Tree Diversity, Environmental Heterogeneity, and Productivity in a Mexican Tropical Dry Forest

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ABSTRACT

Species diversity–environmental heterogeneity (D–EH) and species diversity–productivity (D–P) relationships have seldom been analyzed simultaneously even though such analyses could help to understand the processes underlying contrasts in species diversity among sites. Here we analyzed both relationships at a local scale for a highly diverse tropical dry forest of Mexico. We posed the following questions: (1) are environmental heterogeneity and productivity related?; (2) what are the shapes of D–EH and D–P relationships?; (3) what are individual, and interactive, contributions of these two variables to the observed variance in species diversity?; and (4) are patterns affected by sample size, or by partitioning into average local diversity and spatial species turnover? All trees (diameter at breast height ≥ 5 cm) within twenty-six 0.2-ha transects were censused; four environmental variables associated with water availability were combined into an environmental heterogeneity index; aboveground standing biomass was used as a productivity estimator. Simple and multiple linear and nonlinear regression models were run. Environmental heterogeneity and productivity were not correlated. We found consistently positive log-linear D–EH and D–P relationships. Productivity explained a larger fraction of among-transect variance in species diversity than did environmental heterogeneity. No effects of sample size were found. Different components of diversity varied in sensitivity to environmental heterogeneity and productivity. Our results suggest that species' differentiation along water availability gradients and species exclusion at the lowest productivity (driest) sites occur simultaneously, independently, and in a scale-dependent fashion on the tree community of this forest.

RESUMEN

Las relaciones de la diversidad de especies-heterogeneidad ambiental (D-HA) y diversidad de especies-productividad (D-P) rara vez han sido analizadas simultáneamente, aunque este tipo de análisis podría contribuir a un mejor entendimiento de los procesos asociados con cambios en la diversidad de especies entre sitios. En este estudio analizamos ambas relaciones a una escala local para un bosque tropical seco muy diverso de México. Planteamos las siguientes preguntas: 1) están relacionadas la heterogeneidad ambiental y la productividad?; 2) cuáles son las relaciones entre D-HA y D-P?; 3) cuál es la contribución individual e interactiva de las dos variables a la varianza en diversidad de especies observada?; y 4) estos patrones se ven afectados por el tamaño de la muestra, o por la partición de la diversidad en promedio local y recambio ecológico de especies? Se cenizaron todos los árboles (DAP ≥ 5 cm) dentro de veintisiete transectos de 0.2 ha; cuatro variables ambientales asociadas a la disponibilidad de agua se combinaron en un índice de heterogeneidad ambiental; la productividad se estimó utilizando valores de biomasa aérea en pie. Se realizaron regresiones simples y múltiples, lineales y no lineales. La heterogeneidad ambiental y la productividad no estuvieron correlacionadas. Consistently encontramos relaciones D-HA y D-P log-lineales positivas. La productividad explicó una mayor fracción de la varianza en diversidad de especies entre transectos que la heterogeneidad ambiental. No se encontraron efectos del número de árboles. Los distintos componentes de la diversidad mostraron una distinta sensibilidad a la heterogeneidad ambiental y a la productividad. Nuestros resultados sugieren la ocurrencia simultánea, independiente, y de forma dependiente de la escala de diferenciación de especies a lo largo de gradientes de disponibilidad de agua y exclusión de especies de los sitios menos productivos (los más secos).

Key words: aboveground biomass; alpha-diversity; Chamaela-Cuixmala Biosphere Reserve; environmental heterogeneity; productivity; species diversity; species richness; tropical dry forest; Western Mexico.

Understanding how species richness changes over space, and elucidating the driving processes and mechanisms involved have been fundamental aims of ecology. Positive diversity–environmental heterogeneity (D–EH) relationships have been hypothesized from niche-based theories (Whittaker 1972, Huston 1979, Tilman 1982, Wright 2002, Leigh et al. 2004); a higher diversity is expected in more heterogeneous environments because competitive exclusion is prevented from operating when species can differentially use resources. In contrast, neutral theories assume that all species are ecologically equivalent (Bell 2000, Hubbell 2001), and thus no relationship between environmental heterogeneity and species diversity is expected. Recently, more complex models that reconcile neutral and niche differentiation processes and incorporate spatial scale are consistent with the expectation of positive relationships between environmental heterogeneity and species diversity (Leibold et al. 2004, Lortie et al. 2004, Tilman 2004, Sarr et al. 2005).

The shape of the species diversity–productivity (D–P) relationship and their underlying processes continue to be controversial. Hump-shaped, linear positive, linear negative, or U-shaped relationships have been described (Rosenzweig & Abramsky 1993, Waide et al. 1999, Mittelbach et al. 2001) although the first two curve types are the most common ones in vascular plants (Waide et al. 1999, Mittelbach et al. 2001). Both abiotic factors associated with physiological tolerance to certain conditions and biotic factors associated with competitive interactions among species have been shown to play crucial roles in D–P relationships. At low productivity, harsh environments are expected to preclude establishment of a large number of species, while at high productivity, intense competition is expected to contribute to the exclusion of a large number of species (Connell 1961, Grime 1979, Huston 1979, Tilman 1982, Huston 1994). A positive linear D–P relationship

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has been hypothesized to correspond to the lower productivity section of a hump-shaped relationship (Waide et al. 1999, Mittelbach et al. 2001), when low resource levels in the lower productivity end cause large decreases in the probability of a new species to invade (Huston 1994, Davis et al. 2000, Tilman 2004). Neutral processes have also been shown to produce hump-shaped relationships, given that low species numbers at both ends of the productivity gradient may result from a few small individuals at the low resource end and a few large individuals at the high resource end (Oksanen 1996, Stevens & Carson 1999).

Diversity–EH and D–P relationships have seldom been analyzed simultaneously, despite the complex interactions that potentially occur. For example, several workers have proposed that, along a productivity gradient, environmental heterogeneity is highest at intermediate productivity levels, thus confounding the contribution of both factors to species diversity (Tilman 1982, Rosenzweig & Abramsky 1993, Tilman & Pacala 1993, Waide et al. 1999, Mittelbach et al. 2001). Also, the observation of potential competitive exclusion processes associated with productivity may be hindered by the presence of environmental heterogeneity given that species adapted to different conditions may not interact, or that equilibrium may not be detected under such conditions (Huston 1999). Only two studies, one experimental and one observational, have examined simultaneously the contribution of environmental heterogeneity and productivity to diversity. The first study controlled light heterogeneity and average light availability levels in a pasture of northwestern Pennsylvania (Stevens & Carson 2002). The second study measured microspatial heterogeneity of soil depth, soil moisture, and microtopography along a hump-shaped diversity gradient for a limestone pavement alvar in Ontario, Canada (Lundholm & Larson 2003). In both the cases, resource availability rather than resource heterogeneity played an important role in the observed species-diversity pattern, but further analysis of other systems at other spatial scales may show different results.

Understanding the relative contribution of environmental heterogeneity and productivity to species diversity is particularly relevant for highly diverse systems where processes explaining differences in species diversity among sites are still poorly understood. Tropical dry forests are a highly diverse but also highly threatened ecosystem (Janzen 1988, Gentry 1995, Murphy & Lugo 1995), where variation in forest structure and species diversity has been associated with differences in soil water availability (Sussman & Rakotozafy 1994, Mooney et al. 1995, Sampaio 1995, Segura et al. 2003). Yet for these systems, little is known about the shape of the D–EH and D–P relationships. Also, there is poor knowledge of the individual and interactive contribution of environmental heterogeneity and productivity to spatial variation in species diversity, as well as of the processes associated with the maintenance of diversity in species-rich tropical dry forests (but see Kelly et al. 2001).

In this work, we investigate D–EH and D–P relationship at a local scale (<30 ha: 0.2-ha transects) for one of the most diverse (Gentry 1995, Quigley & Platt 2003) and well-conserved tropical dry forests of the Neotropics in Chamela, Jalisco, Western Mexico. We first explore the relationship between environmental heterogeneity and productivity for this system. We then examine the shape of the D–EH and D–P relationships. Next, we analyze the relative contribution of environmental heterogeneity, productivity, and their interaction to the observed intersite variance in species diversity. Considering the well-known effects of sampled number of individuals on species-diversity estimations (Magurran 1988, Palmer et al. 2000, Gotelli & Colwell 2001, Magurran 2004) and on D–EH and D–P relationships (Oksanen 1996, Stevens & Carson 1999, Waide et al. 1999, Wilson et al. 1999, Scheiner et al. 2000, Wilson 2000, Mittelbach et al. 2001, Schmitz et al. 2002), we assess such effects by using several species-richness measures and estimators that are differentially sensitive to sample size. We also explore directly the relationships between species richness or productivity and number of trees and then analyze the residual D–P relationship. We further analyze D–EH and D–P relationships for different components of diversity, including total diversity, average local diversity within homogeneous subsections of the studied plots, and species turnover among such subsections. Finally, we discuss the relevance of our findings for understanding the processes associated with the maintenance of local diversity of tropical dry forests.

**METHODS**

**STUDY SITE.**—The study site is located within the Chamela-Cuixmala Biosphere Reserve (19°30’N, 105°03’W) in the Pacific Coast of Mexico. The climate is warm and dry with a mean annual temperature of 24.9°C; mean annual precipitation is 748 mm, with 80 percent falling between July and October, and 5 mo present severe drought (García-Oliva 1991). The area is dominated by low hills and covered by a short stature (>12 m) tropical deciduous forest (Lott et al. 1987, Durán et al. 2003) that will be hereafter referred to as tropical dry forest. A taller (average 18 m) semideciduous forest is found along temporary streams at the bottom of hills. The tropical dry forest found at Chamela-Cuixmala is considered as one of the most diverse of its kind, with a high percentage of endemic plant species (Lott et al. 1987, Lott 1993, Gentry 1995, Trejo & Dirzo 2002, Durán et al. 2003, Quigley & Platt 2003).

Changes in tree species diversity among sites with contrasting soil water availability have been described for few sites within the Chamela-Cuixmala Reserve. Tropical dry forest on hill tops (deciduous forest) and semideciduous forest found along temporary streams did not differ in species richness or Shannon–Weiner diversity when compared using 0.1-ha Gentry’s compound transects (Lott et al. 1987). In contrast, comparisons among four 0.24-ha transects (30 m × 80 m) located along a small-scale altitudinal gradient, associated with a water availability gradient within hills of similar geological origin showed clear changes in species richness, Shannon–Weiner diversity, and Simpson indices, and in equitability. Valley sites have higher water availability, organic matter content, nutrient availability, and showed higher diversity, basal area, and annual net primary productivity than hilltop sites (Solís 1993, Martínez-Yrízar et al. 1996, Galicia et al. 1999, Segura et al. 2003).

**SAMPLING DESIGN.**—Twenty-six 20 m × 100 m transects (total area = 5.2 ha) were established on geomorphologically independent slope units within three small watersheds, all draining to the
FIGURE 1. Sampling design for exploration of species diversity–environmental heterogeneity and species diversity–productivity relationships within three small watersheds to capture a wide range of water availability conditions for the tree community at a tropical dry forest of western Mexico. Slender lines are altitudinal isolines (in m elev.), heavy lines indicate watershed divide, and long rectangles represent 0.2-ha transects. The mean temporary stream at the lower part of the granite massive is shown in heavy broken lines. Three transects with contrasting environmental heterogeneity (see Table 1) are highlighted: L = low environmental heterogeneity; I = intermediate environmental heterogeneity; H = high environmental heterogeneity.

west, over a granite massif covered with well-preserved tropical dry forest (Fig. 1; Galicia et al. 1995, Maass et al. 2003, Segura et al. 2003). All transects were laid perpendicular to the main stream of the watershed, to maximize topographic heterogeneity within them; the location of the 26 transects was aimed at covering a wide range of water availability within and among transects, from the moister conditions within the lower part of the main stream canal to the drier conditions at the upper part of south-facing slopes. The transects differ with respect to the range of environmental conditions they encompass; transects on very steep north-facing slopes have the highest environmental heterogeneity; transects on flat ridge tops present the most homogeneous slope, aspect, and soil depth conditions (Balvanera 1999, Balvanera et al. 2002, Segura et al. 2003).

For data gathering purposes, including vegetation and environmental data, transects were divided into twenty 10 m × 10 m (0.01 ha) quadrats. Given that these transects encompassed quite contrasting environmental conditions, each was divided into five 0.04-ha square plots (20 m × 20 m), the largest possible section of transects within which environmental conditions could be considered homogeneous, and that result from the combination of four 0.01-ha quadrats.

Species composition.—Within each transect, we measured diameter at breast height (DBH) for all trees with a DBH ≥ 5 cm and identified them to the species level (Balvanera 1999). Voucher specimens are available at MEXU and the herbarium of the Estación de Biología Chamela, both belonging to the Instituto de Biología, UNAM. A reference collection is also available from the authors.

Environmental variables.—Soil water availability has been identified as the most important limiting factor for plant performance and for many ecosystem processes in these forests (Bullock et al. 1995, Jaramillo & Sanford 1995, Maass et al. 2003). Soil water availability is strongly determined by edaphic and topographic variables (Galicia et al. 1999). The variables include: (1) altitude (in m over sea level) that reflects position relative to more mesic temporary streams (at 40 mosl); (2) slope (in degrees) that determines morpho-pedogenic processes and determines runoff and infiltration characteristics (Ruhe 1975); (3) daily insolation (in MJ/m².d) averaged over a whole year that strongly determines evapotranspirative demand and thus soil water availability during the dry season (Galicia et al. 1999); and (4) soil water storage capacity (in l/m²). All these variables were measured for every 0.01-ha (10 m × 10 m) quadrat. Insolation was modeled with the use of Joule 2.0 (Ezcurra 1996) based on slope and aspect data. Soil water storage capacity was evaluated through well-known relationships (Siebe et al. 1996, Schoeneberger 1998) between depth, rockiness, and texture data of horizons, all described from a 1-m core taken at the center of each 10 m × 10 m quadrat. Balvanera (1999) and Balvanera et al. (2002) provide further details on methods for quantifying water availability surrogate variables.

Species-diversity estimators.—We used two different approaches for species-diversity calculations for analysis of D–EH and D–P relationships. The first one addressed the issue of the role played by number of trees in species-richness estimations, while the second one partitioned diversity into different components.

The first approach was to calculate species richness for each 0.2-ha transect with three different indices differentially sensitive to sample size (Magurran 1988, 2004), given that strong contrasts in number of trees (148–400) were found among transects. The indices were: (1) species richness, *i.e.*, the number of recorded species richness per transect (hereafter called *S*); (2) expected species richness (hereafter called *S*) for a fixed number of individuals (lowest value for all 0.2-ha plots size: 148 individuals) obtained through rarefaction techniques (Gotelli & Colwell 2001); and (3) a nonparametric estimator of the number of species found in the full sampling universe. The nonparametric estimator is highly recommended for sets of species in which some species are very abundant and others are very rare (Chazdon et al. 1998, Magurran 2004); evidence of such
contrasts in species’ abundances have been found for this tropical dry forest (Balvanera 1999, Balvanera et al. 2002, Segura et al. 2003). We selected the incidence-based coverage estimator (hereafter called ICE) because this estimator is based on species presence/absence data, and our analysis focuses on how environmental heterogeneity and productivity are related to the species-richness component of diversity. ICE was obtained for rarified samples of 148 individuals. Incidence here is the frequency with which a species is found in any of the twenty 0.01-ha (10 m × 10 m) quadrats that conform the 0.2-ha (20 m × 100 m) transect. Values of $S_i$ and ICE were obtained using Estimates 7.2 program (Colwell 1997).

The second approach partitioned diversity values of each 0.2-ha transect into average within-plot local diversity, and among-plot species turnover (Lande 1996). For this purpose we used the five 0.04-ha (20 m × 20 m) square plots within each transect, assuming that within such plots environmental conditions for trees are homogeneous in terms of water availability. We used the widely accepted Simpson index based formula for diversity partitioning (e.g., Gimaret-Carpentier et al. 1998, Loreau 2000, Arita & Rodriguez 2002), and thus defined:

$$D_{\text{within}} = 1 - \sum_j 0.2 \sum_i p_{ij}$$

$$D_{\text{among}} = D_{\text{total}} - D_{\text{within}}$$

$$D_{\text{total}} = 1 - \bar{p}_i.$$

The three diversity components were calculated for each 0.2-ha transect, made up of five 0.04-ha plots $j$; within them, for each species $i$,

$$p_{ij} = \frac{1}{N}$$

being $N$ the number of species in plot $j$, and

$$\bar{p}_i = \frac{\sum_j p_{ij}}{5}.$$

In this way, the values of the different diversity components were related to species richness rather than to species’ relative abundance, as discussed above for the case of ICE.

ENVIRONMENTAL HETEROGENEITY ESTIMATOR.—Proper environmental heterogeneity measures should be associated with the differential performance of the studied species (Lechowicz & Bell 1991). In our case, four environmental variables linked to water availability (altitude, slope, average daily insolation, and soil water storage capacity) have been shown to affect spatial changes in species composition (Balvanera et al. 2002), and are thus appropriate indicators of differential species performance. Over the studied area these variables vary greatly (Table 1). Slope and insolation are tightly correlated ($r = 0.52$, $P < 0.001$, for 0.1-ha plots) since slope is one of the variables used to model it, although the relationship is U-shaped; north-facing steep slopes have the lowest insolation, south-facing steep slopes the highest insolation, and intermediate insolation values are found at intermediate to low slope conditions. Slope and altitude are correlated ($r = 0.42$, $P < 0.001$, for 0.1-ha plots) due to the configuration of the terrain where steepest slopes are found at lower altitudes (García-Oliva et al. 1995). Soil water storage capacity is not correlated with any of the other three variables. Thus, to incorporate equitably the effects of variation of all variables on species diversity a composite index of environmental heterogeneity was developed. The index is derived from the values taken by the four environmental variables in all the 0.01-ha quadrats of each transect, which were standardized, and for which principal component scores were calculated to account for variance along orthogonal and synthetic axes. Its calculation is simply the sum of the standard deviations of the four resulting principal components (PC):

$$\text{Environmental heterogeneity (EH)} = \sqrt{\frac{\sum PC_{12}^2}{n}} + \sqrt{\frac{\sum PC_{22}^2}{n}} + \sqrt{\frac{\sum PC_{32}^2}{n}} + \sqrt{\frac{\sum PC_{42}^2}{n}}.$$

<table>
<thead>
<tr>
<th>Variable</th>
<th>All quadrats</th>
<th>Less heterogeneous transect</th>
<th>Intermediately heterogeneous transect</th>
<th>More heterogeneous transect</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range</td>
<td>Standard deviation</td>
<td>Range</td>
<td>Standard deviation</td>
</tr>
<tr>
<td>Altitude (mosl)</td>
<td>24–172</td>
<td>0.156</td>
<td>124–135</td>
<td>0.084</td>
</tr>
<tr>
<td>Slope (degrees)</td>
<td>0–46</td>
<td>0.204</td>
<td>3–8</td>
<td>0.030</td>
</tr>
<tr>
<td>Daily insolation (MJ/m².d)</td>
<td>1–18</td>
<td>0.202</td>
<td>11–13</td>
<td>0.036</td>
</tr>
<tr>
<td>Soil water retention capacity (l/m²)</td>
<td>1–165</td>
<td>0.203</td>
<td>58–103</td>
<td>0.021</td>
</tr>
<tr>
<td>Environmental heterogeneity index</td>
<td>0.260</td>
<td></td>
<td>0.369</td>
<td></td>
</tr>
</tbody>
</table>
A similar index has already been used to measure environmental heterogeneity using topographic and edaphic variables, by multiplying the spatial variances in soil depth, soil fertility, and pH (Richard et al. 2000). As shown in Table 1, our environmental heterogeneity index reflects changes in range and standard deviation of the various variables among plots; transects over flat ridge top have lowest environmental heterogeneity values, while those on steep north-facing slopes have the highest environmental heterogeneity (Balvanera et al. 2002).

PRODUCTIVITY ESTIMATOR.—Productivity is the amount of energy that flows through the ecosystem during a certain period (Chapin et al. 2002). Net primary productivity, the first step in this flow, results from the amount of organic matter produced by photosynthetic organisms during a certain period (Clark et al. 2001). Productivity evaluations within the context of species-diversity studies have used either potential or realized productivity. Potential productivity is influenced by the amount of resources available (e.g., nutrients, water), while realized productivity is the actual amount of energy that flowed through the system and was incorporated into it during a certain period of time into biomass. Both direct and surrogate measures of such potential and realized productivity have been used in diversity studies (Waidé et al. 1999, Mittelbach et al. 2001). The most commonly used estimator of potential productivity in the case of trees (Mittelbach et al. 2001) include climatic variables (e.g., Currie & Paquin 1987, Gentry 1988, Phillips et al. 1994); estimations of realized productivity include standing biomass (measured or estimated; e.g., Huston 1980, Zobel & Liira 1997), while only a few (7 of the 56 plant studies analyzed by Mittelbach et al. (2001)) used actual measures of biomass production (Westman & Whittaker 1975, Whittaker & Niering 1975).

We did not have measures of water availability or nutrient availability in order to evaluate potential productivity. Whereas altitude and insolation are surrogates of water availability, no direct and simple relationship could be established between either of these variables and resource availability. Instead, we used here aboveground phytomass (herafter called biomass) as an estimator of realized productivity. Aboveground phytomass was calculated by summing individual stem biomass, estimated from basal area data and with a model developed for the tropical dry forest found in the study site (Martínez-Yrízar et al. 1992):

\[
\text{Biomass (kg)} = -0.5352 + 0.9996 \times \log_{10}(\text{Basal area}).
\]

When stand age is constant, standing phytomass (ot biomass) is an adequate estimator of net primary productivity (Martínez-Yrízar et al. 1992). The Chamela-Cuixmala tropical dry forest belongs to a reserve where no human major disturbances have taken place, at least in the past 100 years. In contrast with tropical rain forests, regeneration does not take place following gap dynamics; instead, trees predominantly die standing, and thus tree replacement and recruitment of new individuals take place on a single tree basis (Maass et al. 2002, Segura et al. 2003). As a consequence, within a 0.2-ha transect, that includes at least 150 trees with DBH ≥ 5 cm, a mosaic of individual tree ages is likely to be found. If disturbance rates are equivalent among transects, average tree age is expected to be equivalent, and thus standing phytomass can be used as an estimator of productivity.

The few annual productivity values available for this forest confirm that total basal area and annual primary productivity are highly correlated in this forest ($R^2 = 0.996, P = 0.003$; data obtained from Martínez-Yrízar et al. 1992, Segura et al. 2003).

GENERALIZED LINEAR MODELS AND CORRELATIONS.—Productivity–environmental heterogeneity relations were explored using Pearson’s correlation for 0.2-ha plots. Biomass and environmental heterogeneity were both log-transformed to comply with normality assumption. To avoid negative values of the logarithm of environmental heterogeneity, variables were multiplied by 100 prior to transformation.

The shapes of D–EH and D–P relationships were analyzed following protocols suggested for the latter relationship (Mittelbach et al. 2001), using generalized linear models (Crawley 1993, Insightful 2003). A Poisson error and a logarithmic link function were used for count data ($S$), while a normal error and an identity function were used for continuous variables ($S$, ICE, $D_{\text{within}}$, $D_{\text{among}}$, and $D_{\text{total}}$). When the Poisson error based model showed data overdispersion, data were properly rescaled as indicated in Crawley (1993, 2002). Three alternative models were tested:

1. Linear models $Z = a + bX$, and $Z = a + bY$
   where $Z$ is the species-diversity estimator, $X$ is the environmental heterogeneity, and $Y$ is the productivity;

2. Polynomial models $Z = a + bX + cX^2$, and $Z = a + bY + cY^2$
   to check for unimodal patterns, only accepted when a significant amount of variance was explained by $X^2$ or $Y^2$ after fitting the linear curve (Mittelbach et al. 2001); and

3. Negative exponential models $Z = a + be^{(-cX)}$, and $Z = a + be^{(-cY)}$
   to check for asymptotic patterns, based on models used in species accumulation functions (Miller & Weigert 1989, Soberón & Llorente 1993, Bojórquez-Tapia et al. 1994).

The analysis of the relative contribution of environmental heterogeneity and productivity to species diversity was analyzed using the model:

\[
Z = a + bX + cX^2 + dY + eY^2 + fXY
\]

that was run following a stepwise procedure (Crawley 1993, Insightful 2003). Percentages of total variance in $Z$ of the final model explained by $X$, $X^2$, $Y$, $Y^2$, and $XY$ were compared.

The sensitivity of the different species-diversity estimators to environmental heterogeneity and productivity were compared using the model parameter standardized beta (SAS 1989–1996; only available for continuous species-diversity estimators). Beta reflected the magnitude of the slope of the simple linear models, and that of the partial regression coefficients of the multiple linear models, when independent variables were standardized. Such standardization allowed for a comparison of the rate of increase in species-diversity
estimators as independent variables increased, irrespective of the magnitude of the independent variable.

Following the same procedures, we explored the relationship between species richness and tree abundance, and between above-ground biomass and tree abundance. To test whether tree abundance contributes to spurious D–P relationships, we used the residuals of the above relationships and tested for relationships among such residuals.

**RESULTS**

Total aboveground biomass within 0.2-ha transects ranged from 16.7 to 61.6 mg/ha. Environmental heterogeneity ranged from 0.26 to 0.73. No correlations between environmental heterogeneity and biomass, our productivity estimator, were found ($r = 0.16; P = 0.45$).

A total of 8144 trees corresponding to 144 tree species and 47 families were registered during this study. A large variance in biomass, our productivity estimator, were found ($r = 0.45$).

**TABLE 2.** Simple and multiple regression models (generalized linear and negative exponential) for several species-richness estimators differentially sensitive to sample size and two independent variables, environmental heterogeneity (EH), and productivity (estimated from biomass) in the case of twenty-six 0.2-ha transects for the tree community at a tropical dry forest of western Mexico. $S = \text{species richness}$, $S_r = \text{rarefied species richness for 148 trees}$, ICE = nonparametric incidence-based species-richness estimator, $\alpha = \text{Fisher’s } \alpha$ index. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$. A Poisson distribution and a logarithmic link function were used for $S$ that is a count variable; in that case a $\chi^2$ test was run to test for significant contribution of the independent variable. In all other cases, a Gaussian distribution and an identity link function were used. For multiple regression models, two values of deviance, and $F$ are given for each independent variable separated by a “/”, the first one corresponds to the entry of the variable in first place, and the second one to its entry in second place; standardized beta remained constant independent of the order of entry.

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Species-diversity estimator</th>
<th>Model</th>
<th>Deviance</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
<th>Percent explained deviance</th>
<th>Standardized beta</th>
</tr>
</thead>
<tbody>
<tr>
<td>Environmental heterogeneity</td>
<td>$S = e^{2.40 + 0.91 \log(EH)}$</td>
<td>log(EH)</td>
<td>11.32</td>
<td>1</td>
<td>***</td>
<td>32.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$S_r = -0.08 + 23.96 \log(EH)$</td>
<td>351.96</td>
<td>16.12</td>
<td>***</td>
<td>40.17</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$S_r = 63.46 - (121.20 e^{-0.98 \log(EH)})$</td>
<td>520.47</td>
<td>22.63</td>
<td>***</td>
<td>59.41</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ICE</td>
<td>ICE = $-63.92 + 78.26 \log(EH)$</td>
<td>3237.80</td>
<td>18.43</td>
<td>***</td>
<td>43.44</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>ICE = $181.21 - (331.83 e^{-0.64 \log(EH)})$</td>
<td>4204.79</td>
<td>13.52</td>
<td>**</td>
<td>56.41</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Productivity</td>
<td>$S = e^{2.25 + 1.57 \log(Biomass)}$</td>
<td>log(Biomass)</td>
<td>30.39</td>
<td>1</td>
<td>****</td>
<td>47.69</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$S_r = -0.12 + 32.31 \log(Biomass)$</td>
<td>409.93</td>
<td>21.10</td>
<td>***</td>
<td>46.79</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ICE</td>
<td>ICE = $-47.58 + 92.29 \log(Biomass)$</td>
<td>3344.40</td>
<td>19.53</td>
<td>***</td>
<td>44.87</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Environmental heterogeneity and productivity</td>
<td>$S = e^{1.20 + 1.32 \log(EH) + 0.77 \log(Biomass)}$</td>
<td>log(EH)</td>
<td>21.24/13.89</td>
<td>1</td>
<td>****</td>
<td>33.30/21.81</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>log(Biomass)</td>
<td>30.39/24.05</td>
<td>1</td>
<td>***</td>
<td>47.69/37.67</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$S_r = -29.80 + 28.30 \log(EH) + 21.96 \log(Biomass)$</td>
<td>log(EH)</td>
<td>351.96/248.65</td>
<td>1</td>
<td>37.22/26.29</td>
<td>****</td>
<td>40.17/28.38</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>log(Biomass)</td>
<td>409.73/306.61</td>
<td>1</td>
<td>43.35/32.43</td>
<td>****</td>
<td>46.79/35.00</td>
<td>0.54</td>
<td></td>
</tr>
<tr>
<td>ICE</td>
<td>ICE = $-138.65 + 79.97 \log(EH)$</td>
<td>log(EH)</td>
<td>3237.80/2342.28</td>
<td>1</td>
<td>43.52/30.48</td>
<td>****</td>
<td>43.42/31.82</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>+ 67.41 \log(Biomass)</td>
<td>log(Biomass)</td>
<td>3344.39/2448.88</td>
<td>1</td>
<td>43.52/31.86</td>
<td>****</td>
<td>44.87/32.85</td>
<td>0.53</td>
</tr>
</tbody>
</table>

D–P relationships were positive log-linear for all three species-richness measures and estimators (Table 2; Fig. 2a,b,c). No unimodal (polynomial) patterns were found. Asymptotic relationships were fit in the case of $S$, and ICE (Fig. 2b,c); these asymptotic relationships explained only a slightly larger amount of variance than the linear model (1.02–1.05 times more explained variance). The amount of variance in species diversity explained by environmental heterogeneity was lower for $S$ than for $S_r$ and ICE, but the patterns remained the same.

D–P relationships were positive log-linear for all three species-richness measures and estimators (Table 2; Fig. 2d,e,f). These relationships were, in part, driven by two transects with much lower aboveground biomass; when these two transects were excluded the relationships were still significant, although the amount of variance explained and the significance of the relationships decreased ($S$: $R^2 = 0.28$, $\chi^2 = 12.79$, $P = 0.0003$; $S_r$: $R^2 = 0.29$, $F_{1,22} = 8.97$, $P = 0.006$; ICE: $R^2 = 0.32$, $F_{1,22} = 10.39$, $P = 0.004$).
FIGURE 2. Species diversity–environmental heterogeneity and species diversity–productivity relationships for three different species-diversity estimators differentially sensitive to sample size for twenty-six 0.2-ha transects of the tree community at a tropical dry forest of western Mexico. $S =$ species richness; $S_r =$ rarified species richness for 148 trees; ICE = nonparametric incidence-based species-richness estimator (rarified). See Table 2 for statistical details. Solid lines indicate linear models fitted to observed data (points), while broken lines show asymptotic models.

No unimodal (polynomial) relationships were found; those with asymptotic patterns were very similar to the linear ones. The nature of D–P relationships, the amount of variance explained by productivity, and the significance of the obtained model were similar for $S$, $S_r$, and ICE.

Multiple linear regressions including the simultaneous contribution of environmental heterogeneity and productivity to species richness were obtained for all three measures (Table 2). No significant interaction between environmental heterogeneity and productivity was found for any of them. Productivity explained consistently a larger amount of variance; nevertheless, standardized beta associated with environmental heterogeneity was higher than that for productivity. Total amount of explained variance by multiple linear regressions ranged between 69 and 76 percent.

Species richness and productivity (aboveground biomass) showed significant positive linear relationships with number of trees ($S$: $\chi_1^2 = 24.09$, $P < 0.0001$, $R^2 = 0.29$; aboveground biomass: $F_{1,24} = 5.64$, $P < 0.05$; Fig. 3a,b); in the case of productivity the relationship was mostly driven by two transects with low number of trees and low basal area; when they were removed, the relationship was no longer significant. The positive D–P relationship was not solely due to effects of the number of trees on the two variables; residuals from those effects on both richness and aboveground biomass showed positive linear relationship among them ($F_{1,25} = 14.36$, $P < 0.001$; Fig. 3c). The relationship between richness residuals and environmental heterogeneity was positive log-linear ($F_{1,25} = 11.88$, $P < 0.001$, $R^2 = 0.33$) and showed similar results to those obtained with species richness (Table 2).
Results obtained for total transect species diversity, $D_{total}$, were mostly consistent with those obtained for the above species richness and residuals analysis (Table 3; Fig. 4c,f). Both $D_{EH}$ and $D_{P}$ relationships were positive log-linear. The $D_{P}$ relationships were also partly driven by two transects with much lower aboveground biomass; when these two transects were excluded the relationships were still significant but the amount of variance explained and the significance of the relationships decreased ($R^2 = 0.17$, $F_{1,22} = 8.98$, $P = 0.007$). Amount of variance explained by productivity was higher than that for environmental heterogeneity; the same patterns were observed for standardized betas. Again, no interaction effect between environmental heterogeneity and productivity was found. The total amount of explained variance by multiple linear regressions was 75 percent.

Very different patterns were found for the components of species diversity. Average within-plot local species diversity ($D_{within}$) was only related to productivity (aboveground biomass) and not to environmental heterogeneity. The $D_{P}$ relationship was positive log-linear or polynomial (Table 3; Fig. 4a,d); both relationships were largely driven by two transects with very low productivity and the significance of the relationship disappeared when they were removed. Instead, among-plot species turnover ($D_{among}$) was only related to environmental heterogeneity, and not to productivity; its relationship with environmental heterogeneity was positive log-linear (Table 3; Fig. 4b,e).

**DISCUSSION**

The positive log-linear relationships between species diversity and environmental heterogeneity observed here for the whole transect species-diversity measures and estimators are consistent with the expectation of differential species performance along resource gradients (Tilman 1982, Shmida & Wilson 1984, Richard et al. 2000, Lundholm & Larson 2003). Yet, limited data are available to support this hypothesis (but see Balvanera 1999, Balvanera et al. 2002 for preliminary evidence) at this particular tropical dry forest and at this particular scale, or in general for other tropical dry forests. Differential performance of species along resource gradients are evident at biogeographic scales (Bridgewater et al. 2004) and at landscape scales ($>100$ ha; Nichols et al. 1998), but the extent of environmental heterogeneity is lower at smaller scales and species diversity may fail to respond to such a low level of environmental heterogeneity. That was the case of fern species diversity at very local scales (<0.01 ha) and soil heterogeneity, based on soil moisture, fertility, and pH data (Lundholm & Larson 2003). The shape of the relationships found in our study reflect the fact that sufficient environmental heterogeneity, relevant to differential species performance, was included by our sampling protocol. Transects in this work were designed to encompass the maximum environmental variation observed within the study site. The area is dominated by small hills, and some of the 100-m long transects (0.2-ha plots) run from the central stream of the watershed to its divide, thus encompassing the widest possible range of water availability at this spatial scale.

![Figure 3](https://example.com/figure3.png)  
**FIGURE 3.** Relationships between species richness, productivity, and number of trees in the case of twenty-six 0.2-ha transects for the tree community at a tropical dry forest of western Mexico. Linear models were fit to the relationship between species richness and number of trees, and that between basal area and number of trees. Residuals from these models were used as an alternative species richness vs. productivity relationship, for which effects of number of trees have been removed.
Among-homogeneous plots species turnover component, i.e., $t$ionship. Previous work on species turnover along such transects diversity, which also showed a positive log-linear D–EH rela-

Due to stressful conditions (Grime 1979, Huston 1979, Rosenzweig 1995, T rejo & Dirzo 2002). The patterns found in our study suggest among 0.01 quadrats within 30 m $\times$ 30 m plots. The highest productivity end of a wider unimodal relationships (Waide et al. 1996). Our results are consistent with those found at local scales for the tropical rain forests of Borneo using a similar productivity estimator as the one used here (Aiba & Kitayama 1999) and for Central American tropical forest at regional scales (Gentry 1988). However, unimodal or nonexistent relationships have been found for Mexican, Central American, and Asian tropical forest at a variety of regional scales (Beadle 1966, Phillips et al. 1994, Gentry 1995, Trejo & Dirzo 2002). The patterns found in our study suggest that species are likely to be excluded at low productivity gradients due to stressful conditions (Grime 1979, Huston 1979, Rosenzweig & Abramsky 1993). The potential existence of such process is further confirmed by the fact that average within-plot local species diversity (calculated for 0.04-ha homogeneous plots within transects) showed a positive linear P–D relationship. In particular, a low number of individuals was found at a couple of transects that also showed the lowest productivity and the lowest species diversity. These two sites are located at the upper part of the watershed; previous work had shown that these sites have the lowest primary productivity (Martínez-Yrizar et al. 1996). There, a less equitable community has been found (Segura et al. 2003), suggesting domination by the few species can withstand such drought conditions. Results for the within-plot local species diversity suggest that at small spatial scales, where environmentally homogeneous conditions are found, the role played by low productivity on species exclusion is sharper. Our results do not support the presence of competitive exclusion processes at high productivity levels.

Interpretation of our results as evidence for species exclusion under low productivity is dependent on our productivity estimator, standing aboveground phytomass. We used here an indicator of productivity that is a measure of vegetation performance, rather than one that would directly account for nutrient or water availability. One critical assumption associated with such an estimator is that all studied sites have similar stand age, which we can argue because trees predominantly die standing, and that tree replacement happens mostly at the single tree level (Maas et al. 2002, Segura et al. 2003), as discussed above. However, this assumption is only true for larger plots, where the age of a large number of trees, each one at different stages of the replacement process, is averaged. Local tree species turnover rates are very likely to affect our productivity estimations,

### TABLE 3. Simple and multiple regression models (generalized linear and negative exponential) for three components of species diversity, using a Simpson-based partitioning proposed by Lande (1996) and two independent variables, environmental heterogeneity (EH) and productivity (estimated from biomass), in the case of twenty-six 0.2-ha transects, each divided into five 0.04-ha plots, for the tree community at a tropical dry forest of western Mexico. $D_{\text{within}} =$ average local species diversity for the five plots within each transect, $D_{\text{among}} =$ species turnover among the five plots within each transect, and $D_{\text{total}} =$ total transect species diversity. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$. Gaussian distribution and an identity link functions were used. All deviance values are 10$^{-6}$ times those expressed in the table. For multiple regression models, two values of deviance, and $F$ are given for each independent variable separated by a “/”; the first one corresponds to the entry of the variable in first place, and the second one to its entry in second place; standardized beta remained constant independent of the order of entry.

<table>
<thead>
<tr>
<th>Species-diversity component</th>
<th>Model</th>
<th>Independent variable</th>
<th>Deviance</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
<th>Percent explained</th>
<th>Standardized beta</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average within plot local species diversity $D_{\text{within}}$</td>
<td>$\hat{D}_{\text{within}} = 0.90 + 0.04 \log(\text{Biomass})$</td>
<td>$\log(\text{Biomass})$</td>
<td>615.28</td>
<td>1</td>
<td>16.56</td>
<td>***</td>
<td>40.84</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\hat{D}_{\text{within}} = 0.77 + 0.29 \log(\text{Biomass}) - 0.12 \log(\text{Biomass})^2$</td>
<td>$\log(\text{Biomass})^2$</td>
<td>202.28</td>
<td>1</td>
<td>6.75</td>
<td>*</td>
<td>13.42</td>
<td></td>
</tr>
<tr>
<td>Among plot species turnover $D_{\text{among}}$</td>
<td>$D_{\text{among}} = 0.01 + 0.01 \log(\text{EH})$</td>
<td>$\log(\text{EH})$</td>
<td>85.43</td>
<td>1</td>
<td>5.02</td>
<td>*</td>
<td>17.21</td>
<td></td>
</tr>
<tr>
<td>Total species diversity $D_{\text{total}}$</td>
<td>$D_{\text{total}} = 0.94 + 0.02 \log(\text{EH})$</td>
<td>$\log(\text{EH})$</td>
<td>270.59</td>
<td>1</td>
<td>10.35</td>
<td>**</td>
<td>30.13</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$D_{\text{total}} = 0.94 + 0.04 \log(\text{Biomass})$</td>
<td>$\log(\text{Biomass})$</td>
<td>505.52</td>
<td>1</td>
<td>30.90</td>
<td>****</td>
<td>56.27</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$D_{\text{total}} = 0.90 + 0.03 \log(\text{Biomass}) + 0.02 \log(\text{EH})$</td>
<td>$\log(\text{Biomass})$</td>
<td>505.52/405.79</td>
<td>1</td>
<td>52.43/28.07</td>
<td>****</td>
<td>56.27/45.18</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>$\log(\text{EH})$</td>
<td>270.58/170.86</td>
<td>1</td>
<td>42.09/17.72</td>
<td>****</td>
<td>30.12/19.02</td>
<td>0.44</td>
<td></td>
</tr>
</tbody>
</table>
as well as have direct effects on species diversity (Phillips et al. 2003, Chalcraft et al. 2004), and these could not be accounted for in our analysis. In particular, drought and water stress-related tree mortality may play an important role in structure of this forest (Segura et al. 2003). Mortality is expected to vary among areas with differential water availability, partially determining tree biomass estimated here for transects and plots within transects. In particular, the two transects with very low biomass are found in south-facing shoulders, including the transition zone between the crest and the slopes; it is possible that these areas are particularly susceptible to high drought-related mortality due to high evapotranspirative demands. There are several alternative explanations for the low biomass levels found in such transects: either the sites are recovering from a relatively recent drought-related mortality event, and thus in average trees are younger, or low potential productivity hinders the establishment and development of trees that are as large, on average, as those found in other transects, or mortality rates are higher at most stressful sites. Soils found in those two particular transects are among the most shallow (with large areas completely devoid of soil), and among those highest in evapotranspirative demand (given by highest insolation values); we believe that low potential productivity contributes greatly to the low biomass levels found there.

The D–EH and D–P relationships observed here were quite robust, and did not show effects of sample size, despite the large variance in tree abundance observed among sites and the strong correlations between diversity, productivity, and tree abundance. The fact that degree of significance and amount of variance explained by environmental heterogeneity when using $S_r$ or ICE was higher than those found with $S$ could be attributed to effects of tree abundance on species richness; this was not confirmed by analysis with residuals that showed similar results to those found with $S$. Yet, it has been proposed that relationships between number...
of individuals and richness follow complex relationships, and that use of rarefaction techniques is a more adequate way to compare species richness among sites with contrasting densities (Gotelli & Collwell 2001); our results are partially consistent with such an approach.

The lack of relationship between environmental heterogeneity and productivity at our sites provides an excellent opportunity to explore the independent relative contribution of these variables to species diversity. In this case, we observed no tendency for higher heterogeneity as productivity increased, contrary to earlier predictions (Tilman 1982, Rosenzweig & Abramsky 1993, Tilman & Pacala 1993, Wäde et al. 1999, Mittelbach et al. 2001). Productivity consistently explained a larger fraction of variance than environmental heterogeneity. Given that no effect of the interaction between environmental heterogeneity and productivity was found on any of the species-diversity estimators, it is plausible that processes associated with both factors operate simultaneously and independently.

The amount of variance explained by environmental heterogeneity was large when 0.2-ha plots were used, decreased when smaller plots are used (e.g., 0.1 ha in Aguirre 2004), and was no longer significant when homogeneous 0.02-ha plots were used. Our results suggest that as the magnitude of environmental heterogeneity increases, its relative contribution to the variance in species diversity also tends to increase. If that is true, then if magnitude increases, its relative contribution to the variance in species diversity also tends to increase. As heterogeneity increases, its relative role in explaining changes in species diversity among sites also increased. Our results are consistent with recent theoretical work that incorporates the simultaneous operation of different processes at different spatial scales (Leibold et al. 2004, Lortie et al. 2004, Sarr et al. 2005), and in particular with those that include both differential niche-use by different species and large decreases in the probability of invasion of a new species where resource levels are low (Huston 1994, Tilman 2004). Nonetheless, experimental work is needed to test directly for the existence of the predicted involved processes.

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