

Functional traits and environmental filtering drive community assembly in a species-rich tropical system

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Abstract. Mechanistic models of community assembly state that biotic and abiotic filters constrain species establishment through selection on their functional traits. Predicting this assembly process is hampered because few studies directly incorporate environmental measurements and scale up from species to community level and because the functional traits' significance is environment dependent. We analyzed community assembly by measuring structure, environmental conditions, and species traits of secondary forests in a species-rich tropical system. We found, as hypothesized, that community structure shaped the local environment and that strong relationships existed between this environment and the traits of the most successful species of the regeneration communities. Path and multivariate analyses showed that temperature and leaf traits that regulate it were the most important factors of community differentiation. Comparisons between the trait composition of the forest's regeneration, juvenile, and adult communities showed a consistent community assembly pattern. These results allowed us to identify the major functional traits and environmental factors involved in the assembly of dry-forest communities and demonstrate that environmental filtering is a predictable and fundamental process of community assembly, even in a complex system such as a tropical forest.

Key words: *abiotic filters; community assembly; drought; functional traits; Isthmus of Tehuantepec, Oaxaca, Mexico; microenvironment; niche; regeneration; seasonally dry tropical forests; secondary succession; temperature.*

INTRODUCTION

Understanding and predicting the key factors that drive community assembly have been major questions in ecology that are presently critical if we are to address or mitigate the problems imposed by global change (Naeem and Wright 2003, McGill et al. 2006). Many of our ideas on plant community assembly are based on the premise that species differ in their environmental requirements for successful regeneration, especially when young (i.e., the regeneration niche; Grubb 1977, Poorter 2007). Mechanistic explanations of community assembly state that community membership is constrained to those species with the appropriate functional traits to reach a site (i.e., overcome a dispersal filter) and establish under the circumstances set by the environment and other organisms (i.e., the abiotic and biotic filters; Belyea and Lancaster 1999).

Numerous studies show how plant traits affect the performance of individual species, but our ability to predict community assembly from these relationships is nevertheless limited. This is partly because the link between plant traits and function to the environment is mostly conceptualized and few studies directly correlate them (McGill et al. 2006, Vile et al. 2006). Also problematic is that the importance of traits differs with ecosystem conditions and the scale of study (Wright et al. 2005, Ackerly and Cornwell 2007). In tropical humid forests, for example, species adaptations to vertical and horizontal light gradients can explain successional change and species coexistence (Poorter et al. 2006, Lusk et al. 2008, but see Hubbell et al. 1999). In tropical dry forests (TDF) however, adaptations to such light gradients are considered less relevant because of the short-statured and seasonally more open canopy (Ewel 1977, Lebrija-Trejos et al. 2008). Instead, adaptations to strong seasonal drought (limited water supply), high solar irradiance, and high evaporative demand seem to largely determine the ecology of TDF species (Borchert 1994, Lüttge 2008, Poorter and Markesteijn 2008). Such adaptations must be especially important in the partic-

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ularly open early-successional communities of TDFs (Ewel 1977), but other adaptations may become important when the forest develops as succession proceeds. Late-successional TDFs have a larger vegetation cover (implying a lower light and nutrient availability), a more complex structure (e.g., guild diversity), and more diverse agents of seedling mortality (e.g., predators, herbivores, pathogens) than early-successional ones (Lieberman and Li 1992, Hammond 1995, Pereira et al. 2003, Read and Lawrence 2003, Saynes et al. 2005). Hence, light capture and protection of acquired resources may become important for plant establishment as succession proceeds.

Scaling up from the species level to the community level is one of the steps needed to advance in understanding and predicting community assembly (McGill et al. 2006). Patterns of traits and trade-offs at the species level can differ from those at the community level and may not correctly predict vegetation change or plant community structure (e.g., Murray and Leishman 2003, Wright et al. 2005). Recent community-level studies analyzing functional traits and species abundances have shown that niche-related processes play a role in community assembly even in tropical forests (Gunatilleke et al. 2006, Engelbrecht et al. 2007, Kraft et al. 2008), where unpredictable chance events are proposed to play a leading role (Hubbell 2001). Some works have further shown that such a community-level approach has a highly predictive value (e.g., Vile et al. 2006, Mouillot et al. 2007, Shipley et al. 2007). Nevertheless, these studies lack the inclusion of environmental data in their analysis. The inclusion of environmental factors is needed to obtain a more comprehensive mechanistic understanding of the role of functional traits in community assembly and to establish the precise links between filtering factors and functional traits in a system.

Secondary succession is community assembly in action. It is a re-colonization process in which community structure, environment, and species composition change over time. If environmental filters and species traits are relevant for community assembly, then communities should have particular combinations of traits under different environmental conditions. This should occur in spite of the heterogenizing effect that factors such as random dispersal or competition may have in the assembly process (Weiher et al. 1998, Hubbell 2001).

We analyze the significance of environmental filtering in community assembly by linking the shifts in environmental conditions, species abundances, and functional traits that occur with the development of TDF fallows differing in successional status (1–60 yr old). Data on the structure of the fallows are used to further analyze the vegetation–environment feedback. First we ask, does forest structural development during secondary succession produce directional changes in abiotic conditions at the forest floor? Second, does the

variation in abiotic conditions at the forest floor shape the functional trait composition of the regenerating communities? We hypothesized that (1) with the development of forest structure, the regeneration environment changes from hot, sunny, and dry to cooler, shady, and moist; and (2) early-successional communities are dominated by species with traits related to fast growth and tolerance to hot and desiccating environments, while late-successional communities are dominated by species with traits related to acquisition and conservation of resources.

METHODS

The study area was located near Nizanda (16°39'30" N, 95°00'40" W), a village on the Pacific Slope of the Isthmus of Tehuantepec, Oaxaca, Mexico. Mean annual temperature is ~26°C and mean total annual precipitation is ~900 mm, with 90% of rainfall occurring between late May and mid-October. The main forest matrix is formed by a low-statured (~7–8 m) tropical deciduous forest (>75% of the species are deciduous). *Sensu* Holdridge's life zone system, it is in the transition from subtropical very dry forest to subtropical dry forest. Of 920 species recorded in the area (90 km²), 430 are present in the dominant deciduous forest, while 191 species are exclusive to it. The other species of the recorded flora are mainly distributed in diverse communities such as savannas, xerophytic scrubs, gallery forests, and semi-evergreen forests. (For more study area details see Pérez-García et al. [2001].)

Species composition and abundance of trees and treelets of the regeneration communities (RC; individuals 0.3–1.0 m tall) of secondary TDFs were measured in 144 2 × 2 m quadrats placed regularly in 18 plots (8 quadrates/plot). These were formerly corn fields with abandonment times ranging from <1 yr to ~60 yr, plus a mature forest (see Plate 1). Abandonment times were obtained from interviews with plot owners and checked by dendrochronological analyses (Brienen et al. 2009). Structure and species composition of the juvenile community (JC; individuals 1 to <5 cm diameter at breast height [dbh; measured at 1.3 m above the ground surface]) and the adult community (AC; individuals ≥5 cm dbh) were additionally obtained. See Lebrija-Trejos et al. (2008) for details in plot selection, layout, and characterization.

Photosynthetic photon flux density (PPFD), air temperature, relative humidity, soil temperature, and soil matric potential (Ψ_m) were measured during the rainy season (late May–November), when most growth occurs and when foliage development creates marked environmental gradients. Nonetheless, to evaluate the influence of seasonal drought, Ψ_m was measured once during the leafless period (in February). Soils of all but one plot were similarly dry by then ($\Psi_m = -49.9 \pm -12.5$ MPa [mean \pm SD]), and no significant relationships were found between dry-season Ψ_m and time or forest

structure; thus, this variable was omitted from further analyses.

Understory PPFD was measured with LI-COR quantum sensors (Li-190, LI-COR, Lincoln, Nebraska, USA) set at 50 cm above soil level in seven randomly chosen quadrates per plot. Another sensor was raised above the canopy to calculate the percentage PPFD reaching the understory. The PPFD measurements during one full day have been shown to provide good estimates of long-term light conditions of differing understory microsites (Engelbrecht and Herz 2001). Two full days per plot were used. Sensors were placed simultaneously in two plots to record 10-min averages with a 5-s sampling interval. After recording a faultless two-day period, sensors were moved to two other plots until all plots were characterized.

Air temperature and relative humidity (RH) were logged every hour from June to October also at 50 cm above soil level. Two HOBO Pro Temp dataloggers (Onset, Bourne, Massachusetts, USA) were placed in eight plots and three HOBO Pro Temp/RH dataloggers in 10 plots. The daily mean temperature (T_{air}) is used across all analyses. The mean daily maximum temperature was nonetheless calculated to illustrate better the differences in stress conditions between the plots. Simultaneous records of temperature and RH were used to calculate air vapor pressure deficit (VPD; $\text{VPD} = \text{saturated air VP} - \text{air VP}$; $\text{air VP} = \text{saturated air VP} \times \text{RH}/100$) and correlate plot-averaged values of air temperature and VPD ($R = 0.95$, $P < 0.01$, $N = 10$). This corroborated the use of temperature both as an indicator of heat and evapotranspirational conditions (mean daily maximum VPD [KPa] = 3.3, $\text{SD} = 0.5$, range = 2.6–4.4). All calculated averages included only daylight records.

Soil temperature was measured using waterproof digital thermometers with 12.7 cm long probes. Thermometers were placed in the same quadrates where soil samples were taken. Temperature was registered every 3 h from 07:00 to 19:00 during the second day of PPFD recordings. For each recording, a relative measure of soil temperature (T_{Srel}) was calculated to compare between plots ($T_{\text{Srel}} = \text{soil temperature} - \text{ambient temperature}$; ambient temperature was registered by a meteorological station located in an open field in the study area).

The Ψ_m was calculated using the filter paper method, a simple and well-documented method employed in several disciplines for measuring soil matric potentials down to -100 MPa (Ophori and Maharjan 2000, Leong et al. 2002, Scanlon et al. 2002, Marthens et al. 2008). Soil samples were taken from the edge of six quadrates of a plot and at a soil depth of 0–10 cm. Tropical dry forests are very shallow rooted, with 70% of all the root biomass found within 1 m of soil depth occurring in just the first 20 cm (Jobbagy and Jackson 2000). Surface Ψ_m (0–10 cm) has marked effects in the survival of tropical forest seedlings (Engelbrecht et al. 2006). All samples were taken within one (overcast) day and individually

sealed in 150-cm³ plastic jars with three Whatman number 42 filter paper discs (55 mm diameter; Whatman, Maidstone, Kent, UK) placed in the middle of the jar. Samples were left to equilibrate during two weeks inside an isolated container. Afterwards, Ψ_m was calculated from the water content of the middle filter paper by following the methods of the D5298-03 American Society for Testing and Materials international standard and using the formulas of Leong et al. (2002).

Thirty-one species were selected for measuring various functional traits related to plant establishment and persistence (Weiher et al. 1999, Westoby et al. 2002, Niinemets et al. 2004, Poorter 2009; Table 1). Traits for dealing with the characteristic environmental stresses of TDF were of particular interest. Selected species were the most common in the RCs as they accounted on average for 91% of individuals in a plot (range = 81–100%) and represented on average 84% of the species (range = 67–100%).

Leaf thickness, leaf size (surface area), leaf slenderness or aspect ratio (lamina length/lamina width), leaf mass per area (leaf dry mass/leaf area), leaf density (leaf mass per area/leaf thickness), leaf dry matter content (leaf dry mass/leaf fresh mass), and petiole length were calculated from field measurements of sun-exposed fully expanded fresh young and undamaged leaves of adult trees. Five trees of comparable size per species were selected, and five leaves per each tree were sampled. Sampled leaves came from the outer layer of the crown, halfway its vertical length. Leaves were collected with their branches and transported in plastic bags to the in situ laboratory for immediate measurement. Collected branches were put in water, and the leaves were detached individually for recording their fresh mass and dimensions. This prevented leaf wilting and the closing of compound leaves after collection. Measurements were performed on entire leaves (including petioles), with the exception of leaf length, width, and area, where leaflets were used in the case of compound-leaved species. Leaf area was calculated from images obtained with a desktop scanner and analyzed with pixel-counting software (Berloo 1998). For measuring dry masses, leaves were oven dried for 48 h at 75°C.

Leaf compoundness (degree of leaf segmentation; simple leaves, 1; compound leaves, 2; double-compound leaves, 3); leaf pubescence (no, 0; yes, 1); leaf pulvination (ranked from 0 for leaves without pulvini to 3 for leaves with up to tertiary pulvini [i.e., at the petiole base and first- and second-order petiolules]); seed shape (variance of seed length, width, and depth, each divided by the maximum quantity so that one of them is unity [see Thompson et al. 1993]; seed shape ranged from 0.003 for nearly spherical seeds to 0.23 for disc-shaped seeds); seed size (as an ellipsoid volume = $\pi/6 \times \text{length} \times \text{width} \times \text{depth}$); and dispersal mode (classified as wind dispersal for propagules with wings, hairs, or plumes; as animal dispersal for propagules with fleshy pulp or an aril; and

TABLE 1. List of functional traits, grouped by their role in plant establishment and persistence, measured as surrogates of difficult-to-measure traits (in italics).

Measured trait	Abbreviation	Functional role	Variation
Establishment			
<i>Dispersion and germination</i>			
Animal dispersal	AD	spatial dispersion (distance and probability)	N
Unassisted dispersal	UD	spatial dispersion (distance and probability)	N
Wind dispersal	WD	spatial dispersion (distance and probability)	N
Seed shape	SSh	seed longevity and survival	0.003–0.228, D
Seed size	SSz	dispersal distance, fecundity, seed longevity	0.003–0.642 cm ³
Persistence			
<i>Stress resistance</i>			
Deciduousness	De	drought avoidance	B
Leaf compoundness	LC	leaf cooling, light capture economics (structural investment)	O
Leaf density	LD	leaf structure/water balance (modulus of elasticity)	0.2–1.1 g/cm ³
Leaf dry matter content	LDMC	leaf structure/water balance (modulus of elasticity)	0.21–0.64 g/g
Leaf pubescence	LPb	leaf cooling, water balance	B
Leaf size	LSz	leaf cooling, light capture efficiency (self-shading)	0.02–96.53 cm ²
Leaf slenderness	LS	leaf cooling, light capture efficiency (self-shading)	0.71–5.76 cm/cm
Maximum height	H _{max}	light competitive ability	3.7–8.8 m
Petiole length	PL	light capture efficiency	0.24–8.89 cm
Leaf pulvination	LPI	irradiance control	O
Seed size	SSz	seedling resource supply	0.003–0.642 cm ³
<i>Growth rate</i>			
Leaf mass per area	LMA	photosynthetic performance, light capture economics	43–160 g/m ²
Nitrogen fixation	N _{fix}	photosynthetic performance	B
<i>Defense</i>			
Exudates (latex and resins)	Ex	against herbivore attack	B
Leaf dry matter content	LDMC	against mechanical and herbivore damage	0.21–0.64 g/g
Leaf pubescence	LPb	against herbivore and fungi attack	B
Leaf thickness	LT	against mechanical and herbivore damage	50.2–301.1 μm
Spininess (spines and thorns)	Sp	against large herbivore attack and pruning	B

Notes: Variations indicate the range of values for each trait along all sampled species; B, N, O, and D, denote binary, nominal, ordinal, or dimensionless variables. The study area was located near Nizanda (16°39'30" N, 95°00'40" W), a village on the Pacific Slope of the Isthmus of Tehuantepec, Oaxaca, Mexico.

as unassisted dispersal for propagules with no obvious dispersal adaptation) were obtained from specimens of the study area deposited in the MEXU herbarium, Universidad Nacional Autónoma de México. For all seed traits, a minimum of three seeds per five individuals (15 seeds) was assessed.

Deciduousness (strictly deciduous species, 1; otherwise, 0); spininess (spines or thorns, 1; absent, 0); and exudates (latex or resins, 1; absent, 0) were determined from botanical expertise; maximum height (H_{\max}) was calculated following Thomas (1996) using data taken from unpublished regional databases of forest structure and composition (E. A. Pérez-García and J. A. Meave); and nitrogen fixation (yes, 1; no, 0) was obtained from the database of the Germplasm Resources Information Network (*available online*).⁵ This information was unavailable for three species, *Havardia campylacantha* (L. Rico et M. Sousa) Barneby et J. W. Grimes, *Lonchocarpus lanceolatus* Benth., and *Mimosa goldmanii* B. L. Rob. Nonetheless, as taxonomy and phylogeny are good indicators of nodulation (Doyle 1994), they were

assumed to nodulate because most studied species within the genera do so.

A path model was used for an integrated analysis of our hierarchical and process-based hypothesis, i.e., that the successional development of vegetation structure modifies the regeneration environment (hypothesis 1) and that such modified environment acts as a filter that determines the functional trait composition of the regenerating communities (hypothesis 2; Fig. 1). With such approach we could identify the differential role of forest structural and environmental factors (filters) on community assembly. The plots' total basal area (BA), crown area, and density of individuals were calculated using individuals ≥ 1 cm dbh. To perform the simple and multiple linear regressions of the path model (Fig. 1), time, crown area, tree density, PPFD, T_{air} , and Ψ_m were transformed using square-root, arcsine, and logarithmic functions to improve normality and homoscedasticity (the original names of the variables are used at all times). For a clearer description of the successional trends of change, the bivariate relationships between the untransformed variables were additionally analyzed using simple (two-parameter) linear, quadratic, and exponential models.

⁵ <http://www.ars-grin.gov/~sbmljw/cgi-bin/taxnodul.pl?language=>

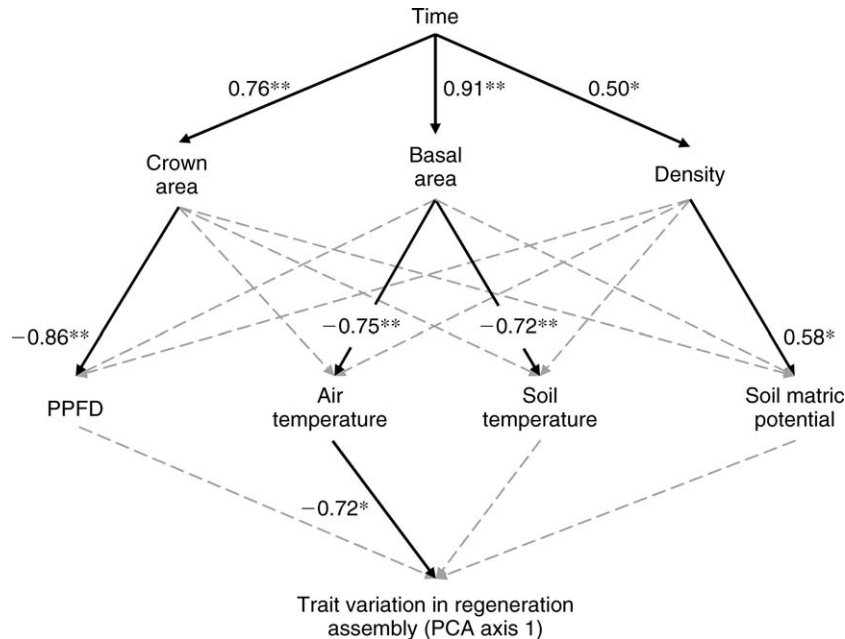


FIG. 1. Path model showing the causal relationships (arrows) between abandonment time, structural development, environmental variability, and trait composition of the regeneration assembly of secondary forests in a species-rich tropical system. Dashed lines show the full models tested by multiple linear regression. Solid lines indicate significant effects (* $P < 0.05$, ** $P < 0.01$); values are standardized regression coefficients. All axes of the principal components analysis (PCA) of the regeneration assembly trait composition were tested, but only axis 1 was significantly related to the environment. Time, crown area, mean air temperature, and the percentage of open-sky photosynthetic photon flux density (PPFD) were transformed to comply with linear models assumptions (see *Methods*), but the original names are kept for simplicity. The study area was located near Nizanda, a village on the Pacific Slope of the Isthmus of Tehuantepec, Oaxaca, Mexico.

A detailed mechanistic explanation of filter-mediated community assembly was obtained by analyzing, with principal component analysis (PCA; McCune et al. 2002), the multivariate relationships between the species functional traits, their community-level variation, and the gradients of environmental change. First, a species' PCA using the species \times traits matrix (species ordination) was performed to reveal the combined variation in their functional traits (i.e., plant strategies). Second, by combining species abundances with species functional traits, a plot \times traits matrix was constructed to perform a PCA of the RCs based on the community-level abundance-weighted trait data. This weighted-average ordination was used to analyze the variation in the functional-trait composition of the RCs in relation to the gradients of environmental change; this included testing the relationships of PCA axes with the environment (path analysis final step; Fig. 1). A similar analysis using only species presence/absence data (i.e., all species weighted equally; unweighted-average ordination) was used to differentiate between the effects of filters on the probability to occur and on the probability to become dominant. A final PCA using a size-stratified plot \times traits matrix containing the abundance-weighted data of each plot's regeneration, juvenile, and adult communities was used to provide an indirect test of the environmental filtering. If the regeneration environment

controls community assembly via filtering, then the trait assembly patterns of the juvenile and adult communities should reflect the RC patterns of previous successional stages. The relationships between the compositions of traits of the size-stratified communities were analyzed by regressing the first PCA axis scores of the communities on their fallow basal area (as an indicator of vegetation development) using nonlinear models. Selection of the best model depended upon statistical methods for model comparisons, namely on R^2 differences when the models had equal numbers of parameters, on the results of an F test when one model was a simpler case of the other (i.e., nested), or on the difference between the models' Akaike Information Criterion values, corrected for small sample sizes, when the models were non-nested (Motulsky and Christopoulos 2004). As trait variables had different scales, they were relativized by their standard deviates (trait means, 0; variances, 1) for all the multivariate analyses.

The PCAs' validity was tested by redoing the ordinations using nonmetric multidimensional scaling (MDS), which makes no assumptions on data distribution (McCune et al. 2002), and by performing Monte Carlo randomizations (500 runs). The sample scores obtained with PCA and MDS (stress < 11.1 , for two-dimensional solutions) were highly correlated (for all cases $R \geq 0.94$) and Monte Carlo tests P were < 0.01 .

This meant that PCAs' assumptions of linearity and normality were met and that ordinations were unlikely to result from chance. A further test of the strength of the trait's weighted-average PCA was performed by eliminating three out of four theoretically interdependent traits that could potentially bias the relative importance of any of such traits (leaf size, compoundness, slenderness, and petiole length; Appendix). No significant differences were found between the complete and the partial PCAs: the percentage of total variation explained by the first two axes of both PCAs was the same (61%) and the loadings of the functional traits on their first two axes were strongly correlated ($R = 0.99$, $P < 0.001$).

RESULTS

Forest structure and environment

Forest structure changed significantly with time (Figs. 1 and 2). Crown area increased rapidly (within 10 yr) while BA increased more gradually. These two patterns were largely regular and contrasted with the more variable, though also significantly increasing, pattern for density of individuals.

Significant environmental changes accompanied the structural development (Fig. 1). The increase in crown area explained best the reduction in PPFD (74% to 6%; Fig. 3a). Both T_{air} (29.1° to 27.4°C; daily mean maximum temperature, 39.8° to 34.2°C) and T_{Srel} decreased with forest development. Relative soil temperature changed from being higher than open-sky temperature (+3.1°C) in less developed fallows to lower than open-sky temperature (−2.6°C) in more developed ones. Basal area explained best these temperature changes (Fig. 3b, d). Differences in Ψ_m (−45.7 to −1.2 KPa) were only related to tree density; three early-successional plots with very low densities mainly caused the positive relationship (Fig. 3c).

Traits and species

The first two species PCA axes explained 31% and 17% of the variation (Fig. 4a). Species with compound and slender leaves, high leaf pulvination, high leaf density and leaf dry matter content (LDMC), nitrogen fixation (N_{fix}), spininess, unassisted dispersal, and a flattened seed shape loaded high on the first PCA axis (loadings ≥ 0.5). Common early- and late-successional legumes had high species scores on the first axis. Species extending towards the PCA's left side had increasing leaf size, leaf thickness, and seed size (first axis loads ≤ -0.5). Evergreen or brevi-deciduous species with high leaf mass per area (LMA) and animal dispersal and species with deciduous leaves, long petioles, and wind dispersal (all traits' absolute loadings ≥ 0.5) were found on opposite sides of the second PCA axis.

Traits, environment, and community assembly

The RCs varied in their weighted-average trait composition (Fig. 4b), reflecting that combinations of

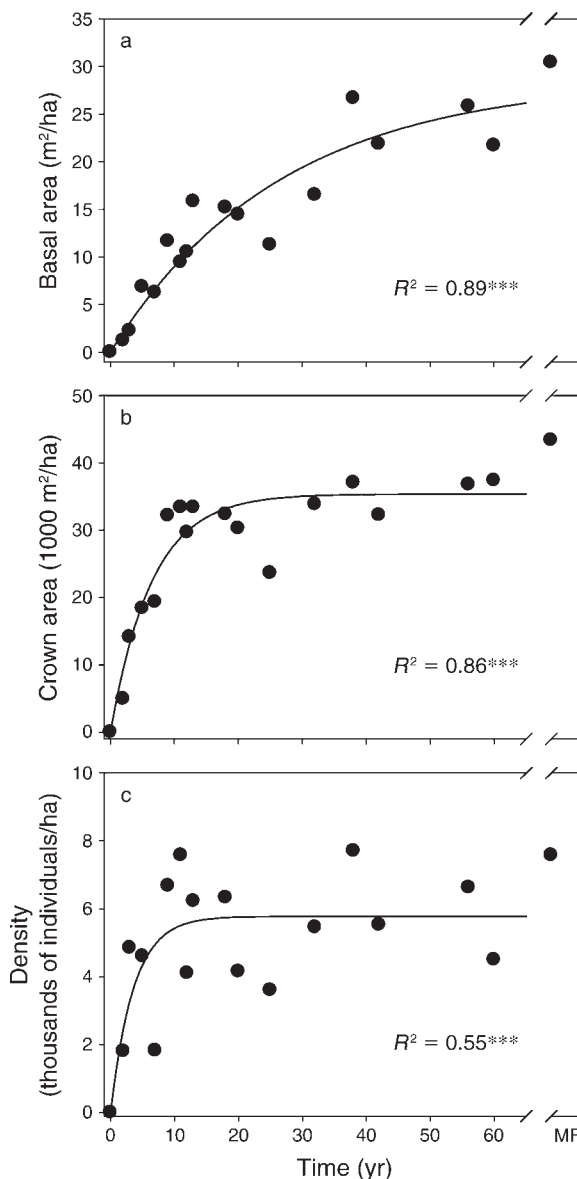


FIG. 2. Structural characteristics of secondary forests stands, with abandonment times ranging from <1 yr to ~60 yr, and a mature forest (MF) at Nizanda, Mexico: (a) basal area, (b) crown area, and (c) density of individuals. All values are expressed per hectare and include individuals ≥ 1 cm diameter at breast height. Continuous curves represent modeled nonlinear (exponential) changes (***) $P < 0.001$.

species with different set of traits occur (cf. Fig. 4a). The first two PCA axes explained 61% of the variation (40% and 21%). Most of this variation (first axis) was strongly correlated (absolute loadings ≥ 0.75) to leaf traits involved in control of water and temperature status (LDMC, density, slenderness, leaf pulvination, compoundness), growth rate (N_{fix}), and defense (spininess and exudates; Fig. 4b, Table 1). Air temperature and PPFD were the only environmental variables signifi-

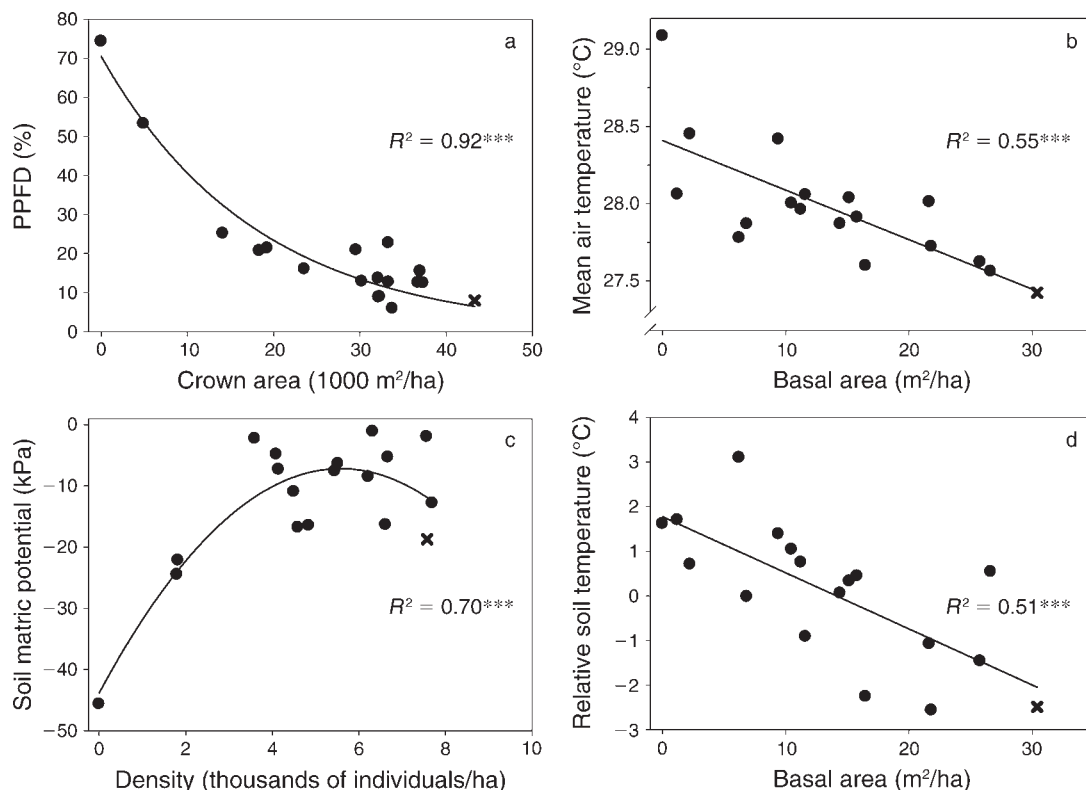


FIG. 3. Regeneration environment of secondary forests (circles), with abandonment times ranging from <1 yr to ~60 yr, and a mature forest (crosses) at Nizanda, Mexico, as a function of their canopy structure (individuals ≥ 1 cm dbh): (a) percentage of open-sky photosynthetic photon flux density (PPFD) reaching the forest understory (i.e., 50 cm above soil level); (b) daily mean air temperature at the forest understory; (c) soil matric potential (0–10 cm depth); and (d) soil temperature (~13 cm depth) relative to ambient air temperature.

cantly correlated with the first axis ($R = 0.72$, $P < 0.001$ and $R = 0.52$, $P < 0.05$, respectively), although only T_{air} was selected by the multiple regression (Fig. 1). An increase in T_{air} concurred with an increase in the community weighted average of traits such as LDMC, leaf slenderness, leaf density, leaf pulvination, leaf compoundness, spininess, and N_{fix} . Traits strongly correlated with the second axis (absolute loadings ≥ 0.70) showed a gradual change from RCs dominated by individuals with small seeds, unassisted dispersal, and deciduous leaves to RCs dominated by individuals with larger seeds, animal dispersal, and thick, high LMA, and evergreen or brevi-deciduous leaves (Fig. 4b). None of the environmental variables was significantly correlated with the second axis.

When only the traits unweighted average was used for the community-level PCA (not shown), the variation explained was similar (38% and 23% for axis 1 and 2) and similar trait associations were found (correlation between trait loadings of the weighted and unweighted average PCAs, $R = 0.93$, $P < 0.001$ and $R = 0.72$, $P < 0.001$ for axes 1 and 2, respectively). Nevertheless, the values of the trait loadings were lower (i.e., the strength of trait correlations with the axes declined), and no

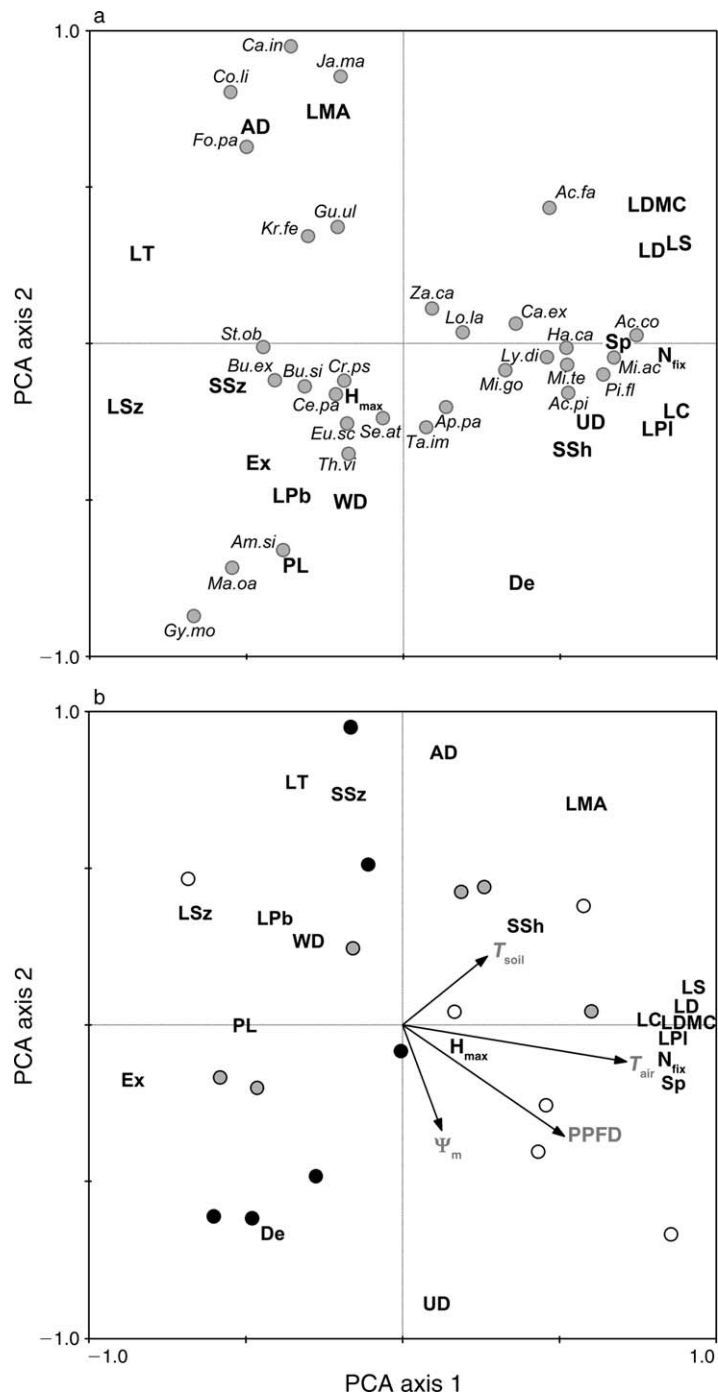
significant correlations were found between the axes and the environmental variables.

The weighted-average trait composition of the size-stratified communities (i.e., their first PCA axis scores; ordination not shown) changed directionally during stand development, from high scores related to compound and dense leaves in low BA plots to low scores related to large leaves and exudates in high BA plots (Fig. 5). The trait composition of the RC shifted strongly within ~10 yr, with lower differences occurring afterwards (logarithmic fit), while in the JC and the AC, the changes in time were gradual and continuous (linear fits). Regeneration, juvenile, and adult communities differed strongly in average trait values early during stand development, but converged towards similar values in structurally fully developed stands (Fig. 5). Additionally, the trends showed that the trait composition of the AC of the most developed stands was similar to that of the JC of mid-developed stands and to the RC of the least developed and recently colonized stands.

Path analysis

Path analysis showed that an increase in abandonment time led to an increase of all forest structural

FIG. 4. Principal components analysis (PCA) ordination of Nizanda's tropical dry forest: (a) species in the two-dimensional space of selected species traits and (b) regeneration communities of secondary-forest plots and a mature-forest plot, based on the community-level abundance-weighted mean of the traits of the most successful species in the regeneration assembly. The scaling of the ordinations reflects the relationships between the species traits (in boldface) and their approximate loadings on the ordination axes; see Table 1 for explanations of trait abbreviations. Species (in italics and abbreviated) are: *Ac.co*, *Acacia cochliacantha*; *Ac.fa*, *A. farnesiana*; *Ac.pi*, *A. picachensis*; *Am.si*, *Amphipterygium simplicifolium*; *Ap.pa*, *Apoplanesia paniculata*; *Bu.ex*, *Bursera excelsa*; *Bu.si*, *Bursera simaruba*; *Ca.ex*, *Caesalpinia exostemma*; *Ca.in*, *Capparis incana*; *Ce.pa*, *Ceiba parvifolia*; *Co.li*, *Coccoloba liebmanii*; *Cr.ps*, *Croton pseudoniveus*; *Eu.sc*, *Euphorbia schlechtendalii*; *Fo.pa*, *Forchhammeria pallida*; *Gu.ul*, *Guazuma ulmifolia*; *Gy.mo*, *Gyrocarpus mocinnoi*; *Ha.ca*, *Havardia campylacantha*; *Ja.ma*, *Jacquinia macrocarpa*; *Kr.fe*, *Krugiodendron ferreum*; *Lo.la*, *Lonchocarpus lanceolatus*; *Ly.di*, *Lysiloma divaricatum*; *Ma.oa*, *Manihot oaxacana*; *Mi.ac*, *Mimosa acantholoba* var. *eurycarpa*; *Mi.go*, *M. goldmanii*; *Mi.te*, *M. tenuiflora*; *Pi.fl*, *Piptadenia flava*; *Se.at*, *Senna atomaria*; *St.ob*, *Stemmadenia obovata*; *Ta.im*, *Tabebuia impetiginosa*; *Th.vi*, *Thouinia villosa*; *Za.ca*, *Zanthoxylum* aff. *caribaeum*. The different symbols in panel (b) indicate the plots' time since abandonment (open circles, <10 yr; shaded circles, 10–30 yr; solid circles, >30 yr), and the overlaid arrows represent the direction of increase of the environmental variables (in gray) and the approximate correlation strength (R) between the environment and the axes of variation. Other abbreviations are: PPF, percentage of open-sky photosynthetic photon flux density reaching the forest understory (i.e., 50 cm above soil level); T_{air} , daily mean air temperature at the forest understory; Ψ_m , soil matric potential (0–10 cm depth); and T_{soil} , soil temperature (~13 cm depth) relative to ambient air temperature.



variables (Fig. 1). The structural variables had, in turn, a different effect on the environmental factors; crown area led to a significant reduction in PPF, basal area led to a reduction in air and soil temperature, and tree density led to a reduction in Ψ_m . Strikingly, air temperature was the main environmental variable leading to trait variation of the regeneration assembly, which indicates that it is a key environmental filter driving TDF succession.

DISCUSSION

Successional changes of forest structure and regeneration environment

As expected, BA, crown area, and density showed directional developments with time. Although these successional changes can follow individual pathways of development (Chazdon 2008), our results prove that regeneration conditions at a site change predictably with

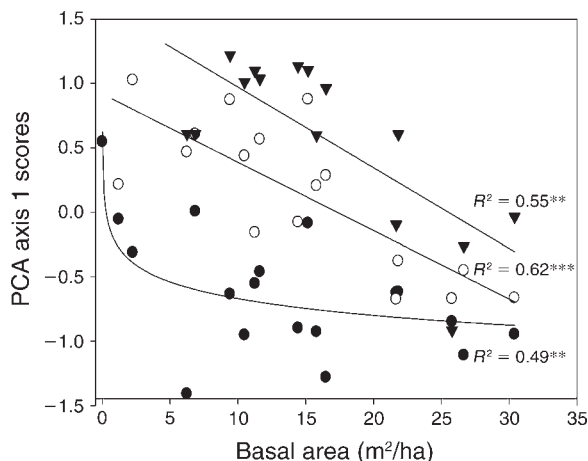


FIG. 5. Community-level abundance-weighted mean of traits (principal components analysis [PCA] axis 1 scores) of the regeneration (solid circles), juvenile (open circles), and adult (solid triangles) communities of secondary forests stands with abandonment times ranging from <1 yr to ~60 yr and a mature forest (basal area ~31 m²) at Nizanda, Mexico, as a function of forest development. Continuous lines represent modeled changes for each community stratum (regeneration, logarithmic model, $R^2 = 0.49$, $P < 0.01$; juvenile, linear model, $R^2 = 0.62$, $P < 0.001$; adult, linear model, $R^2 = 0.55$, $P < 0.01$).

overstory development. Increased crown area enhances absorption of light and, as expected, led to reduced PPFD levels at the forest floor (Fig. 3a). Soil and air temperatures dropped also, as expected (Fig. 3b, d). As leaf area scales positively with BA, BA explained better the temperature changes probably because of the increased reflection and the decreased transmission of infrared radiation with increased stand leaf area and the substantial infrared-reflective properties of wood (Asner 1998). The expected increase in Ψ_m was variable and caused by a few low-density stands (Fig. 3c). Reduced Ψ_m at depths <20 cm are nevertheless common in open areas, even under rainy conditions (e.g., Ashton 1992). The more negative Ψ_m in open early-successional environments result from combined factors such as high evaporation because of high radiation loads and vapor pressure deficits, low water retention capacity of bare or poorly developed soils, and higher exposure to wind desiccation (Ashton 1992, Camargo and Kapos 1995). As hypothesized, from young to old-growth sites, forest structural development creates predictable environmental gradients that go from sunny to shady, hot to cool, and dry to moist.

*Functional traits, environmental change,
and community assembly*

As could be expected from the large differences in abandonment time between fallows (>60 years), the group of common species found in them had different sets of functional traits, which reveals differences in plant strategies (Fig. 4a). The first PCA axis mostly

reflected differences in traits for heat load reduction and water status control (leaf compoundness, slenderness, pulvination, leaf density, and LDMC), while the second PCA axis reflected differences in species drought-coping strategies (cf. Givnish 2002), separating evergreen drought-tolerant species (that are active during the dry season) with high LMA from deciduous drought-avoiding species (that are active only during the rainy season) with low LMA.

The lack of relationship between the scores of the unweighted-average PCA of the RCs with the environmental variables indicates that species with different combinations of traits can persist under the variety of abiotic conditions found along the plots. This implies that species can occur under suboptimal conditions (cf. Pulliam 2000) and/or that community assembly is strongly influenced by propagule dispersal, which produces heterogeneous assemblies by random dispersal (Hubbell 2001) or by competition, which limits the ecological similarity of coexisting species (cf. Weiher et al. 1998, Stubbs and Wilson 2004). However, the abundance-weighted ordination showed groupings of traits that were closely related to light and, primarily, temperature conditions (Figs. 1 and 4b). Community-level patterns of functional-traits convergence occur when abiotic conditions determine establishment success, i.e., filter species according to their functional traits (e.g., Weiher et al. 1998, Holdaway and Sparrow 2006, McGill et al. 2006). Our results hence clearly indicate that environmental filtering makes a difference: only the best suited species are abundant.

Adequate light and water availability do not necessarily guarantee carbon gain under high irradiance; short periods of high evaporative demand or atmospheric drought (i.e., 30–40 min of VPD >3 KPa; cf. average VPD values in *Methods*) may lead to strong reductions of net photosynthesis that parallel the effects of long periods (days) of soil drought (Shirke and Pathre 2004). As VPD increases exponentially with leaf temperature (Lambers et al. 1998), these results imply that plants incapable of keeping low leaf temperatures under high irradiance actually face extended periods of water stress, even if soil water supply is adequate. Accordingly, and as hypothesized, the sunny, hot, and dry early-successional sites in our system were dominated by species with traits that control irradiance load (leaf orientation by pulvinal movement), favor convective over transpirational cooling (compound leaves with small and slender leaflets), and maintain leaf structural integrity and low water potentials under water stress (high leaf density and LDMC; Fig. 4b; Koller 2000, Niinemets 2001, Westoby et al. 2002, Poorter and Markesteijn 2008). Many of these species were N-fixing legumes (with leaves with high N content) capable of photosynthesizing and accumulating biomass at high rates (Wright et al. 2004). These traits further imply that the dominant early-successional species are able to enhance

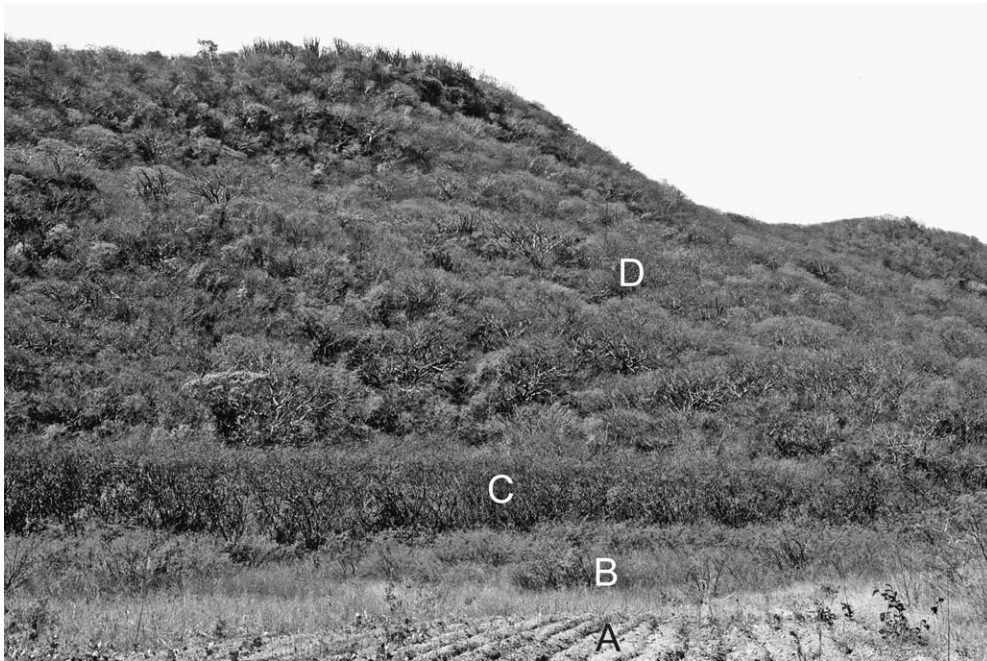


PLATE 1. Early dry season view of a hill in the study area (11 January 2008). Different stages of successional development are represented: (A) a recently cropped field; (B) a recently abandoned field, ca. 1 yr old, dominated by herbs and shrubs; (C) an early successional field, 2-3 yr old, dominated by even-aged legume trees; and (D) an old-growth tropical dry forest of unknown age, characterized by a wider range of growth forms. Photo credits: E. A. Pérez-García.

wet-season carbon gain and hence increase dry-season survival by (1) maximizing the use of high irradiance by keeping favorable photosynthetic leaf temperature and water balances for longer times; (2) avoiding the negative effects on net carbon gain of sharp temperature-induced increments in transpiration and respiration; and (3) enhancing water use efficiency through high-N-content leaves that create steep CO_2 gradients by quickly depleting the internal C concentration (Lambers et al. 1998, Wright et al. 2004).

Under the shady, relatively cool and moist conditions of closed-canopy sites, the RCs were instead dominated by species with simple, large leaves with long petioles (Fig. 4b). Large leaves and long petioles reduce self-shading and enhance light interception per leaf area, which in turn increase net carbon gain under shaded conditions (Falster and Westoby 2003). Evidence of the expected increase of defensive traits with forest development was only found in the increased abundance of plants with exudates.

Although the second PCA axis of community-level traits was not related to the measured environmental variables, it separated RCs with combinations of average traits linked to drought-avoidant and drought-tolerant species, which implies that the RCs were dominated by species of either one strategy or the other. Such variation in dominance might be related to local scale variation in soil nutrient status and deep soil water availability, as deciduous species are favored by drier environments through an increased advantage of

reducing water and carbohydrate losses during dry periods, while evergreen species are favored in nutrient-poor environments through an increased advantage of reducing nutrient losses with leaf shedding (see Givnish 2002).

In addition to the evidence provided by the close link between the environment and the traits of the most successful species in the RC (Fig. 4b), two further facts support that environmental filters and plant traits consistently shape community assembly. First and as expected, JCs of early- to mid-successional fallows (BA $\sim 10\text{--}15\text{ m}^2$) and ACs of mid- to late-successional fallows (BA $\sim 20\text{--}25\text{ m}^2$) have similar average trait values compared to RCs in recently colonized area (BA $\sim 0\text{ m}^2$), suggesting that they passed through similar environmental filters (Fig. 5). Second, regeneration, juvenile, and adult communities converge towards similar community-level average trait values when succession proceeds (Fig. 5).

The rapid shift in the RC attributes implies that the regeneration window for early-successional species is relatively short, just as the open-canopy period with high light (Figs. 3 and 5). Reductions in light availability and temperature during succession are likely to decrease the carbon gain advantage of early dominant species both as a result of a loss in the trait advantages and their intrinsic high costs (Koller 2000, Niinemets 2001, Vitousek et al. 2002, Falster and Westoby 2003). The early dominance and later decrease of legumes with functional traits like ours is common in other secondary

TDFs (Donfack et al. 1995, Pereira et al. 2003, Saynes et al. 2005, Romero-Duque et al. 2007). The gradual decline in air temperature with forest development is paralleled by a gradual increase in dominance of species with simple and large leaves (Figs. 3 and 5), which are typical mature-forest dominants (Pérez-García et al. 2001). Other studies have shown that in temperature and water-stressed systems, the establishment of late-successional species is conditional on facilitation by early-successional species that reduce such abiotic stresses (Holmgren et al. 1997, Aerts et al. 2007) and that seedlings of mature TDF species survive better in shaded than in open sites (e.g., Lieberman and Li 1992, McLaren and McDonald 2003).

In this study, community assembly was best predicted by air temperature (which is strongly related to VPD), rather than by light or Ψ_m as we measured it (Fig. 1). Maximum height, important for the species' competitive performance in systems with stronger vertical light gradients (100–1% PPFD; Thomas 1996, Westoby et al. 2002, Poorter et al. 2006), was therefore irrelevant for succession in this TDF community. Leaf mass per area, another key trait for light competitive performance (Westoby et al. 2002), was only of secondary importance during succession and was linked to drought tolerance rather than to shade tolerance. (See Wright et al. [2005] for changes in the significance of LMA with climate stress.) As species most likely differ in their rooting depths, measurements of Ψ_m in deeper soil layers could have revealed stronger links between Ψ_m and the variation in traits related to avoidance or tolerance of drought (PCA axis 2). Additionally, unmeasured traits, for example, traits related to the plant's water status or to belowground processes, could further play a role in determining community assembly. The stronger correlation of drought tolerance and avoidance with the second and not the first axis of community functional-trait variation is nonetheless consistent with the fact that all species in our system, pioneer or non-pioneer, experience a strong dry season. The key for seedling survival during periods of negative carbon balances produced by resource shortages (like light and water) is previous growth and accumulation of sufficient carbohydrate and water reserves (Lieberman and Li 1992, Lopez and Kursar 2007, Myers and Kitajima 2007). Our results indicate that along the successional gradient, it is especially the interaction between the effects that the environmental conditions (temperature and light) have on plant growth and carbon gain during the rainy season, with its implications for plant survival during the dry season, that determines species establishment success and the relative importance of plant traits.

Final remarks

As hypothesized, successional changes in the forest structure led to predictable changes in the understory

environment, which in turn molded community assembly on the basis of specific plant functional traits. Nevertheless, part of the variation was unexplained, suggesting that other processes such as landscape configuration, disturbance history, biotic interactions, and dispersal limitation, may contribute further to the shaping of community structure. The relative importance of these factors may vary with disturbance intensity. For instance, small-scale disturbances such as forest gap dynamics (more typical in humid forests than in dry forests) will modify the environment only to a limited extent, and under those conditions the role of chance processes (such as advance regeneration and seed dispersal) may become more important for community assembly (Hubbell et al. 1999, Brokaw and Busing 2000, Dalling et al. 2002). Certainly there is much to advance in our understanding of the historical, ecological, and spatial circumstances that alter the relative importance of community structuring factors (e.g., Getzin et al. 2008). This emphasizes the need of conducting empirical studies that incorporate direct measurements of causal factors. By including environmental measurements, our community-level approach allowed the identification of the specific functional traits and environmental factors that are responsible for major ecological responses in an ecosystem and rigorously confirmed that environmental filtering is a fundamental process of community assembly, even in complex systems such as tropical forests.

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APPENDIX

Comparison between PCA results using all measured traits and a subset excluding theoretically interdependent traits (*Ecological Archives* E091-029-A1).