



Tropical tree species diversity in a mountain system in southern Mexico: local and regional patterns and determinant factors

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ABSTRACT

Mechanisms explaining patterns of biodiversity along elevation gradients in tropical mountain systems remain controversial. We use a set of climatic, topographic, and soil variables encompassing regional, landscape, and local-level spatial scales to explain the spatial variation of tree species diversity in the Sierra Madre of Chiapas, Mexico. We sampled 128 circular plots (0.1-ha each) in four elevational bands along four elevation gradients or transects encompassing 100–2200 m. A total of 12,533 trees belonging to 444 species were recorded. Diversity patterns along the elevation gradient and the explanatory power of independent variables were dependent on spatial scale (regional vs transect) and functional group (total vs late-successional or pioneer species). Diversity of all species and late-successional species (1 – proportion of pioneer species) showed a constant pattern at the regional and transect scales, with low predictive power of climatic variables and/or elevation. A linear decrease in either number or proportion of pioneer species diversity was observed with increasing elevation, which was correlated with temperature, rainfall, and human disturbance trends. Total species diversity showed an increase with rainfall of the warmest quarter, indicating a regional-level limiting effect of seasonality (drought duration). Yet the explanatory power of climatic and topographic variables was higher at the individual transect level than at the regional scale, suggesting the parallel but differential influence of evolutionary and geological history factors on diversification not so far studied to explain elevation patterns of species diversity in tropical mountain systems.

Abstract in Spanish is available with online material.

Key words: climatic factors; diversity determinants; elevation gradient; Sierra Madre of Chiapas; tropical mountains.

MECHANISMS EXPLAINING PATTERNS OF SPATIAL VARIATION OF BIODIVERSITY IN TROPICAL MOUNTAIN SYSTEMS REMAIN CONTROVERSIAL (Sanders & Rahbek 2012, Guo *et al.* 2013, Arellano *et al.* 2016). A number of hypotheses have been proposed involving both deterministic and random processes (Sanders & Rahbek 2012, McCain & Beck 2015). Deterministic processes, acting on broad temporal and spatial scales, involve biogeographic, ecological, evolutionary, and geological history causal factors (Ricklefs 1987, 2004, Lomolino 2001).

Mechanisms to explain these biodiversity patterns involve climatic variables such as rainfall, temperature, or their combinations (Grytnes 2003, Körner 2007, McCain 2007). Guo *et al.* (2013) and Rahbek (2005) propose that a unimodal pattern of species richness is most frequent along broad elevation gradients. In many tropical mountain systems, the combination of climatic variables may reduce richness of any taxonomic group at high elevations, which is more clearly observed in those mountain systems exceeding

4000 m asl. A decrease in temperature by itself may have physiological consequences on plants, as few species may develop tolerance traits allowing them to adapt to the extreme conditions characteristic of high elevations (Givnish 1999, Becker *et al.* 2007).

Diversity patterns may vary according to taxonomic group and region (tropical vs temperate). For plants, inconsistent responses have been reported (Grytnes 2003, Oommen & Shanker 2005, Watkins *et al.* 2006, Wang *et al.* 2009), reflecting complex interactions among rainfall, temperature, soil parental material, and the different ability of plant species to use nutrients and water (Tanner *et al.* 1998, Benner *et al.* 2010, Dalling *et al.* 2016). As rainfall often also decreases toward higher elevations in combination with low temperatures, this may lead to lower nutrient availability because of slower rock weathering, microbial activity, and plant absorption. Causal mechanisms determining local plant species richness tend to vary according to differences in physiological tolerance among species and niche partitioning (Silvertown 2004, Arellano *et al.* 2016).

Species richness is typically evaluated along a single elevation transect (Guo *et al.* 2013, Peters *et al.* 2016). Often, a clear

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pattern is detected in which variation in richness is related to trends in climatic variables. Yet it is questionable whether studies on a single transect may allow testing hypotheses with some climatic variables as the principal drivers of diversity at a regional level (Kessler *et al.* 2011, Laurance *et al.* 2011). Further studies focused on a broad regional level may help to ascertain the relative importance of other climatic variables that are often not evaluated when attempting to define the relationship between diversity and the elevation gradient. For example, variables related to seasonality of rainfall contribute to better explaining the distribution of diversity in the tropics (Esquivel-Muelbert *et al.* 2016). Yet also non-climatic variables should be considered (*e.g.*, edaphic variables) that are relevant to processes related to plant communities (Condit *et al.* 2013), and which are only occasionally considered in studies of mountain systems (Homeier *et al.* 2010, Chain-Guadarrama *et al.* 2012). Therefore, broadening the geographic scope of a study to include replicates of elevation gradients (see Hargrove & Pickering 1992) may provide information essential to understanding the mechanisms that determine patterns of diversity on different scales (Rahbek 2005, McCain & Beck 2015).

Human disturbance modifies patterns of species richness in tropical mountain systems. It is common that forests located at lower and intermediate elevations in the tropics are subjected to greater human pressure (Nogués-Bravo *et al.* 2008, Ensslin *et al.* 2015, Averett *et al.* 2016). To avoid this complicating factor, some studies on elevation gradients have only been carried out above 500 m, and most have focused on evaluations of diversity in supposedly pristine or old growth forests (Rahbek 1995). The effect of human disturbance on species richness is rarely considered in studies of spatial variation of biodiversity of plants along elevation gradients, which makes it difficult to propose hypotheses aimed to disentangle the underlying mechanisms that determine these patterns (Nogués-Bravo *et al.* 2008).

As most of the mountain systems show some level of anthropogenic disturbance (Nogués-Bravo *et al.* 2008), it is important to identify its influence among those mechanisms responsible for patterns of species richness, particularly in highly populated biodiverse tropical regions for which little information has been generated. The Sierra Madre of Chiapas—a mountain range in southern Mexico parallel to the Pacific coast—is located within one of the most diverse regions in the Neotropics (a biodiversity hotspot *sensu* Myers *et al.* 2000). This region has been a major target for conservation efforts and includes three major biosphere reserves (El Triunfo, La Sepultura, and Volcán Tacaná), as well as a Mexican Federal Flora and Fauna Protection Reserve (La Fraylesca), and a Chiapas State Ecological Conservation Zone (Pico El Loro-Paxtal); together these protected areas encompass 4962 km²—approximately 28 percent of the Sierra Madre orographic system (Cortina-Villar *et al.* 2012). The region also contains one of Mexico's most extensive and well-preserved cloud forest remnants (Toledo-Aceves *et al.* 2011). Nevertheless, in the lower and intermediate parts of the elevational gradient, forests have been greatly reduced and degraded, principally through changes in land-use to croplands, pastures, and human

settlements, following widespread forest logging and fires, and selective extraction of firewood and timber (Cortina-Villar *et al.* 2012).

Our objective was to evaluate the effect of factors operating on a local (edaphic and topographic variables) and on a regional level (temperature, rainfall, and seasonality) in structuring spatial variation of tree diversity in a tropical mountain region in southern Mexico. We focused on trees as they are fundamental in the composition and structure of plant communities and provide ecosystem goods and services that determine the biophysical conditions for other taxonomic groups to thrive and coexist (Novotny *et al.* 2006, Chazdon 2008, 2014). We identified four elevation gradients (transects) along a NW-SE longitudinal axis spanning 160 km; in each transect, we defined four elevation bands (ranging from 100 to 2000 m in length) and sampled eight 0.1 ha plots as replicates in each intersection of elevation band and transect. Two hypotheses were tested as follows: (1) Climatic variables are the main drivers of major patterns of tree diversity at a regional scale; and (2) variables associated with soil and topography are relevant in determining species subgroups at the transect level (landscape and local scales).

METHODS

STUDY AREA.—We carried out the study on the Pacific slope of the Sierra Madre of Chiapas (15°20' to 16°9'N latitude, 92°29' to 93°42'W longitude). This steep mountain range in southern Mexico extends for approximately 250 km from NW to SE, parallel to the Pacific Coast (Fig. S1—Online Supplementary Material). Granitic rocks predominate in the bedrock along the main axis of the Sierra Madre of Chiapas, yet other igneous and metamorphic materials are scattered in elevated sites or in those subjected to recent volcanic activity; gneiss and acid tuff are also present in the NW extreme, and limestone and sandstone in the SE portion of the Sierra (Müllerried 1957). Elevation is a proxy for a number of physical variables determining local and microregional climatic patterns. Sampling plots were located along a wide elevation gradient (100–2100 m asl) with mean annual temperatures between 16.8°C and 26.2°C and an annual total rainfall between 1223 and 2573 mm (Karger *et al.* 2016).

We set four elevation transects 35–40 km apart along a NW-SE axis (Fig. S1): (1) Pico de Loro, (2) Triunfo, (3) Pijijapan, and (4) Sepultura. Due to the steep slopes and difficult access to intermediate and high elevation areas, it was not possible to carry out a more continuous sampling (*e.g.*, every 100 m along the gradient) in each transect. Therefore, four elevation bands were defined as follows: (1) Lowlands: 100–300 m asl, (2) Middle-low elevations: 700–900 m asl, (3) Middle-high elevations: 1300–1500 m asl, and (4) High elevations: 1800–2200 m asl. Within each band, eight circular 0.1 ha plots were sampled (total of 128 replicate plots). Complexity of the transect's topography and altitudinal band dictated position of the plots close to paths or, in their absence, makeshift paths were established in the forest as needed; plots were established within the band at least 100 m from each other. The low and middle-low bands of the Sierra

Madre of Chiapas are hilly with gentle slopes, which facilitates cattle raising and monoculture agriculture (mostly rainfed maize and shade-coffee plantations). On the other hand, the middle-high and highest areas of the elevation gradient have steep slopes that limit both accessibility as well as the practice of rainfed agriculture; in such areas, the principal land-use is for shade-coffee plantations (Schroth *et al.* 2009). Furthermore, the high elevation stands are within federally protected conservation areas, which have favored conservation of a continuous forest cover throughout the Sierra Madre of Chiapas (Toledo-Aceves *et al.* 2011). Sampling plots were located in the more preserved forest stands; canopy gaps were avoided. In lower sites, most of the plots were located in isolated old growth forest patches and in mid-successional secondary stands; it was not possible to determine for each plot its major human disturbance drivers and successional trajectory. We recorded all trees with a diameter at breast height (dbh) ≥ 5 cm in each plot and identified species at a morphospecies level in the field, and when possible at the species level. For each morphospecies, we obtained voucher specimens for taxonomic determination in the herbarium. Only two morphospecies remained identified at the family level and 31 at the genus level (see Table S1). A complete set of voucher specimens was deposited at the UNICACH herbarium in Tuxtla Gutierrez, Mexico.

PHYSICAL VARIABLES.—We quantified climatic, topographic, and edaphic variables. Historical climatic information for each site was obtained for a number of climatic variables from the CHELSA database (Karger *et al.* 2016) (1 km^2 resolution) and is often used when empirical site-level information is lacking. (We used WorldClim in a first instance for selection of climatic variables, but found a large number of cases, particularly related to rainfall trends, that were at odds with what we could expect from our field experience.) We evaluated collinearity among the 19 variables provided by the CHELSA database using a Pearson test. We selected *a priori* the variables average annual temperature ($^{\circ}\text{C}$) and total annual rainfall (mm), which are often used in studies correlating species richness and elevation gradients (McCain 2007, Sanders & Rahbek 2012). Then, we selected those variables with a correlation coefficient in which $r < 0.70$ (Dormann *et al.* 2012; Table S2). The following variables were considered, with values averaged for 1979 to 2013: mean annual temperature ($^{\circ}\text{C}$), total annual rainfall (mm), seasonality of rainfall (coefficient of variation of annual rainfall), rainfall of the warmest quarter (mm), isothermality (mean diurnal range/temperature annual range), temperature annual range ($^{\circ}\text{C}$), rainfall of the driest month (mm), and rainfall of the warmest quarter (mm).

We measured edaphic variables at the plot level. In each plot, we collected two mineral soil samples obtained from a depth of 20–30 cm after eliminating leaf and soil organic layers: One 10 m north of the center of the plot, and the other 10 m south from the center. Each sample was a composite of four subsamples collected from points 4 m apart from each other, for a total of 256 soil samples. Physical and chemical analyses were conducted at ECOSUR's nationally certified soils laboratory. Due to the high cost of evaluating soil variables for a large number of

samples, we gave higher priority to those which are typically correlated with plant richness (Lieberman *et al.* 1996, Abril & Bucher 2008, Condit *et al.* 2013): Clay content (%), Bouyoucos method), cation exchange capacity (C mol/kg, ammonium acetate method), nitrogen (%), semi-micro-Kjeldahl method), organic matter (%), Walkley-Black method), pH (H_2O method), and phosphorus (mg/kg, Olsen method). We recorded at the center of each plot elevation (m)—measured with a Garmin© GPS—and slope (%)—estimated using a Suunto© clinometer.

TREE DIVERSITY.—We defined two functional groups of trees. First, pioneer species that are capable of establishing themselves in disturbed sites or in sites undergoing initial stages of secondary succession, have high growth rates, are shade-intolerant, have a low specific wood density and a low lignin content. The second group—late-successional species—includes those found in well-preserved old growth forests and in stands undergoing intermediate or advanced successional stages; these species are slow-growing and shade-tolerant, with a high specific wood density and a high lignin content (Chave *et al.* 2006). In the late-successional group, we also included those species termed mid-successional species (Table S1). To assign species to each group, we consulted lists previously published by Rocha-Loredo *et al.* (2010) and González-Espinosa and Ramírez-Marcial (2013). We calculated species diversity using the exponential of the Shannon index (Jost 2006). We selected this index of true diversity as it is easy to interpret and because it considers the abundances among species to be equivalent; that is, all species abundances had the same probability of being detected in the analysis (Jost 2006). We initially calculated the tree diversity index with (1) total number of species; (2) number of late-successional species; (3) number of pioneer species; and (4) the quotient pioneer species diversity/total species diversity (see Molino & Sabatier 2001). Preliminary analyses indicated that diversity calculated with the number of late-successional species was redundant with pioneer diversity (their proportions add up to 1) and showed similar results to those obtained using total species diversity; also, we found redundant results obtained with proportion of pioneer species; therefore, we report only diversity estimates based on total and pioneer number of species.

ANALYSIS.—We generated species accumulation curves for all combinations of transects and elevation bands. To determine the pattern of elevational distribution of total and pioneer species diversity, we adjusted simple regression models. We calculated Pearson correlations between pairs of predictor variables to detect collinearity (Table S2). Analyses to detect collinearity indicated high correlation values among groups of predictor variables. This was the case between elevation and some of the edaphic variables (*e.g.*, cation exchange capacity); and elevation and climatic variables (mean annual temperature, total annual rainfall, rainfall of the hottest quarter, and seasonality of rainfall [coefficient of variation]). Due to collinearity, the number of variables (Table S3) was reduced to nine (climatic: Isothermality, temperature annual range, rainfall of the driest month, rainfall of

warmest quarter; topographic: elevation and slope; edaphic: cation exchange capacity, clay content, phosphorous). In the analysis, we selected elevation as a variable for environmental and topographic heterogeneity instead of the climatic variables mean annual temperature ($R^2 = -0.98$, $P < 0.001$) and total annual rainfall ($R^2 = 0.72$, $P < 0.001$).

For the whole data set, and for each transect, we evaluated the effect of the predictor variables using generalized linear models (GLM) for total and pioneer species diversity. In all models, a gamma distribution and a log-link function were used. A quadratic term was introduced into the models as in some cases we detected a unimodal pattern in the relationship between species richness and some of the predictor variables. We used significance tests (chi-squared tests) based on reduction of deviance and reduction of variables to increase the parsimony of the models. In a complementary manner, variance partition models were used with the hierarchical partitioning approach, a method useful for determining the relative contribution of the predictive variables to variance (Chevan & Sutherland 1991). Hierarchical partitioning (HP) analyses were carried out using the hier.part package. Additionally, the value of Z was obtained to determine the significance of the variables, using a randomization routine (999 randomizations) to generate the Z scores and a 95% confidence interval ($Z \geq 1.65$; Walsh & Mac Nally 2015). All analyses were carried out using the R software (R Development Core Team 2016).

RESULTS

ELEVATIONAL PATTERNS OF TREE DIVERSITY.—We counted 12,533 individual trees belonging to 444 species, 225 genera, and 80 botanical families. Estimates of species richness were more variable among elevations at the Triunfo and Pico de Loro transects vs Pijijiapan and Sepultura, where estimates at low elevation sites showed some of the lowest values; a maximum of species richness at higher elevations was recorded at the Pico de Loro transect (Fig. 1). In general, the pattern of spatial distribution of total species diversity was fairly constant along the elevation gradient (Fig. 2A), although an increase was observed toward the highest elevation in Pico de Loro (Figs. 1, 2C), and at intermediate elevations of the Triunfo transect (Fig. 2E). For the Pijijiapan and Sepultura transects, total species diversity was fairly constant (Figs. 2G and I). Patterns of diversity of pioneer species in all transects combined (overall) and for each individual transect were

linear, decreasing as elevation increased (Figs. 2B, D, F, H and J). Similar results were obtained when diversity of pioneer species was calculated with their proportion instead of their number of species (Fig. S2—Online Supplementary Material).

EXPLAINING PATTERNS OF SPECIES DIVERSITY.—The GLM explained a small proportion of the variance for total species diversity (11.2%; Table 1), with rainfall of the warmest quarter and isothermality as significant variables. Upon generating models for each transect and their determining variables, elevation, isothermality, and temperature annual range accounted for 38.5 percent of variation of total species diversity at Pico de Loro; elevation alone accounted for 27.7 percent of variation of total species diversity at Triunfo.

Some discrepancies among significant variables emerged through the use of either GLM or HP (Fig. 3). The variable rainfall of the warmest quarter (HP = 29.6% of variation; Fig. 3A) explained more variance in total species diversity than did isothermality (HP = 21%). When considering transects separately, only for Pico de Loro temperature annual range was significant (HP = 24.2%; Fig. 3C); for Triunfo, three variables (isothermality, rainfall of driest month, and rainfall of warmest quarter) were significant (Fig. 3E), although none of these corresponded to the variable detected through GLM (elevation); for Pijijiapan, phosphorus was significant (HP = 30.8%; Fig. 3G) and none for Sepultura (Fig. 3I).

The GLM for overall pioneer diversity explained 48.9 percent of variance in species diversity (Table 1), and a negative correlation was found between pioneer diversity and the elevation gradient. This negative correlation was detected through GLM in all transects. The results of hierarchical partitioning were consistent with those from GLM and indicate that elevation was the variable which mostly contributed to explain overall pioneer diversity and in all transects separately (Figs. 3B, D, F and H), but at Pico de Loro temperature annual range was detected as significant by GLM (explaining 49.4% of total variation; Table 1). For the Triunfo transect, temperature annual range and cation exchange capacity were significant (66.4%), as were isothermality and temperature annual range for Pijijiapan (57.4%).

DISCUSSION

We studied a broad and highly diverse mountain system within a region with a high tree species richness (González-Espinosa *et al.*

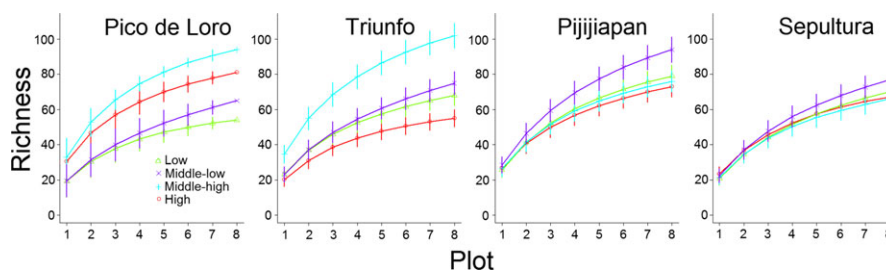


FIGURE 1. Species accumulation curves for each elevation band within transects sampled at the Sierra Madre of Chiapas mountain range in southern Mexico.

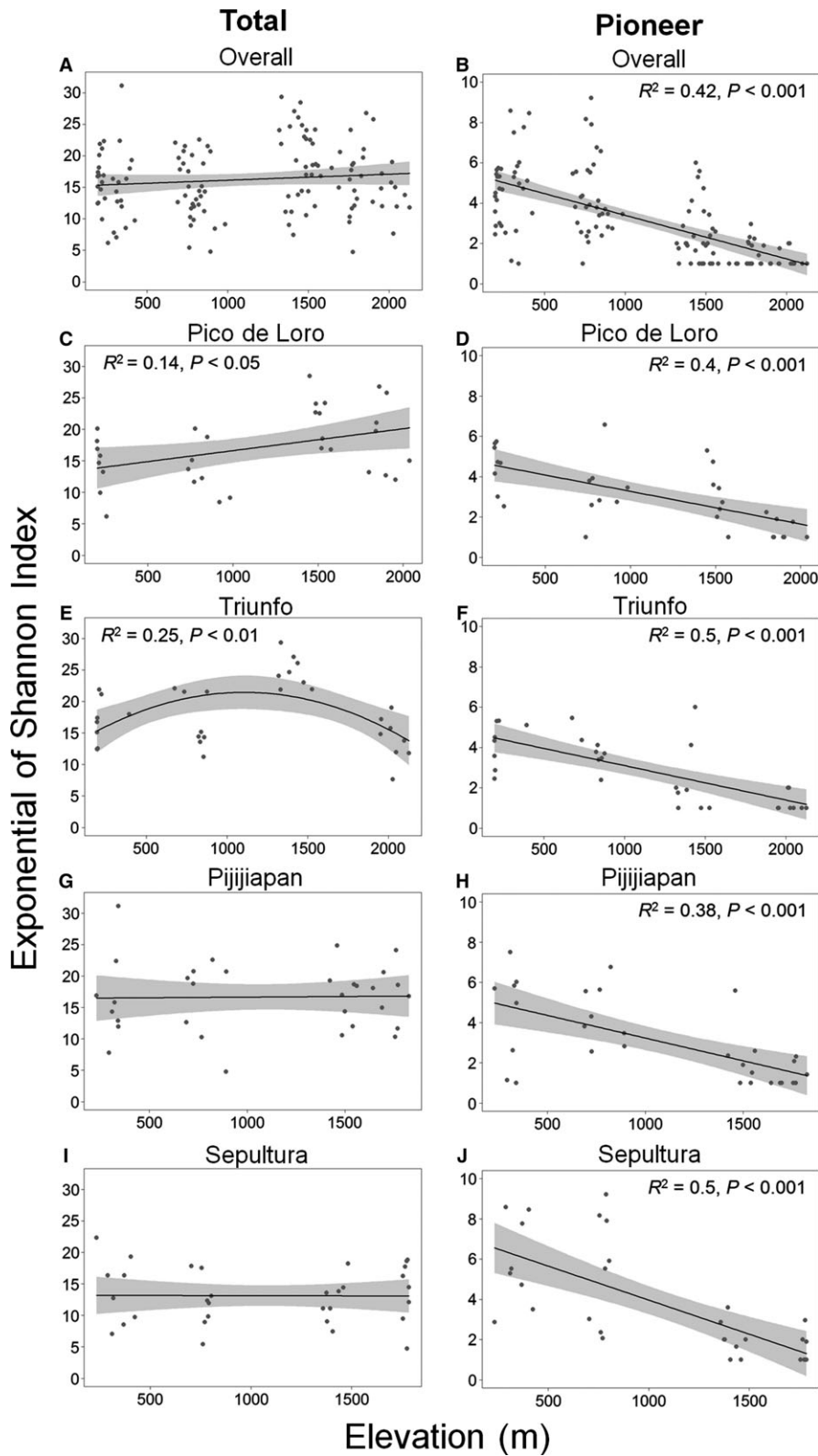


FIGURE 2. The relationship between total tree diversity and pioneer species diversity and the elevation gradient at the Sierra Madre of Chiapas mountain range in southern Mexico. A quadratic term was included in the regression linear model for Triunfo.

TABLE 1. Summary of the generalized linear models for total tree species diversity (TD) and pioneer species diversity (PD) for all transects together and separately. Non-significant variables (phosphorus and slope) are not shown. D^2 = explained variance.

| Response variable | Transect | Model parameters | | | | | | | | D^2 |
|-------------------|--------------|------------------|------------|------------|-----------|-----|-----------|------|------------|-------|
| | | Intercept | Elev | Isot | Tar | Rdm | Rwq | Clay | CEC | |
| TD | Overall | -2.2647329 | | 0.0654345 | | | 0.0008197 | | | 11.2 |
| | Pico de Loro | 1.395e+02 | -1.263e-04 | -2.124e+00 | 1.123e+00 | | | | | 38.5 |
| | Triunfo | 2.584e+00 | 9.135e-04 | | | | | | | 27.7 |
| | Pijijiapan | | | | | | | | | |
| | Sepultura | | | | | | | | | |
| PD | Overall | 2.060e+00 | -6.535e-04 | | | | | | -1.366e-02 | 48.9 |
| | Pico de Loro | -3.037e+01 | -1.868e-03 | | 2.094e+00 | | | | | 49.4 |
| | Triunfo | -9.0423167 | -0.0007908 | | 0.6946189 | | | | -0.0203388 | 66.4 |
| | Pijijiapan | -2.617e+02 | -4.255e-03 | 2.880e+00 | 3.583e+00 | | | | | 57.4 |
| | Sepultura | 2.3007575 | -0.0010670 | | | | | | | 58.7 |

CEC, cation exchange capacity; Clay, clay content; Elev, Elevation; Isot, Isothermality; Rdm, rainfall of driest month; Rwq, rainfall of warmest quarter; Tar, temperature annual range.

2004). We found that spatial patterns of species diversity and the relative importance of associated climatic, topographic, and soil variables vary along the environmental gradient according to the spatial scale of analysis (transect vs regional level) as well as to the functional groups considered. We suggest that no single model can be proposed to account for biodiversity patterns along elevational tropical gradients that clearly are scale- or taxa-dependent. Thus, some climatic variables (*e.g.*, rainfall of warmest quarter) show a predictive value at a regional scale that may differ in their contribution to explain variance within a given transect. We found that elevation, temperature, and rainfall were related to functional groups of tree species that we could differentiate (either pioneer or late-successional species). This idiosyncratic response to physical factors has been reported in regard to plant taxonomic groups (Guo *et al.* 2013, Krömer *et al.* 2013, Peters *et al.* 2016), growth forms (Bhattarai & Vetaas 2003, O'Brien 2003, Watkins *et al.* 2006), and groups differing in their phytogeographical affinity—temperate vs tropical (Oommen & Shanker 2005).

Few studies on elevation gradients analyze putative environmental drivers along a broad regional spatial scale and evaluate different quasi-parallel elevation transects using standardized methods. In such cases, tree diversity has been found to be constant throughout the elevation gradient and among different transects (Lovett 1996, Zhang *et al.* 2016), whilst transects themselves show either unimodal or linear patterns (Grytnes 2003). Yet, most of the studies conducted with plant groups have included a single elevational transect with a commonly emerging unimodal pattern, often related to temperature and/or rainfall as major climatic drivers (Bhattarai & Vetaas 2003, Hemp 2005, Acharya *et al.* 2011, Guo *et al.* 2013, Peters *et al.* 2016). The results on woody species reported from the Himalayan region by Oommen and Shanker (2005) are interesting as the same unimodal species richness pattern was found over five nested spatial scales, from one at a local level ($\sim 30 \text{ km}^2$) up to one encompassing a large

geographical region ($\sim 200,000 \text{ km}^2$). We found in a few cases for all tree species lumped together (and for late-successional species) evidence of the influence of elevation (temperature and rainfall); yet the relationship between elevation and species richness in our system was not as clear-cut as reported in other studies (*e.g.*, McCain 2007). In our study system, another climatic variable, in this case related to seasonality (rainfall of the warmest quarter), explains overall tree diversity variation across all transects; seasonality has also been recently proposed to explain tree distribution in tropical forests (Condit *et al.* 2013, Esquivel-Muelbert *et al.* 2016).

Some plots showed an increase in tree richness in those areas with higher rainfall within the warmest quarter, as in the intermediate parts of the Pico de Loro and Triunfo transects, which are not necessarily the areas receiving the highest annual rainfall. The intensity of drought relates to an increase in water deficit of trees, with the result that a smaller number of species have been able to evolve physiological and reproductive mechanisms allowing them to thrive under such conditions (Esquivel-Muelbert *et al.* 2016). However, we frequently found a fairly constant diversity along the elevation gradient. There is no simple and straightforward explanation to account for the constant tree diversity pattern along elevation in our study system. Actually, non-significant variables were identified either with the GLM or with the HP approaches in some cases (Pijijiapan and Sepultura transects). Guo *et al.* (2013) suggest that the constant diversity pattern along elevation gradients and the lack of a well-defined set of climatic predictions may result from a rather limited extent of the gradient being evaluated, which may restrict biological and/or climatic variation. Yet this is not the case with our study system, as a considerable span of elevation (195–2127 m asl) and climatic variables (*e.g.*, temperature from 16.8°C up to 26.2°C) is clearly observed, with a striking trend toward lower temperatures and increasing rainfall at the highest elevations. Facing the lack of an evident climatic driver that could be identified at a regional

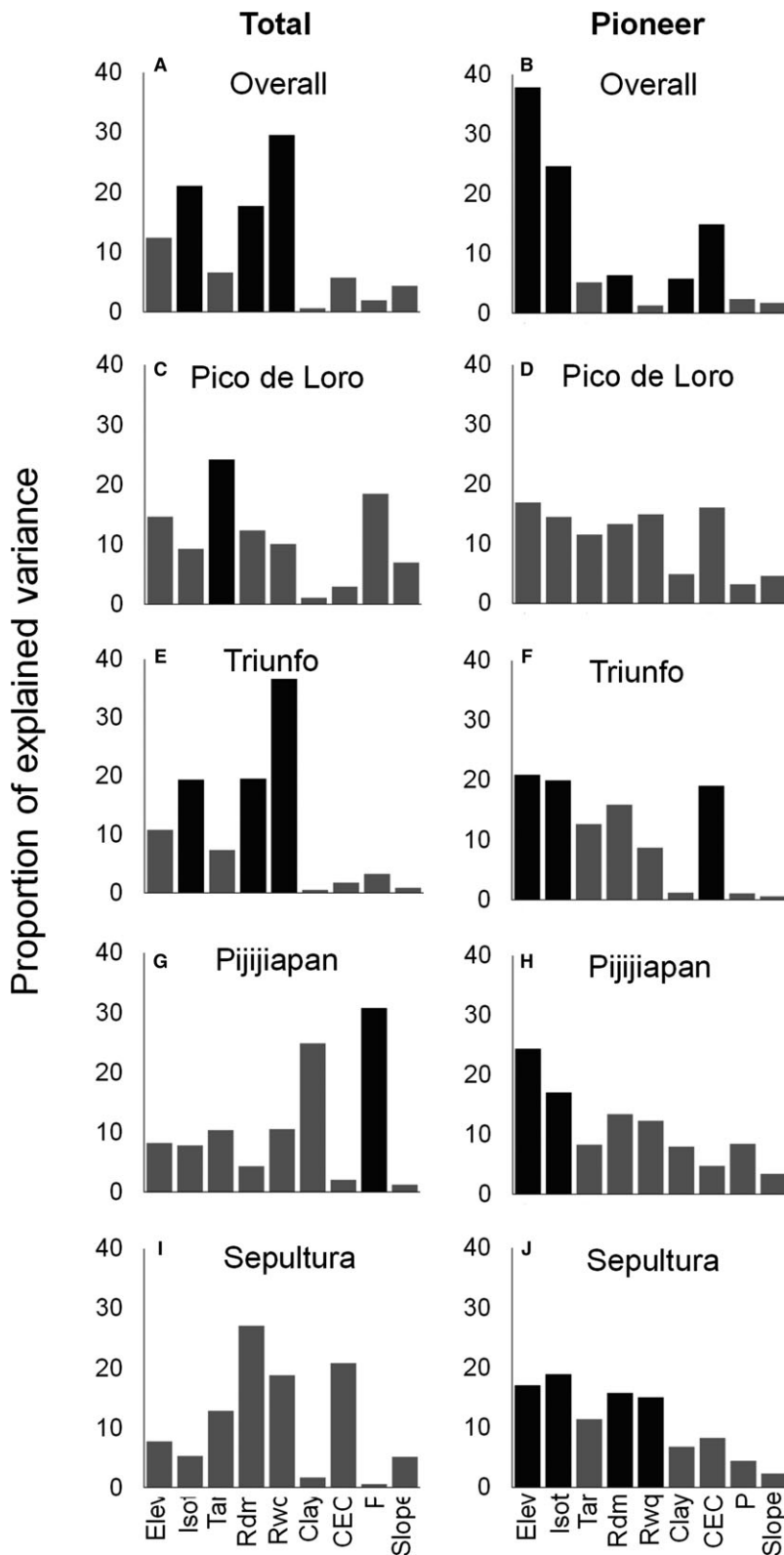


FIGURE 3. Distribution of percent independent effects of climatic, edaphic, and topographic variables on tree diversity (total and pioneer species). Black bars represent significant effects as determined by randomization test (Z -score based on the upper 95% confidence limit, $Z \geq 1.65$). Gray bars represent non-significant effects. CEC, cation exchange capacity; Clay, clay content; Elev, elevation; Isot, Isothermality; P, phosphorus; Rdm, rainfall of driest month; Rwc, rainfall of warmest quarter; Tar, temperature annual range.

scale, we suggest that a constant species diversity along elevation may be driven by very dynamic evolutionary and biogeographical mechanisms that have been proposed to operate in mountain systems (Lomolino 2001). It remains as a pending issue to be dealt with in the mountain systems of southern Mexico and Guatemala, untangling the role of these biological and geological historical mechanisms and their interaction with elevation-related climatic variables in molding a constant diversity pattern along the whole mountain system. We suggest two relevant biogeographical and evolutionary issues. On the one hand, undergoing processes of biological exchange and integration of the biota in the whole mountain system, as the regional plant species pool, includes elements with several phylogeographical origins (Nearctic, Neotropical—mainly South American, Central American, and autoctonous; Quintana-Ascencio & González-Espinosa 1993, Graham 2010); also, it has been found in other tropical mountain systems that the occurrence of taxa from different biogeographical groups varies along the elevation gradient (Li & Feng 2015). On the other hand, evolutionary processes occurring at smaller spatial scales may also contribute to the observed patterns (or lack of them), such as constant diversification rates along the elevation gradient (Rohde 1992). However, a recent global-level study reveals that due to geographical isolation, diversification rates and endemism increase toward the higher areas of elevation gradients, in particular in tropical mountain systems (Steinbauer *et al.* 2016). Also, it has been proposed identifying regions with higher species diversity in coincidence with areas where speciation rates may be higher (Harrison & Cornell 2008, Schluter & Pennell 2017). Finally, we should mention our almost exclusive attention in this study to diversity of tree species. Further analyses also including other plant groups with different growth forms such as terrestrial herbs, epiphytes, shrubs, and lianas would probably result in different diversity patterns to those detected with tree species (*e.g.*, Peters *et al.* 2016). Within our study area, D. A. Jiménez-López (unpubl. data) has detected at the Triunfo transect that richness of epiphyte species increases linearly with lower temperatures and higher humidity as elevation increases.

We found that different functional groups of tree species differ in their distribution patterns as well as in their relationship to possible physical drivers at the transect and regional levels. The causes of these different patterns of diversity may reside in differences among groups of species regarding their ecological niche requirements along pathways of secondary succession (Shmida & Wilson 1985, Quintana-Ascencio & González-Espinosa 1993) as well as with respect to their physiological tolerance in relation to the elevation gradient (Guo *et al.* 2013). Regarding diversity of pioneer tree species, the relevance of the elevational gradient as the main predictor in most of the models is noteworthy. In addition to physical variables correlated with elevation such as temperature and rainfall, it should be mentioned in our study system the effect of human disturbance on forest fragments and on remnants of old growth forests, with a linear decrease toward the highest areas of the elevational gradient. The pattern detected for pioneer diversity is clearly associated with greater human disturbance in the lower areas of our study area, which

has a negative effect on forest richness and composition. Notwithstanding that plant species richness in forest fragments may be related to forest fragmentation, fragment age, and disturbance (Ross *et al.* 2002), the influence of human activities on diversity patterns has been poorly documented in studies on plant richness along elevation gradients. However, it is repeatedly mentioned that the effect of human disturbance is more severe in lower areas (Nogués-Bravo *et al.* 2008, Ensslin *et al.* 2015, Averett *et al.* 2016); in this study, species diversity of early-successional species at low elevation sites accounted for an average 32 percent of total tree diversity, with one plot where this functional group of tree species surpassed 74 percent.

Soil variables may be strong predictors of spatial variation of plant diversity in tropical lowlands (Huston 1980, Condit *et al.* 2013), but few studies have addressed their relevance to explain diversity patterns along elevational gradients in tropical mountain systems (Hemp 2005, Homeier *et al.* 2010). In this study, soil variables showed their relevance mostly at the transect spatial scale and in a lower proportion than climatic variables and topography (elevation). This was more clearly evidenced with cation exchange capacity (Table 1, Fig. 3), associated to a higher diversity of pioneer tree species in the lower parts of the watersheds. Huston (1980) also reported a direct relationship of this soil variable with high tree diversity in Costa Rican lowland forests, which may be more diverse in poor and highly disturbed soils, as we have observed in the lower areas of the Sierra Madre of Chiapas. Yet we still lack more detailed studies linking soil properties to tree diversity along elevation gradients.

Finally, the difficulty that still exists in identifying drivers of tropical tree diversity along elevation gradients may be influenced by a relatively low overall sampling density (Guo *et al.* 2013), the use of widely different protocols for sampling and field methods (Karger *et al.* 2011), or insufficient use of stratified and replicated sampling schemes like the one we followed in this study. We consider that the number of plots that we used is fairly adequate (Fig. 1) and that the stratified sampling scheme used does not represent an obstacle for applying regression methods in an aim to identify determinant drivers of tree diversity at different spatial scales along the elevational gradients included in the Sierra Madre of Chiapas mountain system.

CONCLUSION

This study shows that elevational patterns of tree diversity in a complex and diverse tropical mountain system located in southern Mexico vary with respect to components of overall regional diversity, location of the transect, spatial scale, and functional group. Variation in total tree diversity is mostly explained by regional climatic and topographic factors. The predictive power of significant variables was generally low or non-significant. Possible causal factors remain debatable, but our results point toward the need to consider the spatial scale of analysis and contingent regional geological and evolutionary historical facts. We suggest conducting further studies on elevation patterns of species diversity (both trees and other plant groups) in tropical mountain

systems with the explicit consideration on the parallel but differential influence of historical and evolutionary factors on local and regional diversification.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n41j7> (Martínez-Camilo *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. Checklist of tree species belonging to three functional groups included in the sampling at the Sierra Madre of Chiapas, southern Mexico.

TABLE S2. Pearson correlation coefficients for climatic variables.

FIGURE S1. Study area and location of sampling plots within four elevational transects along the Sierra Madre of Chiapas, southern Mexico.

FIGURE S2. Relationship between tree diversity and elevation when the former is calculated with percentage of pioneer diversity at the Sierra Madre of Chiapas mountain range in southern Mexico.

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