

## Tree diversity in the northern Neotropics: regional patterns in highly diverse Chiapas, Mexico

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Physical factors that may account for regional patterns of plant species diversity remain controversial. We aim to determine the relationship of tree species diversity to environmental factors identifiable at regional scale in the northern Neotropics. We use a high-resolution data set based on herbarium collections of all native tree species known to occur in the highly diverse and physiographically heterogeneous Mexican state of Chiapas. We analyzed 114 grid cells (5 min latitude  $\times$  5 min longitude each) with 40 or more vouchers. We obtained from maps (scale 1:250 000) data on temperature, rainfall, elevation, and soils, and calculated for each grid cell mean actual evapotranspiration (AET), its ratio during the rainy and dry seasons (RET), average fertility/quality of soils (SFQ), and elevation (coarse-scale topography) variance (SDE). These variables were largely independent of each other, and were entered in multiple regression models to predict species diversity assessed with Simpson's index of concentration. A model that accounted for 41.4% of the total variance in tree diversity showed positive effects of AET and seasonality (RET), whereas SFQ had a negative effect. A curvilinear model described well the relationship between tree diversity and AET ( $R^2=0.45$ ), and an intermediate maximum was detected. The data pattern suggested an asymptotic relationship as well, which was confirmed with a two-part regression. Regression quantiles provided better estimates of the effect of SFQ with the upper envelope of the data (0.85–0.90 quantiles). Minimum diversity at intermediate rainfall values hints at a bimodal model of tree diversity along a rainfall gradient, in opposition to the frequent contention of a positive linear relationship. We suggest that broad-scale climatic gradients interact with intraregional landscape-level influences, thus leading to the observed nonlinear responses of tree diversity to environmental predictors.

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Explaining the distribution of diversity along broad environmental gradients continues to challenge ecologists (Pianka 1966, Francis and Currie 2003, Qian and Ricklefs 2004). Spatial patterns of plant diversity have been related to both regional macro-scale processes such as the proliferation and extinction of species, as well as

to local processes determining the carrying capacity of environments to support coexisting species (Ricklefs 1987, 2004). Environmental attributes such as climatic stability and predictability, spatial heterogeneity of resources, and primary productivity determine the variation of habitats to support plant diversity (Pianka

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1966, Huston 1994, Bailey et al. 2004). Whereas there is consensus on the relationship between plant diversity and some possible causal factors (e.g. spatial environmental heterogeneity created by coarse-scale topography or major disturbances), the effects of other factors continue to dispute (e.g. available energy).

The energy-diversity (or energy-species) hypothesis explains the decrease of many terrestrial taxa by decreases in primary productivity or energy as latitude increases (Fischer 1960, Simpson 1964, Wright 1983, Currie 1991, Scheiner and Rey-Benayas 1994, Whittaker et al. 2001). It is not uncommon that information is lacking for variables more directly related to plant productivity (available energy), like solar radiation, temperature, rainfall, and evapotranspiration, which has led to the occasional use of latitude as a surrogate independent variable to explain plant diversity (Rosenzweig 1968, 1995, Mittelbach et al. 2001). Some evidence with vascular plants supports a linear increasing function of evapotranspiration as predictor of species diversity over large scales (Currie 1991, Wright et al. 1993, Austin et al. 1996, Mittelbach et al. 2001, Rey-Benayas and Scheiner 2002). At local scales most of the relationships between primary productivity (or its surrogates) and vascular plant diversity are hump-shaped (Grime 1979), but a unimodal relationship has also been proposed at global or regional scales (Huston 1979, 1994, Rosenzweig and Abramsky 1993, Mittelbach et al. 2001). Austin and Smith (1989) proposed a bimodal pattern of plant species diversity along environmental gradients, notably rainfall. On the other hand, it has been suggested that the interaction of local and regional level factors leading to the observed diversity patterns can only be detected at relatively fine spatial scales (Huston 1999). Tests using vegetation diversity and plant species distribution along regional climatic gradients interacting with local attributes and processes such as site productivity, population interactions, and major disturbance would help to assess some of the proposed hypotheses (Austin and Smith 1989, Givnish 1999, Huston 2004).

Biological and environmental information at the regional or macro-scale level is scarce for most tropical regions (O'Brien 1993, 1998, Lawton et al. 1998), and this hampers comparisons of diversity patterns within the tropics, as well as with other better-known extratropical regions. Available studies frequently depend on information assembled over widely varying spatial scales, from continental to local, which complicates analyses of relationships (Huston 1999, Willis and Whittaker 2002, Ricklefs 2004). Broad scale climatic variables have proved to be useful in modeling predictable macro-scale patterns (Woodward 1987, O'Brien 1998, Whittaker et al. 2001, Francis and Currie 2003, Venevsky and Veneskaia 2003); yet, a comprehensive framework aimed to reconcile the effects of biogeogra-

phical and ecological factors that drive processes at different temporal and spatial scales has been proposed (Ricklefs 2004). Predicting the spatial distribution of tree diversity is particularly relevant in the tropics because of their high diversity and threatened status (Lawton et al. 1998). Understanding the spatial variation of plant species diversity and its interaction with other factors defined at regional and landscape levels may support land use planning, monitoring the consequences of human disturbance (e.g. fire, deforestation, agriculture), and ecological restoration of tree diversity (Lindenmayer and Franklin 2002, Huston 2004).

In this paper, we analyze the interaction among some environmental factors and the diversity of native trees at a regional scale (e.g. several hundreds or thousands of squared kilometers; Mittelbach et al. 2001, Qian and Ricklefs 2004). We use a data set compiled for Chiapas (southern Mexico) that has a consistent scale (1:250 000) and high resolution for taxonomical, geographical and habitat data. The raw data come from the labels of herbarium specimens of trees collected over a period of 135 yr and from published maps. The study region has high biodiversity and environmental heterogeneity (Breedlove 1981, 1986, Ceballos et al. 1998, Wolf and Flamenco 2003), thus enhancing its relevance as a case study of regional scale patterns of tree diversity in the tropics.

## Objective and hypotheses

We aim to determine the relationship of tree species diversity to environmental determinants identifiable at regional scale in the northern Neotropics. Based on classical hypotheses about ecological gradients and diversity, we predict that tree diversity will be associated with 1) increasing environmental favorableness, measured as actual evapotranspiration and soil fertility/quality (Francis and Currie 2003; but see Huston 1994), 2) increasing temporal fluctuation of climatic conditions (seasonality of temperature, rainfall, and evapotranspiration; but see Givnish 1999), and 3) increasing spatial heterogeneity, measured by both coarse-scale topographical variance and the variety of soils within diversity samples (Ricklefs 1977, O'Brien et al. 2000).

## Materials and methods

### Study region

This study is limited to the political boundaries of Chiapas (75 634 km<sup>2</sup>), the southernmost Mexican state (Fig. 1). Its latitudinal range, orography and geological history create a large variety of physiographic regions and ecological conditions (Müllerried 1957, Breedlove 1981). The vascular flora of Chiapas is estimated at over

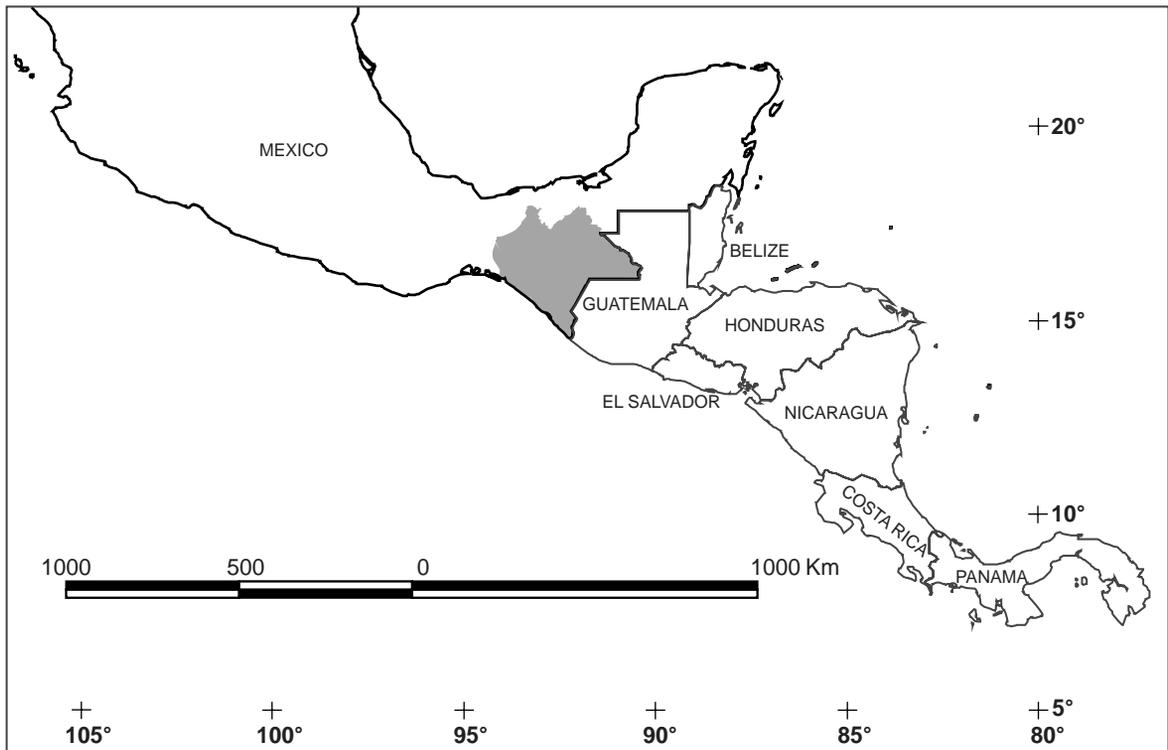


Fig. 1. Location of the state of Chiapas (shaded area) within the northern Neotropics. The upper borderline of the figure approximates the Tropic of Cancer.

9000 species (Breedlove pers. comm.; see web page about Chiapas at <[www.calacademy.org](http://www.calacademy.org)>). Vegetation formations range from lowland evergreen tropical forests up to subalpine scrubland, and from mangroves up to high-elevation evergreen cloud forests and pine forests (Miranda 1952, Breedlove 1981). Local microclimates are very fine-grained (32 Koeppen types have been recognized; García 1987). Most of the territory receives the largest proportion of rainfall in May–October; the “dry season” may last 1.5–6 months, starting in November at the earliest, and may be interrupted by short rainy spells in December–February (García 1987).

### Tree species database

Mexico and Central America are usually not included in macroecological analyses because available accounts of plant species distributions in these regions are regarded as incomplete or not useful (Currie 1991). Yet, conceding that better inventories of species diversity are badly needed in all tropical regions, our study addresses one of the most botanically explored regions within tropical Mexico, and possibly the world (see Ibarra-Manríquez et al. 2002 and Parnell et al. 2003 for comparison with recent studies including the tree flora of the Yucatan Peninsula, and the vascular flora of Thailand, respectively). Chiapas is second only to the neighboring state

of Oaxaca in its floristic diversity within Mexico (Rzedowski 1993).

We compiled a database with information from labels of herbarium sheets of all native tree species collected over a period of 135 yr [i.e. woody plants with diameter at breast height (dbh)  $\geq 3$  cm and height  $\geq 3$  m that grow in Chiapas and that have not been introduced from elsewhere, including other regions of Mexico]. Thus, specimens occasionally identified by collectors as tall shrubs or treelets (monopodic plants  $< 3$  m high) are included if their maximum recorded height exceeds 3 m. We verified the life form of most taxa from species descriptions in Standley (1920–1926), Standley and Steyermark (1946–1966), Standley and Williams (1961–1975), Gentry and Standley (1974), Fryxell (1994), Daniel (1997), Farjon and Styles (1997), and Strother (1999). We looked for specimens at seven different herbaria. We reviewed all vouchers of tree species in the botanical holdings of the California Academy of Sciences (CAS and DS herbaria), covering the period from 1864 through 1996, and at El Colegio de la Frontera Sur (ECOSUR, San Cristóbal de Las Casas, Chiapas, 1974–1999). We also examined a partial set (estimated as ca 60%) of available specimens at MEXU (Univ. Nacional Autónoma de México, Mexico City; years 1896–1999), including all tree collections from the Central Highlands and the Selva Lacandona regions. We

examined a smaller proportion of specimens at XAL (Inst. de Ecología, Xalapa, Veracruz), CHAPA (Colegio de Postgraduados, Montecillo, México), and ENCB (Inst. Politécnico Nacional, Mexico City). Further information on herbaria visited (except ECOSUR) appears in Holmgren et al. (1990). We also looked at georeferenced Chiapas collections available in W<sup>3</sup> TROPICOS, an online database managed by the Missouri Botanical Garden. Our database includes at least 85–90% of the vouchers available worldwide, as CAS and DS jointly hold what possibly is the largest collection of Chiapas flora in the world (ca 70 000 vouchers; Bartholomew and Breedlove pers. comm.). The other herbaria that we visited (except ECOSUR) include many duplicate specimens that we reviewed previously at CAS and DS. All records in the database included information on taxonomical nomenclature, collectors, and collecting dates and localities. Information on habitat, accompanying species, and geographical data (latitude, longitude, elevation) was appended if available. Botanical synonymy was checked and the most recent genus name was used based on Breedlove (1986) and Mabberley (1997).

For each record we obtained geographical coordinates to the nearest five seconds (or checked those appearing on the labels), based on locality data in voucher labels and interpolation using topographical maps (scale 1:50 000; Anon. 1988–1994). We used the ArcView software (Anon. 2000) to overlay a grid with cells 5 min latitude  $\times$  5 min longitude (ca 9.29  $\times$  8.30 km, respectively). The entire territory of the state was included in the whole or partial area of a total of 1020 grid cells (Fig. 2). These are assumed to have a squared shape and a constant area (ca 77.11 km<sup>2</sup>) due to the low latitude of the study region and its relatively small geographical span (3.5 degrees of latitude). We obtained counts of vouchers and the number of tree species that they represented within each grid cell. Analyses were conducted only on grid cells with  $\geq 40$  herbarium collections ( $n = 116$  grid cells); a smaller sample size was considered inadequate. Two grid cells were further discarded from the analyses because only one botanist had collected almost all specimens (>92%) within each of them.

### Climatic variables

We used GIS files with climatic data digitized from published maps (scale 1:250 000; Anon. 1984a, b). Records cover at least 15 yr, with an average  $\pm$  SE of  $30.6 \pm 0.84$  yr, recorded in at least 130 weather stations. The raw climatic variables available were: minimum and maximum mean temperatures for both the May–October and November–April periods (isotherms separated by 3.0°C), minimum and maximum number of days in a year with early morning frost (0, 3, 4, 5, 16, 24, 32, or 40 d), total rainfall

during the May–October rainy season (MRR, isopleths separated by 100 mm when total values <1000 mm, and by 300 mm intervals when total values >1700 mm), and during the November–April “dry season” (MRD, isopleths separated by 25–100 mm depending on the total value). Mean annual temperature (MAT) and rainfall (MAR) for each grid cell were calculated with proportional weights of grid area between contour lines.

Mean annual actual evapotranspiration (AET, mm yr<sup>-1</sup>) was estimated for each cell with Turc’s model (1954),  $AET = P/[0.9 + (P/L)^2]^{1/2}$ , where  $L = 300 + 25 T + 0.05 T^3$ ,  $P$  = mean annual precipitation, and  $T$  = mean annual temperature. This index has been used in large-scale hydrological maps of Mexico (1:4 000 000; Maderey and Torres-Ruata 1990). Seasonality of evapotranspiration (RET) was estimated as the ratio of proportional values of evapotranspiration during the rainy (May–October, AER) and dry (November–April, AED) periods.

### Edaphic variables

Soil taxa (combinations of soil units, subunits, and physical phases) in the FAO-UNESCO Soil Map of the World (Anon. 1974) were obtained for each grid cell from published soil maps (scale 1:250 000; Anon. 1992–1993). These soil maps are based upon at least 490 field sample sites and interpretation of aerial photographs. A total of 59 soil taxa were identified within the selected 114 grid cells, out of 84 soil taxa for the whole of Chiapas. We calculated an index of soil fertility/quality (SFQ) based on interpretation of physical and chemical properties of soil taxa as described in the legend of the FAO-UNESCO map (Anon. 1974, Duchaufour 1987), in addition to information on soil texture and physical phases available from the maps. We adapted soil productivity criteria suggested by Riquier et al. (1970) to assign to each soil taxon a categorical value (1–8) for each of the following attributes: drainage, effective depth, texture/structure, base saturation, organic matter content, mineral reserves, and mineral exchange capacity/nature of clay. Thus, a eutric gleysol received an array of values for these seven criteria as (1, 3, 2, 8, 5, 5, 5). Soil fertility/quality for each soil taxon was assigned as the sum of category points, and it was ranked as the percentage of the highest total obtained (haplic phaeozem, score = 56). Values of SFQ in each grid cell were weighted by percentage area covered by each soil taxon.

### Soil and topographic heterogeneity

We counted the number of soil taxa (SOT) in each grid cell (Rey-Benayas and Scheiner 2002), and estimated soil diversity (DSO) with Shannon’s  $H'$ , using their percentage area on soil maps as a measure of their “relative

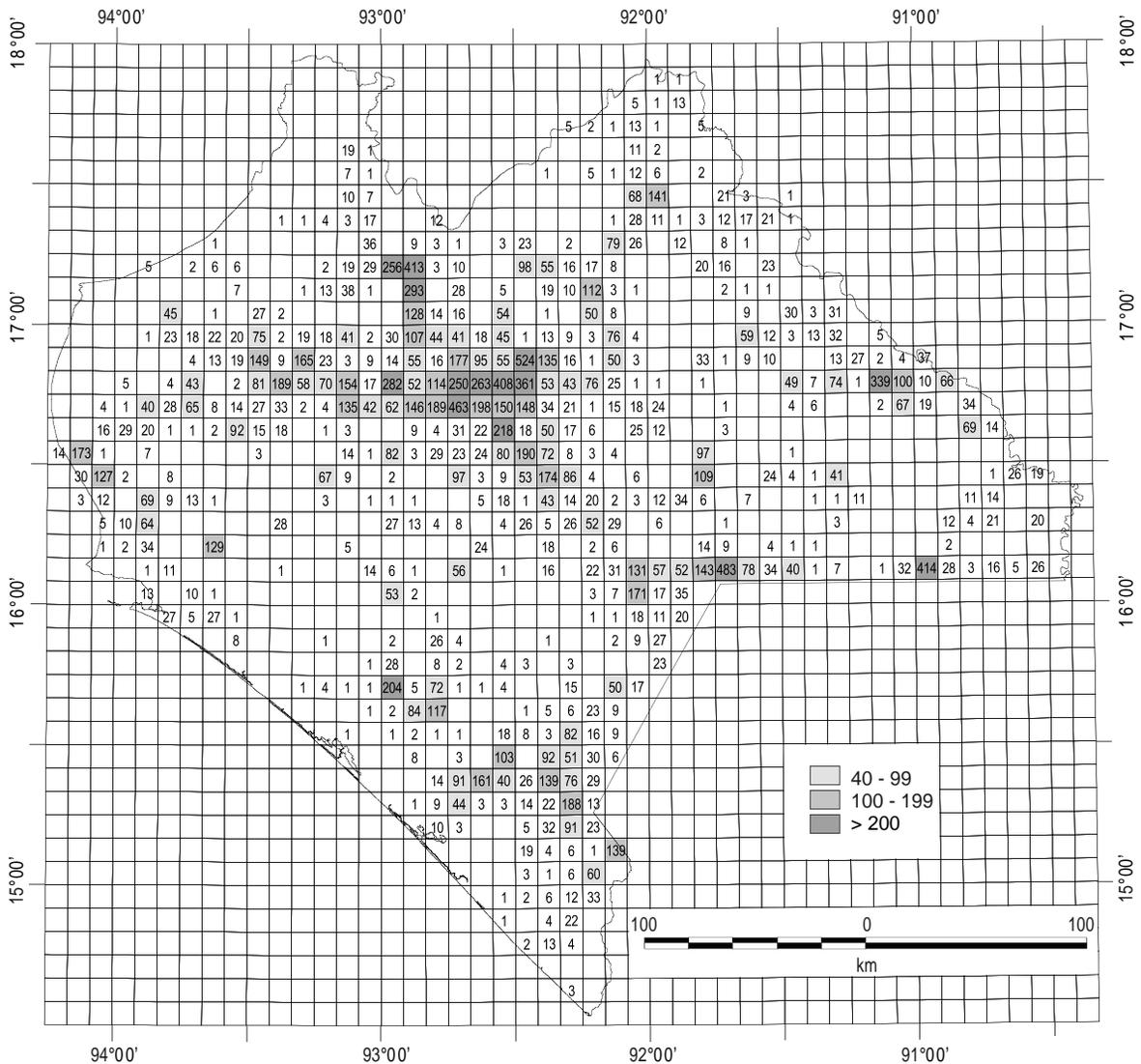


Fig. 2. Map of Chiapas showing the location of 5 × 5 min grid cells with and without herbarium collections of native tree species accumulated during the period 1864–1998. Figures in the grid cells are counts of voucher specimens recorded. Only the 114 shaded cells were used in this study.

abundance". Topographic heterogeneity in each cell was calculated as the number of altitudinal isolines, elevation range, and as the weighted mean and standard deviation of elevation belts within the cell (MEL and SDE, respectively).

### Diversity indices and species richness estimators

We obtained means and standard deviation of estimators of species richness and diversity indices with the program EstimateS ver. 6.0b1 (Colwell 2001). This program constructs species accumulation curves with a protocol that shuffles the samples without replacement, and

calculates a variety of estimators with abundance or incidence data. We used 500 iterations. Only Fisher's  $\alpha$ , Simpson's index of concentration (SI), and estimators based on accumulation and rarefaction Michaelis-Menten curves (M-M, both the runs and means options), were not correlated with the number of herbarium collections within the grid cells ( $p < 0.0001$ ,  $n = 114$ ). Simpson's index was highly correlated with Fisher's  $\alpha$  ( $r = 0.97$ ) and M-M curves ( $r > 0.86$ ). Since results from their use were almost identical in all instances we only report results on tree diversity estimated with  $-\ln SI$ , where  $SI = \sum [(n_i^2 - n_i) / (N^2 - N)]$ ,  $n_i$  is the number of individuals in species  $i$ ,  $i = 1, \dots, S$ , and  $N$  is the total number of individuals of all species (Rosenzweig 1995).

## Analysis

We used Mann-Whitney U tests to assess bias and completeness of the sample dataset (114 grid cells) against the remaining territory of Chiapas (906 grid cells; Fig. 3). Several physical variables may account for environmental favorableness and its temporal and spatial heterogeneity within the grid cells. Predictors of tree diversity were chosen among 24 variables or their combinations to represent these three environmental attributes (Table 1). Linear regression models (both forward and backward methods of variable selection) were fitted to explore prediction of tree diversity as a function of factors that were not correlated (AET, RET, SFQ, SOT, and SDE) and their multiplicative two-way interactions; only RET and SOT had significant correlation ( $p < 0.001$ ; Fig. 4). Frequently used predictors of plant diversity such as MAR (Gentry 1982, 1988a, b, Wolf and Flamenco 2003) and MAT, MRR, MRD, AER, and AED, were not entered in the models because of their high correlation with AET (Fig. 4).

Multiple regression models were fitted to predict tree diversity using only the five variables that showed independence. These variables were used to test hypotheses on variation of tree diversity with habitat favorableness (AET and SFQ), temporal heterogeneity or seasonality (RET), and spatial heterogeneity (SOT and SDE). We tested whether the shape of the function between tree species diversity and AET was curvilinear unimodal with an interior maximum with the Mitchell-Olds and Shaw test (1987), with a null hypothesis of a non-intermediate maximum. The data pattern and locally weighted linear regression (LOWESS curve smoothing) guided further model fitting between tree diversity and physical factors. We used regression quantiles (Cade et al. 1999, Huston 2002) to estimate multiple rates of change (slopes) of tree diversity as a function of subsets of values (upper quantiles, 0.75th–0.95th) of those variables expected to be affected by

known or unknown limiting factors. The 0.50th quantile is the median and its corresponding regression model passes through the center of the distribution, analogous to a standard regression. Cade and Noon (2003) provide a detailed account of the rationale and some useful applications of quantile regression in ecology. Regression quantiles were calculated with the BLOSSOM Statistical Software (ver. W2001.08d, Cade and Richards 2001).

Spatial autocorrelation is to be expected in environmental data of the type used in this study (Liebhold and Gurevitch 2002). We did not fit spatial autoregressive models that assume spatially autocorrelated residuals, but assumed that the spatial pattern would have a negligible effect if the residuals in the ordinary least squares (OLS) regression were less autocorrelated than the original  $-\ln SI$  values (Cressie 1993, Venables and Ripley 1997). We used the library *gstat* (Pebesma 2004) within the open source statistical language R (Anon. 2004) and fitted exponential covariance models to the sample semivariograms of the standardized  $-\ln SI$  values and residuals to compare the extent of their autocorrelation. Except when otherwise indicated we computed all analyses with the SPSS (ver. 10.0) software (Anon. 1999).

## Results

### Tree species and climatic databases

The database comprised 16 677 records of native tree species collected by >320 collectors between the years 1864 and 1999. It included 105 families, 463 genera, and 1871 species or intraspecific taxa. A file with detailed taxonomic information is available on request. Most (88.61%) of the 1020 grid cells had none (49.85%) or fewer than 40 herbarium collections (Fig. 2); only 48 grid cells included 100 or more collections. The mean number of collections in the analyzed 114 grid cells was  $124 \pm 9.6$

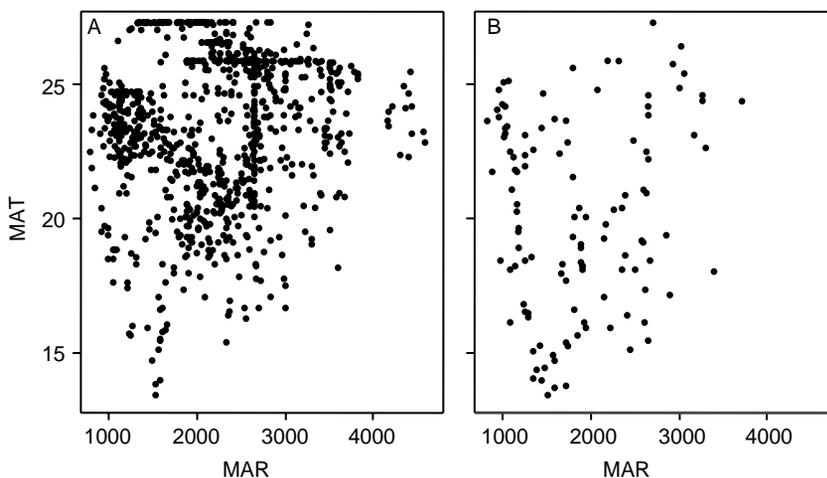


Fig. 3. Scatter plot of mean annual temperature (MAT, °C) and mean annual rainfall (MAR,  $\text{mm yr}^{-1}$ ) for (A) the set of grid cells not included in this study ( $n = 906$ ) because of having <40 herbarium collections, and for (B) the set of grid cells used in the analysis ( $n = 114$ ).

Table 1. Mean, standard error of the mean, median, and minimum and maximum values of climatic, edaphic, topographical, and tree diversity variables in the selected 114 grid cells. Whenever possible, values calculated for the remaining 906 grid cells in Chiapas are shown in parentheses. A file with geographical and environmental data for the complete set of 1020 grid cells is available on request. See Materials and methods for details on variable definition.

Variable	Mean	SE	Median	Minimum	Maximum
<b>Climate</b>					
Mean minimum temperature during the rainy season (°C)	16.2 (19.2)	0.30 (0.08)	16.2 (19.5)	10.5 (10.7)	21.8 (23.0)
Mean minimum temperature during the dry season (°C)	12.0 (15.3)	0.33 (0.10)	12.1 (14.9)	4.5 (4.8)	18.8 (20.0)
Mean annual minimum temperature (°C)	14.1 (17.3)	0.31 (0.09)	13.9 (16.9)	7.6 (7.8)	20.3 (21.5)
Mean maximum temperature during the rainy season (°C)	27.2 (30.8)	0.38 (0.11)	26.9 (31.5)	19.5 (19.8)	33.8 (35.0)
Mean maximum temperature during the dry season (°C)	24.2 (27.6)	0.38 (0.12)	23.7 (28.3)	17.7 (18.0)	34.0 (34.0)
Mean annual maximum temperature (°C)	25.7 (29.2)	0.37 (0.11)	25.2 (29.8)	19.1 (18.9)	33.9 (33.9)
Mean annual temperature, MAT (°C)	19.9 (23.2)	0.33 (0.09)	19.6 (23.5)	13.3 (13.3)	27.1 (27.1)
Mean temperature during the rainy season, MTR (°C)	21.7 (25.0)	0.33 (0.09)	21.2 (25.5)	15.1 (15.3)	27.8 (29.0)
Mean temperature during the dry season, MTD (°C)	18.1 (21.4)	0.34 (0.10)	18.0 (21.7)	11.6 (11.4)	26.4 (26.4)
Mean rainfall during the rainy season, MRR (mm)	1603 (1790)	51.6 (16.9)	1506 (1835)	815 (750)	3100 (3100)
Mean rainfall during the dry season, MRD (mm)	307 (419)	19.9 (11.7)	257 (375)	37 (37)	1003 (1790)
Mean annual rainfall, MAR (mm yr <sup>-1</sup> )	1909 (2209)	64.8 (25.4)	1803 (2200)	914 (828)	3760 (4640)
Mean annual actual evapotranspiration, AET (mm yr <sup>-1</sup> )	994 (1221)	21.6 (7.8)	928 (1196)	683 (684)	1631 (1715)
Mean actual evapotranspiration in rainy season, AER (mm)	508 (613)	10.7 (3.7)	473 (617)	360 (356)	821 (865)
Mean actual evapotranspiration in dry season, AED (mm)	146 (191)	8.5 (4.6)	131 (186)	20 (20)	423 (584)
Mean AER/AED ratio (RET)	5.36 (6.13)	0.41 (0.17)	3.66 (2.99)	1.52 (1.39)	23.88 (25.94)
Mean number of days with morning frosts, MFR	4.0	0.6	0.0	0.0	19.0
<b>Soils</b>					
Sum of relative fertility/quality of soil taxa, SFQ	75.6 (72.4)	0.51 (0.25)	75.2 (73.6)	65.5 (45.7)	88.6 (98.4)
Diversity of soils, DSO (Shannon's H')	2.0	0.0	2.1	0.7	3.2
Number of soil taxa, SOT	5.6 (4.5)	0.28 (0.08)	5.0 (4.0)	1 (1)	16 (18)
<b>Topography</b>					
Altitudinal range, ARA (m)	823	49.9	770	0	2850
Mean elevation, MEL (m)	1420 (797)	60.1 (18.0)	1450 (750)	88 (88)	2750 (2694)
Standard deviation of elevation belts, SDE (m)	445 (281)	17.8 (7.2)	427 (289)	0.0 (0.0)	1080 (1131)
Number of elevation isolines (ELI)	4.39 (3.50)	0.19 (0.08)	4.0 (3.00)	1 (1)	15 (15)
<b>Tree diversity</b>					
Number of collections, N	124.4	9.57	83	40	524
Number of tree species, S	68.2	3.64	59	20	275
Number of species represented by "singletons"	45.9	2.15	44	10	185
Proportion of species represented by "singletons"	0.70	0.012	0.72	0.38	0.90
Michaelis-Menten asymptote (runs)	252.0	15.97	206.1	34.8	1008.4
Michaelis-Menten asymptote (means)	219.5	11.64	185.7	34.3	812.4
Fisher's $\alpha$	97.7	5.60	81.4	13.8	357.5
Simpson's index of concentration (-ln SI)	4.3	0.07	4.36	2.47	6.00

(mean  $\pm$  SE), which on average represented  $68 \pm 3.6$  tree species (Table 1).

Villaseñor and Ibarra-Manríquez (1998) estimate that the Mexican flora has 3639 known native tree species. In 106 out of 463 genera we found 279 vouchers that were left conservatively undetermined as "sp." This happened on several occasions after a family or genus specialist

had made a revision of the specimens in recent years, suggesting that a possibly new or poorly known taxon was involved. Similarly, we included in our data set 298 vouchers determined only as "aff." A more conservative current estimate of the total number of tree species in our study area would therefore include at least 1294 taxa (= 1871 - 279 - 298). It is possible that when all synonyms

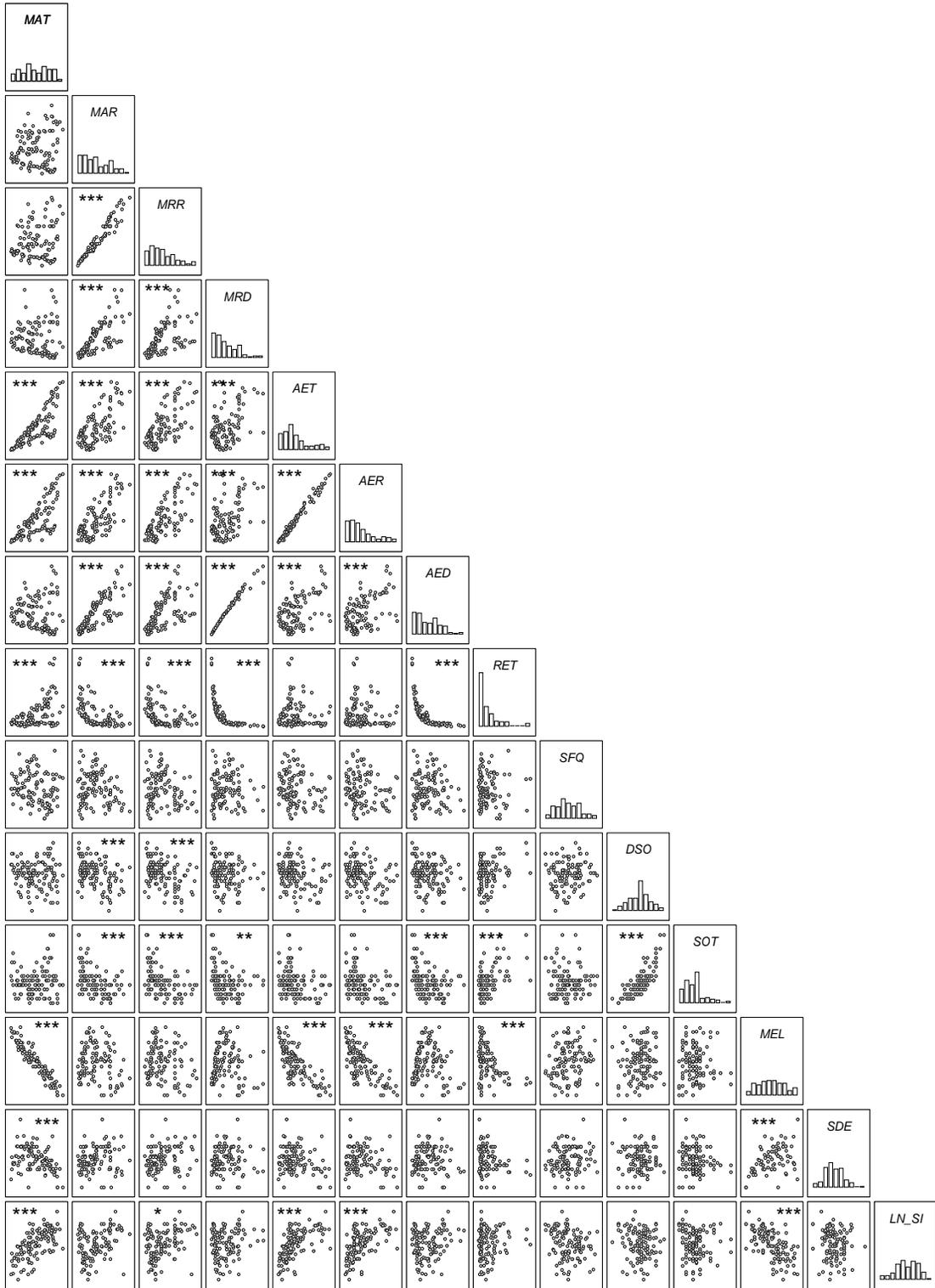


Fig. 4. Matrix of scatter plots of selected environmental variables and Simpson's index ( $-\ln SI$ ). The histogram of each variable at the top of columns includes values of the 114 grid cells grouped in 10 classes. Lack of asterisks inside the square frame indicates that correlation was not significant ( $p > 0.05$ ); \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; overall error rates after Bonferroni's correction for number of tests.

are thoroughly worked out and new species described from vouchers available the estimate for Chiapas will probably reach 1400–1500 tree species.

Mean temperature and rainfall gradients included in our analyses largely overlapped those of the entire study area (Table 1, Fig. 3). However, Mann-Whitney U-tests between the two sets of grid cells ( $n_1=114$ ,  $n_2=906$ ) indicated that the distributions of environmental variables over the whole territory of Chiapas were different from those in our sample ( $p < 0.01$  in all cases, but RET, which had  $p = 0.73$ ; Table 1). Tree collections from very rainy ( $MAR > 4.0 \text{ m yr}^{-1}$ ) and dry warm ( $MAR < 1.0 \text{ m yr}^{-1}$ ,  $MAT > 25^\circ\text{C}$ ) habitats were under represented in our sample (Fig. 3).

### Tree diversity and environment

An exploratory model (forward procedure) included AET ( $t = 6.7$ ,  $p < 0.001$ ), SFQ ( $t = -2.0$ ,  $p < 0.05$ ), and the interaction term  $RET \times SDE$  ( $t = 6.7$ ,  $p < 0.01$ ) as largely independent predictors of tree diversity ( $R^2 = 0.413$ ; collinearity tolerance  $> 0.93$ ). However, the term  $RET \times SDE$  was strongly correlated with both single RET ( $r = 0.81$ ,  $p < 0.0001$ ,  $n = 114$ ) and SDE ( $r = 0.29$ ,  $p < 0.002$ ,  $n = 114$ ). Models fitted with the backward criterion accounted for a slightly larger proportion of total variance (44%); yet, most terms had strong collinearity (tolerance was as low as 0.020), indicating potential low accuracy in estimating the regression coefficients. Because of this violation of statistical assumptions and the correlation of pairwise interactions with their component factors, we decided in subsequent analysis to use only the set of five independent factors.

A multiple regression model using data from all 114 cells accounted for 41.4% of the total variance (model 1 in Table 2; backward variable elimination). Actual evapotranspiration (AET) and seasonality (RET) had positive relationship to tree diversity, whereas soil fertility/quality (SFQ) had a negative coefficient. Neither topographical (SDE,  $t = 1.71$ ,  $p = 0.09$ ) nor edaphic heterogeneity (SOT,  $t = 0.002$ ,  $p = 0.99$ ) in each grid cell contributed to explaining the spatial variability in  $-\ln SI$ . The predictors were largely independent (tolerance  $> 0.86$  in all cases) and similar results were obtained with forward variable selection. Small spatial autocorrelation was observed in the original  $-\ln SI$  values (range of 0.17 decimal degrees in a semivariogram, ca 15 km), but it was non-existent for contiguous grid cells when assessed on the residuals of the OLS model (0.08 degrees, ca 7 km). We also extracted residuals from a predictive kriging model of the original data (leave-one out crossvalidation) and correlated them with residuals from the multiple regression model ( $R^2 = 0.59$ ,  $n = 114$ ).

Table 2. Results of multiple linear regression of effects of single environmental variables on the negative logarithm of Simpson's index ( $-\ln SI$ ). Backward selection of variables. Decreasing number of degrees of freedom result from case selection based on proportion of species within the grid cells represented as singletons (full set of cases,  $n = 114$ , model 1;  $\leq 85\%$  singletons, 94 cases, model 2;  $\leq 80\%$  singletons, 83 cases, model 3; and  $\leq 75\%$  singletons, 62 cases, model 4). SE = standard error of estimates, SC = standardized coefficients. Acronyms of environmental predictors as in Table 1.

Model	Steps	Adj. $R^2$	DF	F	p	Predictors	Estimates	SE	SC	t	p	Tolerance
1	2	0.414	113	20.99	<0.001	AET RET	2.01E-03 3.36E-02	0.000 0.013	0.629 0.197	8.22 2.64	<0.001 0.010	0.885 0.931
						SFQ SDE	-2.41E-02 5.15E-04	0.010 0.000	-0.169 0.132	-2.31 1.71	0.023 0.090	0.963 0.864
2	4	0.427	93	35.68	<0.001	AET RET	2.15E-03 3.56E-02	0.000 0.013	0.639 0.218	8.13 2.77	<0.001 0.007	0.997 0.997
3	4	0.427	82	31.53	<0.001	AET RET	2.25E-03 3.28E-02	0.000 0.013	0.638 0.209	7.63 2.50	<0.001 0.014	0.998 0.998
4	5	0.381	61	19.80	<0.001	AET RET	2.32E-03 4.08E-02	0.000 0.019	0.607 0.211	6.03 2.10	<0.001 0.040	0.998 0.998

We fitted models to subsets of grid cells selected by the increasing sample size (number of vouchers) and the decreasing proportion of “singletons” in the sample (species represented by only one specimen; Colwell 2001); these two variables were negatively correlated:  $r = -0.64$ ,  $p < 0.0001$ ,  $n = 114$ ). A decrease of the adjusted  $R^2$  (from 0.427 to 0.381) and in the number of significant predictors occurred as the dataset was reduced from 114 to 62 grid cells; singletons varied from  $< 92$  to  $\leq 75\%$  (models 2–4 in Table 2).

The shape of the function related to the energy-diversity hypothesis has been proposed to be linear or unimodal (Mittelbach et al. 2001). A simple linear regression model of  $-\ln SI$  on AET accounted for 36% of total variance ( $t = 7.99$ ,  $p < 0.0001$ ). After fitting a curvilinear model the quadratic term in the model under a null hypothesis of a non-intermediate maximum was significant at  $p = 0.0001$ ; the variance in  $-\ln SI$  explained by the quadratic model was 44%. A LOWESS curve smoothing suggested an increase of tree diversity until  $AET \approx 950 \text{ mm yr}^{-1}$  (Fig. 5). A two-part linear regression showed a strong positive relationship of  $-\ln SI$  as a function of annual actual evapotranspiration when  $AET \leq 950 \text{ mm yr}^{-1}$  ( $-\ln SI = -0.90 + 0.0059X$ ,  $R^2 = 0.42$ ,  $F_{1,60} = 44.31$ ,  $p < 0.0001$ ); yet, the slope of the regression was much lower at  $AET > 950$  ( $-\ln SI = 3.10 + 0.0013X$ ,  $R^2 = 0.19$ ,  $F_{1,50} = 11.80$ ,  $p = 0.0012$ ), indicating a saturation of tree diversity at intermediate to high levels of AET.

The visual inspection of the relationship between diversity and rainfall hints at an interior minimum (Fig. 6). The quadratic model that would account for an interior minimum was not significant with  $-\ln SI$  ( $t = 1.69$ ,  $p = 0.095$ ), but it was with Fisher's  $\alpha$  ( $t = 2.24$ ,  $p = 0.027$ ).

Current interest exists about possible relationships of diversity with rainfall in addition to temperature or

altitudinal variation (Givnish 1999, Rahbek and Graves 2001). We explored a model with MAR, MAT and their multiplicative term. The variance explained by this model was higher ( $R^2 = 0.49$ ) than with model 1 in Table 2. Yet MAT and MAR are not independent variables at the spatial scale of our study (collinearity tolerance  $< 0.098$ ). We also tested a model based on MAR and topographic relief (ARA) as given by altitudinal range (maximum minus minimum elevation recorded in each grid cell), and its product. The multiplicative term was not significant ( $t = 0.935$ ), variance explained was low ( $R^2 = 0.135$ ), and ARA (–) and MAR (+) had independent and contrary effects on tree diversity. No evidence of a synergism between climatic variables and topographic heterogeneity was suggested in relation to tree diversity at the spatial scale of our analysis, as found by Rahbek and Graves (2001) and Ruggiero and Kitzberger (2004) in studies at coarser scales with South American birds and mammals, respectively.

### Evapotranspiration and soils as limiting factors of tree diversity

Only AET and SFQ among the five independent single environmental predictors were correlated, with opposite effects, with tree diversity (AET:  $r = 0.603$ ,  $p < 0.0001$ ; SFQ:  $r = -0.265$ ,  $p = 0.004$ ). We examined their limiting effects with multiple regression quantiles across a range of medium and upper quantiles (0.50–0.95; Table 3). A smaller positive estimate was observed with the chosen quantiles in AET [ $b_1(0.50) = 0.00205$  to  $b_1(0.90) = 0.00148$ ], but a more negative slope was obtained for SFQ [ $b_2(0.50) = -0.0184$  to  $b_2(0.90) = -0.0449$ ; Table 3, Fig. 7]. Thus, the rate of change in the upper envelope of the distribution (90th quantile) of tree diversity as a

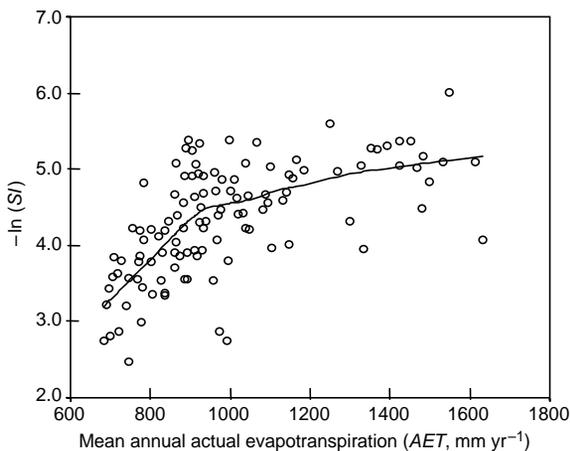


Fig. 5. Local weighted curve smoothing (LOWESS) for tree diversity ( $-\ln SI$ ) as a function of mean annual actual evapotranspiration ( $\text{mm yr}^{-1}$ ).

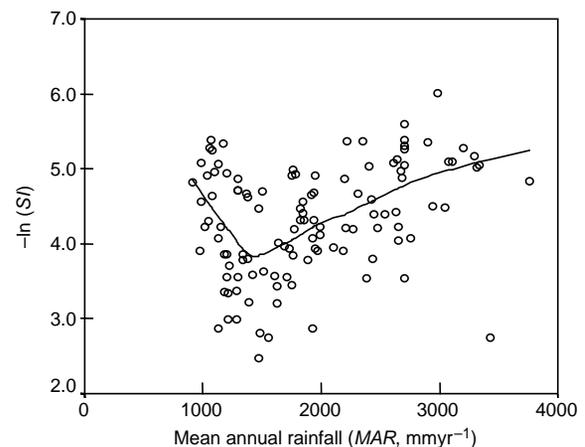


Fig. 6. Local weighted curve smoothing (LOWESS) for tree diversity ( $-\ln SI$ ) as a function of mean annual rainfall ( $\text{mm yr}^{-1}$ ).

Table 3. Parameter estimates of models to predict tree diversity with Simpson's index ( $-\ln SI$ ) as a function of mean annual actual evapotranspiration (AET) and soil fertility/quality (SFQ) for selected upper regression quantiles (0.75, 0.90, 0.95). The asymptotic rank score statistic is distributed as  $\chi^2$  with degrees of freedom equal to the difference in number of parameters between full and reduced models. The 0.50 quantile describes the median (Cade et al. 1999).

Quantile		Estimates	$\chi^2$	p
0.50	Model		35.13	<0.0001
	AET	2.05E-03	22.23	<0.0001
	SFQ	-1.84E-02	1.75	0.1856
0.75	Model		40.80	<0.0001
	AET	1.43E-03	24.30	<0.0001
	SFQ	-4.50E-02	5.92	0.0149
0.90	Model		16.07	0.0003
	AET	1.48E-03	14.88	0.0001
	SFQ	-4.49E-02	9.12	0.0025
0.95	Model		8.36	0.0153
	AET	1.29E-03	9.18	0.0024
	SFQ	-2.03E-02	8.03	0.0046

function of AET was 39% smaller than that estimated through the center of its distribution (50th quantile), but it was up to 240% larger than that at the 50th quantile for SFQ. This means that the statistical effect of AET is relatively less affected by other environmental factors (i.e. it or its correlates are an important limiting factor of tree diversity by itself). However, the effects of soil fertility/quality seem to be more dependent on the interactions with other limiting factors, and may be underestimated or obscured by OLS models as those in Table 2.

## Discussion

### AET and energy/productivity

We used Turc's model of AET as an estimator of joint temperature and rainfall conditions that may be related to plant growth. AET is a commonly used predictor of gradients of net primary productivity at global, continental, and regional scales (Rosenzweig 1968, Mittelbach et al. 2001, Rey-Benayas and Scheiner 2002). Yet, we note that for a number of reasons related to its construction and interpretation AET is at best an indirect indicator of biologically available energy or plant productivity. First, it does not use information on solar radiation (adequate density of energy recording sites is generally lacking in tropical regions anyway). Further, at broad spatial scales correlation of AET with energy or NPP may primarily be the consequence of increased growing season, by either shorter winters or shorter dry seasons, and not necessarily because of the growth rate of plants when they are actually growing. At smaller spatial scales a substantial quantity of rain in tropical storms runs off and is ineffective for plant

growth, and its proportion may increase with mean rainfall in a non-linear manner. Finally, the effectiveness of AET as a predictor of plant productivity may also be reduced at local scale by dependence on availability of mineral nutrients and light.

### Tree diversity and AET

There has been considerable interest in the shape of the relationship and the possible mechanisms underlying the energy-species hypothesis at different spatial scales (Rosenzweig and Abramsky 1993, Whittaker et al. 2001). In this study the diversity-evapotranspiration relationship was found to be significant in all multiple linear models. The proportion of total variance explained by either linear (36%) or quadratic (44%) models was higher than a previously reported median of 30% for plant diversity and energy-related factors at similar regional scales; Francis and Currie (2003) report 80% from a global scale study with plant families.

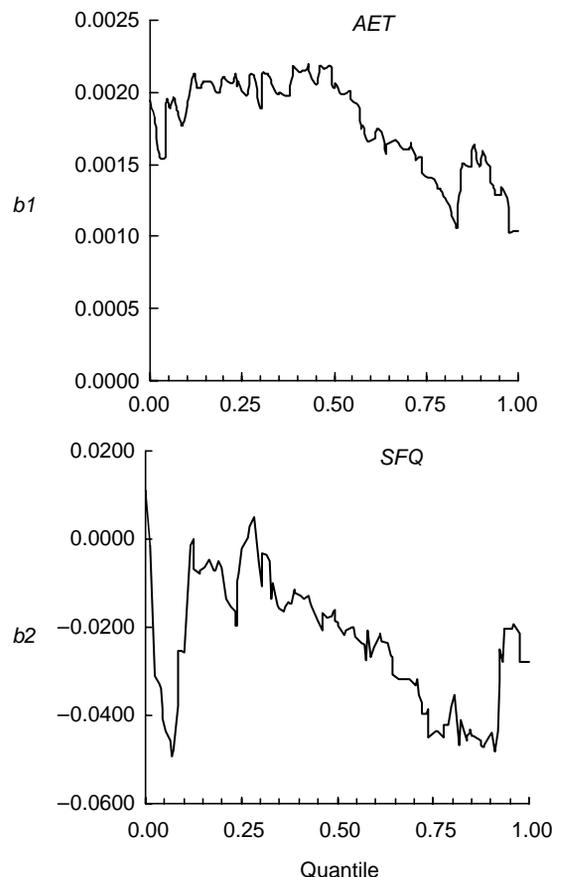


Fig. 7. Estimated rates of change in tree diversity ( $-\ln SI$ ) at all quantiles as a function of annual actual evapotranspiration (AET, b1) and soil fertility/quality (SFQ, b2).  $n = 114$  cases.

Wright et al. (1993), Scheiner and Rey-Benayas (1994), and Mittelbach et al. (2001) at a global scale, and Rey-Benayas (2001) in the Mediterranean biome, concluded that, over broad spatial scales, diversity shows a linear trend with higher energy/productivity. At the regional spatial scale used in this study a quadratic model with an interior maximum adequately describes the relationship between tree diversity and AET. Yet, a more conservative interpretation of the data pattern (Fig. 5) suggests a pronounced linear increase of tree diversity up to mid-range values of AET and a steady but slower increase up to a leveling off at higher values. Consistently with our results, Hawkins et al. (2003) found in their descriptive meta-analysis that variables including water inputs emerge as the primary predictor of plant species richness on regions extending over 800 km<sup>2</sup>.

Currie and Paquin (1987) found that the diversity of trees in North America fits a logistic (asymptotic) model with AET as the only independent variable. As in our study, they also found a large scatter of their data at the highest values of annual evapotranspiration (900–1000 mm). Kerr and Packer (1997) also found large scatter of species richness of North American mammals in high energy regions (potential evapotranspiration >1000 mm yr<sup>-1</sup>). They suggested that the diversity-energy hypothesis pertains only where climatic energy levels are relatively low, and not to the whole range of values encompassed by the continental scale. Local variation in coarse scale topographic heterogeneity was a better predictor of mammal diversity at high levels of AET. We found that both the most diverse and some relatively low diversity assemblages were associated with high AET conditions (Fig. 5). The unimodal or asymptotic relationship between diversity and evapotranspiration (both models were found statistically supported) may result from the interaction with other non-climatic factors that become limiting when soil moisture availability and/or temperature are adequate. For example, rainfall effectiveness may not be linearly related to plant growth because of increasing proportions of runoff due to water infiltration rates, tree cover, and slope, among others (Ashton pers. comm.). Yet, the negative effect of runoff is not necessarily highest at high AET; where AET is high, the soil moisture is likely to be high, regardless of runoff. Local or landscape-level influences like salinity and low soil nutrients are affected by freshwater flow, successional age, disturbance regime, and patch size and isolation (Brown 1981, Huston 1994), and have been proposed to account for species-poor tropical old-growth forests in habitats with high AET (e.g. coastal patches of mangrove or *Pterocarpus*-dominated forests in southern Costa Rica (Richards 1952, Hartshorn 1983, Hart et al. 1989, Ricklefs and Latham 1993)).

## Tree diversity and soils

We found considerable spatial heterogeneity of soils over the 114 cells in our study. 59 out of 84 soil taxa identified in the whole of Chiapas occurred in our study area, which comprised only 12% of the total area of Chiapas (González-Espinosa and Ramírez-Marcial unpubl.). The number of soil types (SOT) did not appear as a significant term in the models accounting for tree diversity, but the SFQ factor had significant negative effects. A higher rate of decline in tree diversity as a function of SFQ at a given level of AET was detected when only the upper 0.75–0.90 quantiles of the data were used (Table 3, Fig. 7), suggesting that other factors in addition to SFQ operate as limiting factors when this variable is used at regional scales.

Current concepts about tropical soils emphasize their previously unrecognized heterogeneity, resulting from a wide variety of parent materials, landforms, climatic influences, and biological interactions during soil formation over variable periods (Richter and Babbar 1991, Sánchez and Logan 1992). This edaphic heterogeneity in the Neotropics has been related to floristic diversity, habitat affinity, and species distribution at landscape scale (Tuomisto et al. 1995, 2003, Clark et al. 1999, Phillips et al. 2003). However, the rapid weathering and leaching of lowland soils in high rainfall areas would tend to eliminate the chemical signature of parent material (limestone) at local and landscape scales and may lead to less heterogeneity than might otherwise be expected (Sánchez 1976, Richter and Babbar 1991). At a regional level, we found a negative correlation of annual rainfall (MAR) with soil diversity (DSO) and number of soil types (SOT). Contrary to Huston (1980), we found no negative correlation between SFQ and MAR (actually SFQ was not related to any climatic variable; Fig. 4). This lack of correlation could result from the structure of the SFQ index, which included some properties of the soil profile that may not be directly related to chemical fertility and which are less likely changed by precipitation (e.g. soil depth, drainage and texture).

## Tree diversity and rainfall

Some grid cells with relatively high tree diversity were associated with the least productive dry end of the rainfall gradient; lower diversity was associated with intermediate rainfall conditions and then it increased at the highest level of precipitation. This bimodal pattern of distribution of plant diversity along environmental gradients is consistent with the hypothesis proposed by Austin and Smith (1989). Rey-Benayas (2001) found that low plant diversity was extremely rare at intermediate levels along different ecological gradients in the Mediterranean biome (resources and regulators, major disturbances, environmental het-

erogeneity, and successional age). As far as we know, our study is one of the first to provide macro-scale support for this hypothesis. We propose that under dry conditions not many species grow well, the trees are relatively small and perhaps scattered, competition for light is relatively weak, and competition for water may be unpredictable because of climatic variability (savanna-like systems in tropical regions). Diversity may be composed of multiple species occupying the canopy, with none dominating, and with relatively few understory tree species because of the short and open canopy [Huston 1994; Quigley and Platt (2003) report a high number of subcanopy trees and shrubs in closed seasonal neotropical forests]. With wetter conditions, the canopy becomes denser, with increased dominance and reduced diversity, but there is greater opportunity for a shade tolerant understory (Smith and Huston 1989, Huston 2004). With high rainfall, soil nutrients may be depleted through weathering and leaching and growth rates and tree height may be reduced; dominance in the canopy is reduced, so diversity increases as a result of higher canopy richness plus the understory richness.

Positive correlations between tropical lowland tree species richness and annual rainfall have been interpreted as supporting the diversity-energy hypothesis (Gentry 1982, 1988b, Givnish 1999); yet, using this variable separately from temperature has been recently criticized by Francis and Currie (2003). In this study we found significant correlations for the whole set of data of tree diversity with rainfall during the rainy season (MRR;  $r=0.33$ ,  $p<0.05$ ), but not with mean annual rainfall (MAR;  $r=0.31$ ,  $p>0.05$ ; Fig. 4). Further, in those cells with elevation comparable to Gentry's sites ( $<400$  m) we found no correlation between tree diversity and MAR ( $r=0.39$ ,  $p>0.21$ ,  $n=12$ ). Conceding that the power of this test is low due to the limited number of adequate cases for comparison, the rainfall gradient among our lowland sites (MAR = 990–3315 mm yr<sup>-1</sup>) is not as long as that studied by Gentry (1982; 1100–5700 mm yr<sup>-1</sup>).

Based on forest stand inventories and associated chemical data from soil samples, Huston (1980, 1994) reports negative correlations between local tree species richness (dbh > 10 cm) and soil nutrient availability in tropical lowland forests in Costa Rica, Ghana, and West Malaysia. He proposed that an interaction of high precipitation with temperature (i.e., high AET) may produce low-fertility soils due to high rates of weathering, litter decomposition, and nutrient leaching from the rooting zone. In this study these were also the physical conditions where forests showed highest diversity; yet, low diversity forests were associated with all nutrient conditions in the study area, from extremely low to very high nutrient availability, possibly indicating the effects of other factors that limit diversity (and motivated the use of quantile regression methods).

Diversity responses to rainfall along regional gradients seem to be quite complex. For example, Wolf and Flamenco (2003) report a decrease in epiphyte diversity in Chiapas when the annual amount of rainfall exceeded 2500 mm, contrary to their expectations. Some of the most species-rich communities within our region of study are located in the lowland forests of the Selva Lacandona, in the SE portion of the state. Mean annual evapotranspiration is high there (AET > 1250 mm), but soils on flats (gleysols and rendzinas) or on gentle slopes (lithosols and regosols) are rather poor, as is typical of lowland tropical soils when viewed at broad scales around the world (Sánchez 1976, Richter and Babbar 1991, Huston 1993). We fitted a model to a subset of grid cells including only lowland areas ( $<700$  m elevation, i.e. more directly comparable to the Costa Rican data from moist, wet, and rain forest sites, swamp and tidally inundated sites excluded; Holdridge et al. 1971, Huston 1980, 1994). Soil fertility/quality was an inverse predictor of the regional pool of tree species in lowland sites ( $F_{1,18}=7.89$ ,  $p=0.012$ ,  $t=-2.808$ ; SFQ explained 31% of total variance; AET and RET were not significant in the lowland model ( $t<0.76$ ).

## Coda

Our study uses herbarium and environmental data from published maps to address a major ecological issue, the regulation of tree species diversity in tropical forests. Our study region has considerable environmental heterogeneity with altitudinal gradients that create climatic conditions resembling habitat sequences along a latitudinal gradient from the tropics to the lower temperate zone. We started our analysis of patterns of tree species diversity with environmental factors (including climatic, physiographic, and edaphic factors) that we thought would be relevant at a regional macro-scale. Estimated actual evapotranspiration is closely related to tree diversity and shows a unimodal or asymptotic relationship (both models were valid). Another positive factor related to tree diversity is the seasonality of climatic conditions and a negative influence is given by the intraregional, landscape-level soil fertility/quality. An intriguing relation of minimum diversity at intermediate rainfall values hints at a bimodal model opposing the frequent contention of a positive linear relationship for plant species. Our findings may be dependent on the spatial scale of analysis (Rahbek and Graves 2001, Willis and Whittaker 2002), but they support the hypothesis that regional diversity is mostly explained by climatic gradients (Francis and Currie 2003). However, in addition to climatic variables other factors operating at finer spatial scales help to explain the observed patterns. While some ecologists might argue that the spatial diversity pattern shown in Fig. 2 might support the

“mid-domain effect” null model (Zapata et al. 2003, Colwell et al. 2004), our data show that spatially structured environmental gradients are correlated with the diversity patterns. Broad-scale factors that correlate with latitude and climatic gradients have been proposed to predict diversity of plant species pools where data are lacking or questionable (O’Brien 1998). Our study represents a well-documented macro-scale case of how such broad climatic gradients may interact with intraregional influences, leading to non-linear responses of tree diversity to environmental predictors. Anthropogenic and natural disturbances may affect diversity mostly at local scale (Willis and Whittaker 2002); yet, widespread and long-term deforestation in some areas of our study region (Ochoa-Gaona and González-Espinosa 2000) may influence tree diversity at coarser spatial scales. Further research on our data set – with possible additions from actual nested local inventories and satellite-provided data on plant productivity and widespread human disturbance – could test for different taxonomical hierarchies and levels of grain and extent (sensu Palmer and White 1994) to explore how regional determinants of tree diversity interact and condition patterns and processes at smaller spatial scales.

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