

Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán

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Summary

1 Data on the composition, structure and diversity of plant communities were gathered along a 1000-m altitudinal transect from tropical seasonal dry forest to cloud forest on calcareous Cerro Grande in Jalisco, México.

2 A total of 470 species, 292 genera and 103 families of vascular plants occurred in 43 samples of 0.1 ha, stratified at 100-m elevational intervals between 1500 and 2500 m a.s.l. There were 97 tree species, 76 shrubs, 70 vines, 181 terrestrial herbs, 39 epiphytes, 3 hemiparasites, 3 succulent rosette shrubs and 1 saprophyte.

3 Forest composition varied continuously with altitude, based on the Shipley & Keddy (1987) test, ordination via reciprocal averaging, and elevational trends in the Sorenson similarities of samples at adjacent altitudes, supporting the individualistic hypothesis of plant community organization.

4 Understorey herbs, shrubs and vines showed the greatest decline in species number with increasing altitude. This pattern is hypothesized to result from the more open, more frequently disturbed, and more completely deciduous canopies at lower, drier elevations. The proportion of evergreen woody plants was greater at higher altitudes, reflecting less seasonal aridity and greater soil leaching. The proportion of endozoochorous species increased with altitude, while the proportion of pterochorous and ectozoochorous species decreased, reflecting trends in the hypothesized efficacy of these mechanisms of seed dispersal.

5 Total basal area of woody plants > 2.5 cm d.b.h. and basal area per tree both increased roughly fourfold between 1500 and 2500 m.

6 Species richness decreased sharply with altitude, due mainly to decreases in terrestrial herbs, and (to a lesser extent) shrubs and vines. The average number of species per 0.1 ha declined from 134 at 1500 m to 43 at 2500 m. The numbers of species, genera and families per sample declined linearly with elevation. Species composition of samples within an altitudinal band showed greater horizontal turnover (β diversity) at lower elevations, showing that low-elevation forests are not only locally more diverse, but spatially more patchy. Community composition varies roughly six times as rapidly with elevation as with the same distance horizontally.

7 A cascading series of effects of elevation on soil fertility, anti-herbivore defences, and the level of density-dependent mortality may account for the observed drop in diversity with elevation, and would be consistent with lower β diversity and greater basal area at higher elevations.

Keywords: gradient analysis, growth-forms, seed dispersal, species turnover, Meso-American vegetation

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Introduction

Tropical forests are among the most species-rich and structurally complex plant communities on earth (Ashton 1964; Brünig 1973; Gentry 1982a, 1988, 1992; Hubbell & Foster 1985; Whitmore 1990; Gomez-Pompa *et al.* 1991; Ashton & Hall 1992; Phillips & Gentry 1994; Phillips *et al.* 1994; Condit *et al.* 1996). Recently, several detailed studies have focused on trends in the composition, structure, and diversity of tropical forests along various ecological gradients, including rainfall (Gentry 1982b, 1986, 1988), edaphic conditions (Huston 1980; Gartlan *et al.* 1986; Gentry 1988; Ashton 1989; Clinebell *et al.* 1995; Duivenvoorden 1996), successional time (Terborgh *et al.* 1996), and rate of tree mortality (Phillips *et al.* 1994). A number of studies have examined such community properties along substantial altitudinal gradients (Beals 1969; Gentry 1988; Beaman & Beaman 1990; Kitayama 1992; Nakashizuka *et al.* 1992; Kitayama & Mueller-Dombois 1994; Lieberman *et al.* 1996), but few have sampled a substantial number of elevations, and none have investigated the transition from seasonal dry forest to cloud forest in a semi-arid region of the Neotropics.

This paper reports the results of an intensive investigation of elevational gradients in forest composition, physiognomy, leaf phenology, horizontal structure, and species richness between 1500 and 2500 m elevation on Cerro Grande in the Sierra de Manantlán Biosphere Reserve in south-western México (Fig. 1). Our aim is to address the following questions.

- 1** How do community composition, structure and diversity vary with altitude and each other in species-rich tropical forests?
- 2** Do the elevational distributions of individual species in such forests conform to the individualistic hypothesis (Gleason 1917, 1926; Ramensky 1924), supported by studies on various temperate mountains (Whittaker 1956, 1960; Whittaker & Niering 1965; Peet 1980), or provide evidence for vegetational discontinuities, as has been claimed for some tropical mountains (Holdridge 1967; Beals 1969; Holdridge *et al.* 1971; Kitayama 1992)?
- 3** Which growth-forms contribute most heavily to vascular plant diversity? Do shifts in their relative abundance accord with hypotheses regarding their context-dependent contribution to competitive ability? Which families and genera dominate at different elevations?
- 4** What are the implications of the observed patterns for conservation of biodiversity in the Sierra de Manantlán Biosphere Reserve and similar montane areas in southern México?

Our approach is direct gradient analysis (Whittaker 1972, 1973; Austin 1985; Stohlgren & Bachand 1997), in which various aspects of community composition,

structure, diversity and/or dynamics are related to gradients in obvious ecological factors (e.g. elevation, slope, aspect). Direct gradient analyses have provided many insights into the nature of ecological communities, the factors influencing the distribution of individual species, the adaptive significance of particular growth forms and their contribution to competitive success in different environments, and potential controls on productivity, biomass and biological diversity (e.g. Whittaker 1956, 1960; Terborgh 1973, 1985; Peet 1978, 1980; Gentry 1982b, 1988, 1992; Austin 1985; Phillips *et al.* 1994; Lieberman *et al.* 1996; Terborgh *et al.* 1996). Gradient analyses in tropical forests can be particularly challenging, given the large number of species involved, frequent absence of local taxonomic treatments, and difficulty of access to the diagnostic parts of many canopy trees, vines and epiphytes. Such studies can also be especially rewarding, given the large number of species and interspecific comparisons available for analysis.

STUDY AREA

Forest inventories centred on a relatively undisturbed strip of montane vegetation between 1500 and 2500 m elevation on Cerro Grande (2560 m) in the Sierra de Manantlán Biosphere Reserve (139 000 ha), located in Jalisco, in south-western México, roughly 50 km from the Pacific Ocean at 19°30' N, 103° 59' W (Fig. 1). After field reconnaissance and visual interpretation of aerial photographs, topographic maps and satellite images, the altitudinal transect was located on the west flank of Cerro Grande, based on the presence of a continuously forested and relatively undisturbed landscape, limited variation in exposure and slope aspect, absence of ravines, and workable (< 70%) slope inclinations over a compact elevational gradient.

GEOLOGY

Unlike the volcanic Sierra de Manantlán proper to the west, Cerro Grande is a calcareous, mostly Cretaceous flat-topped massif. It is clearly delimited from the surrounding landscape by bedrock geology and a surrounding network of rivers and seasonal streams. Between 400 and 2000 m, the slopes are steep ($\approx 45^\circ$) but fairly regular, and locally dissected by many shallow ravines that run nearly parallel to each other. On the plateau above 2000 m, slopes are much gentler. The landscape includes a diversity of geological features typical of a karstic topography, including towers and hundreds of large sinkholes and caves (CET-ENAL 1975–76; Lazcano 1988). Despite a calcareous bedrock of lutite, calcite and dolomite, most soils on Cerro Grande are derived from volcanic ash; these include andosols and cambisols on the plateau, and lithosols and regosols on the steep surrounding slopes (Lazcano 1988). Soils derived from calcareous

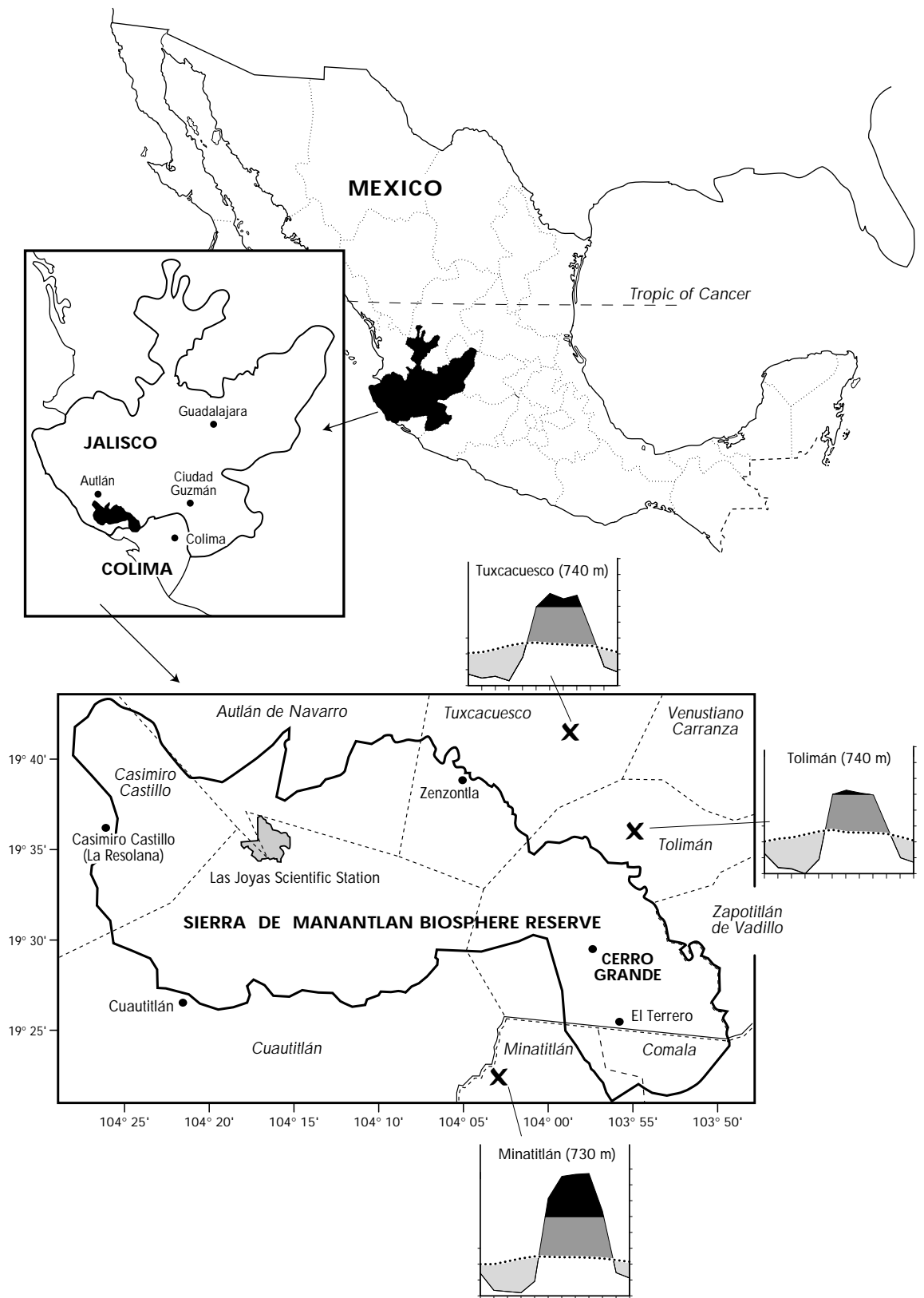


Fig. 1 Location of Cerro Grande and the Sierra de Manantlán Biosphere Reserve in south-western México. Climatic diagrams show monthly means of temperature and precipitation, according to the conventions of Walter (1985).

material are confined to very small areas along the transect, mainly terra rosa around sinkholes.

CLIMATE

Conditions on the Cerro Grande transect range from tropical warm subhumid to mild subhumid (Martinez *et al.* 1991); frost can occur frequently in winter at higher elevations. Mean annual temperatures vary from 16° to 24°C, based on a lapse rate of 0.4°C per 100 m. Rainfall occurs mainly from mid-June to early October, with a harsh dry season from late January to early June (Fig. 1). Mean annual precipitation at lower elevations decreases from ≈ 1500 mm in the south-west to ≈ 700 mm near the north-eastern edge of Cerro Grande (Martinez *et al.* 1991). Reliable data on precipitation are unavailable for higher elevations, but are likely to be high because large amounts of intercepted fog may be involved.

FLORA

The entire 140 000-ha Sierra de Manantlán Biosphere Reserve (400–2860 m a.s.l.) supports 180 families, 900 genera and over 2770 species of vascular plants; some species remain to be described, and many more to be discovered (Vázquez *et al.* 1995). Endemism is high. According to preliminary studies by Hernandez (1995), about 11% of species are restricted to western México, 3% to the state of Jalisco, and 1.2% strictly to Manantlán. Included in the latter are economically promising species such as perennial teosinte (*Zea diploperennis*), a wild relative of maize (Iltis *et al.* 1979), and Guzman's cottonwood (*Populus guzmanantlensis*), a highly productive tree and potential tropical pulpwood producer (Vázquez & Cuevas 1989). The flora of Cerro Grande was botanically unknown until recently, with significant explorations beginning only in 1986 as part of the Flora de Manantlán project (Vázquez *et al.* 1995) and the current study. Though phytogeographical data are still being compiled, it appears that Cerro Grande harbours several narrow endemics not found elsewhere, including *Sideroxylon* sp. nov. (Sapotaceae) (J.A. Vázquez G., unpublished data), *Cheilanthes pellaopsis* Mickel (Adiantaceae), *Pittocaulon hintonii* var. nov. (Asteraceae) (B. Clark, unpublished data), and *Salvia santanae* and *S. vazquezii* (Lamiaceae) (H. H. Iltis, unpublished data) (Vázquez 1995).

VEGETATION

Plant cover on Cerro Grande ranges from tropical seasonal dry forest at low and middle elevations (< c. 1900 m) to tropical cloud forest (montane rain forest) at higher elevations (Vázquez *et al.* 1995). Previous studies of plant communities on mountains near Cerro Grande have largely been descriptive and quali-

tative in nature (Rzedowski & McVaugh 1966; COTECOCA 1979; SPP 1981; Guzmán 1985; Vázquez *et al.* 1990, 1995); a few are physiognomic classifications based on aerial photography (CETENAL 1975–76; Cruz 1984–90, unpublished data). Floristics of the Manantlán cloud forests and their relation to similar communities elsewhere in México and the Neotropics are discussed by Vázquez (1995), Santiago & Jardel (1995), and Jardel & Santiago (1995) and have also been addressed in a number of unpublished theses. Studies on succession, fire, disturbance, and the role of conservation in the surrounding Sierra de Manantlán have been reported by Saldana & Jardel (1991) and Sanchez & Garcia (1993).

The study transect on Cerro Grande was located above the lowlands most heavily disturbed by humans, notably via anthropogenic fire, browsing by livestock, charcoaling, logging, and the gathering of *Dioscorea* roots and *Helicocereus* fruits. Several of these activities were widespread below 1000 m, particularly to the south-east of Cerro Grande, due partly to the access provided by a railroad laid down early in this century. However, the steep topography and remote location of most of the transect on the north-west slopes of Cerro Grande, and the cool, wet climate and unproductive conditions at its upper end, appear to have limited – but not completely excluded – overt human impacts on the vegetation in our study sites (see Results).

Methods

FIELD SAMPLING

During 1992–93, a total of 43 study sites were located between 1500 and 2500 m on the Cerro Grande transect. There were five sites in each 100-m altitudinal belt from 1900 and 2500 m. Much greater effort is required to sample the highly diverse stands at lower elevations, so only two sites were studied in each 100-m altitudinal belt between 1500 and 1800 m. Each 0.1-ha study site consisted of ten 0.01-ha circular quadrats placed in a stratified random design within a 48 m × 60 m plot; centres of potential quadrats (each 11.28 m in diameter) were spaced 12 m apart on a 4 × 5 grid, so as to avoid any overlap between adjacent quadrats. Sites at a given elevation were placed lengthwise in an array along the contour line, with 100-m horizontal intervals between site centres; all sites were located in relatively undisturbed vegetation with a closed or nearly closed canopy, on relatively smooth, west-facing slopes lacking ravines or other major erosional features at any elevation.

All vascular plant species within a quadrat were tallied by presence/absence; woody individuals > 2.5 cm d.b.h. rooted within the quadrat were tallied by species and basal area (BA), with the latter measured by tape at breast height. Growth-form (tree,

shrub, herb, vine, epiphyte), diaspore type, and leaf phenology (evergreen, semi-deciduous, deciduous) of each species were noted in the field, based on observations made during two summers of ecological sampling and a more extensive period of collecting associated with producing the local flora (Vázquez *et al.* 1995). Plants were identified in the field whenever possible, but in doubtful cases vouchers were collected and deposited in the herbaria of the Universidad de Guadalajara-Costa Sur (ZEA) and the University of Wisconsin-Madison (WIS). Species determinations were made by the senior author, the staff of ZEA and WIS, or by specialists in the taxonomic groups involved. Nomenclature followed Vázquez *et al.* (1995), which cites voucher specimens from the Sierra de Manantlán for almost all the taxa in this study; vouchers for recently named or problematic species are cited in the Appendix, which can be found in the *Journal of Ecology Archive* on the World Wide Web.

At each elevation in 1998, observations were made in ten 10-m² quadrats on the occurrence of different kinds of natural (*) and human-related (†) disturbance. These included the *numbers* of (1) browsed or grazed plants*†, (2) fallen woody stems*, (3) cattle droppings†, and (4) diggings for *Dioscorea* roots†, as well as the *presence/absence* of (5) cattle footprints†, (6) cattle trails†, (7) evidence of fire (e.g. charred tree stems) during the past 30 years†*, (8) stumps†, (9) evidence of past maize culture†, (10) evidence of wood extraction†, (11) gathering of *Heliocereus* fruits†, (12) antler rubs*, (13) natural salt-licks*, and (14) soil/peat extraction†.

DATA ANALYSIS

Similarity in community composition was estimated for each pair of samples using the Sorenson index ($S = 1 - 2w/[a + b]$, where a and b are the numbers of species in each of two samples, and w is the number of species held in common). Elevational turnover T in woody plant composition was estimated in units of half-changes of species composition per 1000 m of elevation:

$$T = (\ln x - \ln y) / \ln 2, \quad (1)$$

where x is the Sorenson similarity between 'replicate' samples at the same elevation (inferred from the intercept of the $\ln S$ vs. elevational difference line), and y is the average similarity between pairs of samples located 1000 m apart in elevation (Whittaker & Woodwell 1973).

Tests of whether species' distributions conform to the individualistic or super-organism hypotheses of community structure were conducted by (i) visual inspection of species distributions for apparent discontinuities (ecotones) in community composition (Whittaker 1956; Peet 1978); (ii) visual inspection of elevational trends in the average Sorenson similarity ($D = 2w/[a + b]$, where a and b are the numbers of

species richness in two site samples, and w is the number of species held in common) of samples at adjacent elevations; (iii) statistical analysis of the spatial aggregation of species' elevational limits (Shiple & Keddy 1987); and (iv) regression of ordination scores of individual sites obtained via reciprocal averaging (Hill 1973) against elevation. To avoid artefacts due to changes in the area sampled with elevation, the Shiple & Keddy test was applied to data for two adjacent sites in each elevational belt.

The total density (individuals ha⁻¹), basal area (m² ha⁻¹), and basal area per tree (dm²) of woody plants > 2.5 cm d.b.h. was calculated for each site and related to elevation. The number and fraction of species with a particular growth form, diaspore type, or leaf phenology, averaged over sites at a given elevation, were separately plotted against elevation to determine trends in these aspects of community structure and their relationship to plant species diversity.

Three indices of species diversity were calculated for each site, and then individually averaged across sites within an altitudinal belt:

1 N = number of vascular species present, commonly known as species richness;

2 $e^H = \exp(\sum p_i \ln p_i)$ = modified Shannon diversity index, where p_i is the relative frequency of species i (absolute frequency of species i divided by the total of the absolute frequencies of all species, so that $\sum p_i = 1$); and

3 $e^H N$ = modified Shannon equitability index (Peet 1974). Measures of species richness, diversity and equitability were related to altitude via regression, as were numbers of vascular plant genera and families at each elevation. The 10 plant families contributing the greatest numbers of species to site (α) diversity at each elevation were identified, as were the 10 families and genera contributing the greatest numbers of species to the study transect as a whole.

To assess the degree of horizontal patchiness and its contribution to overall diversity at a given elevation, β diversity (Whittaker 1972; Bratton 1975; Pielou 1990) was calculated as the slope of the regression of the logarithm of Sorenson dissimilarity ($D = 1 - S$) against the horizontal distance between samples. This calculation differs from the usual measurement of β diversity in relating turnover in species composition not to position on an ecological gradient, but to distance within an otherwise uniform habitat. We compared our measure of horizontal β diversity with altitudinal β diversity, obtained by regressing $\ln(1 - S)$ against the vertical distance between samples in different elevational belts. Species-area curves at a given elevation were calculated using the linear (S vs. area) and power-law ($\ln S$ vs. \ln area) models (Newmark 1986). The power-law exponent z and species richness at 0.2 ha were then regressed against elevation to determine how α and β diversity vary with altitude.

Results

SPECIES DISTRIBUTIONS

The vascular flora of the elevational transect totalled 470 species in 292 genera and 103 families. Many of the species for which adequate data are available showed unimodal distributions along the elevational gradient (see Appendix on WWW), similar to the pattern usually seen elsewhere (e.g. Peet 1978; Terborgh 1985; Kitayama & Mueller-Dombois 1994; Lieberman *et al.* 1996; but see Minchin 1989). Woody species composition showed 2.8 half-changes per 1000 m of elevation on the Cerro Grande transect, compared with 1.8 half-changes per 1000 m in the

warm temperate forests of the Great Smoky Mountains (Whittaker 1973), and 4.0 half-changes per 1000 m in the cool temperate forests of the Colorado Front Range (Peet 1978, 1981).

Dominant tree species at each elevation were defined as the two taxa with the highest relative importance value (= [relative frequency + relative density + relative basal area]/3 (Curtis 1959)). The 12 species thus identified were *Heliocarpus terebinthinaceus* (Tiliaceae), *Alstonia longifolia* and *Euphorbia cotinifolia* (Euphorbiaceae), *Leucaena esculenta* (Mimosaceae), *Pouzolzia* sp. (Urticaceae), *Chiococca pachyphylla* (Rubiaceae), *Eugenia culminicola* (Myrtaceae), *Picramnia guerrerensis* (Simaroubaceae), *Zinowiewia concinna* (Celastraceae),

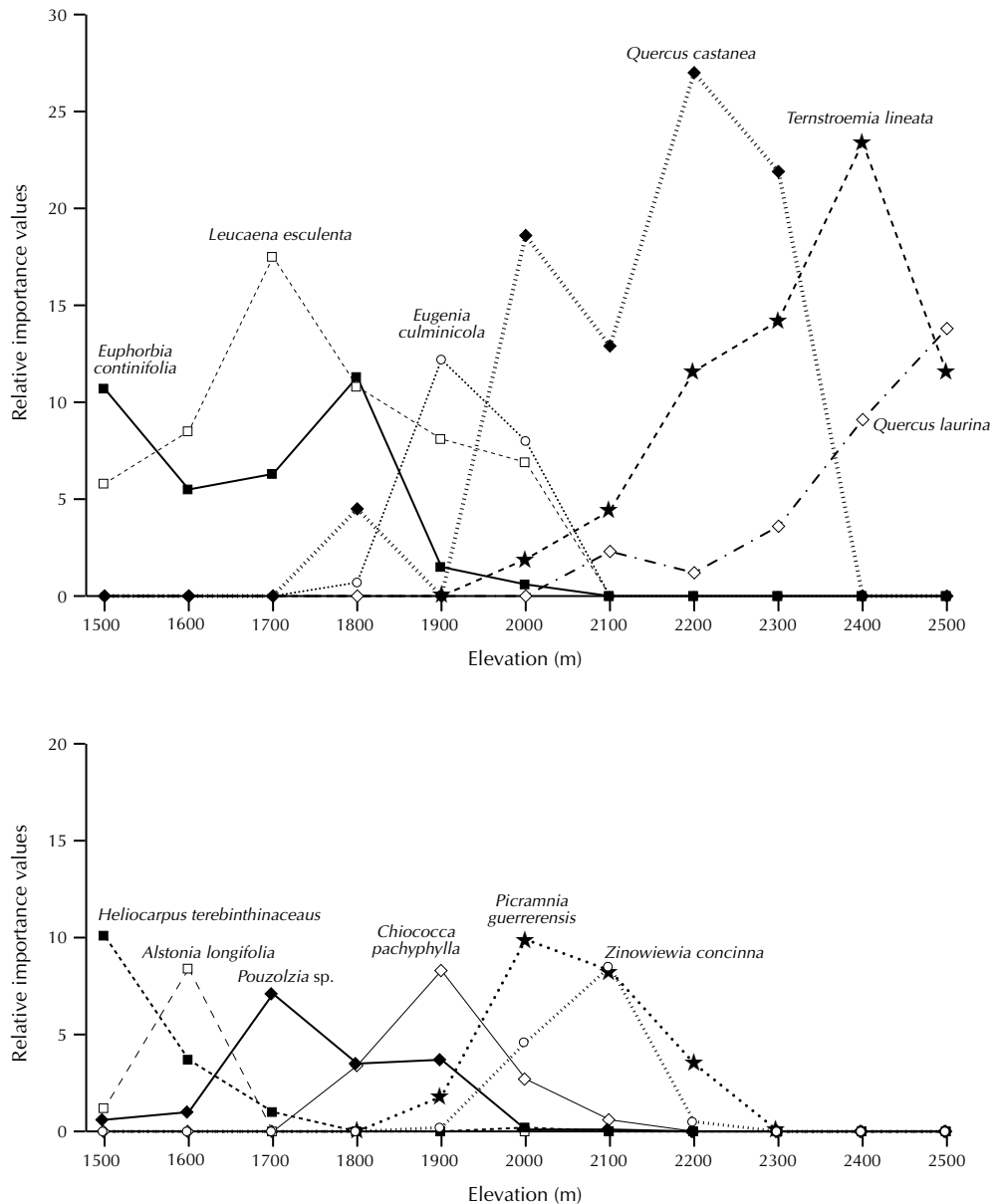


Fig. 2 Importance values (Σ [relative density, frequency, basal area]/3) of dominant tree species as a function of elevation. Upper panel shows distributions for primary dominants, which had the highest importance value for at least one elevation; lower panel shows distribution of secondary dominants, which attained the second highest importance for at least one elevation.

Quercus castanea and *Q. laurina* (Fagaceae), and *Ternstroemia lineata* (Theaceae). These dominants had distributional modes spaced in an apparently regular fashion by altitude, with importance value declining more or less smoothly above and below the modal elevation in each case (Fig. 2).

Overall, however, both woody and herbaceous species were distributed individually along the elevational gradient, with relatively little evidence for sharp discontinuities in species abundance or community composition (see Appendix). Elevational trends in the average Sorensen similarity between samples at adjacent altitudes (Fig. 3) indicated somewhat higher rates of compositional turnover between 1900 and 2000 m (corresponding to a shift from seasonal dry forests to cloud forests), and between 2300 and 2400 m (corresponding to a shift from cloud forests dominated by *Quercus castanea* to those dominated by *Q. laurina*).

However, tests for the aggregation of species's distributional limits using the technique advocated by Shipley & Keddy (1987) showed no evidence of significantly higher (or lower) rates of species turnover anywhere along the gradient (Table 1). The ratio of the number of species reaching an altitudinal limit to those present not reaching such a limit does not depart significantly from the mean, whether data from a given elevation are included (standard analysis, controls for the effects of differences in total species richness) or excluded (jackknife analysis). According to this method, therefore, the shift from tropical dry forest to cloud forest between 1900 and 2000 m is not

Table 1 Number of species reaching elevational limits (E) vs. the number not reaching elevational limits of those present (N) in adjacent pairs of elevational bands on Cerro Grande. Two adjacent sites per elevational band were included in Shipley–Keddy analyses, to avoid artefacts due to different numbers, areas or contiguity of samples at different elevations. Standard scores $((x_i - \mu)/\sigma)$ for E/N are given for an analysis including all elevations (SS₁), and a jackknife analysis excluding the elevation in question from the mean μ and standard deviation σ of E/N (SS₂). The absolute value of the standard scores never exceeded 1.96, so there was no pair of elevational bands at which there was a significant aggregation of species distributional limits

Elevation (m)	E	N	E/N	SS ₁	SS ₂
1500–1600	87	138	0.64	-0.08	-0.08
1600–1700	88	131	0.67	0.08	0.08
1700–1800	81	89	0.91	1.17	1.34
1800–1900	82	109	0.75	0.45	0.48
1900–2000	89	93	0.96	1.38	1.66
2000–2100	58	97	0.60	-0.26	-0.27
2100 ≈ 2200	29	90	0.32	-1.52	-1.88
2200–2,1 m	42	79	0.53	-0.56	-0.60
2300–2400	49	59	0.83	0.81	0.88
2400–2500	19	57	0.33	-1.47	-1.80

$$\chi^2 = 33.3, P < 0.001 \text{ for } 9 \text{ d.f.}$$

accompanied by a significantly higher rate of compositional turnover, even though the average Sorensen similarity between samples at these elevation is relatively low (see Fig. 3).

In a linear regression, altitude explained 95.1% of the variation in reciprocal ordination scores based

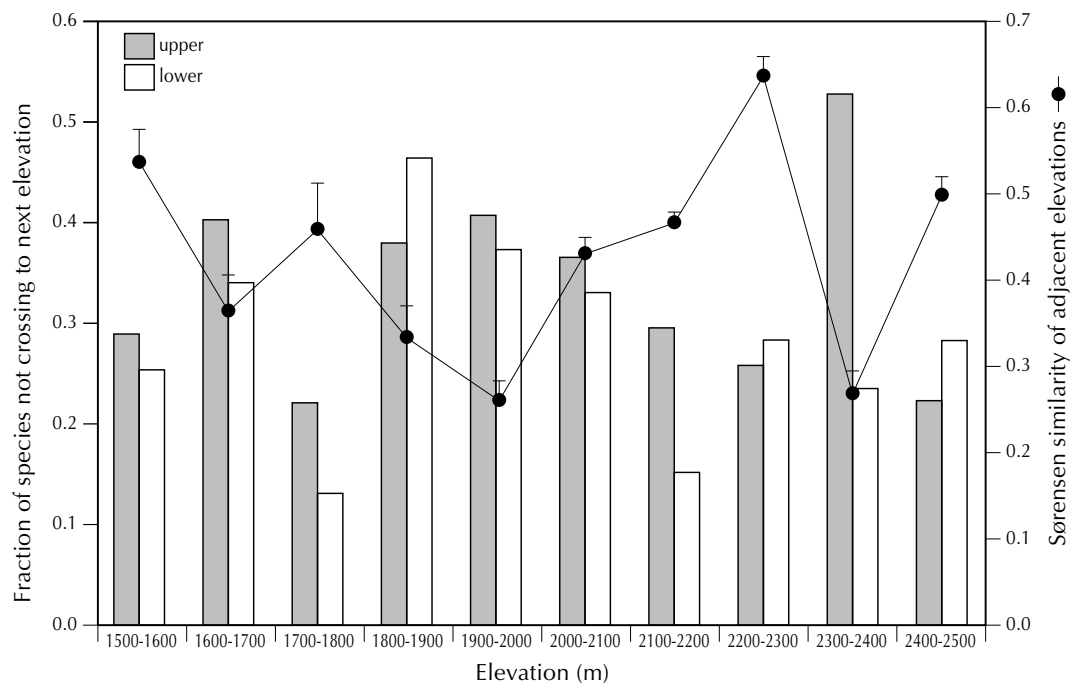


Fig. 3 Average Sorensen dissimilarity D between pairs of samples found in adjacent elevational bands, together with the number of species not crossing to the next upper elevational band (left-hand bar) and the number of species not crossing to the next lower elevational band (right-hand bar).

on community composition ($P < 0.0001$, two-tailed t -test with 41 d.f.). Together with the data just presented, this result demonstrates that (i) altitude is the dominant factor correlated with community composition along the study transect; (ii) composition varies in an essentially continuous fashion with altitude; and (iii) discrete floristic zones based on elevation do not exist on Cerro Grande.

COMMUNITY STRUCTURE

The growth-form spectrum for the entire transect consisted of 97 species of trees (21% of the transect flora), 76 shrubs (16%), 70 vines (15%), 181 terrestrial herbs (39%), 39 epiphytes (8%), 3 hemiparasites (0.6%), 3 succulent rosette-shrubs (0.6%), and 1 saprophyte (0.2%). At each elevation, herbs constituted a greater number of species, and a greater fraction of the vascular species present, than did members of any other growth-form (Fig. 4a,b). The number of herbaceous species per 0.1 ha decreased roughly fourfold with

elevation, from an average of 55.0 species in tropical seasonal dry forests at 1500 m to 13.6 species in evergreen cloud forests at 2500 m; this shift accounted for nearly half of the decline in vascular species richness over the entire gradient (Fig. 4a). The numbers of shrub and vine species decreased with elevations by comparable or greater proportions, but the absolute changes in species number in these species-poor guilds were much smaller than that seen in herbs. The absolute numbers of tree and epiphyte species showed relatively little change with elevation, with each showing a modest peak in mid-elevation cloud forests near 2100 m (Fig. 4b). The fractions of species in each growth-form showed smooth trends with elevation, with trees and epiphytes accounting for less of the flora at lower elevations, herbs and vines accounting for more, and the floristic fraction of shrubs remaining roughly constant (Fig. 4b). Tree ferns accounted for very few species/stems, unlike the cloud forests on the wetter Volcan Barva transect in Costa Rica (Lieberman *et al.* 1996).

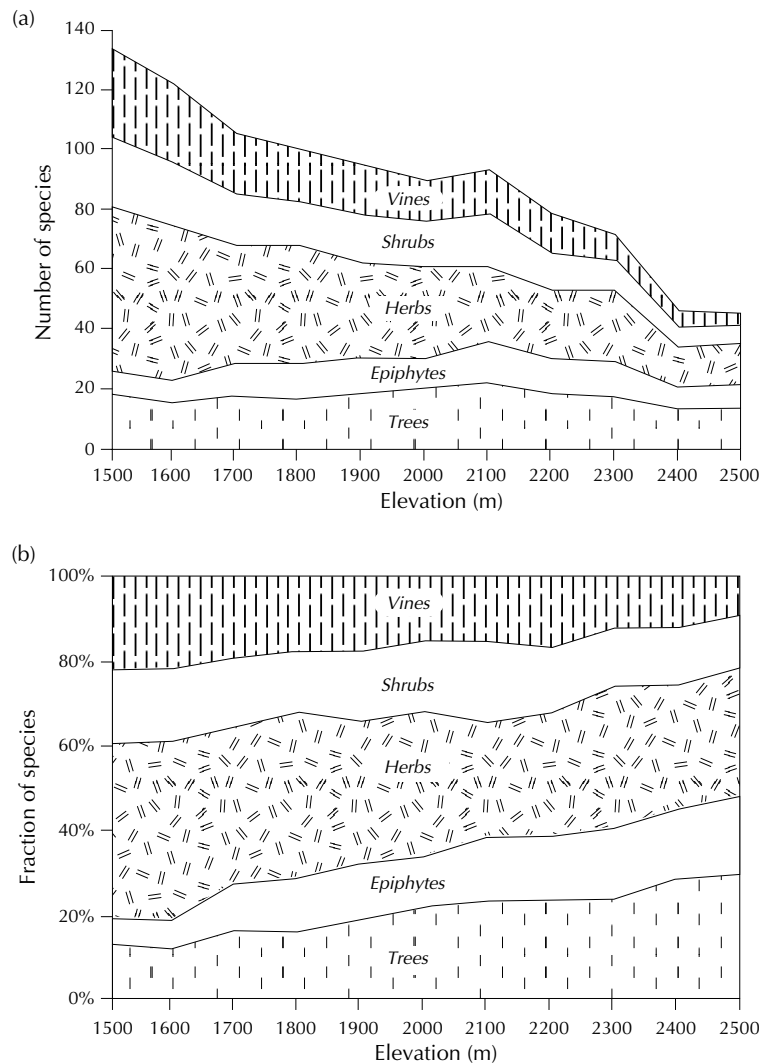


Fig. 4 (a) Numbers of species per 0.1 ha of trees, shrubs, vines, terrestrial herbs and epiphytes at each elevation. (b) Fractions of species per 0.1 ha in each growth-form guild.

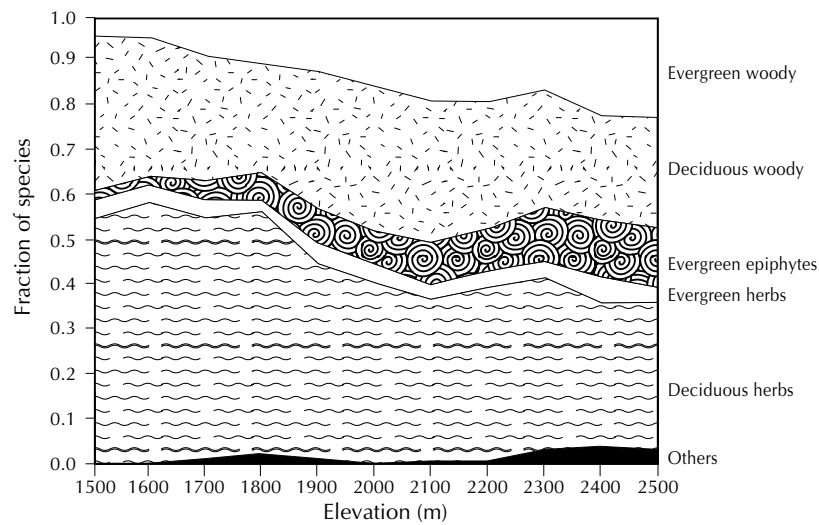


Fig. 5 Fractions of evergreen vs. deciduous species per 0.1 ha as a function of elevation.

The number and proportion of woody species that are evergreen increased sharply with elevation, rising from just above zero at 1500 m to 42% of the woody flora at the top of the transect (Fig. 5). The great majority of tree, shrub, vine and herb species seen on the transect were deciduous; a few species (including some *Quercus*) were semi-deciduous. Evergreen woody species included (i) laurel-like trees and shrubs with sclerophyllous foliage (e.g. *Arbutus* spp., *Quercus laurina*, *Sideroxylon* sp., *Symplocos citrea*, *Ternstroemia lineata*); (ii) two species of needle-leaved conifers (*Abies religiosa*, *Pinus pseudostrobus*); and (iii) a few species of deep-rooted shrubs (e.g. *Acacia acatensis*, *Zizyphus mexicana*). Interestingly, the number and proportion of herbaceous species that are evergreen decreased with elevation, a trend opposite to that seen in woody plants (Fig. 5). Evergreen herbs included essentially all the epiphytes (e.g. several bromeliads, orchids, ferns, lycopods), and a substantial number of small, fleshy terrestrials (e.g. *Achimenes*, *Begonia*, *Peperomia*, *Ponthieva*), many of which were saxicoles.

A total of 128 species on the transect bore fleshy fruits (berries, drupes, etc.) and were presumed endozoochorous (27% of the vascular flora); 140 species (30%) were barochorous (including some species with mildly ballistic seed dispersal, and oaks and a few other

species whose seeds were scatter-hoarded); 24 species (5) had burr-like or stick-tight fruits and were ectozoochorous; 173 species (37%) were anemochorous, with winged, plumed, or dust-like seeds or spores. Five species (1% of the flora) were not assignable to a dispersal type. Trees showed a significant excess of endozoochory; vines, of anemochory; herbs and shrubs, of barochory; and epiphytes, of dust-like seeds and spores (Table 2). The relative incidence of endozoochory increased with elevation, while that of ectozoochory decreased (Fig. 6, Table 2, Appendix). Although the relative proportion of anemochory remained constant, dust-like seeds and spores tended to replace winged seeds at higher elevations.

Tree basal area ($\text{m}^2 \text{ha}^{-1}$) increased nearly fivefold from 1500 to 2500 m, while tree density (individuals ha^{-1}) increased only slightly (Fig. 7). The average basal area per individual increased nearly fivefold from 1500 to 2000 m, and then remained relatively constant at higher elevations. The co-occurrence of low tree density, low basal area per tree, and low total basal area at the lower end of the transect suggests that drought or sporadic disturbance by humans (e.g. fire, firewood extraction) may be affecting the forests there, or that the natural rate of mortality relative to the rate of tree growth is higher at lower altitudes.

Table 2 Number of species with various dispersal syndromes in the five most common growth-forms on the Cerro Grande transect. Note strong association of anemochory with epiphytes and vines; of barochory with herbs and shrubs; and of endozoochory with trees ($\chi^2 = 129.4$, $P < 0.0001$ for 12 d.f.)

	Anemochory	Barochory	Ectozoochory	Endozoochory
Trees	18	19	2	57
Shrubs	12	34	7	22
Vines	33	13	4	19
Terrestrial herbs	73	73	8	25
Epiphytes	33	1	0	5

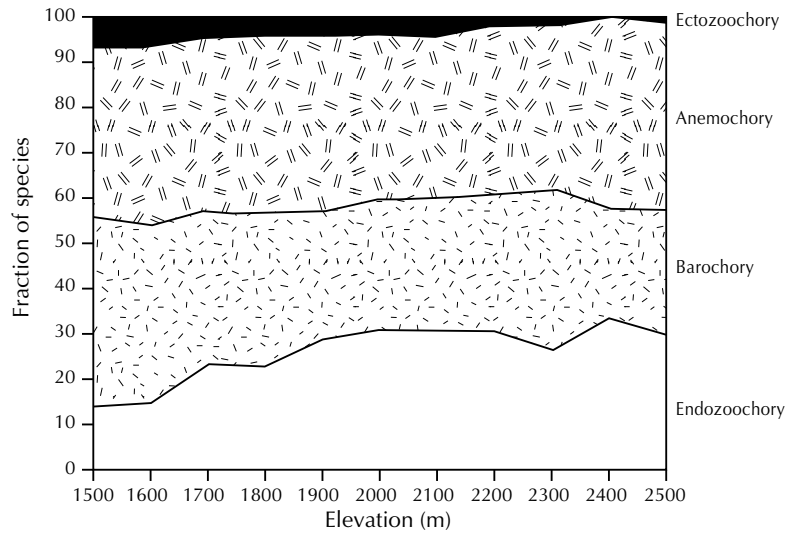


Fig. 6 Elevational gradient in the average fraction of species per 0.1 ha with each dispersal mechanism.

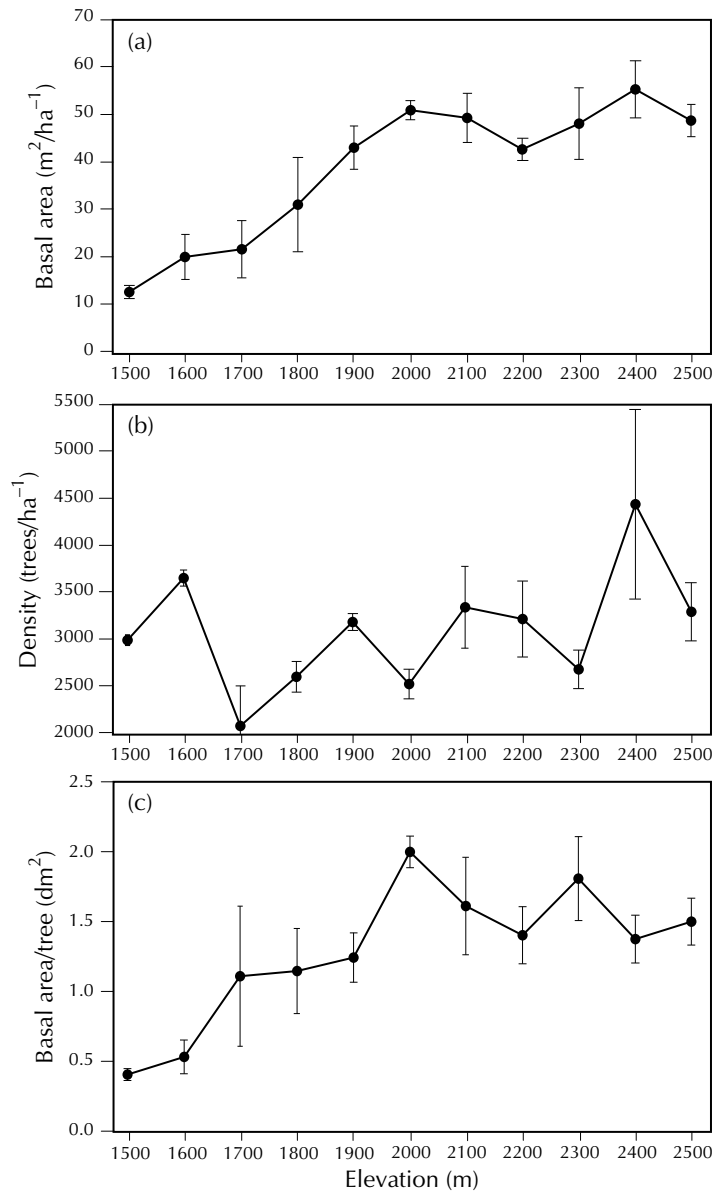


Fig. 7 Tree basal area, density and basal area per individual as a function of elevation.

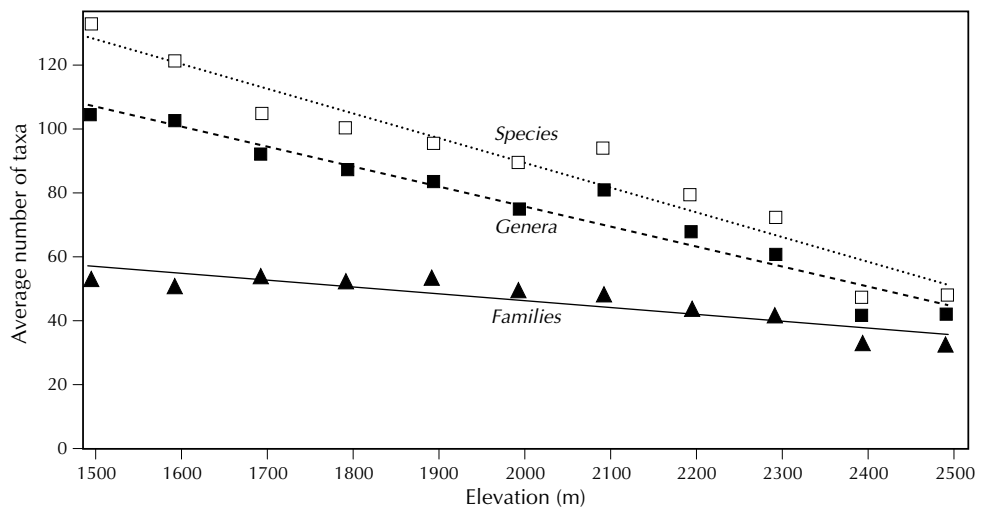


Fig. 8 Total number of vascular plant species, genera and families as a function of elevation. Lines represent least-mean-squares regressions. For species $y = 137.96 - 8.10x$, $r = -0.97$, $P < 0.001$ (9 d.f.); for genera $y = 115.09 - 6.64x$, $r = -0.97$, $P < 0.001$ (9 d.f.); and for families $y = 59.39 - 2.44x$, $r = -0.91$, $P < 0.001$ (9 d.f.).

TRENDS IN SPECIES DIVERSITY

Alpha diversity

The average numbers of vascular plant species, genera and families per 0.1 ha declined in a regular, nearly linear fashion with increasing elevation (Fig. 8). Each additional 100 m of elevation resulted, on average, in 8.2 fewer species per plot, 6.6 fewer genera, and 2.4 fewer families. Species richness and diversity of the tree layer also declined with elevation, though with somewhat greater noise about the central tendency; equitability changed very little. The distribution of abundance of tree species (data not shown) varied from roughly log-normal at lower elevations to roughly log-series at elevations above 2200 m, par-

alleling the trend observed in the Great Smoky Mountains by Whittaker (1956, 1965).

The plant families that contributed most to overall species richness varied rather little over the elevational transect, with Asteraceae being by far the largest family at almost all elevations (Fig. 9). The shift in dominance from Euphorbiaceae, Fabaceae, Burseraceae and Mimosaceae in seasonal dry forests at lower elevations, to Fagaceae and epiphytic Orchidaceae and Peperomiaceae in cloud forests at high elevations, parallels trends seen elsewhere in the Neotropics (see Gentry 1988); a trend toward high species richness of Lamiaceae in cloud forests had not previously been noted, but can also be seen in data from Hawaii (see Wagner *et al.* 1990). The average number of species

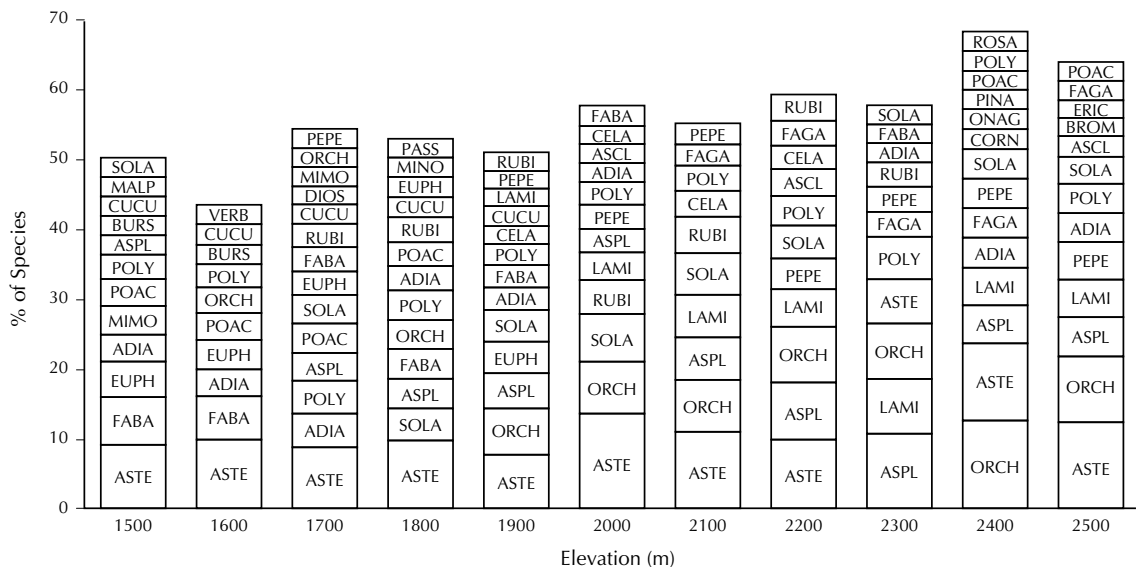


Fig. 9 Percentage of species in the 10 most diverse plant families (including ties) at each elevation. Family names are represented by their initial four letters; POLY = Polypodiaceae.

sampled per genus was quite low, averaging 1.8–3.3 over the entire transect for each of the most species-rich families. This would seem to contrast with the pattern observed in many lowland tropical rain forests, in which a few large genera of understorey elements and/or epiphytes (e.g. *Inga*, *Piper*, *Pleurothallis*, *Psychotria*, *Solanum*) contribute substantially to species richness at the 0.1-ha scale (Gentry 1988). The genera with the greatest number of species on the Cerro Grande transect are *Peperomia* (7 spp.), *Solanum* (7 spp.), *Salvia* (6 spp.), and *Poly-podium* (5 spp.).

Beta diversity

Horizontal β diversity decreased sharply, with elevation (Fig. 10), indicating a decline in the proportional turnover of species composition observed when moving a fixed distance at a given elevation. In other words, forest composition is more patchy at lower elevations, at least at the spatial scales examined (100–500 m) in this study. Given this fact, and given that individual plots are also more species-rich at lower elevations, overall species richness within an elevational belt increases more sharply as a larger area is sampled – and reaches a higher overall level – at lower elevations. Species–area curves show an excellent fit to a power-law function ($S = kA^z$). There is a highly statistically significant, regular tendency for the intercept k (a measure of diversity) but not the slope z (a measure of β diversity) to decline with increasing elevation (Fig. 11).

For woody plants, there is a regular decline in the logarithm of Sorensen similarity with increased ver-

tical separation between pairs of samples (Fig. 12). Based on the mean rates of decline in Sorensen similarity with horizontal vs. vertical distance, the compositional change for a 100-m change in elevation (≈ 200 m along slope) is roughly 6 times as large – but not in the same direction – as that for the same change in horizontal position. Hence, for the tropical forests on the study transect and for the scale of sampling used here, horizontal distance is about 17% as effective as vertical distance in fostering compositional divergence of forest tree and shrub communities and species richness at the landscape scale.

DISTURBANCE

Traces of natural and human-related disturbances were present along most of our transect (Table 3). Among the 11 sites examined, past fires were seen at or below 1800 m; digging of *Dioscorea* roots, at or below 1900 m; and gathering of *Heliocereus* fruits, at or above 2400 m. Browsing, the most common kind of disturbance (often involving natural populations of white-tailed deer), showed no regular association with elevation and was most common at 1500 m, 1900 m and 2400 m. Fallen trees – which mainly reflect a recent windstorm – were roughly twice as common on the lower half of the transect as on the upper half, and were especially high at 1700 and 1800 m. Taken as a whole, these limited data suggest that most forms of human disturbance show no clear trend with elevation, with the exception of forest fires over the past 30 years and *Dioscorea* digging, both of which are relatively common at lower elevations, close to the regional centres of human populations.

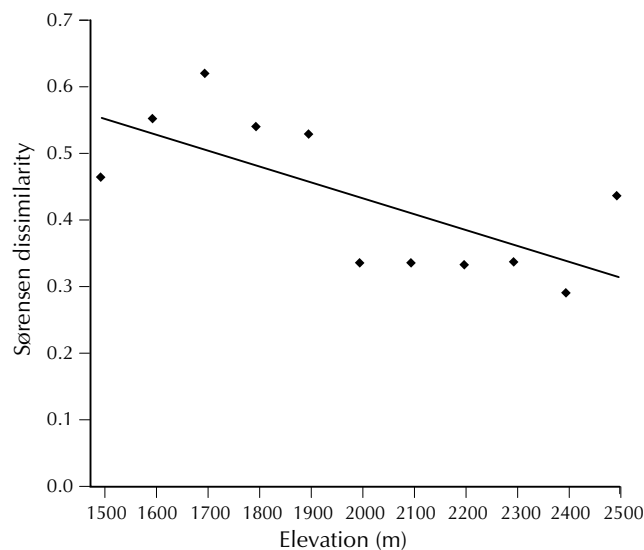


Fig. 10 Average Sorensen dissimilarity D between pairs of woody-plant samples 100 m apart horizontally, plotted against elevation. D can be considered a simple, two-point estimate of β diversity. Line represents least-mean-squares regression: $y = 0.92 - 0.0002x$, $r = -0.71$, $P < 0.05$ (9 d.f.).

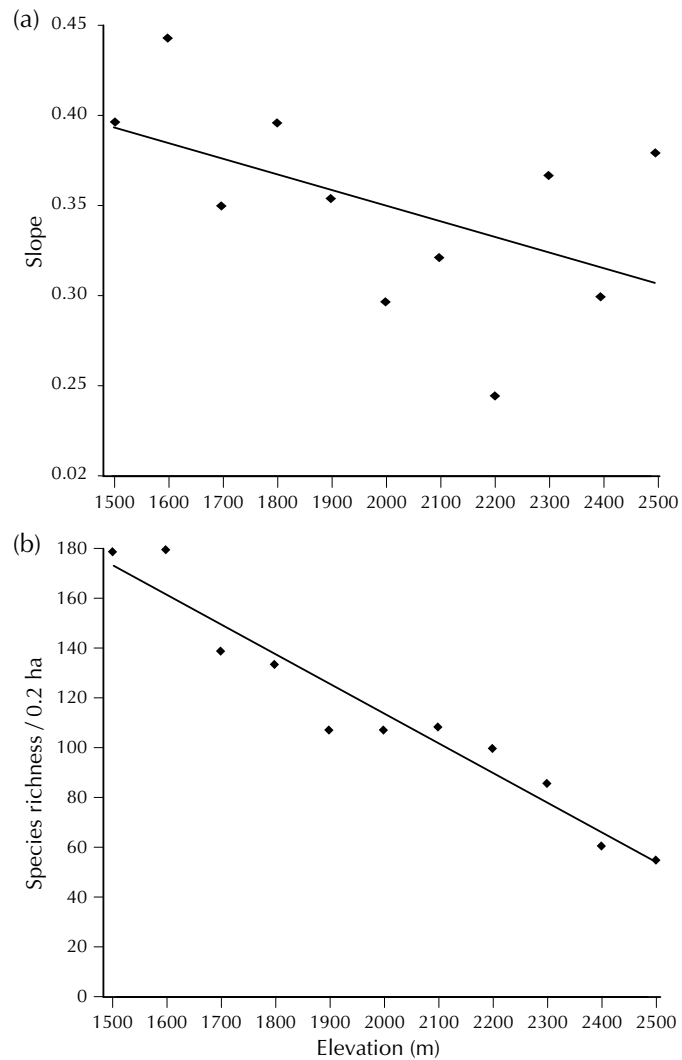


Fig. 11 Slopes and intercepts (at 0.2 ha) of log–log species–area curves at each elevation. Lines represent least-mean-squares regressions. For the slope: $y = 0.53 - 0.00009x$, $r = -0.52$, $P > 0.05$. (9 d.f.). For the intercept (species richness at 0.2 ha): $y = 353.29 - 0.1197x$, $r = -0.97$, $P < 0.001$ (9 d.f.).

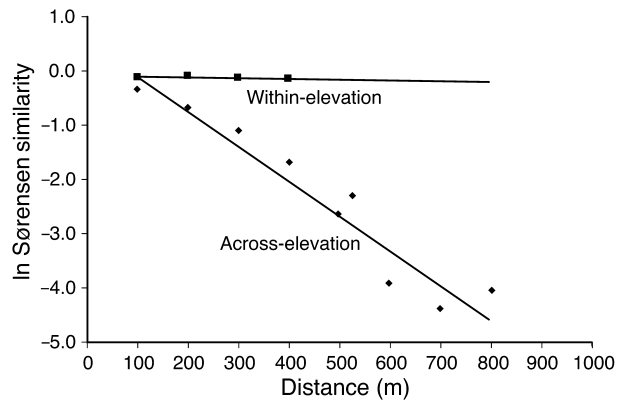


Fig. 12 Logarithm of Sørensen similarity ($1-D$) – based on presence/absence data for woody species – as a function of (i) the horizontal distance between pairs of samples at the same elevation, averaged across elevations (upper set), or (ii) the vertical distance between pairs of samples at different elevations (lower set). Lines are the least-mean-squares regressions. Slopes are measures of vertical and horizontal β diversity, respectively. For similarity within an elevation, $y = -0.0785 - 0.0002x$, $r = -0.84$, $P > 0.05$ (2 d.f.); for similarity across elevations, $y = 0.59 - 0.0065x$, $r = -0.97$, $P < 0.001$ (6 d.f.).

Table 3 Disturbance per 100 m² as a function of elevation (see text). Note apparent absence of any regular trend in total amount of disturbance with elevation, the relative high incidence of forest fire and *Dioscorea* extraction at low elevations, and the relatively high incidence of *Heleocereus* fruit harvest at higher elevations

Elevation (m)	1500	1600	1700	1800	1900	2000	2100	2200	2300	2400	2500	Total
Browsed plants	45	0	0	0	45	5	3	5	3	19	8	133
Fallen woody stems	4	6	11	8	4	2	4	2	4	1	7	53
Cattle droppings	5	0	0	0	1	0	0	0	0	2	0	8
<i>Dioscorea</i> digging	0	2	0	1	1	0	0	0	0	0	0	4
Forest fires	1	1	1	1	0	0	0	0	0	0	0	4
Cattle footprints	0	0	0	0	0	0	0	0	0	3	0	3
Cattle trail	0	0	0	0	0	0	0	1	0	0	0	1
Skimps	0	0	0	0	0	0	0	0	0	2	0	2
<i>Heleocereus</i> harvest	0	0	0	0	0	0	0	0	0	1	1	2
Firewood extraction	1	0	0	0	0	0	0	0	0	1	0	2
Past maize culture	1	0	0	1	0	0	0	0	0	0	0	2
Antler rubs	0	0	0	0	0	0	0	0	0	1	0	1
Natural salt licks	0	0	0	0	0	0	0	0	1	0	0	1
Soil extraction	0	0	0	0	0	0	0	0	0	0	1	1
Totals	57	9	12	11	51	7	7	8	8	30	17	217

Discussion

COMMUNITY COMPOSITION

The distributions of plant species along the altitudinal transect (Figs 2 and 3, Table 1, Appendix) support the individualistic hypothesis of community organization (Gleason 1917, 1926; Ramensky 1924), which posits that the distribution of each species is determined by its own ability to survive, compete and reproduce successfully in different environments, resulting in each species having its own distinctive distribution, and in community composition changing more or less continuously along ecological gradients. Numerous studies, mainly in temperate areas, support the individualistic hypothesis (e.g. Whittaker 1956, 1960; Curtis 1959; Whittaker & Niering 1965; Peet 1978; Ogden & Powell 1979; Austin 1985; Syuzo 1991; Auerbach & Schmida 1993; Palmer & Cowling 1994; Rawal, Pangtey-T. 1994). However, this report is one of the few detailed studies of community composition along substantial elevational gradients in the tropics (Beals 1969; Gentry 1988; Beaman & Beaman 1990; Kitayama 1992; Lieberman *et al.* 1996; see Terborgh 1971, 1977 and Navarro 1992 for elevational continua in tropical bird communities), is based on an unusually fine (100-m) spacing of samples along the elevational gradient, and is the only study to investigate the shift from seasonal dry forests to cloud forests, in the semi-arid Neotropics.

The staggered elevational distribution of dominant tree species (Fig. 2) is consistent with the individualistic hypothesis and with the fact that such ecological dominants are likely to be each other's most important competitors, and thus among the most important determinants of each other's distributions (Whittaker 1972). The characteristic pattern of elevational dominance by particular plant families (e.g.

Euphorbiaceae and Mimosaceae at lower elevations, Fagaceae and Orchidaceae at higher elevations) is consistent with the notion that different lineages are adapted to different ecological conditions (Whittaker 1956; Whitmore 1975; Gentry 1982a,b, 1988; Terborgh *et al.* 1996). The tendency for certain plant families to be among the most species-rich across almost the entire elevational gradient parallels a similar finding for the dominance of certain families across rainfall gradients in the lowland tropics (Gentry 1982b, 1988). The existence of such species-dominant families may reflect the high probability that plants in certain lineages may (i) acquire inter-populational barriers to mating (e.g. limited seed dispersal, variability in flower form or phenology), leading to reproductive isolation and speciation; or (ii) partition resources effectively (by habitat, phenology or successional status), leading to ecological isolation and species coexistence in sympatry.

Alternatively, the high species richness of a given family may reflect the past ability of a lineage to disperse to a remote area and then undergo an extensive adaptive radiation in the absence of many potential competitors. For example, on Hawaii the Campanulaceae – a group that is nowhere else dominant in tropical montane forests – evolved a kaleidoscopic diversity of species with different growth forms, leaf shapes and flower morphologies, and became the largest family in the native flora (Givnish *et al.* 1995; Givnish 1998a). The overwhelming species richness and varied growth forms of the Asteraceae on the Cerro Grande transect is likewise unusual for tropical montane forests (though common in open, higher-elevation communities in the Andes and East Africa), and tends to support the hypothesis that western México is perhaps the most important centre of diversification, speciation, and endemism in this family,

with nearly 3000 species so far described (McVaugh 1984; Villaseñor 1991; Turner 1996). Many members of the Asteraceae have evolved adaptations to semi-arid conditions (e.g. short life-cycle, small seeds, wind dispersal, strong chemical defences) and the group has often speciated extensively in dry regions (e.g. California, Chile), which may partly account for its success in western México.

Our results support the individualistic hypothesis, with the Shipley & Keddy test showing that no elevation has a significantly higher rate of turnover in community composition (Table 1). Sporadic ecotones along otherwise continuous gradients have been reported in other studies (e.g. Whittaker 1956; Beals 1969; Peet 1978; Ogden & Powell 1979; Stohlgren & Bachand 1997). It is important in such cases to distinguish abrupt shifts in community composition along spatial gradients (which may simply reflect abrupt shifts in ecological conditions, or the edge of a local disturbance) from abrupt shifts in composition along ecological gradients abstracted from a variety of spatial gradients. In addition, spatial and ecological scale must be weighed when describing vegetational discontinuity, because many patterns that are discontinuous at a coarse scale may appear continuous when viewed at finer scales (Whittaker 1972).

In Ethiopia, Beals (1969) found that the discreteness of the elevational zonation of vegetation increased with steepness of slope, with discontinuities on gentle slopes being practically non-existent. In Borneo, Kitayama (1992) reported marked elevational discontinuities in community composition on Mount Kinabalu. However, this result may be more a reflection of methodology than of nature, given that it was based on only 14 samples spaced at ≈ 200 -m intervals along two separate transects, over a 3600-m altitudinal gradient with extremely high β diversity. Lieberman *et al.* (1996) used a comparable density of sampling (half that used in the current study, but using larger 1-ha plots) to demonstrate continuous change in forest composition and structure with elevation in Costa Rica. In general, tests for discontinuities in community composition and structure along gradients require the study of numerous samples at closely spaced intervals. Furthermore, in tropical vegetation that displays considerable β diversity within an elevational belt, samples should be located along a spatially coherent transect (or a fully stratified series of transects) in order to avoid spurious discontinuities introduced by large horizontal displacements between samples at different elevations. In the present study, all samples were confined to a relatively narrow swath along a single slope, eliminating the possibility of detecting such spurious discontinuities. However, this approach probably also introduces a degree of compositional uniformity within elevations and compositional continuity between elevations that would not be replicated in a more extensive survey of Cerro Grande.

COMMUNITY STRUCTURE

The essentially continuous shifts in growth-form, leaf phenology, and mode of seed dispersal along the Cerro Grande gradient (Figs 4–6) provides added support for the individualistic hypothesis, and points to context-dependent shifts in the competitive advantage associated with different growth forms, leaf types, and kinds of diaspores. The greater absolute and relative numbers of vine species at lower elevations parallel a general increase in the incidence of vines at lower altitudes and latitudes (Gentry 1991). Vines are structural parasites that gain a competitive edge by allocating relatively little material to support tissue to achieve a given increase in length/height; thus, they often bear xylem vessels with large diameters, which can provide a high level of hydraulic conductivity in a slender stem (Carlquist 1991). Large vessels are inherently more subject to failure via cavitation during frost or drought (Sperry 1995), which may partly account for the lower importance of vines at higher altitudes and latitudes (Putz 1991). However, the decline in vine abundance at higher elevations on Cerro Grande does not seem explicable in these terms, given that drought is far less common at higher elevations, and winter frosts are rare except above 2300 m (F. Gutierrez, personal communication). An alternative explanation for the decline of vines in cloud forests is suggested by Givnish (1984), who proposed that the heavy allocation to roots imposed by leached, highly organic, mineral-poor soils in cloud forests (and lowland wet forests on white sands) may rob vines of much of their growth advantage. In addition, the somewhat higher incidence of human disturbance to the canopy (e.g. logging, firewood gathering, grazing) at lower elevations may favour vines, which have an advantage in mobility with which to invade and exploit ephemeral openings (Givnish 1984, 1995).

The greater absolute and relative numbers of shrub and herb species at lower elevation are probably a consequence of the more open canopy of forests at low elevations. Incomplete canopy closure in seasonal dry forests may result partly from recurrent droughts, or from a higher incidence of human disturbance. A more open canopy allows more light into the understorey, and may permit understorey herbs and shrubs to exceed their ecological compensation point (Givnish 1988, 1995). Whittaker (1960) provided support for such a 'structural constraint' on plant diversity, documenting a much higher absolute and relative diversity of shrubs and herbs under the relatively open canopies of forests on infertile or drought-prone sites in the Siskiyou Mountains than under closed canopies on fertile, well-watered sites.

The representation of herb species decreases much more than that of shrubs in ascending from 1500 m to 2100 m, but then the number of shrub species decreases more than that of herbs between 2100 m and 2500 m (Fig. 4). Shrubs tend to have deeper root

systems than herbs, and should be more drought-tolerant, at least in areas that receive a moderate amount of precipitation (Givnish 1995). However, the difference between precipitation and potential evapotranspiration is so great at the bottom of the Cerro Grande transect that there may not be enough soil moisture to ensure that shrubs (or any other understorey species with permanent above-ground parts) can survive recurrent droughts. This may open the field for herbs adapted for growth during periods of relatively high moisture supply, and equipped with ephemeral leaves and/or an annual life-history.

The increase in the relative proportion of tree and epiphyte species at higher elevations corresponds to a greater decline of herbs, shrubs and vines, and is perhaps a result of the extent to which high rainfall and humidity favours trees and epiphytes (Gentry & Dodson 1987). The peak at ≈ 2100 m in the absolute number of vascular epiphytes corresponds to a peak in mid-elevation cloud forests in other areas of the tropics (Grubb 1977). At lower elevations, there may be inadequate precipitation, fog and/or humidity to sustain certain groups of epiphytes, particularly tank-forming species (McWilliams 1974; Benzing 1980); the highest elevations appear to work against vascular epiphytes and instead favour bryophytes (Grubb 1977).

Deciduous leaves are usually considered an adaptation to seasonal drought (Chabot & Hicks 1982) provided that such drought is not coincident with other seasonal changes in the environment (e.g. increased temperature, irradiance or nutrient availability) that would tend to enhance whole-plant photosynthesis. Evergreen foliage should be favoured by either a lack of seasonality in the potential rate of net whole-plant energy capture (Montague & Givnish 1996), or by nutrient-poor soils which increase the cost of replacing the unretranslocated minerals and carbohydrates (Monk 1966; Chabot & Hicks 1982). The low thermal and solar seasonality on Cerro Grande, and the lower incidence of drought and higher incidence of leached, highly organic, mineral-poor soils in cloud forests at higher elevations, should thus favour an increase with elevation in evergreenness among woody plants, as we observed (Fig. 5). The greater incidence of deciduous trees at lower elevations may be another 'structural' factor promoting a more open canopy, and thus a greater diversity of understorey herbs, shrubs and vines there.

The high frequency of deciduousness among terrestrial herbs at low elevations (Fig. 5) seems puzzling. The dry season restricts the supply of moisture to herbs, but increases the light supply as canopy trees shed their leaves, leading to complementary seasonalities of moisture and light availability for understorey plants, and would be expected to favour evergreen foliage. However, the shallow rooting of most herbs may make it impossible for them to photosynthesize during the dry season, thus giving the deciduous habit a net advantage. One exception is the

guild of rock-dwelling herbs, almost all of which are evergreen. The nutrient shortages they face (particularly on calcareous substrates, where P may be complexed with calcium carbonate), and the small difference in their access to moisture during the rainy and dry season may favour the evergreen habit among such saxicoles. The near ubiquity of evergreenness among the epiphytic herbs on Cerro Grande may be related to the extreme nutrient shortages to which epiphytes are routinely exposed (Benzing 1990).

The higher incidence of endozoochory in evergreen cloud forests than in less humid, relatively drier deciduous forests (Fig. 7) parallels a general trend in the Neotropics toward more endozoochory in rainier sites and seasons (Smythe 1970; Croat 1978; Gentry 1982b, 1988). The usual explanation for this pattern is that anemochory is advantageous for seed dispersal in tropical seasonal forests during the dry season, given that wind speeds are high, the canopy is open, and penetration of winds into the forest makes wind dispersal relatively effective. Conversely, wetter and calmer conditions work against wind dispersal, and may indirectly favour other mechanisms of seed dispersal. Givnish (1998a) proposes a specific advantage of endozoochory in tropical forests in rainier localities and/or seasons, arguing that (i) most avian frugivores require a 'protein subsidy' of leaf-eating insects (Snow 1976); (ii) the incidence of folivory is greater on young, recently flushed leaves in tropical forests (see Coley 1983); and (iii) wetter conditions are likely to stimulate more (or more continuous) leaf flushing, thereby providing a protein subsidy to potential frugivores and fostering the evolution of fleshy fruits.

The traditional argument for the advantage of anemochory also needs revisiting in light of our results: only winged seeds (e.g. samaras) decrease in importance with increasing elevation, while dust-like seeds or spores increase, and plume-like seeds remain essentially unchanged. The greater incidence of dust-like seeds or spores at higher elevations is due largely to their strong association with the epiphytic habit and the increase in the incidence of epiphytes (mainly ferns and orchids) toward higher elevations (Fig. 4). Among wind-dispersed seeds, those bearing wings are often more massive than those bearing plumes, and always far more massive than spores or dust-like seeds; consequently, winged seeds may face an especially great disadvantage in closed forests. Winged seeds occur primarily in lianas and some trees (primarily Sapindaceae, Malpighiaceae, Bignoniaceae and Meliaceae), in which large seeds may be needed to provide the reserves necessary to penetrate the litter below a woody canopy (Givnish 1998). Dust-like seeds/spores are thought to provide an advantage to epiphytes via increased dispersal to (and settling on) open, ephemeral perches atop the twigs and branches of other plants (Benzing 1980); given the lack of litter and root competition on these perches, small seeds probably also carry little disadvantage for epiphytes.

About half of the decline in vascular species richness toward higher elevations reflects a drop in the number of species of terrestrial herbs, the largest growth-form guild on the Cerro Grande transect; most of the remainder results from a lower number of vines and shrubs (Fig. 4). This trend is likely to be due, at least in part, to the increased amount of light penetrating the canopy (see Givnish 1988, 1995), reflecting the greater incidence of drought, fire and human disturbance at lower elevations and the greater abundance of deciduous trees. The species richness of trees and epiphytes shows surprisingly little variation with elevation. These growth forms are strongly favoured by well-watered, humid conditions, which become more prevalent with increasing elevation on Cerro Grande. On transects from cloud forests to semi-arid tropical lowlands, the tendency for overall plant species diversity to increase toward lower elevations may interfere destructively with the worsening of conditions for trees and epiphytes, leading to little change or a decline in their diversity.

Species richness of trees > 2.5 cm d.b.h., shrubs and woody vines at the 0.1-ha scale decreases in a regular fashion with elevation on the Cerro Grande transect (Fig. 4), paralleling a pattern seen in wet forests in Ecuador (Fig. 13) and Costa Rica. Woody plant species richness at each altitude on the Cerro Grande transect is roughly half of that seen on Gentry's (1988) transect in Ecuador, but appears to be closer to the levels observed on Lieberman *et al.*'s (1996) transect in Costa Rica. These differences may partly reflect the much higher rainfall on the Andean gradient, situated in one of the wettest areas of the Neotropics – Gentry (1982a, 1986, 1988) showed that tree species richness in neotropical lowland forests increases sharply with precipitation. In addition, species richness on the Costa Rican transect (Lieberman *et al.* 1996, personal communication) is based on trees > 10 cm d.b.h., and so is substantially lower than the values expected had individuals > 2.5 cm d.b.h. been included. The Central American samples in México and Costa Rica may still be being invaded by elements of the richer Amazonian and Andean floras (see Lieberman *et al.* 1996), with the influence of the latter being greater in Costa Rica, especially under the wetter conditions prevailing along the Volcan Barva transect. Although tropical tree species richness is often correlated with the number of woody stems sampled at local scales (Denslow 1995; Condit *et al.* 1996) and across climatic and edaphic gradients among lowland sites (Givnish 1999), there is no significant correlation of tree species richness and stem number on the Cerro Grande transect, whether elevation is included as a covariate or not. Presumably, this result partly reflects the small range of variation in tree species richness across the study transect.

The remarkable regularity of the changes in the species richness of vascular plants with elevation (on the Cerro Grande, Andean, and Costa Rican transects), precipitation, and rate of tree turnover (Gentry 1982b; Phillips & Gentry 1994; Phillips *et al.* 1994) in Neotropical forests – as well as a less well marked, diatonic relationship of species richness to soil fertility (Huston 1980; Tilman 1982; Ashton 1989) – provides additional support for the view (Gentry 1982b; Phillips & Gentry 1994; *contra* Whittaker 1972) that plant species richness is related in a predictable way to environmental conditions.

What factors might underlie the regular decline in plant species richness with increased elevation? As indicated previously, the much lower numbers of herbs, shrubs and vines in closed cloud forests undoubtedly play a role in determining this pattern on the Cerro Grande transect. But this 'structural' factor cannot provide a general explanation for what is undoubtedly a widespread pattern. For example, on the Andean transect studied by Gentry (1988) most of the additional species at lower elevation are small trees, not herbs or shrubs, and there is no indication that the lowland forests there have a more open canopy than those at higher elevation.

Four general kinds of explanations might be invoked to explain the widespread decline in plant species richness with elevation in the tropics. The first is based on the theory of island biogeography. Local regions at higher elevations are smaller in area and more isolated from similar habitats than those at low elevations, and should thus support a lower equilibrium number of species (MacArthur & Wilson 1963). The second is based on the theory of equal species-packing along gradients (Terborgh 1973), which predicts that more species should evolve in portions of ecological gradients that occupy more area. The first model is based on the balance of immigration and local extinction, while the second also incorporates differences in speciation rates. Both seem plausible, but although they provide potential explanations for the relative sizes of the floristic pools within entire elevational belts, they do not necessarily account for plant species richness at the 0.1-ha scale. A third explanation is structural and based on elevational differences in nutrient availability, forest stratification and plant speciation. Most woody species in moist tropical forests are understorey shrubs, treelets or small trees (e.g. Whitmore 1975; Gentry 1982b; Condit *et al.* 1996). The greater availability of nutrients at lower elevations (see below) and of moisture on rainier sites should reduce whole-plant compensation points (Givnish 1988, 1995, 1999) and thus permit more individuals and species to persist in the understorey. In addition, seed dispersal by forest-interior birds may accelerate speciation in rain-forest

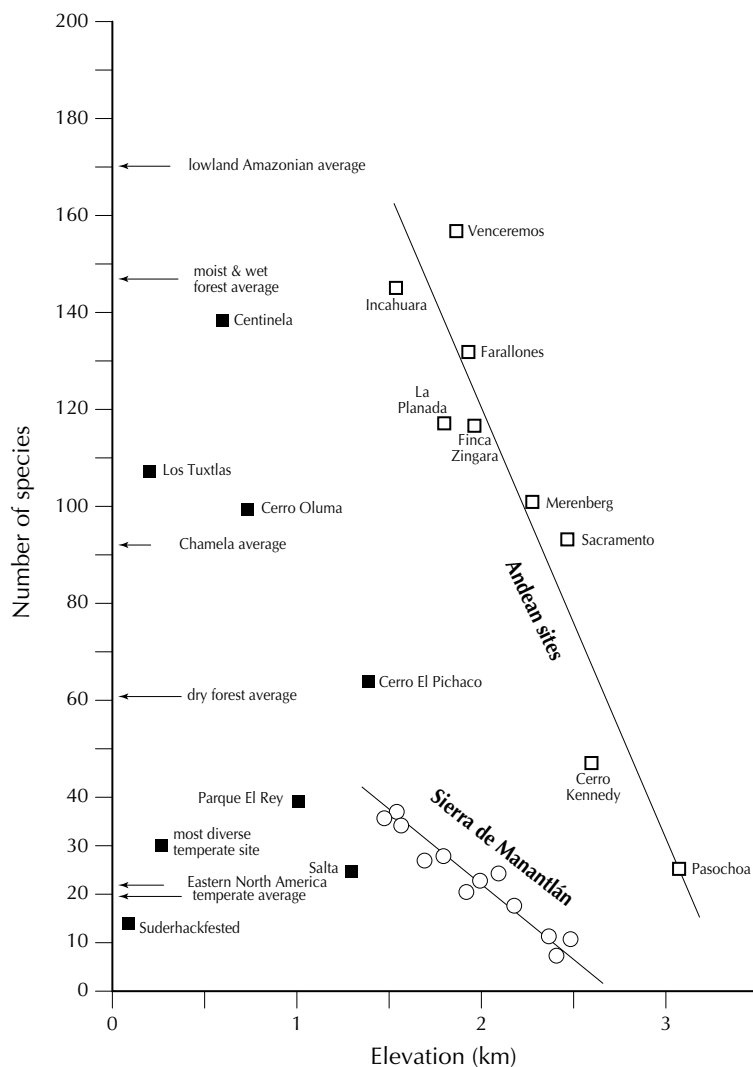


Fig. 13 Summary of woody plant species richness per 0.1 ha vs. elevation in the Neotropics, adapted from Gentry (1988) and including data from the Cerro Grande transect. Note the much lower levels of species richness on the Cerro Grande transect relative to those on the Andean sites, which far more rainfall. Lines represent least-mean-squares regressions. For the Cerro Grande transect, $y = 70.56 - 0.023x$, $r = -0.94$, $P < 0.001$ (9 d.f.); for the Andean sites, $y = 294.4 - 0.87x$, $r = -0.93$, $P < 0.01$ (7 d.f.).

understorey plants, given that such birds are notoriously loathe to cross habitat barriers (Givnish 1998). Wetter and more nutrient-rich conditions should favour a greater incidence of endozoochory, based on the expected increase in the 'protein subsidy' to frugivores (Givnish 1998).

A final possibility is that the decline in forest diversity with elevation on tropical mountains (and possibly elsewhere) may be related to elevational declines in the rates of plant growth and forest turnover and the allocation to plant anti-herbivore defences (Givnish 1999). At higher elevations the rates of plant growth, competitive exclusion and mortality might be expected to slow as a consequence of cooler temperatures, decreased rates of N mineralization and nitrification (Marrs *et al.* 1988; Heaney & Proctor 1989; Tanner *et al.* 1990), increased soil leaching, and increased soil organic matter (which decreases the

volumetric concentration of most mineral nutrients and should render them more costly to extract from the soil). Soil infertility (or other factors that reduce plant productivity) favours heavy allocation to defences against natural enemies (Janzen 1974; Coley 1983). Such defences may, in turn, reduce tropical tree diversity by reducing the overall rate and specificity of herbivory, thereby diminishing the density-dependent forces that help maintain high plant diversity in tropical forests (Givnish 1999), and possibly increasing total basal area.

The higher levels of β diversity at lower elevations (Fig. 11) is consistent with the hypothesis that temporal turnover and host-specific herbivory is greater under warmer, sunnier, more nutrient-rich conditions, and supports MacArthur's (1972) conjecture that lowland tropical forests may be more diverse than those at higher altitudes or latitudes because the

former show more spatial turnover in species composition. However, neither our data (Figs 10 and 12) nor those of Lieberman *et al.* (1996) show any evidence of greater proportional turnover in species composition with elevation in the lowlands. Finally, the tendency toward a log-series distribution of abundance for tree species at higher elevations, and a log-normal distribution of abundance at lower elevations parallels the pattern seen along a temperate elevational gradient by Whittaker (1956) in the Great Smoky Mountains. It is also consistent with May's (1975) suggestion that pre-emption of resources in species-poor communities leads naturally to a log-series distribution of abundance, and with Sugihara's (1980) model for generating a canonical log-normal distribution via the sequential division of resources by a large series of competitors.

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