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Successional changes in functional composition contrast for dry and wet tropical forest

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Abstract. We tested whether and how functional composition changes with succession in dry deciduous and wet evergreen forests of Mexico. We hypothesized that compositional changes during succession in dry forest were mainly determined by increasing water availability leading to community functional changes from conservative to acquisitive strategies, and in wet forest by decreasing light availability leading to changes from acquisitive to conservative strategies. Research was carried out in 15 dry secondary forest plots (5–63 years after abandonment) and 17 wet secondary forest plots (<1–25 years after abandonment). Community-level functional traits were represented by community-weighted means based on 11 functional traits measured on 132 species. Successional changes in functional composition are more marked in dry forest than in wet forest and largely characterized by different traits. During dry forest succession, conservative traits related to drought tolerance and drought avoidance decreased, as predicted. Unexpectedly acquisitive leaf traits also decreased, whereas seed size and dependence on biotic dispersal increased. In wet forest succession, functional composition changed from acquisitive to conservative leaf traits, suggesting light availability as the main driver of changes. Distinct suites of traits shape functional composition changes in dry and wet forest succession, responding to different environmental filters.

Key words: acquisitive traits; community-weighted mean; conservative traits; dry deciduous forest; Mexico; secondary succession; wet evergreen forest.

Introduction

Secondary succession is community assembly in action (Lebrija-Trejos et al. 2010). Species replacement during secondary succession is often explained in terms of species' adaptations to changing light environments (e.g., Bazzaz and Pickett 1980), reflecting a trade-off in plant design. Fast-growing species with a rapid acquisition of resources thrive at the rich light environment of early-successional stages, while slow-growing species that conserve resources dominate under the poor light environment of late-successional stages (Reich et al. 2003, Poorter et al. 2004). This trade-off in plant design is maintained across different geographic regions and is consistent across floras, life forms, and phylogenetic groups (Díaz et al. 2004, Wright et al. 2004).

In reality, the acquisitive-conservative trade-off points to the extremes of a continuum in plant strategies and a species' position along this continuum can be quantified by its functional traits (Wright et al. 2004). In this study, we focus on 11 leaf, stem, whole-plant, and regenerative traits that are important for light acquisition, carbon gain, stress resistance (heat, drought, shade), resource conservation, dispersal, and establishment (see Appendix: Table A1).

Leaf traits run from cheap, short-lived leaves with high assimilation rates on the acquisitive end of the spectrum to tough, resistant leaves that have long leaf

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lifespans on the conservative end (Wright et al. 2004). Acquisitive leaf traits include long petioles (Takenaka 1994), large leaf laminas (Bazzaz and Pickett 1980), high specific leaf area (SLA; Poorter et al. 2009) and compound leaves (Niinemets 1998). Conservative leaf traits include high leaf dry matter content (LDMC), leaf density, and leaf thickness (Reich et al. 1991, Kitajima and Poorter 2010).

The acquisitive-conservative continuum for stem traits runs from cheap-to-construct, low-density wood, facilitating high volumetric stem growth rates, to high-density wood, facilitating stem protection, and hence, high survival rates (Chave et al. 2009). Deciduous species are conservative since they efficiently reabsorb nutrients before shedding the leaves (Aerts 1996, Givnish 2002); moreover, deciduousness is a good predictor of drought survival (Poorter and Markesteijn 2008). Seed size and biotic dispersal are good indicators of per-capita reproductive effort (Dalling and Hubbell 2002). Early-successional species produce many small seeds and late-successional species few large seeds (e.g., Foster and Janson 1985) that are more often animal dispersed, enhancing directed dispersal to safe sites (Jansen et al. 2008).

Studies on successional change from acquisitive to conservative strategies have been mainly conducted in tropical wet forests, where species assemble along a gradient of decreasing light availability (e.g., Kobe 1999, Montgomery and Chazdon 2002). This classical idea may not hold for tropical dry forests where light is not a major limiting resource for plant performance since these forests are less stratified and species are short statured (Lebrija-Trejos et al. 2008). During tropical dry forest succession, conditions change from dry and hot to relatively moister and cooler environments (Lebrija-Trejos et al. 2011, Pineda-García et al. 2013). Early-successional species have better drought-coping strategies and enhanced water use efficiency compared to late-successional species (Lebrija-Trejos et al. 2010, Alvarez-Añorve et al. 2012). Dry forest species may therefore experience highly stressful conditions during the dry and hot early stages of succession, and wet forest species during the shaded late stages of succession. Therefore, in dry forests, we expect that species occurring at early stages of succession have conservative strategies whereas those occurring at late-successional stages have acquisitive strategies, based on increasing water availability. In contrast, we expect that in tropical wet forests early-successional species are acquisitive and late-successional species are conservative, based on decreasing light availability. These expectations hold for leaf, stem, and whole-plant traits that reflect the use and conservation of internal resources and depend on the resources available (light, water). Traits related to the regenerative phase are largely decoupled from those related to the established phase (Grime et al. 1997). We expect both dry and wet forest successional changes to reflect increased importance of per capita reproductive effort indicated by large seeds and animal dispersal, because small-seeded, wind-dispersed species are favored in open (recently abandoned) sites (Hammond and Brown 1995) and because of increased abundance of potential dispersers with succession.

To test these predictions, we analyze how 11 functional traits measured on 132 species in dry and wet tropical forest change with secondary succession.

METHODS

Research locations

Tropical dry forest originally covered about 17.1% of Mexico's land cover, and is presently reduced to 11.3%, of which roughly two-thirds is secondary forest (Challenger and Soberón 2008). Dry forest research plots were established close to the village of Nizanda on the Pacific slope of the Tehuantepec Isthmus in Oaxaca, southern Mexico (16°39′ N, 95°00′ W). Mean annual temperature is 26°C and mean annual precipitation is 900 mm, of which over 90% is concentrated between late May and mid-October (Lebrija-Trejos et al. 2008). The vegetation is predominantly tropical dry deciduous forest, characterized by a low canopy stature (~7 m tall) with a high biodiversity (Pérez-García et al. 2001, 2010). The 15 secondary forest plots (900 m^2 each) with different fallow ages (5–63 yr) are established on abandoned maize fields. Within each plot, four parallel 5 × 20 m transects were established, further divided into four 5 × 5 m sub-quadrats. In one sub-quadrat all individuals with dbh $\geq$1 cm were identified and measured, in a second all individuals with dbh $\geq$2.5 cm and in the remaining two all individuals with dbh $\geq$5 cm. Species-level variables were scaled up according to sampling effort per size class (see also Lebrija-Trejos et al. 2008).

Tropical wet forest originally covered about 9.1% of Mexico's land cover, and is presently reduced to 4.8%, of which two-thirds is secondary forest (Challenger and Soberón 2008). Wet forest research plots were established close to the village of Loma Bonita, in Marqués de Comillas, Chiapas, southeastern Mexico (16°01′ N, 90°55′ W). Mean annual temperature is 24°C and mean annual precipitation is 3000 mm, with a dry period (<100 mm/month) from February through April (van Breugel et al. 2006, 2007). The research area is characterized by small hills and valleys with sandy or limestone soils of low pH (<5.5). The 17 secondary forest plots (1000 m^2 each) with different fallow ages (<1–25 yr) were established on abandoned maize fields. Each plot was divided into two 10 × 50 m subplots. In one subplot, all individuals with dbh $\geq$1 cm were identified and measured, in the second, all individuals of dbh $\geq$5 cm were identified and measured. Again, species variables were scaled up according to sampling effort per size class.

Functional traits

A total of 132 species were evaluated: 51 dry forest species and 81 wet forest species. Those species that made up at least 80% of the basal area in the plots were selected (excluding cacti in dry forest, as functional traits are hard to compare) because they accurately describe the community-weighted mean (Garnier et al. 2004, Pakeman and Quested 2007). Seven leaf traits, one stem trait, one whole-plant trait, and two regenerative traits were considered that are important for the carbon, water, and nutrient balance of plants. Traits were measured following standardized protocols (Cornelissen et al. 2003; for a detailed description of the methods for each trait, see the Appendix). Traits were measured in the study areas on 5–10 individuals per species, with the exceptions of wood density (where, for wet forest, 15 of the 81 species were taken from comparable Mexican ecosystems), and the binary traits leaf compoundness, deciduousness, and dispersal syndrome (which were scored based on field observations, local informants, herbaria, and literature). In wet forest, data for some species for seed volume (14 species) and dispersal type (13 species) were missing and average wet forest trait values were used in the analyses; these missing values made up for an average of 6% of the total basal area (range 0–8.7%) in the case of seed volume and 2% (range 0–29%) in the case of dispersal type.

Species' average trait values were used although we recognize that intraspecific trait variation may play an important role in species adaptation along environmental gradients. Considering the extensive species-level trait data set available (132 species) and the high species turnover during succession, for the purpose of this research we consider the use of species average trait values legitimized.

Statistical analysis

Each functional trait is scaled up from species level to community level using the community-weighted mean (CWM; Garnier et al. 2004, Lavorel et al. 2007), a parameter that can be seen as the functional value of an average plant from the community. It is calculated as

$$\mathrm{CWM} = \sum_{i=1}^{S} w_i \times x_i$$

where S is the total number of species, w_i is the relative basal area of the ith species, and x_i is the trait value of the ith species. The relative basal area is used, rather than abundance, because it reflects the species' biomass, an indicator of plant performance and adaptation to local conditions. This is a species' relative contribution to the functional spectrum available in each plot (which is at least 80% of total basal area in a plot).

Regression analysis was used to relate CWM trait values with the successional age (years after abandonment of maize field) and the stand basal area (which is a structural variable of succession; including cacti in dry forest). Stand basal area is logarithmically related to age in both forest types (Appendix: Fig. A1). Statistical analyses were carried out using R v. 2.13.1 (R Development Core Team 2011).

RESULTS

The dry forest showed clear community-level functional trait changes with succession: many traits (8 out of 11) directionally changed, with similar patterns for stand basal area and age (Fig. 1, Appendix: Table A2). Traits related to large and efficient leaf display (specific leaf area [SLA]), wood density, and the proportion of plants with compound and deciduous leaves decreased with succession. Leaf thickness, seed volume, and proportion of biotic seed dispersal increased with succession.

In wet forest, only four traits changed directionally (Fig. 1, Table A2) of which one trait only responded to age (leaf thickness), and others only to stand basal area (LDMC, leaf density), with SLA responding to both. Only leaf traits changed with succession; SLA decreased whereas LDMC and leaf density increased with stand basal area. Leaf thickness increased with age (Table A2).

DISCUSSION

In both forest types, the functional composition of the community changes with succession, though distinct suites of traits matter for dry and wet forest succession. More traits changed during dry forest succession compared to wet forest succession. This may partly be due to the length of the chronosequence, which is notably longer in dry forest (5–63 yr after abandonment) than in wet forest (<1–25 yr). Despite the relatively short sequence for wet forest, we do think that the most important changes are captured, as high rates of species turnover as well as rapid changes in species and functional diversity have been shown to take place in early successional stages (i.e., the first two decades; van Breugel et al. 2006, 2007, Lohbeck et al. 2012).

Dry forest succession.—We predicted that, during tropical dry forest succession, there is a shift from early-successional species with conservative traits to cope with the harsh, dry, and hot environment, toward late-successional species with acquisitive traits that benefit from the higher water availability and the cooler environment. We partially found decreases in the conservative strategy; wood density decreased with succession but LDMC and leaf density did not. Wood density limits volumetric growth and reflects resistance to drought (Poorter and Markesteijn 2008) and the need for being drought resistant is greater at early-successional stages where soil water potential is lower (Lebrija-Trejos et al. 2011, but see Pineda-García et al. 2013). Remarkably, SLA and leaf area decreased with succession, against expectations, as high values of these traits are generally associated with high resource conditions (Poorter et al. 2009). Including a gradient of deciduousness, number of months without leaves (Méndez-Alonzo et al. 2012), and rooting depths may reveal how species

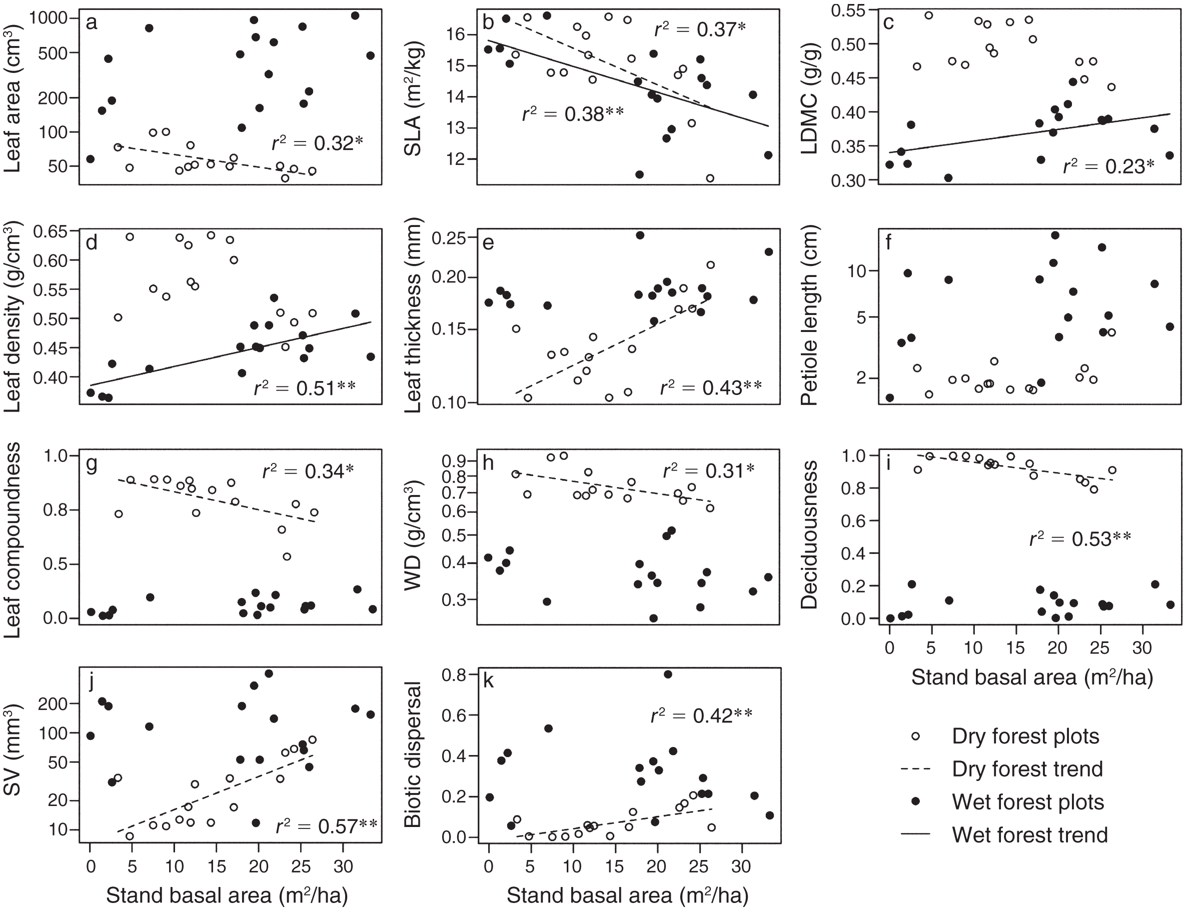

FIG. 1. Changes in community-weighted mean trait values (weighted by relative basal area) against stand basal area (structural variable of succession) in successional dry (open symbols, $N = 15$ plots) and wet (solid symbols, $N = 17$ plots) forest plots in southern Mexico. Regression lines (broken in dry forest, continuous in wet forest) and coefficients of determination are given, in the case of significant relationships. In the case of the binary variables leaf compoundness, deciduousness, and biotic dispersal, the value 1 represents compound leaves, deciduous leaf habit, and biotically dispersed seeds, respectively. Abbreviations are LDMC, leaf dry matter content; SLA, specific leaf area; WD, wood density; SV, seed volume.

* $P < 0.05$; ** $P < 0.01$.

with large and cheap leaves are able to prosper in these dry early-successional sites (cf. Pineda-García et al. 2013).

The small increase in relative abundance of evergreen species with succession (note that deciduous species dominate throughout the successional gradient) was in line with expectations, as the forests become denser, close their canopy, hold more humidity, and the soil water content increases (Lebrija-Trejos et al. 2011). This confirms previous studies showing that deciduousness is especially important during the extra-dry environments in early-successional stages (Pineda-García et al. 2013). Also the importance of having compound leaves decreased with succession: additional to the ability of some species to avoid desiccation by folding leaflets, compound leaves are able to drop individual leaflets rather than the whole leaf thereby fine-tuning leaf area under drought stress (Poorter and Markesteijn 2008). Leaf thickness increased with dry forest succession, as in wet forest succession (only with time after abandonment; Appendix: Table A2). Thick leaves mostly have higher stomatal density (but see Bongers and Popma 1990) and lower chlorophyll contents (Loranger and Shipley 2010), are expensive to construct and associated with longer leaf lifespans (Reich et al. 1991; but see Kitajima et al. 2012). Lastly the importance of species that depend on animals for seed dispersal increases with tropical dry forest succession, as does the volume of the seeds. This confirms that early-successional species invest in many small seeds that can travel large distances (e.g., by wind), whereas late-successional species invest in fruits that attract biotic dispersers to allow directional dispersal.

Wet forest succession.—We predicted that during tropical wet forest succession there is a shift from early-successional species with acquisitive strategies toward late-successional species with conservative strategies to cope with the low light conditions. We indeed found the acquisitive trait SLA to decrease with succession and the conservative traits leaf density, LDMC, and leaf thickness to increase with succession, confirming earlier results from other vegetation types (Garnier et al. 2004, Kahmen and Poschlod 2004, Dahlgren et al. 2006). Remarkably, only leaf traits showed significant changes. These clear changes from an acquisitive to a conservative strategy show that the leaf economics spectrum plays an important role in species turnover during tropical wet forest succession, and suggests light availability to be one of the main drivers of species turnover. Community traits related to reproductive strategies, wood density, and deciduousness showed no directional changes with succession. The lack of a role for wood density is surprising, given the fact that the biomass proportion of high wood density trees increases with succession (Brown and Lugo 1990) and that it is one of the best predictors for growth and survival of wet forest species (Poorter et al. 2008, Wright et al. 2010). The proportion of deciduous species does not change during wet forest succession, likely because deciduousness is a rare ($<10\%$ of the wet forest species is deciduous) and a maladaptive strategy in extremely wet conditions. Surprisingly, we found no increase in biotically dispersed trees for wet forest. In our plots, biotic dispersal is common throughout the successional gradient (Fig. 1k), in line with previous studies (Young et al. 1987). We therefore hypothesize that, instead of changes from abiotic to biotic dispersal, changes in animal dispersal groups could play an important role during wet forest succession.

Of the 11 traits studied, only one trait was irrelevant to both successional gradients (petiole length). Two traits (SLA and leaf thickness) showed community-level changes during succession in both forest types, following the same direction. This indicates that SLA is a crucial trait for secondary succession and may be applicable across vegetation types (cf. Garnier et al. 2004, Poorter et al. 2009). A similar argument can be given for leaf thickness although due to the uncertainties in its functional role (mainly its relation to the leaf economics spectrum) we argue that this needs further study. Most traits are either related to dry forest succession (leaf area, leaf compoundness, wood density, deciduousness, biotic dispersal, seed volume) or to wet forest succession (LDMC, leaf density).

This study shows that secondary succession directionally changes functional composition in two contrasting tropical forest types that differ strikingly in their annual precipitation, but largely distinct suites of traits matter for dry and wet forest succession. Dry forest trait changes can be partially explained by water limitations in early succession. In wet forest succession, community functional composition changed from acquisitive to conservative leaf traits, suggesting decreasing light availability to be the main driver.

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Literature Cited

Aerts, R. 1996. Nutrient resorption from senescing leaves of perennials: Are there general patterns? Journal of Ecology 84: 597–608.

Alvarez-Añorve, M. Y., M. Quesada, G. A. Sánchez-Azofeifa, L. D. Avila-Cabadilla, and J. A. Gamon. 2012. Functional regeneration and spectral reflectance of trees during succession in a highly diverse tropical dry forest ecosystem. American Journal of Botany 99:816–826.

Bazzaz, F. A., and S. T. A. Pickett. 1980. Physiological ecology of tropical succession: a comparative review. Annual Review of Ecology and Systematics 11:287–310.

Bongers, F., and J. Popma. 1990. Leaf characteristics of the tropical rain forest flora of Los Tuxtlas, Mexico. Botanical Gazette 151:354–365.

Brown, S., and A. E. Lugo. 1990. Tropical secondary forests. Journal of Tropical Ecology 6:1–32.

Challenger, A., and J. Soberón. 2008. Los ecosistemas terrestres. Pages 87–108 *in* Capital natural de México, vol 1: Conocimiento actual de la biodiversidad. Conabio, México, D.F., Mexico.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. Ecology Letters 12:351–366.

Cornelissen, J. H. C., et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335–380.

Dahlgren, J. P., O. Eriksson, K. Bolmgren, M. Strindell, and J. Ehrlén. 2006. Specific leaf area as a superior predictor of changes in field layer abundance during forest succession. Journal of Vegetation Science 17:577–582.

Dalling, J. W., and S. P. Hubbell. 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. Journal of Ecology 90:557–568.

Díaz, S., et al. 2004. The plant traits that drive ecosystems: evidence from three continents. Journal of Vegetation Science 15:295–304.

Foster, S., and C. H. Janson. 1985. The relationship between seed size and establishment conditions in tropical woody plants. Ecology 66:773–780.

Garnier, E., et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85:2630–2637.

Givnish, T. J. 2002. Adaptive significance of evergreen vs deciduous leaves: solving the triple paradox. Silva Fennica 36:703–734.

Grime, J. P., et al. 1997. Integrated screening validates primary axes of specialisation in plants. Oikos 79:259–281.

Hammond, D. S., and V. K. Brown. 1995. Seed size of woody plants in relation to disturbance, dispersal, soil type in wet Neotropical forests. Ecology 76:2544–2561.

Jansen, P. A., F. Bongers, and P. J. van der Meer. 2008. Is farther seed dispersal better? Spatial patterns of offspring mortality in three rainforest tree species with different dispersal abilities. Ecography 31:43–52.

Kahmen, S., and P. Poschlod. 2004. Plant functional trait responses to grassland succession over 25 years. Journal of Vegetation Science 15:21–32.

Kitajima, K., A.-M. Llorens, C. Stefanescu, M. V. Timchenko, P. W. Lucas, and S. J. Wright. 2012. How cellulose-based leaf toughness and lamina density contribute to long leaf lifespans of shade-tolerant species. New Phytologist 195:640–652.

Kitajima, K., and L. Poorter. 2010. Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. New Phytologist 186: 708–721.

Kobe, R. K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. Ecology 80:187–201.

Lavorel, S., K. Grigulis, S. McIntyre, N. S. G. Williams, D. Garden, J. Dorrough, S. Berman, F. Quétier, A. Thébault, and A. Bonis. 2007. Assessing functional diversity in the field—methodology matters! Functional Ecology 22:134–147.

Lebrija-Trejos, E., F. Bongers, E. A. Pérez-García, and J. A. Meave. 2008. Successional change and resilience of a very dry tropical deciduous forest following shifting agriculture. Biotropica 40:422–431.

Lebrija-Trejos, E., E. A. Pérez-García, J. A. Meave, F. Bongers, and L. Poorter. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. Ecology 91:386–398.

Lebrija-Trejos, E., E. A. Pérez-García, J. A. Meave, L. Poorter, and F. Bongers. 2011. Environmental changes during secondary succession in a tropical dry forest in Mexico. Journal of Tropical Ecology 27:477–489.

Lohbeck, M., L. Poorter, H. Paz, L. Pla, M. van Breugel, M. Martínez-Ramos, and F. Bongers. 2012. Functional diversity changes during tropical forest succession. Perspectives in Plant Ecology, Evolution and Systematics 14:89–96.

Loranger, J., and B. Shipley. 2010. Interspecific covariation between stomatal density and other functional leaf traits in a local flora. Botany 88:30–38.

Méndez-Alonzo, R., H. Paz, R. C. Zuluaga, J. A. Rosell, and M. Olson. 2012. Coordinated evolution of leaf and stem economics in tropical dry forest trees. Ecology 93:2397–2406.

Montgomery, R., and R. Chazdon. 2002. Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. Oecologia 131:165–174.

Niinemets, Ü. 1998. Are compound-leaved woody species inherently shade-intolerant? An analysis of species ecological requirements and foliar support costs. Plant Ecology 134:1–11.

Pakeman, R. J., and H. M. Quested. 2007. Sampling plant functional traits: What proportion of the species need to be measured? Applied Vegetation Science 10:91–96.

Pérez-García, E. A., J. A. Meave, and C. Gallardo. 2001. Vegetación y flora de la región de Nizanda, Istmo de Tehuantepec, Oaxaca, México. Acta Botanica Mexicana 56: 19–88.

Pérez-García, E. A., J. A. Meave, J. Villaseñor, J. Gallardo-Cruz, and E. Lebrija-Trejos. 2010. Vegetation heterogeneity and life-strategy diversity in the flora of the heterogeneous landscape of Nizanda, Oaxaca, Mexico. Folia Geobotanica 45:143–161.

Pineda-García, F., H. Paz, and F. C. Meinzer. 2013. Drought resistance in early and late secondary successional species from a tropical dry forest: the interplay between xylem resistance to embolism, sapwood water storage and leaf shedding. Plant, Cell and Environment 36:405–418.

Poorter, H., Ü. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist 182: 565–588.

Poorter, L., and L. Markesteijn. 2008. Seedling traits determine drought tolerance of tropical tree species. Biotropica 40:321–331.

Poorter, L., M. van de Plassche, S. Willems, and R. G. A. Boot. 2004. Leaf traits and herbivory rates of tropical tree species differing in successional status. Plant Biology 6:746–754.

Poorter, L., et al. 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. Ecology 89:1908–1920.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Reich, P. B., C. Uhl, M. B. Walters, and D. S. Ellsworth. 1991. Leaf lifespan as a determinant of leaf structure and function among 23 Amazonian tree species. Oecologia 86:16–24.

Reich, P. B., I. J. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation: traits, spectra, and strategies. International Journal of Plant Sciences 164:S143–S164.

Takenaka, A. 1994. Effects of leaf blade narrowness and petiole length on the light capture efficiency of a shoot. Ecological Research 9:109–114.

van Breugel, M., F. Bongers, and M. Martínez-Ramos. 2007. Species dynamics during early secondary forest succession: recruitment, mortality and species turnover. Biotropica 39: 610–619.

van Breugel, M., M. Martínez-Ramos, and F. Bongers. 2006. Community dynamics during early secondary succession in Mexican tropical rain forests. Journal of Tropical Ecology 22:663–674.

Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Wright, S. J., et al. 2010. Functional traits and the growth–mortality trade-off in tropical trees. Ecology 91:3664–3674.

Young, K. R., J. J. Ewel, and B. J. Brown. 1987. Seed dynamics during forest succession in Costa Rica. Plant Ecology 71: 157–173.

SUPPLEMENTAL MATERIAL

Appendix

Additional details on functional traits, methods, and results. (*Ecological Archives* E094-109-A1).