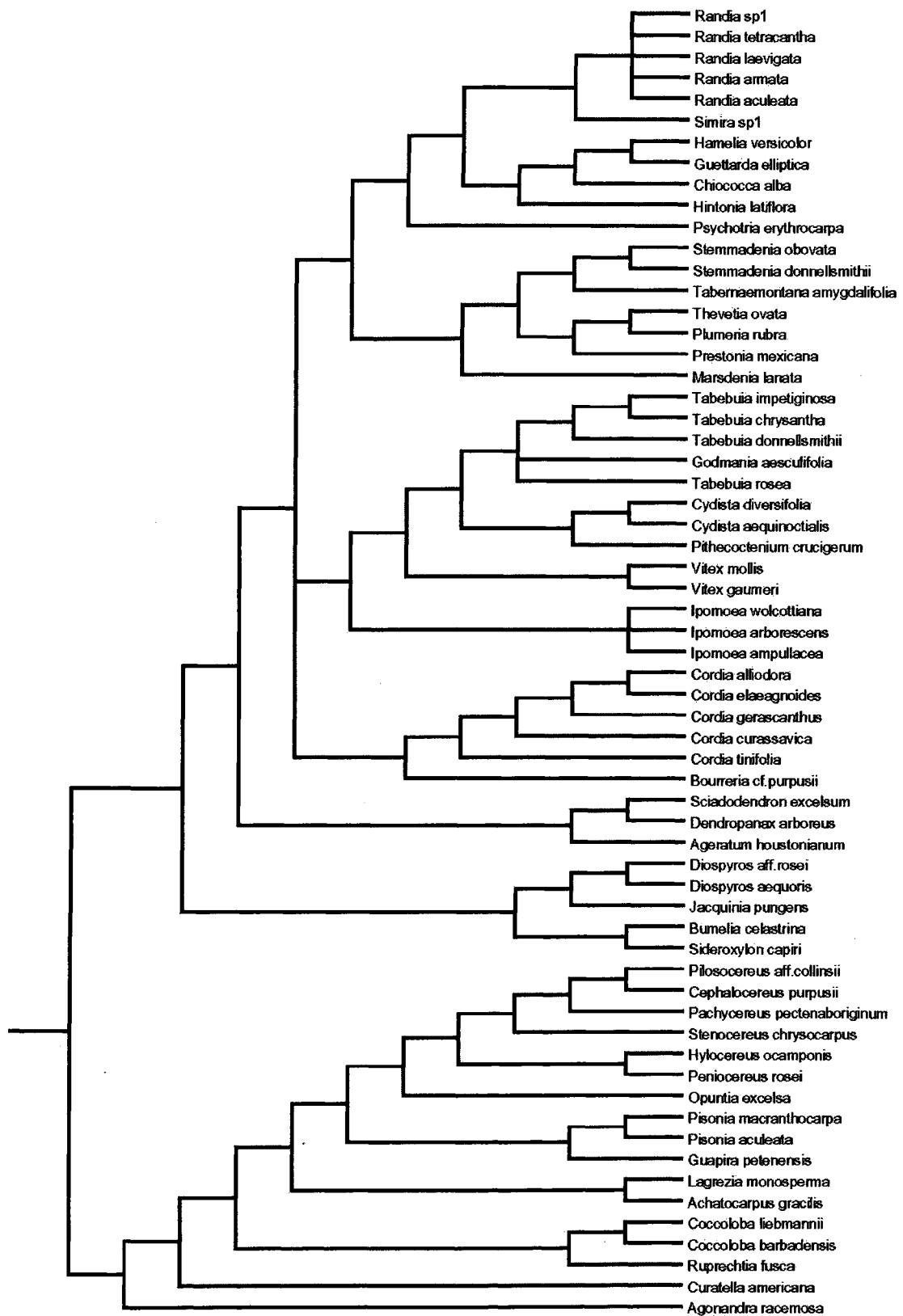
Jalisco Site Phylogeny – Eurosids I and Myrtales without Fabaceae



Jalisco Site Phylogeny – Eurosids II



Jalisco Site Phylogeny – Euasterids



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