Species richness and diversity along edaphic and climatic gradients in Amazonia

Hanna Tuomisto*, Gabriela Zuquim and Glenda Cárdenas
Department of Biology, University of Turku, 20014 Turku, FINLAND
* corresponding author; e-mail hanna.tuomisto@utu.fi

Abstract

The number of species is known to decrease from the humid tropics towards drier and colder climates, but how species richness varies along environmental and spatial gradients within the tropical rain forests is not clear. We inventoried 214 transects of 0.25 ha to document species diversity patterns in an example plant group (ferns and lycophytes) across non-inundated rain forests of western and central Amazonia, and assessed how well these conformed with proposed hypotheses about species richness. The observed number of species varied between 6 and 71 per transect. The effective number of species (emphasising the degree of unevenness in species abundances) varied between 1.02 and 8.60, and diversity profiles revealed considerable differences among transects in community structure. Although the density of individuals varied over almost two orders of magnitude, species diversity was better explained by other variables. In particular, within-transect species diversity increased substantially with increasing soil cation concentration. It also increased with soil aluminium concentration, heterogeneity in soil chemistry, annual rainfall and dry season rainfall, and was higher in western than in central Amazonia. Multiple regression models explained up to 70% of the variance in species diversity, but the relationships between species diversity and the environmental gradients became progressively weaker as species abundances were given more weight in the calculation of diversity. Our results conformed to the proposal that site productivity promotes species diversity. This seemed to arise from larger species pools on more fertile soils and in wetter climates, even when it could be expected that the older and more widespread infertile soils would have provided more opportunities for speciation.

Introduction

“Despite the handicap of insufficient ecological data, or
perhaps because of it, theorization and speculation as to the
possible causes of diversity gradients has been frequent
and varied.” (Pianka 1966)

Species diversity and gradients in it have long intrigued biologists. Tree species richness is known to reach a maximum in tropical rain forests and to decrease towards higher latitudes and drier climates (e.g., Beard 1944). Numerous hypotheses have been proposed to explain both such global trends and the fact that some areas have larger species pools and/or higher species densities than others. Several attempts have also been made to classify these hypotheses to provide an overview of the alternatives (e.g., Pianka 1966, Diamond 1988, Palmer 1994, Gaston 2000, Hill and Hill 2001). However, within the tropical rain forests, it is often not even clear what the species richness patterns themselves are, and it is far from obvious which external factors they may correlate with. In Amazonia, this is largely because the available floristic information is both scanty and biased (Nelson et al. 1990, Schulman et al. 2007, Sousa-Baena et al. 2014).

Here, we document patterns in species diversity and related community properties in an example plant group (pteridophytes: ferns and lycophytes) using data from 214 non-inundated Amazonian forest sites. We then test how well the observed patterns conform to predictions of two kinds of hypotheses: those emphasising present-day environmental factors (which can be directly measured) and those focusing on the cumulative effect of historical and spatial factors (which need to be inferred). Although most hypotheses are concerned with just the numbers of species, our quantitative data allow taking into account relative species abundances as well. This gives a more detailed picture of the trends in species diversity and other aspects of community structure. Since local species density generally increases with the size of the relevant species pool (e.g., Caley and Schluter 1997), we use the former as an indicator of the latter (without assuming saturation of local communities; Gonçalves-Souza et al. 2013).

Hypotheses based on present-day environment

It is a general notion that species richness increases with ecosystem productivity, which itself is a complex concept related to favourableness in temperature, water availability and soil chemistry. We focus on testing diversity patterns along gradients of annual and dry season rainfall, soil cation concentration and soil aluminium concentration. Soil cations are important plant nutrients, whereas aluminium is potentially toxic.

Long rainfall gradients at continental to global extents clearly show a positive correlation between annual rainfall and local species richness of plants (Beard 1944, Brown 1988, Bjorholm et al. 2006, Eiserhardt et al. 2011). In the Neotropics, species densities of woody plants seem to increase with increasing annual precipitation and decreasing dry season length even within the evergreen tropical forests (Gentry 1988, Phillips et al. 1994, Clinebell et al. 1995, ter Steege et al. 2003, Stropp et al. 2009, Van Der Heijden and Phillips 2009, Kristiansen et al. 2011). Since ferns and lycophytes are known to favour moist growing conditions, we expect their diversity to increase with climatic water availability as well.

Earlier results related to the soil fertility gradient have been varied, and different kinds of responses need to be considered. It has been proposed that the general relationship is hump-shaped (Grime 1979, Tilman 1982, Mittlebach et al. 2001, Pausas and Austin 2001), although most studies globally seem to have found plant species density to increase with soil fertility (Wright 1992, Gillman and Wright 2006),. Within tropical forests, most studies have found species density to increase with soil fertility (Gentry 1988, Phillips et al. 1994, Duivenvoorden 1996, Tuomisto and Poulsen 1996, Tuomisto et al. 2003a, Tuomisto and Ruokolainen 2005, Costa 2006, Cárdenas et al. 2007, Laurance et al. 2010), but some have found it to decrease (Huston 1980, Tuomisto et al. 2002, Slik et al. 2009). A peak in species density at intermediate soil fertility has also been found (Ashton 1989, Tuomisto and Ruokolainen 2005), as has lack of relationship (Clinebell et al. 1995, Tuomisto et al. 2002, Kristiansen et al. 2011).

The relative contribution of rainfall and soil fertility gradients to local plant species density has rarely been addressed within Amazonia. A few studies on trees and palms have suggested that rainfall is more important (Gentry 1988, Clinebell et al. 1995, Kristiansen et al. 2011). We test if this is the case for understory ferns and lycophytes.

Sites with heterogeneous soils can be expected to support more species than sites with more homogeneous soils. Even within Amazonian non-inundated forests, it has been shown that plant species composition varies along a soil fertility gradient (e.g., trees: Gentry 1988, Duivenvoorden 1996, Ruokolainen et al. 2007; palms: Vormisto et al. 2004; ferns and lycophytes: Tuomisto et al. 2003a,b,c, Higgins et al. 2011, Zuquim et al. 2012). We test the prediction that species density increases with within-site edaphic heterogeneity.

Hypotheses based on history and space

A classic explanation for high tropical species richness is that equatorial areas have experienced stable tropical climates for a long time, which has allowed a large number of species to accumulate (e.g., Fischer 1960, Baker 1970). Recent reconstructions of past Amazonian climates postulate climatic instability at the edges of the current rain forest realm (Colinvaux et al. 2001, Mayle et al. 2000, Bush and de Oliveira 2006). Therefore, we assess whether the instable peripheral areas have lower species richness than the central stable ones.

The age of a habitat depends also on geological history. This determines how old the land surface itself is, and since when it has been available for terrestrial organisms to live and evolve on. Within Amazonia, the geologically oldest surfaces are found in the Guianan and Brazilian pre-Cambrian shield areas. Western Amazonia is more recent as a terrestrial ecosystem, since much of it was affected by a marine incursion in the Miocene and was then covered by wetlands consisting of a complex of swamps and open water areas (the Pebas system; Hoorn 1993, Räsänen et al. 1995, Hoorn et al. 2010, Hoorn and Wesselingh 2010). We assess whether the geologically old central Amazonian sites have higher species richness than those in the younger western Amazonia.

Nutrients are gradually leached out of exposed sediments, so the old central and eastern parts of Amazonia have predominantly soils with low nutrient availability (Sombroek 1984, 2000), whereas western Amazonia also has high-nutrient soils. The latter can be derived from the Pebas Formation or from fresh (even volcanic) material eroded from the Andean slopes and deposited in the floodplains of white-water Amazonian rivers, which become substrate for non-inundated forests when rivers abandon their former floodplains (Salo et al. 1986, Räsänen et al. 1987, Hoorn et al.

2010, Higgins et al. 2011). Such nutrient-rich soils may not have been present in western Amazonia at all before the drainage of the Pebas system. For a long time they were probably covered by the more nutrient-poor sediments of the Nauta formation, whose removal by rainwater denudation still continues (Higgins et al. 2011). We assess whether rich soils have a smaller species pool than poor soils, as could be expected because the latter have been available as a habitat for a longer time.

Large areas generally provide more opportunities for speciation and colonization than small areas do. At the basin-wide scale, poor to intermediate soils are more common in Amazonia than rich soils are (Quesada et al. 2011), so we test if the former also have more species than the latter. If intermediate conditions are more common than extreme conditions, species richness should peak in the former (Terborgh 1973, Mittlebach et al. 2001, Pausas and Austin 2001). In addition, an ecological version of the mid-domain effect (Colwell and Lees 2000) may occur: if species are randomly distributed along an ecological gradient, more species ranges will overlap at intermediate than at extreme conditions.

Finally, it is possible that the regional species pool is enriched by immigration from other biogeographical areas. The Andes have been an important center of speciation for ferns and lycophytes, which is evident both from the high overall number of species and from the high degree of endemism (Moran 1995). We assess if higher species richness is found in western Amazonian sites close to the Andes than in sites of comparable environments further away, which could be indicative of a spill-over effect.

Material and methods

Study sites and field data collection

We established a total of 214 line transects of 5 m by 500 m in old-growth non-inundated rain forests in lowland Amazonia (Fig. 1). Each transect was placed so as to cover as much as possible of the local topographical variation. Within each transect, all terrestrial ferns and lycophytes with at least one green leaf (leafy stem in the case of lycophytes) longer than 10 cm were identified to species and recorded. Epiphytic and climbing ferns were also included if they had large enough leaves at a height less than 2 m above ground. Two climbing filmy fern species whose leaves are inconspicuous because they are tightly pressed against tree trunks were excluded. The number of individuals was used to quantify abundance of the species. In the case of clonally reproducing species such as many *Selaginella*, the abundance measure was actually the number of ramets: each rooting stem was counted as one individual whether or not it was connected to another rooting stem.

We collected at least one representative voucher specimen of each species during each field trip (several field trips were made to Ecuador and NE Peru), and additional specimens were collected whenever observed plants could not be assigned with certainty to a species already represented by a recent voucher. Duplicates of the vouchers are deposited in TUR and in national herbaria (SINCHI for Colombia, QCA and QCNE for Ecuador; USM, AMAZ and/or CUZ for Peru; SP and INPA for Brazil). All voucher specimens were cross-checked at TUR and identified to species by HT. In some cases, individuals that in the field were thought to belong to the same species were assigned to two or more species in the herbarium. If it was not possible to deduce with certainty which of the observed individuals belonged to which species, the entire complex was treated as a single species in the analyses. As a result, the numbers of species used in the analyses were in some cases smaller than the numbers of species actually observed, but this is less important for the purposes of the present paper than consistency in species delimitation across all sites.

Soil characteristics of the transects were documented with surface soil samples from the top 5 cm of the mineral soil. Each soil sample consisted of five subsamples taken within an area of about 5 m by 5 m. Three composite samples were usually taken in each transect: one near the beginning, one near the middle and one near the end. If the topography was hilly, two samples were generally taken from hill tops and one from an intervening valley bottom. The soil samples were analysed for exchangeable bases (Ca, Mg, K, Na) and aluminium using extraction in ammonium acetate at pH 7. The vast majority of the soil samples were analysed at MTT Agrifood Finland. Some of the samples from northern Peru were analysed at the Geological Survey of Finland or at ISRIC (The Netherlands).

A topographic profile for each transect was obtained with the help of a Suunto clinometer and a 50-m measuring tape. We used the measured elevation difference between the highest and lowest points within a transect as a measure of topographic variability. Altitude of the transect above sea level was extracted from SRTM (Shuttle Radar Topographic Mission) data, which has a nominal vertical resolution of 1 m and a pixel size of 90 m. The SRTM mosaic was filtered with a moving window of 5 by 5 pixels, and for each window centered on a transect we extracted the mean altitude value in ArcGIS 10.1.

Climatic data were derived from monthly temperature and rainfall values available in Bioclim (Hijmans et al. 2005). Out of many possible but highly intercorrelated climatic variables, we chose total annual rainfall (bioclim 12) and the mean precipitation of the driest quarter (bioclim 17), which we considered relevant measures of climatic water availability. The data were downloaded from the WorldClim database (http://www.worldclim.org/bioclim) at a 2.5 arc-minutes resolution (about 4.7 km near the Equator line). Climatic values for each transect were extracted using DIVA-GIS (Hijmans et al. 2012).

Most transects were georeferenced using several coordinate readings obtained with a hand-held GPS. For a few transects, georeferencing was based on landmarks in satellite images and aerial photographs, but even then the georeferencing error is estimated to be less than 1 km. Latitude and longitude were used to model spatial trends in the data.

Numerical analyses

In all analyses, we used entire transects as sampling units, which leads to a uniform sampling unit size of 0.25 ha. Therefore, all our results are interpretable in terms of the density of individuals or species observed at this spatial grain. For simplicity, the term ‘species density’ will be used to refer both to the actual number of species (= species richness) and to the effective number of species (= species diversity) observed per transect.

The number of species that can be observed within a transect is constrained both by its limited surface area (not all heterogeneity present at a locality is included within the transect) and by the number of individuals it contains (the number of species can never exceed the number of individuals, and is usually considerably smaller). When the interest is in species diversity of communities larger than the sampling unit, undersampling can bias conclusions about species richness gradients, especially in such species-rich systems as the tropical rain forests. To estimate how representative the sampling units were of the local species pool, we calculated the Chao 1 (Chao 1984) and ACE (Chao and Lee 1992) estimators of species richness for each locality. These estimators aim to quantify how many species are actually present in the local community, even if some were missed by the corresponding transect. The smaller the difference between the estimated and observed number of species, the better the sampling.

To assess changes in community structure along edaphic and climatic gradients, we first calculated the number of individuals, the actual number of species (species richness, R) and the effective number of species (species diversity, ${}^qD$) for each transect. Species diversity depends not only on the number of species but also on how similar their abundances are, and it equals the inverse of mean proportional species abundance. In other words, diversity is the number of equally-abundant species that would give the same mean species abundance as the actually observed species have on average. "On average" is here based on the weighted generalized mean with exponent q−1, with the species proportional abundances themselves used as weights (Hill 1973, Jost 2006, Tuomisto 2010, 2011). The equation is:

$${}^qD = 1 \Big/ \sqrt[q-1]{\sum_{i=1}^{R} p_i p_i^{q-1}}$$

The parameter q defines which mean is used, and thereby controls how much weight is given to abundant *vs.* rare species when calculating mean species abundance. Large values of q pull the mean towards the abundance of the most abundant species, which causes the effective number of species to decrease. Small values of q pull the mean towards the abundance of the least abundant species, which causes the effective number of species to increase. At q=0, diversity obtains the same value as richness. As q approaches infinity, diversity approaches the inverse of the proportional abundance of the most abundant species (Tuomisto 2010, 2011). If all species are equally abundant in the data, diversity equals richness no matter what the value of q. Plotting diversity calculated with different values of q against q can therefore give useful insight to community structure.

Diversity (${}^qD$) can be thought to consist of two components, richness (R) and evenness (${}^qE$), and these may behave in different ways along external gradients. We calculated evenness (${}^qE = {}^qD/R$) to quantify how many effective species there are for each actual species in the dataset (Tuomisto 2012). This can also be thought of as the degree to which the potential diversity (which has an upper limit equaling richness) has been realized in the data, and it varies in the range [1/R, 1]. We also report unevenness ($^qU = 1/^qE$), because this facilitates seeing the differences among communities with high degree of dominance by the most abundant species. An additional advantage of unevenness is that it is independent of diversity, and the two therefore allow decomposing richness into two mathematically independent components. The decomposition of diversity into richness and evenness components is not as elegant, because evenness is constrained by richness (Jost 2010, Tuomisto 2012).

We used linear and polynomial regression analyses to assess to what degree the variation in the observed number of species (actual or effective), evenness and unevenness is explained by the observed number of individuals. The number of individuals was logarithmically transformed before analysis, because the probability that a new individual added to the dataset also adds a new species decreases as the number of individuals already contained in the dataset increases.

We assessed trends along edaphic, climatic and spatial gradients for species richness, diversity, evenness and unevenness as well as for density of individuals using linear and polynomial regressions. Soil cation concentrations (Ca+Mg+K+Na in cmol+/kg) were logarithmically transformed before analysis to model relative rather than absolute changes in cation concentration: a unit change in nutrient concentration can be expected to be more important for plants when the nutrient in question is scarce than when it is abundant.

Linear multiple regressions were used to assess which (combinations of) variables explained the variance in species diversity best. To simplify these analyses and make getting an overview of the results easier, only explanatory variables that had a significant relationship with species diversity in simple linear regressions were used, and these were grouped into four thematic pairs: soil chemistry (average aluminium concentration and log-transformed average cation concentration); variability in soil chemistry (range of average aluminium concentration and range of log-transformed average cation concentration); space (longitude and altitude); and climate (annual and dry season rainfall). Each pair was then used alone and in various combinations to assess their relative explanatory powers. In addition, we constructed for each diversity measure an optimised multiple regression model. The initial model contained all explanatory variables that were significant on their own. We then eliminated any variables that did not make a significant contribution to the model, starting from the one with the highest p value, until all remaining variables were significant at the $p < 0.05$ level. All reported coefficients of determination are based on adjusted R^2 values.

Analyses were carried out in R version 2.15.1 (R Development Core Team) using either the 'vegan' package (Oksanen et al. 2013) or code written by HT.

Results

Community structure

A total of 396,000 fern and lycophyte individuals were registered in the inventories. The number of individuals per transect varied between 56 and 11,370, with the overall average being 1,850 and median 1,480. When viewed by geographical region (Table 1), it appeared that the Ecuadorian and Brazilian transects had higher density of ferns and lycophytes (mean >2300 individuals/transect) than the Colombian and Peruvian transects (mean <1800 individuals/transect).

For the numerical analyses, the individuals were classified into 293 species. The number of observed species ranged between 6 and 71 per transect, with an average of 29.3 and median of 27.5. The Ecuadorian and Brazilian transects differed from the Colombian and Peruvian ones, but in opposite ways. The minimum species density observed in Ecuador was higher than the average observed in any of the other regions, whereas the average observed in Brazil was lower than the minimum in most other regions (Table 1).

Our transects seemed to sample the local pteridophyte species pool rather well. When the Chao 1 estimator was used, the number of species estimated for a locality was, on average, 11.8% larger than the number of species observed (median 6.3%); with the ACE estimator, the mean difference was 13.4% (median 9.0%). Both estimators suggested a difference of more than 50% in three out of the 214 localities, and one (but not both) did so in nine localities. The estimated proportion of unseen species was weakly or not at all correlated with the observed number of species, the observed number of individuals, or the measured environmental variables (|Pearson's r| ≤ 0.21 in all cases).

Species diversity (which takes abundances into account) within the transects was only weakly related to the number of individuals present (Fig. 2 A-C). Transects with any number of individuals could have about as low species diversity as transects with the fewest individuals did, but the highest diversity values were concentrated to transects with intermediate numbers of individuals. The transects with most individuals had slightly higher diversity than the transects with fewest individuals at q=0, but the situation was reversed at larger values of q. This is related to species evenness showing a very clear decreasing trend with increasing number of individuals whenever q>0 (Fig. 2 D–F). Often the hyper-abundant species driving the low evenness were clonal, including the eight species that reached highest local densities (four *Selaginella*, two *Adiantum* and two *Trichomanes* species). However, several non-clonal species were also observed with very high abundances at some sites (e.g., species of *Adiantum*, *Polybotrya* and *Danaea*).

Diversity profiles illustrate how species diversity in the transects change with the value of q: at small values of q, diversity reflects mostly the number of species present, but as q increases, dominance by the most abundant species gets more weight (Fig. 3). As a result, average within-transect species diversity decreased from 29.3 effective species at q=0 to 3.4 effective species at very large values of q. At the same time, average evenness decreased from 1.0 to 0.13, and average unevenness increased from 1.0 to 9.8. Many of the trajectories corresponding to different transects crossed each other, which indicates among-transect differences in species relative abundance distributions. Irrespective of the value of q, mean diversity was highest in the Ecuadorian transects and lowest in the Brazilian ones (Table 1). With evenness and unevenness, the differences among regions were less noticeable, although mean unevenness was relatively high in Ecuador at all values of q (Fig. 3, Table 1).

Trends along environmental gradients

The diversity profiles (Fig. 3) suggested that transects on cation-poor soils had lower species diversity than transects on cation-rich soils. This can be seen especially for the maximum values in each cation class and at small values of q. Even at the largest values of q, the transects in the most cation-poor soil class had lower average diversity (2.8 effective species) than transects in the two most cation-rich classes (>4.4 effective species).

It was clear that soil cation concentration and geographical region were strongly interlinked in our data: on average, transects from the western part of the study area had higher soil cation concentrations than transects from the eastern part (Figs. 1, 3). In fact, longitude was negatively correlated with most of the environmental variables, especially dry season rainfall (Table 2). The other environmental variables covaried with each other as well: soil cation concentration was positively correlated with both annual rainfall and elevation, and the within-transect averages and ranges were highly correlated for both soil cation concentration and soil aluminium concentration (Table 2, Fig 4).

Species diversity had a positive linear relationship with almost all of the environmental and spatial variables. Diversity at q=0 (and hence species richness) was best predicted by log(soil cation concentration) and longitude, both with $R^2 \geq 40\%$. The other variables had R^2 values between 24% and 30%, except latitude and within-transect difference in elevation, which had practically no predictive power in the linear models (Table 3, Fig. 5). The relationship between diversity and latitude was better characterised as U-shaped ($R^2=16\%$ at q=0, decreased to 3% at high values of q), and the relationship between diversity and altitude was clearly hump-shaped (Fig. 5I–J). Evenness, unevenness and the number of individuals were in general poorly or not at all explained by the available environmental and spatial variables: the highest R^2 values were only 9–13% (Fig. 5). For example, both number of individuals and unevenness at very large values of q increased with variability in soil cation concentration and had a hump-shaped relationship with mean soil cation concentration.

In order to tease apart the relative contributions of the spatial and environmental variables to explaining the variance in within-transect species diversity, we carried out multiple linear regressions. At q=0, each of the four thematic pairs of explanatory variables explained 32–53% of the variance in species diversity, and a combination of any two pairs explained at least 54% (Table 3). Models combining soil chemistry with either the spatial or the rainfall variables, or variation in soil chemistry with the spatial variables, explained at least 63%. At larger values of q, all the best models included the spatial variables. The explanatory power of all variables decreased with increasing q, but not uniformly: soil chemical variables became relatively less important and spatial variables relatively more important. This can be seen in the R^2 values of both simple and multiple regressions (Table 3). In multiple regression models obtained with backward elimination, soil cation concentration was retained at small values of q but longitude at large values of q (Table 4). The explanatory variables covaried strongly, so the largest unique contribution to R^2 by any variable pair was only 6% (Table 3).

Discussion

Species diversity along environmental gradients

Our results from lowland Amazonia conformed to the hypothesis that local species diversity of ferns and lycophytes increases with resource availability, represented in our data by soil cation concentration and climatic moisture. In addition, there was a general increase in diversity towards sites with higher variability in soil chemistry. Because most of the environmental variables were correlated with each other, it is difficult to draw definite conclusions on which of them, if any, might have a causal relationship with species density. However, the explanatory power of soil cation concentration was much higher than that of any of the other environmental variables. In addition, when the means and variabilities of soil cation concentration and aluminium were used together in a regression model, the explanatory power was only marginally higher than without the variability measures. This suggests that high soil nutrient availability may indeed promote fern and lycophyte species density in its own right, and the association is not merely a byproduct of higher soil heterogeneity.

A hump-shaped relationship between plant species density and soil resource availability could result from a combination of few species being able to cope with resource scarcity and communities becoming dominated by one or a few highly competitive species at high resource availability (Grime 1979, Tilman 1982). Such dominance should cause unevenness to increase towards high resource availability, but our data did not conform to this. At most values of q, unevenness was unrelated to soil cation concentration, and the weak relationship that emerged at high values of q was contrary to expectation: the highest unevenness values were found at intermediate rather than high soil cation concentrations. The decrease in species density at high resource availability could also reflect decreasing resource supply heterogeneity (Tilman 1982), but in our data the variability in both soil cation concentration and soil aluminium concentration increased with their mean values.

In Amazonia, a hump-shaped relationship between species density and soil nutrient concentration has been reported for the Melastomataceae in one study

(Tuomisto and Ruokolainen 2005), although another study found a negative relationship (Tuomisto et al. 2002). The species densities of other plants have been found to either increase with soil fertility (trees: Gentry 1988, Phillips et al. 1994, Duivenvoorden 1996, Laurance et al. 2010; ferns and lycophytes: Tuomisto and Poulsen 1996, Tuomisto et al. 2003a, Tuomisto and Ruokolainen 2005, Costa 2006, Cárdenas et al. 2007) or to have no relationship with it (trees: Clinebell et al. 1995; ferns and lycophytes: Tuomisto et al. 2002; palms: Kristiansen et al. 2011).

Such variability among studies reflects at least two different phenomena. The first is a sampling effect: the results depend on how much and which part of the edaphic gradient is considered (called the veiled gradient problem by McCoy 2002). This explains the differences between the results of Tuomisto et al. (2002) and Tuomisto and Ruokolainen (2005): the former covered a shorter gradient and was restricted to relatively high-nutrient soils. In our data (which cover a longer edaphic gradient than either previous study), a positive trend for ferns and lycophytes was pronounced, but a weak indication of a levelling off or even a decrease in species density could be seen at very high soil cation concentrations. The decrease was due to just a few transects, however, and more data from cation-rich soils are needed to establish if this is a real trend or the effect of some other limiting factor.

The second cause for variable results among studies is that different plant groups may really behave in different ways. It seems obvious that Melastomataceae species density peaks well within the edaphic gradient covered by our sampling, but the species density of ferns and lycophytes does not. Whether such differences between evolutionary lineages are due to differential evolutionary diversification (and hence differences in the numbers of extant species that are able to grow in particular conditions) or to ecological processes that govern within-site co-occurrence of species remains to be clarified.

Two observations indicate that evolutionary processes are involved. Firstly, the collective species lists of ferns and lycophytes have generally been shorter for poor-soil sites than for rich-soil sites (Tuomisto and Poulsen 1996, Tuomisto et al. 2003a, Cárdenas et al. 2007, Zuquim et al. 2009). This indicates smaller species pools for poor soils than for rich soils in Amazonia. Secondly, the different fern genera have attained their highest species richness in different parts of the edaphic gradient, and more genera have apparently diversified on rich soils than on poor soils.

Contrary to earlier studies on woody plants (Gentry 1988, Wright 1992, Phillips et al. 1994, Clinebell et al. 1995, Van Der Heijden and Phillips 2009, Kristiansen et al. 2011), we found that soils explained fern and lycophyte species diversity much better than rainfall did. Again, this discrepancy may reflect real ecological differences between the plant groups, different relative lengths of the environmental gradients covered, or different covariance structures among the explanatory variables in the respective datasets. In our dataset, soil cation concentration was positively correlated with annual rainfall, but in at least one of the tree studies, soil fertility was negatively correlated with rainfall (Clinebell et al. 1995). One or both of the latter factors may also explain why ter Steege et al. (2000) observed that rainfall predicted tree species density better in western and central Amazonia than in eastern Amazonia and the Guianas.

Obviously, covariance between potential explanatory variables can make unraveling their relative contributions impossible. This problem can only be alleviated with large enough sample sizes that provide a balanced representation of different variable combinations from all parts of the study area. Our data would benefit from further sampling especially on cation-rich soils in areas with about 2000 mm or 3500 mm of annual rainfall (Fig. 4B), and a better representation of central and eastern Amazonia. Even with balanced sampling, however, it is reasonable to assume that many factors can limit species density, and that maximum species density may be easier to predict than average species density (ter Steege et al. 2003). Interestingly, in our data the degree to which species density was explainable by environmental and spatial variables decreased substantially as the value of q was increased, i.e. when the emphasis in the calculation of diversity was shifted from species richness to species dominance. This suggests that the number of species per unit area may be under a more deterministic control than the proportional abundances of the most abundant species.

In general, it is of great concern that observed trends in species richness depend strongly on sampling effort, and in tree inventories the number of stems can easily be the single most important predictor of the number of species observed (Condit et al. 1996, He and Legendre 1996, Tuomisto and Ruokolainen 2012). In our data, sampling effort was standardized to a fixed surface area, which means that there can be (and were) large differences among transects in the number of individuals observed. However, it seems unlikely that our results would have been seriously biased by this. Firstly, the density of individuals itself was only marginally or not at all related to the environmental and spatial gradients we were interested in. Secondly, both Chao 1 and ACE estimators indicated that the expected number of species was generally not much larger than the number of species actually observed, and the estimated degree of undersampling was not related to either the number of individuals or to any of the other explanatory variables of interest. Thirdly, although the maximum number of species in a transect increased from low to intermediate density of individuals, overall the relationship was hump-shaped and not very strong. These observations suggest that our results on species richness and diversity gradients can be considered robust.

Species diversity in a biogeographical context

Both the mid-domain effect and the age-and-stability hypothesis as applied to broad-scale geology suggest that the highest species richness should be found in our Brazilian transects. These are closest to the geographical midpoint of Amazonia, and are on old and stable geological formations (Sombroek 2000). The western Amazonian transects are geographically more peripheral, and these areas have been geologically more dynamic in the post-Miocene times (Salo et al. 1986, Räsänen et al. 1987, 1995, Hoorn 1993, Hoorn et al. 2010). However, we actually found the opposite. Among the seven regions we sampled, the Brazilian one stood out in having transects of much lower species density than was typical in the other regions. This seems to have an ecological explanation: the Brazilian transects combined relatively dry climates with cation-poor soils, and this combination appears to be a tough one for ferns and lycophytes to adapt to. Transects with equally poor soils but wetter climates in Colombia and northern Peru had higher species density than the Brazilian transects, as did transects with equally dry climates but more cation-rich soils in southern Peru.

Stability in climate (especially rainfall) seems to have been highest in western Amazonia thanks to convective rain caused by the Andes, and in a belt of about 4 degrees south of the equator (Martin et al. 1997, Hooghiemstra and van der Hammen 1998). The longitudinal trend we observed in fern and lycophyte species diversity could partly be explained by the age-and-stability hypothesis as applied to atmospheric water availability, but we found no indication of any latitudinal trend in species diversity between the equator and 13°S. This is in contrast to earlier results on trees and palms, which were interpreted mostly in terms of past climatic stability and to a lesser degree in terms of present-day rainfall (Stropp et al. 2009, Kristiansen et al. 2011).

How about the age-and-area hypothesis? Extremely poor white sands are relatively scarce, with Arenosols and Podzols together covering 4–5% of the forested area in Amazonia (Quesada et al. 2011). Other cation-poor soils derived from the Precambrian granitic rocks of the Guyanan and Brazilian shields are both old and widespread (Sombroek 1984, 2000): Ferralsols and Acrisols together cover almost 60% (Quesada et al 2011). Cation-rich soils in Amazonia are mostly derived from the Pebas Formation, which was deposited in the Miocene but may not have become available as a forest substrate until much later (Higgins et al. 2011), and from even more recent Andean sediments deposited by rivers. The Alisols and Cambisols derived from such substrates cover about 6% of Amazonia (Quesada et al. 2011).

If the species pool size (and species density) were primarily determined by the age and/or surface area of the corresponding habitat, we should expect most species on relatively poor soils, and clearly fewer both in the extremely poor white sands and in the rich soils. Typically, the white sands indeed harbor very few plant species, including ferns and lycophytes (Tuomisto and Poulsen 1996, ter Steege et al. 2003). However, both our data and earlier studies on ferns and lycophytes are in conflict with the prediction for rich soils, which typically have both high species densities and a large species pool (Tuomisto and Poulsen 1996, Cárdenas et al. 2007, Zuquim et al 2012).

If the relative ages and surface areas of the rich *vs.* poor soils in Amazonia have been deduced correctly, the net diversification rate (difference between speciation rate and extinction rate) must have been higher among fern and lycophyte species adapted to rich soils than among those adapted to poor soils. In one tree group (the tribe Protiae of the Burseraceae), it has been suggested that the ancestral state of the clade was adapted to intermediate soils, and that repeated adaptation has taken place both into the nutrient-rich Pebas-derived soils and into the nutrient-poor white sand soils (Fine et. al 2005). The numbers of species per plot were not reported for the Protiae, but the regional species pools for the intermediate and rich soils were of similar sizes, whilst clearly fewer species were found in the white sands. This may indicate that the net diversification rates on the contrasting substrates have differed in the Burseraceae as well.

A final biogeographical consideration is the potential role of the Andes in promoting high fern and lycophyte species richness in western Amazonia. The Andes harbour approximately 2000 species of pteridophytes, whereas only about 300 have been estimated for Brazilian Amazonia (Moran 1995). As expected if many of the Amazonian species are of Andean origin, we found a decreasing trend in fern and lycophyte species diversity towards the east, and also that longitude was one of its best predictors in multiple regression models. Unfortunately, it is difficult to separate the effect of geographical proximity to the Andes from the effects of soil cation concentration and annual rainfall, both of which covary with longitude. Indeed, more data are needed especially from Brazilian Amazonia to obtain a better understanding of these biogeographical patterns.

Acknowledgements

We thank numerous colleagues for collaboration in the field, especially Kalle Ruokolainen, Jefferson Prado, Mark Higgins and Adriana Zegarra, the even more numerous local field assistants who made the fieldwork possible, and all the villages and private landowners who gave us permission to work in their territory. During data collection, GC was based at Universidad Nacional de la Amazonia Peruana (UNAP – Iquitos, Peru) or Instituto de Investigaciones de la Amazonia Peruana (IIAP – Iquitos, Peru) and GZ at Instituto Nacional de Pesquisas da Amazônia (INPA – Manaus, Brazil). We thank these institutions and Pontificia Universidad Católica del Ecuador (PUCE - Quito, Ecuador), Universidad de los Andes (Bogotá, Colombia), SINCHI (Bogotá, Colombia) and Universidad San Antonio Abad del Cusco (Cusco, Peru) for collaboration and logistic support. The SRTM data was extracted by Gabriel M. Moulatlet. Funding from the Academy of Finland to HT is gratefully acknowledged. The field data were accumulated during various earlier projects funded mostly by the Academy of Finland and the European Union. We thank the national authorities for granting the research and collection permits [e.g. Brazilian National Council for Scientific and Technological Development (CNPq) and the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio)].

References

Ashton, P. S. 1989. Species richness in tropical forests. p. 239-251. – In Holm-Nielsen, L. B. et al. (Eds.) Tropical Forests: botanical dynamics, speciation and diversity. Academic Press Limited, London. 380 pp.

Baker, H. G. 1970. Evolution in the tropics. – Biotropica 2: 101-111.

Beard, J. S. 1944. Climax vegetation in tropical America. – Ecology 25: 127-158.

Brown, J. H. 1988. Species diversity. – In: Myers, A. A. and Giller, P. S. (eds.), Analytical biogeography: an integrated approach to the study of animal and plant distributions. Chapman and Hall, pp. 57-89.

Bush, M. B. and de Oliveira, P. E. 2006. The rise and fall of the Refugial Hypothesis of Amazonian Speciation: a paleoecological perspective. – Biota Neotrop. 6.

Bjorholm, S. et al. 2006. Historical legacies in the geographical diversity patterns of New World palm (Arecaceae) subfamilies. – Botanical Journal of the Linnean Society 151: 113 – 125.

Caley, M.J. and Schluter, D. 1997. The relationship between local and regional diversity. – Ecology 78: 70-80.

Cárdenas, G. G. et al. 2007. Riqueza y distribución ecológica de especies de pteridofitas en la zona del Río Yavarí-Mirín, Amazonía Peruana. – Biotropica 39: 637–646.

Chao, A. 1984. Nonparametric Estimation of the Number of Classes in a Population. – Scand. J. Statist. 11: 265-270.

Chao, A. and Lee, SM. 1992. Estimating the number of classes via sample coverage. – J. Am. Statist. Assoc. 87: 210-217.

Clinebell II, R. R. et al. 1995. Prediction of neotropical tree and liana species richness from soil and climatic data. – Biodiver. Conserv. 4: 56-90.

Colwell, R. K. and Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. – TREE 15: 70-76.

Condit, R. et al. 1996. Species-Area and Species-Individual Relationships for Tropical Trees: A Comparison of Three 50-ha Plots. – J. Ecol. 84: 549-562

Colinvaux, P. A. et al. 2001. A paradigm to be discarded: Geological and paleoecological data falsify the HAFFER & PRANCE refuge hypothesis of Amazonian speciation. – Amazoniana XVI: 609-646.

Costa, F. R. C. 2006. Mesoscale gradients of herb richness and abundance in Central Amazonia. – Biotropica 38: 711-717.

Diamond, J. 1988. Factors controlling species diversity: overview and synthesis. – Ann. Missouri Bot. Garden 75: 117-129.

Duivenvoorden, J. F. 1996. Patterns of tree species richness in rain forest of the middle Caquetá area, Colombia, NW Amazonia. – Biotropica 28: 142-158.

Eiserhardt, W. L. et al. 2011. Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. – Ann. Bot. 108: 1391-1416

Fine, P. V. A. et al. 2005. The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the western Amazon. – Evolution 59: 1464-1478.

Fischer, A. G. 1960. Latitudinal variations in organic diversity. – Evolution 14: 64-81.

Gaston, K. J. 2000. Global patterns in biodiversity. – Nature 405: 220-227.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. – Ann. Mo. Bot. Gard. 75: 1–34.

Gillman, L. N. and Wright, S. D. 2006. The influence of productivity on the species richness of plants: a critical assessment. – Ecology 87: 1234-1243.

Gonçalves-Souza, T. et al. 2013. A critical analysis of the ubiquity of linear local-regional richness relationships. – Oikos 122: 961-966.

Grime, J. P. 1979. Plant strategies and vegetation processes. – J. Wiley & Sons, Chichester.

He, F. and Legendre, P. 1996. On species-area relations. – Am. Nat. 148: 719-737.

Higgins, M. A. et al. 2011. Geological control of floristic composition in Amazonian forests. – J. Biogeogr. 38: 2136-2149.

Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – Int. J. Climatol. 25: 1965-1978.

Hijmans, R. J. et al. 2012. DIVA-GIS Version 7.5. Manual. – URL: http://www.diva-gis.org/docs/DIVA-GIS_manual_7.pdf

Hill, J.L. and Hill, R.A. 2001. Why are tropical rain forests so species rich? Classifying, reviewing and evaluating theories. – Progress in Physical Geography 25: 326-357.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. – Ecology 54: 427–432.

Hooghiemstra, H. and van der Hammen, T. 1998. Neogene and Quaternary development of the neotropical rain forest: the forest refugia hypothesis, and a literature overview. – Earth-Sci. Rev. 44: 147 183.

Hoorn, C. 1993. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: Results of a palynostratigraphic study. – Palaeogeogr. Palaeoclimatol. Palaeoecol 105: 267-309.

Hoorn, C. et al. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. – Science 330:927–931.

Hoorn, C. and Wesselingh, F. 2010. Amazonia: landscape and species evolution. A look into the past. – Wiley-Blackwell, Oxford. 447 p.

Huston, M. 1980. Soil nutrients and tree species richness in Costa Rican forests. – J. Biogeog. 7:147-157.

Jost, L. 2006. Entropy and diversity. – Oikos 113: 363-375.

Jost, L. 2010. The relation between evenness and diversity. – Diversity 2: 207-232.

Kristiansen, T. et al. 2011. Local and regional palm (Arecaceae) species richness patterns and their cross-scale determinants in the western Amazon. – J. Ecol. 99: 1001–1015.

Laurance, S.G.W. et al. 2010. Influence of soils and topography on Amazonian tree diversity: a landscape-scale study. – J. Veget. Sci. 21: 96–106.

Mayle, F.E. et al. 2000. Millennial-scale dynamics of southern Amazonian rain forests. – Science 290: 2291–2294.

Martin, L. et al. 1997. Astronomical forcing of contrasting rainfall changes in tropical South America between 12,400 and 8800 cal yr BP. – Quat. Res. 47: 117–122.

McCoy, E. D. 2002. The “Veiled Gradients” Problem in Ecology. – Oikos 99:189-192.

Mittelbach, G. G. et al. 2001. What is the observed relationship between species richness and productivity? – Ecology 82: 2381–2396.

Moran, R. C. 1995. The importance of mountains to Pteridophytes, with emphasis on Neotropical montane forests. – In: Churchill, S.P. (ed.). Biodiversity and conservation of Neotropical montane forests. New York Botanical Garden, pp. 359–363.

Nelson, B. W. et al. 1990. Endemism centers, refugia and botanical collection density in Brazilian Amazonia. – Nature 345: 714-716.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. and Wagner, H. 2013. vegan: Community Ecology Package. – R package version 2.0-7. http://CRAN.R-project.org/package=vegan

Palmer, M. W. 1994. Variation in species richness: towards a unification of hypotheses. – Folia Geobotanica et Phytotaxonomica 29: 511-530.

Pausas, J. G. and Austin, M. P. 2001. Patterns of plant species richness in relation to different environments: An appraisal. – J. Veg. Sci. 12: 153-166.

Phillips, O. L. et al. 1994. Dynamics and species richness of tropical rain forests. – Proc. Natl. Acad. Sci. USA. 91: 2805-2809.

Pianka, E.R. 1966. Latitudinal gradients in species diversity: a review of concepts. – Am. Nat. 100: 33-46.

Quesada, C. A. et al. 2011. Soils of Amazonia with particular reference to the RAINFOR sites. – Biogeosciences 8: 1415-1440.

Ruokolainen, K. et al. 2007. Are floristic and edaphic patterns in Amazonian rain forests congruent for trees, pteridophytes and Melastomataceae? – J. Trop. Ecol. 23: 13-25.

Räsänen, M. E. et al. 1987. Fluvial perturbance in the Western Amazon Basin: Regulation by Long-Term Sub-Andean Tectonics. – Science 238: 1398-1401.

Räsänen, M. E. et al. 1995. Late Miocene tidal deposits in the Amazonian foreland basin. – Science 269:386–390.

Salo, J. et al. 1986. River dynamics and the diversity of Amazon lowland forest. – Nature 322: 254-258.

Schulman, L. et al. 2007. Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. – J. Biogeogr. 34: 1388-1399.

Slik, J. W. F. et al. 2009. Environmental correlates for tropical tree diversity and distribution patterns in Borneo. – Diversity Distr. 15: 523-532.

Sombroek, W. 1984. Soils of the Amazon region. – In: Sioli, H. (ed.), The Amazon: limnology and landscape ecology of a mighty tropical river and its basin. Dr. W. Junk Publishers, pp. 521-535.

Sombroek, W. 2000. Amazon landforms and soils in relation to biological diversity. – Acta Amazonica 30: 81-100.

Sousa-Baena, M.S. et al. 2014. Completeness of digital accessible knowledge of the plants of Brazil and priorities for survey and inventory. – Diversity Distrib. 20: 369–381.

Stropp, J. et al. 2009. Disentangling regional and local tree diversity in the Amazon. – Ecography 32: 46-54.

ter Steege, H. et al. 2000. An analysis of Amazonian floristic composition, including those of the Guiana Shield. – J. Trop. Ecol. 16: 801-828.

ter Steege, H. et al. 2003. A spatial model of tree α- diversity and tree density for the Amazon. – Biodivers. Conserv. 12: 2255–2277.

Terborgh, J. 1973. On the notion of favorableness in plant ecology. – Am. Nat. 107: 481-501.

Tilman, D. 1982. Resource competition and community structure. – Monog. Biol. 17. Princeton University Press, Princeton, NJ. 296 p.

Tuomisto, H. and Poulsen, A.D. 1996. Influence of edaphic specialization on the distribution of pteridophytes in neotropical forests. – J. Biogeogr. 23: 283-293.

Tuomisto, H. et al. 2002. Distribution and diversity of pteridophytes and melastomataceae along edaphic gradients in Yasuni national park, Ecuadorian Amazonia. – Biotropica 34: 516-533.

Tuomisto, H. et al. 2003a. Floristic patterns along a 43-km long transect in an Amazonian rain forest. – J. Ecol. 91: 743–756.

Tuomisto, H. et al. 2003b. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. – Ecol. Appl. 13: 352-371.

Tuomisto, H. et al. 2003c. Dispersal, environment, and floristic variation of western Amazonian forests. – Science 299: 241-244.

Tuomisto, H. and Ruokolainen, K. 2005. Environmental heterogeneity and the diversity of pteridophytes and Melastomataceae in western Amazonia. – Biologiske Skrifter 55: 37-56.

Tuomisto, H. 2010. A consistent terminology for quantifying species diversity? Yes, it does exist. – Oecologia 164: 853-860.

Tuomisto, H. 2011. Commentary: do we have a consistent terminology for species diversity? Yes, if we choose to use it. – Oecologia 167:903-911.

Tuomisto, H. 2012. An updated consumer´s guide to evenness and related indices. – Oikos 121: 1203-1218.

Tuomisto, H. and Ruokolainen, K. 2012. Comment on “Disentangling the drivers of β diversity along latitudinal and elevational gradients”. – Science 335: 1573.

Van Der Heijden, G. M. F. and Phillips, O. L. 2009. Environmental effects on Neotropical liana species richness. – J. Biogeog. 36: 1561–1572.

Vormisto, J. et al. 2004. Diversity and dominance in palm (Arecaceae) communities in *terra firme* forests in the western Amazon basin. – J. Ecol. 92: 577-588.

Wright, S. J. 1992. Seasonal drought, soil fertility and the species density of tropical forest plant communities. – TREE 7: 260–263.

Zuquim, G. et al. 2009. An annotated checklist of ferns and lycophytes from the Biological Reserve of Uatumã, an area with patches of rich-soils in central Amazonia, Brazil. – Fern Gaz. 18:286-306.

Zuquim, G. et al. 2012. Broad scale distribution of ferns and lycophytes along environmental gradients in Central and Northern Amazonia, Brazil. – Biotropica 44: 752-762.

Tables

Table 1. Means and ranges of selected variables related to the diversity of ferns and lycophytes in 214 transects in Amazonian non-inundated forests. For geographical locations, see Fig. 1.

Region	Ecuador	Colombia	NW Peru	NE Peru	C Peru	S Peru	Brazil
Individuals	2393 (734–10655)	1471 (263–3045)	1520 (286–5750)	1710 (497–4178)	1189 (206–2656)	1571 (249–4488)	2360 (56–11370)
Species richness	46.77 (33–58)	24.54 (15–34)	27.7 (15–42)	28.79 (15–46)	20 (8–35)	30.69 (11–71)	12.62 (6–38)
Diversity (q=1)	15.67 (2.63–24.77)	8.78 (3.55–14.57)	9.73 (4.14–23.47)	9.37 (2.35–16.13)	7.28 (2.06–12.48)	10.85 (1.47–25.51)	3.02 (1.11–8.06)
Diversity (q->Inf)	4.59 (1.26–8.6)	3.46 (1.49–5.38)	3.54 (1.54–7.08)	3.35 (1.22–6.54)	3.09 (1.19–4.79)	3.76 (1.08–7.81)	1.59 (1.02–2.93)
Evenness (q=1)	0.33 (0.06–0.47)	0.36 (0.15–0.53)	0.36 (0.13–0.62)	0.33 (0.11–0.52)	0.37 (0.13–0.58)	0.35 (0.13–0.56)	0.28 (0.07–0.67)
Evenness (q->Inf)	0.1 (0.03–0.2)	0.15 (0.05–0.24)	0.13 (0.05–0.26)	0.12 (0.04–0.24)	0.18 (0.05–0.32)	0.13 (0.06–0.28)	0.15 (0.04–0.38)
Unevenness (q=1)	3.8 (2.11–16.37)	3.21 (1.89–6.52)	3.09 (1.62–7.98)	3.47 (1.92–8.93)	3.44 (1.71–7.77)	3.22 (1.79–7.5)	5.45 (1.49–15.33)
Unevenness (q->Inf)	12.95 (5–36.02)	8.25 (4.16–20.38)	9.03 (3.82–22.19)	10.01 (4.18–23.61)	7.83 (3.13–18.64)	8.91 (3.55–18.15)	9.04 (2.62–23.16)

Table 2. Correlations among variables that might explain variation in fern and lycophyte species diversity in 214 transects in Amazonian non-inundated forests. Pearson correlation coefficients exceeding 0.50 are highlighted in bold.

	log(Mean cat.)	Range log(cat.)	Mean Al	Range Al	Ann. rain	Dry s. rain	Lat	Long.	Mean alt.	Range elev.
log(Mean cat.)	1	**0.58**	0.34	**0.50**	0.21	0.16	0.03	-0.40	**0.55**	0.10
Range log(cat.)		1	0.28	0.43	0.18	0.05	-0.07	-0.26	0.38	0.03
Mean Al			1	**0.71**	0.45	0.44	0.36	-0.34	0.17	-0.14
Range Al				1	0.39	0.41	0.34	-0.36	0.19	0.02
Ann. rain					1	**0.60**	0.00	-0.42	0.39	-0.24
Dry s. rain						1	**0.55**	**-0.73**	0.00	-0.19
Lat.							1	-0.07	**-0.52**	0.10
Long.								1	-0.46	0.17
Mean alt.									1	0.04
Range elev.										1

Table 3. Contribution of environmental and spatial variables (rows) to explaining variance in the within-transect species diversity of ferns and lycophytes (columns) in 214 transects in Amazonian non-inundated forests. Adjusted R^2 values (expressed in %) from linear regressions are shown (the unique contributions of each pair of explanatory variables to the multiple regression containing all 4 pairs is given in parentheses). Latitude and elevation difference were not used in multiple regressions, because they had no explanatory power. All other variables produced statistically significant simple regressions ($p<0.001$, except $p<0.01$ for the two smallest R^2 values for q approaching infinity).

	Diversity (q=0)	Diversity (q=1)	Diversity (q-> Inf)
log(cations)	42	25	11
Longitude	40	33	23
Range Al	30	20	9
Altitude	29	22	13
Range log(cations)	29	14	4
Al	28	11	3
Annual rainfall	27	20	12
Dry season rainfall	24	18	12
Latitude	1	0	0
Elevation difference	0	0	0
Pair 1: log(cations) and Al	53 (4)	28 (1)	11 (1)
Pair 2: longitude and altitude	47 (4)	39 (6)	25 (6)
Pair 3: ranges of log(cations) and Al	41 (2)	24 (1)	10 (1)
Pair 4: annual and dry season rainfall	32 (3)	24 (2)	14 (1)
Pairs 1 and 2: log(cations) and Al; longitude and altitude	65	44	25
Pairs 2 and 3: longitude and altitude; ranges of log(cations) and Al	63	45	26
Pairs 1 and 4: log(cations) and Al; annual and dry season rainfall	63	40	21
Pairs 3 and 4: ranges of log(cations) and Al; annual and dry season rainfall	56	35	17
Pairs 1 and 3: log(cations) and Al; ranges of log(cations) and Al	55	30	12
Pairs 2 and 4: longitude and altitude; annual and dry season rainfall	54	42	26
All 4 variable pairs	70	48	28

Table 4. The most parsimonious multiple linear regression models explaining within-transect species diversity of ferns and lycophytes in 214 transects in Amazonian non-inundated forests. Backward elimination was used to exclude from the models the explanatory variables with highest p values until all remaining variables were significant at the $p < 0.05$ level. Adjusted R^2 values (expressed in %) are shown for each model.

Order of diversity	R^2	Explanatory variables in model
q=0	70	log(cations), Al, dry season rainfall, elevation, range log(cations)
q=1	46	log(cations), annual rainfall, longitude
q-> Inf	28	Al, annual rainfall, elevation, longitude, range Al

Figure captions

Fig. 1. Distribution of the 214 transects inventoried in Amazonian non-inundated forests. Inset shows the general distribution of the localities in South America, and the large map their distribution in relation to elevation as obtained from SRTM. Circles are scaled in proportion to soil cation concentration in the transects. The same colour scheme is used in the other figures to indicate which transects come from which of the seven regions. In Ecuador (green), Colombia (orange) and Brazil (red), all transects were considered part of the same region, but the Peruvian transects were separated into four regions: NW Peru (dark blue), NE Peru (purple), central Peru (intermediate blue) and S Peru (pale blue).

Fig. 2. The relationship between species diversity (A–C) or evenness (D–E) and number of individuals of ferns and lycophytes in 214 transects in Amazonian non-inundated forests. Linear and second-order polynomial regression lines are shown if statistically significant at $p<0.05$. Colours refer to geographical regions as shown in Fig. 1, and symbols are sized in relation to soil cation concentration. Species diversity at $q=0$ equals species richness, so evenness at $q=0$ invariably equals unity.

Fig. 3. Diversity profiles (top row), evenness profiles (middle row) and unevenness profiles (bottom row) for ferns and lycophytes in 214 transects in Amazonian non-inundated forests. Each panel contains transects with mean soil cation concentration in the specified range, and the colours refer to the regions as shown in Fig. 1. Small values of the parameter q give more weight to species richness, large values to the degree of dominance by the most abundant species. The values obtained with $q=0$ are disjoint because of the logarithmic x axis.

Fig. 4. Distribution of fern and lycophyte species richness (size of symbols) within 214 transects in Amazonian non-inundated forests across the environmental space defined by two environmental variables at a time. Linear and second-order polynomial

regressions between the environmental variables are shown if statistically significant at $p<0.05$. Colours refer to geographical regions as shown in Fig. 1.

Fig. 5. Trends in species richness, diversity, unevenness and number of individuals of ferns and lycophytes in 214 transects in Amazonian non-inundated forests as a function of soil cation concentration (A–C), annual rainfall (D–F) and altitude (I–L). Colours refer to geographical regions as shown in Fig. 1. Symbols are sized in relation to annual rainfall in A–D and soil cation concentration in E–L. Linear and second-order polynomial regression lines are shown if statistically significant at $p<0.05$.

Figure 1.

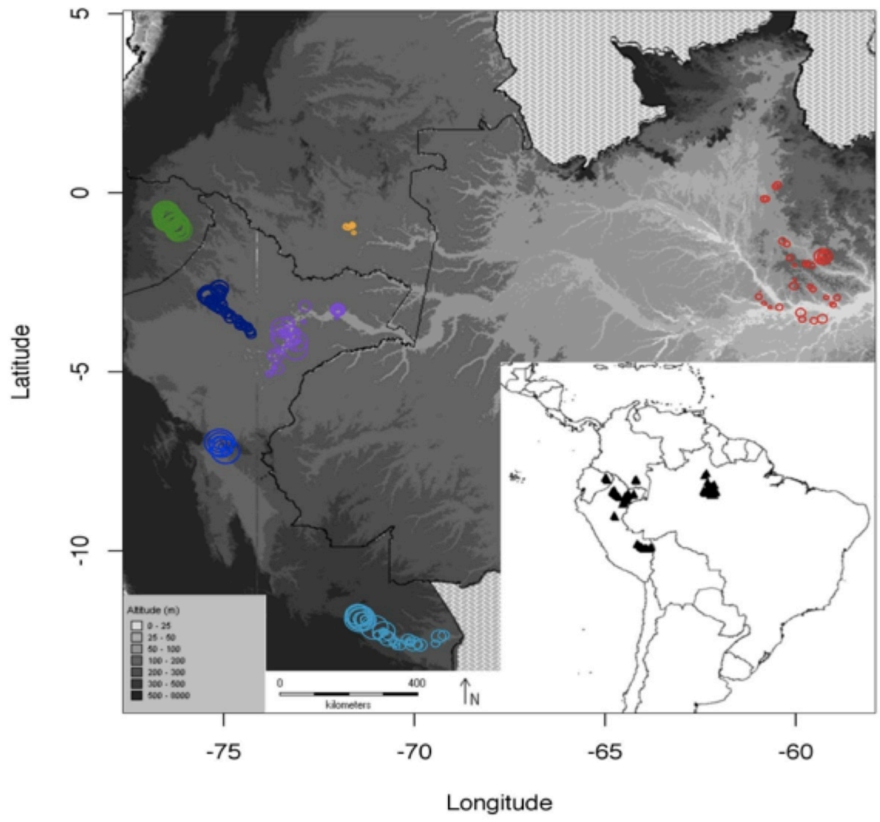


Figure 2.

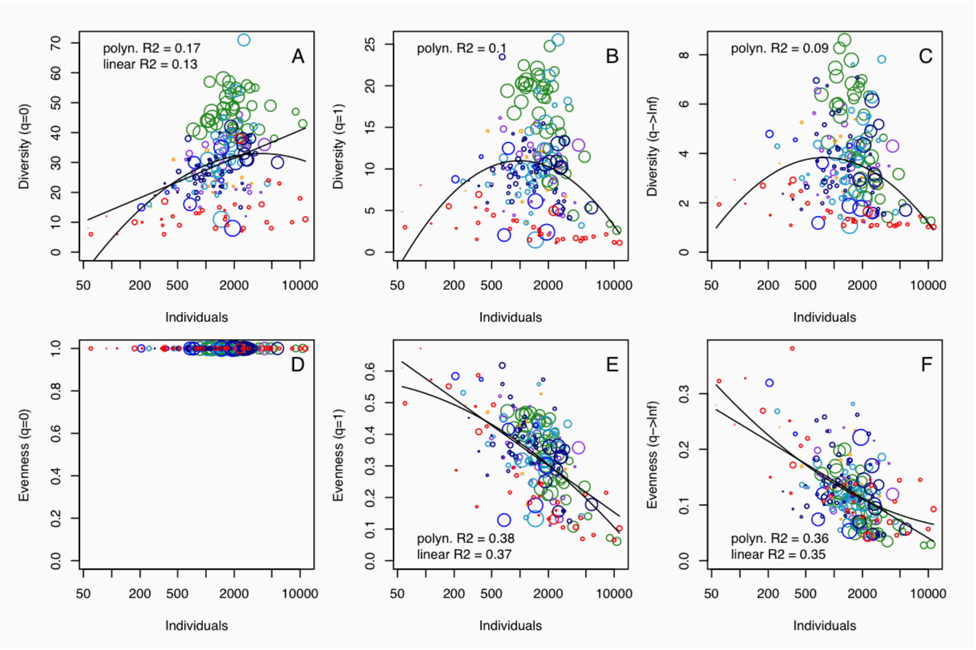


Figure 3.

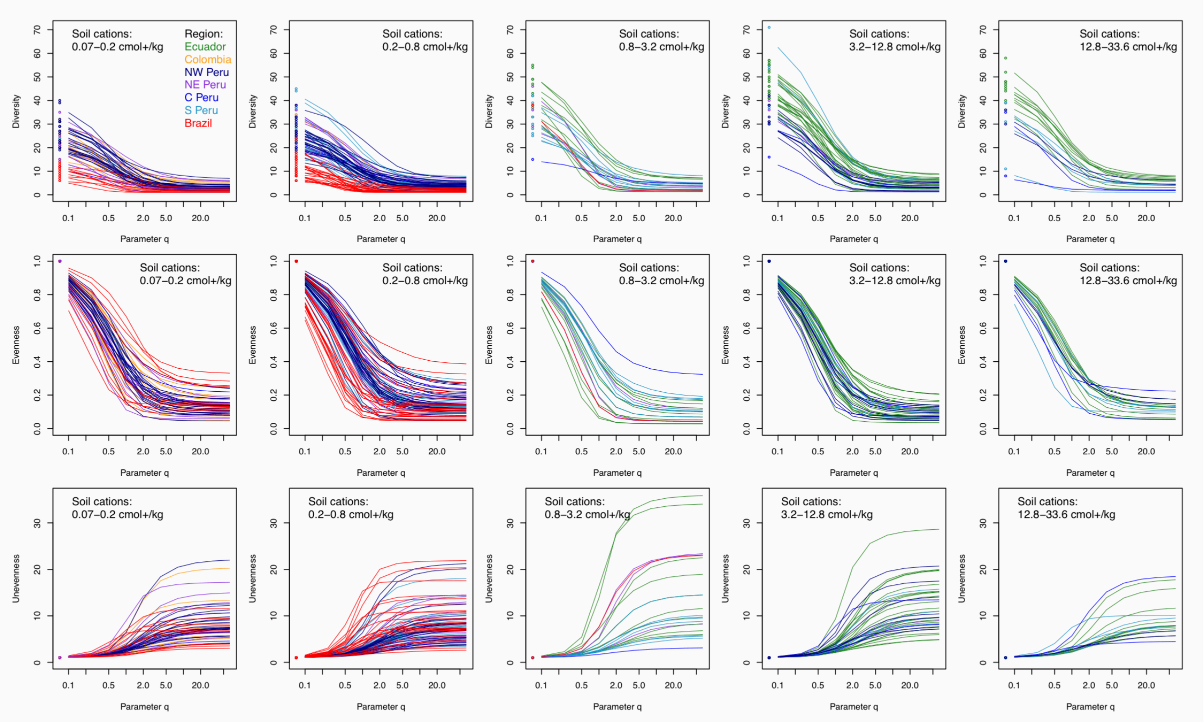


Figure 4.

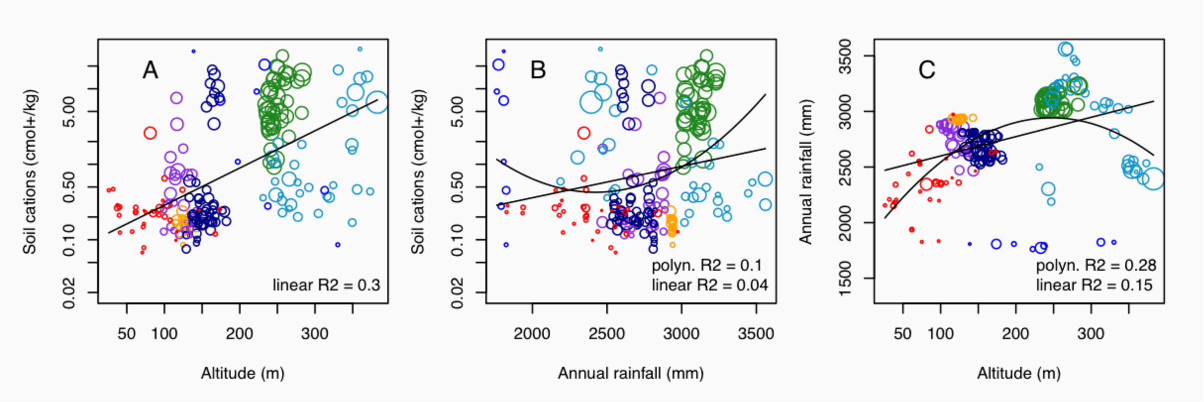
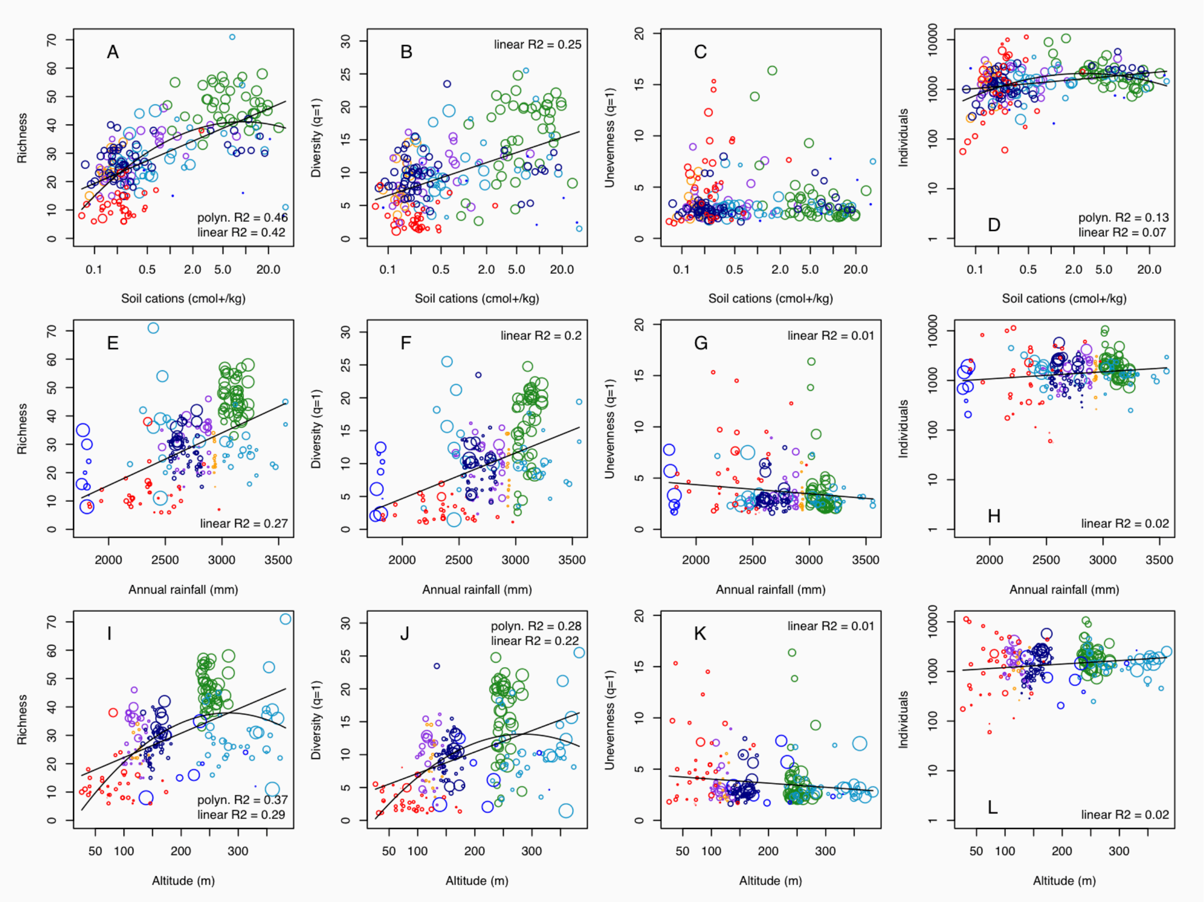


Figure 5.


A
Richness
polyn. R2 = 0.46
linear R2 = 0.42
Soil cations (cmol+/kg)
B
Diversity (q=1)
linear R2 = 0.25
Soil cations (cmol+/kg)
C
Unevenness (q=1)
Soil cations (cmol+/kg)
D
Individuals
polyn. R2 = 0.13
linear R2 = 0.07
Soil cations (cmol+/kg)
0.1
0.5
2.0
5.0
20.0
E
Richness
linear R2 = 0.27
Annual rainfall (mm)
F
Diversity (q=1)
linear R2 = 0.2
Annual rainfall (mm)
G
Unevenness (q=1)
linear R2 = 0.01
Annual rainfall (mm)
H
Individuals
linear R2 = 0.02
Annual rainfall (mm)
2000
2500
3000
3500
I
Richness
polyn. R2 = 0.37
linear R2 = 0.29
Altitude (m)
J
Diversity (q=1)
polyn. R2 = 0.28
linear R2 = 0.22
Altitude (m)
K
Unevenness (q=1)
linear R2 = 0.01
Altitude (m)
L
Individuals
linear R2 = 0.02
Altitude (m)
50
100
200
300
0
10
20
30
40
50
60
70
0
5
10
15
20
25
30
1
10
100
1000
10000