MORPHOLOGICAL CHARACTERISTICS OF FERN ASSEMBLAGES ALONG AN ELEVATIONAL GRADIENT: PATTERNS AND CAUSES

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Abstract. Based on species distribution data of 477 fern species along a tropical elevational gradient of 3300 m altitude, we analyzed the morphological patterns of species assemblages and related the patterns to environmental factors. Although close correlations of morphological traits and environmental drivers do not necessarily imply causality or function, a number of those morphological characteristics are also found in seed plants and have been tested widely regarding their relation to the ambient environment, and the results found within this study are in accordance with the main results for seed plants. High values of laminar thickness, combined with limited laminar dissection, are interpreted as defensive strategies against climatic extremes, especially at high elevations. High stomatal densities have also frequently been reported to occur at sites with low CO_2 concentrations approaching high elevations. The main indument types, hairs and scales, although often assigned similar functions, may serve different functions, namely, respectively repelling and retaining water; comparable studies with seed plants have advocates for both hypotheses. Correlations between morphological traits and environmental drivers among plant groups of different lineage point to the increasing plausibility of such arguments. However, for pteridophytes, more studies of whole vegetation assemblages along extended environmental gradients are needed to verify the results found within this study. *Accepted 15 March 2007.*

Key words: pteridophytes, morphology, environment, climate, elevational gradient, tropical forest, Costa Rica.

INTRODUCTION

The morphology of plants has often been interpreted as an indicator of environmental conditions. Size and shape of leaves and other special characters affect the performance of plants within their environment by optimizing the exploitation of resources, and by providing defense strategies against harmful impacts, e.g., climatic extremes and herbivory. If the environment acts as a selective force then we would expect a similar coincidence of characteristics within similar environments, regardless of the taxonomic composition of the species assemblage (Halloy & Mark 1996). The identification of such 'functional groups', and their relation to their ambient biotic and abiotic world, not only serves for mechanistic explanations of the character under consideration, but also allows analyses of environmental changes over time. Plants as a 'key to past climates' are the subject of a long discussion in

reconstructing climate history (e.g., Chaloner & Creber 1990, Uhl & Mosbrugger 1999), for instance through the comparison of recent and ancient climates based on the correlation between atmospheric CO_2 and stomatal density (Woodward 1987, Beerling & Chaloner 1993, McElwain 1998, McElwain *et al.* 1999, Chen *et al.* 2001). Actual CO_2 gradients, as for example along elevational gradients, do alter mean stomatal densities, with highest densities at sites with lowest CO_2 concentrations (Körner *et al.* 1979).

Plants are morphologically diverse, and the underlying biotic and abiotic drivers of these morphologies (in the context of whole species assemblages) provide a useful tool for characterizing and comparing habitat conditions within and beyond biogeographic boundaries. Broad attention on this issue has been focused on the architecture of leaves, the constraints including aspects of support and resistance. Water-use efficiency and gas-exchange requirements affect the development of blade shapes, as well as mechanical demands to withstand wind, temperature, and hu-

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midity extremes. Common examples of leaf structure convergence are seen in high mountain environments with wide temperature oscillations and strong winds, leading to small, ericoid leaves (e.g., Hedberg & Hedberg 1979, Körner 1999). The indument of leaves – hairs and scales – is hypothesized as improving water assimilation and protecting against solar radiation, thus retarding water loss in dry environments (Ehleringer & Mooney 1978, Müller *et al.* 1981, Körner 1999), but the indument may also protect stomata in wet environments (Gates 1980). This apparent contradiction in functional significance is an example of how morphological characteristics depend on the environment where the species occur (Press 1999).

Traditionally, correlations of particular morphological characteristics of vegetation assemblages or single species to habitat qualities are referred to as adaptations (e.g., Bock & von Wahlert 1965, see Koehl 1996 for a review), i.e., promoting the fitness of species in their particular habitat. The conceptual pathway "morphology – performance – fitness" (Koehl 1996) circumscribes a methodology which is more descriptive rather than mechanistic, since experimental analyses of the investigated mechanisms are, if possible at all, very difficult. Consequently, many studies rely on statistical correlations and assign patterns of morphological traits to the most probable environmental drivers. Thus the soundness of conclusions is determined by a predominance of the morphology-environment correlation found. Not surprisingly, this procedure may be hampered by the fact that unmeasured drivers (that correlate with those that are measured) can be responsible for morphological traits, and that unmeasured morphological traits (that correlate with those measured) may be the actual reasons for the fitness of the species. Moreover, phylogenetic constraints of the plant taxa involve may limit the range of morphological adaptations that can be realized, potentially influencing the patterns observed in nature. The simplest way to overcome all these uncertainties in linking morphology and environment is to find similar patterns in different lineages, because effective strategies to deal with certain environmental factors are hypothesized to have evolved independently and more than once.

The primary goal of this paper is to present morphological patterns among fern assemblages along an elevational gradient in Costa Rica. This gradient covers 3300 m, from nearly sea-level to *páramo* above the treeline, involving steep gradients in important environmental factors such as temperature and humidity. The range of environmental extremes between the opposite ends of the gradient, and the large variability of morphological features within ferns, offer a solid basis for comparison of species assemblages and their prevailing morphological structures within their environmental setting. The relationship between form and function of morphological traits not only serves as a characterization of different existing habitats, but also for analyses of changes in habitats over time by comparing morphological changes in fossil species assemblages (Mosbrugger & Utescher 1997). Because most previous studies using plants as indicators of paleoclimatic changes, as a key to past climates, have dealt with seed plants and gymnosperms (e.g., Pyykkö 1979, Körner 1988, Chaloner & Creber 1990, Wolfe 1993, Niklas 1996, 1999, McElwain 1998, Uhl 1999, Chen *et al.* 2001, Roth-Nebelsick *et al.* 2001), there is a need for data on pteridophytes (Uhl & Mosbrugger 1999), especially since ferns have been dominant in several geological periods, contribute considerably to present-day vegetation assemblages, particularly in the wet tropics, and show a high morphological diversity. The data presented here should help to enhance the knowledge about environmentally driven morphological traits among ferns in particular and vascular plants in general.

METHODS

Climate. We measured temperature and air humidity with 27 Microdaq data loggers HoboPro RH/Temp at 4 elevational steps (40, 650, 1800, and 2800 m) along the gradient (at intervals of 10 minutes, from July 2002 to November 2003 – a period of 18 months). We used minimum humidity values, because occurrences of drought likely reflect limiting growing conditions for drought-sensitive organisms like most ferns. Additionally, as bryophyte abundance is supposed to reflect air humidity (Frahm & Gradstein 1991, Wolf 1993), we visually estimated the cover of bryophytes on trunks and branches in each plot, and used the mean of all plots at each elevational step as a proxy for air humidity. Precipitation data came from seven meteorological stations within 15 km of the transect region (Instituto Meterologico Nacional, San José), with additional data from Kappelle *et al.* (1989) and Heaney & Proctor (1990) and an observation period of 5–47 years (mean 24 years). For analyses, we interpolated linearly between these measuring points for every elevational step of 100 m. The resulting elevational lapse of annual precipitation

values with maximum at about 1100 m is in good accordance with modelled data from the WorldClim data bank (Hijmans et al. 2004).

Vegetation sampling. In Costa Rica, the Biological Station La Selva and adjacent Braulio Carrillo National Park are known as the most extensive protected elevational gradient of primary tropical forests in Central America (Pringle *et al.* 1984, Pringle 1988, Herrera-McBryde 1997), with an outstandingly high fern diversity and endemism (Mehltreter 1995, Kluge *et al.* 2006, Watkins *et al.* 2006). This area covers 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). To complete the gradient to vegetation zones above the timberline, we chose 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 at higher elevations (Kappelle *et al.* 1989) (Holdridge life zones "montane rain forest" and "subalpine rain *páramo*"). Along this elevational gradient we sampled the pteridophyte vegetation in 156 plots in elevational steps of 100 m with four to five plots each. Plot area was constantly 400 m^2 to control for sampling effort and area (Rahbek 1997, Lomolino 2001). This size is small enough to keep environmental factors and forest structure more or less homogeneous within the plots, and is the minimum area required for representative pteridophyte surveys in humid tropical forests (Kessler & Bach 1999). Canopy and high trunk epiphytes were recorded using binoculars and collecting poles, and by searching for recently fallen trees and branches within the plot or

TABLE 1. Morphological traits according to information from Moran and Riba (1995), Rojas (1996, 1997, 2001a, b, 2002a, b), and herbarium studies, and their assignment to classes. Source of information is given as: a: literature information; a(b): literature information checked by own observations; b: own observations.

Characteristic	Description	Class	Source
Rhizome type	absent / unknown	0	a
	upright to short-creeping	1	a
	creeping	2	a
	(stout) tree-like	3	a
Laminar dissection	entire	0	a
	once-pinnate (to once-pinnate-pinnatifid)	1	a
	twice- or more-pinnate	2	a
Laminar morphology	monomorphic	1	a
	slightly dimorphic	2	a
	dimorphic (incl. heterophyllous)	3	a
Laminar thickness	thin (membranaceous to thin herbaceous)	1	a (b)
	medium (herbaceous to paper-like)	2	a (b)
	thick (thick paper-like to very coriaceous, stiff)	3	a (b)
Scale and hair density	absent (0%)	0	b
	very sparse / weak (> 0% to 1%)	1	b
	sparse (1% to 10%)	2	b
	numerous (10% to 50%)	3	b
	very numerous to covering surface (> 50%)	4	b
Hydathodes	absent	0	a
	present	1	a
Indusium	absent	0	a
	present (incl. false indusium, involucrum, synangium)	1	a
Buds	absent	0	a
	present	1	a

adjacent locations (Gradstein *et al.* 2003). Each plot was sampled exhaustively for 4–8 hours per plot, depending on the species richness of the habitat.

Morphological characteristics. Within our 156 study plots we found 477 species of ferns and fern allies. The morphological characteristics of these species were compiled by analyzing literature data (Moran and Riba 1995, Rojas 1996, 1997, 2001a, b, 2002a, b), complemented by the study of collections for such characters as scales and hair density and stomatal densities. Other characteristics studied were the shape of rhizomes and blades, the presence of hydathodes, vegetative buds, slime and indusia, and the density of scales and hairs on different parts of the plants. Some of these characteristics, especially indument density values and laminar thickness, are rather subjective, and so to avoid a pretense to accuracy we used an ample class division. All characteristics were assigned to classes (Table 1).

Patterns of stomatal density along the elevational gradient were assessed by studying specimens of the most species-rich genus on the transect, *Elaphoglossum* (Lomariopsidaceae). We used all collected 333 specimens of 72 *Elaphoglossum* species (1 to 16 specimens per species, depending on total frequency), which was about one-third of all *Elaphoglossum* records (N = 980) along the elevational gradient between 100 m and 3400 m (the elevational distribution of analyzed specimens were random, therefore elevation and number of analyzed specimens were totally uncorrelated; R = 0.08, p = 0.676). We used only mature fronds for assessment of stomatal densities because young immature leaves often show relatively high stomatal densities (Chen *et al.* 2001). We applied clear nail polish on the abaxial surface at the tip, center, and base of each blade. When dry, we pulled the polish film from the frond surface, counted the stomatal cells within 5 squares of $1 \, mm^2$ each (stomatal density) by transmitted light microscopy and used the mean values for analysis.

Data analysis. To assess morphological patterns of species assemblages with elevation and climatic factors, we counted the number of species (percentage values) with the respective characteristic within each species assemblage at every elevational step of 100 m and regressed against the driving factors. However, there might be close relationships between pteridophyte morphological characteristics, and in order to reduce the complexity within the set of characteristics we used principle component analysis (PCA). This procedure extracts artificial variables ('factors') from the original data matrix. As a result, the original variables are represented by fewer factors, and the correlation of each variable with each factor ('factor loading') is given. Thus high factor loadings (> 0.4) of variables on the same factor indicate strong covariance of the respective characteristics (i.e., they occur significantly in combination, or, if factor loadings have different signs, they significantly exclude each other). These factors were also tested on correlation with the driving factors. Correlations and regressions of morphological characteristics and factors with temperature are not shown, as temperature is strongly negatively correlated with elevation (r = −0.96, p < 0.001), and correlations and regressions with temperature are therefore simply the inverse of those with elevation. ANOVA was applied to test the differences in frequencies of morphological characteristics between Holdridge Life Zones, and differences in stomatal densities between laminar thickness classes. All analyses were carried out with SPSS 11.5; trendlines were set by distance-weighted least-square smoothing with tension 0.5, using SYSTAT 7.0.

RESULTS

Climate. The transects on the Atlantic slope of Volcán Barva and Cerro de la Muerte, 35 km apart with a total elevational extent of 3400 m, showed steep climatic gradients. Mean annual temperature declined linearly from 24.2°C at 40 m to 9.8°C at 2800 m (lapse rate 0.53°C / 100 m) (Fig. 1C). The daily variation of mean temperature was comparable at all four sites, with a slightly higher variability in the dry season from January to April (Fig. 1A). The variability of daily humidity values was considerably higher during the dry season, with frequent dry spells even within the rainy season (May to December), and least at 1800 m (Fig. 1B); total variability was most pronounced at the lower and upper ends of the transect. The relatively constant humidity conditions at mid-elevations therefore led to highest mean humidity values over the whole observation period (Fig. 1D), with decreasing humidity towards both ends of the transect. This was also reflected by comparing the humidity lapse over the whole gradient with estimated bryophyte cover on trunks and branches (Fig. 1D, triangles). From sea-level to mid-elevations, we found a strong increase in mean bryophyte cover, from 5 % to about 90 %. Towards the upper treeline, bryophyte cover was still high, whereas air humidity decreased.
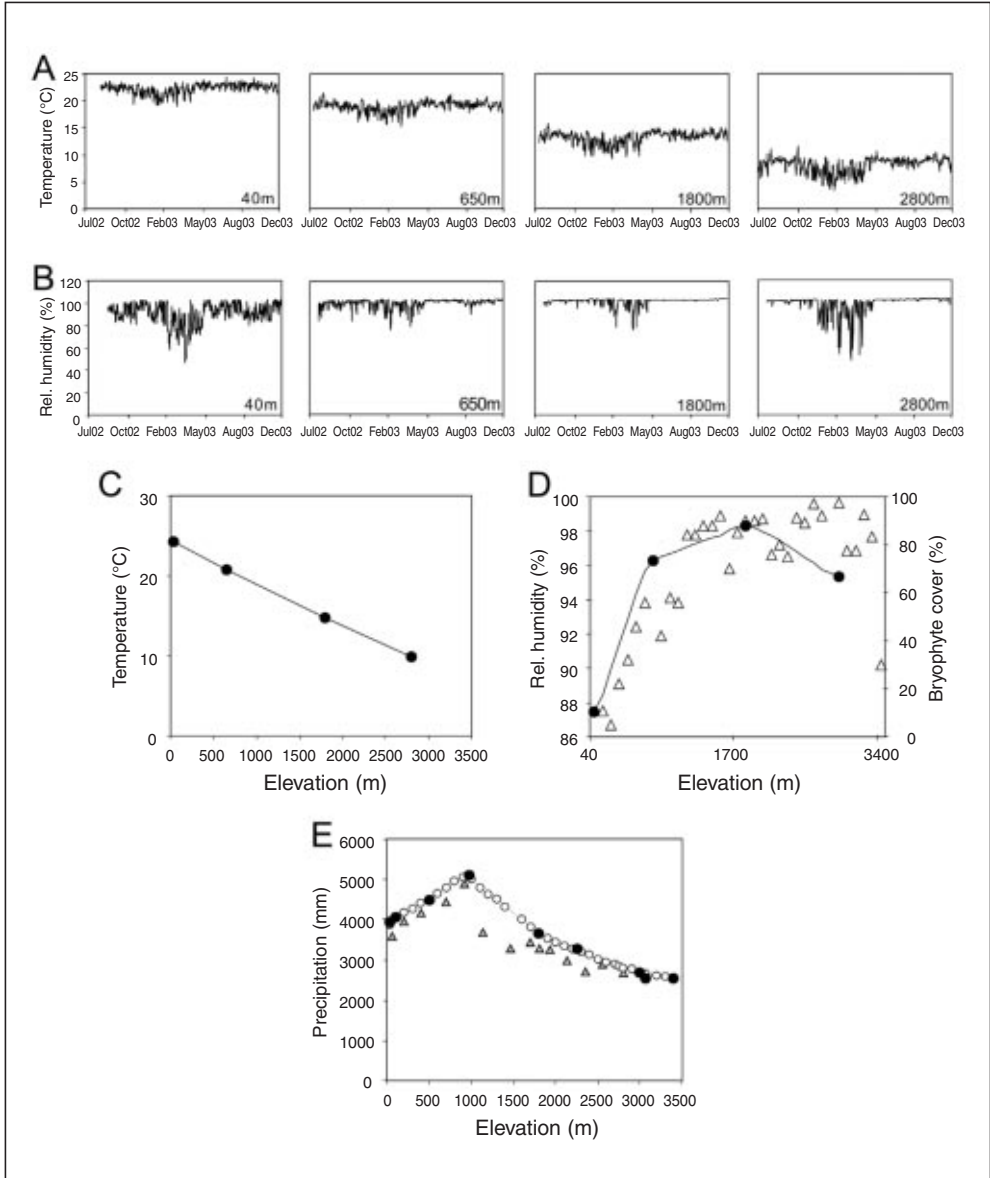
FIG. 1. Climatic characteristics of the elevational gradient: temperature, air humidity, and precipitation. (A) Mean daily temperature and (B) Mean minimum daily air humidity, measured at four elevational steps (40, 650, 1800, 2800 m) from July 2002 to November 2003. (C) Mean annual temperature at four elevational steps, mean lapse rate was 0.53°C / 100 m. (D) Mean minimum air humidity at four elevational steps (filled circles) and bryophyte cover on trunks and branches (triangles) at every elevational step of 100 m; both data-lines are correlated with R = 0.84 (p < 0.001). (E) Mean annual precipitation from 9 meteorological stations within a distance of 15 km from the transect area. Filled circles: data from IMN - Instituto Meteorológico Nacional, 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).

However, over the whole gradient, air humidity and bryophyte cover were closely correlated (R = 0.84, p < 0.001). Mean annual precipitation peaked at 1100 m (Fig. 1E) and decreased towards both ends of the gradient.

Morphological characteristics. The first three factors (F1–F3) of the PCA explained more than half of the variance in the distribution of morphological characteristics among fern species (Table 2), and high factor loads in the same direction indicated a covariance of the respective characteristics.

Most morphological variables were combined in the first two factors, which explain nearly the half of the variance; scales, dimorphism, and thickness on the one, and hairs on the other hand, showed oppo-

site trends. Most other characteristics showed unclear relationships to individual PCA factors with factor loadings below 0.4, only the distribution of values of laminar thickness, dimorphism (both positive), and laminar dissection (negative) among fern species having a considerable influence.

Correlations of the first two factors with environmental variables show a contrary trend of indument types (scales and hairs) along humidity and temperature gradients (Table 2). Laminar thickness, laminar dissection, rhizome type, and indusia may also play a role in reflecting environmental conditions.

The basic rhizome types (upright or very short and creeping with a compact arrangement of fronds (class 1) and creeping with distant fronds (class 2))

TABLE 2. Covariance of morphological characteristics of all species, derived by reduction of dimensions using principle component analysis (PCA). Seventeen morphological characteristics were reduced to 4 factors (F1–F4). Eigenvalue of factors, explained variance (%) of factors, factor loadings (> 0.4) of morphological characteristics, and correlation values (Pearson's R) of factors and environmental variables are given. * p < 0.01, ** p < 0.005, *** p < 0.001.

|	F1	F2	F3	F4
Eigenvalue	4.99	2.53	2.18	1.39
% variance explained	29.3	14.9	12.8	8.2
% cumulated variance	29.3	44.2	57.0	65.2
Factor loads				
Scales on rhizome	0.41	0.65		
Scales on stipe	0.65		0.60	
Scales on rachis	0.73		0.59	
Scales on axes	0.72		0.60	
Scales laminar tissue	0.76			
Dimorphism	0.60			
Laminar thickness	0.58			
Hairs on rhizome	−0.48			−0.47
Hairs on stipe	−0.66	0.42		
Hairs on rachis	−0.65	0.56		
Hairs on axes	−0.61	0.51	0.44	
Hairs on laminar tissue	−0.52	0.57		
Laminar dissection	−0.47	−0.47		
Indusium		−0.60		
Rhizome type		−0.41		−0.44
Hydathodes				
Buds				0.62
Correlations	R	R	R	R
Precipitation	−0.63***	−0.74***	0.17	0.36
Bryophyte cover	0.04	0.55**	−0.18	0.28
Temperature	−0.50**	−0.77***	0.16	0.25
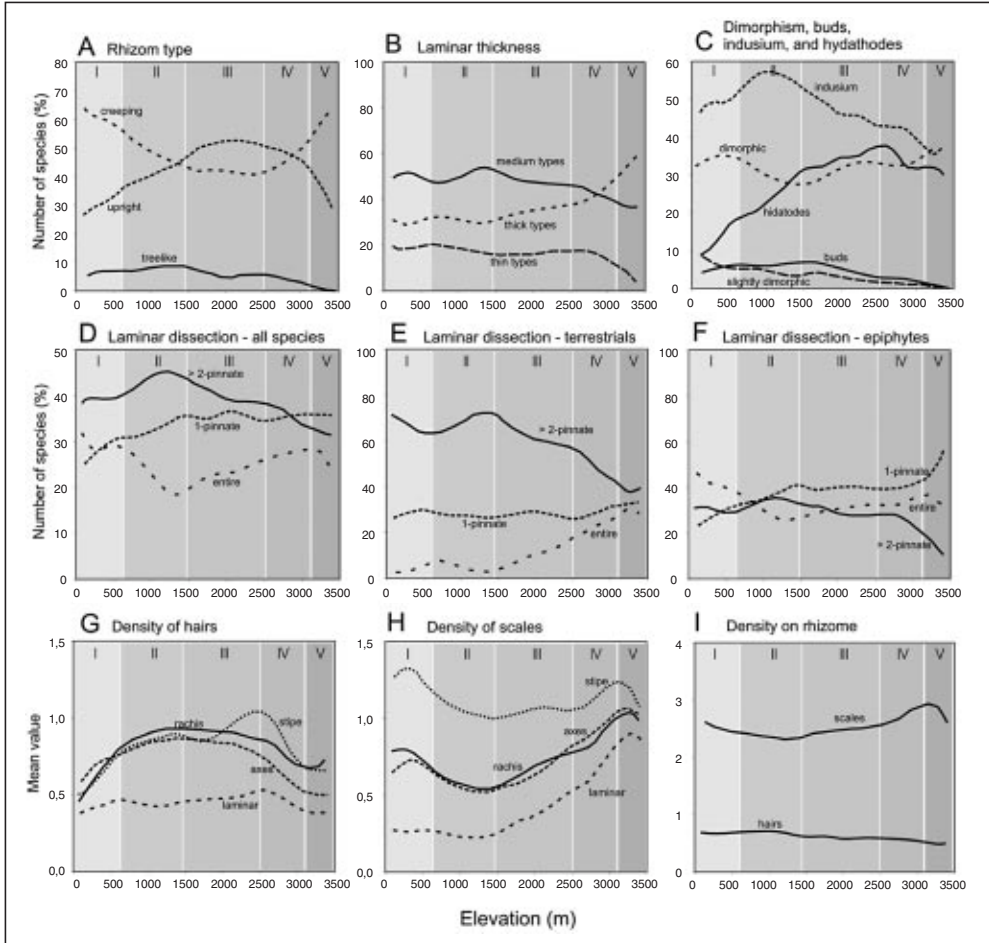
FIG. 2. Morphological traits in relation to elevation and Holdridge Life Zones. Holdridge Life Zones (Holdridge 1967) are given in gray shades (for Life Zones see legend to Table 3). Mean number of species (%) at every elevational step of 100 m between 100 m and 3400 m along the elevational gradient possessing indicated features regarding (A) rhizome type, (B) laminar thickness, (C) dimorphism, buds, indusium, and hydathodes, (D) laminar dissection of all species, (E) of terrestrial species and (F) epiphytic species, (G) mean density of hairs and (H) mean density of scales on different parts of blades, and (I) mean density of hairs and scales on rhizomes. For clarity of presentation only trendlines are given. Trendlines were set by distance- weighted least square smoothing with tension 0.5, using SYSTAT 7.0.

both showed a clear pattern with elevation (Fig. 2A). Species assemblages at mid-elevations had the highest values of upright rhizome types, whereas creeping types showed the opposing trend. The third rhizome type (tree-like) was the rarest and its frequency pattern was more or less diffuse along the elevational gradient, except for a marked decline towards its upper end.

Species with thin laminar types (i.e., membranaceous and herbaceous species) showed a significant decline in frequency towards high elevations, especially above mid-elevations (Fig. 2A, Table 3), and species with thick blades showed the opposing trend. Particularly in Holdridge Life Zones above 2500 m (i.e., montane rain forest and subalpine rain páramo) thick types, comprising 50 to 60 % of the fern spe-

TABLE 3. Correlations of morphological characteristics of fern species assemblages with climatic parameters (correlations with temperature are not shown because of its directly inverse correlation with elevation). For a clearer overview, in rhizome types, and laminar thickness and dissection, some classes were combined. Analyses of variance (ANOVA) of morphological characteristics of fern species assemblages with respect to Holdridge Life Zones; lowercase letters indicate affinity of Life Zones to homogeneous subgroups using Student-Newman-Keuls procedure; I: tropical wet forest (< 600 m), II: premontane rain forest (600–1450 m), III: lower montane rain forest (1450–2500 m), IV: montane rain forest (2500–3200 m), and V: subalpine rain *páramo* (> 3200 m). * $p < 0.01$, ** $p < 0.005$, *** $p < 0.001$.

| Morphological variables		Correlations			ANOVA		Life Zones				
		Elevation	Precipi-tation	Bryophyte cover	F	p	I	II	III	IV	V
Rhizome type											
	upright	0.45***	–0.33***	0.63***	46.06	0.000	a	b	c	c	d
	creeping	–0.28***	0.14	–0.61***	40.22	0.000	a	b	c	bc	a
	tree-like	–0.47***	0.55***	–0.05	22.75	0.000	a	b	ac	c	d
Laminar	slightly dimorphic	–0.64***	0.54***	–0.48***	18.91	0.000	a	b	c	d	d
	dimorphic	0.00	–0.08	–0.18	3.49	0.009	ab	a	a	a	b
Laminar dissection											
all species	entire	–0.04	–0.08	–0.17*	4.53	0.002	a	b	ab	ab	ab
	once-pinnate	0.42***	–0.31***	0.42***	8.42	0.000	a	b	b	b	b
	twice- or more-pinnate	–0.25**	0.29***	–0.13	4.48	0.002	ab	a	ab	b	b
terrestrials	entire	0.62***	–0.61***	0.31***	30.12	0.000	a	a	b	c	d
	once-pinnate	0.07	–0.08	–0.09	1.64	0.167	ab	a	ab	ab	b
	twice- or more-pinnate	–0.59***	0.58***	–0.22*	31.49	0.000	ab	a	b	c	d
epiphytes	entire	–0.23**	0.03	–0.43***	12.23	0.000	a	b	bc	bc	c
	once-pinnate	0.51***	–0.37***	0.33***	15.14	0.000	a	b	b	b	c
	twice- or more-pinnate	–0.37***	0.41***	0.06	17.38	0.000	ab	a	ab	b	c
Laminar thickness											
	thin	–0.39***	0.36***	–0.05	15.04	0.000	a	a	a	a	b
	medium	–0.36***	0.34***	–0.12	7.97	0.000	a	a	ab	b	c
	thick	0.59***	–0.54***	0.16	40.32	0.000	a	a	b	c	d
Buds	(present)	–0.47***	0.46***	–0.18	11.12	0.000	a	a	a	b	c
Hydathodes	(present)	0.72***	–0.57***	0.77***	56.54	0.000	a	b	c	c	c
Indusium	(present)	–0.46***	0.58***	–0.12	22.14	0.000	a	b	ac	c	d
Scales (density)											
	rhizome	0.37***	–0.45***	0.11	12.76	0.000	a	a	a	b	b
	stipe	–0.14	-0.01	–0.29***	6.29	0.000	a	b	b	ab	ab
	rachis	0.34***	–0.48***	–0.08	21.44	0.000	bc	a	b	c	d
	minor axes	0.46***	–0.55***	0.06	26.30	0.000	a	b	a	c	d
	laminar	0.71***	–0.72***	0.28***	59.41	0.000	a	a	b	c	d
Hairs (density)											
	rhizome	–0.35***	0.37***	–0.13	6.62	0.000	ab	a	bc	bc	c
	stipe	0.27**	–0.13	0.48***	13.60	0.000	a	b	b	b	a
	rachis	0.13	0.08	0.38***	14.70	0.000	a	b	b	c	ac
	minor axes	–0.26**	0.38***	0.14	20.12	0.000	a	b	b	a	c
	laminar	0.12	–0.11	0.14	3.67	0.007	ab	ab	a	a	b
Stomata (number / mm²)		0.78***	–0.71***	0.34***	51.27	0.000	a	b	c	d	d
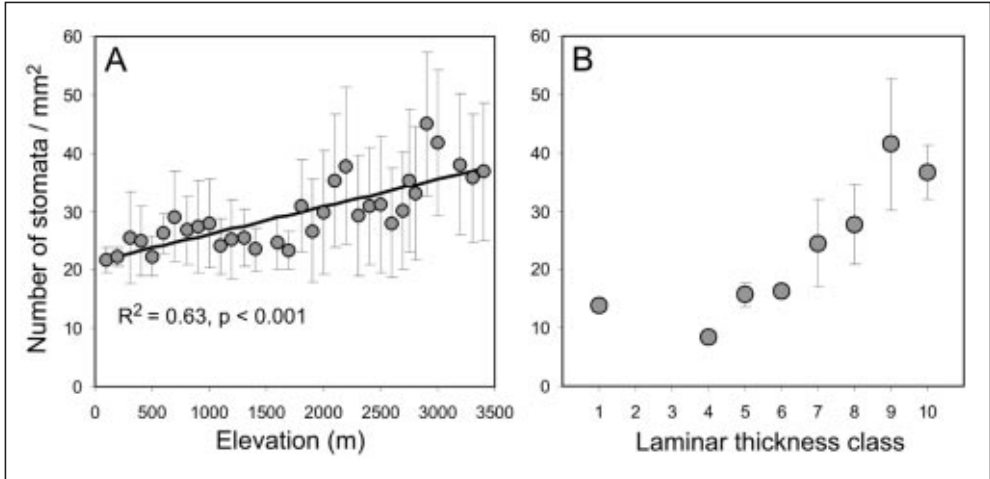
FIG. 3. Stomata of 333 specimens involving 72 *Elaphoglossum* species. (A) Mean density of stomata (N*mm^{-1}) (with 1 SD and regression line) at every elevational step of 100 m between 100 m and 3400 m along the elevational gradient. (B) Mean density of stomata (N*mm^{-1}) (with 1 SD) plotted against the laminar thickness class of the respective species.

cies assemblages, became dominant over thin types, and showed an affinity to cold and dry environments.

Also, both extreme dissection types (entire vs. twice- or more-pinnate) showed opposing trends with elevation. Highly dissected types predominated at mid-elevations, and both gradient ends showed a tendency towards entire blades. The once-pinnated blades held a intermediate position with a slightly increasing trend towards high elevations (Fig. 2D, Table 3). This pattern is basically confirmed when the species are separated into the major lifeforms (terrestrials and epiphytes; Figs. 2E, 2F). The only exception was that the increase in entire blades towards the lower end of the gradient was exclusively caused by epiphytes, whereas terrestrial species attained only very low frequencies. Overall, highly dissected species showed a tendency towards wet and warm environments, as represented by Holdridge Live Zones tropical wet to lower montane rain forest.

The density of hairs was highest at mid-elevations, and in contrast the density of scales was lowest at mid-elevations, with highest values towards the ends of the gradient, especially the upper end. This overall pattern was also observed when considering the indumentum densities on the different parts of the blades (Figs. 2G, 2H). The density of both indumentum types decreased almost throughout from lower to higher and exposed parts of the blade, i.e., from the stipe to the laminar surface.

We observed 135 species (28.3 %) with laminar dimorphism, but this characteristic showed no clear trend along the elevational or environmental gradients (Fig. 2C, Table 3). In contrast, the small number of 21 species (4.4 %) that had slightly dimorphic fronds, showed significantly decreasing frequencies towards high elevations and an affinity to warm and wet environments.

All other special morphological characteristics (buds, hydathodes, and indusia) showed strong relationships to elevation and environment (Fig. 2C, Table 3). Whereas buds and indusia were negatively related to elevation and positively to precipitation and temperature, the contrary was the case for hydathodes. Moreover, hydathodes were strongly positively associated with bryophyte cover, i.e., air humidity.

The mean stomatal density of assemblages of the 72 *Elaphoglossum* species increased significantly with elevation by about 4.7 stomata*mm^{-1}*1000m^{-1} (Fig. 3A, Table 3). The distribution of stomatal densities was strongly negatively related to precipitation and positively, but more weakly, related to bryophyte cover (air humidity). Additionally, the stomatal density of the studied *Elaphoglossum* species was positively related to laminar thickness (ANOVA, F = 10.94, p < 0.001, Fig. 3B).

DISCUSSION

One of the crucial problems in interpreting patterns of variation of morphological traits along environmental gradients is that causal relationships are hard to establish given the paucity of experimental studies and the phylogenetic linkage of many characters that determine morphological patterns, even in cases where no actual adaptation occurs. Below we mention several cases, especially involving the large and common genera *Elaphoglossum* and *Hymenophyllum*. However, we refrained from an in-depth phylogenetic analysis for two reasons. First, too little phylogenetic information is available on the majority of fern taxa in the study region to reliably address the question of which morphological character states evolved how often. Second, there is the issue of causality. Just as the preponderance of a certain taxon at a given elevation may influence the morphological traits observed there at community level, it is also conceivable that it is precisely those morphological traits that enable the taxon to thrive at this elevation. For these reasons we have followed a two-way approach in the presentation and interpretation of the results. First, we have documented the observed patterns because, even without a causal interpretation, these relationships can be used to make climatic inferences from fossil floras. Second, rather than providing a detailed discussion of all possible and mostly untested causal or phylogenetic relationships, we present the most likely explanations as a guideline for future experimental work.

Climate. Observing all climatic variables in context, the mid-elevations offer the most suitable growing conditions for many ferns, since high and constant humidity coincides with relatively mild temperatures (lack of drought or frost events). Accordingly, these zones support the highest species richness (Kluge *et al*. 2006). This observation underlines the climate-based dependency of fern species richness (Bhattarai *et al*. 2004, Kessler *et al*. 2001; see also Francis & Currie 2003, Hawkins *et al*. 2003). The contrast of the species-rich mid-elevations with their benign climatic conditions with the two extremes of the gradient will be a recurring theme in our interpretation of the observed morphological patterns.

Morphological interrelation among fern species. The principle component analysis (PCA) showed that some morphological characteristics of the fern species frequently co-occurred, and certain groups of morphological characteristics have inverse distribution trends.

The most obvious feature is that species with scales and species with hairs are at opposite ends of the factors. This means that species with many scales have few or no hairs and vice versa. However, scales and hairs are often considered to represent just two subtypes of the same characteristic, namely the indument. Whether these two different indument types indicate different functional strategies will be discussed below.

Among the other morphological variables, laminar thickness, dimorphism, and dissection showed trends aligned to both indumentum types, indicating that species with scales tend to have thicker, dimorphic, and less dissected leaves (factor 1). It is conjecture whether such a joint set of characteristics reflects a common strategy in dealing with environmental conditions. This pattern is probably caused by the high fraction of just one genus within the whole species set, namely *Elaphoglossum*. This was by far the most species-rich genus in the study, including 74 of the 477 species (15.5 %). All species of *Elaphoglossum* have scales and are dimorphic, and many of them, especially at high elevations, have a very stiff and thick blade texture. We therefore ran the PCA again and excluded the *Elaphoglossum* species, but the results remained about the same, with the exception of laminar dimorphism and dissection, which showed minor influence on factor 1, leaving indument types and laminar thickness as the most prominent drivers of the factor analysis.

As the first two factors in the PCA show significant correlations with temperature and humidity gradients, it is likely that the morphological characteristics constraining these factors may reflect – analyzed separately – their ambient environment as well. Disentangling all morphological characteristics step by step will give further insight into the arrangement of species within their environment according to their habit and texture.

Rhizome types. The basic rhizome types (upright/stout vs. creeping) show contrary trends along the gradient, with species assemblages at mid-elevations having a strong tendency towards short and upright rhizomes, whereas at both ends of the transect creeping rhizomes prevail (Table 3, Fig. 2A). Most likely this reflects two opposing trends. On the one hand, mid-elevations not only have the highest species richness, but also the highest numbers of individuals of ferns and epiphytes in general (Cardelús *et al*. 2006). Therefore the dominance of stout to erect rhizomes may reflect competition for space and light. At the elevational extremes, terrestrial and epiphytic herb communities
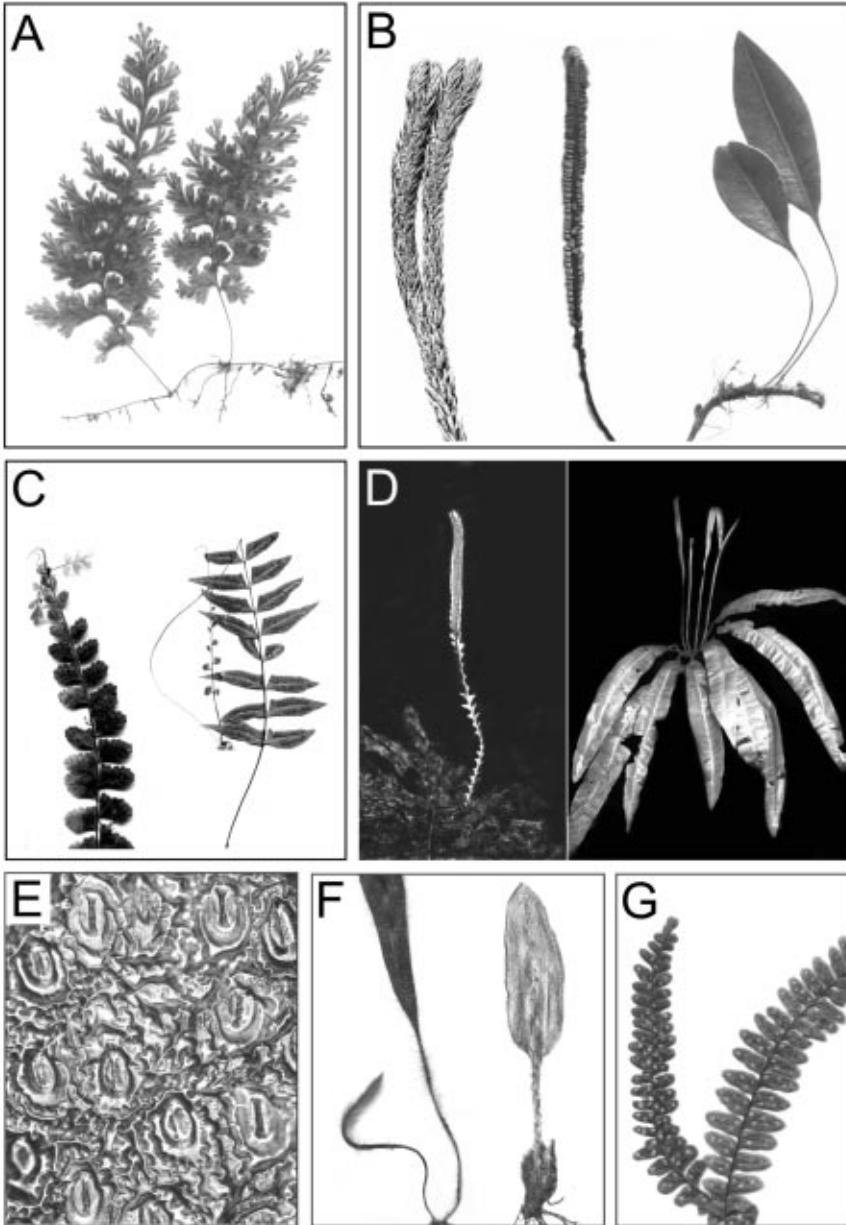
FIG. 4. Examples of laminar thickness types: (A) Thin types (*Hymenophyllum costaricanum*), and (B) thick types (*Huperzia talamancana*, *Jamesonia alstonii*, *Elaphoglossum hoffmannii*); (C) Plantlet formation by buds: left *Asplenium rosenstockianum* and right *Asplenium cirrhatum*; (D) Dimorphism in ferns: hemidimorphism, with fertile apical portion of frond modified (left, *Cochlidium serrulatum*) and holodimorphism, with whole fertile frond modified (right, *Elaphoglossum lankesteri*); (E) Stomatal cells of *Elaphoglossum proximum*. Scale of figure 0.2*0.25mm^2; (F) Indument types of ferns: Hairs (left, *Elaphoglossum siliquioides*) and scales (right, *Elaphoglossum muscosum*); (G) Hydathodes at the end of veins on the adaxial surface of *Terpsichore subtilis*. Note chalky secretion ('lime dots').

are rather open, but environmental conditions are less favorable. In these situations, creeping rhizomes can enable the plants to reach optimal microhabitats.

The tree-like life form, although much lower in species richness, shows no clear trend along most of the gradient (Fig. 2A), but the high regression values with elevation (Table 3) are caused by the marked decline at the upper end. A possible explanation for this might be found in vegetation structure and climatic factors, especially temperature. The overall lower height of the vegetation strata (Lieberman *et al.* 1996), as well as frequent low temperatures and strong winds at high elevations, may select against this growth form with its unprotected exposure of the vegetative organs. Tree ferns have been observed to be particularly sensitive to frost events both in Mexico (K. Mehltreter, pers. comm.), Kenya (Hemp 2001), and in Bolivia (MK, pers. obs.).

Laminar thickness. Laminar thickness showed a strong correlation with environmental factors. Many ferns are poikilohydric, and very thin laminar types are more sensitive to low humidity and drought (Dubuisson *et al.* 2003). There is great diversity in laminar structures in pteridophytes, from onecell thick in blades of *Hymenophyllum* to compact, entire, leathery blades that are often very stiff and almost brittle (many *Elaphoglossum* and *Huperzia*, Figs. 4A, B). The first extreme resembles the laminar structure of bryophytes, which are in many cases also strongly dependent on humid environments (Frahm & Gradstein 1991, Proctor 2003, León-Vargas *et al.* 2006). The other extreme is analogous to the leaf structure of high alpine ericoid shrubs, and interpreted as an adaptive strategy to environments with climatically harsh ('xeromorphism') or nutrient-limited ('peinomorphism') conditions (Körner 1999).

Overall, species with thin laminar (i.e., membranaceous and herbaceous) types were dominant at low and mid-elevations (up to two-thirds of all species in the respective assemblages, Fig. 2B). Up to mid-elevations, the dominance of thin laminar species is therefore in accordance with the common image of ferns as drought-sensitive organisms, primarily distributed in shaded forest habitats. Towards the upper treeline this pattern gradually changes. Above the upper limit of the condensation layer (*ca.* 2500 m), and with a gradual opening of the forest structure, species encounter an increasingly unfavorable environment with greater extremes of temperature and air humidity (Fig. 1) and frequent strong winds. Under these conditions firm-leafed adaptation

strategies gain increasing importance. Near the upper treeline at about 3200 m, thick, robust species predominate and ferns with ample and soft-herbaceous lamina structure disappear (see also species list given by Mehltreter 1995).

Laminar division. Laminar dissection patterns were highly variable along the elevational gradient, and so an assignment to ecological function is difficult. There have been very few attempts to relate blade shapes of pteridophytes to environmental settings, and some authors have stated that there is no evidence of relationships between dissection and ecological traits (e.g., Kramer *et al.* 1995, Kessler *et al.* 2001). However Kessler *et al.* (2001) showed intriguing similarities in blade shape between regions with a very small taxonomic overlap (Bolivia and Borneo). At these sites, niches for certain dissection types were filled by different taxa, often in different families (e.g., the predominance of entire blades represented in Borneo by Grammitidaceae, in Bolivia by *Elaphoglossum*, Dryopteridaceae). In both regions species with entire blades showed a tendency to grow at high elevations, a result confirmed by Halloy & Mark (1996), who found negative correlations with temperature. In contrast, an increase in species with entire leaves in warmer climates was reported by Wolfe (1971) and Kerr (1993) for fossil plants. Twice- or more-pinnate species showed a mid-elevational maximum in Bolivia and Borneo (Kessler *et al.* 2001), which probably indicates a positive correlation with environmental wetness.

Both trends in blade dissection patterns of pteridophytes (entire at high elevations, highly dissected at mid-elevations) are confirmed in this study (Fig. 2D), although entire leaves were also frequent at the lower end of the elevational gradient in Costa Rica. In the studies mentioned above (Kramer *et al.* 1995, Kessler *et al.* 2001), no attempt was made to distinguish between major life forms, namely terrestrials and epiphytes, although both habitats offer markedly different environmental conditions. Our data first revealed that leaves of terrestrial species have higher degrees of dissection than those of epiphytic species (Fig. 2E and 2F). Further, the common patterns mentioned above for all species also held true for both life forms. The major difference was that terrestrial assemblages included very few species with entire blades at low elevations, whereas epiphytic species here gained maximum values, therefore showing an U-shaped trend with elevation. The ecological settings driving species with entire blades to occur at low elevations seem to

be primarily an epiphytic phenomenon. In fact, at low elevations the vertical gradients (temperature, humidity) from forest floor to outer canopy is much steeper than at the upper treeline, where the low, open forest structure limits the microclimatic differences from soil to canopy. A high fraction of species at high elevations often occurred in all microhabitats, whereas at low elevations soils and canopy did not share any species, indicating a high microhabitat segregation (Kluge & Kessler, *in review*). The special conditions of the epiphytic habitat at low elevations are high solar radiation and highly variable air humidity, and therefore for epiphytes both ends of the elevational gradient share similar conditions of temporary low humidity, despite differences in absolute temperature. Entire blades (coupled with thick textures, Table 2) appear to be favored in habitats having marked temperature and humidity oscillations, a pattern also shown by Halloy & Mark (1996), who found that entire blades were dominant in open habitats but rare in dense shady forests. This blade morphology may offer greater mechanical stability and reduced evapotranspiration (Wolfe 1971, Körner *et al.* 1989, Kerr 1993).

Laminar indumenta. One of the most obvious features of fern morphology is the presence of epidermal appendages. Epidermal outgrowth often takes the form of hairs and/or scales, collectively referred to as indument (Fig. 4). Indument types and, especially, the density of hairs and scales are diverse, and accordingly we have assigned density classes to the two most commonly observed types. Categorization into hairs (uniseriate structures) and scales (flat, multiseriate structures) may be too simplified, but we use this basic division because it is widely applied for classification purposes, and because we lack understanding of homologies of various indument types (Kramer *et al.* 1995, Lellinger 2002).

Our data suggest opposing trends of both indumentum types along the elevational gradient (Figs. 2G and 2H). Similar results, with the highest density of hairs in the wettest sites and the lowest density in the driest, were found by Halloy & Mark (1996) in a study of functional traits of leaf characteristics across a wide taxonomic and geographical range. By contrast, density of scales was lowest at mid-elevations while highest values were observed towards the ends of the gradient, especially the upper end. This trend is more pronounced for the more exposed parts of the leaves, especially for the laminae (Table 3).

These opposing trends of hair and scale density along an elevational gradient are noteworthy, because

both indument types have been assigned the same functions, including reduction of solar radiation and water loss, and facilitating water absorption (Ehleringer & Mooney 1978, Müller *et al.* 1981, Körner 1999). The distribution of hairs and scales on pteridophytes within this study, however, suggests that they may serve different functions. Scales appear to have a protective function in dry and/or cold environments (Müller *et al.* 1981), whereas hairs may facilitate stomatal function by preventing blockages by closed water films and particles, impeding entry of pathogens (Gates 1980), or, especially on young blades, impeding herbivory by insects and vertebrates (Levin 1973, Woodman & Fernandes 1991, Grubb 1992, Gutschick 1999). Hairs prevent water droplets from forming on the leaf surface and the stomata, thus improving gas exchange (Smith & McClean 1989, Brewer & Smith 1995). Moreover, they prevent the deposition of minerals and other substances, which may result in stomata closure, as shown for calcicolous species by DeSilva *et al.* (1996). In our study area, hairs apparently do not play a role in defense against water loss (not necessary, because humidity at mid-elevations is always high, Fig. 1), nor against solar radiation (which is low in zones with high hair densities because clouds form at mid-elevations). This contrasts with the function of hairs in arid environments (Press 1999), where they lower leaf temperature and reduce water loss (Ehleringer & Mooney 1978).

Dimorphism. A high fraction of the species within our study (28.3%) has dimorphic leaves. This characteristic occurs over a wide range in ferns, and involves the modified shape of the whole fertile frond (holodimorphism, as, e.g., in *Polybotrya* and *Elaphoglossum*, Fig. 4D, right) or of, in rare cases, only a part (usually apex) of a blade (hemidimorphism, some Grammitidaceae, Fig. 4D). Dimorphism is usually manifested in a reduction of the blade area of fertile leaves, and in some species the fertile blades are 'skeletal' without any photosynthetic laminar tissue (e.g., *Polybotrya*, *Olfersia*). The fertile fronds are mostly elevated above the level of the sterile ones, often forming a sterile rosette with upright fertile fronds in the center (Fig. 4D). An intermediate stage exists, where the surface area of the sterile frond is only slightly reduced compared to the sterile fronds and not elevated above the level of the sterile fronds. This slightly dimorphic type is relatively rare (in our study only 21 species, 4.4 %), and is mostly comprised of large species of the genera *Pteris* and *Diplazium*.

The elevated exposition of fertile fronds in dimorphic species has been interpreted as a functional adaptation for spore dispersal (Kramer *et al.* 1995): the fertile leaves are more exposed to air movement, and probably desiccation of sporangia is improved. However, we know nothing about the ecology of dimorphism in ferns, and the distribution of this characteristic over a wide range of taxa indicates that it has evolved several times (Kramer *et al.* 1995). Along environmental gradients the occurrence of dimorphism within this study does not indicate a preference for special settings, neither along temperature nor humidity gradients (Table 3, Fig. 2C). Why slightly dimorphic species showed a tendency towards warm and wet environments remains unclear, but might be induced by the respective species showing a highly divided and herbaceous appearance.

Special characteristics: buds, indusia, and hydathodes. The development of buds, indusia, and hydathodes are well known characteristics that are important for classification purposes, especially for species delimitations within genera. However we lack clear evidence about the benefit in function of these features in ferns (Kramer *et al.* 1995).

Plantlet formation by buds, mainly on the rachis (Fig. 4C) is a vegetative reproduction mode present in many ferns. Thirty-two species in our data set (6.8%) exhibited buds; one of them is not known to have sexual reproduction (*Blechnum proliferum* Rosenst.). This is a low number compared with a study from the nearby Monteverde cloud forest reserve (Koptur & Lee 1993), where about 19% of fern species were found to produce plantlets from buds. This and other studies (e.g., Farrar 1968, Mickel 1976) suggest that plantlet production increases with environmental wetness, coinciding with our results where a significant positive correlation with precipitation and negative correlation with elevation were observed (Table 3), with highest values of bud-bearing species found between 500 m and 1700 m (Fig. 2C). The ecological significance of that relationship is yet not understood, but the developing process of plantlets from buds, where a tiny but fully developed new plant arises from the parent plant without contact to the substrate, is certainly favored in the absence of harsh environmental conditions, namely drought and frost events. On the other hand, vegetative reproduction among angiosperms is often linked to harsh abiotic conditions (Klimes *et al.* 1997).

The same may be valid for the presence of hydathodes (Fig. 4G). Within our data set, 116 species (24.3%) possess these organs, which occur at the end of veins near the blade margin. The presence of hydathodes was strongly correlated with elevation and humidity, with highest percentages of ferns with hydathodes occurring in species assemblages of cold, humid environments (Table 3, Fig. 2C). It has been assumed that hydathodes facilitate the secretion of water (Kramer *et al.* 1995), but there is little evidence suggesting this function (e.g., Sperry 1983). It is likely that in environments with high and constant air humidity the secretion (and evaporation) of water, and thus the emission of minerals (many species show hydathodes with lime dots, e.g., *Melpomene*), is – under a given root pressure – hindered by high ambient air humidity, and dilation of the vein ends may compensate for this disadvantage.

The presence of indusiate sori show nearly the opposite pattern to that of the hydathodes (Table 3, Fig. 2C). Of 477 species, 228 (47.8 %) have indusiate sori, and the distribution pattern of these species showed strongest correlation with precipitation. This suggests that indusia may represent a mechanical defense strategy against high amounts of falling and running water.

Stomata. Stomatal density shows an inverse relationship to ambient CO_2 levels, in response both to temporal changes (Woodward 1987, Woodward & Bazzaz 1988, Peñuelas & Matamala 1990, Beerling 1993, Beerling & Chaloner 1993, McElwain 1998, McElwain *et al.* 1999, Chen *et al.* 2001) and elevational changes (Körner *et al.* 1979, Woodward 1986, Beerling *et al.* 1998). The increase in stomatal density in accordance with the decrease in CO_2 concentration with elevation (as a result of decrease in atmospheric pressure) was also found by us (Fig. 3A). Although the mechanism that controls the stomatal density response to CO_2 concentration remains unknown to date, this parameter has been successfully used as an indicator to calibrate paleo-CO_2 levels for different historical times (e.g., McElwain 1998, Chen *et al.* 2001). The adaptive functions of stomata are to optimize the balance of CO_2-uptake and water loss and regulate temperature by transpirational cooling (Jones 1998, Gutschick 1999). Since transpiration rate depends on temperature and atmospheric vapor pressure, the positive correlation with elevation might explain high stomatal densities with increasing elevation

(thus inverse to temperature) and with bryophyte cover (thus with air humidity). At the same time, high stomatal densities have been reported to coincide with thick cuticles for rapid water and gas exchange during photosynthetically active periods, while better protecting against water loss during inactive periods (Begon *et al.* 1990). This has also been found within our study, as stomatal density and laminar thickness were significantly correlated (Fig. 3B).

Conclusions. In most cases, pteridophyte assemblages in our study showed morphological patterns that changed considerably with elevation, but not all of these traits can at present be plausibly interpreted or assigned functional significance. A number of the morphological patterns found by us have previously also been documented among seed plants and have been subjected to tests of their functionality. For example, thick and undivided or moderately divided leaves can be interpreted as a defense strategy against climatic extremes like low temperatures and drought events, and consequently vegetation assemblages at high elevations are prone to show this morphological trait. Similarly, high stomata densities have frequently been reported to occur at sites with low CO_2 concentrations at higher elevations. Surprisingly, the main indument types, hairs and scales, although often assigned similar functions follow opposing trends, namely repelling and retaining water respectively. However all these lines of reasoning (probably with the exception of arguments regarding stomatal density) lack experimental testing and a phylogenetic perspective. Future research should be directed at providing experimental support and eliminating shared history for the proposed causal relationships.

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