# EDAPHIC FACTORS AND THE LANDSCAPE-SCALE DISTRIBUTIONS OF TROPICAL RAIN FOREST TREES

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*Abstract.* Tropical rain forests have the highest tree diversity on earth. Nonrandom spatial distributions of these species in relation to edaphic factors could be one mechanism responsible for maintaining this diversity. We examined the prevalence of nonrandom distributions of trees and palms in relation to soil type and topographic position (''edaphic biases'') over a mesoscale (573 ha) old-growth tropical rain forest (TRF) landscape at the La Selva Biological Station, Costa Rica. All trees and palms ≥10 cm diameter were measured and identified in 1170 circular 0.01-ha plots centered on an existing 50 × 100 m grid. Topographic position was classified for each plot, and slope and aspect were measured. Soil type data were taken from a previous study (Clark et al. 1998). A total of 5127 trees and palms were identified in 267 species. Detrended Correspondence Analysis and Canonical Correspondence Analysis showed that highly significant edaphic gradients were present, with swamp or highly fertile soils separated from the less fertile, well-drained upland soils. Species composition remained significantly related to topographic position when soil type was controlled for. The main floristic gradients were still significant when flooded sites were excluded from the analyses. Randomization tests on a weighted preference index were used to examine the relations of individual species to soil types and, within the dominant soil type, to topographic position. Of the 132 species with $N \geq 5$ individuals, 33 showed significant associations with soil type. Within the dominant soil type, 13 of 110 analyzable species were nonrandomly associated with one or more topographic positions.

For a variety of reasons, including issues relating to sample size and adequate edaphic characterization of landscapes, we suggest that the ~30% of species shown to be edaphically biased in this study is an underestimate of the true degree of edaphically related distributional biases. To evaluate this hypothesis will require mesoscale vegetation sampling combined with quantitative soil analyses at the same scale in a range of tropical rain forests. If edaphic distributional biases are shown to be common, this suggests that edaphically linked processes leading to differential recruitment are similarly common.

*Key words: Costa Rica; edaphic biases; edaphic gradients; landscape ecology; mesoscale landscapes; randomization tests; topographic position effects; trees; tropical rain forest; tropical soils.*

## INTRODUCTION

Two characteristics distinguish lowland tropical rain forests (TRF) from other terrestrial biomes: they harbor the highest density of tree species, and most of these species are locally rare. There can be >300 tree species/ ha in TRF (Valencia et al. 1994), and the median density of trees ≥10 cm diameter is ≤1 individual·species$^{-1}$·ha$^{-1}$ (Valencia et al. 1994, data in Lieberman et al. 1985*a*). How do all these species coexist? Are there really >300 distinct ways per hectare to partition the basic requirements of plant life; i.e., water, light, nutrients, and physical space? Or are other factors such as chance or history playing a decisive role (Poore 1968, Hubbell and Foster 1986*a*)? The answers to these questions are critical to understanding how tropical forest landscapes are organized and how they might be maintained in the future.

One route for maintaining the high local diversity of TRF trees could be nonrandom distributions related to edaphic factors (Ashton 1969, Gentry 1981). If tree species are nonrandomly distributed among edaphic patch types and patch types are mixed over the landscape, under certain conditions this could lead to higher numbers of species at the regional scale. Working at the plot or transect scale, several researchers have indeed demonstrated significant edaphic biases (i.e., nonrandom associations with the analyzed factors) of old-growth TRF plant species (Newbery and Proctor 1984, Hubbell and Foster 1986*b*, Basnet 1992, Gentry and Ortiz 1993, Tuomisto and Ruokolainen 1994, Poulsen 1996). Other studies have demonstrated broad edaphic biases at much larger spatial scales (Baillie et al. 1987, Swaine 1996).

There is an intermediate spatial scale, however, that is critical to understanding the role of edaphic effects on TRF plant communities and that has been little stud-

ied. This is the scale from ~1 to 100 km², which we term a "mesoscale landscape" (Heikkinen 1996). Landscapes of this size are larger than those investigated in most plot studies, but are smaller than major river basins. At this scale tropical forest landscapes are complex mosaics of edaphic types (Gartlan et al. 1986, ter Steege et al. 1993, Duivenvoorden 1995, Tuomisto et al 1995, Clark et al. 1998). Our goal in this research was to assess the extent of edaphically biased distributions of TRF tree species over such a mesoscale landscape.

Any landscape-level study in tropical rain forest faces two major challenges. One is unique to the tropics: the extreme rarity of most species. We addressed this issue by using highly replicated sampling and by developing randomization methods for analyzing species with low sample size. We also used multivariate analyses to assess the major gradients in species composition and to determine their environmental correlates. The second challenge is common to all studies where the objectives include landscape-scale inference: how does one take a representative sample of an entire landscape (Botkin and Simpson 1990)? Plot-based studies tend to be either unreplicated for studies of edaphic factors, or based on sites deliberately chosen to minimize topographic variation. To obtain unbiased estimates of both the vegetation and edaphic factors over our study area, a mesoscale landscape of old-growth TRF, we used a regularly spaced sample grid covering the entire area.

We found that edaphically biased distributions were common. At the same time, we discovered some important limitations of these types of analyses. This led us to consider the implications of these limitations, and to suggest that the data presented here present a minimum estimate of edaphic biases in old-growth TRF. Finally, we build on the results of this work to suggest new directions for research on mesoscale edaphic variation and its impact on the structure of TRF plant communities.

## METHODS

The study was carried out in a 573-ha area of old-growth forest (Clark 1996) at the La Selva Biological Station in the Atlantic lowlands of the Republic of Costa Rica. The area is a mosaic of several distinct edaphic zones (Sollins et al. 1994): alluvial terraces formed by contemporaneous or historic flooding, areas of residual soil formed by in-place weathering of lava flows, swamps, and infertile colluvial soils of small stream valleys (Fig. 1). Elevation within the study area ranged from ~34 to 131 m above sea level.

Trees and palms ≥10 cm in diameter were counted and identified to species or morphospecies in 1170 circular 0.01-ha plots centered on the posts of a previously established 50 × 100 m grid that covers the La Selva reserve (D. A. Clark 1998). Four people determined species identifications in the field: D. B. Clark, D. A.
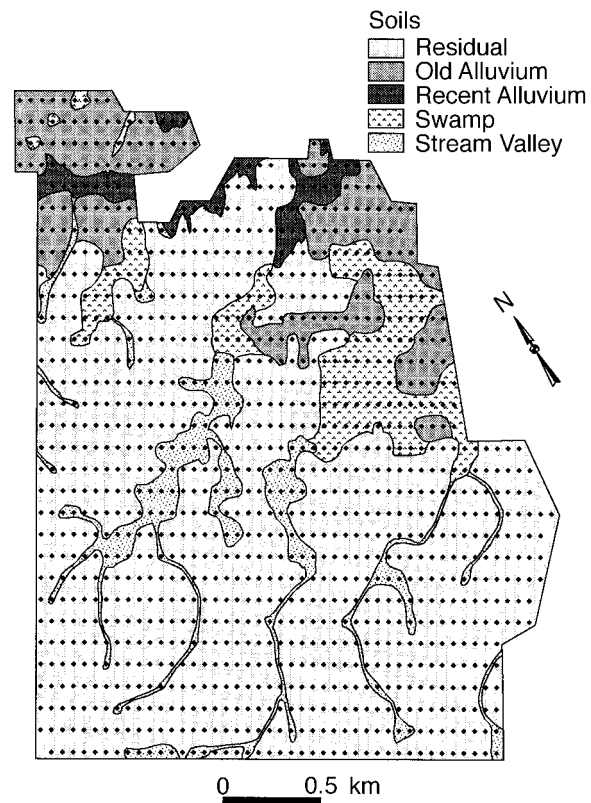


FIG. 1. The distribution of soil types and the locations of vegetation plots at the La Selva Biological Station, Costa Rica. A 0.01-ha quadrat was established at each grid point. Soils data are taken from Clark et al. (1998).

Clark, and two local technicians (Leonel Campos and William Miranda). Prior to the field work this group worked together in the La Selva arboretum and herbarium to develop a list of species that could be reliably identified in the field. Species that could not be consistently identified were always collected. A shotgun was used for collecting from taller trees. Vouchers were subsequently identified by the four field identifiers, Orlando Vargas (La Selva's Station Naturalist), Nelson Zamora (Instituto Nacional de Biodiversidad de Costa Rica), and Barry Hammel and Michael Grayum (Missouri Botanical Garden). Vouchers for all species are currently stored at La Selva. A list of the species' names, species' authorities, and a voucher number in a public collection for all species discussed in this article is given in the Appendix. A complete listing for all the species will be published separately (D. B. Clark, D. A. Clark, L. Campos, W. Miranda, and O. Vargas, *unpublished data.*)

Within each 0.01-ha plot, slope angle at the grid point was measured with a clinometer over a distance of 2 m in the direction of greatest slope, and aspect was determined with a compass. Topographic position of the plot was classified as one of four categories: flat/ridgetop, upper slope, mid-slope, base of slope/ripar-

ian. We used an existing data set on soil type that was based on sampling in each plot; development of this database is described in Clark et al. (1998). Briefly, a soil sample at 40–50 cm depth was collected adjacent to the grid point. Soil samples were classified based on color, slope position, elevation, and geographic location into one of five soil types following the concepts developed by Sancho and Mata (1987) and further amended by Sollins et al. (1994) and Clark et al. (1998). The soil types were: Residual soils (well-drained high-clay, low-nutrient soils formed by weathering of lava flows, mainly ultisols), Stream Valley soils (colluvial high-clay soils washed off the ultisol ridges, moderately drained, acidic and low nutrient content), Old Alluvial soils (well drained high-clay inceptisols of intermediate nutrient status), Recent Alluvial soils (moderately drained sandier soils of high fertility), and Swamp soils (poorly drained, acid, high-clay gleyed and mottled soils). Further details on soil classification and underlying site geology are given by Sollins et al. (1994) and Clark et al. (1998).

We used multivariate analyses to look for floristic and environmental gradients in the data, and to assess the relative importance of environmental factors in determining the observed species distributions. We used the program CANOCO (ter Braak 1987, 1988a) version 3.12 to perform a Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) on all 940 plots with at least three tree stems. We checked our results with CANOCO 4 (ter Braak and Šmilauer 1998) to confirm that the DECORANA bug (Oksanen and Minchin 1997) did not influence the outcome. DCA is an indirect gradient analysis technique (Hill and Gauch 1980) that detects gradients in species composition from species abundance data. DCA simultaneously ordinates species and samples, so that one can immediately relate species to the samples in which they occur. CCA is a direct gradient analysis technique (ter Braak and Prentice 1988) that relates species composition to measured environmental variables. Environmental variables included in the CCA were slope, aspect, elevation, soil type, and topographic variables. Because aspect is a circular variable, we transformed it into two derived variables, northness = cosine(aspect) and eastness = sine(aspect). We coded soil type and topography as dummy (1/0) variables. We performed two CCAs: one with all variables included, and a second with only soil types included.

CANOCO permits partial analyses in which the effects of covariables are factored out (ter Braak 1988b). In addition to the analyses described above, we performed a partial CCA in which the effects of soil type were factored out, and a partial DCA in which the effects of all measured variables were factored out. This partial DCA will determine if there are residual gradients in species composition that are unrelated to topography or soil types.

We developed a randomization method to analyze species' distributions in relation to soil types. For each species we calculated a weighted preference index (WPI) for each species based on the standard deviation of the proportions among samples, weighted by the number of samples per soil types, or

$$\text{WPI}_j = \sqrt{\left[ \sum_{i=1}^{S} p_i (n_{ij}/p_i - N_J/P)^2/P \right]}$$

where $i$ = soil types 1 to $S$, $S$ is the number of soil types analyzed, $p_i$ is the number of plots with soil type $i$, $P$ is the total number of plots, $n_{ij}$ the number of plots containing species $j$ on soil type $i$, and $N_j$ the total number of plots in which of species $j$ occurred. The WPI is zero for a perfect generalist (i.e., equal frequencies in all soil types) and increases with increasingly nonrandom distributions. At each sample size from 5 to 517 (the largest number of plots occupied by one species), we drew 500 random samples without replacement of that number of plots. We then compared each species' WPI to the 95th percentile of the WPIs calculated from the randomly simulated data. Because we expected Swamp soils to be the most extreme edaphic condition, we repeated this analysis for non-Swamp plots in order to examine finer degrees of distributional biases. We also experimented using the chi-square statistic as a measure of nonrandomness, and calculated the distribution of values for 500 random samples without replacement for each sample size. Although the results were virtually identical to the WPI analyses (data not shown), the chi-square confidence limit was more irregular at small sample sizes, presumably because of continuity problems at small sample sizes. We discuss only the WPI results in this paper.

We were also interested in topographic biases within a given soil type. We calculated the WPI for species' occurrence among the four topographic positions within the dominant soil type (Residual), for species occurring in at least five plots on that soil. We then compared these indices to the 95th percentile values from randomizations for each sample size based on 500 samples drawn randomly and without replacement from the Residual soil plots.

## RESULTS

### Species diversity and frequency

We encountered a total of 5127 individuals belonging to 267 species of trees and palms. Trees accounted for 261 species and 3819 individuals, while palms totaled 6 species and 1308 individuals. *Pentaclethra macroloba* (Mimosoideae) was the most common species, with 13.6% of all stems. The next three most common species were palms (Arecaceae): *Iriartea deltoidea* (7.7% of stems), *Socratea exorrhiza* (7.7%), and *Welfia regia* (7.5%). Rare species, those occurring at a density of ≤1 individual/ha, comprised 74% of the total species sample. Of the 267 species, 57 (21%) were represented by only a single individual among the 5127 stems.

### Multivariate analyses of species distribution

The first DCA axis separated samples and species occurring on Swamps and Recent Alluvial sites from those on Residual soil (Fig. 2a). Although there is considerable overlap among soil types, Swamp and Recent Alluvial sites are clustered towards the left of Axil, Residual soils are concentrated on the right, Stream Valleys predominate in the middle, and Old Alluvium is dispersed throughout. Species scores (Fig. 2b) are consistent with a wetland to upland interpretation. *Astrocaryum alatum* and *Carapa nicaraguensis* were most common in swamps, *Colubrina spinosa* most common on Recent Alluvium, and *Lonchocarpus oliganthus* preferred all the floodable habitats including Stream Valleys. On the right end of DCA axis 1 *Faramea parvibractea, Euterpe precatoria,* and *Protium costaricense* all preferred the better drained uplands. The four most frequent species (*P. macroloba* and the palms *W. regia, I. deltoidea,* and *S. exorrhiza*) occupy intermediate positions along this gradient. The beta diversity of the first axis is quite high (Table 1A), indicating a strong gradient in species composition. We could not interpret the second or third axes ecologically, but the importance of the gradients they represent are indicated by the relatively high eigenvalue and beta diversity (Table 1A). There are no consistent patterns along this axis with respect to soil type or topographic classes (not shown).

Direct gradient analysis using CCA revealed that tree species composition is related to both soil type and topography. The first CCA axis segregates steeper, higher elevation sites (usually midslopes or upper slopes on Residual soils) from flat swampy sites and sites on Recent Alluvium (Fig. 3). This reconfirms the major swamp–upland gradient found with the DCA (Fig. 2), and the species scores along the first CCA axis (not shown) are very similar to those along the first DCA axis (Fig. 2b), although in reversed order. The second CCA axis segregates soil types in the sequence Swamp, Stream Valley, Residual Soil, Old Alluvium, and Recent Alluvium and may represent either a soil texture gradient and/or a soil oxygen gradient. The first CCA axis, as well as the overall analysis, was statistically significant ($P < 0.0001$). Nevertheless, the CCA eigenvalues were substantially lower than those of the corresponding DCA, and the environmental variables only explained a small portion (2.2%) of the variance in species composition. This indicates that there is substantial noise in species composition (a certainty with small plots) and/or that other unmeasured gradients are important.

It may seem counterintuitive that the frequently flooded and chemically reduced Swamp soils are not more extreme along the first axis than the fertile, infrequently flooded Recent Alluvium. This might be because the three common palms (*W. regia, I. deltoidea,* and *S. exorrhiza*) occur occasionally in Swamps but rarely on Recent Alluvium. Alternatively, soils classified as Swamps might include slightly elevated microsites (as found by Lieberman et al. 1985b) and therefore include species more typical of upland sites.

A CCA using soils as the only environmental variable (Table 1C) revealed centroids of soil types and species scores (not shown) virtually identical to the CCA using all environmental variables, reconfirming a swamp to upland gradient. A partial CCA test (ter Braak 1988b) with soil types as covariables revealed that within soil types, topographic position is highly significantly related to species composition ($P < 0.001$ for the first eigenvalue and for the overall analysis, Table 1D). The topographic categories were arranged along the first axis in the order: Upper Slope, Midslope, Base of Slope, and Flat. The second axis separated Base of Slope from Flat. Species scores indicated preferences consistent with the topographic WPI analysis.

We also performed a partial DCA factoring out all of the environmental variables (Table 1E). The eigenvalues and beta diversities of the first two axes are quite high, implying there is much variation in species composition that was not explained by our environmental variables. The species scores and sample scores along the first partial DCA axis (not shown) are almost identical to that of the second DCA axis (Fig. 2). We were not able to interpret the gradient biologically.

To examine a shorter edaphic gradient, we excluded the fertile Recent Alluvial sites as well as the frequently flooded Swamp sites (Table 1F and G). The overall results were similar to the analysis of the full data set. The DCA was highly significant, but in the CCA environmental factors explained a minimal portion of the variation in species' distributions. Old Alluvial sites were at one end of CCA Axis 1, with the less fertile Residual and Stream Valley sites at the other extreme. The second CCA axis separated sites on steeper slopes and at intermediate slope positions from flatter sites such as terraces, hilltops, and slope bases.

### Species' distributions in relation to soil type and topographic position

Of the 132 species with five or more occurrences, 33 showed a nonrandom distribution with respect to soil type (WPI randomization analysis, Fig. 4 and Table 2). Of these 33 species, only one occurred on a single soil type; the more common pattern was a biased distribution that spanned more than one soil type. We considered the Swamp soils to be the most extreme edaphic environment due to the combination of frequent flooding, low pH, and anoxic conditions. To determine how many of the distributional biases were due to this extreme soil type, we repeated the soil preference analysis excluding all plots on Swamp soil. Of the 127 species that occurred at least five times in non-Swamp plots, 23 were significantly associated with one or more non-Swamp soils (data not shown).
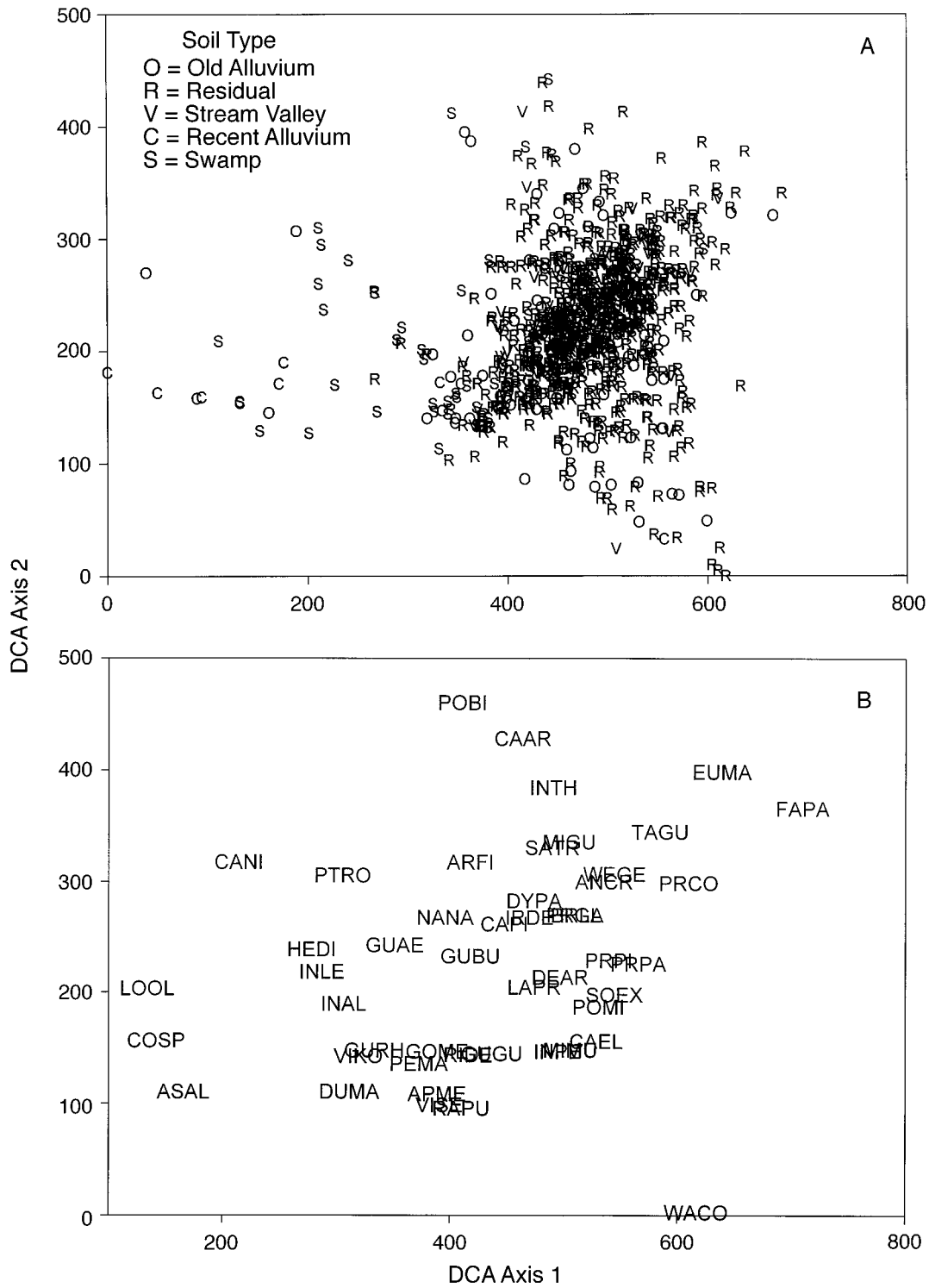
Fig. 2. Detrended Correspondence Analysis. Axes are scaled in 100 × sd beta diversity units (Hill and Gauch 1980). (A) Sample scores. (B) Species scores of the 48 most abundant species. Summary statistics are given in Table 1A. Species abbreviations in (B) correspond to the first two letters of the genus and species given in the Appendix.

TABLE 1. Results of multivariate analyses of species distributions using only species data (stem counts)(DCA) or species occurrences including environmental data (CCA).

| Analysis and data | Axis | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| A) DCA, full data set | | | | |
|   Eigenvalues | 0.404 | 0.378 | 0.330 | 0.308 |
|   Beta diversity | 6.75 | 4.42 | 6.10 | 4.01 |
| B) CCA, full data set and all environmental variables | | | | |
|   Eigenvalues | 0.105 | 0.056 | 0.044 | 0.033 |
|   (Sum of all unconstrained eigenvalues = 15.715) | | | | |
|   (Sum of all canonical eigenvalues = 0.340) | | | | |
| C) CCA, full data set, only soil type for environmental data | | | | |
|   Eigenvalues | 0.089 | 0.049 | 0.031 | 0.015 |
|   (Sum of all unconstrained eigenvalues = 15.715) | | | | |
|   (Sum of all canonical eigenvalues = 0.185) | | | | |
| D) Partial CCA, full data set, soil type factored out, topographic variables retained (four categorical variables, hence three axes) | | | | |
|   Eigenvalues | 0.033 | 0.028 | 0.012 | |
|   (Sum of all unconstrained eigenvalues after fitting covariables = 15.530) | | | | |
|   (Sum of all canonical eigenvalues after fitting covariables = 0.073) | | | | |
| E) Partial DCA, full data set, all environmental variables factored out | | | | |
|   Eigenvalues | 0.375 | 0.329 | 0.312 | 0.294 |
|   Beta diversity | 6.13 | 6.99 | 4.36 | 3.20 |
| F) DCA, only upland sites (no Swamp or Recent Alluvial sites) | | | | |
|   Eigenvalues | 0.382 | 0.335 | 0.313 | 0.291 |
| G) CCA, only upland sites, all environmental variables | | | | |
|   Eigenvalues | 0.053 | 0.047 | 0.030 | 0.021 |
|   (Sum of all unconstrained eigenvalues = 13.754) | | | | |
|   (Sum of all canonical eigenvalues = 0.212) | | | | |

*Notes:* The complete environmental data set included slope, aspect, northness, eastness, soil type, and topographic position. Beta diversity is expressed in units of standard deviations of species turnover (Hill and Gauch 1980).

Topographic positions varied nonrandomly among the five soil types. Alluvial terraces and swamps were flatter than the Residual soil areas, which occurred on moderately broken terrain. To separate the effects of soil type and topography on species distributions, we calculated the WPI for topographic position of each species within the most common soil type (Residual). Of 110 species with at least five occurrences on Residual soil, 13 had WPI values exceeding the 95% randomization values (Table 3). Preference patterns were diverse. Some species preferred ridgetops and upper slopes; others slope bases and riparian sites, while others were biased towards mid-slope positions.

## DISCUSSION

### Gradients in species composition

Both indirect and direct gradient analyses revealed that the dominant gradient in tree species composition in the old-growth portion of La Selva is significantly related to soil type. The effects of soil type and topographic position within soil types were both statistically significant. Nevertheless, the proportion of variation explained by the measured environmental variables was low. This is probably caused to a large extent by noise. Because there was only a median of four trees per plot, there is much stochastic variation in terms of which species were present or absent. This noise effect is exacerbated by the large number of tree species present at La Selva. Because of this, the location of sample scores (e.g. Fig. 2a) is likely to be less informative than the positions of species scores (Fig. 2b) and environmental variables (Fig. 3). Despite the stochastic variation, even very small plots, highly replicated at the landscape scale, were sufficient to detect major gradients in species composition.

The magnitude of the DCA eigenvalue and beta diversity suggest a strong secondary gradient in tree species composition that was unrelated to soil or topography (Table 1A). This gradient, which segregates sites with *Casearia arborea* and *Pourouma bicolor* from those with *Warszewiczia coccinea, Virola sebifera, Rauvolfia purpurascens,* and *Dussia macroprophyllata*
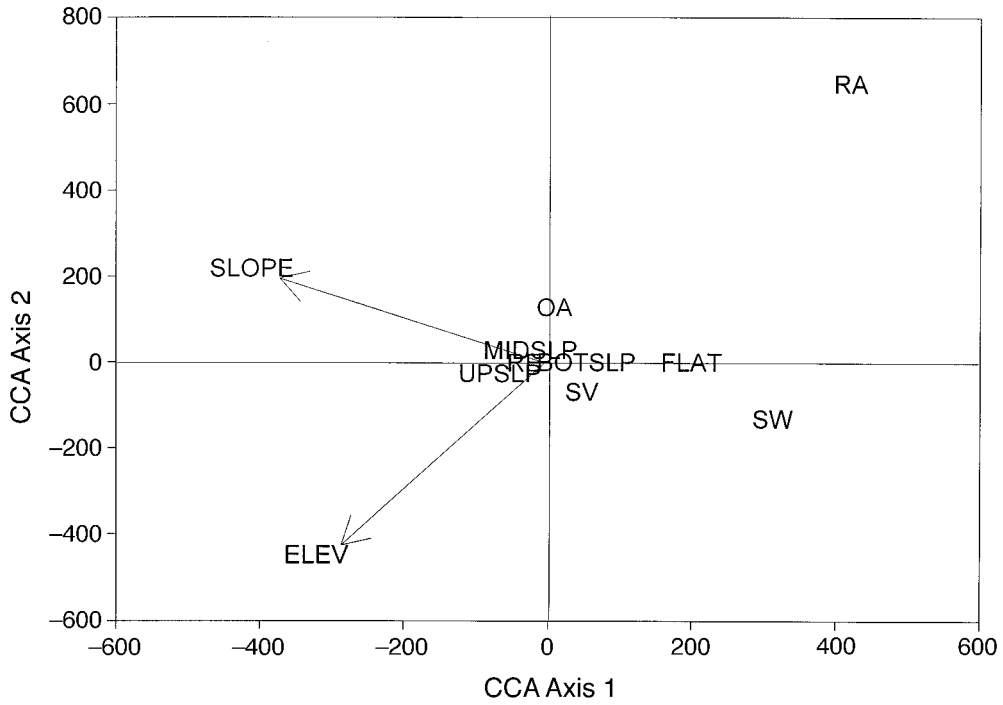
FIG. 3. Canonical Correspondence Analysis scores for environmental variables. Categorical variables (soil type, topographic position) are represented by plot centroids; continuous variables (elevation, slope) are represented by "biplot arrows." Soils types are SW = Swamp, OA = Old Alluvium, SV = Stream Valley, RE = Residual, RA = Recent Alluvium. Topographic positions are FLAT = ridgetop or flat, UP = top of slope, MID = mid-slope, BASE = base of slope.
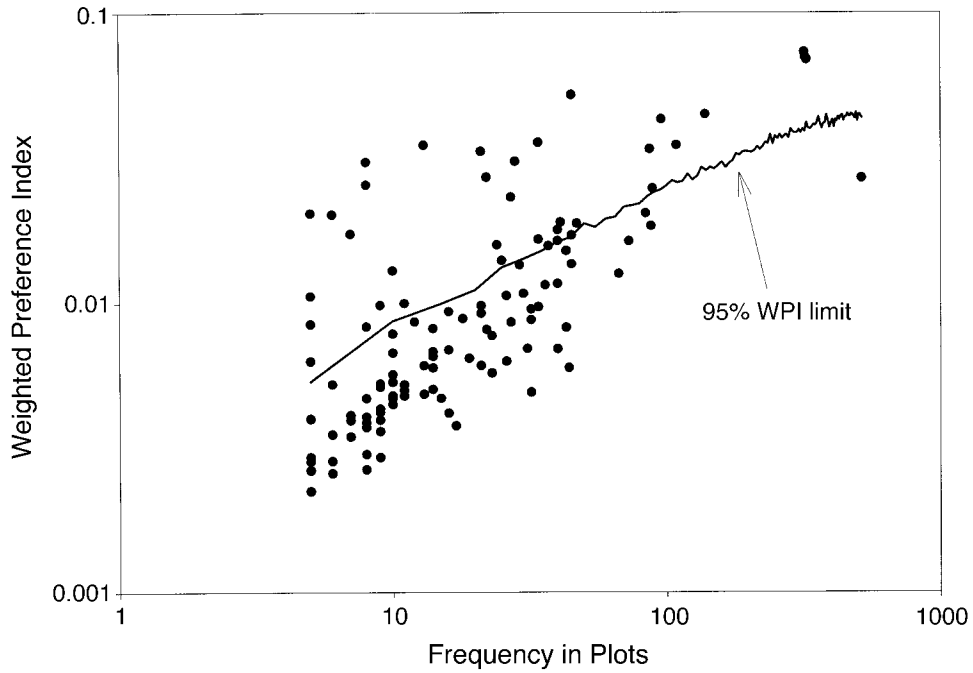


FIG. 4. The distribution of species with $N \geq 5$ individuals (132 species) in terms of Weighted Preference Indices (WPI) for soil type. The solid line indicates the 95th percentile value from randomization calculations. Points falling above the line are significantly ($P < 0.05$) nonrandomly distributed in relation to soil type (species names given in Table 2).

TABLE 2. The percentage of plots on each of five soil types occupied by trees species that were significantly ($P < 0.05$) associated with specific soil types according to their Weighted Preference Index (WPI; see Fig. 4).

| Preferred soil type | Species (Family) | % RA | % OA | % RE | % SV | % SW | Frequency |
|---|---|---|---|---|---|---|---|
| RA | *Simira maxonii* (Rubiaceae) | 15.6 | 0.7 | 0 | 0 | 1.9 | 8 |
| RA | *Colubrina spinosa* (Rhamnaceae) | 21.9 | 4.3 | 1.4 | 3.2 | 6.6 | 34 |
| RA | *Spondias* spp. (Anacardiaceae) | 12.5 | 0 | 0 | 1.1 | 0 | 5 |
| RA | *Jacaratia dolichaula* (Caricaceae) | 12.5 | 0 | 0.1 | 0 | 0.9 | 6 |
| RA | *Pleuranthodendron lindenii* (Flacourtiaceae) | 18.8 | 0 | 0 | 0 | 1.9 | 8 |
| RAOA | *Castilla elastica* (Moraceae) | 9.4 | 2.9 | 0 | 0 | 0 | 7 |
| RAOA | *Inga densiflora* (Mimosaceae) | 3.1 | 2.1 | 0 | 0 | 0.9 | 5 |
| RAOA | *Hampea appendiculata* (Malvaceae) | 6.3 | 2.9 | 0.3 | 0 | 1.9 | 10 |
| RASVSW | *Lonchocarpus oliganthus* (Papilionoideae) | 9.4 | 0 | 0.3 | 10.6 | 5.7 | 21 |
| RASW | *Otoba novogranatensis* (Myristicaceae) | 3.1 | 0.7 | 0.5 | 1.1 | 3.8 | 11 |
| OA | *Rauvolfia purpurascens* (Apocynaceae) | 0 | 8.6 | 1.5 | 1.1 | 1.9 | 27 |
| OA | *Dussia macroprophyllata* (Papilionoideae) | 0 | 5.7 | 1.5 | 2.1 | 2.8 | 25 |
| OA | *Chrysophyllum venezuelanense* (Sapotaceae) | 0 | 2.9 | 0.4 | 0 | 0.9 | 8 |
| OARE | *Warszewiczia coccinea* (Rubiaceae) | 3.1 | 15.0 | 13.8 | 7.4 | 0 | 139 |
| OARESV | *Welfia regia* (Arecaceae)† | 3.1 | 31.4 | 30.5 | 26.6 | 11.3 | 325 |
| OARESV | *Protium pittieri* (Burseraceae) | 0 | 6.4 | 11.3 | 9.6 | 0.9 | 109 |
| OARESV | *Socratea exorrhiza* (Arecaceae) | 3.1 | 31.4 | 30.5 | 21.3 | 10.4 | 319 |
| OARESW | *Protium panamense* (Burseraceae) | 0 | 10.0 | 8.4 | 1.1 | 6.6 | 89 |
| OASV | *Apeiba membranacea* (Tiliaceae) | 0 | 6.4 | 2.8 | 7.4 | 1.9 | 40 |
| OASW | *Lacistema aggregatum* (Flacourtiaceae) | 0 | 1.4 | 0.1 | 0 | 1.9 | 5 |
| RE | *Dystovomita paniculata* (Clusiaceae) | 0 | 0 | 4.8 | 2.1 | 0.9 | 41 |
| RE | *Protium costaricense* (Burseraceae) | 0 | 1.4 | 4 | 0 | 0 | 34 |
| RE | *Faramea parvibractea* (Rubiaceae) | 0 | 5.0 | 9.6 | 1.1 | 1.9 | 87 |
| RESV | *Sacoglottis trichogyna* (Humeriaceae) | 0 | 0 | 2.3 | 6.4 | 0 | 24 |
| RESV | *Euterpe precatoria* (Arecaceae)‡ | 0 | 0 | 10.2 | 13.8 | 1.9 | 96 |
| RESV | *Iriartea deltoidea* (Arecaceae) | 9.4 | 16.4 | 31.6 | 29.8 | 15.1 | 322 |
| RESV | *Minquartia guianensis* (Olacaceae) | 0 | 1.4 | 5.1 | 4.3 | 0 | 47 |
| SVSW | *Hernandia didymantha* (Hernandiaceae) | 0 | 2.1 | 0.9 | 7.4 | 10.4 | 28 |
| SW | *Pachira aquatica* (Bombacaceae) | 0 | 0 | 0.1 | 0 | 3.8 | 5 |
| SW | *Pterocarpus officinalis* (Papilionoideae) | 0 | 0 | 0 | 0 | 12.3 | 13 |
| SW | *Cecropia obtusifolia* (Cecropiaceae) | 0 | 0 | 0.6 | 0 | 3.8 | 9 |
| SW | *Carapa nicaraguensis* (Meliaceae) | 0 | 3.6 | 1.6 | 6.4 | 19.8 | 45 |
| SW | *Astrocaryum alatum* (Arecaceae) | 3.1 | 0.7 | 0.9 | 2.1 | 10.4 | 22 |

*Notes:* Soil types were Recent Alluvium (RA), Old Alluvium (OA), Residual (RE), Stream Valley (SV), and Swamp (SW). Sample sizes (number of 0.01-ha plots per soil type) were: Swamp, 106; Recent Alluvium, 32; Old Alluvium, 140; Stream Valley, 94; and Residual, 798. Frequency is the total number of sample plots in which a species occurred (of 1170 total sample plots).

† *Welfia georgii* in Clark et al. (1995).

‡ *Euterpe macrospadix* in Clark et al. (1995).

TABLE 3. Species whose Weighted Preference Index among topographic categories on Residual soil exceeded the 95% bound from 500 random draws (see *Methods*).

| | Percentage of plots of each topographic class occupied | | | | |
|---|---|---|---|---|---|
| Species (Family) | Flat-Ridgetop | Upper slope | Mid-slope | Base of slope–riparian | Frequency |
| *Ardisia fimbrillifera* (Myrsinaceae) | 0 | 0 | 2.5 | 7.1 | 19 |
| *Colubrina spinosa* (Rhamnaceae) | 4.3 | 0 | 1.3 | 4.1 | 11 |
| *Euterpe precatoria* (Arecaceae) | 13.0 | 15.1 | 9.7 | 1.0 | 81 |
| *Faramea parvibractea* (Rubiaceae) | 4.3 | 17.6 | 7.6 | 4.1 | 77 |
| *Guarea bullata* (Meliaceae) | 13.0 | 1.5 | 4.0 | 4.1 | 29 |
| *Guarea rhopalocarpa* (Meliaceae) | 0 | 1.0 | 2.3 | 8.2 | 21 |
| *Miconia multispicata* (Melastomataceae) | 8.7 | 5.4 | 1.7 | 1.0 | 22 |
| *Ocotea meziana* (Lauraceae) | 0 | 3.9 | 1.3 | 0 | 14 |
| *Pouteria torta* (Sapotaceae) | 4.3 | 1.0 | 0.6 | 4.1 | 10 |
| *Protium costaricense* (Burseraceae) | 4.3 | 7.3 | 3.2 | 1.0 | 32 |
| *Sacoglottis trichogyna* (Humeriaceae) | 0 | 1.0 | 2.1 | 6.1 | 18 |
| *Socratea exorrhiza* (Arecaceae) | 4.3 | 39.5 | 29.7 | 21.4 | 243 |
| *Welfia regia* (Arecaceae) | 21.7 | 38.0 | 27.3 | 31.6 | 243 |

*Notes:* All species ($N = 110$) with $\geq 5$ individuals on Residual soil were analyzed. Frequency is the number of plots (out of 793) on Residual soil in which a species occurred.

(Fig. 2*b*), awaits biological interpretation. Our inability to interpret such a strong gradient indicates that there is still much to learn about the basic natural history of even fairly common rain forest tree species.

### Edaphically biased distributions at landscape scales: detection and interpretation

Even with the simplified representation of environmental variation used in this study, we found a number of different patterns of edaphic biases in tree species distributions across this old-growth TRF landscape (Tables 2 and 3). Species biased towards the Recent Alluvial soil, for example, experience the highest soil fertility but must be able to tolerate occasional flooding. At the opposite extreme, species on Residual soil rarely experience flooding but are exposed to poor nutrient conditions. Species on Residual or Stream Valley soils can tolerate both low nutrients and occasional flooding. In contrast, species associated with Old Alluvium and Recent Alluvium can tolerate occasional flooding but appear to require more nutrient-rich soils.

We identified more than a dozen different patterns of edaphic biases related to soil type and topographic positions (Tables 2 and 3). These biases were mostly differential distributions among soil types or topographic positions, not complete restriction to one condition (Tables 2 and 3). A similar result was found by Clark et al. (1998) for the nine species they studied over a subset of the landscape discussed here. Nevertheless, the differences in densities for the edaphically biased species between the "preferred" and "nonoptimal" habitats were frequently 100–200%, even among the nonflooded upland soil units. Biases of smaller magnitude among the upland soils, which would still be of significant interest, would require larger sample sizes to detect.

Using the WPI randomization approach, we determined that ~30% of the 132 most common species of trees and palms were significantly nonrandomly distributed with respect to soil type and/or topographic position. For the reasons given below, we believe that our data present a minimum estimate of the prevalence of edaphic biases in TRF tree species distributions.

First, we used highly aggregated qualitative variables to examine soil and topographic preferences. We consolidated the 13 soil units recognized in our study area by Sancho and Mata (1987) into five major classes. The only soils data available for all 1170 plots were qualitative (Clark et al. 1998). There was certainly significant intra-soil unit edaphic variation that was not included in our analyses and that affected the distribution of these species. For example, Vitousek and Denslow (1987) showed significant phosphorus differences within our Residual soil unit, and Lieberman et al. (1985*b*) found significant variation in tree species compositions over small spatial scales within our Swamp soil unit. Other edaphic factors, such as microsite topography (Davies et al. 1998) and within-gap nutrient variation (Denslow
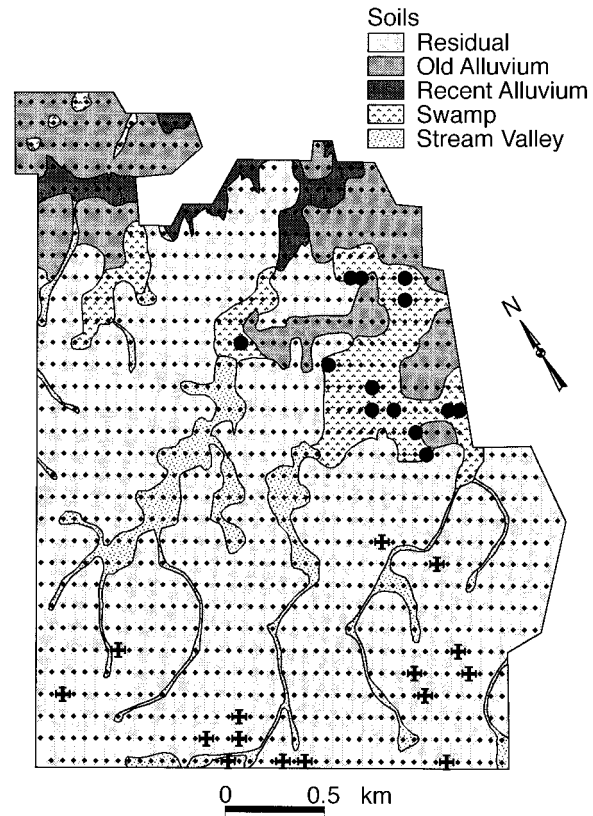


FIG. 5. The distribution of plots with *Pterocarpus officinalis* (Papilionoideae; solid circles) and *Quararibea ochrocalyx* (Bombacaceae; Maltese crosses). Compare with the distribution of points sampled shown in Fig. 1. All 13 plots with *P. officinalis* were located on Swamp soil; all 15 plots with *Q. ochrocalyx* were located on Residual soil.

et al. 1998), that could also potentially affect species' distributions, were also not considered here.

An additional obstacle to detecting distributional biases is illustrated in Fig. 5. The distribution of *Pterocarpus officinalis* fits one reasonable concept of a species with a highly biased distribution related to soil type. All 13 plots with *P. officinalis* occurred on Swamp soils, and the WPI was highly significant. At first glance, the data for *Quararibea ochrocalyx* (Fig. 5) are an even clearer demonstration of the same type of distributional bias. All 15 plots with this species are on Residual soils. The WPI value for this species, however, is not significant. The reason for this is shown in Fig. 6. Our a priori question for each species was, "Does this species occur nonrandomly in relation to the distribution of the five major soil types at La Selva?" These soil types occupied very different percentages of the landscape. Recent Alluvium accounted for only 3% of the sample plots, while 68% were on Residual soil. Statistically, for a given sample size it will always be easier to detect a bias toward a rare soil type than towards a common one. *P. officinalis* (Fig. 5) occurred only on Swamp soil, a relatively rare soil type. *Q. ochrocalyx,* on the other hand, was restricted to the

FIG. 6. The Weighted Preference Index (WPI) obtained if all individuals at different sample sizes occurred only in Residual soil, and the WPI randomization 95th percentile values. A sample of ~18 individuals occurring only on Residual soil would be necessary to obtain a significant result with this data set.
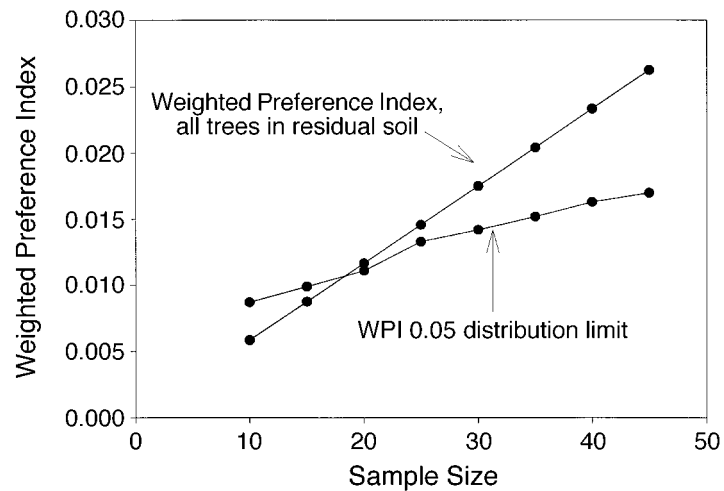
most frequent soil type. Given the frequencies of soil types in this sample, a perfect Residual soil species would have to have been present in 18 plots to be detectable as significantly biased toward Residual using the WPI randomization approach (Fig. 6). Had our a priori hypothesis been, "Is *Q. ochrocalyx* significantly associated with Residual soil vs. all other soil types?," the answer would have been "Yes" ($\chi^2 P < 0.008$).

This study clearly demonstrated that a major limitation to landscape analysis of tropical tree distributions is sample size. About half the species we sampled occurred as fewer than five individuals in the sample of 5127 trees, and 56 species (21%) occurred as singletons. This is typical for TRF inventories (Valencia et al. 1994), and for a community-wide sampling effort it is probably unavoidable. Larger sample sizes lead to greater statistical power (Zar 1996), or in this case, a greater ability to detect real edaphic biases in the mesoscale distribution of these species. The effect of increasing power with sample size was evident in the WPI analyses. The median sample size for the species detected with soil-biased distributions was 24, while the median for species not significantly related to soil types was 10 (Mann-Whitney $P_{one-tail} < 0.01$).

One approach to increasing sample size per species in inventories is to increase plot size. This clearly increases the cost of sampling for a given number of plots, but it has another less obvious consequence. With the small plot size used in this study (diameter = 11.3 m), our edaphic characterizations of each plot were likely to apply to all trees in the plot. Indeed, at all levels of analysis we found evidence that tree distributions in these small plots were significantly related to the edaphic factors we measured at this scale. Increasing the plot size would have increased the within-plot edaphic heterogeneity. There is thus a trade-off between adequate edaphic characterization for each sampled tree and plot size (Lieberman et al. 1985b, Palmer and Dixon 1990). The fine-scale structure of edaphic heterogeneity over

an entire old-growth TRF landscape has not yet been adequately characterized. However, results at several different spatial scales suggest that such heterogeneity is likely to be substantial in TRF (Richter and Babbar 1991, Johnston 1992, Tuomisto et al. 1995). When larger plots are used to study edaphic responses of TRF trees, the spatial structure of edaphic variance within these plots will need to be assessed.

There are thus several reasons why our methods should tend to underestimate edaphic biases. This expectation is consistent with the results of our multivariate analyses. All permutations of the DCA and CCA analyses showed that soil type and/or topographic position were highly significant factors affecting tree distributions. Nevertheless, the measured environmental factors accounted for very little of the variance in these distributions. Almost all of the nonrandom distributions shown in Tables 2 and 3 are differences in degree of occupancy of different edaphic conditions, not complete restriction to one soil type or topographic position. From previous studies there are additional data on edaphic biases for nine species of trees and five species of palms at La Selva. Nonrandom distributions in relation to soil type, topographic position, or slope angle were found for all five species of palms (Clark et al. 1995) and all nine species of trees (Clark et al. 1998) examined in these studies. What accounts for the much higher frequency of edaphic responses found by these studies compared to the results presented here? One reason may be taxonomic. Four of the five palms previously found to be edaphically biased by Clark et al. 1995 were also found in this study to be significantly associated with particular soil types (Table 2). Palms have been shown to be an edaphically sensitive group in other tropical sites (Kahn and de Castro 1985); generalizing from them to dicotyledonous trees may be unwarranted. Of the nine species of dicot trees examined in Clark et al. (1998), only two were found to be nonrandomly distributed in the analyses presented here. In this case, however, the

difference between the studies is purely a sample size effect. Clark et al. (1998) focused on nine species, with sample sizes from 10 to >130 times larger than those obtained for the same species in this study. The most extreme case was for *Dipteryx panamensis,* for which *N* = 240 in Clark et al. (1998) but zero in this study. In the former study, Swamp and Recent Alluvial soils were excluded. Even over this shorter environmental gradient, with large sample sizes edaphic biases were detected for all nine species. There are two main disadvantages to this intensive approach, however. One, illustrated by the case of the palms, is that generalization from a few species to the whole tree community may be misleading. Secondly, obtaining the large samples of trees used by Clark et al. (1998) involved several person-years of field work. This will not be possible for the vast majority of tropical tree species. One is therefore left with the options of studying a few species in detail, or as in the case presented here, accepting the limitations of a community-wide survey and attempting to deal with them.

### Other factors influencing landscape-scale distributions

We were unable to interpret the strong gradient in species' distributions indicated by the second axis in the DCA analyses (which was the same gradient uncovered by the first partial DCA axis). In addition to soil type and topographic position, a variety of other factors can lead to such nonrandom spatial patterns of old-growth tree species over mesoscale TRF landscapes (D. B. Clark 1999). One such factor is anthropogenic impacts. Previously we found (Clark et al. 1995) that the edible palm *I. deltoidea* is missing from one section of the old-growth on Old Alluvium at La Selva. Multiple lines of evidence pointed to past human harvesting for heart of palm in this area. Other factors that could lead to nonrandom spatial distributions include stand disturbance history, local environmental heterogeneity not reflected in the existing soils map, mass effects (Shmida and Wilson 1985), and chance (Hubbell and Foster 1986a).

Fig. 5 illustrates a type of potentially nonrandom distribution that was not detectable by our analyses. All the plots with *Q. ochrocalyx* were restricted to the southern half of the Residual soil area. With our sample size of 798 Residual soil plots, this is unlikely to be a chance occurrence. The WPI randomization method, however, did not incorporate any spatial information other than soil type per se. Clearly there is scope to develop randomizations that include proximity to soil type boundaries, watercourses, successional forests, and other landscape elements likely to influence species' distributions. Similarly, randomization approaches could be used to examine spatial relations among plots and within soil units.

The distributions within any study area may also be related, in potentially complex ways, to human activities
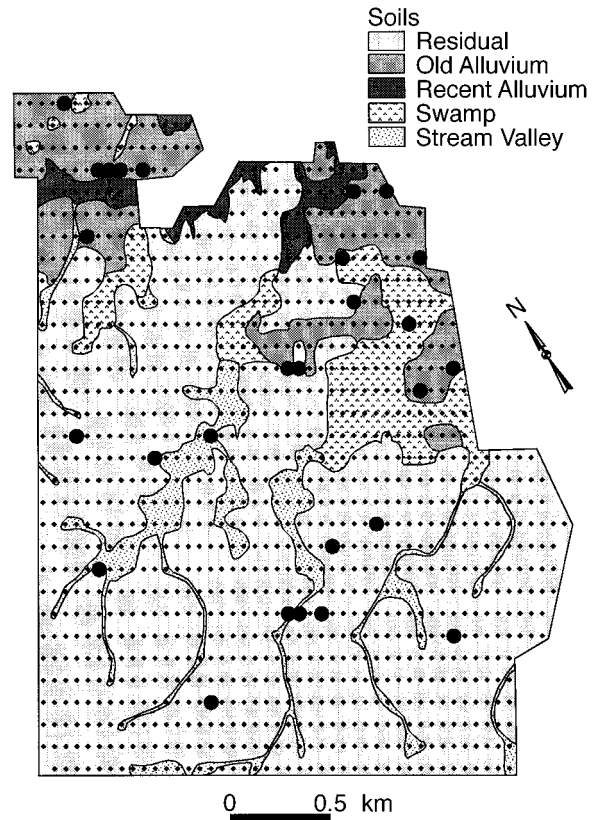


FIG. 7. The distribution of *Rauvolfia purpurascens* (Apocynaceae; solid circles) compare with the distribution of points sampled shown in Fig. 1.

outside of the study area (Janzen 1983). For example, within La Selva *Rauvolfia purpurascens* was highly significantly associated with Old Alluvium, with a density of ~9 individuals/ha on that soil compared to only 2 individuals/ha on Residual soil (Fig. 7, Table 2). Nevertheless, because Residual soil is much more extensive in the study area, 44% of the *R. purpurascens* sampled were on the "nonpreferred" soil type. Without knowing the larger regional distribution of soil types it is not possible to know what percentage of the regional population occurs on each of these soil types. This result does raise the possibility, however, that most individuals of *R. purpurascens* occur in very poor habitat (by a factor of 9/2 = 4.5) for this species. At a larger spatial scale than the study area, the species' preferred and more fertile soil type has been extensively deforested throughout the region (Butterfield 1994). Disproportionate deforestation on more fertile soils is a common pattern in tropical landscapes (Veldkamp et al. 1992, Huston 1993). It is probable that species like *R. purpurascens* once maintained much larger populations at a regional level on their preferred soil type, but that the percentage of the population on nonpreferred soils has increased with deforestation. Whether the populations of *R. purpurascens* on poorer soil were sustained by a mass effect

(Shmida and Wilson 1985) is unknown. The condition of edaphic biases toward preferentially deforested soils with remnant populations in suboptimal habitats is likely to be a common occurrence in tropical trees, and merits further study.

### Future research directions

With the approaches discussed above, even with their limitations, we have shown that nonrandom spatial distributions of tree species are common over old-growth TRF landscapes. These spatial biases are observable even when extreme environments like swamps are excluded (see also Clark et al. 1998). However, the ecological origins of these nonrandom distributions are almost unstudied. How do these distributions arise? How are they maintained? At what life stage(s) do the different structuring processes operate? How important are factors such as inter- or intraspecific competition, disturbance history, mycorrhizae, and dispersal limitation?

One line for future research is to transplant species of different edaphic biases into different microenvironments in the field (cf. ter Steege 1994, Itoh 1995). The environmental complexity of field conditions can be minimized and studied by similar experiments under controlled conditions (Vitousek and Denslow 1987, Burslem et al. 1994, Veenendaal et al. 1996, Van der Heijden et al. 1998). However, translating the results of these experiments into an understanding of species' mesoscale distributions will require understanding the distribution of edaphic factors at this spatial scale. To our knowledge there is no TRF landscape of this size (1–100 km$^2$) for which there currently exists a spatially explicit database on quantitative soil chemistry at a scale sufficient to address the hypotheses raised by descriptive studies such as this one. Here we analyzed tree species distributions using highly aggregated soil categories based on the limited soils data currently available. It would be far preferable to base such a study on analyses of soil chemistry and texture for each sample plot. This combining of mesoscale vegetation sampling with quantitative soil analyses has yet to be done in old-growth TRF. We believe this approach is likely to show that many tropical tree species, more than the 30% shown here and possibly even the majority, are nonrandomly distributed in relation to edaphic factors when analyzed at the scale of moderately sized landscapes.

If the generality of edaphic structuring of tropical rain forest tree species is confirmed, it will have major implications for understanding the regeneration of TRF tree species over mesoscale landscapes. The basic requirement for edaphic structuring to arise is differential recruitment, related to edaphic conditions, among species. There are numerous theoretical routes to differential recruitment (Huston 1994), including differential growth, survival, and dispersal. In turn, these performance differences may or may not be mediated by inter- and/or intra-specific competition with plants of the same or different sizes. Understanding the mech-

anisms that lead to differential recruitment among edaphic conditions may lead to a substantially revised paradigm of tropical rain forest regeneration.

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**APPENDIX**

Species name and authority, family name, voucher number, and location for the species discussed in this paper.

| Species name and authority | Family | Voucher number and location |
|---|---|---|
| *Anaxagorea crassipetala* Hemsl. | Annonaceae | D. Smith 586, Duke |
| *Apeiba membranacea* Spruce ex Benth. | Tiliaceae | B. Hammel and J. Trainer 10868, Duke |
| *Ardisia fimbrillifera* Lundell | Myrsinaceae | L. Campos and W. Mirando MV 129, La Selva |
| *Astrocaryum alatum* H. F. Loomis | Arecaceae | W. D. Stevens 24625, HN |
| *Brosimum lactescens* (S. Moore) C. C. Berg | Moraceae | C. Alvarado 31, INBIO |
| *Capparis pittieri* Standl. | Capparidaceae | M. H. Grayum 2090, HN |
| *Carapa nicaraguensis* C. DC. | Meliaceae | G. S. Hartshorn 1274, Duke |
| *Casearia arborea* (Rich.) Urb. | Flacourtiaceae | B. Hammel and J. Trainer 12766, HN |
| *Cassipourea elliptica* (Sw.) Poir. | Rhizophoraceae | J. Sperry 545, HN |
| *Castilla elastica* Sessé | Moraceae | J. Sperry 662, Duke |
| *Cecropia obtusifolia* Bertol. | Cecropiacae | J. Folsom 8979, Duke |
| *Chrysophyllum venezuelanense* (Pierre) T.D. Penn. | Sapotaceae | B. Hammel 10575, Duke |
| *Colubrina spinosa* Donn. Sm. | Rhamnaceae | B. Hammel 10622, Duke |
| *Dendropanax arboreus* (L.) Decne. & Planch. | Araliaceae | G. S. Hartshorn 1525, HN |
| *Dipteryx panamensis* (Pittier) Record & Mell | Papilionoideae | R. Robles 1199, HN |
| *Dussia macrprophyllata* (Donn. Sm.) Harms | Papilionoideae | B. Hammel 10340, Duke |
| *Dystovomita paniculata* (Donn. Sm.) Hammel | Clusiaceae | B. Hammel 10966, Duke |
| *Euterpe precatoria* Mart.† | Arecaceae | M. H. Grayum 7813, HN |
| *Faramea parvibractea* Steyerm. | Rubiaceae | B. Hammel 8052, HN |
| *Goethalsia meiantha* (Donn. Sm.) Burret | Tiliaceae | B. Jacobs 2939, HN |
| *Guarea bullata* Radlk. | Meliaceae | L. Campos & W. Miranda MV430, La Selva |
| *Guarea guidonia* (L.) Sleumer | Meliaceae | L. Campos & W. Miranda MV 796, La Selva |
| *Guarea rhopalocarpa* Radlk. | Meliaceae | L. Campos & W. Miranda MV 50, La Selva |
| *Guatteria aeruginosa* Standl. | Annonaceae | C. Alvarado 50, HN |
| *Hampea appendiculata* (Donn. Sm.) Standl. | Malvaceae | G. S. Hartshorn 1358, La Selva |
| *Hernandia didymantha* Donn. Sm. | Hernandiaceae | L. Campos & W. Miranda MV 87, La Selva |
| *Inga alba* (Sw.) Willd. | Mimosoideae | A. Gentry and R. Ortiz 78571, INBIO |
| *Inga densiflora* Benth. | Mimosoideae | L. Campos & W. Miranda MV 385, La Selva |
| *Inga leiocalycina* Benth. | Mimosoideae | L. Campos & W. Miranda MV 11, La Selva |
| *Inga pezizifera* Benth. | Mimosoideae | A. Gentry and R. Ortiz 78524, INBIO |
| *Inga thibaudiana* DC. | Mimosoideae | L. Campos & W. Miranda MV 220, La Selva |
| *Iriartea deltoidea* Ruiz & Pav. | Arecaceae | Chacón, Chacón, Mora 1968, HN |
| *Jacaratia dolichaula* (Donn. Sm.) Woodson | Caricaceae | Herrera 1869, HN |
| *Lacistema aggregatum* (Bergius) Rusby | Flacourtiaceae | G. S. Hartshorn 1402, HN |
| *Laetia procera* (Poepp.) Eichler | Flacourtiaceae | B. Hammel and J. Trainer 12854, HN |
| *Lonchocarpus oliganthus* F. J. Herm. | Papilionoideae | Isidro Chacon 1261, HN |
| *Miconia multispicata* Naudin | Melastomataceae | B. Hammel 12190, HN |
| *Minquartia guianensis* Aubl. | Olacaceae | G. Herrera 2250, HN |
| *Naucleopsis naga* Pittier | Moraceae | A. Gentry and R. Ortiz 78638, INBIO |
| *Ocotea meziana* C. K. Allen | Lauraceae | L. Campos and W. Miranda MV 192, La Selva |
| *Otoba novogranatensis* Moldenke | Myristicaceae | R. Aguilar 2457, INBIO |
| *Pachira aquatica* Aubl. | Bombacaceae | M. Ballestero 2, HN |
| *Pentaclethra macroloba* (Willd.) Kuntze | Mimosoideae | B. Hammel 8440, Duke |
| *Pleuranthodendron lindenii* (Turcz.) Sleumer | Flacourtiaceae | M. H. Grayum and J. Sperry 1866, HN |
| *Pourouma bicolor* Mart. | Cecropiaceae | T. McDowell 423, Duke |
| *Pourouma minor* Benoist | Cecropiaceae | D. Smith 345, Duke |
| *Pouteria torta* (Mart.) Radlk. | Sapotaceae | B. Hammel 10568, Duke |
| *Protium costaricense* (Rose) Engl. | Burseraceae | B. Hammel 8157, HN |
| *Protium glabrum* (Rose) Engl. | Burseraceae | G. S. Hartshorn 1774, HN |
| *Protium panamense* (Rose) I. M. Johnston | Burseraceae | B. Jacobs 2148, HN |
| *Protium pittieri* (Rose) Engl. | Burseraceae | J. Folsom 10078, HN |
| *Pterocarpus officinalis* Jacq. | Papilionoideae | B. Hammel and M. Grayum 14130, HN |
| *Pterocarpus hayesii* Hemsl. | Papilionoideae | N. Zamora and T. D. Pennington 1569, INBIO |
| *Quararibea ochrocalyx* (K. Schum.) Vischer | Bombacaceae | Damon Smith 521, HN |
| *Rauvolfia purpurascens* Standl. | Apocynaceae | M. Grayum 1283, HN |
| *Rinorea deflexiflora* Bartlett | Violaceae | A. Gentry, R. Ortiz, J. Bradford, and I. Shonle |
| *Sacoglottis trichogyna* Cuatrec. | Humiriaceae | B. Hammel 8444, Duke |
| *Simira maxonii* (Standl.) Steyerm. | Rubiaceae | J. H. Beach 1476, HN |
| *Socratea exorrhiza* (Mart.) H. Wendl. | Arecaceae | W. D. Stevens 24559, HN |
| *Spondias radlkoferi* Donn. Sm.‡ | Anacardiaceae | B. Hammel 10497, Duke |
| *Tapirira myriantha* Triana & Planch. | Anacardiaceae | B. Hammel 11085, HN |
| *Virola koschnyi* Warb. | Myristicaceae | F. Araya 197, HN |
| *Virola sebifera* Aubl. | Myristicaceae | F. Araya 766, INBIO |
| *Warszewiczia coccinea* (Vahl) Koltzsch | Rubiaceae | I. A. Chacon G. 595, HN |
| *Welfia regia* H. Wendl. ex André§ | Arecaceae | M. Weimann and P. M. Rich 137, HN |

*Notes:* INBIO = Instituto Nacional de Diversidad, Santo Domingo de Heredia, Costa Rica; HN = Herbario Nacional, San José, Costa Rica; La Selva = Herbarium of the La Selva Biological Station, Costa Rica; Duke = Duke University Herbarium, Durham, North Carolina, USA. Species names follow the usage of the Handbook of Costa Rican Plants Project (B. Hammell and M. Grayum, *personal communication*).

† *Euterpe macrospadix* in Clark et al. (1995).

‡ May include some *Spondias mombin L.*

§ *Welfia georgii* in Clark et al. (1995).