

Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak

CATHERINE L. CARDELÚS*, ROBERT K. COLWELL and
JAMES E. WATKINS JR†

Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269, USA, and
†*Department of Botany, University of Florida, Gainesville, FL 32611, USA*

Summary

1 We examined *in situ* diversity and distribution of vascular epiphytes, as well as site environmental variables at six sites along a continuous elevational gradient (30–2600 m a.s.l.) of old-growth forest in Costa Rica.

2 A total of 555 species of vascular epiphytes from 130 genera of 53 families were identified to species or morphospecies. The ferns were the most diverse group, with 138 species, followed by orchids (112 species). Cloud forest at 1000 m was the richest site, representing the maximum of a pronounced mid-elevation peak in epiphyte species richness.

3 Spatial randomizations of recorded elevational ranges suggest that the overall elevational richness pattern of most epiphyte groups on this transect is substantially influenced by the mid-domain effect (MDE, the mid-elevation overlap of large-ranged species). Among the environmental factors considered (rainfall, temperature and canopy light environment), only rainfall was significantly correlated with richness.

4 Different patterns of richness for vascular epiphytes and for trees indicate that mechanisms differ between life forms.

5 We collected 26% of the estimated epiphyte species of Costa Rica along a single mountain transect. This, together with the finding that different groups and life forms varied in the elevation at which species richness peaked, highlights the need to conserve the few remaining intact elevational gradients in Latin America.

Key-words: Barva Transect, beta diversity, Chao-Sørensen, elevational gradient, epiphyte diversity, Mantel test, mid-domain effect, mid-elevational bulge, species richness

Journal of Ecology (2006) **94**, 144–156

doi: 10.1111/j.1365-2745.2005.01052.x

Introduction

Vascular epiphytes in tropical rain forests are a hyperdiverse group. Although they are often overlooked because of their isolation in the treetops, their contribution to the lowland rain forest vascular flora is significant, with estimates of 25% (Nieder *et al.* 2001) and 22% (in Costa Rica, where this study takes place, Zamora *et al.*, in press) of the total vascular flora. The high diversity of epiphytes and their ubiquity in tropical forests make them an ideal group with which to address questions about species richness patterns on a regional level. Although there is little evidence of host specificity

(Zimmerman & Olmstead 1992; Hietz & Ausserer 1998), vascular epiphytes are dependent on canopy trees for their habitat. The degree to which their diversity is linked to that of their host trees is unclear, because we lack large, synthetic studies on vascular epiphyte diversity patterns across complete landscape gradients with known canopy tree diversity patterns. This study quantifies vascular epiphyte diversity along the Barva Transect, spanning 2906 m elevation in Costa Rica, where long-term studies on canopy tree distributions (Lieberman *et al.* 1996) allow comparisons of epiphytes and their host trees.

For over a century botanists have studied patterns of species richness along elevational gradients without agreeing on a definitive pattern and without being able to satisfactorily account for the various patterns they did find. Based on climatic parallels with latitude, species

*Present address and correspondence: Catherine L. Cardelús, Department of Botany, University of Florida, Gainesville, FL 329611, USA (fax 352 392 3993; e-mail cardelus@botany.ufl.edu).

richness was thought to decrease with increasing elevation (Stevens 1992), but recent evidence suggests that, although diversity does decrease at high elevations, the trend is generally not monotonic. A number of well-designed studies on both plants and animals have documented a unimodal pattern, with a mid-elevation peak in richness patterns (Terborgh 1977; McCoy 1990). Rahbek (1995) suggested that the lack of a mid-elevation peak in many other studies may be caused by a failure to study complete gradients or to account for sampling effort or sample area (there is more land area in lowlands than at higher elevations, Rosenzweig 1995; McCain 2004).

Factors that have been suggested to explain mid-elevation peaks in species richness include intermediate productivity (Rosenzweig 1995), maximum humidity (Rahbek 1995), an upslope mass effect for certain taxa (Kessler 2000) and the mid-domain effect (MDE, Colwell & Lees 2000; Grytnes 2003). The mid-domain effect arises from geometric constraints on species ranges within a bounded domain (Colwell & Lees 2000; Colwell *et al.* 2004). Based on chance alone, the likelihood of the elevational ranges of many species overlapping is higher at mid-elevations than for the lower and higher elevations, producing a richness 'bulge' that is either not driven by environmental gradients or amplifies or distorts an environmentally driven mid-domain richness peak. The MDE thus emerges from the assembly of species ranges that may, individually, be determined by underlying evolutionary, ecological or historical effects.

Although a mid-elevation richness bulge has been suggested for vascular epiphytes in general (Schimper 1888; Madison 1977; Nieder *et al.* 2001; Wolf & Alejandro 2003), no canopy-based study has previously been conducted over a full elevational transect. Many epiphyte diversity studies have relied on ground-based methods, either collecting from the ground (fallen branches), or using binoculars and/or tree pruners to 10 m above ground level to assess diversity (Gentry & Dodson 1987a; Kessler 2001). Ground-based assessments underestimate species richness because they capture only a subset of

the vascular epiphytes that are actually present in the canopy (Flores-Palacios & García-Franco 2001; Cardelús 2002). Other canopy-based studies have assessed incomplete elevational spans (e.g. Wolf 1994; Hietz & Hietz-Seifert 1995a), or elevational gradients that span markedly different wetness gradients (Kessler 2001), making it difficult to assess overall patterns.

We used canopy-based sampling, exclusively, to explore patterns of elevational distribution, species richness and beta diversity of vascular epiphyte taxa. Epiphyte species richness along a continuous elevational transect in wet forest was compared statistically with tree species richness, with the predictions of a mid-domain effect model and with elevational patterns of precipitation, temperature and canopy light environment, while accounting for spatial autocorrelation.

Methods

The study was conducted in the Volcán Barva-La Selva Transect in Braulio Carrillo National Park Costa Rica (PNBC), i.e. from 30 to 2906 m a.s.l. The Barva Transect is the only remaining uninterrupted tract of mature forest that spans such a large elevational gradient in Central America (Norman 1985), connecting La Selva Biological Station with Volcán Barva on the Atlantic slope of the Cordillera Central and covering an area of 19 000 acres across four life zones in the Holdridge System (tropical wet forest, tropical premontane rain forest, tropical lower montane rain forest, and tropical montane rain forest, Holdridge 1967). The frost line occurs between 1300 m and 1600 m (Hartshorn & Peralta 1988). Rainfall is consistently above 3200 mm year⁻¹, with over 5000 mm year⁻¹ of rainfall at mid-elevations (Hartshorn & Peralta 1988). Fieldwork was conducted from January 2001 to August 2001 at 30, 500, 1000, 1600, 2000 and 2600 m elevation (Table 1).

We sampled 10 canopy trees at each of the 1000 m, 1600 m and 2000 m sites, nine at the 500 m site, eight at the 30 m site and five at the 2600 m site, where no new

Table 1 Six study sites along Barva Transect, Costa Rica. Estimated mean annual rainfall and temperature values for the six sites (italics) were obtained from a polynomial (cubic) regression on elevation, fitted to the data from meteorological stations for nearby reference sites (place names in the table)

Site	Elevation (m)*	Rainfall (mm)*	Temperature °C†	Vegetation type*	Coordinates
Study site 1	30	<i>3942</i>	<i>25.6</i>	Lowland	N 10°25.591', W 084°00.137'
La Selva	42	4015	25.3	Lowland	
Study site 2	500	<i>4807</i>	<i>22.8</i>	Lowland	N 10°19.617', W 084°03.690'
San Miguel	500	4627	23.6	Lowland	
Cariblanco	970	5096	19.7	Premontane	
Study site 3	1000	<i>4804</i>	<i>20.3</i>	Premontane	N 10°16.111', W 084°05.051'
Study site 4	1600	<i>4063</i>	<i>17.5</i>	Lower Montane	N 10°11.690', W 084°07.484'
Vara Blanca	1804	3426	16.8	Lower Montane	
Study site 5	2000	<i>3425</i>	<i>15.7</i>	Montane	N 10°10.563', W 084°06.672'
Sacramento	2260	3268	14.5	Montane	
Study site 6	2600	<i>2734</i>	<i>12.8</i>	Montane	N 10°08.821', W 084°06.890'
Villa Mills	3000	2701	10.7	Montane	

*Hartshorn & Peralta 1988, †Boyle 1996.

Table 2 The family, genus, species and number of individuals of each canopy tree species sampled at each of the six study elevations along the Barva Transect

Genus species	Family	30 m	500 m	1000 m	1600 m	2000 m	2600 m
<i>Calophyllum brasiliense</i>	Clusiaceae	–	1	–	–	–	–
<i>Chrysophyllum</i> sp.	Sapotaceae	–	–	1	–	–	–
<i>Ficus</i> sp. 1	Moraceae	–	–	1	1	–	–
<i>Ficus</i> sp. 2	Moraceae	–	–	1	–	–	–
<i>Ficus</i> sp. 3	Moraceae	–	–	–	1	–	–
<i>Hyeronima alchorneoides</i>	Euphorbiaceae	4	2	–	–	–	–
<i>Lecythis ampla</i>	Lecythidaceae	4	2	–	–	–	–
<i>Licania kallunkiae</i>	Chrysobalanaceae	–	1	–	–	–	–
<i>Quercus copeyensis</i>	Fagaceae	–	–	–	2	4	5
<i>Quercus seemanii</i>	Fagaceae	–	–	–	–	6	–
<i>Sapium rigidifolium</i>	Euphorbiaceae	–	–	–	3	–	–
<i>Sapium</i> sp.	Euphorbiaceae	–	–	1	–	–	–
<i>Sloanea</i> sp.	Elaeocarpaceae	–	1	–	–	–	–
<i>Vochysia allenii</i>	Vochysiaceae	–	2	2	–	–	–
<i>Zinowiewia integerrima</i>	Celastraceae	–	–	–	2	–	–
Unknown	Unknown	–	–	4	1	–	–

vascular epiphyte species were collected after the second tree had been sampled. We selected trees at random from 15 to 20 healthy, intact, large individuals suitable for climbing, except at the 30 m site, where only two tree species were sampled due to restrictions from a study on canopy microclimate at this site (Cardelús & Chazdon 2005). A total of 52 trees in 15 families were studied (Table 2). Tree diameter at breast height ranged from 70 to 200 cm. Elevation and exact location of study trees were recorded using a Garmin Etrex Summit global positioning system.

The entire trunk was sampled as one quadrat, from the first bifurcation to 3 m above the ground. Branch collections were made by establishing a 4.0 × 0.5 m transect on each of two large, lower branches of each tree, although, in a few cases, a tree limb was somewhat narrower than 0.5 m. Each branch transect was subdivided into eight quadrats measuring 0.5 × 0.5 m. All vascular epiphytes within each quadrat were collected and identified to morphospecies, and we recorded species occurrence for each quadrat. A total of 884 quadrats were established, 832 on branches and 52 on trunks.

Plant specimens were identified at the Instituto Nacional de Biodiversidad (InBio) in San José, Costa Rica, the Museo Nacional de Costa Rica, and the New York Botanical Gardens (NYBG). Approximately 90% of the vascular epiphytes could be positively identified. The large proportion of specimens that were infertile were necessarily identified based on vegetative characters, with reference to fertile specimens that we determined to be conspecific. For this reason, it is more likely that species richness was underestimated due to failure to discriminate between similar species that differ little in vegetative characters, rather than being overestimated due to splitting. Two orchid genera, *Stelis* and *Pleurothallis*, and members of the Melastomaceae and Gesneriaceae were identified only to morphospecies. Given the current state of flux of familial and generic level phylogenies for the ferns, all species were grouped

under Pteridophyta. The few (13) specimens of Cactaceae were eliminated from all analyses because of international importation problems. Hemi-epiphytes, vascular plants that live some part of their lives with no root attachment to the forest floor, were included in the analysis as epiphytes. Duplicates were deposited according to the following priority: Museo Nacional de Costa Rica, InBio, NYBG.

To determine crown transect light environment, we took a hemispherical photograph of the canopy from a point 10 cm above the centre of each branch transect. Because photographs were necessarily taken only on uniformly cloudy days, trees sampled on sunnier days were excluded, resulting in a total of 77 hemispherical photographs. Digital photographs were taken with a Nikon Coolpix 950 digital camera with a Nikon fisheye lens attachment. Hemispherical photographs were imported directly into Gap Light Analyser software (Frazer *et al.* 1999) and percentage total transmittance was calculated for each image. To determine if light transmittance differed among study sites, we used analysis of variance (ANOVA). We assessed the relationship between light transmittance and species richness with quadratic regression (SAS 1999).

For data from all sites combined and separately for each of the six elevations, a sample-based rarefaction curve (species accumulation as a function of occurrence, with 95% confidence intervals, Colwell *et al.* 2004) was computed to assess inventory completeness. These curves allow richness comparisons among sites, while accounting for differences between sites in the number of individuals sampled (Gotelli & Colwell 2001; Longino *et al.* 2002). As a second method for comparing richness among sites, we computed ICE, a non-parametric, incidence-based richness estimator, which reduces the bias that undersampling imposes on estimated total species richness (Chazdon *et al.* 1998). We also computed ICE and sample-based rarefaction curves for major taxonomic groups of epiphytes, to compare richness

among these groups. Species richness estimates (ICE) and sample-based rarefaction curves (with confidence intervals) were computed from incidence data using EstimateS software (Version 7.5, Colwell 2005a).

To examine overall floristic similarity among sites, we used EstimateS software (Version 7.5, Colwell 2005a) to compute Chao's abundance-based Sørensen index (Chao *et al.* 2005), a measure 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, reducing substantially the negative bias that undermines the usefulness of traditional similarity indices, given incomplete sampling of rich communities. Because only incidence (presence-absence) data were collected, 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).

We considered the potential effects on species richness at our six sites of mean annual rainfall, mean annual temperature, canopy light environment, tree species richness and geometric constraints (mid-domain effect). Temperature and rainfall values were estimated by polynomial interpolation from long-term data at nearby government meteorological stations (Table 1). Relative tree richness was estimated from the individual-based rarefaction curves of Lieberman *et al.* (1996; their Fig. 2a), for a uniform count of 400 stems. To represent empirical richness for our epiphyte data, we followed the common practice (Rahbek 2005) of using the interpolated richness for each sampling site. In other words, each species was assumed to occur at all sites between (and including) its lowest and highest recorded occurrences among our study sites, even if not actually recorded at all intermediate sites.

Expected richness under the influence of the mid-domain effect was generated using RangeModel Version 4 (Colwell, 2005b) by randomizing the placement of the complete set of empirical ranges along a continuous gradient, under the geometric constraint that no range may extend beyond the limits of the domain (the Barva Transect, from 0 m to 2906 m elevation). These randomizations simulate a scenario in which the position of species' ranges along the transect is collectively random with respect to any biological or environmental gradients along the transect, while the distribution of possible range sizes remains characteristic of the biology of these epiphytes in relation to the empirical characteristics of the transect (McCain, 2003, and Colwell *et al.*, 2004, explain why empirical ranges must be used).

Species recorded at only a single site (which were numerous) had an observed elevational range of zero, even after interpolation, and would thus fail to properly influence the predicted richness based on shuffled ranges. To remedy this problem, we assumed that the

actual elevational range of each species (including not only species that occurred at just one site, but all species) extended beyond each end of its recorded range by 250 m elevation, approximately halfway, in terms of elevation, to the next sampling site (the mean half-distance between sites was 257 m). The only exceptions were species recorded at the 30 m sampling site, which were incremented only 30 m on the downhill end. None of these range augmentations had any effect on richness at the sampling sites, because no augmented range extended far enough to reach the next site.

In the randomization algorithm used (based on McCain 2004), empirical ranges were selected one at a time, without replacement, then placed independently and at random on the domain by choosing a midpoint from the uniform random distribution of feasible midpoints, given the size of the range. For each simulation, after all ranges had been randomly placed on the domain, site richness (the number of overlapping shuffled ranges) was recorded at the six empirical sampling elevations. One thousand randomizations were carried out, and predicted mean richness and its 95% confidence interval was computed for each of the six sampling elevations, based on the 1000 predicted richness values for each site.

We carried out range randomizations for the full dataset (all species) and separately for each of the major higher taxa of epiphytes: ferns, aroids, bromeliads and orchids. Mid-domain theory predicts that geometric constraints will be stronger, and thus mid-domain richness peaks more pronounced, for large-ranged species than for small-ranged species (Colwell *et al.* 2004). To assess this prediction, we divided each dataset (the all-species set and the taxon subsets) into the 50% of species with largest ranges and the 50% of species with the smallest ranges and repeated the randomizations separately for each range-size subset.

To explore the explanatory potential of the mid-domain effect, we plotted the empirical richness distributions (including interpolated presences) and the means and 95% confidence intervals for the simulated richness distributions as a function of elevation. We also computed coefficients of determination for observed richness values vs. mean predicted richness values for each dataset. Because the patterns are spatially autocorrelated, we assign no significance level to the coefficients of determination for these exploratory analyses.

To assess the statistical relationship between species richness and its potential predictors (mean annual temperature, mean annual rainfall, canopy light environment, tree species richness and geometric constraints), we used a stepwise, multiple Mantel regression technique (Legendre *et al.* 1994), as implemented in the application Permute! (Casgrain 2004). This approach relies on multiple regression among the corresponding elements of resemblance matrices for the dependent variable and for each independent variable. In our case, each resemblance matrix was a 6×6 symmetric matrix of differences between site values for a given variable. To assess and control for spatial autocorrelation among the

Table 3 Epiphytes at six elevations along the Barva Transect. The first six columns show the number of vascular epiphyte specimens, species, genera, families identified at each study site along the Barva Transect, followed by the number of species found in only one and in exactly two quadrats (parentheses denote percentage of species in these categories). In addition to the recorded number of species (third column), the last three columns show other ways of examining richness along the transect: by range interpolation, by rarefaction (to 389 occurrences, see Fig. 3), and by richness estimation (ICE, numbers in parentheses represent the percentage estimated species that were recorded). Values in the Pooled Elevations row (except for Specimens) are less than the sum of elevational values because some species occurred at more than one elevation

Elevation	Specimens	Species	Genera	Families	One quadrat	Two quadrats	Interpolated	Rarefied	ICE
30 m	571	57	28	21	16 (28)	4 (7)	57	48.84	71 (80)
500 m	713	148	59	30	59 (40)	18 (12)	153	107.68	217 (68)
1000 m	1187	215	82	38	89 (41)	34 (16)	223	118.73	326 (66)
1600 m	937	171	68	29	67 (39)	30 (18)	183	106.10	248 (69)
2000 m	978	146	60	28	59 (40)	17 (12)	149	91.89	218 (67)
2600 m	322	43	28	17	21 (49)	4 (9)	43	43.00	86 (50)
Pooled elevations	4710	555	130	53	198 (36)	75 (14)	555	197.13	783

sampling sites in the multiple regressions, we also included a matrix of map distances between all pairs of sites (great-circle distances between the latitude-longitude coordinates in Table 1), as well as a matrix of elevational differences between all pairs of sites.

In the multiple Mantel tests, sampling distributions for partial regression slopes and for multiple R^2 are produced by repeatedly permuting the rows and columns of the resemblance matrix for the dependent variable, re-computing the multiple regression after each permutation. In our tests, we used 999 permutations for each test. The stepwise procedure examines the significance of the multiple R^2 and partial regression slope with the inclusion of each candidate variable, then selects the most explanatory variable if it passes a predetermined, Bonferroni-corrected P -value-to-enter for both the R^2 and regression slope. After the first variable is selected, the remaining variables are tested in the same way, until no additional variable can pass the P -value test to enter the model. After each step, we performed a backward elimination check, removing any variable from the model for which the partial regression slope was not significant at a predetermined, Bonferroni-corrected P -value-to-remove. We used a generous $P = 0.10$ for both the addition and the removal threshold. We carried out a stepwise, multiple Mantel analysis for all epiphyte species, with and without including geometric constraints among the candidate predictors. We repeated these analyses for large and small ranges, separately, to compare the role of candidate predictors for range size classes (following Jetz & Rahbek 2002). As recommended by Legendre (2000), we examined resemblance matrix elements for each variable for skewness and outliers.

Results

Our tree crown and trunk samples yielded a total of 555 epiphyte species in 130 genera, representing 53 angiosperm families, plus ferns (Table 3), an average of 32 species tree⁻¹. These species represent 26% of the estimated epiphyte flora of Costa Rica. A total of 419 specimens (8.9%), were not identifiable to species or morphospecies,

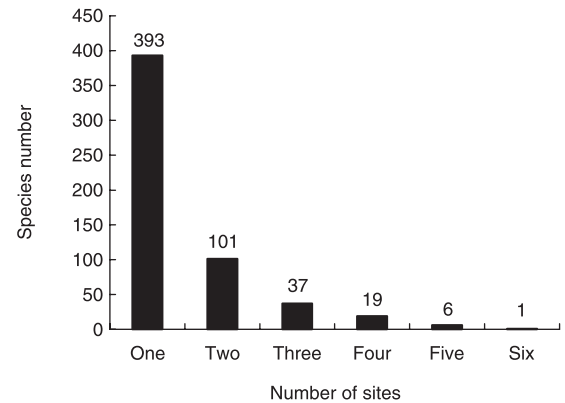


Fig. 1 Number of vascular epiphyte species found at 1, 2, 3, 4, 5 or all 6 elevational study sites.

usually because they were too young to identify, and were excluded from the analyses. The great majority of species (71%) had a small elevational range, being recorded at only one site. The number of species recorded declined steadily with increasing range size (Fig. 1) and only one species, *Anthurium consobrinum* Schott (Araceae), was found at all six sites. About half the species found at only one site were recorded from only a single quadrat at that site (36% of all species). Fourteen per cent of all species were recorded in only two quadrats (sometimes, but not always, at the same site, Table 3).

The overall species accumulation curve as a function of occurrence (sample-based rarefaction curve) for the pooled data from all sites did not reach an asymptote (Fig. 2). Species richness peaked at 1000 m elevation and was lowest at 2600 m: 2600 m \approx 30 m < 2000 m < 500 m \approx 1600 m < 1000 m (Fig. 3, Table 3). As expected, ICE estimated greater minimum species richness than was actually observed at each elevation (Table 3). For example, we collected 215 species at the 1000 m site, but ICE estimated a minimum species richness of 326. The ICE estimates for true richness at the sampling sites, like the rarefaction estimates, portray a clear mid-elevation peak in richness (Table 3).

Overall floristic similarity between the epiphyte assemblages at sampling sites declined with increasing

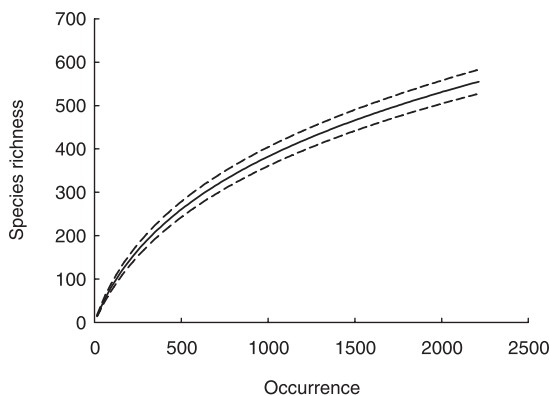


Fig. 2 Sample-based rarefaction curve and 95% confidence intervals for all vascular epiphytes species collected at any of six sites (30 m, 500 m, 1000 m, 1600 m, 2000 m and 2600 m) along the Barva Transect, Costa Rica. Total species number is 555.

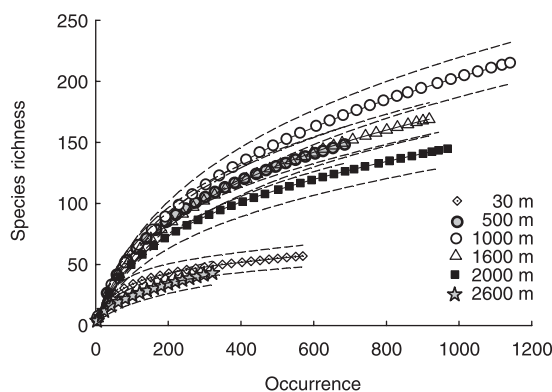


Fig. 3 Sample-based rarefaction curves for observed vascular epiphytes at each elevational study site along the Barva Transect elevational gradient, Costa Rica.

difference in elevation between sites, based on Chao's abundance-based Sørensen index (Fig. 4). As expected, the estimator for the index (open circles), which corrects for under-sampling bias, shows a higher level of floristic similarity than the corresponding raw index value (crosshatch). Note that the difference between the raw value and the corrected value is generally greater for floras at nearby elevations, which would be expected to have more undetected species in common than floras at distant elevations.

Together, orchids and ferns constituted nearly half of the species recorded (250, Table 4). Only 13 angiosperm families (plus ferns) each contributed 1% or more of the species, together comprising 88% of the total species richness, with the remaining 36 families accounting for only 12% (Table 4). Pooling species from all elevations, sample-based rarefaction curves for the four most species-rich groups reveal that the two dominant groups, ferns and orchids, have a greater rate of increase and higher projected asymptote than those of the aroids and bromeliads (Fig. 5a). Richness differences are evident when these groups are compared at a common number of occurrences (389) by rarefaction (Fig. 5b). ICE predicts species richness of ferns to be 177 species

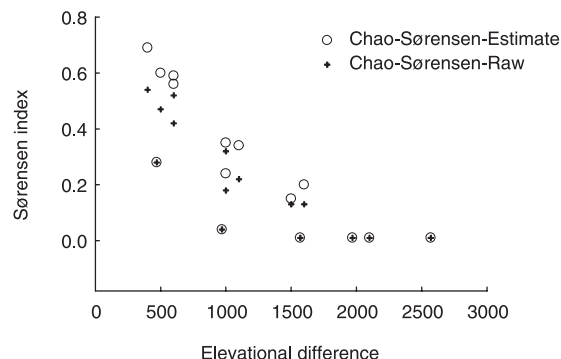


Fig. 4 The decay of the Chao-Sørensen similarity index estimator (O) and the corresponding raw Chao-Sørensen index (+) as a function of elevational difference between sites, for all species combined.

Table 4 Families/groups, genera, species and ICE species richness estimates of vascular epiphytes with greater than 1% of species represented in sample collections along the Barva Transect. Numbers in parentheses represent the percentage of ICE-estimated species that were recorded on the transect

Family/Group	Genera	Species	Percent	ICE
Ferns	27	138	25	177 (78)
Orchidaceae	18	112	20	199 (56)
Araceae	5	60	11	82 (73)
Bromeliaceae	7	41	7	56 (73)
Ericaceae	10	28	5	28 (100)
Melastomataceae	3	28	5	43 (65)
Clusiaceae	2	21	4	22 (95)
Gesneriaceae	4	18	3	42 (43)
Piperaceae	3	14	3	19 (74)
Rubiaceae	3	13	2	15 (87)
Araliaceae	2	8	1	9 (89)
Marcgraviaceae	4	8	1	9 (89)
Cyclanthaceae	3	7	1	8 (88)
Total	91	496	88	687 (72)
Other groups	39	59	12	104 (57)
Total all groups	130	555	100	783 (71)

and orchids to be 199 species, 22% and 44% above observed species richness, respectively (Table 4).

Ferns exhibit their greatest observed species richness at 1000 m, while the orchid richness peaked at higher elevations, 1600 m and 2000 m (Fig. 6, left column). For both groups, species rarefaction curves were levelling off at the 2600 m site, indicating that the site was well sampled. The ferns also seemed to be well sampled at the 500 m site.

Light availability in the lower crown varied considerably among trees, with median percentage light transmittance highest at 500 m and 1000 m. There was no significant relationship, however, between species richness and light levels on the microsite (branch) level or averaged among trees within elevations (quadratic regression, $P = 0.80$, $R^2 = 0.14$). However, there was a significant difference in light levels among sites, (single-factor ANOVA, $P = 0.002$), with Tukey's test indicating that the 500 m and 1000 m sites had significantly higher light than the 2000 m site.

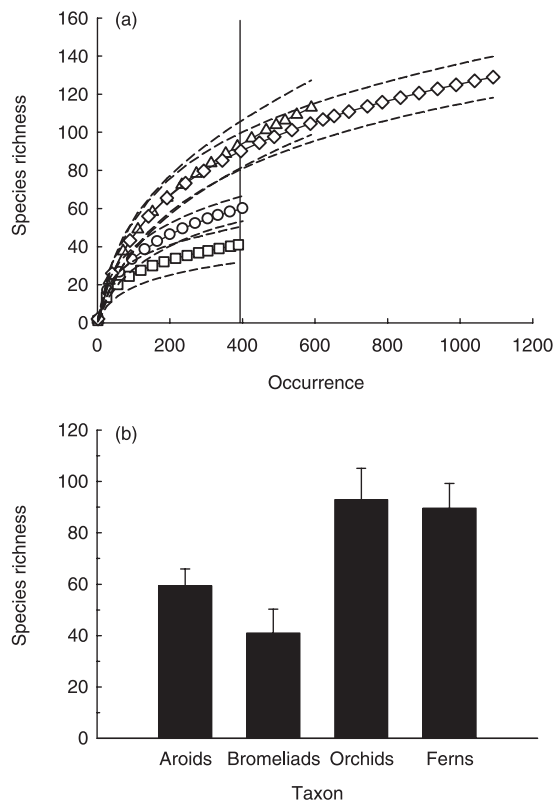


Fig. 5 (a) Sample-based rarefaction curves for the four dominant epiphyte groups: aroids (○), bromeliads (□), orchids (△) and ferns (◇) documented at each of six sites along the Barva Transect. (b) Rarefied species number and upper 95% confidence interval of four dominant epiphyte groups at the maximum common incidence number, 389 (vertical line in upper figure).

Patterns of species richness for interpolated elevational distributions as a function of elevation appear in Fig. 6. Clearly, observed species richness (solid points) peaks at mid-elevation not only for all species considered together (first row of graphs), but also for most dominant groups (ferns, bromeliads and orchids) considered individually (as well as for all non-dominant families pooled, not shown). Aroid richness, in contrast, peaks at the lower end of the transect. Predicted species richness at the field sampling elevations, based on randomizing the elevational placement of interpolated species ranges, is shown in Fig. 6 as open points within a 95% confidence envelope (fine lines). Observed species richness differs from predicted richness significantly only at elevations for which the solid point lies outside this envelope. The coefficient of determination (R^2) in each graph provides an indication of fit useful for comparisons among the graphs in Fig. 6 in which mid-domain peaks occur.

Overall, when all ranges for each group are considered (left column of graphs in Fig. 6), the mid-domain effect potentially accounts for much of the mid-elevation peak in richness. Significant deviations from predicted richness are somewhat concordant, in that ferns, aroids and bromeliads, but not orchids, are richer (aroids much richer) than predicted at the lowest elevation (30 m).

The theoretical prediction that large-ranged species should show a substantially more pronounced mid-domain peak than small-ranged species (compare the middle column of graphs with the right column in Fig. 6) is fulfilled for all species of epiphytes (first row of graphs in Fig. 6), for three of the four dominant groups considered separately (but not for aroids, Fig. 6), and for all non-dominant families pooled (not shown). Without exception, considering large-ranged species alone yields a better fit to mid-domain model predictions than considering species of all range sizes together, as predicted by theory. (Compare each graph in the left column of Fig. 6 with the corresponding graph in the middle column; the same is true for non-dominant groups pooled.)

When all five site variables plus geographical distance were entered as candidate independent variables in a stepwise, multiple Mantel regression (Test 1, All Ranges, Table 5, Fig. 7), mid-domain predicted richness (MDE) was the first variable selected followed by geographical distance (negative slope) and rainfall (Table 5). No additional factors passed the criteria to enter the model in this test. When MDE was excluded from consideration *a priori*, none of the other factors explained enough variance to enter the model (Test 2, All Ranges, Table 5). When elevation *per se* was included among candidate variables, including MDE, only MDE and elevation were included in the final model (Test 3, All Ranges, Table 5). Including elevation in a reduced model without MDE yielded no significant variables in the resulting model (Test 4, All Ranges, Table 5). When richness due exclusively to species with large elevational ranges was considered, MDE was the only variable included in the final models for Test 1 and Test 3, with no variables explaining any richness variation in Tests 2 and 4, with MDE excluded *a priori* (Table 5, Large Ranges). When richness due exclusively to species with small elevational ranges was considered, no site variables entered any model (Table 5, Small Ranges). Examination of resemblance matrix elements for each variable for skewness and outliers revealed no instances of extreme skewness or outliers (Legendre 2000).

In summary, the results of the multivariate tests indicate that geometric constraints (MDE) accounted for much of the variation in richness over the transect, with a significant independent effect of rainfall in explaining residual variation, but not a strong enough effect for rainfall to enter the model on its own when MDE was excluded. Temperature, canopy light environment and tree richness failed to explain a significant portion of the pattern of epiphyte richness. Because the entire transect was on a relatively constant slope, map distance and elevational difference were correlated, both accounting inversely for residual variation in richness after MDE had entered the model. The reason for the negative partial slope for map distance and elevation difference is that some distant pairs of sampling points were even more similar than nearby pairs of sampling points (a lagged autocorrelation), because of the relatively

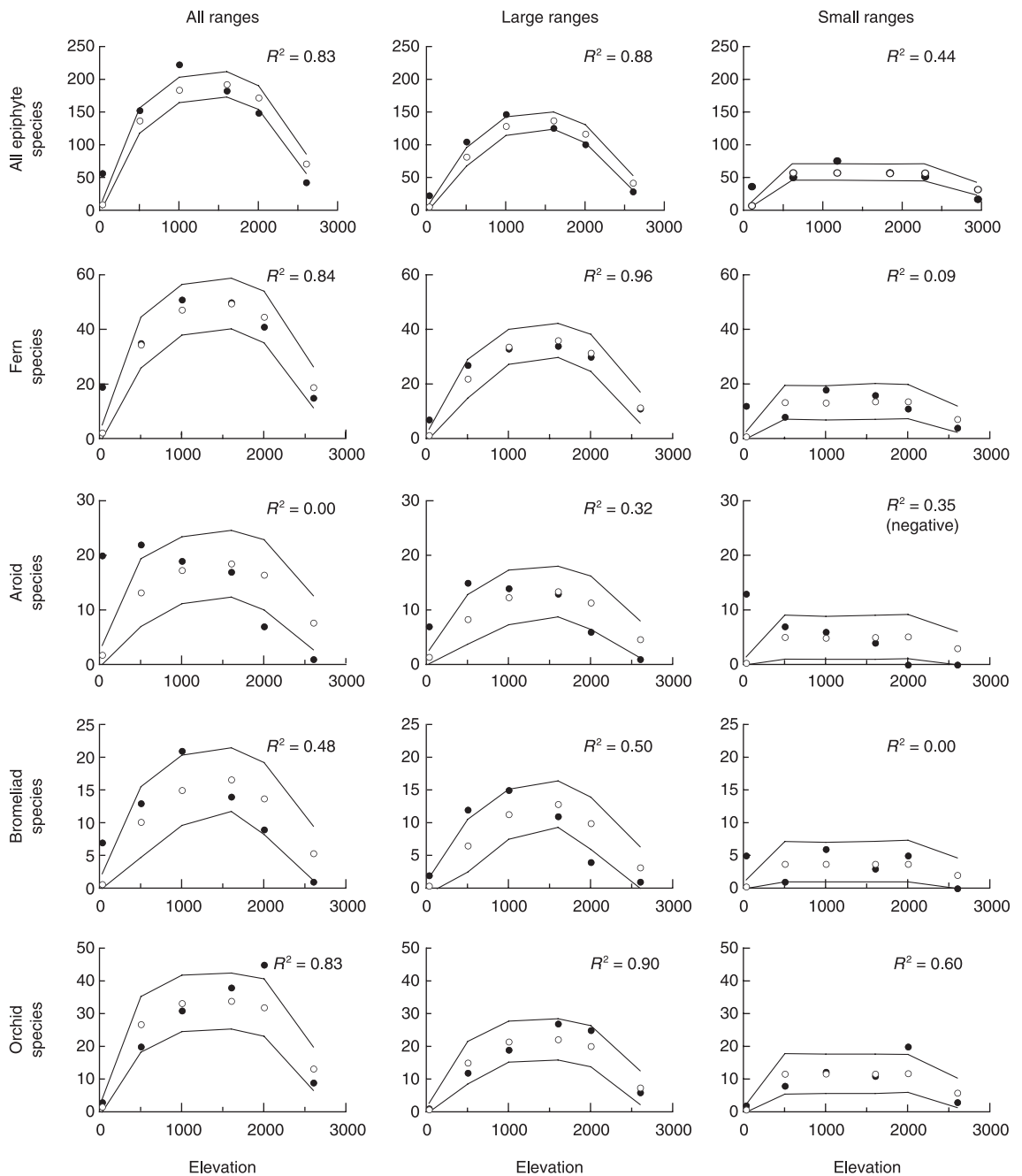


Fig. 6 Observed and predicted species richness as a function of elevation for all epiphyte taxa (top row of graphs) and separately for ferns, aroids, bromeliads and orchids (remaining rows of graphs). The left column of graphs displays results for all species within each group, whereas the middle and right columns of graphs show the 50% of species for each group with larger and smaller ranges, respectively. Solid points indicate observed richness for each field sampling elevation. Open points show mean richness and fine lines give the 95% confidence intervals predicted by the mid-domain effect randomization model. The coefficient of determination for the regression of observed on expected appears on each graph.

symmetrical pattern of richness and sampling points with increasing distance or elevational difference.

Discussion

The species richness estimator ICE suggests that between 50 and 80% of the true species richness along the gradient was sampled at each study elevation (Table 3). This result is not surprising as high species richness in tropical biotas often results in unsaturated species

accumulation curves (e.g. Longino *et al.* 2002), similar to those observed in this study. The 555 species we recorded represent 26% of the estimated Costa Rican epiphyte flora (Zamora *et al.*, in press). While the Barva transect connects to one of the most studied tropical forests in the world, La Selva Biological Station, the transect remains essentially unstudied. Clearly, many more species of epiphytes remain to be documented, judging from the non-asymptotic species accumulation curves for all elevations and for pooled data (Figs 3, 4

Table 5 Results of stepwise, multiple Mantel regression on candidate explanatory variables for epiphyte species richness over the Barva Transect. The variables listed in the top panel are those considered for inclusion in the model for each test. Variables that entered each model are numbered in the order of entry. Delta R^2 is the increase in total variance explained as each variable enters the model. Slope is the standardized partial regression slope of the variable in the final model, whereas P for slope is P for the associated t -statistic

Data set	Model	Test 1	Test 2	Test 3	Test 4	
		Rainfall Temperature Light Tree richness Distance MDE	Rainfall Temperature Light Tree richness Distance	Rainfall Temperature Light Tree richness Distance Elevation MDE	Rainfall Temperature Light Tree richness Distance Elevation	
All ranges	Var selected	1. MDE	None	1. MDE	None	
	Delta R^2	0.509		0.509		
	Slope	0.990		0.967		
	P for slope	0.009		0.011		
	Var selected	2. Distance		2. Elevation		
	Delta R^2	0.141		0.231		
	Slope	-0.471		-0.544		
	P for slope	0.002		0.006		
	Var selected	3. Precipitation				
	Delta R^2	0.157				
	Slope	0.405				
	P for slope	0.028				
	Model R^2	0.807		0.741		
	P for R^2	0.005		0.011		
	Large ranges	Var selected	1. MDE	None	1. MDE	None
		Slope	0.802		0.802	
P for slope		0.007		0.007		
R^2		0.643		0.643		
	P for R^2	0.007		0.007		
	Small ranges	Vars selected	None	None	None	None

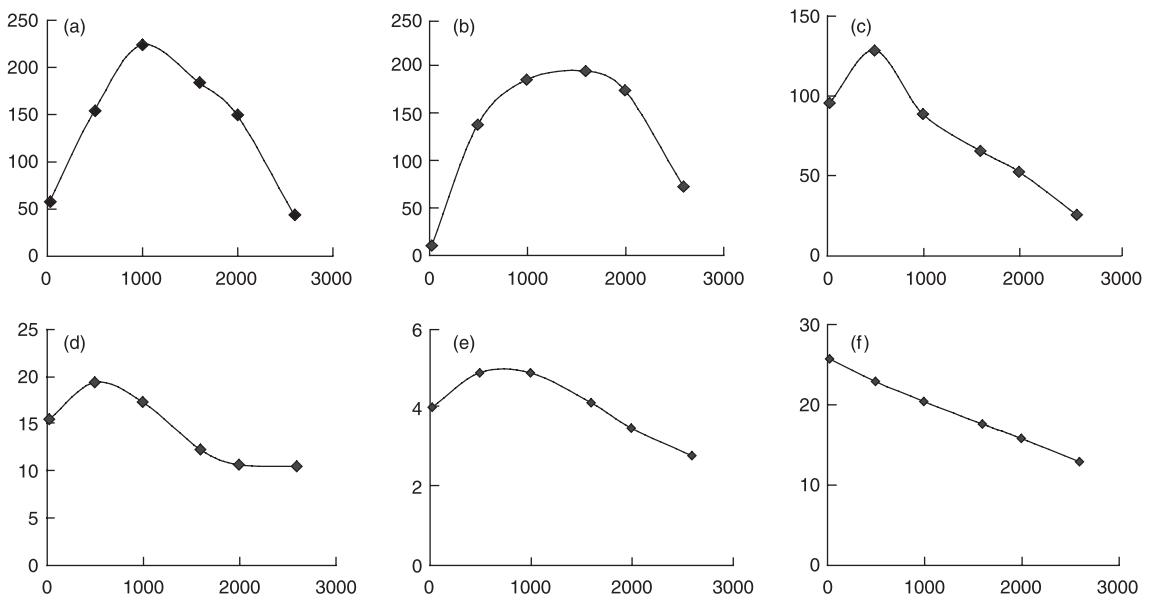


Fig. 7 Epiphyte species richness, MDE predictions and environmental variables along the Barva Transect. (a) Observed species richness, including interpolated presences. (b) Species richness expected under MDE. (c) Species richness of trees, per 400 stems (Lieberman *et al.* 1996). (d) Percentage light transmittance. (e) Mean annual precipitation (m). (f) Mean annual temperature (°C). All abscissa scales are m above sea level.

and 5a) and the proportion of species observed only once or twice (Table 3).

Nevertheless, by using sample-based approaches that do not assume complete inventory, we can make some headway towards understanding biogeographical patterns of vascular epiphytes along the Barva Transect. Sample-based rarefaction curves and richness estimators (ICE) for each elevation demonstrate that the 1000 m site is the most species rich, with the steepest rate of species accumulation, whereas the 30 m (La Selva) and 2600 m sites are the least rich in species (Fig. 3, Table 3), i.e. a typical mid-elevation bulge (Terborgh 1977; Rosenzweig 1995), as shown in Fig. 7(a). This pattern has been observed in other vascular epiphyte studies, both those based on secondary data compilations (Madison 1977; Nieder *et al.* 2001) and those based on primary data gathered on a ground-area basis (Gentry & Dodson 1987b; Hietz & Hietz-Seifert 1995b; Nieder *et al.* 2001). The mid-elevation bulge has also been reported for numerous studies on non-epiphytic plants and indeed appears to be the most common pattern of distribution of life-forms along elevational gradients (Rahbek 2005).

In their landmark paper on vascular epiphyte diversity, Gentry & Dodson (1987a) pointed out that a few plant families contribute disproportionately to the high number of vascular epiphyte species. Our results corroborate their finding; 88% of the species richness along the gradient was contributed by just 12 of the 53 plant groups found. Only three groups contributed over 5% and two groups over 20% (Table 4). Rarefaction curves of the four dominant epiphytic groups show that fern and orchid species richness is significantly higher than that of aroids and bromeliads across all elevations (Fig. 5a). Although more species of ferns than orchids were recorded on the transect, the high proportion of orchid species found only once (47% vs. 29% for ferns) leads to the prediction that there are actually more species of orchids than ferns (Fig. 5a). Species occurring in only one quadrat are important contributors to species richness estimates (Longino *et al.* 2002). Increasing the sample size would enhance the likelihood of discovering species that have low frequency of occurrence in a forest, such as the orchids. Although orchids are the most diverse group, this high diversity is not driving the mid-elevation peak, as orchid species richness is highest at 1600 m and 2000 m (Fig. 6a) while total species richness peaks at 1000 m.

Mid-elevation richness peaks in vascular epiphyte richness have traditionally been attributed exclusively to environmental factors (e.g. Gentry & Dodson 1987b; Küper *et al.* 2004) or to source-sink population dynamics (Kessler 2000), on the unstated assumption that richness would be constant over elevational gradients in the absence of such factors. The demonstration that simple geometric constraints on random range placement can produce mid-domain richness peaks (Colwell & Hurtt 1994) and increasing evidence that this phenomenon contributes to real-world biogeographical patterns (Colwell *et al.* 2004) calls this assumption into question.

No one doubts that environmental factors change over elevational gradients, or that species that live at different elevations are differentially adapted to these factors. The question is, rather, how much do environmental factors and geometric constraints each contribute to the elevational patterns of richness that emerge from these population-level processes?

When placed at random within the elevational constraints (sea level at 0 m a.s.l. and the upper bound of montane forest of the Barva Transect at 2850 m a.s.l.), ranges for the 555 epiphyte species produced mid-elevation richness peaks that tend to match empirical richness patterns for most groups of vascular epiphytes, but match most closely for large-ranged species (Fig. 6). Because the placement of a small-ranged species is only slightly constrained by domain boundaries, mid-domain theory suggests that small-ranged species may be the best indicators of environmental influences on richness. In keeping with MDE theory, small-ranged species distributions (Fig. 6, right hand column) displayed a variety of patterns, showing neither constant richness over the transect nor a prominent mid-elevation richness peak (although a modest peak occurs for all species pooled, Fig. 6, top right graph).

The departure of aroids from the mid-elevation peak common for other epiphyte groups (Fig. 6) may be due to true epiphytic aroid diversity and distribution being masked by the inclusion of both hemi-epiphytes and epiphytes, a phenomenon noted by Watkins (personal communication) for ferns along the Barva Transect. The growth forms of aroids are often difficult to distinguish when collected from fallen specimens, as done by most taxonomists, or even *in situ*, as the roots are embedded in canopy soil organic matter and all aroids were therefore considered as epiphytes. Hemi-epiphyte diversity is in fact lower at mid-elevations than in the lowlands (Küper *et al.* 2004), suggesting that the high species richness found at the lowland sites is probably influenced by hemi-epiphytes.

When the available data for environmental factors (canopy percentage light transmittance, rainfall, temperature), as well as tree species richness, geographical distance and the mid-domain effect, were used as candidate variables in a stepwise multiple Mantel regression, MDE, distance and rainfall were the only significant factors (Test 1, Table 5). Results of the Mantel test for large-ranged species corroborate the prediction of MDE theory that large-ranged species will overlap at mid-elevation (Table 5). What is intriguing is that no factor entered the model for small-ranged species that might be expected to be governed by environmental variables (but see below).

For the range placement randomizations in the statistical analysis to make any sense, each species must be assumed to have a coherent (continuous), non-zero elevational range. The alternative approach of randomizing discrete occurrences fails to incorporate the observations that real ranges tend to be coherent on a biogeographical scale and that real populations have

some minimum viable range size. For these reasons, we interpolated the occurrence pattern for each range, an adjustment that affected the richness pattern for observed occurrences by slightly amplifying richness at all sampling sites except the lowest and highest sites (Table 3), while similarly increasing the total number of site-by-species occurrences in the simulations. To deal with species that each occurred at only one site, we augmented all ranges by an amount not large enough to affect observed range limits by reaching as far as an adjacent sampling site, but large enough to allow species recorded from a single site to affect richness patterns after randomization. Of course, this adjustment is also a realistic one, at least qualitatively, because point sampling on a gradient routinely underestimates true range size. Grytnes & Vetaas (2002) pointed out that the common practice of range interpolation itself can amplify mid-elevation richness humps. This occurs to a modest degree in our analysis (Table 3), but it is important to note that both observed (after interpolation) and predicted (MDE) richness patterns are equally affected, and that both rarefaction and richness estimation approaches also portray a strong, mid-elevation peak in epiphyte species richness for the Barva Transect (Table 3).

Although this project required intense field sampling under challenging conditions, our sample size of six sites (15 resemblance pairs for the Mantel regressions) must be viewed, from a statistical point of view, as small, especially in relation to the number of candidate variables in the multiple Mantel regression analysis. However, there is no reason to suggest that the significant roles demonstrated for MDE, distance and rainfall are artifacts of small sample size, but it could be the case that with more sampling sites, additional factors would enter the final model as power increased, or that rainfall would enter the model on its own with MDE removed from candidacy *a priori* (Table 5, Test 2). Of course, some unmeasured environmental variable (e.g. net primary productivity, potential or actual evapotranspiration, relative humidity, or seasonal patterns, maxima or minima of any factor) or biotic, rather than abiotic, variables could prove to be highly correlated with richness. While it is certainly possible that MDE would be displaced from prominence for all species, or for large-ranged species (Fig. 6), this seems unlikely. In contrast, the slightly humped elevational pattern of richness for small-ranged species (each of which occurs at a single site, in our data), which is poorly matched by MDE predictions, might prove significantly correlated with environmental factors with increased sampling (Fig. 6, all taxa pooled).

A new factor, the mid-domain effect, significantly influences vascular epiphyte species richness patterns, although our data also validate long-standing observations that high rainfall is correlated with high epiphyte species richness (Gentry & Dodson 1987b). Sampling in greater depth as well as studying the role of other biotic factors, such as dispersal syndrome, foliar nutrient

content, soil chemistry or physiology, may give us further understanding of the mechanisms underlying both local and regional species distributions.

The Mantel tests show that tree species richness in no way predicts epiphyte species distributions along the Barva Transect. Rarefied tree richness patterns (Lieberman *et al.* 1996) peaked at 300 m and 500 m, below the 1000 m peak for epiphytes, and then decreased with increasing elevation (Fig. 7c, Lieberman *et al.* 1996). The difference in distribution patterns of trees and epiphytes is most likely due to differences in life history as well as differences in nutrient and moisture demands. Epiphytes in non-cloud forests experience low humidity (Cardelús & Chazdon 2005) and extreme events that dry out their substrate and can cause plant death (Benzing 1990). Cloud forest, where mist is always present to some degree during the day, perhaps provides a more permissive environment for epiphyte lineages that have little tolerance for drought. Trees, with access to soil water, are likely to be less sensitive to drying events in lower-elevation forests.

The discordance between distribution patterns of tree species richness (Lieberman *et al.* 1996) and epiphyte richness could, at first sight, be perceived as a sampling artifact based on the low number of tree species sampled for epiphytes in this study; more tree species were sampled at mid-elevation than at lower elevations (Table 2). However, epiphyte host-tree specificity, although thoroughly studied, has never been documented and is not a known mechanism for epiphyte species distributions (Zimmerman & Olmstead 1992; Hietz & Ausserer 1998; Cardelús 2002).

Macro- and microclimatic conditions at different elevations apparently affect species richness peaks in distinct ways, not only for different life-forms (trees vs. epiphytes) but also for different groups of epiphytes. The lack of concordance in species richness patterns for trees and for different groups of vascular epiphytes makes planning for the conservation of all groups difficult. The lesson from our study seems to be that unbroken elevational gradients of forest are the only certain way to protect the largest number of plant species.

Acknowledgements

Special thanks are due to R.L. Chazdon, who provided vital advice throughout this work, and to the Organization for Tropical Studies, which provided logistical support along the Barva Transect. We thank the taxonomists and parataxonomists at Instituto Nacional de Biodiversidad in San Jose, Costa Rica, for their help in plant identification, particularly B. Hammel, and O. Vargas at OTS. We are grateful to J.S. Silander and K. Holsinger, for advice and comments on earlier versions of this manuscript as well as two anonymous reviewers. We also thank D.A. Clark and D.B. Clark for logistical support at La Selva and R. Gonzalez-Vargas and K. Wendelberger for field assistance. C.L.C. was supported by: NSF Research Fellowship and Dissertation Improvement Grant,

Organization for Tropical Studies Pilot and Research Grants, Ronald Bamford Endowment to the University of Connecticut Department of Ecology and Evolutionary Biology, University of Connecticut Natural History Museum, and University of Connecticut Graduate School and Research Foundation. R.K.C. was supported by US-NSF grant DEB-0072702. J.E.W. was supported by an OTS Pilot Grant and Pohl Fellowship, Iowa State University.

References

- Benzing, D. (1990) *Vascular Epiphytes*. Cambridge University Press, Cambridge.
- Boyle, B.L. (1996) *Changes on altitudinal and latitudinal gradients in neotropical montane forests*. PhD Dissertation, Washington University, St Louis, Missouri.
- Cardelús, C.L. (2002) *Distribution and abundance of vascular epiphytes in tropical wet forests*. PhD Dissertation, University of Connecticut, Storrs, Connecticut.
- Cardelús, C.L. & Chazdon, R.L. (2005) Inner-crown micro-environments of two emergent tree species in a lowland wet forest. *Biotropica*, **37**, 238–244.
- Casgrain, P. (2004) *Permute! Multiple Regression Over Distance, Ultrametric and Additive Matrices with Permutation Test, Version 3.4, Alpha 9 – User's Manual*. Département de Sciences Biologiques, Université de Montréal, Montréal. <http://www.bio.umontreal.ca/Casgrain/en/labo/permute>
- Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, **8**, 148–159.
- Chazdon, R.L., Colwell, R.K., Denslow, J.S. & Guariguata, M.R. (1998) Statistical estimation of species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. *Forest Biodiversity in North, Central and South America and the Caribbean: Research and Monitoring* (eds F. Dallmeier & J. Comisky), pp. 285–309. Parthenon Press, Paris.
- Colwell, R.K. (2005a) *Estimates: Statistical Estimation of Species Richness and Shared Species from Samples, Version 7. User's Guide and Application*. <http://viceroy.eeb.uconn.edu/estimates>. [Persistent URL: <http://purl.oclc.org/estimates>]
- Colwell, R.K. (2005b) *Rangemod: a Monte Carlo Simulation Tool for Assessing Geometric Constraints on Species Richness, Version 4. User's Guide and Application*. <http://viceroy.eeb.uconn.edu/rangemod>.
- Colwell, R.K. & Hurtt, G.C. (1994) Nonbiological gradients in species richness and a spurious rappid effect. *The American Naturalist*, **144**, 570–595.
- Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution*, **15**, 70–76.
- Colwell, R.K., Mao, C.X. & Chang, J. (2004) Interpolating, extrapolating and comparing incidence-based species accumulation curves. *Ecology*, **85**, 2717–2727.
- Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist*, **163**, E1–E23.
- Flores-Palacios, A. & Garcia-Franco, J.G. (2001) Sampling methods for vascular epiphytes: their effectiveness in recording species richness and frequency. *Selbyana*, **22**, 181–191.
- Frazer, G.W., Canham, C.D., Sallaway, P. & Marinakis, D. (1999) *Gap Light Analyzer*. Simon Fraser University and Institute for Ecosystem Studies, Burnaby, British Columbia, Canada.
- Gentry, A.H. & Dodson, C. (1987a) Contribution of nontrees to species richness of a tropical rain forest. *Biotropica*, **19**, 149–156.
- Gentry, A.H. & Dodson, C.H. (1987b) Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Gardens*, **74**, 205–233.
- Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.
- Grytnes, J.A. (2003) Ecological interpretations of the mid-domain effect. *Ecology Letters*, **6**, 883–888.
- Grytnes, J.A. & Vetaas, O.R. (2002) Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *The American Naturalist*, **159**, 294–304.
- Hartshorn, G. & Peralta, R. (1988) Preliminary description of primary forests along the La Selva-Volcán Barva altitudinal transect, Costa Rica. *Tropical Rain Forests: Diversity and Conservation* (eds F. Almeda & C.M. Pringle), pp. 281–306. California Academy of Sciences and Pacific Division, American Association for the Advancement of Science, San Francisco, California.
- Hietz, P. & Ausserer, J. (1998) Population dynamics and growth of epiphytes in a humid montane forest in Mexico. *Selbyana*, **19**, 281.
- Hietz, P. & Hietz-Seifert, U. (1995a) Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. *Journal of Vegetation Science*, **5**, 487–498.
- Hietz, P. & Hietz-Seifert, U. (1995b) Structure and ecology of epiphytic communities of a cloud forest in central Veracruz, Mexico. *Journal of Vegetation Science*, **6**, 719–728.
- Holdridge, L.R. (1967) *Life Zone Ecology*. Tropical Science Center, San Jose, Costa Rica.
- Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297**, 1548–1551.
- Kessler, M. (2000) Upslope-directed mass effect in palms along an Andean elevational gradient: a cause for high diversity at mid-elevations. *Biotropica*, **32**, 756–759.
- Kessler, M. (2001) Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. *Biodiversity and Conservation*, **10**, 1897–1921.
- Küper, W., Kreft, H., Nieder, J., Koster, N. & Barthlott, W. (2004) Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. *Journal of Biogeography*, **31**, 1477–1487.
- Legendre, P. (2000) Comparison of permutation methods for the partial correlation and partial Mantel tests. *Journal of Statistics and Computer Simulation*, **67**, 37–73.
- Legendre, P., Lapointe, F.-J. & Casgrain, P. (1994) Modeling brain evolution from behavior: a permutational regression approach. *Evolution*, **48**, 1487–1499.
- Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G.S. (1996) Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology*, **84**, 137–152.
- Longino, J.T., Coddington, J. & Colwell, R.K. (2002) The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology*, **83**, 689–702.
- Madison, M. (1977) Vascular epiphytes: their systematic occurrence and salient features. *Selbyana*, **2**, 1–13.
- McCain, C.M. (2003) North American desert rodents: a test of the mid-domain effect in species richness. *Journal of Mammalogy*, **84**, 967–980.
- McCain, C.M. (2004) The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography*, **31**, 19–31.
- McCoy, E.D. (1990) The distribution of insects along elevational gradients. *Oikos*, **58**, 313–322.

- Nieder, J., Prosperi, J. & Michaloud, G. (2001) Epiphytes and their contribution to canopy diversity. *Plant Ecology*, **153**, 51–63.
- Norman, C. (1985) Virgin rain forest reprieved. *Science*, **227**, 273.
- 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**, 224–293.
- Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- SAS Institute (1999) *The SAS System for Windows*. SAS Institute, Cary, North Carolina.
- Schimper, A.F.W. (1888) *Die Epiphytische Vegetation Amerikas*. Gustav Fischer, Jena.
- Stevens, G.C. (1992) The elevational gradient in altitudinal range: an extension of Rapaport's latitudinal rule to altitude. *American Naturalist*, **140**, 893–911.
- Terborgh, J. (1977) Bird species diversity on an Andean elevational gradient. *Ecology*, **58**, 1007–1019.
- Wolf, J.H.D. (1994) Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio*, **112**, 15–28.
- Wolf, J.H.D. & Alejandro, F. (2003) Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography*, **30**, 1689–1707.
- Zamora, N., Hammel, B.E. & Grayum, M.H. (in press) Vegetación/Vegetation. *Manual de Plantas de Costa Rica*, Volume I (eds B.E. Hammel, M.H. Grayum, C. Herrera & N. Zamora). Missouri Botanical Garden, St Louis.
- Zimmerman, J.K. & Olmstead, I.C. (1992) Host tree utilization by vascular epiphytes in a seasonally inundated forest (Tintal) in Mexico. *Biotropica*, **24**, 402–407.

Received 5 January 2005

Accepted 21 June 2005

Handling Editor: Gerhard Zotz