Diversity patterns of ferns along elevational gradients in Andean tropical forests

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Introduction

The latitudinal gradient of increasing species richness across most taxa from the Arctic regions towards the tropics is, on a coarse scale, one of the best documented patterns in ecology, but the causes determining these patterns are still being discussed (Rohde 1992; Rosenzweig 1995; Gaston and Blackburn 2000; Hillebrand 2004; Ricklefs 2007). In addition, patterns of species richness along elevational gradients have also recently received considerable attention (e.g., Sanders et al. 2003; Bhattarai et al. 2004; Kluge et al. 2006; Kessler et al. 2011) because they form a natural experimental setting along which environmental conditions (e.g., dry to wet, warm to cold) change steeply within relatively short horizontal distances (few tens of km). Relative to the latitudinal gradients from the Equator to the North and South Poles, elevational gradients have the advantage that they are not strongly influenced by dispersal limitation (due to shorter distances) and that they can be replicated (Lomolino 2001).

While the diversity of trees in neotropical forests (Gentry 1988, 1995) is outstanding, most plant species in neotropical forests belong to herbaceous (both terrestrial and epiphytic) life forms (Gentry and Dodson 1987; Ibsch 1996; Balslev et al. 1998). While trees have been the focus of tropical forest research, they are known to present methodological sampling problems due to their large size, often low population densities and difficulties in identifying species, and are unsuitable for answering all the questions in tropical ecology (e.g., Jones et al. 2008). As a result, numerous researchers have focused on other life forms to study diversity patterns, ecology and biogeography in tropical forests (e.g., Poulsen and Pendry 1995; Tuomisto et al. 1995; Kluge et al. 2008; Kessler et al. 2011; Willingham et al. 2012).

Ferns and lycophytes (henceforth called ferns for simplicity) are globally distributed, with a total of ca. 11,000 species (Smith et al. 2006), and are most diverse in tropical montane forests (Moran 2004; Kreft et al. 2010; Kessler et al. 2011). In humid tropical forests, ferns are among the most abundant and diverse plant groups, making up 6.5–25% of the vascular plant flora at local scales (0.01–1 ha) (Whitmore et al. 1985; Ibsch 1996; Balslev et al. 1998; Linares-Palomino et al. 2009). Numerous studies have shown that fern species richness commonly...
displays a hump-shaped richness pattern with a peak at mid-elevations (Kessler 2000, 2001a, 2001b; Hemp 2001, 2002; Bhattarai et al. 2004; Krömer et al. 2005; Kluge et al. 2006, 2008). A global analysis recently showed that this was especially true for extensive tropical elevational gradients, i.e., those ranging from the lowlands up to the timberline (Kessler et al. 2011).

However, little is known about the diversity of ferns at regional scales within the tropics. Thus, it is unknown if fern species richness peaks around the Equator or if it remains relatively constant within the tropical realm. In the neotropics, for example, previous studies have shown that fern species richness at the local scale was similar along elevational gradients in Costa Rica (10° N) and Bolivia (18° S) (Kessler 2001c; Kluge et al. 2006), but quantitative comparisons from mountains close to the Equator are lacking. The only available data on a national scale have shown that Ecuador harbours about 1400 fern species, although it is the smallest of the Andean countries (Jørgensen and León-Yánez 1999; Ulloa Ulloa and Neill 2005; Neill and Ulloa Ulloa 2011). In this study, we tested the hypothesis that, in common with many other groups of organisms, although regional richness is stated to decline with distance from the Equator (Lomolino et al. 2005), species richness patterns and composition of ferns along elevational gradients in Andean tropical forests are comparable overall, despite different species pools. Specifically, we tested a set of inter-related secondary hypotheses that are outlined with their associated predictions in Table 1, leading to a panel of hypothetical elevational species richness curves (Figure 1).

### Material and methods

#### Study areas

The Napo transect was studied in 24 plots at eight elevations separated by about 500 m elevation on the eastern Andean slope in Napo province, Ecuador (Figure 2, Table 2). This gradient spanned localities from lowland forests in the vicinity of Rio Napo (Reserva Jatun Sacha) at 400 m, Sumaco-Napo-Galeras National Park, Reserva Ecológica Antisana, Estación Biológica Yanayacu and Guango lodge up to highest elevations at Reserva Ecológica Cayambe-Coca close to the timberline at 4000 m. These sites were selected because they harboured well-preserved forest habitats along the whole gradient from lowlands up to the treeline ecotone.

| Hypotheses | Predictions |
|-------------|-------------|
| (a) Despite different species pools, species composition patterns are similar between gradients. | − Family species numbers are strongly correlated across all gradients. Elevational ranges and centres of distributions of families are strongly correlated across all gradients. |
| (b) Due to gradually changing climatic conditions with increasing distance from the Equator, species richness of gradients declines gradually. | − Species richness of gradients show highest values at the Equator; thus, with respect to Figure 1, species richness curves move down within the panel of all gradients with increasing distance from the Equator. |
| (c) Due to gradually changing climatic conditions with increasing distance from the Equator, the elevation of highest richness declines gradually. | − Elevational species richness patterns show gradually declining peak values; thus, with respect to Figure 1, species richness curves move left within the panel of all gradients with increasing distance from the Equator. |

In the present study, we established the first plot-based fern transects at the Equator in the Napo province on the eastern (Amazonian) slope of the Andes and at Pichincha on the western (Pacific) slope. The Napo transect presents entirely new data, whereas the Pichincha transect was already included in part in a comparative analysis by Kessler et al. (2011), but is reported here for the first time in its entirety. In this study, we first evaluated the elevational patterns of species richness of terrestrial and epiphytic fern species along both elevational gradients and related these patterns to climatic variables (temperature, relative humidity and rainfall) to assess their relative importance in relation to fern richness patterns. Second, we examined our results within the context of comparable data from other neotropical elevational gradients between Mexico and Bolivia.
Our measurements indicated that the depth of the organic layer and plant-available phosphorus (P) concentration increased with elevation, whereas nitrogen (N) availability tended to decrease with elevation. Also, calcium (Ca), magnesium (Mg) and potassium (K) in the organic layers increased with elevation; the acidity of the organic layer was moderate to high (data from 500 m to 2000 m from Unger et al. 2010, 2012). Concerning the forest structure (up to 2000 m), the above-ground biomass did not decrease with elevation (Unger et al. 2012). The Pichincha transect covered 22 plots between 450 m and 3600 m on the western Andean slope in Pichincha province (Figure 2, Table 2).

Data from studies carried out in Mexico (one transect), Costa Rica (one transect) and Bolivia (three transects) were used to compare elevational gradients at different latitudes in the neotropics; see Table 2 for sources of data and main characteristics of all gradients.

**Climatic measurements**

Along both gradients we collected data on temperature and precipitation, and calculated their respective variability (seasonality: coefficient of variation). Additionally, we assessed ambient humidity. Temperature and its variability in Napo were measured between October 2009 and June 2011 with three HOBO Pro loggers at each elevation. The loggers were positioned at a height of 2 m on tree trunks and covered by a plastic cap to avoid direct rain and sunlight. Measuring frequency was at every 30 min to account for unusual outliers (minimum measuring duration was 12 months). We compared our measured data with data for the same localities extracted from the WorldClim database (Hijmans et al. 2005), using a correlation analysis. No data loggers were used along the Pichincha transect; here we used data from the WorldClim database (Hijmans et al. 2005). Daily mean values of relative air humidity measured from the on-site data loggers in tropical forest are almost 100% and therefore not very informative. Instead we quantified dry spells, which may cause severe damage to hygrophilous organisms such as thin-
structured filmy ferns (Hymenophyllaceae). We expressed the relative frequency of values below 60, 70 and 80% relative humidity as a Humidity Index (HI). For Pichincha no such data were available and so, as in previous comparable studies (e.g., Kluge et al. 2006), we used the estimated cover of bryophytes on trunks and branches in each plot as a proxy for humidity (Karger et al. 2012). Precipitation values along both gradients were compiled from the WorldClim database (Hijmans et al. 2005). This database provides interpolated climate surfaces at a spatial resolution of 1 km² from a time range from at least 50 years, although use of such interpolated data has been criticised because they may not reflect true conditions (e.g. Killeen et al. 2007). Long-term on-site measurements are clearly ideal, but these type of data were not available for our study region. We are, however, fairly confident about their accuracy because, in the context of a previous study in Costa Rica, we were able to directly compare long-term data from meteorological stations with WorldClim data (see Figure 3 in Krömer et al. 2013). Although differing slightly in the total amount of precipitation, the elevational trend in that study was almost identical for on-site and WorldClim data.

**Vegetation sampling**

Along the Napo transect, fern diversity was sampled in three permanent plots of 400 m² at each elevation, resulting in a total of 24 plots, whereas along the Pichincha transect, we inventoried 22 plots of identical size at irregular intervals between 450 m and 3600 m. A plot size of 400 m² has previously been used for surveys of local fern diversity (e.g., Kessler 2001b; Kluge et al. 2006), not only because it is large enough to be representative, but also because it is small enough to be ecologically homogeneous and to allow rapid and efficient surveys (Kessler and Bach 1999). All plots were placed in representative stands of forest, avoiding special geomorphological features such as deep valleys and exposed ridges, as well as canopy gaps. We collected species separately for terrestrial and epiphytic ferns. Canopy 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). For every species we counted the number of individuals. All species were collected for identification at the herbarium of the Pontificia Universidad Católica del Ecuador (QCA) and by specialists for difficult groups. Family delimitation followed Smith et al. (2006).

**Data analyses**

To assess the relationship between climatic variables and the distribution of species richness, we used multiple linear regression models. The best model was chosen by inspection of the Akaike Information Criterion (AIC). Since the number of observations in our study (‘plots’) is low with respect to the number of parameters (‘variables’), we chose the bias-corrected form AICc (Burnham and Anderson 2002):

\[
AICc = AIC + \left(2 \frac{k(k+1)}{n-k-1}\right) + \left(\frac{n}{n-k-1}\right) - 2
\]

where \(n\) is the number of observations and \(k\) is the number of parameters in the model. With increasing \(n\), AICc asymptotically converges to AIC.

The model with the lowest AICc value may be assigned the ‘best model’. However, differences in the AICc values (\(\Delta\)) between nested models are often small and the exclusive acceptance of a single model may lead to wrong conclusions about the performance of the parameters (Wagenmakers and Farrell 2004). Models with \(\Delta < 2\) have substantial support and models with \(\Delta > 4\) should definitely be excluded (Burnham and Anderson 2002). Based on \(\Delta_i\), the Akaike weight \(wi\) quantifies the plausibility that a given model \(i\) is actually better than the next model within the set of all models. With these weights we assessed the

| Locality                              | Abbreviation | Elevation sampling range (m) | Coordinates                      | Data source and date of collection |
|---------------------------------------|--------------|-------------------------------|----------------------------------|-----------------------------------|
| Mexico, Los Tuxtlas, Veracruz          | TUXT         | 140–1675                      | 95°12’–95°04’ W                  | TK 2005–2006                      |
| Costa Rica, Braulio Carrillo National Park and Cerro de la Muerte | CR           | 100–3400                      | 83°41’–67°55’ W                  | JK 2001–2002; Kluge & Kessler (2005) |
| Northeast Ecuador, Jatun Sacha to Oyacachi, Napo | NAPO | 500–4000                      | 78°05’–77°36’ W                  | LS, SA 2011 (this study)          |
| Northwest Ecuador, Felipe Carrillo Puerto to Volcán Pichincha, Pichincha | PICH | 450–3600                      | 78°35’–79°05’ W                  | LS, SA 2011 (this study)          |
| Northern Bolivia, Pilón Lajas to Cotapata, La Paz | LAPAZ | 350–3500                      | 67°07’–67°54’ W                  | MK et al., Jun–Nov 1997          |
| Central Bolivia, Carrasco National Park, Cochabamba | CARR | 200–3750                      | 83°44’–83°41’ W                  | MK et al. 1996–1997;              |
| Central Bolivia, Masicuri Valley, Santa Cruz | MASI | 500–2450                      | 63°42’–63°34’ W                  | MK et al. May–Jun 1996;          |
|                                       |              |                               | 18°40’–19°03’ S                  | Kessler (2000)                    |
relative importance of all variables across all models by summing the weights of all competing models including the respective variables (Burnham and Anderson 2002); the sums for the variables were then compared. We report the best models for all species and separately for life forms, as well on adjusted $R^2$, $P$, AICc, $\Delta$AICc and model weight $w_i$.

Multimodel inference and model averaging were carried out with package MuMIn (Barton 2010) within the statistical platform R (R Development Core Team 2011).

Since, for example, Costa Rica and Bolivia share less than 40% of their fern species (Kluge and Kessler 2005), we tested whether gradients were similar with respect to their family and genus composition despite real different species pools. We compared the gradients if they differed in species richness within the same fern families and if different families occupied different ranges along the elevation gradient, expressed by their centres of distribution (= elevation of highest richness), and if these patterns were similar across families. To assess these floristic and compositional similarities between all pairs of elevational transects along the latitudinal gradient on the basis of family richness and distribution, we compared (i) the numbers of species in each family in every pair of transects by applying Pearson’s $R$ (i.e., $R$ is high when the same fern families are species-rich or species-poor respectively in both compared transects) and (ii) the elevations of maximum species richness likewise (i.e., $R$ is high when the same fern families show similar elevations of maximum species richness). The elevation of maximum species richness for a particular family was assessed by locally weighted scatterplot smoothing (loess models). A loess model fits a non-parametric curve to a
point cloud to demonstrate their main characteristics; for example, in our case, the maximum. The elevation, where the loess curve of a particular family richness peaks was taken as its centre of distribution.

Results

Climate variables

Along the Napo transect, temperature declined with elevation, at a lapse rate of 5.6°K km\(^{-1}\) (Figures 3a and 3c), fitting well to the WorldClim data (\(R = 0.98, P < 0.001\)). The variability of temperature showed a unimodal pattern with elevation: it was lowest at medium elevations and increased towards the upper and lower ends of the gradient (Figure 3c). Likewise, relative air humidity showed the strongest influence of dry spells towards both ends of the gradient (Figure 3b). Accordingly, our Humidity Index showed a unimodal relation with elevation (Figure 3d). Highest rainfall values occurred between 1000 m and 2000 m, just below the condensation layer (Figure 3e).

Along the Pichincha transect, temperature showed virtually the same pattern as on the Napo transect (Figure 3c), whereas rainfall values were considerably lower and lacked a pronounced hump at low elevation compared with the Napo gradient (Figure 3c). SPECIES RICHNESS

Along the Napo transect, we found a total of 91 terrestrial fern species in 34 genera and 20 families (see full species data table in the Supplementary online material). The most abundant species were Diplazium costale (Sw.) C. Presl, Cyclodium trianae (Mett.) A.R. Sm. and Maxonia apiifolia (Sw.) C. Chr. For terrestrial taxa, the families with highest numbers of species were Dryopteridaceae with 16, Cyatheaceae with 13 and Woodsiaaceae with eight species. The largest fern genus was Cyathea with 11 species, followed by Thelypteris and Diplazium with eight species each. Dryopteridaceae and Thelypteridaceae were found along the entire elevational gradient from 500 m to 4000 m, while most of the other families showed elevational preferences. This was especially the case for Lindsaeaceae, Metaxyaceae, Ophioglossaceae and Schizaceae. Among the epiphytic species, we found about 259 species distributed in 49 genera and 21 families based on preliminary identifications and sorting to morphospecies. The most species-rich families were Polypodiaceae (90 spp., mainly from the former family Grammitidaceae) and Dryopteridaceae (77 spp., mainly Elaphoglossum with 68 spp.).

Along the Pichincha transect, we recorded 164 terrestrial species distributed in 44 genera and 24 families, whereas we found 155 epiphytic species in 30 genera and 9 families (see full species data table in the Supplementary online material). The most species-rich families were Dryopteridaceae (39 spp.) and Cyatheaceae (19 spp.) among the terrestrials, and Polypodiaceae and Dryopteridaceae among the epiphytes. The most species-rich genera were Elaphoglossum and Cyathea for terrestrials and Elaphoglossum and Asplenium for epiphytes.

Along the Napo transect, species richness of all, terrestrial and epiphytic species showed clear hump-shaped patterns with elevation (Figure 4a), with peaks at about 2000 m, where a total of up to 70 species per plot were found for all species combined. Along the Pichincha transect all species and the epiphytes showed very similar patterns to the Napo transect, whereas the terrestrial ferns showed more variable numbers with a less pronounced peak at about 1000 m (Figure 4b).

Species richness and climate variables

Relating the patterns of species richness of both the Napo (Table 3a) and the Pichincha transect (Table 3b) to climate variables, we found that all climatic variables were important...

![Figure 4](image-url). Species richness along the study elevational gradient in Napo province, Ecuador (a). Species richness along the elevational gradients in Pichincha province, Ecuador (b), based on data from Kessler et al. (2011). Different symbols and trend lines (quadratic models) as well as \(R^2\) values of model fit are given for all species and major life forms (terrestrials and epiphytes).
Table 3. Results of multiple regression analyses and Multi-Model Inference of the relationship between climatic variables and fern species richness along elevational gradients in (a) Napo (500 m–4000 m above sea level (a.s.l.)) and (b) in Pichincha (450 m–3600 m a.s.l.), Ecuador. Results are given separately for all species, terrestrials and epiphytes. hum.index, measure of amount of drought events (%); prec, mean annual precipitation (mm); temp, mean annual temperature (°C); var, seasonality (variation coefficient) of temp and prec. Beta coefficients are given for all variables which entered the models; all models are given with delta AICc < 4; var.imp, variable importance due to model averaging are given for all variables. Significances of beta coefficients and $R^2$ values are given with: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. For additional information see Methods.

(a) Beta coefficients (standardised)

| Dependent variable | Model | hum.index | prec | var(prec) | temp | var(temp) | $R^2$-adj | AICc | deltaAICc | weight |
|--------------------|-------|-----------|------|-----------|------|-----------|-----------|------|-----------|--------|
| ALL SPECIES        | 1     | -0.12     | 1.43** | -0.85*    | -0.48* | 0.66***   | 173.4     | 0.00 | 0.29      |        |
|                    | 2     | 0.16      | -0.45 | 1.00***   | -0.36* | 0.66***   | 173.8     | 0.48 | 0.23      |        |
|                    | 3     | 0.13      | 0.71*** |          |       | 0.55***   | 174.5     | 1.19 | 0.16      |        |
|                    | 4     | 0.22      | 0.65*** |          |       | 0.59***   | 174.6     | 1.29 | 0.15      |        |
|                    | 5     | 0.07      | -0.27 | 0.94**    |       | 0.56***   | 176.5     | 3.14 | 0.06      |        |
|                    | var.imp | 1.00 | 0.32 | 1.00 | 0.33 | 0.75 |          |      |          |        |
| TERRESTRIALS       | 1     | -0.07     | -0.87*** | 1.37***  | -0.41** | 0.78*** | 121 | 0.00 | 0.77      |        |
|                    | 2     | 0.07      | -1.07** | 1.14**   | 0.42  | 0.78*** | 124.9 | 3.92 | 0.11      |        |
|                    | var.imp | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |          |      |          |        |
| EPIPYHTES          | 1     | 0.21      | 0.64**  |         |       | 0.51*** | 160.8 | 0.00 | 0.30      |        |
|                    | 2     | 0.30      | 0.58**  |         |       | 0.56*** | 161.1 | 0.29 | 0.26      |        |
|                    | 3     | 0.05      | 1.14*   | -0.61    | -0.42* | 0.58** | 162.8 | 1.95 | 0.11      |        |
|                    | 4     | 0.51**    | 0.54**  |         |       | 0.44** | 163.7 | 2.86 | 0.07      |        |
|                    | 5     | 0.20      | -0.05   | 0.68*   |         | 0.48** | 164.3 | 3.46 | 0.05      |        |
|                    | 6     | 0.19      | 0.67    | -0.03   |         | 0.48** | 164.3 | 3.49 | 0.05      |        |
|                    | 7     | 0.27      | -0.20   | 0.74*   | -0.31  | 0.55** | 164.3 | 3.49 | 0.05      |        |
|                    | var.imp | 1.00 | 0.12 | 0.92 | 0.26 | 0.47 |          |      |          |        |

(b) Beta coefficients (standardised)

| Dependent variable | Model | hum.index | prec | var(prec) | temp | var(temp) | $R^2$-adj | AICc | deltaAICc | weight |
|--------------------|-------|-----------|------|-----------|------|-----------|-----------|------|-----------|--------|
| ALL SPECIES        | 1     | 0.93      | -2.20 | 2.67      | -1.19 | 0.83***   | 157.5     | 0.00 | 0.26      |        |
|                    | 2     | 0.15      | 2.06  | -2.99     | 3.84  | 0.81***   | 157.9     | 0.45 | 0.21      |        |
|                    | 3     | 1.53      | 0.19  | 0.33      | -1.76 | 0.78***   | 158.5     | 1.05 | 0.15      |        |
|                    | 4     | 1.78      | 0.69  | -2.36     | 2.93  | 0.82***   | 158.6     | 1.13 | 0.15      |        |
|                    | 5     | 0.08      | 0.75  | 0.79      | 1.00  | 0.79***   | 159.9     | 2.37 | 0.08      |        |
|                    | 6     | 0.20      | 1.70  | -2.83     | 3.42  | 0.83***   | 161.1     | 3.64 | 0.04      |        |
|                    | var.imp | 0.62 | 0.75 | 0.79 | 1.00 | 1.00 |          |      |          |        |
| TERRESTRIALS       | 1     | -0.03     | 1.72  | 3.42      | -1.34 | 0.52**    | 139.7     | 0.00 | 0.37      |        |
|                    | 2     | 1.63      | 0.05  | -1.36     |       | 0.48***   | 141.5     | 1.73 | 0.15      |        |
|                    | 3     | 1.73      | -0.02 | -1.36     |       | 0.40**    | 143.1     | 3.35 | 0.07      |        |
|                    | 4     | 0.09      | 0.31  |          |       | 0.40**    | 143.1     | 3.38 | 0.07      |        |
|                    | var.imp | 0.79 | 0.31 | 0.31 | 0.31 | 1.00 |          |      |          |        |
| EPIPYHTES          | 1     | 0.13      | -2.99 | 3.85      | -0.72 | 0.93***   | 123.6     | 0.00 | 0.46      |        |
|                    | 2     | 0.63      | -2.48 | 3.07      | -1.14 | 0.93***   | 124.7     | 1.07 | 0.27      |        |
|                    | 3     | -3.12     | 3.96  | -0.70     |       | 0.92***   | 125.4     | 1.86 | 0.18      |        |
|                    | 4     | 0.09      | 0.35  | -2.67     | 3.38  | 0.93***   | 126.8     | 3.19 | 0.09      |        |
|                    | var.imp | 0.55 | 0.36 | 1.00 | 1.00 | 1.00 |          |      |          |        |
but to variable extents. The explained variances ($R^2$) of the best models for all species ranged between 66% for Napo and 83% for Pichincha ($P < 0.001$). Across all models, the variability of temperature and precipitation had better information value along both gradients than the respective raw values (variable importance due to model averaging equal or close to 1); in Napo humidity considerably added explanatory power to the models. With respect to life form, in Napo the terrestrial and in Pichincha the epiphytes showed clearer patterns than the respective other life forms.

Comparison of elevational transects

The elevational richness patterns of the seven transects showed similar hump-shaped patterns along the five central transects and also hump-shaped but noticeably lower richness curves along the southernmost and northernmost transects (Figure 5). The residuals of species richness between the individual transects and the overall richness trend derived from all transects in combination (bold regression line in Figure 5) showed that the southern- and northernmost transects (Masicurí and Los Tuxtlas) were significantly different from all other transects, whereas the five central transects were mostly indistinguishable from each other (Figure 6). Only the Bolivian transect close to the southern limit of tropical cloud forests had slightly lower values than the other four transects (Figure 6).

The number of species per family was highly correlated among transects ($R$ values of pair-wise correlations ranged between 0.76 and 0.97; all $P < 0.001$). Similarly, the elevations at which each family reached its maximum species richness were also correlated between most transects, with the exception of cases where one of the outermost gradients (Masicuri or Los Tuxtlas) were involved (Table 4).

![Figure 5](image-url)

![Figure 6](image-url)

### Table 4. Pair-wise Pearson correlations of gradients with respect to elevations of highest species richness within families for six elevational gradients in Napo (NAPO) and Pichincha (PICH), Ecuador; Costa Rica (CR); Carrasco (CARR) and Masicuri (MASI), Bolivia; and Los Tuxtlas (TUXT), Mexico. Gradient in La Paz was excluded because of gaps in the elevational coverage.

| Transect 1 | Transect 2 | $n$ | $R$   | $P$     |
|------------|------------|-----|-------|---------|
| CARR       | CR         | 22  | 0.71  | <0.001  |
| CARR       | NAPO       | 22  | 0.67  | 0.001   |
| CARR       | TUXT       | 14  | 0.76  | 0.002   |
| CARR       | PICH       | 22  | 0.56  | 0.007   |
| CARR       | MASI       | 16  | 0.69  | 0.003   |
| CR         | NAPO       | 21  | 0.60  | 0.004   |
| CR         | TUXT       | 14  | 0.49  | 0.074   |
| CR         | PICH       | 21  | 0.59  | 0.005   |
| CR         | MASI       | 16  | 0.66  | 0.006   |
| NAPO       | TUXT       | 15  | 0.54  | 0.036   |
| NAPO       | PICH       | 22  | 0.72  | <0.001  |
| NAPO       | MASI       | 16  | 0.43  | 0.098   |
| TUXT       | PICH       | 14  | 0.45  | 0.107   |
| TUXT       | MASI       | 13  | 0.59  | 0.034   |
| PICH       | MASI       | 16  | 0.52  | 0.038   |
Discussion

Our study shows that fern species richness in the Ecuadorian Andes follows a hump-shaped elevational pattern with highest values at about 2000 m for all species in general, as well as for terrestrial and epiphytic species. With our on-site climatic measurements of temperature and ambient humidity, and precipitation data from global climatic models (Hijmans et al. 2005), we were able to simultaneously characterise the elevational climatic conditions for the gradients. The relationships of both patterns fit very well to general hypotheses about climatically driven species richness distributions, including ferns.

Climatic conditions and fern diversity

As in other mountain ecosystems, temperature declines linearly with elevation whereas annual sums of precipitation show a pattern typical for tropical mountains with highest values between 1000 m and 2000 m, just below the major cloud condensation layer (Kluge et al. 2006). Air humidity was on average close to saturation at all elevations which is not surprising for tropical wet mountain ecosystems with no marked ‘dry’ season. However, even short-term drought events may cause irreversible damage to ferns, since they have a low capability to actively control their water balance, unlike the angiosperms (Brodribb and McAdam 2011; MacAdam and Brodribb 2012). As a result, balanced humidity conditions without extreme events (dry spells) may be physiologically more important for ferns than a particular absolute level. Thus, the variability of humidity and temperature may provide more information with which to characterise the relationship between species richness and ambient conditions of the study region. Most clearly, the course of both climatic parameters showed that extreme deviations from mean values predominantly occurred at the gradient extremes. The mid elevations, in this study region around 1500 m to 2000 m, harboured the most balanced climatic conditions with medium, scarcely fluctuating temperatures and highest rainfall values that created an ever-wet habitat with modest air humidity oscillations.

The peak of fern species richness at mid elevations has often been interpreted as reflecting the ambient conditions of a balanced climate without extremes, such as drought at low elevations and frost at high elevations (Kessler 2001b; Hemp 2002; Bhatarai et al. 2004; Krömer et al. 2005; Kluge and Kessler 2007; Kessler et al. 2011). Consequently, across all regression models, the variable importance in our study showed that balance-related climatic parameters (var(TEMP), var (PREE) and hum.index) had a better performance than the respective parameters based just on annual means (PREE and TEMP) (see Tables 3a and 3b). But however appealing and expectable is the congruence of a climatic setting and species richness distributions (Moran 2004), it does not explain any mechanism. There are two such possible mechanistic explanations. First, the influence of climate may be indirect, as it is possibly related to ecosystem productivity which, in turn, is supposed to be related to species richness (Currie et al. 2004; Evans et al. 2005). Second, the high richness at mid elevations may be an evolutionary result of higher speciation rates or lower extinction rates under the respective climatic conditions (Barrington 1993). A differentiation of these possibilities requires data beyond the scope of the present study.

Comparison of the elevational transects

In general, we found a similarity of the richness and taxonomic composition among the elevational transects spanning the latitudinal range between 18° N and 18° S. The two transect at the northern and southern extremes of our latitude range, located around the transition from tropical to subtropical conditions, showed significantly reduced species numbers. This might have been caused by drier and colder climatic conditions. However, these two transects showed similar trends to each other of species richness as well as comparable taxonomic composition (Kessler 2000; Krömer et al. 2013).

Excluding these transitional transects, we found that within the tropics there was basically no latitudinal gradient in the shape of local scale fern species richness patterns, although fern species richness values differ strongly at the regional scale. The latitudinal decrease of regional fern species richness has also been documented at the global scale (Kreft et al. 2010) and parallels the patterns found in many other groups of organisms (e.g., Rodriguez and Arita 2004 for non-volant mammals; Quian 2007 for vascular plants). However, it appears that this latitudinal pattern of high regional diversity of ferns does not translate to the local scale fern species richness studied here, because decreasing regional richness towards tropical edges does not cause decreasing local richness. This may suggest that, within small scale localities in the tropical habitats we studied, fern species richness has an upper limit and is bound by the number of species that can co-occur. This in turn implies that small-scale fern communities are saturated, perhaps due to limitations of the available niche space. However, the discrepancy between regional and local richness patterns of ferns suggests that spatial species turnover (i.e., beta diversity), for example between different habitats (Kessler et al. 2009a, 2009b; Jones et al. 2011), might be higher in Ecuador than further away from the Equator. A test of this hypothesis requires spatially consistent and replicated plot data along the latitudinal gradient that are currently unavailable.

In addition to the concordance of species numbers, we also found that species numbers per family, as well as the
elevations at which individual families reached their maximum diversity, largely coincided between transects. This pattern has recently also been found by Girardin et al. (2013) for forest trees in Ecuador, Peru and Bolivia, and in general for vascular plants by Grau et al. (2012) in different localities across the Pyrenean and Catalonian mountains (both Iberian Peninsula). Within our study, in all transects the most species rich families are Polypodiaceae and Dryopteridaceae, which together comprised about half the total species richness along each study gradient, usually followed by the filmy ferns (Hymenophyllaceae). Given that all these groups display distinct morphological features, which reflect certain ecological adaptations like shape and structure of leaves or density of scale indumentum (Kluge and Kessler 2007), and considering the high dispersal ability of ferns (Barrington 1993), it is not surprising that taxonomic composition reflects common patterns of ferns in tropical montane forests. Such pattern are upheld across continents, with transects in Bolivia and Borneo showing a high degree of concordance (Kessler et al. 2001). Similar patterns of ‘family niches’ are also found among trees across the tropics and suggest that different major taxa have different abilities to develop and maintain species (Ricklefs and Renner 2012).

Conclusions

We found that local fern communities at the local scale show a high degree of similarity within mountain forests of the neotropics and possibly more generally. This similarity concerns both the richness and the taxonomic composition of the assemblages and shows no latitudinal trend within the tropical realm. It is at the transition to the subtropical regions that the latitudinal decline of species richness and changes in taxonomic composition become apparent.

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Laura Salazar is interested in the ecology and conservation of ferns in Ecuador and their diversity along elevational gradients. Jürgen Homeier is a plant ecologist interested in the performance of tropical plants along environmental gradients. Michael Kessler is interested in the diversity and biogeography of tropical montane plant and animal communities, with a special focus on ferns. Stefan Abrahamszczak is interested in diversity patterns and plant–animal interactions, especially of hummingbirds. Marcus Lehner is interested in plants systematics, biogeography and DNA barcoding, with a focus on cryptogams. Thorsten Krömer is interested in diversity, ecology, systematics and conservation of vascular epiphytes, with a special focus on Bolivia and Mexico. Jürgen Kluge is a biogeographer interested in the spatial patterns of plant distributions, especially along tropical elevational gradients.

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