



What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica

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ABSTRACT

Aim We studied pteridophyte species richness between 100 m and 3400 m along a Neotropical elevational gradient and tested competing hypotheses for patterns of species richness.

Location Elevational transects were situated at Volcán Barva in the Braulio Carrillo National Park and La Selva Biological Station (100–2800 m) and Cerro de la Muerte (2700–3400 m), both on the Atlantic slope of Costa Rica, Central America.

Method We analysed species richness on 156 plots of 20 × 20 m and measured temperature and humidity at four elevations (40, 650, 1800 and 2800 m). Species richness patterns were regressed against climatic variables (temperature, humidity, precipitation and actual evapotranspiration), regional species pool, area and predicted species number of a geometric null model (the mid-domain effect, MDE).

Results The species richness of the 484 recorded species showed a hump-shaped pattern with elevation with a richness peak at mid-elevations (*c.* 1700 m). The MDE was the single most powerful explanatory variable in linear regression models, but species richness was also associated strongly with climatic variables, especially humidity and temperature. Area and species pool were associated less strongly with observed richness patterns.

Main conclusions Geometric models and climatic models exclusive of geometric constraints explained comparable amounts of the elevational variation in species richness. Discrimination between these two factor complexes is not possible based on model fits. While overall fits of geometric models were high, large- and small-ranged species were explained by geometric models to different extents. Species with narrow elevational ranges clustered at both ends of the gradient to a greater extent than predicted by the MDE null models used here. While geometric models explained much of the pattern in species richness, we cannot rule out the role of climatic factors (or vice versa) because the predicted peak in richness from geometric models, the empirical peak in richness and the overlap in favourable environmental conditions all coincide at middle elevations. Mid-elevations offer highest humidity and moderate temperatures, whereas at high elevations richness is reduced due to low temperatures, and at low elevations by reduced water availability due to high temperatures.

Keywords

Climatic variables, Costa Rica, elevational gradient, geometric constraints, Neotropics, null model, pteridophytes, species richness.

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INTRODUCTION

Patterns of species richness have long been of interest to biologists. The best known patterns are the species–area relationship (e.g. Rosenzweig, 1995) and the latitudinal increase of species richness from the poles towards the equator (e.g. Rahbek & Graves, 2001; Hawkins & Diniz-Filho, 2004). The causes for the latitudinal diversity gradient are still debated hotly, but current research focuses mainly on energy availability, evolutionary time, habitat heterogeneity, area and geometric constraints (e.g. Rahbek & Graves, 2001; Jetz & Rahbek, 2002; Ricklefs, 2004).

A third environmental gradient, elevation, has often been linked to the latitudinal gradient. It was long believed that a monotonic decrease of species richness with increasing elevation was the universal pattern (Stevens, 1992) and that the elevational pattern therefore reflected the latitudinal pattern (e.g. Begon *et al.*, 1990). However, recent studies have shown that species richness and elevation show complex relationships (Rahbek, 1995, 1997; Lomolino, 2001), dependent on the taxonomic group and gradient considered (e.g. Rahbek, 1997; Kessler, 2002). Rahbek (1995, 2005) recognized three basic types of species richness patterns with elevation, of which the hump-shaped pattern was found to be most common. Monotonic declines in richness with elevation may often actually be hump-shaped patterns, because in numerous studies species richness estimates have not been controlled or corrected for the effect of area, which could inflate species number at low elevations (see examples in Rahbek, 1995; Kessler, 2001a; Bachman *et al.*, 2004). Further, many elevational transects were not sampled down to the lowest possible elevations, potentially masking a hump at low elevations (Lomolino, 2001; Rahbek, 2005). For example, in Costa Rica, Lieberman *et al.* (1996) found a peak of tree species richness at just 300 m.

The causes of the hump-shaped patterns of diversity and the location of the peak are not fully understood. Explanations fall into two broad categories, namely those considering optimal environmental conditions (maximum humidity, optimum temperature–precipitation conditions, maximum productivity) in the middle of the gradients (e.g. Hawkins & Diniz-Filho, 2004) and those considering geometrical constraints (e.g. see review by Colwell *et al.*, 2004).

In the present study we describe the pattern of pteridophyte species richness along a tropical elevational gradient in Costa Rica, Central America and evaluate a suite of hypotheses meant to explain patterns of diversity. We focused on two environmental variables, temperature and humidity, each of which was measured for 18 months along the elevational gradient. In addition to these variables, we consider area, species-pool and geometric constraints, each of which is cited frequently as a common or even general explanation for patterns of diversity with elevation.

We did not include one variable often thought to influence diversity, namely productivity. Productivity is clearly driven by climatic factors (Francis & Currie, 1998; Ricklefs *et al.*, 1999; González-Espinosa *et al.*, 2004), but we do not know which part of the energy input in the ecosystem is actually available to ferns that represent a varying part of the total vegetation. This uncertainty prevented us from introducing and testing hypotheses

related to productivity, such as the ‘more individuals hypothesis’ (Srivastava & Lawton, 1998).

We chose pteridophytes as the focal group of organisms due to their global distribution, high but manageable species richness, relatively stable species-level taxonomy and outstanding contribution to local tropical floras (Young & León, 1991; Kappelle & Gomez, 1992; Pearson, 1995; Tuomisto *et al.*, 2003).

METHODS

Study area

Braulio Carrillo National Park and adjacent La Selva Biological Station are located on the Atlantic slopes of Volcán Barva within the Central Cordillera of Costa Rica between 45 m and 2906 m (Fig. 1). The Braulio Carrillo transect is the most extensive protected elevational gradient of primary tropical forests in Central America (Pringle *et al.*, 1984; Pringle, 1988; Herrera-McBryde, 1997), covering four Holdridge life zones (Holdridge, 1967): tropical wet forest (35–600 m); premontane rain forest (600–1450 m); lower montane rain forest (1450–2500 m); and montane rain forest (2500–2900 m). Elevations surpassing timberline were investigated on the Atlantic slope of the adjacent mountain complex of Cerro de la Muerte between 2750 m and 3491 m with a timberline at 3200 m and páramo vegetation higher up (Kappelle *et al.*, 1989) (Holdridge Life Zones ‘montane rain forest’ and ‘subalpine rain páramo’) (Fig. 1).

Our main study transect was on Volcán Barva (2906 m) with an elevational extent from 100 m to 2800 m. Because the peak of Volcán Barva is below timberline elevation, we included a second transect on Cerro de la Muerte (3491 m) between 2700 m and 3400 m to extend the study to timberline and into the páramo vegetation. The two mountains are about 50 km apart and are of different geological origin (Coates, 1997), which potentially calls into question whether the subtransects can be combined for data analysis. We tested the validity of considering the two transects as one by conducting a detrended correspondence analysis as well as a Monte Carlo simulation of the distribution of species range limits. Both tests showed that species turnover was not significantly elevated at the transition between both subtransects (data not shown, but available upon request). While the lack of significant turnover among subtransects suggests that both belong to a single floristic unit, the delimitation of the domain extent for mid-domain effect (MDE) analysis is still potentially problematic. If we consider solely the Barva transect between 100 m and 2800 m, the upper hard boundary should be set at 2906 m (the mountain top of Volcán Barva, as in Candelús *et al.*, 2006). Combining the two subtransects and setting the upper hard boundary at 3491 m (mountain top of Cerro de la Muerte), on the other hand, may violate some assumptions of MDE null models. For example, ranges of individual species may extend to higher elevations on the mountain range of Cerro de la Muerte, simply because larger mountain masses can influence their own climatic conditions and shift habitat zones higher on higher mountains (mountain mass effect, Lomolino, 2001; McCain, 2005). On the other hand, within the MDE null models, the limits of a domain

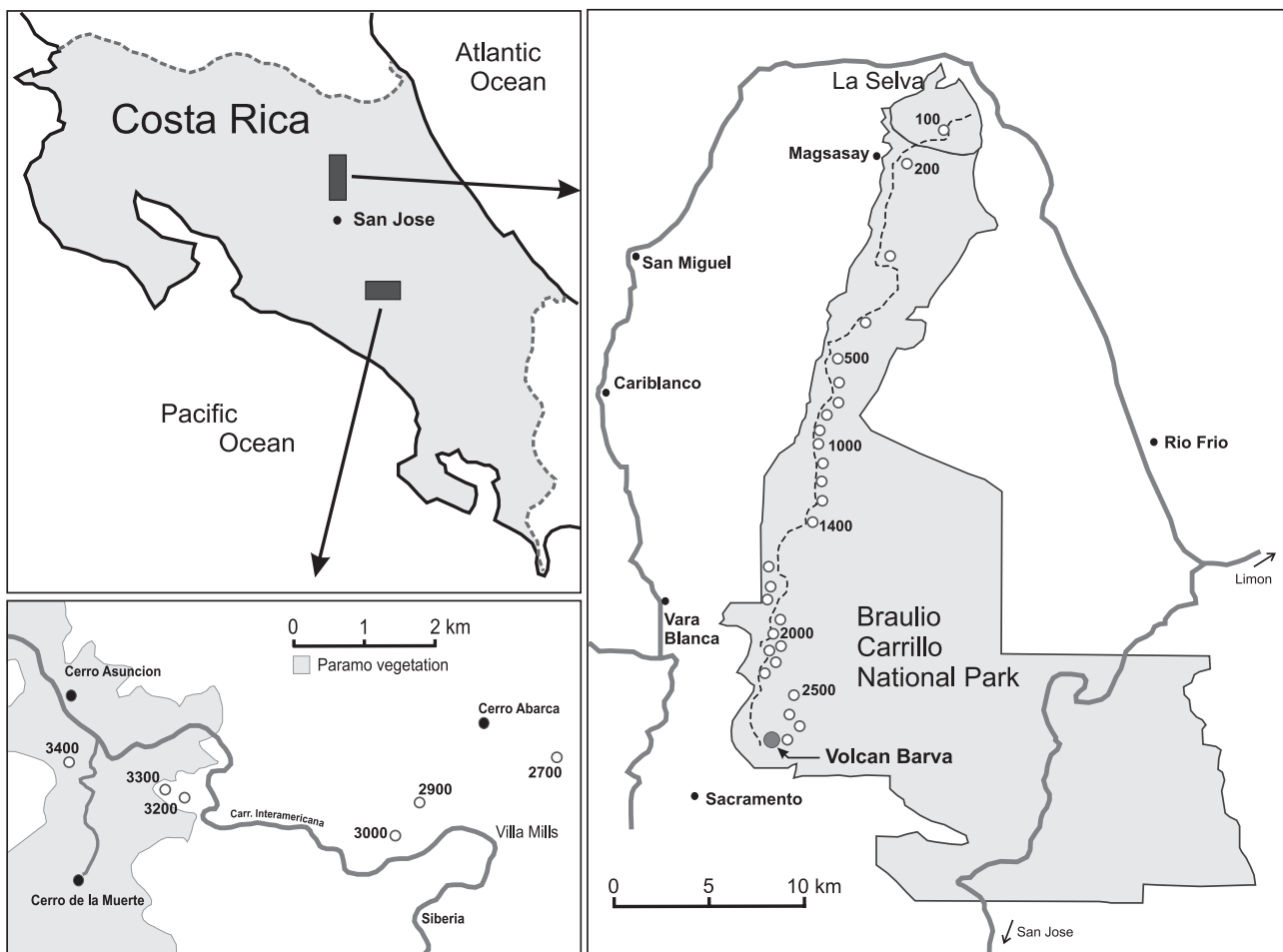


Figure 1 Study areas Volcán Barva (Biological Station La Selva and Braulio Carrillo National Park) and Cerro de la Muerte; open circles: elevational steps, greyish line in Braulio Carrillo map: transect trail.

are understood as dispersal barriers, and because ferns have small, wind-borne spores (Tryon, 1970, 1979; Smith, 1972) the limited distance between the mountains raises the question of whether the top of Volcán Barva is in fact such a dispersal barrier, or if spore dispersal from other mountains influences the fern assemblages near the top of that mountain. Because there is no unambiguous way to define the upper domain limit in this situation, we conducted our analyses both for the Barva subtransect only and for both subtransects combined.

Vegetation sampling

Field research was carried out from August 2002 to September 2003. The pteridophyte vegetation was studied on 156 plots in elevational steps of 100 m (with an elevational range overlap of both subtransects between 2700 m and 2800 m). At every step we established five plots wherever possible, while keeping plot area constant to control for sampling effort and area (Rahbek, 1997; Lomolino, 2001). Plots were 400 m² in size, mainly of square shape (20 × 20 m²). This size is small enough to keep environmental factors and forest structure homogeneous within the plots and is the minimum area required for representative pteridophyte

surveys in humid tropical forests (Kessler & Bach, 1999). Crown and high trunk epiphytes were recorded using binoculars and collecting poles, and by searching recently fallen trees and branches within the plot or adjacent locations (Gradstein *et al.*, 2003). Each plot was sampled exhaustively for 4–8 h per plot, depending on the species richness of the habitat.

Collections were identified at the Herbarium of the National Museum of Costa Rica by JK, with the support of A. Rojas (*Elaphoglossum*), I. Valdespino (*Selaginella*), B. Øllgaard (*Huperzia*), D. Barrington (*Polystichum*) and A. R. Smith, R. C. Moran and L. D. Gomez in cases of doubt. Nomenclature follows the *Flora Mesoamericana* (Moran & Riba, 1995) with few exceptions, mainly in the genera *Elaphoglossum* and *Cyathea* (Rojas, 1996 1997, 2001a,b, 2002a,b). Herbarium specimens were deposited at the Herbarium of the National Museum of Costa Rica (CR), the Herbarium of the University of Costa Rica, San José (USJ) and the Herbarium of the University of Göttingen, Germany (GOET).

Species richness was expressed as point diversity, i.e. the mean species density per plot within every elevational step. Unlike many recent studies (e.g. Grytnes & Vetaas, 2002; Bhattarai *et al.*, 2004), we did not interpolate species distributions between actual records. The underlying reasoning of interpolation is that

gaps in elevational distribution are caused by undersampling. However, interpolation has three problems. (1) It disrupts the crucial control of sampling area and sampling intensity as species are added that were *in fact* not present in the plots. (2) Gaps are filled only *between* lower and upper recorded range limits, which in essence assumes that no individuals of a species have been missed beyond the observed range limits, but that individuals have been missed at sampling points within the range limits. As a result, interpolation increases richness in mid-elevations to a higher degree than at the gradient limits (Grytnes & Vetaas, 2002). (3) Species richness in nearby plots is more similar than in distant plots (distance decay) and the resulting spatial autocorrelation inflates Type I error (Diniz-Filho *et al.*, 2003). The spurious effects of autocorrelation increase when using interpolated distribution data. However, many diversity studies on elevational gradients use interpolated data, and comparisons of such data with our noninterpolated data might prove difficult. We therefore calculated the correlation of our empirical richness patterns and with the related interpolated patterns of richness. Interpolated and empirical richness patterns showed the same pattern along the elevational gradient and were highly correlated ($R = 0.94$, $P < 0.001$). Similarly, regression analyses using interpolated richness showed qualitatively similar results to those analyses using empirical richness measures. We thus present results based only on the empirical richness values without interpolation.

Data treatment and explanatory variables

The relationship between diversity (various measures) and the explanatory variables was calculated for each individual variable using simple linear regression and then overall using stepwise multiple linear regression analyses. Such a linear model tests only for linear relationships between the potential explanatory variables and diversity, but there are several plausible scenarios under which a unimodal model is actually more biologically reasonable. For example, it is possible that the richness pattern is not determined by a single factor, but rather that the increase of species richness in the bottom half of the transect and the decline in the upper half are determined by different sets of factors, e.g. low temperatures at high elevations and low humidity at low

elevations (e.g. Bhattarai *et al.*, 2004). Thus, we also examine a unimodal model to detect such curvilinear relationships. To do this, we included a quadratic term into the regression function [in its general form: $Y = b_0 + b_1X + b_2X^2$; generalized linear model (GLM), with Y : dependent variable, X : independent variable and b_i : coefficients]. Models were examined both with and without the contribution of the MDE as an explanatory variable.

To consider whether different factors influence large and small-ranged species (as has been suggested, e.g. Colwell *et al.*, 2004), we divided the species set into two halves with species of large and narrow elevational ranges and conducted analyses overall and with each of these groups separately.

All analyses were performed with spss 10.0.

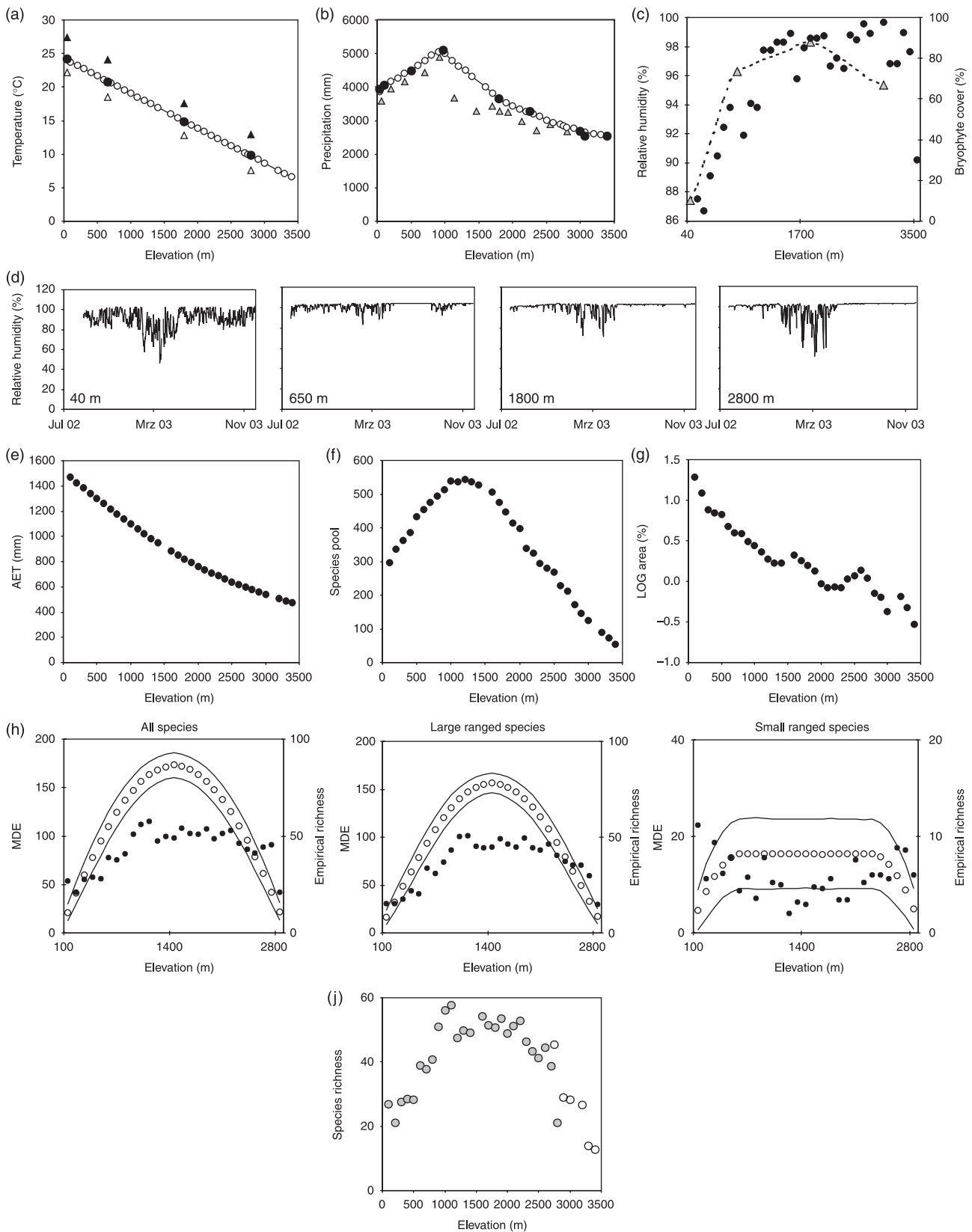
The following explanatory variables were included in the analyses.

Climate: temperature, precipitation and humidity

Temperatures and relative humidity were measured at several locations within four different elevational bands from July 2002 to November 2003 using in total 27 Microdaq data-loggers HoboPro RH/Temp. At each single location we established a set of three data-loggers at 50 cm and 200 cm above the ground and in the inner canopy as high up as possible. The locations of data loggers were chosen so as to have the lowest possible chance of temporary direct sunflecks. Sites were at 40 m (in zonal forest), at 650 m and 1800 m (in zonal, ravine and ridge forest at each site), and at 2800 m (in zonal and ridge forest). Temperature data were collected every 10 min and were averaged afterwards to 1 h to minimize the impact of possible outliers. For the present study we used the averaged mean, minimum and maximum daily temperature and daily minimum values of humidity of zonal forest stands.

The cover of bryophytes on trunks and branches was estimated visually in each plot and the mean of all plots at each elevational step was used as a proxy for humidity, as bryophytes have been well documented to increase with increases in humidity (Frahm & Gradstein, 1991; Wolf, 1993). In order to validate the assumption that bryophyte cover closely reflects relative humidity, we correlated bryophyte cover with the averaged minimum daily relative humidity of all data-loggers at 50 cm and 200 cm above ground (Fig. 2c,d). Minimum values were used because

Figure 2 (a) Temperature (22 August 2002–2 December 2003), this study; circles: mean annual; triangles: mean daily maximum (filled triangles) and mean daily minimum (open triangles) temperature; model (open circles) was estimated by linearly interpolated field data; mean lapse temperature was $0.55\text{ }^\circ\text{C}/100\text{ m}$, which nearly equals estimate of Lieberman *et al.* (1996) ($6\text{ }^\circ\text{C}/1000\text{ m}$). (b) Mean annual precipitation: filled circles: data from Instituto Meteorológico Nacional (IMN), San José (2003), except at 2260 m (Heaney & Proctor, 1990) and 3475 m (Kappelle *et al.*, 1989); open circles: linearly interpolated data; triangles: data from the WorldClim data bank (Hijmans *et al.*, 2004). (c) Bryophyte cover on trunks and branches along the elevational transect between La Selva (40 m) and Volcán Barva (2906 m); mean cover values of all plots within an elevational band of 100 m (filled circles); mean of daily minimum values of relative humidity (%) at four sites along the transect trail (40 m, 650 m, 1800 m, 2800 m) (open triangles, broken line; relation between bryophyte cover and measured relative humidity: $R = 0.84$, $P < 0.001$). (d) Daily minimum values of relative humidity (%) at four elevations between August 2002 and November 2003, combining data from all data loggers at 50 cm and 200 cm above ground at each elevation. (e) Actual evapotranspiration (AET): combination of mean annual temperature and precipitation along the elevational gradient, following Turc's formula (1954), $\text{AET} = P/[0.9 + (P/L)^2]^{1/2}$, with $L = 300 + 25T + 0.05T^3$, P = mean annual precipitation and T = mean annual temperature. (f) Estimated species pool: number of species per elevational belt of 100 m; data source: INBio, herbarium data of specimen of Costa Rica, restricted to the Atlantic slope and data of Moran & Riba (1995). Data for 805 species (number of individual records = 12,235). (g) Area as an explanatory variable; estimated area in elevational bands of 100 m, given in percentage values of total area considered, and afterwards log-transformed due to nonlinear relationship between area and species richness. (h) Empirical (closed circles) and predicted species richness (open circles) for 434 on the Brava transect; predicted species richness under



assumption of random placement (MDE, lines: upper and lower 95% CI limits), computed by 5000 randomizations of observed species ranges using RangeModel (Colwell, 2004); empirical and predicted richness given for: all species, large-ranged species, i.e. the half of all species with wide elevational amplitudes ($n = 218$), and small-ranged species, i.e. the half of all species with narrow elevational ranges ($n = 216$). (j) Species richness along elevational transect between 100 m and 2800 m (closed circles) and between 2750 m and 3400 m (open circles).

occurrences of drought are likely to reflect growth-limiting situations. Least frequency of drought occurrences and day-by-day oscillations of minimum humidity values were observed at 1800 m, indicating the highest and most balanced humidity conditions at this elevational band.

To detect patterns of precipitation, we used the mean annual precipitation values of nine meteorological stations located close to the study transect (maximum distance from transect 12 km for San Miguel) [data from Instituto Meteorológico Nacional (IMN), San José; Kappelle *et al.*, 1989; Heaney & Proctor, 1990] (Fig. 2b). Observation periods for stations were 5–47 years, 24 years on average. Values for steps lacking independent stations were interpolated linearly between values from the closest two stations. The resulting elevational lapse of annual precipitation values with maximum at about 1000 m is in close accordance with modelled data from the WorldClim data bank (Hijmans *et al.*, 2004).

In addition to single climatic variables, we included the actual evapotranspiration (AET) as the predictive variable. AET was calculated using Turc's formula (Turc, 1954; González-Espinosa *et al.* 2004), where $AET = P/[0.9 + (P/L)^2]^{1/2}$, with $L = 300 + 25T + 0.05T^3$, P = mean annual precipitation, and T = mean annual temperature (Fig. 2e).

Regional species pool

The species present at the study transect are a subset of the species occurring in the region and that have the potential to colonize in the study area (Graves & Gotelli, 1983). While a variety of relationships between regional species pool and local diversity might be hypothesized, a linear relationship has been suggested most frequently (e.g. Rosenzweig & Ziv, 1999). To construct the model of a regional species pool, we compiled the number of species in Costa Rica per elevational step based on data from the Instituto Nacional de Biodiversidad (INBio) and on literature data (Moran & Riba, 1995; Rojas, 1996, 1997, 2001a,b, 2002a,b) (Fig. 2f).

Area effect

The effect of area is crucial in species diversity studies and has a strong influence at all scales (Rosenzweig & Sandlin, 1997; Crawley & Hurrall, 2001; Whittaker *et al.*, 2001; van Rensburg *et al.*, 2002). Larger areas contain more individuals and thus more species ('passive-sampling hypothesis', Connor & McCoy, 1979). Because in mountains area typically declines with elevation (Körner, 2000), species numbers can be biased towards lower elevations (Rahbek, 1995). Other things being equal, the number of species should decline with elevation as area declines (Rohde, 1997). As area and species richness do not have a linear relationship, we used log-transformed area as the explanatory variable (Rosenzweig & Ziv, 1999). We estimated the proportion of total area found at intervals of 100 m in a 30-km-wide strip for the area of the Braulio Carrillo National Park and on Cerro de la Muerte (transect area) by counting grid cells on topographical maps (1 : 50,000) between the contour lines and the area of the

elevational bands was expressed as the percentage of the total area considered (Fig. 2g).

Geometric constraints: the MDE

In recent years the MDE, a geometrical null model in which species' ranges are placed randomly along a geographical domain with hard outer boundaries resulting in hump-shaped richness patterns, has been invoked as an explanation for richness patterns along elevational and other gradients (Colwell & Hurrall, 1994; see review in Colwell *et al.*, 2004). While MDE models have been shown to correlate closely to the diversity patterns along some elevational gradients (Kessler, 2000a; Colwell *et al.*, 2004; McCain, 2004), the meaning and implications of such geometric constraints models is debated hotly (Bokma & Mönkkönen, 2000; Colwell & Lees, 2000; Jetz & Rahbek, 2001; Hawkins & Diniz-Filho, 2002; Grytnes, 2003; Colwell *et al.*, 2004; Herzog *et al.*, 2005). Nonetheless, when combined with the effects of area, geometric constraints have in several cases been shown to explain nearly all variation in richness along particular elevational gradients (e.g. Sanders, 2002; Bachman *et al.*, 2004).

An MDE null model was used to estimate the influence of geometrical constraints on the elevational distribution of species (Colwell & Hurrall, 1994; Colwell & Lees, 2000; Jetz & Rahbek, 2001; Colwell *et al.*, 2004) (Fig. 2h). We used RangeModel software (Colwell, 2004) to generate the null distributions (means of 5000 runs) expected if empirical species ranges were placed at random within the domain, under the constraint that none extend beyond domain limits. We used the randomization procedure of model 2 of Colwell & Hurrall (1994), where empirical ranges are assigned random mid-points drawn from a uniform distribution and mid-point–range combinations that extend beyond the domain are omitted and a new mid-point–range pair is drawn with replacement. This model approximates the pattern expected were the position of the range over which each species lives along the elevation gradient to evolve randomly with respect to any biological or environmental gradient along the gradient, while the distribution of possible range sizes remains characteristic of the biology of the taxon. As in Jetz & Rahbek (2002), we split species into two groups, large-ranged and small-ranged, for analysis because large-ranged species are more likely to be constrained by geometry, whereas small-ranged species are more likely to show the effects of underlying environmental or historical drivers. Arita (2005) recently made several theoretical predictions on how range sizes should be distributed along domain gradients if species distribution is determined by Colwell & Hurrall's (1994) model 2 version of the mid-domain effect. We compared our data with two of these predictions, namely that (1) mean range size (in our study: elevational range of the species) should remain constant along the gradient and (2) that skewness of the range sizes should increase towards the extremes of the gradient.

Collinearity among variables

We found that several variables varied in similar ways along the elevational gradient (e.g. temperature and log area both decreased

Table 1 Coefficients of determination (R^2) of average point diversity values of every elevational step of 100 m with explanatory variables for all species and separated for large-ranged and small-ranged species; standard coefficients (beta) for each variable and model fit (R^2) are given for stepwise multiple regression analysis. Analyses are based on data of the Barva subtransect between 100 m and 2800 m, and of the full transect also including the upper subtransect on Cerro de la Muerte (100–3400 m). Model A includes all variables, model B all variables except the MDE. Temperature was excluded from all models because of nearly perfect collinearity with AET. Reduction of dimension: factor analysis reduced variability within explanatory variables to two dimensions, high factor loadings in the same dimension indicate possible collinearity within the variable groups. — = variable not incorporated in model; (.) = variable excluded from analysis (F -significance > 0.5); * $P < 0.01$, ** $P < 0.005$, *** $P < 0.001$

	Range of gradient Variable	100–2800 m			100–3400 m		
		R^2 individual	beta Model A	beta Model B	R^2 individual	beta Model A	beta Model B
All species	MDE	0.66***	0.77***	—	0.83***	0.87***	—
	Bryophyte cover	0.44***	(.)	(.)	0.26**	(.)	(.)
	Precipitation	0.00	(.)	(.)	0.15	0.23**	(.)
	Species pool	0.22	(.)	0.82***	0.49***	(.)	1.26***
	Log area	0.33**	(.)	(.)	0.00	(.)	0.79
	Temperature	0.15	—	—	0.03	—	—
	AET	0.22	–0.38***	–0.82***	0.01	(.)	–1.54
	Model fit (R^2)		0.80***	0.76***		0.87***	0.83***
Large-ranged species	MDE	0.78***	0.85***	—	0.81***	0.84***	—
	Bryophyte cover	0.44***	(.)	(.)	0.16	(.)	(.)
	Precipitation	0.01	(.)	(.)	0.25**	0.35***	(.)
	Species pool	0.30**	(.)	0.90***	0.64***	(.)	1.21***
	Log area	0.32**	(.)	(.)	0.01	(.)	(.)
	Temperature	0.12	—	—	0.08	—	—
	AET	0.19	–0.34***	–0.82***	0.02	(.)	–0.63***
	Model fit (R^2)		0.90***	0.85***		0.93***	0.87***
Small-ranged species	MDE	0.48***	—	—	0.36***	–0.60***	—
	Bryophyte cover	0.20	(.)	(.)	0.33**	(.)	–0.59***
	Precipitation	0.05	(.)	(.)	0.00	(.)	(.)
	Species pool	0.31**	(.)	–0.68***	0.11	(.)	–0.34*
	Log area	0.12	(.)	0.51**	0.07	(.)	(.)
	Temperature	0.01	—	—	0.03	—	—
	AET	0.03	(.)	(.)	0.06	(.)	(.)
	Model fit (R^2)		0.49***	0.55***		0.36***	0.45***
Reduction of dimension		Dimension		Dimension			
		1	2	1	2		
	MDE	0.01	0.98	–0.07	0.97		
	Bryophyte cover	–0.82	0.50	–0.63	0.71		
	Precipitation	0.86	0.45	0.91	0.31		
	Species pool	0.54	0.84	0.74	0.66		
	Log area	0.93	–0.33	0.94	–0.17		
	Temperature	1.00	–0.02	1.00	0.02		
AET	0.99	–0.12	0.99	–0.11			

monotonically with elevation and regional species pool and precipitation both showed hump-shaped patterns with elevation). Such collinearity might influence multiple regression analyses by leading to the exclusion of one of two variables with a similar pattern, which might then mask the possible relative importance of the excluded variable. We ran a factor analysis to detect such possible collinearity (Table 1). The resulting matrix combines the groups of variables with comparable patterns along the elevational gradient into a smaller set of ‘dimensions’ indicated by high ‘factor loads’. Within a given dimension, variables with inferior factor

load have a higher risk of being excluded by running multiple regressions. The exclusion of a variable from a multiple regression therefore does not necessarily indicate insignificance of the excluded variable, especially when factor loads of included and excluded variables of the same dimension were comparable and high.

RESULTS

Within the 156 study plots we recorded a total of 484 pteridophyte species (see Appendix S1 in Supplementary Material).

Table 2 Top: series of second order polynomial regressions for species richness along the Barva transect (100–2800 m) and predictor variables, using generalized linear models (GLM). Equation for second order polynomials following equation term $f = b_0 + b_1 \cdot \text{variable} + b_2 \cdot \text{variable}^2$. Bottom: stepwise multiple linear regression model with all second-order functions; all variables except temperature were excluded (F -significance > 0.5), excluded variables not shown; d.f. = degrees of freedom; * $P < 0.01$, ** $P < 0.005$, *** $P < 0.001$

Variable	GLM order	d.f.	R^2	b_0	b_1	b_2
MDE	2	24	0.66***	21.59	0.20	-0.0001
Bryophyte cover	2	24	0.55**	12.59	0.88	-0.0056
Precipitation	2	24	0.01	65.72	-0.01	0.0000
Species pool	2	24	0.23	41.06	-0.05	0.0001
Log area	2	24	0.53***	46.17	15.67	-32.0660
Temperature	2	24	0.80***	-85.23	17.51	-0.5518
AET	2	24	0.76***	-55.13	0.23	-0.0001
Model (stepwise)	beta	R^2				
Temperature	0.90***	0.80***	(All other variables excluded due to F -statistics)			

Richness of all species showed a clear hump-shaped pattern with maximum around 1700 m and with a steeper decline towards high elevations (Fig. 2j).

Along the Barva subtransect between 100 m and 2800 m, species richness was correlated strongly with the MDE and bryophyte cover ($R^2 > 0.4$), whereas all other variables showed only weak linear correlations (Table 1). A stepwise regression model of all variables (model A) included the MDE and AET, and explained 80% of the variation in species richness. The MDE had the strongest explanatory power within the final model (beta = 0.77, $P < 0.001$) which also included AET (beta = -0.38, $P < 0.001$). A second model with all variables except the MDE (model B) included AET and species pool, and explained 76% of the variation in species richness.

When the species data set was divided into two groups (large and small-ranged species, 218 and 216 species, respectively), the effect of the geometric constraints showed a different pattern in the two different groups (Fig. 2h) relative to that observed for the data set as a whole. Large-ranged species showed a mid-elevation peak in richness. In contrast, small-ranged species had maximal richness at the lower and the upper ends of the gradient, respectively. While the MDE model predictions were well correlated with pteridophyte species richness for all species when considered together and for large-ranged species, the explanatory power of the MDE for the subset of species with narrow elevational ranges was lower. For the large-ranged species, other environmental variables contributed only modestly to the final model, just as for the data set overall. For the subset of small-ranged species only species pool had a significant but low relationship to variation in species richness. Similarly, stepwise multiple regression models for the subset of large-ranged species included the same variables as for the full species set in both models, and explained similar proportions of the species richness as for the full data set. For small-ranged species, on the other hand, the MDE was the only included explanatory variable in model A and species pool and log area in model B, but both models had low explanatory power ($R^2 < 0.5$).

When the Barva subtransect was combined with the additional subtransect on Cerro de la Muerte, all models, except for small-ranged species, revealed only slightly higher fits to those obtained when only the main transect between 100 m and 2800 m was considered, but different variables were significant predictors of richness (Table 1). The MDE remained the single variable with the highest regression values. Coefficients of determination for species pool were higher than in the models for the single subtransect and significant, while regression values of log area were lower than for the single subtransect and not significant (Table 1).

Some of those variables that were poorly correlated with species richness in the linear regressions (Table 1) were highly correlated with species richness when applying curvilinear regression models (Barva transect, Table 2). This was especially true for temperature and AET, for which regression values increased from 0.15 and 0.22 (not significant) in a linear model to 0.80 and 0.76 in a curvilinear model (both $P < 0.001$). In a linear model with all quadratic functions included, only temperature remained in the final model ($R^2 = 0.80$, $P < 0.001$). The same was the case when the Barva transect was combined with the subtransect on Cerro de la Muerte (data not shown), in which case only temperature was incorporated into the final model ($R^2 = 0.87$, $P < 0.001$). Both quadratic models in which only environmental variables were included had very similar overall coefficients of determination to the linear models with the MDE.

The high number of excluded variables in the multiple regression analyses could be due to collinearity among the variables we considered, which might then mask the possible relative importance of single variables. Two groups of variables ('dimensions') were separated (Table 1). Along the main transect (the Barva transect between 100 m and 2800 m), the variables bryophyte cover, log area, precipitation and temperature were combined because of monotonic trends (dimension 1) and the MDE and species pool were combined because of pronounced humped patterns (dimension 2). As a consequence, we cannot exclude the possibility that variables within each of these groups act together

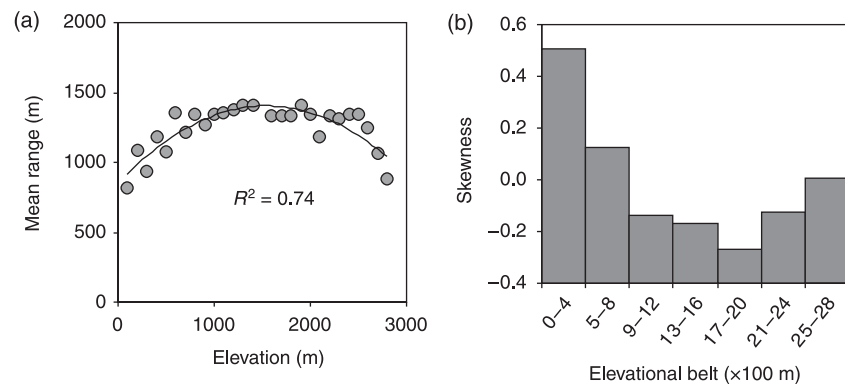


Figure 3 Range size frequencies: (a) mean range size along elevational gradient; (b) skewness of range size frequencies of elevational belts of 400 m.

to govern patterns of diversity, or that variables within groups interact in complex ways. This is probably the case for temperature and AET.

Mean range size varied with elevation and range size skewness increased towards the extremes of the gradient (Fig. 3).

DISCUSSION

Our study revealed both clear elevational patterns of species richness as well as strong relationships between species richness and several sets of potential explanatory variables. At the most general level, our study adds to the growing number of studies (Jacobsen & Jacobsen, 1989; Parris *et al.*, 1992; Kessler, 2001a; Hemp, 2002; Bhattarai *et al.*, 2004) showing that on high mountains pteridophyte species richness shows a strongly hump-shaped elevational pattern, even though the absolute elevations of the richness peaks vary somewhat between the studies (Table 3). Hump-shaped patterns of species richness in pteridophytes have been interpreted as reflecting maximum humidity at mid-elevations (Hemp, 2002; Kessler, 2001a), an optimal combination of humidity and mild temperatures (Bhattarai *et al.*, 2004), or the geometric influence of hard boundaries (Kessler, 2001b). The relative influence of each of these determinants of richness patterns may vary among eleva-

tional gradients and taxa. Below we discuss each of the explanations for the pattern of fern species richness we observed.

Species pool

The regional species pool is the most basic 'null model' for local species richness, based on the assumption that local species are drawn at random from the regional pool (Romdal, 2003), or at least that the proportion of the regional species pool drawn at different elevations is invariant. Considering that our sample included almost half of all pteridophyte species known from Costa Rica, it is somewhat surprising that we observed only a modest correlation between our point diversity data and the regional species richness. The regional species pool peaked at 1200 m, i.e. 500 m below the local peak. The most obvious explanation for the discordance between local and regional diversity is that the effect of area is stronger at the regional scale. In fact, multiplying our local species richness values from the standardized plot design with the log-area values of the respective elevational bands, both local and regional richness curves peak at 1200–1300 m and are better correlated ($R = 0.69$, $P < 0.001$). In any case, a possible good concordance between regional and local species richness might not necessarily indicate a causal relationship, as they reflected the same basic pattern on

Table 3 Studies on pteridophyte species richness along elevational gradients

Source	Study location	Study method	Number of species	Elevational extent (m)	Species diversity peak (m)
Lellinger (1985)	Panamá	Literature survey	687	0–3250	500–1500
Parris <i>et al.</i> (1992), Kessler <i>et al.</i> (2001)	Mt. Kinabalu/Borneo	Literature and herbarium survey combined with 20×20 m ² plots	613	400–4000	1600
Jacobsen & Jacobsen (1989)	Southern Africa	Literature survey	296	0–3482	1000–1500
Jacobsen & Jacobsen (1989)	East Africa, Rwanda-Burundi-Kivu	Literature survey	254	700–4507	1500–2000
Jacobsen & Jacobsen (1989)	East Africa, Kenya Uplands	Literature survey	219	0–5195	1500–2000
Kessler (2001b)	Carrasco National Park/Bolivia	Plots of 20×20 m ²	493	200–3950	1800
Hemp (2002)	Mt Kilimanjaro/Tanzania	Plotless sampling	140	760–4400	1500–2000
Bhattarai <i>et al.</i> (2004)	Himalaya/Nepal	Literature survey	228	100–4800	2000
This study	Costa Rica, Central America	Plots of 20×20 m ²	484	100–2800	1700

different spatial scales. This basic pattern would probably be driven by the same factor(s) discussed below.

Area

Area is a crucial parameter determining biodiversity patterns (e.g. Rahbek, 1995; Rosenzweig & Ziv, 1999; Lomolino, 2001) and can have both indirect and direct effects on species richness (Connor & McCoy, 1979). As long as surveys follow a standardized protocol, there is no direct area-effect. However, even when sampling is standardized for area, the size of the regional area surrounding the investigated area may influence species richness patterns, if such increased area increases the rate of dispersal into the study area (Shmida & Wilson, 1985; see also Lomolino, 2001). This 'echo-effect' (Rosenzweig & Ziv, 1999) can lead to a correlation between area and diversity even when samples are of equal size. In our study, regional area had a very low influence when the full extent of the transect was considered, but because regional area and temperature are highly correlated (Table 1), it is possible that at high elevations both variables are acting in concert to decrease species richness.

MDE

In our study, the MDE was the single most powerful explanatory variable in the regression analyses when all species were considered. Furthermore, as predicted by MDE null models, the effect of geometric constraints decreased with decreasing elevational range of the individual species, a pattern also shown for geographic range size at the continental scale for African birds by Jetz & Rahbek (2002) and in several other studies (reviewed in Colwell *et al.*, 2004). However, we also found an interesting deviation from the MDE expectations of the null model we used (model 2 of Colwell & Hurr, 1994). Contrary to the prediction of Arita (2005), mean elevational amplitude of species did not remain constant along the gradient. Other null models, such as the spreading dye null model (Jetz & Rahbek, 2001, 2002; Jetz *et al.*, 2004), can produce variation in mean elevational amplitude along the domain (e.g. Candelús *et al.*, 2006), but probably not to the extent seen here. The deviation of the elevational amplitude from MDE expectations was caused primarily by an accumulation of species with narrow elevational amplitudes at either end of the gradient. These accumulations of small-ranged species were explained poorly by the MDE or other variables and there are two possible explanations for this. Either we may have missed an important environmental or historical variable or the null model used may be insufficiently complex. The most probable interpretation of this pattern is that the species occurring at the ends of the transect have potential ecological amplitudes exceeding the conditions actually realized along the gradient, i.e. that they could grow above or below the transect. As a result, the observed elevational amplitudes are smaller than those of species occurring in the transect's middle, where they can express their full ecological amplitudes.

A possible test of the above hypothesis (that amplitudes are truncated on the studied domain) would be to compare

elevational transects on mountains of different height within a floristic region. We predict that on all mountains (or other domains for that matter) there will be an accumulation of species with narrow ranges near the top of the mountain, but that on higher mountains species that have restricted ranges on lower mountains will have larger amplitudes because their uphill maximum extends beyond the maximum elevation of lower mountains. For the accumulation of narrow-ranged species at the lower end of the gradient, a latitudinal comparison should show that species with wide elevational ranges in the tropics have gradually reduced ranges as they are climatically 'squeezed out' towards higher latitudes. This hypothesis is contrary to assumptions of MDE model 2 assumptions, where species with amplitudes extending beyond the domain range are excluded (Colwell & Hurr, 1994), but more in line with predictions of spreading dye models (Jetz & Rahbek, 2001, 2002; Jetz *et al.*, 2004) and suggests that biologically more realistic versions of the MDE null model may be useful (Grytnes & Vetaas, 2002).

Climate

Precipitation, temperature, bryophyte cover (as a proxy for humidity) and AET were only weakly correlated with patterns of species richness along the whole gradient. However, our analyses presume a linear relationship between AET or temperature and richness, which is not the most biologically reasonable hypothesis. Instead, a hump-shaped relationship between temperature and AET and richness seems more likely, with richness highest at intermediate temperatures and rainfalls. In fact, the best fit for these variables to the parabolic shape of species richness was a two-order polynomial function). If climatic factors do contribute to observed patterns of pteridophyte richness, it is therefore likely that they operate in different ways on different parts of the gradient: the linear decrease of temperature along the whole elevational gradient therefore affects negatively the increase of species richness at low elevations, and vice versa positively at high elevations. Such a parabolic relationship might be expected if, on the bottom half of the gradient, high precipitation and its potential benefits to pteridophyte richness are offset by high temperatures and therefore high evapotranspiration, reduced humidity and periodic dry periods (Fig. 2c), whereas on the top half of the gradient pteridophyte species richness was limited by low temperatures, especially frost events (Bhattarai *et al.*, 2004). That temperature and not humidity limits growth, abundance and species richness at high elevations is suggested by fern morphological traits: blade thickness of pteridophyte species as expression for xeromorphism is the morphological characteristic correlated most strongly to elevation (and thus temperature), while these morphological characteristics do not have a correlation trend relative to humidity (M. Kessler and J. Kluge, unpublished data).

Potentially, optimal temperatures overlap with a peak in humidity at mid-elevations. Humidity can be critical for pteridophytes both for reproduction (the transport of gametes depends on wet surfaces) and for growth (Kessler, 2001a; Page, 2002; Bhattarai *et al.*, 2004). In the tropics, stable cloud condensation

belts lead to high humidity at mid-elevations (Hastenrath, 1967) through reduced solar radiation and extra 'occult' precipitation (Bruijnzeel & Veeneklaas, 1998; Bhattarai *et al.*, 2004), as also evidenced by our microclimatic measurements. On higher mountain ranges and in drier regions, the elevation of the condensation level tends to lie at higher elevations than in humid regions and on smaller mountain ranges (Bruijnzeel & Veeneklaas, 1998). The higher elevational position of condensation levels may be the reason for the rather high elevation of maximum pteridophyte species richness in fairly dry eastern Africa at 2000 m (Jacobsen & Jacobsen, 1989; Hemp, 2002) compared to the low peaks at 500–1500 m in very wet Panama, which also has lower mountains (Lellinger, 1985).

Taken together, temperature and humidity may thus limit species richness at both extremes of the gradient, but in different ways: at the lower end by a reduction of humidity through high temperatures, and at the upper end by low temperatures. We suspect that an optimal range of temperature and humidity exists at mid-elevations, a conclusion that echoes the findings of Bhattarai *et al.* (2004). Favourable climates may lead to higher species richness either because optimal climatic conditions lead to maximum productive energy available in the ecosystems (e.g. Wright, 1983; Rohde, 1992; Brown *et al.*, 2004; Ferrer-Castán & Vetaas, 2005) or because fewer species can tolerate extreme (cold and/or dry) conditions ('tolerance hypothesis'; see Currie *et al.*, 2004).

CONCLUSIONS

We were unable to consider several potentially explanatory variables, due to limits in our understanding of fern communities. This is the case of historical factors (Bush, 2002) and metapopulation dynamics such as source–sink effects (Kessler, 2000b; Grytnes, 2003). Nonetheless, we did not have a lack of explanatory power; rather the reverse. We found that both the MDE and climatic variables had high explanatory power in the regression models and can be considered as the main potential factors determining the richness pattern of pteridophytes along the study transect. The MDE was the primary driver of the best linear models and temperature of the best curvilinear model, resulting in similar explanatory power for the two sets of models. A discrimination between these factor complexes is not possible through a simple comparison of the regression coefficients, because both the MDE and climatic variables were correlated strongly with fern species richness, with R^2 values > 0.75 . However, our results suggest deviations from Arita's (2005) theoretical predictions about the distribution of range sizes along the study gradient. While this unmet prediction does not necessarily derive from all possible MDE models, it still cautions us against uncritically accepting the MDE model used here as a determining factor without further study. Climatic conditions, on the other hand, provide a biologically reasonable explanation for the richness pattern observed along our study transect, and the relationship between the measured climatic variables and diversity closely mirrors a global latitudinal pattern documented by Hawkins *et al.* (2003). In a meta-analysis across numerous taxa, Hawkins *et al.* (2003) found that — with few exceptions — richness is

generally limited at high latitudes by low temperatures and at low latitudes by water availability. Our study shows that this general pattern is mirrored at least for pteridophytes on elevational gradients. Our results are reconcilable with the hypothesis that temperatures limit richness at high elevations and water availability limits richness at low elevations. Interestingly, Hawkins *et al.* (2003) observed that the point at which the limiting influences of temperature and water availability switch is taxon-dependent, e.g. birds are less temperature-sensitive than butterflies and so switch at higher latitudes. Based on these considerations, we believe that two approaches are most promising in the future to distinguish between the relative influences of the MDE and climate in determining elevational richness patterns. First, a comparison of the richness patterns of numerous taxa differing in temperature- and drought-sensitivity along elevational gradients should be conducted. For example, along our study transect tree diversity peaks at 300 m (Lieberman *et al.*, 1996), indicating that in this case the MDE is unlikely to be the main determining factor and pointing to fundamental ecological differences between ferns and trees. Secondly, it would be useful to study one or several transects where the optimal climatic conditions do not coincide with the middle of the transect, where the MDE also predicts highest richness.

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SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com/loi/geb

Appendix S1 Species of ferns and fern allies along the elevational transects from La Selva to Volcán Barva (100–2800 m) and on Cerro de la Muerte (2700–3400 m), Costa Rica, sorted by family.