Species richness and distribution of ferns along an elevational gradient in Costa Rica[1]

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To better understand changes in the distribution and diversity within plant functional types along an elevational gradient and the potential mechanisms driving such changes, we studied species richness of ferns at six elevations along a forested elevational gradient in Costa Rica, from La Selva Biological Station at 30 m a.s.l. up the slopes of Volcán Barva to 2960 m a.s.l. Among the samples from all the sites combined, we found 264 species from 60 genera. Sixty-nine species were terrestrial, 113 were canopy epiphytes, and 121 were low-trunk epiphytes. Only one species occupied both canopy and terrestrial habitats at any of the study sites. Overlap of canopy and low-trunk species composition was relatively low (18%), and lower still was the overlap of terrestrial and low-trunk species (12%). Total species richness peaked at the 1000-m site for canopy and low-trunk epiphytic species. In contrast, the richness of terrestrial species rose to a mid-elevation maximum and remained relatively constant at higher elevations. In an effort to explain elevational patterns of species richness, we examined mean annual rainfall and temperature, light intensities in the canopy and at ground level, and the mid-domain effect. Of the explanatory factors examined, the mid-domain effect accounted for most of the elevational pattern. We found little evidence that environmental gradients drive patterns of fern species richness on this spatial scale.

Key words: epiphytes; ferns; mid-domain effect; pteridophytes; species richness; tropical mountains.

Geographical variation in patterns of species richness and distribution has intrigued biologists for centuries. Much early work focused on large-scale, cross-continental patterns and was pioneered by botanists such as de Candolle (1874) and Copeland (1939). Modern interest has focused on distributions along latitudinal and elevational gradients and the processes that control these patterns (Scheiner and Reybenayas, 1994; Boyle, 1996; Vetaas and Grytnes, 2002; Li et al., 2003; Willig et al., 2003; Bachman et al., 2004; Colwell et al., 2004b; Kattan and Franco, 2004). Such studies have furthered understanding of the spatial patterns in species richness and the mechanisms behind these patterns. More recent interest in species richness has focused on structurally complex tropical forests. Besides comparisons of species numbers, several studies have attempted to understand how richness patterns vary among different structural or functional groups such as trees, vines, shrubs, and herbs (Gentry, 1982, 1988; Condit et al., 1996; Vazquez and Givnish, 1998; Tuomisto and Poulsen, 2000; Kessler, 2001b; Cardelus et al., 2006).

Studies on elevational gradients have found two main patterns of species richness: first, a monotonic decrease in richness with increasing elevation (or relatively constant richness at lower elevations, with decreasing richness at higher elevations), and second, a "humped" distribution, with species richness highest near the middle of the gradient (Rahbek, 1995; Rahbek, 2005). This humped distribution pattern is by far the most common. Rahbek (2005) found it in 80% of the 204 studies he examined. Given this near-universal richness pattern, many have attempted to explain the causal mechanisms behind it. Explanations range from ecological (Grytnes, 2003) to historical (Rahbek and Graves, 2001) to geometric (Colwell et al., 2004b). Of these, the geometric approach is the most recent and remains poorly studied.

Several authors have suggested that mid-gradient peaks of species richness may arise, at least in part, from geometric constraints on range locations within a bounded domain (Colwell and Lees, 2000; Grytnes and Vetaas, 2002; Grytnes, 2003; Colwell et al., 2004b). Bounded domains are constrained by "hard boundaries" such as those that occur at the top and bottom of elevational gradients or the edges of islands. Terrestrial species cannot physically occur above the highest or below the lowest elevation along a complete gradient nor can their ranges extend beyond the terrestrial extent of an island. Apart from such obvious restrictions, domains can also be defined by ecological discontinuities that bound a given ecosystem or biome. Bounded regions or domains such as these (sensu Colwell and Hurtt, 1994) constrain the location of species ranges. Such constraints force the overlap, particularly of species with larger and thus more centered ranges, toward the middle of domains. This overlap results in a mid-domain peak in diversity, termed the "mid-domain effect" (MDE) (Colwell and Lees, 2000; Colwell et al., 2004b). One common misunderstanding about mid-domain models is the mistaken belief that they hypothesize that en-

TABLE 1. The six studies sites along the Barva Transect, Costa Rica. Mean annual rainfall and temperature for each study site (in italics) were estimated by cubic interpolation from data for nearby meteorological stations, which are listed in the table between study sites. Light transmittance is based on analysis of hemispherical photographs from the study sites. Intersite map distance is based on GPS readings at the study sites.

Site	Elevation (m) [a]	Rainfall (mm) [a]	Temperature °C [b]	Canopy light (% transmittance)	Terrestrial light (% transmittance)	Distance to next study site (km)	Rainforest type [a]
Study site 1	30	*3942*	*25.6*	15.30	8.77	12.84	Lowland
La Selva	42	4015	25.3	—	—	—	Lowland
Study site 2	500	*4807*	*22.8*	19.16	8.17	6.97	Lowland
San Miguel	500	4627	23.6	—	—	—	Lowland
Cariblanco	970	5096	19.7	—	—	—	Premontane
Study site 3	1000	*4804*	*20.3*	17.10	9.07	9.33	Premontane
Study site 4	1600	*4063*	*17.5*	12.10	7.30	2.55	Lower Montane
Vara Blanca	1804	3426	16.8	—	—	—	Lower Montane
Study site 5	2000	*3425*	*15.7*	10.50	7.52	3.26	Montane
Sacramento	2260	3268	14.5	—	—	—	Montane
Study site 6	2600	*2734*	*12.8*	10.35	7.28	—	Montane
Villa Mills	3000	2701	10.7	—	—	—	Montane

[a] Data from Hartshorn and Peralta, 1988.
[b] Data from Boyle, 1996.

vironmental gradients in nature have no effect on the ranges of individual species or on species richness (e.g., Hawkins and Diniz-Filho, 2002). In fact, MDE models predict the pure effects of geometric constraints (domain boundaries) on richness patterns that would be expected in the absence of environmental gradients. The presence of a strong MDE does not exclude the possibility that other factors (such as climate, site nutrients, precipitation) may simultaneously contribute to spatial patterns of species richness over the domain. Moreover, the undisputed fact that the history and biology of each individual species determines its range in no way contradicts the possibility that the aggregate pattern may conform to a stochastic model.

Most studies of plants along elevational gradients have focused on the distribution of terrestrial species; few have focused on epiphytes, and fewer still have compared epiphytic and terrestrial floras (Kessler, 2001a, b) This has resulted in a substantial gap in knowledge given that forest canopies contain much of the world's biodiversity and a significant percentage a forest's biomass (Lowman and Nadkarni, 1995). In addition, ferns are a fascinating study system that combines wind-dispersed spores and free-living gametophytes. This unique character suite adds an additional level of complexity when making biogeographical comparisons of ferns to other vascular plants. By comparing the distribution patterns of fern life forms, we hope to determine whether these forms respond differently with respect to species richness, to climate, and to geometry.

In this paper we examine the distribution of epiphytic and terrestrial ferns along an elevational gradient in Costa Rica. We ask the following questions: (1) How does richness vary as a function of elevation? (2) Does elevation influence the contribution of different life forms (sensu Richards, 1996), i.e., canopy epiphytes, low-trunk epiphytes, and terrestrial species)? (3) Is there habitat fidelity in life form, and if so, does such fidelity break down at high elevations? (4) What factors most likely explain the patterns of richness along the gradient?

MATERIALS AND METHODS

Study area—Ferns were sampled along the La Selva-Volcán Barva gradient located on the Atlantic slope of the Cordillera Central in the Parque Nacional Braulio Carrillo, Costa Rica (known as the "Barva Transect"). The Barva Transect extends for 35 km from La Selva Biological Station, a tropical wet forest at approximately 30 m a.s.l., through four Holdridge life zones (lowland tropical wet forest [0–500 m a.s.l.] premontane wet forest [500–1200 m a.s.l.], lower montane wet forest [1200–2300 m a.s.l.], and montane wet forest [>2300 m a.s.l.]) to its highest point at the top of Volcán Barva, at 2906 m a.s.l. (Table 1) (Hartshorn and Peralta, 1988). This is the only mature, continuously forested elevational gradient of its length in Central America (Norman, 1985). Almost daily cloud cover begins at approximately 800–1000 m a.s.l. and is present at all sites above 800 m a.s.l. Frostline occurs between 1300 and 1600 m a.s.l. (Hartshorn and Peralta, 1988) with a 15°C temperature difference between the 30 m and 3000 m a.s.l. sites. Rainfall is consistently above 3000 mm yr^{-1} for all sites (Table 1) with the 1000-m site receiving the highest rainfall, ~5000 mm yr^{-1}. Additional site information can be found in Lieberman et al. (1996).

Sampling methods—Six study sites were established close to permanent vegetation plots along the gradient at 30, 500, 1000, 1600, 2000, and 2600 m a.s.l. Kessler and Bach (1999) reported that 400 m^2 is the minimum required area for adequate comparisons of the fern flora in species-rich neotropical forests. Given the broken terrain at intermediate elevations along the gradient, it was difficult to maintain habitat homogeneity in transects greater than 200 m^2. Thus at each site, we established four randomly chosen 100 × 2 m transects to sample terrestrial and low-trunk epiphytic ferns to a height of 3 m above ground level. The total terrestrial area sampled per site was 800 m^2, twice the minimum suggested by Kessler and Bach (1999). All terrestrial individuals rooted within the plot were counted, whereas only the presence of low-trunk epiphytes (<3 m above ground level on the host tree) was recorded. Because preliminary tests revealed no significant differences in richness among transects within sampling sites (analyses not included here in the interests of brevity), and this paper focuses on among-site differences, we pooled all data within sites for the analyses reported here.

Different sampling methods were used to determine the distribution and diversity of inner-canopy epiphytic species because the labor-intensive aspect of canopy work made sampling all trees within ground transects prohibitive. All sampled trees were in or near ground transects. Ten emergent trees per site were sampled at the 1000-, 1600-, and 2000-m sites. Only nine trees were sampled at the 500-m site, eight trees at the 30-m site, and five trees at the 2600-m site. At the 2600-m site, we stopped sampling trees when we no longer found new species in two consecutively sampled trees. Only nine trees were sampled at the 500-m site, because rains and flooding prevented further sampling. Only eight trees were sampled at the 30-m site, because they were part of a controlled study on canopy microclimate (Cardelús and Chazdon,

2005). Healthy trees were climbed using single rope techniques (Perry, 1978). Two 4.0×0.5 m transects were established along the two lowest main branches. Lowest branch height was variable among sites and ranged from 10 to 29 m, with the 1000-m sites having the lowest branches and shortest trees along the transect. All epiphytes within both branch transects were collected, and their presence was recorded for each 0.5×0.5 m quadrat. While distance varied, sample trees were close to but not located within the terrestrial transects.

Richness and floristic similarity estimates—All analyses were performed on four data sets: all fern species combined, all canopy epiphytic fern species, all low-trunk epiphytic fern species (those growing on trees less than 3 m above ground level, plus hemiepiphytes), and all terrestrial fern species. Species growing in multiple habitats were included in all of those habitats for the analyses. Total species richness recorded in field studies is subject to a downward bias caused by undersampling in virtually all species richness studies, especially for rich tropical biotas. To assess sampling completeness and control for sampling effort, we computed sample-based rarefaction (species accumulation) curves and their 95% confidence intervals (CI) (Colwell et al., 2004a, b). Curves with overlapping CIs were considered not significantly different. We applied three distinct approaches to reduce the effects of undersampling on richness estimates. In the first approach, we compared richness, based on the rarefaction curves, at a uniform number of occurrences (Chazdon et al., 1998). In the second, we used nonparametric methods to estimate true species richness using two incidence-based estimators, Chao2 and ICE (Chazdon et al., 1998). In the third method, we assumed that the elevational range of each species was continuous, at the scale of our sampling. This assumption yields what we will refer to as the "interpolated" species richness for each sampling site (Grytnes and Vetaas, 2002), which includes each species actually recorded from that site, plus any additional species recorded from at least one site above and at least one site below that site.

To examine overall floristic similarity among sites, we used EstimateS software version 7.5 (Colwell, 2005b) to compute estimators for the abundance-based Sørensen index of similarity developed by Chao et al. (2005). This index is based on the probability that two randomly chosen individuals, one from each site, both belong to species shared by both sites (but not necessarily to the same shared species). The estimator for this index takes into account the contribution to the true value of this probability made by species actually present at both sites, but not detected in one or both samples. This approach has been shown to reduce substantially the negative bias that undermines the usefulness of traditional similarity indices, given incomplete sampling of rich communities. In this study, because only incidence (presence-absence) data were recorded, we pooled occurrences among quadrats at each site and used the summed incidences as a proxy for abundance in computing the similarity index, a procedure described by Chao et al. (2005). To compare statistically the decrease in floristic similarity as a function of difference in elevation between sites, simple Mantel tests (Casgrain and Legendre, 2001) were run on the one-complement of the Sørensen estimator (transforming it into a dissimilarity index) vs. difference in elevation. This test was carried out for all species combined and for each life form (canopy epiphyte, low-trunk epiphyte, and terrestrial).

Mid-domain effect predictions—To model the spatial patterns of species richness expected under the sole influence of geometric constraints, we used RangeModel software (Colwell, 2005a). RangeModel 4 places a set of empirical species ranges at random within a specified, one-dimensional domain (scaled to the 0–2906 m a.s.l. Barva Transect, in this case), without replacement, with the constraint that no species range may extend beyond the limits of the domain (Colwell and Lees, 2000). The program then records the modeled pattern of species richness by counting the number of ranges (species) that occur at each field sampling site (Table 1 gives their elevations). The entire process is repeated N times (we chose $N = 1000$), and mean richness and its 95% confidence interval is reported for each sampling site, following the method of McCain (2003).

We calculated the raw, recorded elevational range for each species on the transect as the difference between the lowest and highest elevation at which

we recorded it as present at our sampling sites. However, species found at only one site, which are numerous in our data set, would thus have a recorded elevational range of zero and "disappear" in the simulations when ranges were shuffled. To treat such ranges more realistically, we assumed that each range in the data set, on average, actually extended half the elevational "distance" to the next sampling site (about 250 m; Table 1) from its highest and lowest recorded occurrences. Thus, we augmented the range of each species in the data set (not just those occurring at only one site) by 250 m at each end for use in RangeModel simulations. The only exceptions were species recorded from the 30-m site. We augmented these ranges by 30 m on the "downhill" end and 250 m on the "uphill" end. Note that this range augmentation scheme has no effect on any of our measures of empirical site richness (recorded richness, rarefied richness, estimated true richness, or interpolated richness).

Mid-domain effect theory indicates that species with larger ranges are more likely to conform to MDE predictions than species with smaller ranges, because, with random placement, options for the location of the midpoint of a large range are more limited than the options for the location of the midpoint of a small range (Colwell et al., 2004b). In this study, we considered a species to have a small range if it was recorded at only one site, whereas any species recorded at two or more sites was considered to have a "large" elevational range. To examine the MDE on small vs. large elevational ranges, we applied the same analyses to the species within each of these two range-size groups, separately.

Environmental variables—To assess the explanatory power of climatic factors on species richness patterns of all species and on the stem density of terrestrial species, we examined the statistical relationship between species richness (or stem density) and four environmental variables (mean annual rainfall, mean annual temperature, understory light environment, and canopy light environment) for each data set. We gathered rainfall and temperature data from the literature for locations as close in elevation and physical proximity as possible to our sites. We then used polynomial interpolation to estimate the values for our sampling elevations (Table 1). To assess light environments, a digital, hemispherical photograph was taken with a Nikon Coolpix 950 digital camera (Melville, New York, USA) with a fisheye lens attachment, then analyzed using Gap Light Analyzer software (Frazer et al., 1999) to estimate the percentage of total transmittance. Photographs were taken every 5 m in the terrestrial transects (understory light environment) and in the center of each canopy study branch (canopy light environment).

Statistical methods—Biogeographical data, by their very nature, are not spatially independent (Pimm and Brown, 2004; Rahbek, 2005). In our study, because adjacent sites along the Barva Transect are more likely to share species and to have similar climates than are sites further apart, neither richness values nor environmental values along the transect are statistically independent among sites. To assess the explanatory potential (for species richness) of environmental factors and MDE predictions, while accounting statistically for distance among sites, we used two approaches. First, we computed partial Mantel tests (Smouse et al., 1986), as implemented in Legendre's R-Package (Casgrain and Legendre, 2001), for observed richness vs. individual environmental variables and for observed richness vs. MDE. In each case, the matrix of Euclidean map distances (computed from site global positioning system [GPS] readings, using the "Geographic Distances" function in the R-Package) between our sampling sites was used as the controlled factor. Second, for richness as a function of all environmental variables plus MDE predictions, we carried out stepwise, multiple regression over distance matrices with permutation tests (Legendre et al., 1994), as implemented in the Permute! program (Casgrain, 2004). Because of the extremely small sample size ($N = 6$ sites), we set a generous $P = 0.10$ to enter the forward selection procedure (with a backward check at each step at $P = 10$), to balance the low power to detect effects.

Voucher specimens—Voucher specimens for all species were collected and stored in 70% ethanol while in the field. Specimens were subsequently dried and deposited in herbaria in the following order: Museo Nacional (CR), Univ-

TABLE 2. Species richness at six sites on the Barva Transect, Costa Rica. The second through fifth columns show recorded species richness at each study elevation for each growth form and for all species combined. Interpolated richness is the richness at each site under the assumption of continuous elevational ranges. Rarefaction estimates represent the expected number of species at 552 occurrences per site. ICE and Chao2 are nonparametric estimates of total species richness, including undetected species. Percentage collected values were computed as (total species/ mean of ICE and Chao2) × 100.

Elevation (m)	Species richness					Rarefaction estimate	ICE	Chao2	Percentage collected
	Canopy	Low-trunk	Terrestrial	All recorded species	Interpolated richness				
30	16	16	10	41	41	39	44	43	94
500	32	29	11	66	75	64	73	71	92
1000	40	38	22	93	106	86	108	108	86
1600	31	24	20	69	87	61	96	88	75
2000	29	29	21	77	85	68	98	96	79
2600	8	23	18	46	50	46	54	55	84
All sites pooled	113	121	69	264	264	154	293	293	90

ersidad de Costa Rica (USJ), Instituto Nacional de Biodiversidad (InBio), and New York Botanical Garden (NY). Taxonomic considerations were made primarily following Flora Mesoamericana (Moran and Riba, 1995).

RESULTS

Distribution of diversity—We recorded a total of 264 species from 60 genera. Of these, 69 species were terrestrial, 113 species were canopy epiphytes, and 121 species were low-trunk epiphytes (Table 2). The five most diverse genera were *Elaphoglossum* (Elaphoglossaceae, 25 species), *Trichomanes* (Hymenophyllaceae, 18 species), *Asplenium* (Aspleniaceae, 15 species), *Hymenophyllum* (Hymenophyllaceae, 13 species), and *Diplazium* (Woodsiaceae, 12 species). Altogether, 162 species were recorded at only one sampling elevation. Among the 102 species that we found at more than one site, 44 were found at two sites, 33 at three sites, 19 at four sites, three at five sites, and only two at all six sites (*Elaphoglossum peltatum* and *Asplenium serra*). The species accumulation curve (sample-based rarefaction curve, Fig. 1) for all sites and all species combined failed to saturate, as expected for very species-rich tropical floras.

Range sizes of ferns varied with life form. Large ranges were defined as ranges of greater than one site, while small ranges were those limited to one site. Terrestrial fern species were predominantly (64%) small-ranged, whereas 50% of can-

opy ferns had small ranges, with low-trunk epiphytes intermediate at 59%.

Canopy and low-trunk species were equally diverse and both significantly more diverse than terrestrial species (Fig. 2). Elevation differentially affected epiphytic and terrestrial species as richness peaks shifted with habitat type (Fig. 3). Total recorded species richness peaked at 1000 m for canopy and low-trunk epiphytes, whereas terrestrial species richness showed no distinct richness peak and was relatively constant from 1000 to 2600 m (Fig. 3).

The pattern of recorded species richness was decidedly humped, reaching its peak (93 species) at the 1000-m site (Fig. 3). Species richness was similar at both the highest and lowest elevations, with the 30-m site having 41 species and the 2600-m site having 46 (Table 2). Interpolated richness (Table 2), not surprisingly (Grytnes and Vetaas, 2002), shows a somewhat amplified hump, compared with recorded richness.

Because most of the rarefaction curves fail to reach an asymptote and somewhat different numbers of individuals were sampled at different sites, we compared rarefied richness at comparable sampling levels. All sites were compared at 552 occurrences (the vertical line in Fig. 4, determined from the expected richness in Table 2). Qualitatively, the mid-elevation hump clearly survives rarefaction. The 95% CIs for the richest site (1000 m), did not overlap with other elevations, indicating that this site was statistically the richest. In all cases, the non-
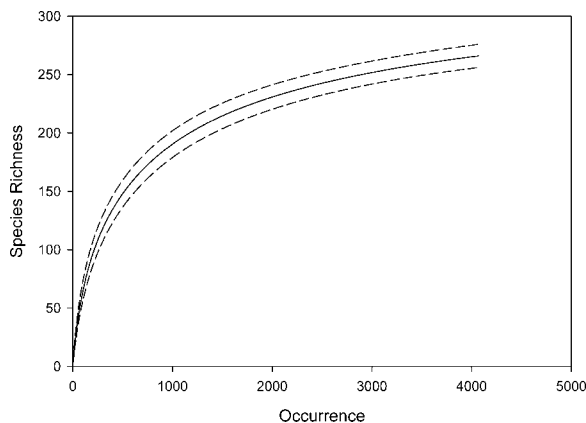

Fig. 1. Pooled sample-based rarefaction curve (solid line) with 95% confidence intervals (dashed line) for all fern species recorded at any of six sites (30-, 500-, 1000-, 1600-, 2000-, and 2600-m elevation) along the Barva Transect, Costa Rica. The total number of species recorded in this study was 264.
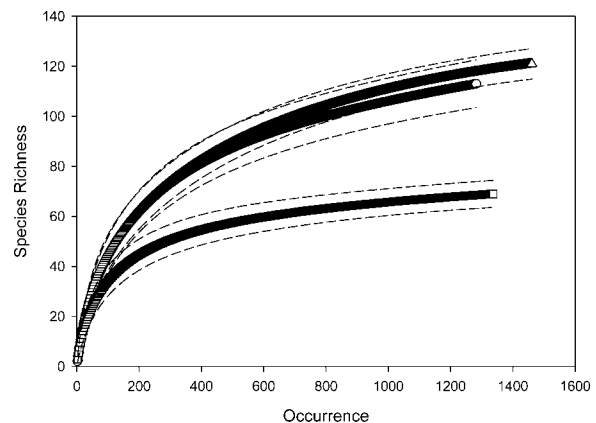

Fig. 2. Sample-based rarefaction curves with 95% confidence intervals (dashed lines) for recorded fern species for each growth form studied, canopy epiphytes (triangles), low-trunk epiphytes (circles), and terrestrial species (squares), along the Barva Transect, Costa Rica (30 to 2600 m a.s.l.).
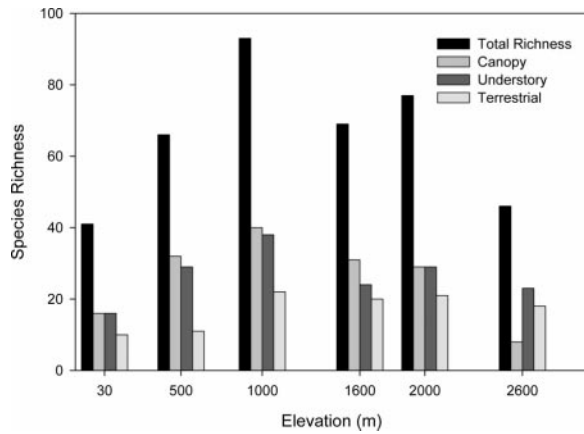
Fig. 3. The number of species recorded for three growth forms (canopy epiphytes, low-trunk epiphytes, and terrestrial species) and for all growth forms collected at each of six sites along the Barva Transect, Costa Rica. The total number of recorded species was 264.

parametric, incidence-based estimators, ICE and Chao2, were similar to, but (necessarily) somewhat higher than the observed number of species at any given site (Table 2). At the 30-m site, for example, 41 species were recorded, whereas ICE and Chao2 estimated a total of 44 and 43, respectively (Table 2). Thus, at this site, recorded species richness was 94% of the estimated true richness. In all cases we were within 75% of the estimators, suggesting that we recorded a substantial proportion of the total species diversity at each site. Again, based on ICE and Chao 2 estimates of true richness, the mid-elevation hump persists. Interestingly, interpolated species richness closely approximates the values of ICE and Chao 2 at most sampling sites (Table 2), although based on an entirely different approach.

Floristic similarity among sampling sites—Floristic similarity for all fern species was relatively high between sites within 500 m elevation of each other but declined quickly with increasing difference in elevation (Fig. 5). Although this decrease in similarity between sites with increasing distance was consistent for all life forms, the degree of decrease varied among forms. Terrestrial species had the highest similarity be-
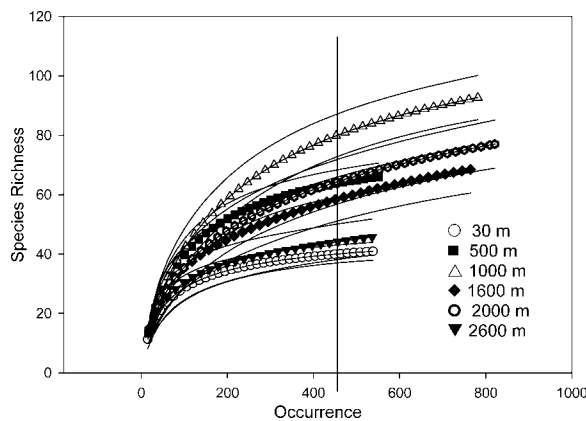

Fig. 4. Sample-based rarefaction curves with 95% confidence intervals (dashed line) for observed fern species for each growth form studied, canopy epiphytes (triangles), low-trunk epiphytes (circles), and terrestrial (squares), along the Barva Transect, Costa Rica.
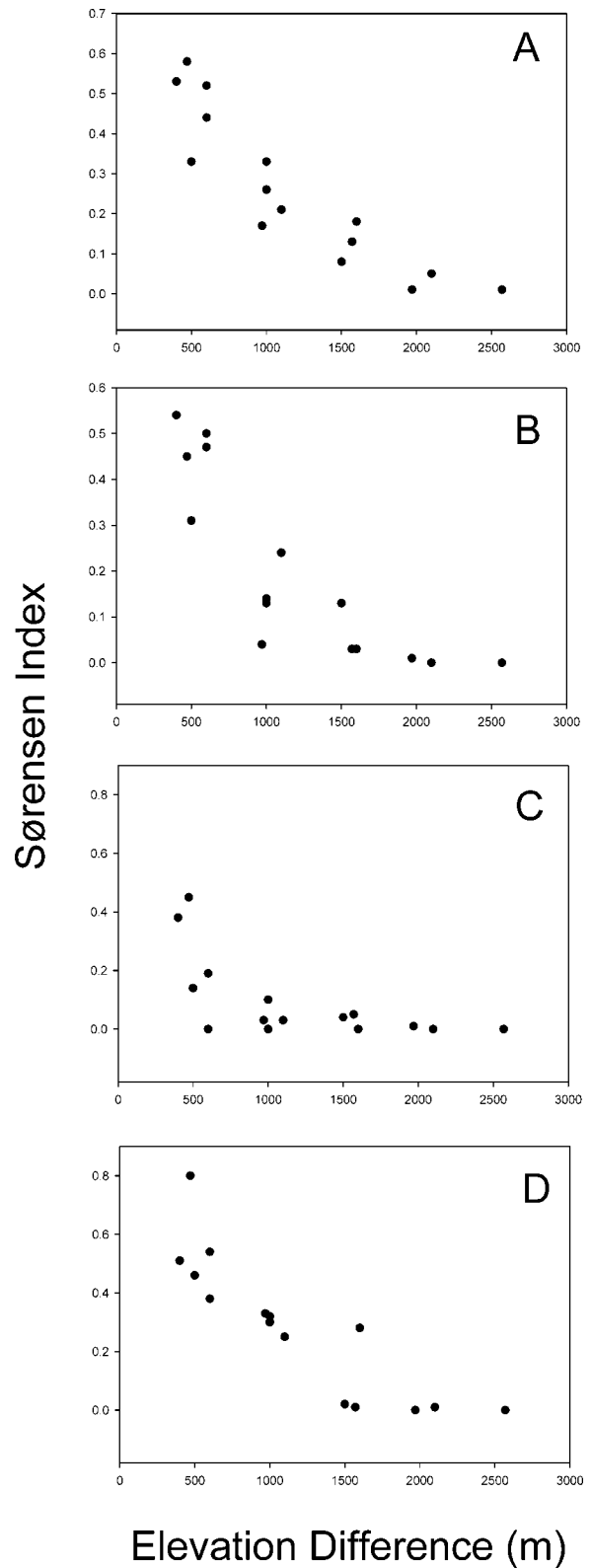

Fig. 5. The decay of Chao's abundance-based, Sørensen similarity estimator as a function of elevational difference between sites for each data set: (A) all species combined, (B) canopy epiphytes, (C) low-trunk epiphytes, and (D) terrestrial fern species.
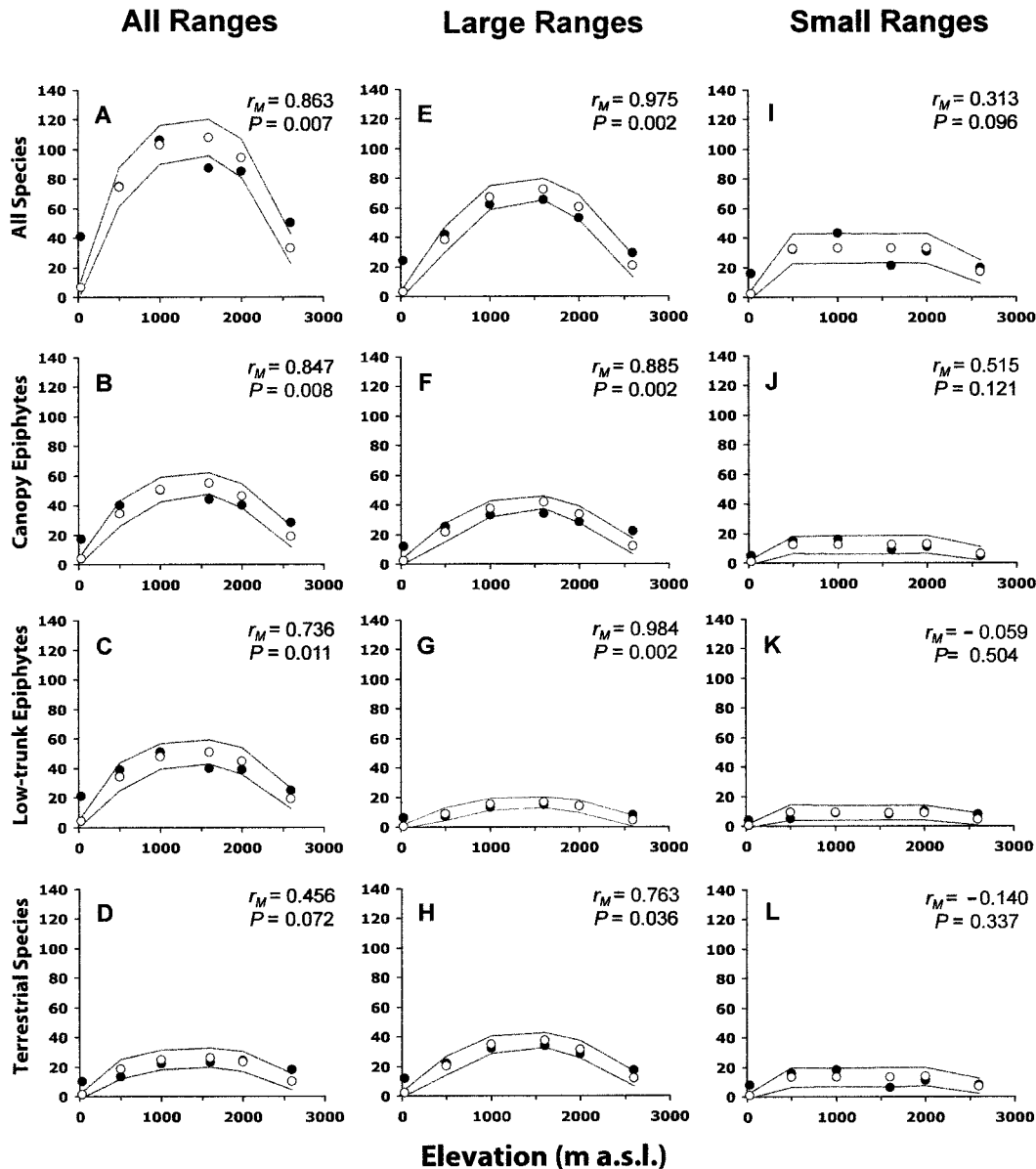
Fig. 6.   Interpolated empirical richness (solid points), predicted richness (open points; the computed means of 1000 mid-domain effect [MDE] randomizations), and the 95% confidence intervals for the MDE richness predictions as a function of elevation for each data set (all species, canopy epiphytes, low-trunk epiphytes, and terrestrial species) and for all the ranges (A–D), large ranges (E–H), and small ranges (I–L). The Mantel statistics (r_M) report the results of partial Mantel tests (intersite differences in interpolated empirical richness vs. intersite differences in MDE prediction, controlling for intersite map distances). P values are rank of the computed statistic among 999 Mantel randomizations.

tween nearby sites while the low-trunk species had the lowest similarity between such sites (Fig. 5). All negative correlations between floristic similarity and difference in elevation were significant at $P < 0.01$ by simple Mantel tests.

Habitat specificity and elevation—We found limited overlap of *epiphytic* species between both low-trunk and canopy habitats with 36 species (18%) shared by the two habitats. There was a similar degree of overlap between low-trunk and terrestrial habitats with 25 species (12%) shared by these habitats. Only a single species, *Elaphoglossum cismense*, was found in both low-trunk epiphytic and canopy epiphytic habitats as well as terrestrial habitats and this at only one site.

Apart from this species, there was no species overlap between terrestrial and canopy habitats. There was no tendency for canopy-terrestrial habitat specificity to decrease with elevation, yet a higher percentage of terrestrial species were recorded as low-trunk epiphytes with increasing elevation.

Correlates of species richness—We found evidence of a substantial influence of MDE for all fern species combined and for each of the three life forms along the elevational gradient (Fig. 6A–D). The fit of the interpolated empirical richness data (Table 1) to corresponding MDE predictions was assessed in two distinct ways. First, by examining the location of the data points for interpolated richness (solid dots in Fig.

TABLE 3. Partial Mantel statistics (r_M) and P values for species richness as a function of mid-domain effect (MDE) predictions, four environmental variables, and density of terrestrial individuals. The columns show results for all species and for species classified by range size and by growth form. The last column shows the relation between terrestrial fern density and the four environmental variables. The Mantel statistics (r_M) report the results of partial Mantel tests (intersite differences in interpolated empirical richness vs. intersite differences in the specified environmental variable or MDE prediction, controlling for intersite map distances). P values are rank of the computed statistic among 999 Mantel randomizations. * $0.01 \le P \le 0.05$; ** $P \le 0.01$.

Factor		All species, all ranges	All species, large ranges	All species, small ranges	Canopy epiphytes, all ranges	Low-trunk epiphytes, all ranges	Terrestrial species, all ranges	Terrestrial individuals, all ranges
MDE prediction	r_M	0.863	0.975	0.313	0.847	0.736	0.456	
	P	0.007**	0.002**	0.096	0.008**	0.011*	0.072	
Rainfall	r_M	−0.018	−0.183	0.066	−0.108	0.081	−0.513	−0.239
	P	0.552	0.285	0.347	0.449	0.403	0.004**	0.185
Temperature	r_M	−0.163	−0.148	−0.321	−0.309	−0.149	−0.286	−0.056
	P	0.374	0.289	0.127	0.181	0.422	0.095	0.587
Terrestrial light	r_M	0.543	0.258	0.630	0.732	0.624	−0.028	−0.329
	P	0.037*	0.114	0.065	0.011*	0.025*	0.416	0.039*
Canopy light	r_M	−0.388	−0.469	−0.012	−0.547	−0.333	−0.341	−0.061
	P	0.048*	0.002**	0.495	0.032*	0.108	0.076	0.496
Terrestrial individuals	r_M	0.106	0.405	−0.324	−0.056	−0.068	0.482	—
	P	0.258	0.108	0.153	0.542	0.490	0.091	—

6) in relation to the 95% confidence intervals for the MDE randomizations, it is evident that empirical richness is significantly higher than the MDE prediction at the lowest elevation (30-m) site and marginally higher than predicted at the highest site (2600 m). In the second approach, we computed partial Mantel tests for interpolated richness vs. predicted species richness, controlling statistically for the effect of site proximity. Figure 6 shows, for each data subset, the partial Mantel statistic (r_M) and it significance based on matrix permutation tests. The correspondence between predicted and observed (interpolated) richness is highly significant for all ferns considered together, as well as for canopy epiphytes, and for low-trunk epiphytes (Fig. 6A–C) and nearly significant ($P = 0.072$) for terrestrial ferns (Fig. 6D).

When each data set was divided into range size quantiles, consisting of large (more than one sampling site; 102 species) vs. small (only one site; 164 species) ranges, the fit of the empirical richness data to MDE predictions fully confirmed the expectations of MDE theory (Colwell et al., 2004b). For each habitat category, the fit was better for species with large ranges (Fig. 6E–H) and worse for small ranges (Fig. 6I–L), compared to the fit for all range sizes considered together (Fig. 6A–D). In fact, all results were highly significant for large ranges, and none was significant for small ranges.

To assess the correlates of empirical species richness in a multivariate context, we first carried out separate partial Mantel tests on empirical richness vs. each of six independent variables: MDE richness predictions, mean annual rainfall, mean annual temperature, canopy light, understory light, and number of terrestrial fern individuals (the last as a test for sampling effort bias). In each case, the matrix of map distances among sampling sites was entered as the controlled factor. We repeated these tests for all species, for species with large ranges (all life-forms pooled), small ranges (all life-forms pooled), and separately for each of the three life-forms (all range sizes pooled). The results of these spatially adjusted, univariate tests appear in Table 3. Because many tests were carried out to produce this table, some of them using the same data in different ways (small and large ranges are subsets of all ranges and life form categories are yet another partitioning of the same data), the P values should be viewed as comparative,

rather than exact, although patterns of multiple P values below 0.01 (referred to as ''strong'' below) are unlikely to be fortuitous (Moran, 2004). Interpolated richness was strongly correlated with MDE predictions for all categories except (all) terrestrial species, and species with small ranges, as already noted for Fig. 6. The only other significant relationships were (1) a strong negative relationship between rainfall and the richness of terrestrial ferns, (2) a moderate positive relationship between terrestrial light levels and richness of small-ranged and canopy ferns, and (3) a strong negative relationship between canopy light levels and the richness of large-ranged species (mirrored by weaker negative relationships with canopy species and all species).

Using stepwise, multiple regression over distance matrices with permutation tests (Legendre et al., 1994), all four environmental variables, plus predicted richness based on MDE simulations, were considered together as potential explanatory factors for species richness, with the site-to-site distance matrix included to control for spatial effects. The results were clear-cut: the first factor selected by the procedure was MDE (standardized slope $b = 0.826$, $P(b) = 0.007$, $R^2 = 0.682$), after which no additional variables qualified to be added in the second step (not even map distance). When the same procedure was run without including MDE predicted richness among the candidate variables, terrestrial light was the only variable to enter the model (standardized slope $b = 0.509$, $P(b) = 0.039$, $R^2 = 0.259$). With all variables forced into the model, $R^2 = 0.856$.

We repeated the same battery of tests for life-form data subsets. For canopy ferns, the first variable to enter the general model was terrestrial light (slope $b = 0.759$, $P(b) = 0.007$, $R^2 = 0.576$), followed by MDE predicted richness for canopy ferns (slope $b = 0.646$, $P(b) = 0.003$, delta $R^2 = 0.287$). With MDE forced out, both terrestrial light (slope $b = 0.7592$, $P(b) = 0.007$, $R^2 = 0.576$) and canopy light (slope $b = −0.2599$, $P(b) = 0.016$, delta $R^2 = 0.067$) enter the model. For low-trunk epiphytes, only MDE predicted richness (slope $b = 0.7148$, $P(b) = 0.012$, $R^2 = 0.511$) entered the general model. With MDE forced out, only terrestrial light (slope $b = 0.5499$, $P(b) = 0.045$, $R^2 = 0.302$) entered the model. Finally, for terrestrial ferns, the first variable to enter the general model

was map distance (slope $b = 0.654$, $P(b) = 0.028$, $R^2 = 0.427$), followed by rainfall (slope $b = -0.389$, $P(b) = 0.007$, delta $R^2 = 0.151$). Because MDE did not enter the general model, the model with MDE forced out was identical. The factors that entered the multivariate models correspond quite closely to those with the most significant univariate correlations (Table 3).

Density of terrestrial ferns—Partial Mantel tests relating the number of individual terrestrial ferns to each of four environmental variables, with the effect of intersite distance removed, did not reveal any significant effects of these variables on terrestrial fern density, with the exception of a modest ($P = 0.039$) negative correlation with terrestrial light (Table 3, last column). In a multiple regression over distance matrices with permutation tests, with all environmental variables and map distance included, no variables were sufficiently explanatory to enter the model.

DISCUSSION

We recorded 264 species from six sites covering a total sampling area of 3600 m² and an elevational range of nearly 2600 m, over a ground distance of less than 60 km (average of 46 species/site). The total species accumulation (sample-based rarefaction) curve fails to saturate, suggesting that the actual numbers are higher (Fig. 1). Other regional and local surveys have recorded far fewer species. Tuomisto et al. (2003) recorded 280 species in 163 Amazonian transects, each 500 × 5 m. Similar methods were employed by Tuomisto et al. (2002), who sampled 27 transects and recorded 140 species. In a larger study, Tuomisto and Poulsen (2000) examined a combined area of more than 35 000 m² in lowland sites in Peru and Ecuador, and they recorded only 40 species. Higher species counts have been reported from the mountains of Bolivia by Kessler (2001b), who reported 755 fern species from 65 sites spanning a distance of more than 800 km. In another elevational gradient study (450–3905 m), Kessler (2001a) recorded 493 ferns from 204 plots of 400 m² each. Our inventory of 264 species from 24 transects at six sites (3600 m²) highlights the hyper-diversity of the Central American cordillera and the importance of mountain ranges for plant diversity (Moran, 1995). Here we ask what factors influence this diversity and how they do so.

Perhaps the most intriguing biogeographical aspect of species-rich tropical forests is the repeatable mid-elevation peak in species richness along elevational gradients in these systems. In his recent review of 204 data sets from 140 studies on elevational patterns of species richness, Rahbek (2005) described four patterns of the relationship between species richness and elevation. By far the most common was the "hump-shaped" pattern, which was reported from c. 80% of the sites that covered complete gradients. Most elevational gradient studies on plants have conformed to this pattern (Parris et al., 1992; Kessler, 2000, 2001b, 2002; Kessler et al., 2001). We were able to find only a single fern study that deviated from this trend and reported a positive monotonic increase in richness with elevation (Bhattarai and Vetaas, 2003). This study took place on a much smaller elevational scale compared to other fern studies. In fact, most cases in which a mid-domain peak is not found lack a sufficient elevational range to detect it, even if present (Rahbek, 2005). Indeed, in a follow-up study that increased the elevation range on the same gradient, Bhat-

tarai et al. (2004) did report evidence of a distinctive mid-elevation peak in diversity.

In our study, total species richness (all life forms combined) exhibited the classic mid-elevation peak (Figs. 3 and 6). This pattern, however, did not hold for all individual life forms (Fig. 3). Epiphytic (both canopy and low-trunk) species exhibited peak diversity at mid-elevations, whereas terrestrial species maintained a relatively steady richness after an initial increase at lower elevations (Figs. 3 and 6D). Life form also influenced within-site species richness. With the exception of the 2600-m site, the rank order of richness between different life forms was relatively constant, with canopy species exhibiting highest richness, followed by low-trunk epiphytes and terrestrial species. These data suggest that combining data between epiphytic and terrestrial species may mask patterns of species richness intrinsic to specific life forms.

An additional difference associated with life form was the disparity in range sizes between the epiphytic and terrestrial species. Sixty-four percent of terrestrial species occurred at a single site compared to 50% of the epiphytic species. Mode of dispersal may play a role in the broader distribution of epiphytic vs. terrestrial fern species. While both groups use wind as their primary dispersal mechanism, taller terrestrial and elevated epiphytic species might be expected to disperse spores greater distances and thus be more widespread (Peck et al., 1990). Epiphytic fern species in general tend to grow in more extreme habitats. These attributes make them potentially more flexible in their abilities to cope with environmental variation and may help explain their abilities to grow in a larger range of microenvironments. Additional support for this conjecture comes from recent phylogenetic analyses, which suggest that the majority of fern epiphytes fall in the recently derived Polypodiidae lineage that is potentially undergoing adaptive radiation in epiphytic habitats (Pryer et al., 1995).

Apart from biological differences, there are many environmental factors that influence species richness. Forests at higher elevations tend to have consistently lower mean vapor pressure deficit and lower mean temperature than lowland forests. Within forests, differences in humidity and temperature between the canopy and forest floor also tend to be lower in montane relative to lowland forests (Proctor et al., 1988; Richards, 1996). Such homogenization of microclimate and more consistent wind in montane forests led us to predict that habitat specificity (canopy vs. terrestrial species), seen so dramatically in lowland forests (J. Watkins, Jr., unpublished data), should break down at higher elevations. This should be especially true for ferns that rely on wind dispersal of miniscule spores and on aqueous media for reproduction. Surprisingly, however, there was remarkable habitat fidelity at all sites along the Barva Transect especially in regard to canopy vs. ground transects. We encountered only a single species, *Elaphoglossum cismense*, at a single site (2000 m) that occurred in canopy, low-trunk, and terrestrial positions. Some terrestrial species tended to grow as low-trunk epiphytes with increasing elevation. Although we only observed a single case of reciprocal (terrestrial to canopy and vice versa) establishment, a more unexpected observation was the limited overlap of species between sites (Fig. 5). Thus, in spite of the potential for long-distance dispersal, ferns demonstrate strong habitat specificity in general and especially for terrestrial vs. canopy epiphytic habitats. This habitat fidelity adds further support to the hypothesis that even

closely related life forms behave differently along this gradient.

Environmental variables played a more apparent role when life-form groups were considered separately. Both the univariate (Table 3) and multivariate results point to a negative correlation between rainfall and species richness of terrestrial ferns (controlled for the effect of intersite distance). Examination of the data shows that this result is driven primarily by discordance between the rising phase of terrestrial fern richness (Fig. 6D), which peaks at 2000 m and then declines little, and the declining level of rainfall above 1000 m.

A similar negative correlation was found between canopy light environment and species richness (Table 3). This relationship is largely influenced by large-ranged canopy epiphytes (note the lack of significance of canopy light for small-ranged species, low-trunk, or terrestrial species). This negative correlation can perhaps be explained by the stress caused by high light. Canopy habitats experience rapid dry-down periods, which cause plant water stress. These rapid dry-downs compounded by a higher light environment and colder temperatures at higher elevations pose a unique set of physiological constraints that could make the canopy habitat unsuitable for many epiphytes and thus result in a lower diversity. The positive canopy fern richness with understory light environment is paradoxical, and possibly fortuitous. The positive effect of light on low-trunk epiphyte richness, with MDE forced out of the model, may reflect a genuine influence that might become more apparent with more sampling sites. One potential explanation is that the relationship may be driven by the 30% of low-trunk species that were also recoded from canopy or terrestrial plots, two habitats with species that did not exhibit a positive richness–light correlation. Low-trunk species may represent adaptive transitions from terrestrial to epiphytic (or vice versa) and thus exhibit different behavior from either group. This would be especially true if the driving mechanism for the evolution of epiphytism is competition for light (Benzing, 2000).

Literature both old and new emphasizes microclimatic factors such as light, temperature, and precipitation as explanations for species richness distributions along elevational gradients. A series of recent studies have added a new consideration for studies of species richness: the influence of geometric constraints (Colwell et al., 2004b). Our data and analyses, for all species and for life-form categories separately, show that species distributions of ferns along the elevational gradient can be largely explained by MDE while the environmental variables explained less of the pattern. We recognize that the number of sampling sites is quite small for multiple regression. A similar study with a larger number of sampling points might reveal significant effects of some of the variables that show significance or near-significance in the partial Mantel tests (Table 3). However, an increased number of sites would not likely overturn the significance of the MDE to fern species richness patterns, particularly epiphytic ferns, along the Barva Transect.

Like other null models (Gotelli and Graves, 1996), MDE models are designed to exclude the influence of specific, potentially causal factors, while maintaining biological realism in other key variables. In the case of MDE models, the factors excluded by design are any environmental gradients within the domain that might structure geospatial patterns of species richness. Such environmental gradients may then be considered explicitly as candidate causes of patterns of species richness, as we did in our multivariate tests, together with the predicted effects of stochastic processes operating within geometrically constraining boundaries (the MDE model predictions). Although MDE models exclude the effect of environmental gradients on range location, these models retain biologically determined species ranges (as estimated by our methods) in their observed frequencies. In no way do MDE models contradict the role of biology or the environment in shaping the dynamics and location of individual species ranges. Rather, they generate emergent patterns that result from species ranges that are individually determined by other factors. For example, in a manner closely resembling tree diversity along the gradient (Lieberman et al., 1996), terrestrial fern species (but not canopy or low-trunk epiphytic species) maintained a relatively steady richness after an initial increase at lower elevations (Figs. 2A and 6D). This deviation from the predictions of the null model suggests, perhaps, that some aspect of the environment, biology, or history more strongly influences spatial gradients of the distribution of terrestrial as compared to epiphytic species.

Conclusions—In this paper we demonstrate that species richness varies in a predictable manner along the Barva Transect. Among the ferns, the variation in spatial pattern of richness is related to life form, as evidenced by the different patterns of distribution between epiphytic and terrestrial species along the gradient. The actual mechanism controlling these patterns likely lies in a combination of factors related to biology, the environment, and geometric constraints on geographic ranges. That a group with essentially unlimited dispersal capacity has many species with narrow elevational ranges implies that there are strong biological limitations to range size. While we find that much of the variation in fern species richness over the Barva Transect can be explained by the mid-domain effect, additional local-level microclimatic monitoring is required to understand how and to what degree environmental variables influence the distribution of individual species.

LITERATURE CITED

BACHMAN, S., W. J. BAKER, N. BRUMMITT, J. DRANSFIELD, AND J. MOAT. 2004. Elevational gradients, area, and tropical island diversity: an example from the palms of New Guinea. *Ecography* 27: 299–310.

BENZING, D. 2000. Bromeliaceae: profile of an adaptive radiation. Cambridge University, Cambridge, UK.

BHATTARAI, K. R., AND O. R. VETAAS. 2003. Variation in plant species richness of different life forms along a subtropical elevation gradient in the Himalayas, east Nepal. *Global Ecology and Biogeography* 12: 327–340.

BHATTARAI, K. R., O. R. VETAAS, AND J. A. GRYTNES. 2004. Fern species richness along a central Himalayan elevation gradient. *Journal of Biogeography* 31: 389–400.

BOYLE, B. L. 1996. Changes on altitudinal and latitudinal gradients in neotropical montane forests. Ph.D. dissertation, Washington University, St. Louis, Missouri, USA.

CARDELÚS, C. L., AND R. CHAZDON. 2005. Inner-crown microenvironments of two emergent tree species in a lowland wet forest. *Biotropica* 37: 238–244.

CARDELÚS, C. L., R. K. COLWELL, AND J. E. WATKINS, JR. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology* 94.

CASGRAIN, P. 2004. Permute! Multiple regression over distance, ultrametric, and additive matrices with permutation test. Computer program and documentation available at website http://www.bio.umontreal.ca/Casgrain/en/labo/permute.

CASGRAIN, P., AND P. LEGENDRE. 2001. The R Package for multivariate and spatial analysis, version 4.0 d6. User's manual. Computer program and

documentation available at website http://www.bio.umontreal.ca/Casgrain/en/labo/R/v4/index.html.

CHAO, A., R. L. CHAZDON, R. K. COLWELL, AND T.-J. SHEN. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters* 8: 148–159.

CHAZDON, R. L., R. K. COLWELL, J. S. DENSLOW, AND M. R. GUARIGUATA. 1998. Statistical estimation of species richness of woody regeneration in primary and secondary rainforests of NE Costa Rica. *In* F. Dallmeier and J. Comisky [eds.], Forest biodiversity in North, Central, and South America and the Caribbean: research and monitoring, 285–309. Parthenon Press, Paris, France.

COLWELL, R. K. 2005a. RangeModel: a Monte Carlo simulation tool for assessing geometric constraints on species richness, version 4. User's guide and application available at website http://viceroy.eeb.uconn.edu/rangemodel.

COLWELL, R. K. 2005b. EstimateS: statistical estimation of species richness and shared species from samples, version 7.50. User's guide and computer program available at website http://purl.oclc.org/estimates.

COLWELL, R. K., AND G. C. HURTT. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist* 144: 570–595.

COLWELL, R. K., AND D. C. LEES. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution* 15: 70–76.

COLWELL, R. K., C. X. MAO, AND J. CHANG. 2004a. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85: 2717–2727.

COLWELL, R. K., C. RAHBEK, AND N. J. GOTELLI. 2004b. The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist* 163: E1–E23.

CONDIT, R., S. P. HUBBELL, J. V. LAFRANKIE, R. SUKUMAR, N. MANOKARAN, R. B. FOSTER, AND P. S. ASHTON. 1996. Species–area and species–individual relationships for tropical trees: a comparison of three 50-ha plots. *Journal of Ecology* 84: 549–562.

COPELAND, E. B. 1939. Fern evolution in Antarctica. *Philippine Journal of Science* 70: 157–235.

DE CANDOLLE, A. P. A. 1874. Constitution dans le Règne Vègetal de Groupes Physiologiques Applicables à la Gèographie Ancienne et Moderne. Bibliothèque Universelle de Genève, Paris, France.

FRAZER, G. W., C. D. CANHAM, P. SALLAWAY, AND D. MARINAKIS. 1999. Gap light analyzer. Simon Fraser University, Burnaby, British Columbia, Canada, and Institute for Ecosystem Studies, Millbrook, New York, USA.

GENTRY, A. H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden* 69: 557–593.

GENTRY, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75: 1–34.

GOTELLI, N. J., AND G. R. GRAVES. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C., USA.

GRYTNES, J. A. 2003. Ecological interpretations of the mid-domain effect. *Ecology Letters* 6: 883–888.

GRYTNES, J. A., AND O. R. VETAAS. 2002. Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *American Naturalist* 159: 294–304.

HARTSHORN, G., AND R. PERALTA. 1988. Preliminary description of primary forests along the La Selva–Volcán Barva altitudinal transect, Costa Rica. *In* F. Almeda and C. M. Pringle [eds.], Tropical rainforests: diversity and conservation, 281–306. California Academy of Sciences and Pacific Division, American Association for the Advancement of Science, San Francisco, California, USA.

HAWKINS, B. A., AND J. A. F. DINIZ-FILHO. 2002. The mid-domain effect cannot explain the diversity gradient of Nearctic birds. *Global Ecology and Biogeography* 11: 419–426.

KATTAN, G. H., AND P. FRANCO. 2004. Bird diversity along elevational gradients in the Andes of Colombia: area and mass effects. *Global Ecology and Biogeography* 13: 451–458.

KESSLER, M. 2000. Altitudinal zonation of Andean cryptogam communitites. *Journal of Biogeography* 27: 275–282.

KESSLER, M. 2001a. Pteridophyte species richness in Andean forests in Bolivia. *Biodiversity and Conservation* 10: 1473–1495.

KESSLER, M. 2001b. Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. *Biodiversity and Conservation* 10: 1897–1921.

KESSLER, M. 2002. Range size and its ecological correlates among the pteridophytes of Carrasco National Park, Bolivia. *Global Ecology and Biogeography* 11: 89–102.

KESSLER, M., AND K. BACH. 1999. Using indicator groups for vegetation classification in species rich Neotropical forests. *Phytocoenologia* 29: 485–502.

KESSLER, M., B. S. PARRIS, AND E. KESSLER. 2001. A comparison of the tropical montane pteridophyte floras of Mount Kinabalu, Borneo, and Parque Nacional Carrasco, Bolivia. *Journal of Biogeography* 28: 611–622.

LEGENDRE, P., F.-J. LAPOINTE, AND P. CASGRAIN. 1994. Modeling brain evolution from behavior: a permutational regression approach. *Evolution* 48: 1487–1499.

LI, J. S., Y. L. SONG, AND Z. G. ZENG. 2003. Elevational gradients of small mammal diversity on the northern slopes of Mt. Qilian, China. *Global Ecology and Biogeography* 12: 449–460.

LIEBERMAN, D., M. LIEBERMAN, R. PERALTA, AND G. S. HARTSHORN. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology* 84: 137–152.

LOWMAN, M. D., AND N. M. NADKARNI. 1995. Forest canopies. Academic Press, San Diego, California, USA.

MCCAIN, C. M. 2003. North American desert rodents: a test of the mid-domain effect in species richness. *Journal of Mammalogy* 84: 967–980.

MORAN, M. D. 2004. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100: 403–405.

MORAN, R. C. 1995. The importance of mountains to pteridophytes, with emphasis on Neotropical montane forests. *In* S. P. Churchill, H. Balslev, E. Forero, and J. L. Luteyn [eds.], Biodiversity and conservation of montane forests, 359–363. New York Botanical Garden Press, Brooklyn, New York USA.

MORAN, R. C. AND R. RIBA [VOL. EDS.]. 1995. Psilotaceae a Salviniaceae. *In* G. Davidse, M. Sousa, and S. Knapp [gen. eds.], Flora mesoamericana, vol. 1. Universidad Nacional Autónoma de México, Ciudad Universitaria, Mexico City, Mexico.

NORMAN, C. 1985. Virgin rain forest reprieved. *Science* 227: 273.

PARRIS, B. S., R. S. BEAMAN, AND J. H. BEAMAN. 1992. The plants of Mount Kinabalu. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

PECK, J. H., C. J. PECK, AND D. R. FARRAR. 1990. Influences of life history attributes on formation of local and distant fern populations. *American Fern Journal* 80: 126–142.

PERRY, D. R. 1978. A method of access into the crowns of emergent and canopy trees. *Biotropica* 10: 155–157.

PIMM, S. L., AND J. H. BROWN. 2004. Domains of diversity. *Science* 304: 831–833.

PROCTOR, J., Y. F. LEE, A. M. LANGLEY, W. R. C. MUNRO, AND T. NELSON. 1988. Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. I. Environment, forest structure and floristics. *Journal of Ecology* 76: 320–340.

PRYER, K. M., A. R. SMITH, AND J. SKOG. 1995. Phylogenetic relationships of extant ferns based on evidence from morphology and *rbcL* sequences. *American Fern Journal* 85: 205–282.

RAHBEK, C. 1995. The elevational gradient of species richness: a uniform pattern? *Ecography* 18: 200–205.

RAHBEK, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* 8: 224–239.

RAHBEK, C., AND G. R. GRAVES. 2001. Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences, USA* 98: 4534–4539.

RICHARDS, P. W. 1996. The tropical rainforest. Cambridge University Press, Cambridge, UK.

SCHEINER, S. M., AND J. M. REYBENAYAS. 1994. Global patterns of plant diversity. *Evolutionary Ecology* 8: 331–347.

SMOUSE, P. E., J. C. LONG, AND R. R. SOKAL. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology* 35: 627–632.

TUOMISTO, H., AND A. D. POULSEN. 2000. Pteridophyte diversity and species composition in four Amazonian rain forests. *Journal of Vegetation Science* 11: 383–396.

TUOMISTO, H., K. RUOKOLAINEN, M. AGUILAR, AND A. SARMIENTO. 2003. Floristic patterns along a 43-km long transect in an Amazonian rain forest. *Journal of Ecology* 91: 743–756.

TUOMISTO, H., K. RUOKOLAINEN, A. D. POULSEN, R. C. MORAN, C. QUINTANA, G. CANAS, AND J. CELI. 2002. Distribution and diversity of pteridophytes and Melastomataceae along edaphic gradients in Yasuni National Park, Ecuadorian Amazonia. *Biotropica* 34: 516–533.

VAZQUEZ, J. A., AND T. J. GIVNISH. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology* 86: 999–1020.

VETAAS, O. R., AND J.-A. GRYTNES. 2002. Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. *Global Ecology and Biogeography* 11: 291–301.

WILLIG, M. R., D. M. KAUFFMAN, AND R. D. STEVENS. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Annual Review of Ecology and Systematics* 34: 273–309.