Individual Canopy-tree Species Effects on Their Immediate Understory Microsite and Sapling Community Dynamics

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ABSTRACT

Canopy trees are largely responsible for the environmental heterogeneity in the understory of tropical and subtropical species-rich forests, which in turn may influence sapling community dynamics. We tested the effect of the specific identity of four cloud forest canopy trees on total solar radiation, canopy openness, soil moisture, litter depth, and soil temperature, as well as on the structure and dynamics of the sapling community growing beneath their canopies. We observed significant effects of the specific identity of canopy trees on most understory microenvironmental variables. Soil moisture was higher and canopy openness lower beneath *Cornus disciflora*. In turn, canopy openness and total solar radiation were higher beneath *Oreopanax xalapensis*, while the lowest soil moisture occurred beneath *Quercus laurina*. Moreover, *Chiranthodendron pentadactylon* was the only species having a positive effect on litter depth under its canopy. In spite of these between-species environmental differences, only *C. pentadactylon* had significant, negative effects on sapling density and species richness, which may be associated to low seed germination and seedling establishment due to an increased litter depth in its vicinity. The relevance of the specific identity of canopy trees for natural regeneration processes and species richness maintenance depends on its potential to differentially affect sapling dynamics through species-specific modifications of microenvironmental conditions.

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Key words: canopy openness; cloud forest; forest regeneration; litter depth; sapling density; soil moisture; species richness; specific identity.

NATURAL FOREST REGENERATION IS ONE OF THE DRIVING MECHANISMS influencing community diversity maintenance. Several authors have emphasized the need to examine this process in the context of environmental heterogeneity and heterospecific replacement of individuals (Nicotra *et al.* 1999, Bellingham & Tanner 2000, Webb & Peart 2000, Harms *et al.* 2001). Research that fully incorporates the analysis of such heterogeneity, however, and examines its causes and its role in community diversity maintenance is still scanty (Hutchings *et al.* 2000, Beckage & Clark 2003, Potts *et al.* 2004).

Vegetation structure and composition at present are largely the products of the different processes that take place during forest regeneration (Hartshorn 1980, Runkle 2000). Newly established seedlings and young saplings in a forest understory face a much heterogeneous environment across space (Hurtt & Pacala 1995, Aiba *et al.* 2004, Queenborough *et al.* 2007b). The prevailing microenvironmental conditions during the early life of a canopy tree affect the probability of such tree eventually reaching the canopy or of dying before succeeding (Augspurger 1984, Spies & Turner 1999, Poorter 2007). Many forest dynamics studies that have analyzed environmental heterogeneity have related such variation to the opening of canopy gaps, which often modifies profoundly the understory environment (Grant 1997, Denslow *et al.* 1998, Arriaga 2000, Aiba *et al.* 2004). There is increasing recognition, however, that some features of the community's overstory such as tree density, size, or shape, may also have similar effects (Tremmel & Bazzaz 1993, Montgomery & Chazdon 2001, Acevedo *et al.* 2003). The

known effects of canopy trees on the understory microenvironment are complex and include local modifications of light quality and quantity, air temperature and relative humidity, and soil properties including fertility, soil structure, litter characteristics, and water contents (Molofsky & Augspurger 1992, LePage *et al.* 2000, Acevedo *et al.* 2003, Becerra *et al.* 2004, Ayres *et al.* 2009). The overall microenvironmental effects of canopy trees may also differentially limit the germination success of seeds newly arrived in the area (Hurtt & Pacala 1995; Schupp 1995; Gray & Spies 1996; Hubbell *et al.* 1999, 2001; Pearson *et al.* 2003). Studies on the regeneration niches (*sensu* Grubb 1977) of tree species have found large between-species differences in this regard (Webb & Peart 2000, Yamada *et al.* 2006, Queenborough *et al.* 2007a, Russo *et al.* 2008).

The recognition of the specific identity of canopy trees as an ecological factor in the study of forest dynamics offers interesting new perspectives. For example, by using the species of canopy trees as a reference, one may be able to detect more readily the degree of heterogeneity in a forest understory or to assess to what extent this factor interacts with baseline heterogeneity, given the potential of each species to maintain the existing environmental conditions or to transform them, creating new ones (Pickett *et al.* 2000). Also, this approach may help to gain insight on the potential interactions experienced by propagules deposited under the canopies of different species (Hurtt & Pacala 1995, Harms *et al.* 2001). In this context, the case of Mesoamerican cloud forests is particularly interesting, as these communities host complex mixtures of tree species with different ecological affinities, including those with lowland tropical forests and temperate forests of higher altitudes and latitudes (Rzedowski 1978). These varying ecological affinities are related to different morphologies, leaf phenologies, and functional

patterns (*e.g.*, Arriaga 1988, Williams-Linera 1997, Saldaña-Acosta *et al.* 2008), which further suggests the possibility that the different canopy-tree species could make a significant contribution to the heterogeneity of the regeneration microsites associated to them.

The aim of the present study was to test the hypothesis that the effects of cloud forest canopy trees on the regeneration processes are species-specific due to the differential abilities of the species to shape the regeneration microsites. The specific goals were the following: (1) to analyze the effects of the specific identity of canopy individual trees on total solar radiation, percent canopy openness, percent soil moisture, litter depth, and soil temperature; (2) to assess the effects of the specific identity of trees on seedling community structure and dynamics; and (3) to determine whether the species effect remains the same throughout the year, considering the seasonal variation of the habitat.

MATERIALS AND METHODS

STUDY AREA.—The study was conducted in a cloud forest in Santo Tomás Teipan (hereafter Teipan), Oaxaca state, southern Mexico (16°15′ N; 95°58′ W; 2400 m asl), which occurs across an elevational range from 2200 to 2500 m. Yearly total rainfall in this area ranges between 1400 and 1500 mm, and mean annual temperature is *ca* 12.3°C (Instituto de Geografía, Universidad Nacional Autónoma de México [IG-UNAM] 1970, García 2004). Mean temperature for the coldest month (January) is 8°C, and for the hottest one (May) is 26°C; the highest and lowest temperature extremes recorded in the region are -4°C and 32°C, respectively (IG-UNAM 1990). In Teipan the climate is considerably seasonal, with 96.8 percent of total annual rainfall concentrating between May and October (Mejía-Domínguez *et al.* 2004).

FIELD SURVEY.—Fieldwork was conducted in a 1-ha permanent plot that was first established in 2002, located *ca* 1 km north from Teipan, on the lower slope of Mt. Calabazo (Mejía-Domínguez *et al.* 2004). The lowest elevation in the plot (the NW corner) is 2300 m, and the highest point is 60 m higher. In this plot, the dynamics (survivorship, recruitment, and mortality) of the forest canopy (trees with dbh ≥ 2.5 cm) was monitored yearly between 2002 and 2007.

In May 2007, 153 1-m^2 quadrats were established and permanently marked with metal stakes throughout the large plot. These quadrats were located either in areas under the single influence of the crowns of one of four selected canopy species (listed below), or in areas of mixed canopy influence, where no single-species effect could be identified. Areas under mixed canopies only containing the four focal species in any combination were discarded, *i.e.*, areas of mixed influence always included several of the remaining species forming part of the canopy in this forest (Mejía-Domínguez *et al.* 2004). We produced a map of the 1-ha plot showing potential locations for 1-m^2 quadrats, considering the desired condition, based on crown projections of all canopy trees with heights ≥ 10 m (up to 35 m) measured in the first forest census; in the field we verified that the quadrats met unambiguously the selection criterion. Between-plot independence was maximized by incorporating areas as much as possible located under different individuals and in different sectors of the plot.

The cloud forest of Teipan has a relatively simple vertical structure. Under the largest canopy trees, there is one readily distinguishable subcanopy layer of low trees (5–10 m in height), strongly dominated by two species (*Psychotria galeottiana* and an as yet undescribed *Miconia* species). They occur everywhere together in the 1-ha plot, and show a significant positive association between them (Mejía-Domínguez *et al.* 2004). Their joint occurrence results in a homogenous light attenuation across space. This situation justifies ascribing understory environmental differences mainly to canopy trees (10–35 m in height), which account for *ca* 87 percent of total community crown cover. The relatively little overlap between the crowns of different canopy species enabled us to identify areas that were almost exclusively influenced by a single species.

The selection of canopy species for examining their specific effects (specific identity [SI]) on understory environment and dynamics was based mostly on their relative importance values (RIV) (*i.e.*, the sum of their relative frequencies, densities, and basal areas) in the canopy; additionally, the selection was also based on some physiognomic traits such as leaf form and crown geometry. The following canopy species were chosen: (1) *Cornus disciflora* DC. (Cornaceae), which had the highest RIV in every previous census; (2) *Quercus laurina* Bonpl. (Fagaceae), which always had the second largest RIV and the second largest cover despite a low density; (3) *Oreopanax xalapensis* (Kunth) Decne. & Planch. (Araliaceae), a species ranking sixth in RIV among canopy trees, but first in the understory community; and (4) *Chiranthodendron pentadactylon* Larreat. (Sterculiaceae), a species ranking eighth according to RIV but of interest due to its potential effect on the light environment and litter properties under its crowns, as it is the tree species with the largest leaves in this forest. Hereafter, these species will be referred by their generic epithets only.

The selected species differ in several attributes with potential effects on the environment under their canopies (Table 1). Two of the four species are deciduous (or nearly), whereas the other two are evergreen: *Cornus* remains completely leafless, while *Quercus* retains some of its hard, sclerophyllous leaves during the dry season. The two evergreen species also differ in their phenological behavior, as *Chiranthodendron* sheds leaves continuously throughout the year but *Oreopanax* does not. Moreover, *Quercus* has the deepest crowns, in contrast to the very flat crowns of *Cornus* and *Chiranthodendron*. Leaf size, a trait related both to litter accumulation on the soil and canopy openness, also differs greatly among species, with *Chiranthodendron* and *Oreopanax* having much larger leaves than the other two. The crowns of *Cornus* and *Oreopanax* are evidently more open than those of *Quercus* and *Chiranthodendron*, apparently because of a prevalence of orthotropic branches in the former vs. a larger proportion of plagiotropic branches in the latter, but this architectural trait has not been formally assessed. These differences in crown architecture may not be related to a differential light interception only, but also to the particular proportions of throughflow and stemflow for each species, and consequently their abilities to funnel water into their surrounding soils (Loustau *et al.* 1992, Park & Cameron 2008).

TABLE 1. *Characteristics of the four selected canopy tree species. Shown values are those recorded in a 1-ha plot in Teipan, Mexico. Leaf length includes both leaf blade and petiole.*

Species	Maximum height (m)	Leaf phenology	Mean crown depth (m)	Maximum crown depth (m)	Leaf length (cm)
Cornus disciflora	27	Deciduous	5.5	10.0	4–5
Quercus laurina	35	Subdeciduous	7.0	13.0	6–7
Oreopanax xalapensis	26	Evergreen	5.0	12.5	15–16
Chiranthodendron pentadactylon	26	Evergreen	5.3	10.3	14–15

Every sapling of tree and shrub species with a height $\leq 50\,cm$ and lacking cotiledonary leaves occurring in the 153 plots was individually marked with aluminum tags, and its height (to stem apex) and cover (two perpendicular diameters) were measured. Additionally, their exact location in the quadrat was recorded on a grid to the nearest centimeter; this information was used in subsequent surveys to verify the fate of each plant. Subsequently, seedlings were surveyed at 3 mo intervals (August and November 2007, and February and May 2008) until data for an entire yearly cycle were gathered. Newly recruited saplings, *i.e.*, those already fulfilling the inclusion criteria, were tagged and measured, and their locations noted.

In addition to assessing seedling community structure and dynamics, at each census we also measured three soil variables in each quadrat (the first two at a depth of 20 cm): (a) percent relative soil moisture (Aquaterr T-300, Aquaterr Instruments and Automation LLC, Costa Mesa, California, USA), (b) soil temperature (Aquaterr T-300), and (c) litter depth (flexometer, to the nearest mm). Concurrently, hemispherical photographs were taken horizontally 1 m above the ground at the center of each quadrat (Nikon Coolpix 990 digital camera and an 8-mm FC-E8 fisheye lens); percent canopy openness and total solar radiation for 3-mo periods were estimated from the photographs with the gap light analyzer (GLA) software (Frazer *et al.* 1999). Photographs were taken near ground level because we were interested in characterizing the light environment of the understory, where seedling establishment and initial sapling growth occurs, but not in potential differences at other heights through the forest profile that could not be perceived by such small plants.

DATA ANALYSIS.—In order to discard potential site-specific effects unrelated to the main investigated factor (SI), we used a generalized linear model (GLM) and an analysis of deviance to test for differences in slope inclination (arcsine transformed) between quadrats associated to the different specific identities.

Sapling density was estimated as the number of saplings per 1-m² quadrat, and percent cover of this community (hereafter referred to simply as cover) as the percentage of area (m²) covered by saplings in the same area. Species richness was defined as the number of species per quadrat. We assessed seedling community dynamics by estimating mortality (M) and recruitment (R) rates with the following equations (Sheil 1995, 2001):

$$M = \{1 - [(N_0 - m)/N_0]^{1/(\Delta t)}\} \times 100,$$

$$R = \{[(N_0 + r)/N_0]^{1/(\Delta t)} - 1\} \times 100,$$

where N_0 is the initial density, m is the number of dead seedlings, Δt is the time period (months), and r is the number of recruited seedlings. Total observation period was 12 mo.

Because of nonnormality of some variables (even after attempting various transformations), we used GLMs and analyses of deviance to analyze the species effect on the environment in the immediate neighborhood of each canopy focal species, as well as on the understory community's structure and dynamics. The quasi-binomial distribution was used for canopy openness and recruitment and mortality rates, instead of the binomial one, due to overdispersion; in turn, for sapling density and species richness we used a quasi-Poisson for the same reason (Bolker *et al.* 2009). Gaussian distribution was used for the rest of variables. GLMs have been increasingly used when modeling variables with nonnormal distributions due to their higher statistical power compared with nonparametric analysis of variance tests (Crawley 2007, Bolker *et al.* 2009).

In a first analysis we took species as the influencing factor or covariate, and we performed individual statistical tests for each of the following response variables: (a) percent relative soil moisture, (b) soil temperature, (c) litter depth, (d) percent canopy openness, and (e) total solar radiation. For the understory community, response variables were: (a) sapling density, (b) species richness, (c) percent cover, (d) recruitment rate, and (e) mortality rate. For these analyses we used the mean values of all ten response variables (*i.e.*, five environmental and five for the understory community) measured at different times. The factor species took five values: the four focal species and the mixed (nonmonospecific) canopy. These analyses were performed using the GLM function in R (R Development Core Team 2010). For significant models, pairwise comparisons were performed with *post-hoc* Tukey HSD tests.

Finally, by combining all data from the seasonal censuses (instead of their means), we used generalized linear mixed models (GLMMs) to examine the effect of the specific identity (SI, as a fixed factor), and of sampling period (*t*, as a random factor) on the same ten response variables. The error distribution for these variables is shown in Table 2. The following five models were pairwise and sequentially compared with the likelihood ratio test (Burnham & Anderson 2002, Bolker *et al.* 2009) for each response variable: (1) α, which excludes the two analyzed effects; (2) $\alpha + \beta SI$, which only included the effect of SI; (3) $\alpha + \gamma t$, which only included the effect of time; (4) $\alpha + \beta SI + \gamma t$; and (5) $\alpha + \beta SI + \gamma t + \delta t SI$. Model selection was based according to the lowest values of the Akaike

TABLE 2. *Models with minor Akaike information criterion (AIC) derived from generalized linear mixed models of the effects of specific identity (SI) and random seasonal variation (τ) on five microenvironmental variables and five sapling community variables assessed in a cloud forest understory of southern Mexico. Pairwise comparisons of models for each response variable based on likelihood ratio tests (lrt).*

Response variable	Model	Error distribution	AIC	Factor	lrt
Understory microenvironment					
Soil moisture	$\alpha+\beta SI+\gamma t$	Gaussian	−1219.97	SI	**
				t	***
Soil temperature	$\alpha+\gamma t$	Gaussian	1441.02	t	***
Litter depth	$\alpha+\beta SI+\gamma t$	Gaussian	3271.70	SI	***
				t	***
Canopy openness	$\alpha+\beta SI+\gamma t$	Quasi-binomial	19.54	SI	NS
				t	a
Total solar radiation	$\alpha+\beta SI+\gamma t$	Gaussian	2061.40	SI	***
				t	***
Sapling community					
Sapling density	$\alpha+\beta SI+\gamma t$	Poisson	1628.27	SI	***
				t	***
Species richness	$\alpha+\beta SI$	Poisson	2447.24	SI	***
Mortality rate	$\alpha+\gamma t$	Quasi-binomial	134.33	t	a
Recruitment rate	$\alpha+\gamma t$	Quasi-binomial	35.43	t	a
Sapling cover	$\alpha+\beta SI$	Gaussian	−1041.61	SI	NS

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

[a]Factor significance could not be assessed because of quasi-binomial distributions; for these models in the AIC column are quasi-AIC values.

NS, not significant.

information criterion (AIC) (Akaike 1974). For overdispersed variables with binomial or Poisson distributions, we calculated quasi-AIC (Tjur 1998, Bolker *et al.* 2009); these analyses were performed using the lme4 package (Bates & Maechler 2009) in R.

RESULTS

The analysis of deviance performed to compare slope inclination between the five species identity treatments did not show significant differences ($F_{4, 93} = 1.69$, $P = 0.15$). In contrast, GLMs showed that the species identity had significant effects on most microenvironmental forest understory variables: soil moisture ($F_{4, 148} = 5.5612$, $P = 0.0003$), litter depth ($F_{4, 148} = 6.3325$, $P = 0.0001$), canopy openness ($\chi^2_4 = 0.0308$, $P = 0.0208$), and total solar radiation ($F_{4, 148} = 3.4390$, $P = 0.0102$). Soil temperature was the only variable without significant variation between different species ($F_{4, 148} = 1.9858$, $P = 0.0996$). Similarly, the analyses of deviance showed significant effects of species on two of the five understory community variables analysed: sapling density ($\chi^2_4 = 26.89$, $P = 0.0200$) and species richness ($\chi^2_4 = 11.394$, $P = 0.0130$).

The *post-hoc* pairwise comparisons of the environmental and understory community variables showed a considerable heterogeneity regarding which species affects which variables (Fig. 1), *i.e.*, no single species had the strongest effects, although *Chiranthodendron* quadrats differed with respect to more response variables than any other canopy type (one microenvironmental variable

and two sapling community variables). Mean soil moisture ($\pm 1\,SD$) was significantly higher under *Cornus* canopies ($48.3 \pm 7.2\%$), but values recorded for this variable under this species differed significantly only from those recorded under the canopies of *Quercus* ($41.4 \pm 6.8\%$) and the mixed canopies ($42.1 \pm 6.6\%$). Mean litter depth was significantly larger under *Chiranthodendron* (6.5 ± 1.6 cm; range: 4.47–5.11 cm), with this species differing from the means of all other treatments. Regarding canopy openness, the areas under *Oreopanax* canopies ($6.8 \pm 1.4\%$) showed larger values that differed significantly only from those sites located under *Cornus* ($5.6 \pm 0.9\%$). Similarly, the largest mean total solar radiation values were recorded in sites beneath the crowns of *Oreopanax* trees (3.5 ± 0.5 mol m^2/d), which differed significantly from those associated to mixed canopies (3.1 ± 0.5 mol m^2/d). Regarding understory community structure, under the canopy of *Chiranthodendron* we recorded a lower mean sapling density (1.2 ± 1.6 ind./m^2) and mean species richness (0.8 ± 0.8 species), but significant differences were observed only for comparison of these values with those from mixed canopies (2.9 ± 3.2 ind./m^2, and 1.7 ± 1.3 species, respectively).

In short, *Cornus* canopies had a positive effect on soil moisture and a negative one on canopy openness, but did not affect total solar radiation. In contrast, *Quercus* affected soil moisture negatively, but had no significant effect either on canopy openness or on total solar radiation. This pattern contrasts with that observed for *Oreopanax*, as canopy openness and total solar radiation were
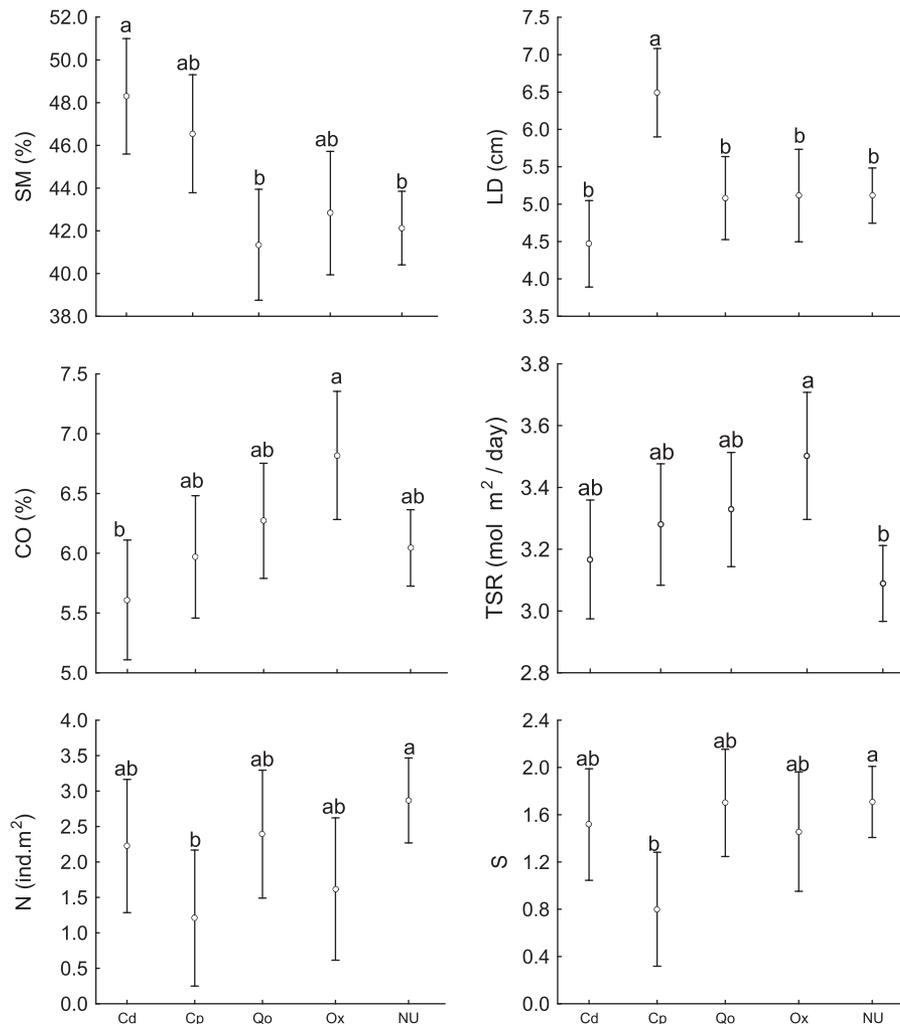
FIGURE 1. Mean values (with 95% CI) of environmental and understory variables under the canopies of four species and under mixed-species canopies (nonuni-specific [NU]) in a cloud forest of southern Mexico. Species abbreviations: Cd, *Cornus disciflora*; Cp, *Chiranthodendron pentadactylon*; Qo, *Quercus laurina*; Ox = *Oreopanax xalapensis*. Response variables abbreviations: SM, soil moisture; LD, litter depth; CO, canopy openness; TSR, total solar radiation; N, seedling density; and S, species richness. Different letters indicate significant differences in a generalized linear model and *post-hoc* Tukey HSD tests.

significantly larger under its crowns, while soil moisture remained unaffected. *Chiranthodendron* was the only species with a positive effect of litter depth, although it did not show significant effects on the other microenvironmental variables. *Chiranthodendron* was also the only canopy type with negative effects on two sapling commu-nity variables (sapling density and species richness); interestingly, these variables differed significantly between this species and the mixed canopies. No species significantly affected soil temperature and the remaining sapling community variables (cover, mortality, and recruitment rates).

In agreement with the results of the analysis of deviance, the GLMMs showed significant effects of SI on three microenviron-mental variables (soil moisture, litter depth, and total solar radia-tion; Table 2). These models also showed significant effects of time on four microenvironmental variables, including soil temperature. Overall mean litter depth peaked in February (6.7 ± 2.1 cm), near

the end of the dry season, and showed a minimum in November, at the end of the rainy season (3.5 ± 1.7 cm) (Fig. 2). Likewise, soil moisture was at its highest in August ($65.4 \pm 15.1\%$), in the middle of the rainy season, and dropped to a minimum in February ($26.2 \pm 8.8\%$). Conversely, canopy openness had its lowest value in August ($4.9 \pm 2.0\%$) and showed two peaks, one in November ($6.9 \pm 2.6\%$) and another in February ($6.8 \pm 1.6\%$). Total solar radiation peaked in May (4.0 ± 1.1 mol m^2/d), and decreased as winter approached, returning to high levels in the following May (3.8 ± 0.9 mol m^2/d). With respect to sapling community vari-ables, sapling density and species richness were significantly affected by species identity, and sapling density was also affected by time (Table 2). It must be noted that in some cases the selected models according to the AIC included nonsignificant factors; this was particularly clear in the case of the model constructed for sapling community cover.
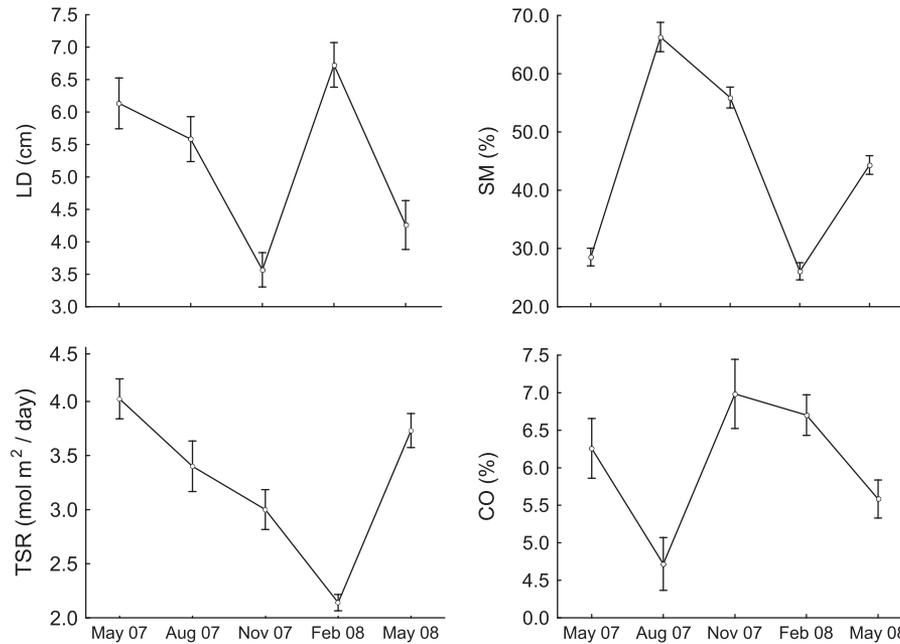
FIGURE 2. Temporal variation throughout the year of environmental variables in the understory of a cloud forest of southern Mexico. Values are means (with 95% CI) of measurements made under the canopies dominated by various species. LD, litter depth; SM, soil moisture; TSR, total solar radiation; and CO, canopy openness.

DISCUSSION

SPECIES EFFECTS ON UNDERSTORY MICROSITE AND SAPLING COMMUNITY.—In this study, we demonstrated that canopy trees of different species have differential effects on canopy openness, total solar radiation, soil moisture, and litter depth. These results are in agreement with earlier studies that have demonstrated between-species differences in a number of plant traits that can influence litter chemistry, litter biomass, and soil temperature and moisture (Eviner & Chapin 2003, Eviner 2004, Barbier *et al.* 2008). When considering the temporal variation of these environmental variables (*i.e.*, between-season significant differences), the species effects on them were still apparent. This indicates that the temporal variation is independent of canopy-tree species, in agreement with the lack of significant interactions observed in the GLMMs. This result also implies that the species effects can override the seasonal variations of the light and humidity regimes, which in our study forest are not negligible due to the seasonal partial loss of foliage that characterizes it.

The different ways in which the four focal species affect understory microenvironment is not a mere question of magnitude: each analyzed variable changed significantly according to at least one species, while being indifferent to others. For example, *Cornus* and *Quercus* significantly affected soil moisture, but in opposite directions, whereas *Chiranthodendron* was the only species with a significant effect on litter depth. Although these results matched our initial expectations regarding the differential effects of canopy species, only one of the four canopy types (*i.e.*, *Chiranthodendron*) had a significant effect on the sapling community, resulting in lower sapling density and species richness beneath its canopy. Interestingly, the mixed (nonmonospecific) canopies were associated

to significantly larger values of these two variables, a result that may be related to a more diverse seed rain than to better germination and establishment conditions. Our results are not conclusive about what factors are responsible for these limitations in the understory community associated to *Chiranthodendron*, but they suggest a crucial role of litter depth, which was significantly larger beneath this species than under any other canopy type (*i.e.*, the remaining three studied species and the mixed-species canopies). Litter depth may potentially have strong effects on understory structure and composition, and the nature of this physical effect—be it positive or negative—on understory vegetation may be nonlinear, reversed beyond certain amount of litter, and species-dependent (Suding & Goldberg 1999). This factor is also known to have both positive and negative effects on understory development by influencing microclimatic soil conditions like moisture (Facelli & Kerrigan 1996, Graae & Heskjaer 1997) and temperature (Becerra *et al.* 2004, Esteso-Martínez & Gil-Pelegrín 2004). Seeds under litter are deprived of light and seeds resting on its surface cannot root easily, limiting both the number of plants that establish in a given microsite, and the number of species represented in them (Vázquez-Yanes *et al.* 1990, Facelli & Pickett 1991, Vázquez-Yanes & Orozco-Segovia 1992, Daws *et al.* 2005). Similarly, *Oreopanax* showed a clear (albeit nonsignificant) trend toward a lower sapling density in their immediate understory, despite being the most abundant species in the understory community. This observation might be related to the better light conditions recorded beneath this canopy type. In Teipan, *Oreopanax* displayed a significant negative association between saplings and adult trees (Mejía-Domínguez 2006), in agreement with a higher survival of this species in darker (more mature) environments reported for

similar forests in nearby Chiapas State (Quintana-Ascencio *et al.* 2004).

   We can conclude that taxonomic identity of canopy trees is related to particular conditions in the forest understory, but the resulting environmental variation linked to the different canopy species has specific effects on the sapling community (and thus in the forest regeneration process) in some cases only. We claim that in searching for causes of a heterogeneous understory environment where the recruitment of a larger array of species is possible, given their differences in regeneration niche (Grubb 1977, Poorter 2007, Queenborough *et al.* 2007a), a deeper examination of canopy species effects is warranted.

Environmental heterogeneity in the forest understory.— Environmental heterogeneity is an implicit component of all ecological studies, but its analysis has preferentially concentrated on its consequences than on its causes (Hutchings *et al.* 2000, Pickett *et al.* 2000, Beckage & Clark 2003). Local heterogeneity has been generally attributed to an uneven distribution of resources and microclimate, often related to fine-scale microtopographic variations (Harper 1977, Bellingham & Tanner 2000, Dalling & Hubbell 2002, Robert & Moravie 2003, Kubota *et al.* 2004). The role of living organisms as sources of heterogeneity has been less emphasized, however, in contravention to the suggestion that many species should be considered 'ecosystem engineers', given their significant ability to produce environmental modifications (Jones *et al.* 1994, Pickett *et al.* 2000, Gutiérrez & Jones 2006). In fact, there is ample evidence that the effects of these biotic sources of environmental variability may be either positive or negative, but that they usually result in an increased heterogeneity compared with that uniquely related to abiotic factors (Jones *et al.* 1997, Pickett *et al.* 2000, Eviner 2004, Barbier *et al.* 2008).

   The few efforts to examine the role of the specific identity of canopy trees in diverse forests have largely restricted to the analysis of the effects of species composition on litter or soil properties (Ayres *et al.* 2009, Cardelús *et al.* 2009, Kamei *et al.* 2009, McCarthy-Neumann & Kobe 2010), and have been mostly conducted in species-poor forest plantations (Parrotta 1995, Powers *et al.* 1997). The role of canopy trees as drivers of environmental heterogeneity in a forest understory has also been analyzed from the perspective of biological neighborhoods, both in tropical and temperate forests (Canham *et al.* 2004; Uriarte *et al.* 2004, 2005; Comita & Hubbell 2009), or with a nurse or facilitative plants approach (Holmgren *et al.* 1997; Flores & Jurado 2003; Gómez-Aparicio *et al.* 2004, 2005b), both of which acknowledge the ecological relevance of species effects. Some differences, however, exist between these two approaches and the study of the general effects of single canopy species. The analysis of biological neighborhoods, mostly restricted to species-rich communities, involves the examination of the effects of multi-specific sets (*i.e.*, comparisons of heterospecific vs. conspecific neighborhoods, distance to neighbors, and size effects; Hubbell *et al.* 2001; Uriarte *et al.* 2004, 2005; Canham & Uriarte 2006; Queenborough *et al.* 2007b), while the nursing role of plants is often assessed in terms of its potential positive effects on nonconspecifics (Gómez-Aparicio *et al.* 2004,

2005b). By dissecting the effects of four cloud forest canopy species and comparing them with those of mixed canopies, we were able to identify more readily the particular role played by each species (including both positive, negative, and neutral effects *sensu* Wiegand *et al.* 2007), and to relate it to the particular ways in which it modifies the environment in its surroundings.

   Microclimatic factors may vary every meter in the forest understory (Nicotra *et al.* 1999, Montgomery & Chazdon 2002, Gómez-Aparicio *et al.* 2005a). Our results agree with this finding because we also documented a large environmental heterogeneity in the understory of our study forest. Nonetheless, a parallel analysis conducted by our group revealed the existence of relatively homogeneous patches, with a mean diameter of *ca* 13 m; interestingly, this figure closely matches the mean ($\pm$ SE) crown diameter of canopy trees in this forest (11.2 $\pm$ 4.5 m, for trees > 15 m tall; N. Mejía-Domínguez, unpubl.). This coincidence suggests that the resolution scale of environmental heterogeneity in the forest understory is related to the physical structure of the forest upper canopy, whose variation could be partly attributed to individual species effects.

Canopy species effects along gradients of overstory tree dominance.—Plant diversity is larger in tropical forests than in their temperate counterparts (Dirzo 2001). Nonetheless, in the tropics steep gradients in the degree of canopy dominance are well-known, ranging from very diverse forests where no single tree has real dominance, to strongly monodominant forests (Hart 1990, Richards 1996). Thus, one may ask how generalized are the microenvironment-mediated species effects on the sapling community dynamics. At one end, monodominance clearly implies that specific identity loses relevance, so that the environmental heterogeneity within such a forest must be explained in terms of inter-individual variations in canopy architecture or tree size, of the particular gap dynamics of that forest, or other local environmental variations (such as topography) (Runkle 2000). Comparisons of two or more single-dominated communities of different species (in particular of monodominant forest plantations), however, have shown very clear species effects on woody species recruitment patterns (Parrotta 1995, Powers *et al.* 1997), a result of great importance in efforts to restore native tree diversity in degraded areas affected by deforestation (Castro *et al.* 2002, Padilla & Pugnaire 2006).

   Increasing the number of species to two is sufficient to generate heterogeneity associated to this taxonomic/ecological factor and, as indicated by our results, the successive inclusion of more species may gradually increase the magnitude of this effect, as long as they prove to affect differentially at least one microenvironmental component. Our study forest comprises many more canopy species than the limited set examined by us (*ca* 40; Mejía-Domínguez *et al.* 2004), and yet we were able to locate points across the forest understory where we could associate the microenvironment to a single canopy species (not necessarily to a single tree). It is conceivable that in much more diverse forests, such as those reported by Gentry (1988) for the Peruvian Amazonia and by Condit *et al.* (1996) for the Malay Peninsula, the individual effects of the different species tend to be confounded due to strong multiple-crown overlap.

Under these circumstances, the biological neighborhood approach may be of greater value in analyzing the causes of understory heterogeneity. Even so, one cannot overlook the fact that the species effects lie at the heart of any biological neighborhood (Wiegand *et al.* 2007), and that the combined effects of various species, probably involving synergisms yet to be studied, plays an important role in the natural regeneration and diversity maintenance of species-rich tropical and subtropical forests.

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