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The elevational gradient of Andean plant endemism: varying influences of taxon-specific traits and topography at different taxonomic levels

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Abstract

Aim Little is known about the elevational gradient of plant endemism. It is mostly assumed that patterns are determined by topographical factors such as area of elevational belts and degree of habitat fragmentation, but comparative studies of different plant taxa along the same elevational gradient are lacking. The aim was to compare the elevational patterns of plant endemism of the entire flora and selected families and genera in a search for commonalities.

Methods The elevational patterns of endemism for the entire Ecuadorean vascular plant flora, for twenty-seven selected families, and for twenty-four selected genera based on the Catalogue of Vascular Plants of Ecuador were analysed.

Results Elevational patterns of endemism were non-random at all taxonomic levels but there was no common elevational pattern. Rather, the study groups showed a wide variety of independent patterns at all taxonomic levels. Most groups had hump-shaped patterns with maxima at different elevations and mostly at the same or at higher elevations than the maxima of species richness. The overall flora showed highest endemism in the narrowest and most fragmented elevational belts, presumably because of the consequent fragmentation of species populations.

Main conclusions Patterns of endemism appear to be influenced both by taxon-specific ecological traits (e.g. life form, reproduction, dispersal, demography, spatial population structure, competitive ability) in their specific interaction with historical processes and by environmental factors such as topographical fragmentation. The degree to which these influences become visible along the elevational gradient are determined by which combination of species is analysed: for a given genus or family, taxon-specific traits dominate the patterns, for the entire flora taxon-specific patterns are blurred by averaging and the signal of topography emerges. Beyond the elevational gradient as such, this study shows that the frequently stated assumption that given biogeographical settings lead to similar patterns of endemism among different taxa is wrong.

Keywords

Andes, Ecuador, elevational pattern, endemism, orography, plants, topography.

INTRODUCTION

Mountains are well known to harbour concentrations of endemic plants (Kruckeberg & Rabinowitz, 1985; Major,

1988). However, unlike the elevational gradient of species richness (Rahbek, 1995), relatively little is known about the elevational pattern of endemism. The few available studies reveal heterogeneous patterns. Plant endemism may increase roughly monotonically with elevation as in the Guyanas (Berry *et al.*, 1995) and as for selected plant groups in Bolivia (Kessler, 2000, 2001a,b, 2002a,b, in press). It may remain roughly constant above mid-levels as in Ecuador

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(Balslev, 1988) or decline in the alpine zone, as documented in the Carpathians and the Tien Shan (Major, 1988), Ecuador (Sklenář & Jørgensen, 1999), and for selected plant groups in Colombia (Gradstein *et al.*, 1989), Peru (Ibisch *et al.*, 1996; León & Young, 1996), and Bolivia (Kessler, 2000, 2001a,b; Kessler *et al.* 2001, in press). It may even be highest in the lowlands, as for bryophytes on the Galápagos islands (Gradstein & Weber, 1982). The explanations put forward for these varying patterns explicitly or implicitly involve abiotic factors such as the biogeographical setting, orography and palaeoecological changes. Thus, the increase of endemism with elevation is generally interpreted as a result of the increasing isolation and decreasing surface area of high mountain regions, leading to small, fragmented species populations which are prone to speciation (Graves, 1985, 1988; Kruckeberg & Rabinowitz, 1985; Major, 1988).

The frequently observed decrease of endemism at highest elevations has been explained by various processes. In some cases recent mountain uplift is assumed to have provided too little time for speciation, while in other cases Pleistocene glaciations might have led to the extinction of alpine endemics (Major, 1988). In the Andes, the higher geographical connectivity of mountain plateaus allows high-montane species to be widely distributed whereas species inhabiting the steep, topographically complex slopes have narrow, fragmented ranges and hence tend towards local endemism (Graves, 1988; Sklenář & Jørgensen, 1999; Kessler, 2001b, 2002a,b, in press).

While these explanations are all logical and intuitively appealing, they do not explain why different plant taxa show different patterns of endemism along one and the same elevational transect. For example, along an elevational gradient from 200 to 3950 m in the Bolivian Andes, Acanthaceae, Arecaceae, Araceae, Bromeliaceae and Pteridophyta all show different patterns, some with monotonic increases and others with hump-shaped patterns with maxima anywhere between 1200 and 3800 m (Kessler, 2001b). Such different patterns along a given transect are unlikely to be caused by topography and/or palaeoecology alone, but must also involve group-specific life-history aspects such as dispersal. These factors have until now only been used to explain varying absolute levels of endemism between different plant groups, for example, lower endemism among spore-dispersed ferns, but not as causes for differing elevational patterns. Overall, this raises the question whether elevational patterns of plant endemism are caused by environmental factors that affect all plant groups alike or whether they are the result of group- or even species-specific processes.

A study of these relationships is of general interest in biogeography, where different schools of thought either (a) consider that environmental and historical factors should influence different higher taxa in similar ways (Nelson & Platnick, 1981; Wiley, 1981; Humphries & Parenti, 1999) or (b) assume independent patterns because the environmental tolerances, behaviours and mobilities of the taxa differ (Wilson, 1992; Brown & Lomolino, 1998). Both possibilities are supported by empirical evidence, and the question is not

whether one view is correct and the other wrong, but rather under which condition one or the other pattern dominates. With respect to the elevational gradient of endemism, until now it is not possible to evaluate these possibilities, because all available studies either analysed the whole flora without subdivisions or because only selected plant families, but not the entire flora, were considered.

In the present paper, I present the first detailed analysis of the elevational gradients of endemism of an entire tropical montane flora as well as of twenty-seven selected plant families. I used the recently published Catalogue of Vascular Plants of Ecuador (Jørgensen & León-Yáñez, 1999) which provides the most complete and up-to-date listing of the elevational distribution and levels of endemism for a tropical flora in a country with high mountains. I correlated the patterns of each individual family to that of the entire flora to search for congruent patterns. Further, I correlated the elevational patterns of endemism of the entire flora and the families to several parameters which could be causally related to endemism, namely to elevation as such, to area of each elevational belt as a proxy for the narrowness and fragmentation of each belt, and to species richness. Finally, to assess whether the elevational patterns of individual plant families are the result of an accumulation at a lower taxonomic level (species or genera), I calculated the correlation of the endemism patterns of selected genera with those of their respective families. This study focuses on patterns of endemism, i.e. relative changes of the percentage of endemic species at different elevations. Different plant groups show highly differing absolute levels of endemism, but this is not further pursued here.

METHODS

All data were extracted from the Catalogue of Vascular Plants of Ecuador (Jørgensen & León-Yáñez, 1999). For all named Ecuadorian vascular plant species this catalogue provides (if known) information on the status (native, endemic, introduced, cultivated) as well as on the occurrence within ten elevational belts (0–500, 500–1000, ..., > 4500 m). I counted the total number of species and the number of species endemic to continental Ecuador occurring in each elevational belt. While this definition of endemism is determined by biogeographically meaningless political subdivisions, it is nevertheless consistent for all study groups and is therefore suitable to compare patterns. Separate counts were made for those twenty-seven plant groups with more than twenty endemic species. In most cases, these groups corresponded to individual families, in other cases I combined closely related families that are frequently treated together in studies of species diversity and endemism: all ferns and fern allies were combined into Pteridophyta; Eremolepidaceae, Loranthaceae and Viscaceae into Loranthaceae s.l.; Caesalpiniaceae, Fabaceae and Mimosaceae into Leguminosae; and Cyrtipediaceae was lumped into Orchidaceae. For simplicity, I refer to all these groups as 'families' here. I excluded introduced and cultivated species as well as hybrids.

Endemism was expressed as the percentage of species endemic to continental Ecuador in each elevational belt relative to its total species number in that belt. To assess how well these patterns correspond to other variables, I calculated bivariate linear correlations of the elevational patterns of endemism at the family level to (a) the elevational patterns of species richness of each family, (b) area of each elevational belt (values from Jorgensen & León-Yáñez, 1999; Table 9), (c) elevation as such (the midpoint of each belt; 4750 m for the belt > 4500 m), and (d) the elevational pattern of endemism of the entire Ecuadorian flora. Elevation is used as a proxy for the change of numerous environmental factors with increasing elevation, for example, the decreases of mean temperatures, air pressure and O₂-concentration, and the increase of daily temperature fluctuations, frost frequency and UV-radiation. While there is no doubt that these are the factors affecting species, rather than elevation as such, I did not analyse them separately because they are highly covarying and cannot be adequately separated in the scope of this study.

To assess whether the elevational patterns of individual families are an accumulation of similar patterns at the generic level, I calculated the elevational patterns of those twenty-four genera with > 20 endemics per genus in continental Ecuador. I excluded genera with > 60% of the endemics of the entire family because their patterns would be almost identical to the family patterns. These generic patterns were then correlated with the elevational patterns of their respective families. *G*-tests were used to test whether the observed patterns at all taxonomic levels (overall, families, genera) differed from randomness.

RESULTS

All species combined showed a bimodal elevational pattern of endemism, with a first maximum at 2500–3500 m, and a second maximum at > 4500 m (Fig. 1). The first peak had a slightly lower percentage of endemic species (27.5%) than the second peak (28.9%). The absolute number of endemics peaked at 2500–3000 m with 1138 species, while at > 4500 m there were only thirty-five endemic species. The elevational pattern of endemism of all species was most strongly correlated to area of each elevational belt ($R = -0.83$) and to a lesser degree to elevation ($R = 0.71$) and species richness ($R = -0.62$) (Table 1). The overall pattern differed highly significantly from a random distribution (*G*-test, $P > 0.0001$).

The twenty-seven individual families showed very heterogeneous patterns (Fig. 1, Table 1). Maxima of family endemism were found in each elevational step, with the largest number (nine cases) at 3000–3500 m. Most families were weakly to moderately correlated (eighteen families with R -values < 0.6) or even anticorrelated (five families with negative R -values) to the general pattern. The elevational patterns of endemism of the individual families differed significantly from that of the overall flora (*G*-tests, all values significant at least at $P < 0.05$ after sequential Bonferroni correction), except for *Maranthaceae* (*G*-test,

$P = 0.47$). The individual family patterns all differed significantly from random distributions (*G*-tests, all values significant at least at $P < 0.05$ after sequential Bonferroni correction).

Correlation values of endemism to species richness varied from 0.98 to 0.99, i.e. they showed enormous variation (Table 1). In twenty-one cases, endemism peaked at a higher elevation than species richness, whereas the peaks of both parameters coincided in the same belt in six cases. Endemism never peaked at a lower elevation than species richness. The correlation values of endemism to area varied from 0.60 to 0.83, with twenty negative values, i.e. revealing a trend towards higher endemism in belts with reduced area. With respect to elevation, correlation values varied from 0.99 to 0.99, with fifteen positive and twelve negative values.

The correlation values of the elevational patterns of endemism between selected genera and their respective families ranged from $R = -0.70$ to 0.99 (Table 2). There was no significant difference between the correlation values of the genera vs. the families compared with those of the families vs. the overall flora (*F*-test, $F = 0.40$, $P = 0.53$). The patterns at genus level differed significantly from randomness for all genera (*G*-tests, all values significant at least at $P < 0.05$ after sequential Bonferroni correction), except for *Burmeistera*, *Dracula* and *Lepanthes*. The peaks of endemism were located at higher elevations than those of species richness in fifteen genera, at the same elevation in two cases (*Guzmania*, *Pleurothallis*) and at lower elevations in seven cases (*Cynanchum*, *Dracula*, *Lepanthes*, *Masdevallia*, *Maxillaria*, *Pentacalia*, *Telipogon*).

DISCUSSION

The main results of the analysis can be summarized in two points: First, elevational patterns of endemism are non-random at all taxonomic levels considered (total flora, family, genus). Secondly, elevational patterns of endemism mostly differ significantly between the different taxonomic groups and levels.

Overall, there is a close negative correspondence of the percentages of endemism of the entire flora to the area of the elevational belts. This relationship is to be expected if endemism depends causally on the degree of habitat fragmentation and/or isolation, i.e. if the topographic setting causes species populations to be fragmented which promotes their genetic divergence. This pattern has been found in several studies of endemism and is the most commonly cited explanation for elevational patterns of endemism (Graves, 1985, 1988; Kruckeberg & Rabinowitz, 1985; Major, 1988; Ibisch *et al.*, 1996; Sklenář & Jørgensen, 1999; Kessler, 2000, 2001a, b; Kessler *et al.* 2001, in press).

The above pattern was, however, only observed in a fraction of study families and genera, indicating that at these taxonomic levels taxon-specific characteristics and evolutionary histories have an overriding effect over the topographical influence. Comparative studies from Bolivia show that the distinctive family level elevational patterns of endemism are geographically constant. There, elevational

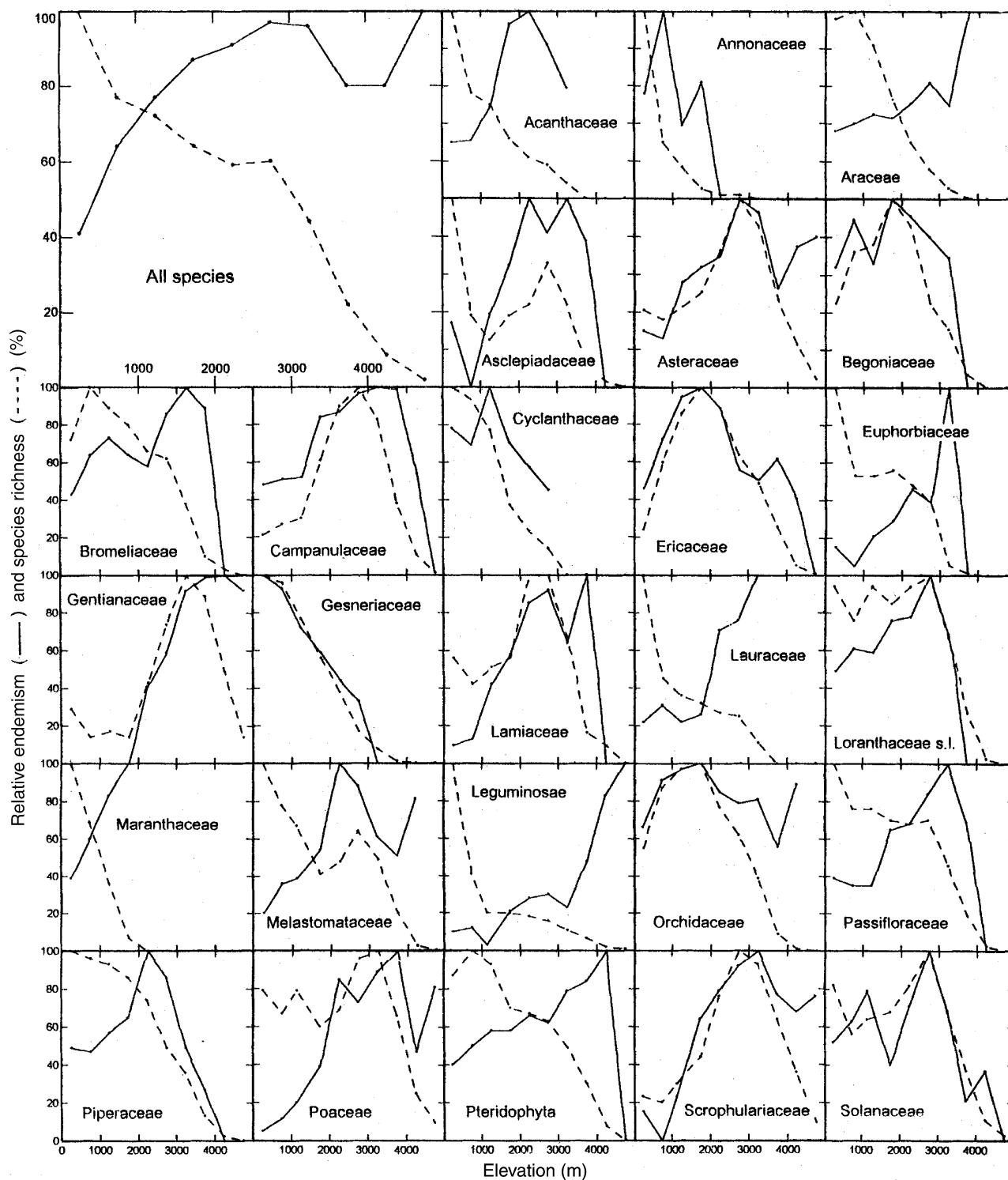


Figure 1 Elevational patterns of endemism (solid lines) and of species richness (dashed lines) of the entire continental Ecuadorean vascular plant flora and of selected plant families. To compare patterns, rather than absolute values, all values of species richness and endemism were rescaled, expressing the maximum of each individual curve as 100%.

Table 1 Elevational patterns of endemism of the whole native continental Ecuadorian vascular plant flora (all species) and of twenty-seven selected plant groups: elevational maxima of endemism, pattern shapes (/ = monotonic increase, \ = monotonic decrease, \cap = hump-shaped, $\cap\cap$ = two peaks), and bivariate linear correlation values with species richness of the respective groups, area of each elevational belt, elevation, and elevational pattern of endemism of the entire flora (overall endemism). Two peaks are recognized when at least two elevational steps with 10% lower endemism are located between the peaks or when a single step has values at least 20% lower. No probability values are reported for the correlations because the adjacent elevational steps are spatially autocorrelated and hence violate the assumption of independence and because the low number of elevational steps implies that after sequential Bonferroni correction only R -values >0.98 remain significant at $P < 0.05$

	Elevational maximum (m)	Curve shape	Species richness	Area	Elevation	Overall endemism
All species	2500–3000 and >4500	$\cap\cap$	–0.62	–0.83	0.71	–
Acanthaceae	2000–2500	\cap	–0.71	–0.53	0.65	0.77
Annonaceae	500–1000	\cap	0.40	0.23	–0.76	–0.62
Araceae	3500–4000	/	–0.72	–0.42	0.79	0.34
Asclepiadaceae	2000–2500 and 3000–3500	$\cap\cap$	0.17	–0.20	0.28	0.63
Asteraceae	2500–3000	\cap	0.46	–0.57	0.67	0.87
Begoniaceae	1500–2000	\cap	0.83	0.01	–0.48	0.13
Bromeliaceae	3000–3500	\cap	0.20	–0.22	–0.04	0.40
Campanulaceae	3000–3500	\cap	0.82	–0.15	–0.06	0.21
Cyclanthaceae	1000–1500	\cap	0.69	0.21	–0.69	–0.49
Ericaceae	1500–2000	\cap	0.90	–0.05	–0.60	–0.12
Euphorbiaceae	3000–3500	\cap	–0.37	–0.23	0.41	0.59
Gentianaceae	4000–4500	\cap	0.66	–0.50	0.94	0.57
Gesneriaceae	0–500	\	0.98	0.60	–0.99	–0.75
Lamiaceae	3500–4000	\cap	0.47	–0.41	0.37	0.67
Lauraceae	3000–3500	/	–0.65	–0.42	0.91	0.71
Leguminosae	> 4500	/	–0.55	–0.42	0.88	0.44
Loranthaceae s.l.	2500–3000	\cap	0.89	0.03	–0.45	0.31
Maranthaceae	1500–2000	/	–0.99	–0.82	0.99	0.99
Melastomataceae	2000–2500	\cap	–0.54	–0.58	0.64	0.78
Orchidaceae	1500–2000	\cap	0.63	–0.38	–0.22	0.26
Passifloraceae	3000–3500	\cap	0.16	–0.17	0.15	0.57
Piperaceae	2000–2500	\cap	0.54	0.03	–0.39	0.32
Poaceae	3000–3500	\cap	–0.05	–0.56	0.77	0.77
Pteridophyta	4000–4500	\cap	–0.05	–0.25	0.12	0.03
Rubiaceae	3000–3500	\cap	0.14	–0.16	–0.31	0.30
Scrophulariaceae	3000–3500	\cap	0.71	–0.52	0.76	0.83
Solanaceae	2500–3000	\cap	0.83	0.08	–0.52	–0.02

patterns of endemism of Acanthaceae, Araceae, Arecaceae, Bromeliaceae and Pteridophyta differ noticeably from each other (Kessler, 2001b) while being closely correlated to the respective family patterns documented here for Ecuador ($R = 0.68$ – 0.94 , P at least < 0.05 in all cases) (M. Kessler, unpubl. data). As by definition both countries do not share endemic species, these studies are independent samples.

The taxon-specific traits influencing patterns of endemism presumably involve aspects of reproduction, dispersal, life-form, demography, spatial population structure and competitive ability (Griggs, 1940; Kruckeberg & Rabinowitz, 1985; Major, 1988; Kunin & Gaston, 1993; McDonald & Cowling, 1994; Walck *et al.*, 1999; Kessler, 2001a). For example, in many plant groups epiphytic species tend to be more widespread than their terrestrial counterparts (Ibisch *et al.*, 1996; Kessler, 2000, 2001b, 2002a,b, in press). As the representation of epiphytic plants varies with elevation, this may well influence the elevational pattern of endemism of a given plant family and override the effect of topography.

Historically, such taxon-specific traits influenced the specific evolutionary history of each taxon, leading to group-specific elevational patterns of plant endemism.

There are two elevational patterns of endemism that apply to most families and genera and that may provide insights to the underlying processes determining family or genus-specific patterns. First, endemism tends to peak at higher elevations than species richness. Secondly, endemism tends to show a hump-shaped distribution. Both patterns appear to be relatively independent of elevation as such, and occur at different elevations depending on the overall elevational richness pattern of a given taxon. One possible explanation is that endemism peaks are located at higher elevations than richness peaks because of a combination of two effects. On the one hand, the more fragmented topography at higher elevations (see above) leads to an increase of endemism with elevation. On the other hand, only the most adaptable and hence widespread species can survive at the highest levels at which a family occurs, leading to a reduction of endemism.

Genus	Family	Elevational maximum (m)	Curve shape	R
<i>Anthurium</i>	Araceae	3500–4000	/	0.99
<i>Burmeistera</i>	Campanulaceae	2500–3000	∩	0.79
<i>Centropogon</i>	Campanulaceae	2500–3500	∩	0.99
<i>Cynanchum</i>	Asclepiadaceae	2000–2500	∩	0.78
<i>Dracula</i>	Orchidaceae	0–500	\	–0.70
<i>Elaphoglossum</i>	Pteridophyta	> 4500	/	–0.68
<i>Epidendrum</i>	Orchidaceae	1500–2000 and 3500–4000	∩∩	–0.30
<i>Guzmania</i>	Bromeliaceae	1000–1500	∩	–0.45
<i>Lepanthes</i>	Orchidaceae	500–1500	∩	0.75
<i>Masdevallia</i>	Orchidaceae	0–500	\	0.68
<i>Maxillaria</i>	Orchidaceae	0–500 and 2500–3000	∩∩	0.25
<i>Miconia</i>	Melastomataceae	2000–2500	∩	0.63
<i>Oncidium</i>	Orchidaceae	2500–3500	∩	0.54
<i>Palicourea</i>	Rubiaceae	2500–3000	∩	0.93
<i>Pentacalia</i>	Asteraceae	0–1000	\	–0.65
<i>Peperomia</i>	Piperaceae	2000–2500	∩	0.84
<i>Piper</i>	Piperaceae	2000–2500	∩	0.97
<i>Pitcairnia</i>	Bromeliaceae	2000–2500	∩	0.36
<i>Platystele</i>	Orchidaceae	2000–2500	∩	0.76
<i>Pleurothallis</i>	Orchidaceae	1500–2000	∩	0.84
<i>Solanum</i>	Solanaceae	2500–3000	∩	0.77
<i>Stelis</i>	Orchidaceae	1500–2000 and 4000–4500	∩∩	0.13
<i>Telipogon</i>	Orchidaceae	500–1000	\	0.40
<i>Tillandsia</i>	Bromeliaceae	3000–3500	∩	0.99

Table 2 Elevational patterns of endemism of twenty-four selected plant genera: Elevational maxima of endemism, pattern shapes (/ = monotonic increase, \ = monotonic decrease, ∩ = hump-shaped, ∩∩ = 2 peaks), and bivariate linear correlation values with the elevational patterns of their respective families. See Table 1 for further details

Because there are several exceptions to both patterns in the data set it is too early to decide if their prevalence is because of an underlying general process and if this interpretation has validity.

Overall, the most likely explanation to the variety of observed patterns is that there are various separate mechanisms determining endemism whose signals are only visible at different levels of observation. If the probability that a given species is endemic is influenced by a number of different factors, specifically by taxon-specific traits and by orographical and historical abiotic factors, then which of these factors become visible along the elevational gradient is determined by the combination of species that is analysed. If we study specific genera or families, then taxon-specific traits and evolutionary histories will dominate the observed patterns. However, if we look at the overall flora, then taxon-specific patterns are blurred by averaging and the signal of the topographical effect becomes visible.

The underlying assumption to this interpretation is that there is no interaction of species in the development of endemism. Unlike species richness, where a low number of species of a given plant family may result in open niches for other families, it is difficult to conceive a mechanism by which low endemism of a given family may prompt other families to evolve a higher number of endemics. Thus, the evolution of endemism takes place at the species level and patterns result from an accumulation of independently evolved cases. The likelihood of the evolution of endemics in

turn is influenced by taxonomic affinity and abiotic factors such as topography and climatic history (Hengeveld, 1990).

In order to further discern the influence of topography and taxon-specific traits on the development of elevational patterns of endemism, comparative studies are needed. Specifically, it should be analysed if plant taxa show similar patterns in similar topographic settings in different biogeographical regions and to which degree different topographic settings influence the patterns within a given biogeographical region. The elevational gradient appears to be particularly suitable to study the evolution of endemism because it represents a very strong environmental gradient that is comparable world-wide.

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BIOSKETCH

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