



## Tree composition and structure in disturbed stands with varying dominance by *Pinus* spp. in the highlands of Chiapas, México

Luis Galindo-Jaimes<sup>1</sup>, Mario González-Espinosa<sup>1,\*</sup>, Pedro Quintana-Ascencio<sup>1</sup> and Luis García-Barrios<sup>2</sup>

<sup>1</sup>Departamento de Ecología y Sistemática Terrestres, División de Conservación de la Biodiversidad, El Colegio de la Frontera Sur (ECOSUR), Apartado Postal 63, 29200 San Cristóbal de Las Casas, Chiapas, México; <sup>2</sup>Departamento de Agroecología, División de Sistemas de Producción Alternativos, El Colegio de la Frontera Sur (ECOSUR), Apartado Postal 63, 29200 San Cristóbal de Las Casas, Chiapas, México; \*Author for correspondence (e-mail: mgonzale@scl.ecosur.mx; phone: +52 967 81883, ext. 4001)

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### Abstract

We studied soil and forest floor conditions, regeneration patterns of trees, and forest structure and floristic composition along a gradient of dominance by *Pinus* spp. in disturbed stands in the highlands of Chiapas, southern Mexico. Seedlings, saplings, and adults of tree species were counted and measured in 2–3 circular plots (1000 m<sup>2</sup> each) in 36 forest stands (a total of 38 tree species). Dominance of broadleaved trees other than *Quercus* spp. was negatively correlated with basal area of *Pinus* spp. ( $P < 0.001$ ). Soils of pine-dominated stands were more compacted, less acidic, and less fertile (lower C.E.C., nitrogen, and organic matter content). Numerous broadleaved trees may depend on an oak-dominated canopy to regenerate, and changes associated to pinelands expansion may compromise their long-term persistence. However, seedlings and saplings of *Quercus* spp. were abundant in stands with both an oak- or pine-dominated canopy. The results suggest that a plan for sustainable forest utilization in the study region, and in other similar populated tropical highlands, could take advantage of the abundant oak regeneration and coexistence with pines in the canopy.

### Introduction

Natural disturbances by events such as treefalls, hurricanes, flooding, fires, landslides etc., may be a major factor accounting for local plant diversity (Connell 1978; Pickett 1980; Pickett and White 1985; Denslow 1987; Huston 1994; but see also Hubbell et al. 1999; Chazdon et al. 1999; Kobe 1999). In addition to the disturbance regime, the responses of communities and ecosystems (Connell and Slatyer 1977; Bormann and Likens 1977) depend on differences in morphology, physiology, tolerance, life-cycle attributes and dispersal and colonizing attributes of the species involved (Grubb 1977; Woods and Whittaker 1981; Leemans 1991; Glenn-Lewin and van der Maarel 1992). As a result of disturbance regimes acting over a historical scale, it is possible to identify

different sets of species with certain plant communities (Denslow 1980).

Low-intensity and sustained human disturbance through selective logging, firewood extraction, grazing, and land clearing for permanent agriculture may influence plant communities and their successional patterns (Jardel 1991; Attiwill 1994; Hong et al. 1995; Fujisaka et al. 1998). Long-term alteration of patterns and processes in forest systems may lead to losses in their biological diversity and may render them more susceptible to invasions (Hobbs and Huenneke 1992). In heavily populated regions, the composition and structure of secondary forests may be the result of the interaction between land-use patterns and species attributes (Hong et al. 1995; Vetaas 1997). In particular, it has recently been documented that widespread biological invasions by species of *Pinus* may follow

drastic changes in the historical disturbance regime (Richardson and Bond 1991; Richardson 1998b, 1998b). Understanding the effects of human disturbance on forest structure and composition, and on the relationships among the component groups of tree species is essential in defining alternative sustainable forestry systems (Halpern and Spies 1995; Lugo 1995; Vetaas 1997).

The landscapes of the highlands of Chiapas have undergone a severe transformation following changes in population and land-use patterns during the last decades (Wagner 1962; González-Espinosa et al. 1995a; De Jong et al. 1999; Ochoa-Gaona and González-Espinosa 2000). The formerly extensive stands of Oak, Pine-Oak, and Evergreen Cloud Forest (Miranda 1952; Breedlove 1981) have been severely fragmented and reduced, with the resulting landscape mostly comprising a complex mixture of secondary forests, shrublands, grasslands, and permanent clearings for agriculture (De Jong et al. 1999; Ochoa-Gaona and González-Espinosa 2000). Secondary forest associations in the area are heavily used for logging, extraction of firewood and charcoal, and as grazing lands (Alemán-Santillán 1989; Ramírez-Marcial et al. 1996; De Jong et al. 1999), with consequences on the regeneration of woody species (Quintana-Ascencio et al. 1992; Ramírez-Marcial et al. 1996), and on the maintenance of the floristic composition and structure of successional forest stands (González-Espinosa et al. 1991, 1995a, 1995b). An observed trend in forest stands previously dominated by oak species is the relatively recent increase of species of pines (less than 50 years), along with severe decreases in the richness of such vascular plant groups as ferns and allies, vines and lianas, shrubs, and understory trees (30–80%; González-Espinosa et al. (1995a, 1995b)). We hypothesize that the observed increase of abundance and distribution of native pine species may change local environmental conditions, making habitats less favorable for the maintenance of the original set of tree species. In this paper, we examine some possible relationships among soil and forest floor attributes, forest structure conditions, and floristic composition of a set of disturbed stands along a gradient of pine dominance.

### Study sites

The study was conducted at Rancho Merced-Bazom (municipality of Huistán) and Mitzitón (municipality

of San Cristóbal de Las Casas) in the central part of the highlands of Chiapas, Mexico. The inventoried forest stands are on gentle slopes at 2,250–2,500 m elevation (INEGI 1984a). Mean annual temperature is 13–14 °C, and mean annual rainfall is 1,200–1,500 mm (García 1987; INEGI 1984b). The soils are moderately deep Luvisols and Rendzinas derived from limestone rock (INEGI 1985). Land-use patterns have caused a landscape mosaic including only small and isolated remnants of original vegetation interspersed with vast expanses of agricultural lands, grasslands, shrublands, and secondary forests showing a varying dominance by either pines or oaks (a detailed description of recent changes in vegetation cover at the municipality of Huistán appears in Ochoa-Gaona and González-Espinosa (2000)). The small patches of remaining original vegetation include associations of Evergreen Cloud Forest, Oak Forest, and Pine-Oak Forest (Miranda 1952; Breedlove 1981; González-Espinosa et al. 1997). The indigenous people of the highlands of Chiapas obtain forest products on a daily basis from both mature and second-growth stands. Oak species (*Quercus laurina*, *Q. crassifolia* and *Q. rugosa* in mesic sites, and *Q. crispipilis*, *Q. skutchii* and *Q. segoviensis* in the drier habitats) are the preferred source for firewood and charcoal. On the other hand, the pines (*P. ayacahuite* var. *ayacahuite*, *P. pseudostrobus* var. *apulcensis*, *P. montezumae* var. *montezumae*, and *P. tecunumanii*; nomenclature follows Farjon and Styles (1997)) are usually logged when they reach 20–25 cm dbh (González-Espinosa et al. 1995b).

### Materials and methods

#### *Floristic inventories and environmental variables*

Floristic and structural inventories were obtained from 36 forest stands along a gradient of dominance by *Pinus* spp., by setting 2–3 circular plots (1000 m<sup>2</sup> each) separated by 50 m (the number of plots depended on the size of the stand being sampled). Elevation, slope angle and slope aspect were obtained for each plot. An average of percent canopy openness was obtained for each plot from 12 readings (at three points on the limits of the concentric circles along each orientation, N, S, E, W) of a convex spherical crown Forestry Suppliers™ densiometer. All large (>25 cm dbh) and small adult trees (5–25 cm dbh) were counted and their dbh and height measured

within these plots. All saplings ( $\geq 50$  cm height and  $< 5$  cm dbh) were counted and their height measured within one 100 m<sup>2</sup> concentric circle. All seedlings ( $< 50$  cm height) of tree species were counted in five circles (1 m<sup>2</sup> each) located at the center and at the four cardinal points on the limit of the largest plot. We grouped tree species as canopy (*Pinus* spp., *Quercus* spp., and occasional *Arbutus xalapensis*) and understory trees (broadleaved species other than *Quercus*). The number of stumps ( $> 10$  cm at the base; mostly due to logging) was obtained within the largest circle. Litter depth was measured at 15 points located throughout the stand, where soil samples were also collected from a depth of  $< 30$  cm. A composite 1 kg soil sample was obtained from these 15 (0.5 kg each) subsamples, and prepared to conduct the following analyses in the laboratory: soil texture, pH, available phosphorus, organic matter content, cation exchange capacity, and bulk density (van Reewijk 1995).

### Analysis

Relative importance values (RIV's) were calculated for all tree species with dbh  $> 5$  cm, based on their relative density and relative basal area (Mueller-Dombois and Ellenberg 1974). The possible relationships among floristic composition, structural variables (RIV's, and density of seedlings, saplings and adults), and soil attributes with the dominance of *Pinus* spp. in the stands were analyzed with linear and polynomial regression (Fisher and van Belle 1993). A classification of the stands was obtained with the TWINSPAN program (Hill 1979); two divisions were effected as recommended by van Groenewoud (1992), using both floristic composition and relative density of tree species. A canonical correspondence analysis (CCA; Ter Braak (1986, 1987)) was used to explore the possible relationships among the RIV's of adult trees and environmental variables; relative density was used for seedlings and saplings.

## Results

### *Tree species richness and basal area*

A total number of 38 tree species with dbh  $> 5$  cm was recorded in the 36 sampled stands, including 10 species that can be considered typical canopy trees and 28 as understory tree species (table with detailed

data structure and floristic composition for each species in each stand is available on request, either in hard-copy or electronic file format). The number of canopy species in each stand was 1–6, and the number of understory species was generally higher, but more variable (0–12 species). Oak-dominated canopies were much less frequent, as *Quercus* spp. (1–4 species) accounted for  $> 50\%$  of the RIV of the canopy in only two stands. A few stands had a diverse canopy dominated by broadleaved understory trees (up to 14 species; Table 1). The number of species of oaks was not linearly related to the dominance of pines in the stand, but a quadratic relationship was obtained (Figure 1a). A significant negative linear relationship was found between the species richness of understory trees and the RIV's of *Pinus* spp. in each stand (Figure 1b). Species of *Quercus* and *Pinus* accounted for 50–80% of the RIV of canopy trees in 24 out of 36 stands. It was found that pines (1–4 species) dominated the canopy ( $> 50\%$ ) in one third of the stands, occasionally exceeding 75% (Table 1). Total basal area in the stands was found to vary widely (24.8 up to 68.4 m<sup>2</sup>/ha), but it was usually high (mean  $\pm 1$  s.e. =  $48 \pm 1.8$  m<sup>2</sup>/ha). Basal area of pines was frequently the highest in the stands ( $24.7 \pm 2.9$  m<sup>2</sup>/ha) as compared with that of oaks ( $16.1 \pm 1.9$  m<sup>2</sup>/ha) and other broadleaved understory species ( $7.1 \pm 1.5$  m<sup>2</sup>/ha; Table 1). The dominance of both *Quercus* spp. and other broadleaved understory tree species were negatively correlated with the RIV and basal area of *Pinus* spp. (all four  $R^2 > 0.32$ ,  $df = 34$ ,  $P < 0.001$ ; Figures 2 and 3).

### *Age/size stand structure*

The number of seedlings and saplings accounting for the regeneration of *Pinus* spp., *Quercus* spp. and broadleaved understory tree species other than *Quercus* varied widely along the gradient of dominance by pine species (Table 2). Seedlings of *Pinus* spp. were considerably scarcer (usually  $< 1000$  pine seedlings/ha) than those of *Quercus* spp. (usually 3,000–7,000 seedlings/ha). As it could be expected, the largest numbers of pine seedlings (5,000–8,000 ind/ha) were recorded under canopies with the highest dominance by reproductive pines ( $> 25$  cm dbh; Figure 4a). However, we also found under these canopies some of the largest numbers of *Quercus* seedlings (10,000–20,000 ind/ha). The number of both pine and oak saplings was not correlated with the RIV of reproductive pines (Figure 4b). The highest num-

Table 1. Attributes of the 36 study sites, arranged according to their increasing relative importance value (RIV) of *Pinus* spp. RIV, BA, and R refer to relative importance values, basal area, and species richness of *Pinus* spp. (P), *Quercus* spp. (Q), broadleaved (B) species other than *Quercus*, and total (T) for each stand, respectively. Roman numerals refer to those stand groups created by TWINSpan with 30 sites.

SITE1	6	7	23	15	11	19	36	13	3	18	10	25	9	14	35	16	12	8	17	26	5	33	34	21	32	31	27	20	30	4	29	28	2	22	24		
GROUP	I	I	I	I	II	II	-	I	II	II	II	II	II	II	-	II	II	IV	II	II	II	-	II	-	-	III	III	III	III	II	III	III	II	III	III	IV	IV
RIVR	0	0	0	2	7	12	12	13	13	13	13	15	24	26	31	32	34	40	40	41	41	45	47	62	72	76	80	80	80	84	85	85	85	94	94	97	
RIVQ	38	27	38	27	46	43	17	27	75	41	44	36	37	30	38	32	45	52	37	22	33	30	39	20	20	19	20	16	11	14	10	15	0	6	3		
RIVB	62	73	62	71	47	45	70	60	12	46	43	49	40	44	30	36	21	8	23	37	26	20	15	18	5	5	1	4	8	0	5	0	0	0	0		
BAPO	0	0	0	1	6	10	8	8	5	13	12	7	28	21	31	37	25	12	33	18	36	28	38	48	42	52	41	39	48	36	54	54	25	34	37		
BAQ7	25	24	28	20	35	36	7	16	21	39	31	24	35	21	22	28	21	17	18	18	22	12	13	4	7	6	2	2	3	4	8	2	0	1	2		
BAB42	13	27	15	22	5	6	22	14	1	6	6	10	2	7	13	4	2	1	4	11	4	6	7	2	2	1	0	0	0	1	0	0	0	0	0		
BAT48	38	51	43	43	46	53	37	38	26	58	49	41	65	50	66	68	49	30	54	47	61	50	59	54	51	59	44	41	52	40	63	56	25	35	39		
RP	0	0	0	1	1	2	1	2	2	2	3	2	2	3	3	3	1	2	2	3	1	2	3	1	2	3	3	2	3	3	2	4	3	1	1		
RQ	1	2	1	2	3	1	2	3	3	3	3	4	2	3	3	3	3	3	3	2	2	4	4	2	4	3	3	2	3	1	3	2	0	2	1		
RB	12	12	12	10	7	10	14	11	8	11	11	8	8	8	6	11	7	7	7	10	9	6	5	9	5	2	1	2	2	0	4	0	0	0	0		
RT	13	14	13	14	10	15	16	15	13	16	16	14	14	12	12	17	11	12	12	15	12	13	12	12	12	8	7	6	8	5	9	6	4	3	2		

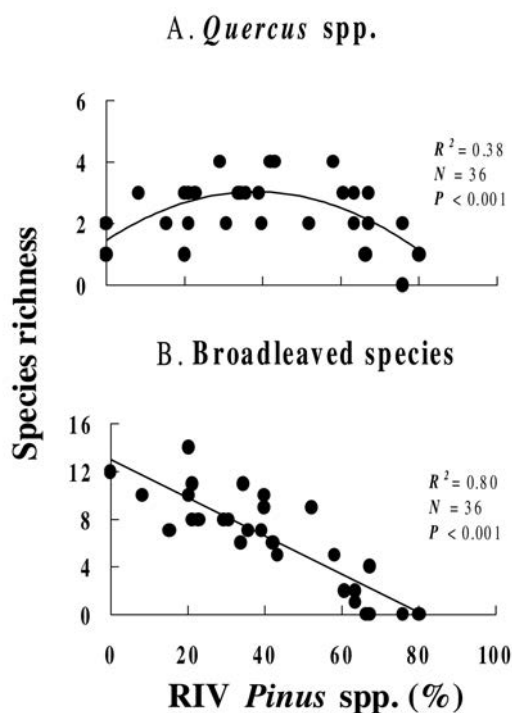


Figure 1. Regression of floristic richness of *Quercus* spp. (A) and broadleaved tree species other than *Quercus* (B) with the relative importance value of *Pinus* spp. in the 36 studied stands.

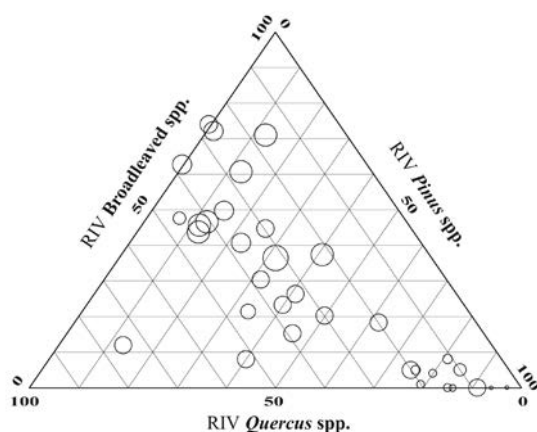


Figure 2. Triangle chart (Batschelet 1979) of relative importance values of *Quercus* spp., broadleaved tree species other than *Quercus*, and *Pinus* spp. in the 36 studied stands. The diameter of each circle is proportional to total richness of tree species in the stand (2–17 species).

bers of adult oaks occurred in those stands with intermediate RIV's of pines (30–70%; Figure 4c). The number of seedlings, saplings and adults of broadleaved

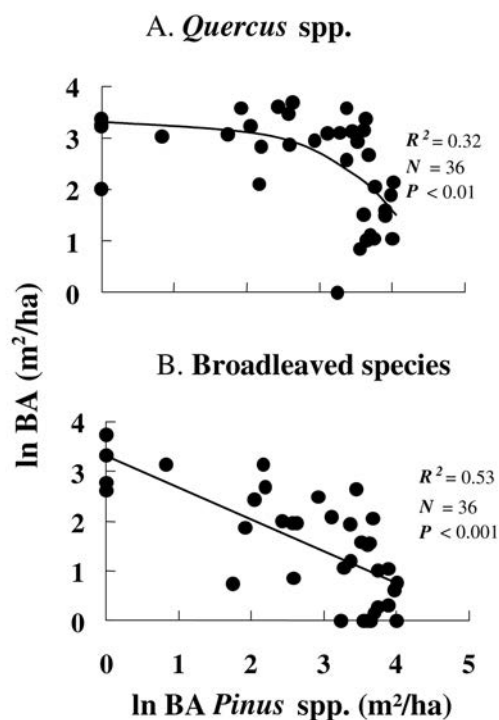


Figure 3. Regression of the natural logarithm of basal area (ln BA) of *Quercus* spp. (A) and broadleaved tree species other than *Quercus* (B) with the ln of basal area of *Pinus* spp. in the 36 studied stands.

aved tree species showed highly significant negative correlations with the RIV's of pines (Figure 4).

#### *Pine dominance and soil variables*

The edaphic variables evaluated in the stands showed consistent changes along the gradient of pine dominance. Pine-dominated canopies were associated to less acidic and porous soils (both  $P < 0.001$ ; Figures 5a,b). A significant ( $P < 0.001$ ) relationship was found between the amount of available phosphorus and the dominance by pines (Figure 5c). A negative relationship with the RIV of *Pinus* spp. was found for the content of organic matter, the cation exchange capacity, and nitrogen content (Figures 5d,e,f). For all variables, an inflection point of the fitted curves is suggested at 60–70% RIV of *Pinus* spp.

#### *Classification of stands*

After two divisions TWINSpan created four groups of sites out of 30 stands including 101 tree “pseu-

Table 2. Density of adults (ind/ha), saplings (ind/100 m<sup>2</sup>), and seedlings (ind/100 m<sup>2</sup>) of *Pinus* spp. (P), *Quercus* spp. (Q) and broadleaved tree species other than *Quercus* (B) in the 36 stands arranged according to their increasing dominance of adult pines.

Sites	Adults			Saplings			Seedlings		
	P	Q	B	P	Q	B	P	Q	B
1	0	60	1140	0	0	127	0	160	139
6	0	160	1550	0	6	188	0	62	390
7	0	70	930	0	0	191	0	0	154
23	0	170	1290	0	0	294	0	24	470
15	10	120	1370	0	3	367	0	1	319
11	10	220	1120	0	0	124	0	20	258
19	60	300	1240	0	2	250	0	20	429
36	80	300	1621	0	0	16	0	0	144
3	100	920	250	1	25	49	0	3	1020
10	20	290	880	0	0	190	0	20	407
13	60	180	1220	0	0	89	1	62	534
18	50	200	1060	0	29	148	0	63	438
25	170	160	860	0	5	85	0	46	327
9	60	290	1090	0	5	111	0	41	295
14	180	250	710	0	1	254	0	26	384
35	300	790	760	0	7	4	0	4	81
16	130	300	840	0	1	154	0	20	308
12	260	740	600	0	6	125	0	20	40
8	430	550	140	13	6	3	7	60	121
17	250	530	480	0	22	84	0	20	249
5	320	390	630	0	3	96	0	2	157
26	530	80	610	3	26	116	0	16	449
33	510	540	310	0	6	11	0	0	62
34	450	860	280	0	4	30	0	23	168
21	410	380	370	0	16	112	0	49	486
32	1140	500	120	0	3	3	0	26	0
31	740	340	110	0	2	2	0	60	141
20	500	200	60	0	10	7	20	42	22
27	740	400	10	0	7	0	0	2	1
30	850	200	200	0	9	30	0	22	65
4	430	100	10	0	22	0	1	125	81
28	700	260	0	1	6	0	0	0	0
29	1610	160	160	3	6	20	0	6	26
2	690	0	80	4	1	1	80	20	0
22	960	90	0	3	7	2	41	205	63
24	1120	20	0	6	12	1	0	184	230

dospecies” *sensu* Carleton et al. (1996). These included 38 species represented by adult individuals, 37 species represented by their saplings, and 26 species represented by their seedlings (Table 3). The first group of stands included a large number of species, either as adults, saplings or seedlings (26, 21, and 16 species, respectively); however, only 13 species had all their three life stages represented, among them

*Cornus disciflora*, *Magnolia sharpii*, *Oreopanax xalapensis*, *Quercus laurina*, *Persea americana*, *Prunus rhamnoides*, *Rapanea juergensenii*, and *Ternstroemia lineata* ssp. *chalicophylla*. All these species are regarded as typical components of old-growth Oak Forests. Only adult individuals of *Pinus tecunumanii* and *P. pseudostrobus* var. *apulcensis* were occasionally found in the stands comprising this group (Table 3). Group II included the largest number of stands and species, although species richness was highly variable (Table 2): 35 species were represented by their adults, 34 by their saplings, and 19 by their seedlings. *Cleyera theaeoides*, *Prunus serotina*, *Rhamnus sharpii*, *Styrax argenteus*, and *Viburnum jucundum* ssp. *jucundum* were well represented components of this second group, in addition to those species mentioned for Group I. Four species of pines (*P. ayacahuite*, *P. montezumae*, *P. pseudostrobus* ssp. *apulcensis*, and *P. tecunumanii*) were represented by both their adults and saplings (Table 3). Group III included stands with lower species richness (13, 12 and 9 species represented by either adults, saplings, or seedlings), and only six species had individuals in all age/size classes. Both *Pinus* (*P. ayacahuite*, *P. montezumae*, *P. pseudostrobus* var. *apulcensis*, and *P. tecunumanii*) and *Quercus* (*Q. laurina* and *Q. crassifolia*) were well represented elements in the canopies of these stands. Finally, a fourth group included stands with the lowest richness of species and a high dominance by *Pinus montezumae*; a few oak species were also present in the canopies (Table 3). Only *Quercus laurina*, *Prunus serotina*, and *Ternstroemia lineata* had all their age/size classes well represented in all four groups; the seedlings of about two thirds of the total number of species were absent or only little represented in the studied stands (Table 3).

#### *Ordination along environmental variables and pine dominance*

The results of CCA ordination for all sites and species are separately shown for adults, saplings, and seedlings (Figures 6a, 6b and 6c, respectively). Only the first two ordination axes were considered (Table 4). The environmental variables that were included accounted for a considerable amount of the observed variation among stands (the eigenvalues for axis 1 were 0.52–0.81); corresponding values for axis 2 were considerably lower (0.22–0.54; Table 4). The cumulative variance accounted by the first two axes of variation was > 24% for species and > 51% for

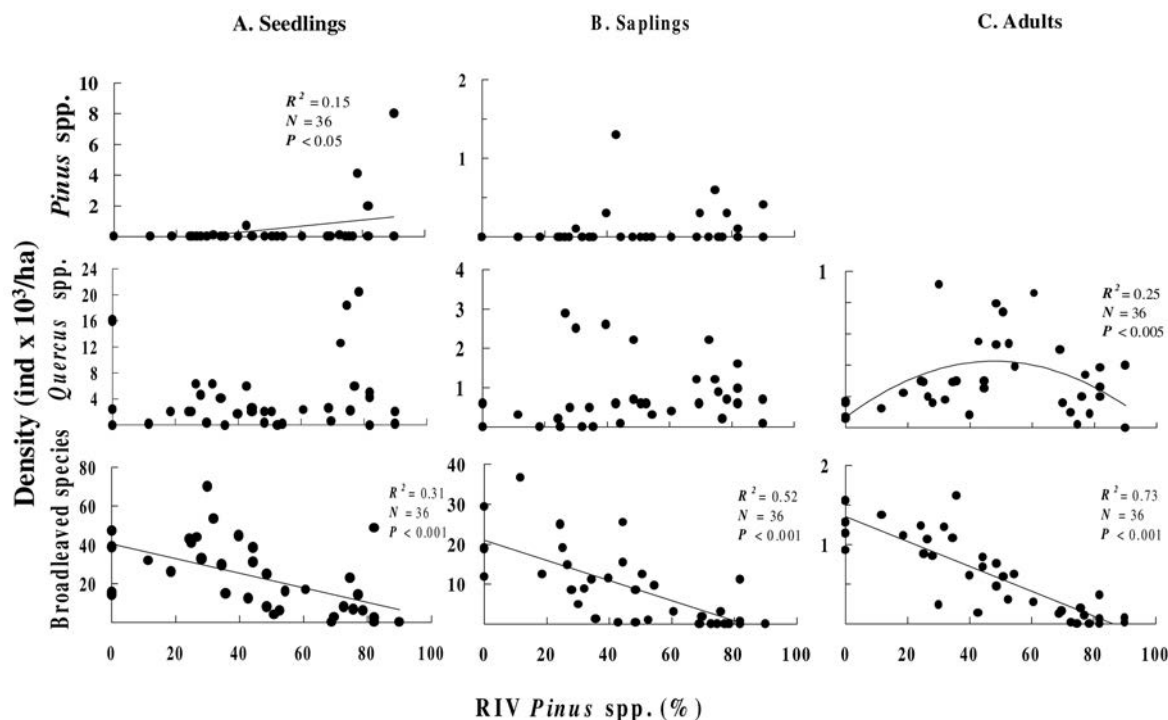


Figure 4. Regression of the density of (A) seedlings, (B) saplings, and (C) adults with the relative importance values of *Pinus* spp. in the 36 studied stands. Only shown are those relationships that were significant ( $P < 0.05$ ). The regression of density of adult *Pinus* spp. and their RIV is not shown as they are autocorrelated variables.

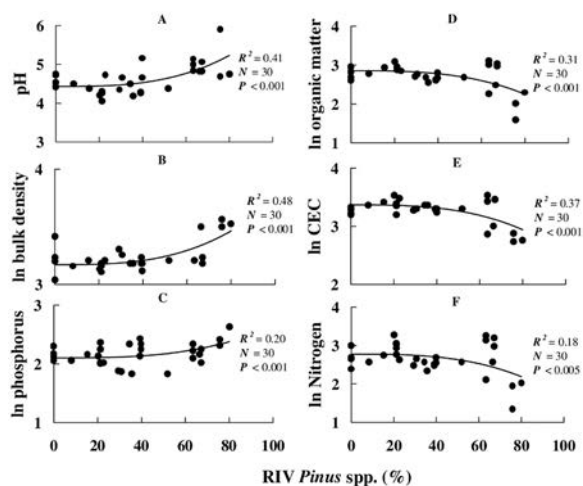


Figure 5. Regression of soil site characteristics with the relative importance values of *Pinus* spp. in 30 stands. (A) pH, (B) bulk density (10 g/mL), (C) available phosphorus (ppm), (D) organic matter content (%), (E) exchangeable capacity, EC (meq/100 g), and (F) nitrogen content (%).

species-environment. Canopy cover had high correlation (negative) with the first ordination axis for saplings and seedlings (data for adults were not analyzed as their crowns account for canopy cover); other

highly correlated variables were soil bulk density, organic matter content in the soil, and soil cation exchange capacity (Figure 6, Table 4). The variables with highest correlation coefficients with axis 2 were, with the exception of soil pH, not consistent for all age/size classes.

## Discussion

### *Oaks and pines in the canopy*

Previous observations from Mexican forests (Rzedowski and McVaugh 1966; Rzedowski 1978; Vázquez et al. 1995), and recent quantitative studies in the highlands of Chiapas (Ramírez-Marcial et al. (2001); M. González-Espinosa, pers. com.) have proposed that *Quercus* and *Pinus* represent two coexisting and ecologically distinct groups of canopy tree species. Pines and oaks (usually 2–3 species of each genus in any given locality) compose the canopy layer of many forest associations in the mountains of tropical Mexico and Central America; however, they have different biological attributes and receive differ-

Table 3. Abundance and frequency of the 38 tree species included in the study. Groupings resulted from classification analysis. Digits in triplets refer to abundance classes of adults, saplings and seedlings, respectively. Abundance classes are: absent (0), rare (1), intermediate (2), abundant (3), and very variable (4). Values of frequency refer to presence/absence of adults, saplings, and seedlings in any of the four groups.

Species	Group I	Group II	Group III	Group IV	Frequency
<i>Arbutus xalapensis</i> (Arbxa)	0 0 0	0 0 0	4 1 0	0 0 0	1 1 0
<i>Pinus ayacahuite</i> (Pinay)	0 0 0	1 1 0	4 1 0	0 0 0	2 2 0
<i>Pinus montezumae</i> (Pinmo)	0 0 0	2 1 0	3 0 0	3 3 2	3 2 1
<i>Pinus tecunumanii</i> (Pinte)	1 0 0	4 1 0	3 2 2	2 0 0	4 2 1
<i>Pinus pseudostrobus</i> (Pinps)	1 0 0	1 1 0	2 2 2	0 0 0	3 2 1
<i>Quercus acatenangensis</i> (Queac)	0 0 0	2 2 0	0 0 0	2 1 0	2 2 0
<i>Quercus crassifolia</i> (Quecra)	1 0 1	4 1 0	4 2 3	2 3 3	4 3 3
<i>Quercus crispipilis</i> (Quecri)	0 0 0	1 0 0	0 0 0	1 3 3	2 1 1
<i>Quercus laurina</i> (Quela)	2 1 2	3 4 2	4 3 3	1 2 4	4 4 4
<i>Quercus rugosa</i> (Queru)	1 0 0	1 0 1	1 2 0	0 0 0	3 1 1
<i>Alnus acuminata</i> (Alnac)	0 0 0	1 0 0	1 0 0	0 0 0	2 0 0
<i>Buddleia cordata</i> (Budco)	1 0 0	1 0 0	0 0 0	0 0 0	2 0 0
<i>Clethra macrophylla</i> (Clema)	2 1 0	1 1 0	0 0 0	0 0 0	2 2 0
<i>Cleyera theaeoides</i> (Cleth)	3 1 1	4 1 1	1 1 0	0 0 0	3 3 2
<i>Cornus disciflora</i> (Cordi)	2 1 4	4 4 2	0 0 0	0 0 0	2 2 2
<i>Cornus excelsa</i> (Corex)	0 0 0	0 1 0	0 0 0	1 1 0	1 1 0
<i>Crataegus pubescens</i> (Crapu)	0 0 0	0 0 0	1 0 0	0 0 0	1 0 0
<i>Drimys granadensis</i> (Drigr)	0 0 0	0 1 0	0 0 0	0 0 0	0 1 0
<i>Eupatorium nubigenum</i> (Eupnu)	2 1 0	1 1 1	0 0 0	0 0 2	2 2 2
<i>Garrya laurifolia</i> (Garla)	0 0 0	1 1 0	0 0 0	0 0 0	1 1 0
<i>Ilex vomitoria</i> (Ilevo)	0 0 0	0 1 0	0 0 0	0 0 0	0 1 0
<i>Licaria</i> cf. <i>campechiana</i> (Licca)	1 1 1	1 4 1	0 0 0	0 0 0	2 2 2
<i>Litsea glaucescens</i> (Litgl)	0 1 0	0 1 4	0 1 1	0 0 0	0 3 2
<i>Magnolia sharpii</i> (Magsh)	3 1 1	1 1 1	0 0 0	0 0 0	2 2 2
<i>Microtropis contracta</i> (Micco)	1 1 0	1 1 0	0 0 0	0 0 0	2 2 0
<i>Myrica cerifera</i> (Myrce)	0 0 0	1 1 0	0 0 0	0 0 0	1 1 0
<i>Olmediella betschleriana</i> (Olmbe)	1 0 0	1 0 0	0 0 1	0 0 0	2 0 1
<i>Oreopanax xalapensis</i> (Orexa)	1 3 3	1 3 3	0 0 0	0 0 0	2 2 2
<i>Persea americana</i> (Peram)	3 3 3	1 2 4	0 0 0	0 0 0	2 2 2
<i>Prunus rhamnoides</i> (Prurh)	4 2 4	1 1 4	0 0 0	1 0 0	3 2 2
<i>Prunus serotina</i> (Pruse)	1 0 1	2 1 2	1 4 4	1 2 3	4 3 4
<i>Rapanea juergensenii</i> (Rapju)	3 2 3	3 3 3	0 1 2	0 0 0	2 3 3
<i>Rhamnus sharpii</i> (Rhash)	1 1 1	2 2 4	0 0 0	0 0 0	2 2 2
<i>Saurauia latipetala</i> (Saula)	1 2 1	1 4 1	0 0 0	0 0 0	2 2 2
<i>Symplocos limoncillo</i> (Symli)	0 4 2	1 1 0	0 0 0	1 0 0	2 2 1
<i>Styrax argenteus</i> (Styar)	1 4 0	1 4 2	0 0 0	0 0 1	2 2 2
<i>Ternstroemia lineata</i> (Terli)	2 2 2	3 3 4	1 1 1	1 0 1	4 3 4
<i>Verbesina perymenioides</i> (Verpe)	1 1 2	4 4 3	0 0 0	0 0 0	2 2 2
<i>Viburnum jucundum</i> (Vibju)	1 1 0	1 2 1	0 0 0	0 0 0	2 2 1
<i>Zanthoxylum melanostictum</i> (Zanme)	1 1 0	1 1 0	0 0 0	0 0 0	2 2 0
Species 1	0 0 0	1 1 0	0 0 0	1 2 0	2 2 0
Number of species	26 21 16	35 34 19	13 12 9	12 8 8	

ent traditional uses, with consequences on their natural regeneration and dispersal ability.

The adults of oak species were found in a variety of habitats (*Q. laurina* was dominant in the more hu-

mid habitats, *Q. rugosa* and *Q. crassifolia* in intermediate conditions, and *Q. crispipilis* in the driest sites), but their dominance was higher in the canopy of stands in mesic habitats. However, seedlings and sap-



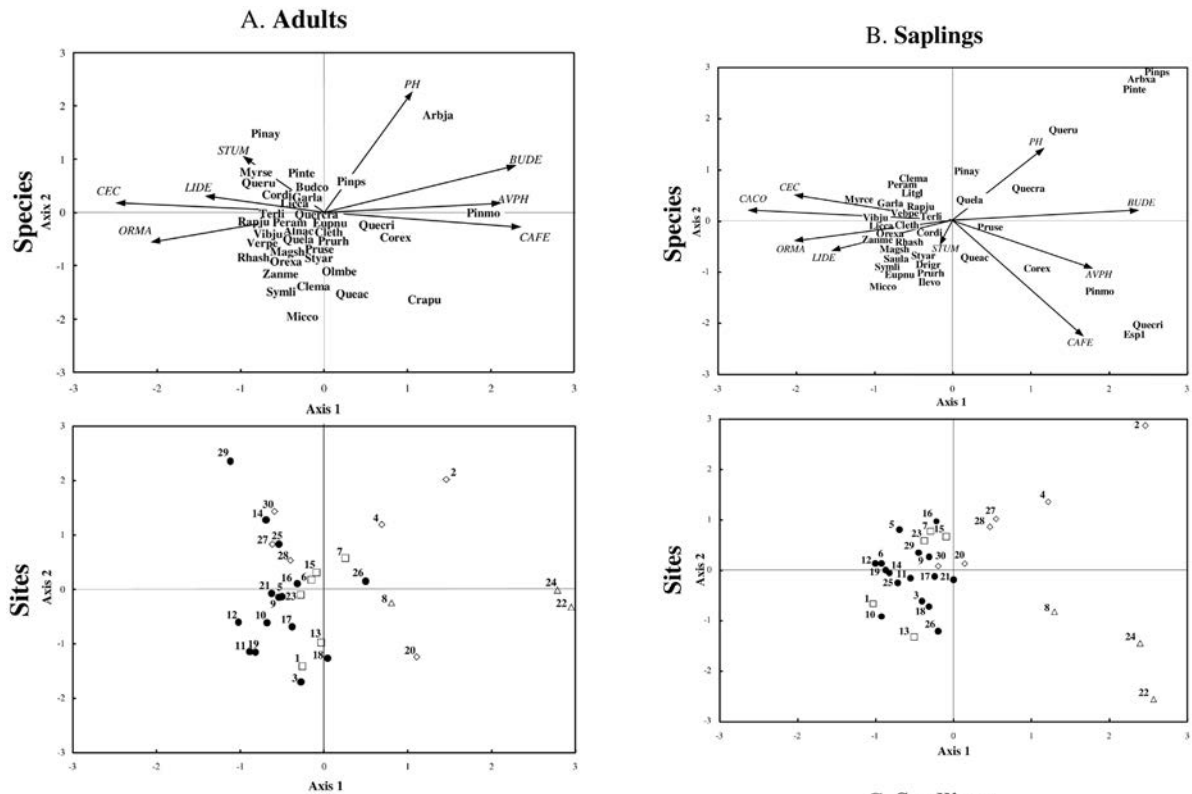


Figure 6. Ordination diagram for sites and species. Identification of environmental variables as in Table 4. Identification of species as in Table 3. Sites are grouped according to classification analysis: open squares (group I), filled circles (group II), open diamonds (group III), and open triangles (group IV).

lings of oak species (including *Q. laurina*) were mostly found under rather open canopies dominated by pines, confirming the favorable effect of incomplete canopy openness (or forest edges) reported in studies on germination and/or establishment of *Q. petraea* (Shaw 1968; Kollmann and Schill 1996), *Q. robur* (Andersson 1991), *Q. crispipilis* (Quintana-Ascencio et al. 1992), *Q. crassifolia* (Ramírez-Marcial et al. 1996), *Q. rugosa* (Cabrera García et al. 1998; López-Barrera and González-Espinosa 2001; Bonfil and Soberón 2000), and *Q. laurina* (Camacho-Cruz et al. 2000). In the highlands of Chiapas oak seedlings can germinate and establish in open areas, including abandoned fields following shifting cultivation, grasslands, and early successional shrublands (González-Espinosa et al. (1991); Ramírez-Marcial et al. (1996); see also Bonfil and Soberón (2000)).

Species of *Pinus* in our study area share the same distributional range of oaks. *Pinus ayacahuite* and *P. tecunumanii* are found in the highest and more humid habitats, and *P. pseudostrobus* ssp. *apulcensis* and *P.*

B. Saplings

C. Seedlings

*montezumae* occupy relatively drier sites. However, all species of pines included in this study do not re-

Table 4. Results of canonical correspondence analysis for tree species data (A) and (B) correlations of environmental variables with axes. See Legend of Figure 6 for codes of environmental variables.

A.

Axis	Adults		Saplings		Seedlings	
	1	2	1	2	1	2
Eigenvalues	0.52	0.22	0.81	0.54	0.68	0.45
Species – environment correlations	0.94	0.75	0.97	0.84	0.94	0.86
Cummulative variance (%)						
Species:	19.1	27.2	16.5	27.5	15.1	24.9
Species – environment:	46.3	65.9	32.6	54.5	31.3	51.7

B.

Axis		Adults		Saplings		Seedlings	
		1	2	1	2	1	2
CACO	Canopy cover (%)	*	*	-0.83	0.07	-0.72	-0.04
LIDE	Litter depth (cm)	-0.48	0.06	-0.49	-0.12	-0.57	0.23
STUM	Number of stumps >10 cm dbh	-0.27	0.22	-0.10	-0.11	-0.34	0.37
CAFE	Number of cattle feces	0.69	-0.03	0.53	-0.58	0.42	-0.36
BUDE	Bulk density (10g/mL)	0.72	0.22	0.77	0.06	0.76	0.08
PH	pH	0.35	0.55	0.43	0.41	0.49	0.39
ORMA	Organic matter (%)	-0.69	-0.11	-0.64	-0.08	-0.75	0.03
AVPH	Available phosphorus (ppm)	0.63	0.01	0.58	-0.24	0.46	0.01
CEC	Cation exchange capacity (meq/100 g)	-0.81	0.02	-0.67	0.10	-0.73	0.15

\* Not included because of autocorrelation.

generate under closed oak-dominated canopies, but their seedlings and saplings may be abundant under an open pine-dominated canopy. It is well established that many species of *Pinus* may germinate and establish successfully in open areas, as those created by severe disturbance or deforestation (Richardson and Bond 1991; González-Espinosa et al. 1991). The ecological attributes of pines allowing them to become successful invaders have been noted by Richardson and Bond (1991); Binggeli (1996); Rejmánek and Richardson (1996); Richardson (1998b), including their small, alate, wind-dispersed seeds, their capacity to reproduce at an early age, and their ability to maintain high growth rates in open habitats.

Our results suggest that either pines or oaks tend to dominate on each other in the canopy of forest stands subjected to varying degrees of disturbance. However, Figure 3a suggests that basal area of *Quercus* spp. may drastically decrease when the basal area of *Pinus* spp. exceeds a threshold value. On the other hand, in stands located in the most humid habitats the oaks also tend to decrease, even if the pines are conspicuously absent. This is the case of Evergreen Cloud Forest stands, where the canopy (25–35 m) in-

cludes a high richness of species of genera like *Persea*, *Styrax*, *Clethra*, *Chiranthodendron*, *Olmediella*, *Liquidambar*, *Cleyera*, and occasional *Quercus acat-enangensis* and *Q. laurina* (González-Espinosa et al. 1997; Ramírez-Marcial et al. 2001).

#### Changes in the soil and forest floor

We have shown that changes in some soil properties can be linked to the varying dominance of *Pinus* spp. in the canopy: the pine-dominated stands had more compacted and less fertile soils. In addition, and contrary to general expectations in soils of conifer forests (e.g. Trudgill (1988); White et al. (1988); Richardson (1998b)), the soils under a dense layer of pine needle litter accumulated for several decades were less acidic. A possible explanation is based on decomposition processes where temperature, water content, porosity, and the lignin content in the litter mostly determine the levels of microbial activity (Lavelle et al. 1993). In our study sites the prevailing temperatures (usually are 13–14 °C, only occasionally > 16 °C) and humidity conditions of the soil may not allow a high microbial activity on the relatively less

degradable lignin-rich litter of pine needles (White et al. 1988). Recent work in some of our stands has documented that soils of pinelands are more compacted, drier, more exposed to higher forest floor temperatures, and have lower microbial biomass (Romero-Nájera 2000).

The regeneration of broadleaved species other than *Quercus* spp. (accounted by density of their seedlings and saplings) was significantly lower in the pine-dominated stands (Figure 4). In addition to the above-mentioned changes in soil variables, the forest floor of the pine-dominated stands typically had a more uniform litter layer (usually < 6 cm deep) than that of the oak-dominated sites (6–14 cm deep), less dead wood, and a sparser or almost absent herbaceous/shrub layer. As a consequence, it could be expected that pinelands might provide a relatively low number of safe sites for seed germination and seedling establishment, as it has been documented with nursery and field experiments by López-Barrera and González-Espinosa (2001) (for *Quercus rugosa*) and Camacho-Cruz et al. (2000) (for *Q. laurina* and several broadleaved species) in the same study region.

#### *Expansion of pines, successional change, and human disturbance*

There is evidence that *Pinus* spp. have increased their area of distribution and local dominance over that of *Quercus* spp. on mesic sites within our study area and in other mountainous regions of tropical Mexico (Jardel (1991); González-Espinosa et al. (1995a, 1995b); Vázquez et al. (1995); del Castillo-Sánchez, pers. comm.). The results of our study indicate that stands with increased dominance by *Pinus* spp. typically are species-poor and structurally simpler. Similar floristic changes due to widespread human disturbance have been documented in the eastern United States (Brender 1974; Plummer 1975; Schneider 1996), as well as in Japan and Korea (Hong et al. 1995). In some instances the Pine-Oak forests have been identified as a temporal successional stage where pines, oaks, and other hardwoods coexist (e.g. Christiansen and Peet (1981), Peet (1992) in the North Carolina Piedmont). In our study region, these floristic changes are linked to the prevailing different uses of oaks and pines. The former are usually logged at an early age to obtain firewood, while the latter are allowed to attain useful sizes for commercial timber or to meet domestic construction needs (González-Espinosa et al. 1995b).

Changes in soil and forest floor variables along a gradient of pine dominance seemed abrupt in some cases, and usually beyond a suggested threshold level (Figure 5; curve-fittings using only values < 60% RIV of *Pinus* spp. were all non-significant). We obtained our data from a set of stands that differed in their history of disturbance, and not from those at a given site following different management practices. Furthermore, we do not know at this stage if releasing the pinelands from their current low-intensity disturbance regime, will allow them to undertake successional change towards more diverse oak-dominated communities, or to maintain them, in the long term, in a new pine-dominated stable state. Chapin et al. (1986, 1987) and Pyšek (1994) have found that releasing environmental limitations (e.g. soil fertility) may not result in community level responses, as expected by successional change in non-stressed systems. Within our study area, human factors may also help to maintain the early successional pinelands, as it has been observed by Hong et al. (1995) in Korean pine forests that are traditionally managed; but see Lust et al. (1998) for the reverse situation following the abandonment of a monoculture of Scots pine.

#### *Some implications for forest management*

We report that richness and dominance of broadleaved tree species decrease as the dominance of *Pinus* spp. increases in the stand. This trend was observed for seedlings, saplings, and adults (Figure 4). In addition, the observed changes in soil and forest floor variables may have consequences on the patterns of recruitment and establishment of tree species along a successional series leading to oak-dominated forest. Species such as *Magnolia sharpii*, *Persea americana*, *Cornus disciflora*, *Rhamnus sharpii*, *Clethra macrophylla*, *Drimys granadensis*, and *Styrax argenteus* appear to be favored by a closed oak-dominated canopy that maintains cool and moist conditions at the forest floor (Camacho-Cruz et al. 2000; Romero-Nájera 2000).

We should note that abundant naturally established seedlings and saplings of *Quercus* spp. may grow under rather open pine-dominated canopies, suggesting that an eventual replacement of pines by oaks in the upper layer may occur, provided that the current regimes of differential disturbance on these two groups of species is interrupted. This would be consistent with findings by Maddelein et al. (1991), *vide* Lust et al. (1998), indicating that oaks planted under the can-

opy of a plantation of Scots pine in Belgium succeeded quite well. However, we have no evidence indicating that the whole pool of tree species typical of old-growth forests will be recovered in pine-dominated stands, provided that these are allowed to develop successionaly. Cavelier and Tobler (1998) have reported that only a fraction of the species pool could establish after abandonment of a *Pinus patula* plantation in the highlands of Colombia. In this study we found some species for which no seedlings or juveniles were found in any of the stands (e.g. *Drimys granadensis*; Table 3).

The recovery of a mixed canopy (mostly composed by *Quercus* spp.) seems to be required for the regeneration and establishment of numerous native hardwood species in our study region, and in similar tropical highland areas. The results of this study are encouraging as they indicate that current pine-invaded stands may support large populations of *Quercus* seedlings and juveniles. A mosaic landscape including fragments of mixed and oak-dominated forests (Lugo 1995; Vetaas 1997) could allow the maintenance of relatively intensive forestry areas based on *Pinus* spp., while most broadleaved trees might naturally persist.

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