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Unraveling the causal links between ecosystem productivity measures and species richness using terrestrial ferns in Ecuador

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Abstract

This work focuses on the relationship between terrestrial fern species richness and productivity, and on the fern nutrient availability along a tropical elevational gradient in Ecuador. During three yearly field phases between 2009 and 2011, field work was carried out at eight elevations (500 m to 4000 m) on the eastern Andean slope in Ecuador. Diversity, biomass, productivity and leaf functional traits of terrestrial ferns were recorded in three permanent plots of $400m^2$ each per elevation. In Chapter 1, I outlined the general purpose of this dissertation, as well as general concepts. In Chapter 2, an alternative to measure air humidity is proposed. In Chapter 3, a total of 91 terrestrial fern species, in 32 genera and 18 families are reported. Hump-shaped patterns along the elevational gradient with a peak at mid elevations adequately described fern species richness, which confirmed that fern diversity is primarily driven by energy-related variables, and that especially low annual variability of these factors favors species rich fern communities. The main results of Chapter 4 showed that along the elevational gradient, terrestrial fern species richness was only weakly related to measures of ecosystem productivity, and more closely to the productivity of the terrestrial fern assemblages as such, which appeared to be determined by an increase in the number of fern individuals and by niche availability. In addition, within elevational belts, a negative relationship between fern species richness and fern productivity was found, which was mainly due to interspecific. In other words, within both spatial scales of this study, fern diversity appears to be limited by the number of available niches by competition to occupy these niches. In Chapter 5, leaf properties, biomass and productivity of terrestrial ferns and trees along our elevational transect were studied. Ferns and trees showed similar elevation gradients for the foliar functional traits; however, a systematic difference in specific leaf area (SLA) between fern and tree leaves was found along the elevational gradient, which reflected the different light regimes of both life forms. In addition, a striking difference between ferns and trees with respect to the patterns of altitudinal change in biomass and productivity was found, which supported the hypothesis that both plant groups are growth-limited by different factors. While biomass and productivity of trees decreased with elevation, which suggests that factors (soil and air humidity, light availability) other than nutrient availability should play a key role for terrestrial ferns.

Table of Contents

Chapter 1

Introduction

1.1 Research focus 1: Species richness patterns and their relationship with productivity along tropical elevational gradients

Elevational gradients are suitable in investigations related to patterns of biodiversity because they provide a natural experimental setting along which environmental conditions change continuously within relatively short distances (few tens of km). Elevational gradients are considered to be analogous to latitudinal gradients, but they have the advantage of not being affected by dispersal limitations (due to short distances) and having frequent replications (in contrast to latitudinal gradients) (e.g. Rahbek, 1995, 2005; Lomolino, 2001; Nogués-Bravo *et al.*, 2008).

Ferns and lycophytes (henceforth called ferns for simplicity) are widely distributed across the world with about 11.000 species (Smith *et al.,* 2006). Ferns are more abundant and diverse in humid tropical forest, especially in montane habitats (Moran, 2004; Kreft *et al.*, 2010; Kessler *et al.*, 2011), where they represent between 6.5 and 25 % of the vascular plants flora at local scales (Whitmore *et al.,* 1985; Ibisch, 1996; Balslev *et al.*, 1998; Linares-Palomino *et al.,* 2009). For instance, Ecuador harbors about 1,400 ferns species, although it is the smallest Andean country with an area of approximately 283.000 km² (Jørgensen and León-Yánez, 1999; Ulloa Ulloa and Neill, 2005; Neil and Ulloa Ulloa, 2011). The overall richness found in Ecuador is considered exceptionally high in comparison to other Andean countries shows that this overall richness is exceptionally high (Peru: 1,200 species: Smith *et al.,* 2005; Bolivia: 1,163 species: Soria-Auza and Kessler, 2007).

Various studies in elevational gradients have found two main patterns of species richness: a monotonic decrease in species richness as elevation increases (Rahbek, 1995) and a hump-shaped richness pattern with the highest number of species at about mid-elevations. The humped distribution is the most common across all taxonomic groups as described by Rahbek (1995, 2005), who found it in 80% of 204 examined studies. Fern species commonly show a hump-shaped richness pattern with a peak at mid-elevations and decreasing diversity above and bellow (Hemp, 2001, 2002; Kessler, 2000a, 2001a, 2001b; Bhattarai *et al.,* 2004; Krömer *et al.,* 2005; Kluge *et al.,* 2006, 2008). A global comparative analysis recently showed that this is especially true for extensive tropical elevational gradients, i.e., those ranging from the lowlands up to the timberline (Kessler *et al.,* 2011).

However, the driving causes of these richness patterns are only partially understood and may include area, climatic variables (e.g. temperature and humidity as well as energy availability and ecosystem productivity), historical and evolutionary processes, null models and neutral theories, and processes at the population level such as source-sink dynamics.

Possible drivers within the scope of the present research are described in detail bellow.

Source-sink dynamics: At a local scale**,** species richness could be influenced by dispersal capacities, in which source-sink dynamics (Pulliam, 1988) offer an explanation. This process occurs when propagules of a species are dispersed to suboptimal habitats and survive, but are unable to produce enough offspring to maintain self-sustaining populations (Kessler, 2009). Grytnes (2003a) proposed that sink populations are commonly established from source populations within the domain if ecological conditions are similar. For instance, in mid-elevation habitats, dispersal of species from both lower and higher elevations are possible, which reflects a relatively higher diaspore input than areas close to the endpoints of the elevational gradient, which mostly have diaspore input higher than areas close to the end points of the elvational gradient that have diaspore input from one direction only (Grytnes, 2003a, b; Grytnes and Vetaas, 2002; Kattan and Franco, 2004; Kessler, 2000b; Lomolino, 2001; Rahbek, 1997). In two recent studies, Grytnes *et al.* (2008) and Kessler (2009) sterile individuals were assumed to be a sink population and their pattern of species richness were compared to those of fertile individuals. Sterile richness showed hump-shaped patterns more strongly than fertile richness, which suggested that the source-sink effect influenced patterns of species richness in an altitudinal gradient and demonstrated the importance of sterile and fertile individuals' inclusion vegetation surveys (Kessler, 2009).

Climate and energy availability: Climatic variables, e.g. temperature, rainfall and ambient humidity, are considered to be the main drivers of local species richness patterns (e.g. Heaney, 2001; Kessler, 2001c; Bhattarai *et al.,* 2004; Kluge *et al.,* 2006; Kessler *et al.,* 2011). High humidity favors the growth and reproduction of fern communities because gametophyte generation depends on water for the transport of gametes (Barrington, 1993). In addition, a number of studies have documented a highly positive correlation between fern species richness and temperature, precipitation and air humidity (e.g. Hawkins *et al.,* 2003; Currie *et al.,* 2004; Kessler, 2001b; Bhattarai *et al.,* 2004; Kluge *et al.,* 2006; Kreft and Jetz, 2007). Furthermore, the peak of fern species richness at mid elevation has often been interpreted to reflect the ambient conditions of a balanced climate without extremes like drought at low elevations and frost at high elevations (Kessler, 2001b; Hemp, 2002; Battarai *et al.*, 2004; Krömer *et al.*, 2005; Kluge and Kessler, 2007; Kessler *et al.*, 2011). In the tropical montane regions – the hot spots of fern diversity – the stable cloud condensation belts lead to high humidity at mid-elevations (Hastenrath, 1967).

Tropical regions with high rainfall are known to support more species than those with lower rainfall. However, besides rainfall density, rainfall distribution throughout the year also needs to be considered (Moran, 2004). Two regions could receive the same amount of annual rainfall, but if one of the regions experiences an evident dry season, then it will harbor fewer species than the one with more equitably distributed annual precipitation (Clinebell *et al.*, 1995; Moran, 2004). These facts suggest that favorable climatic conditions could lead to higher species richness because optimal climatic conditions are realted to higher productive energy available in the ecosystems (e.g. Wright, 1983; Rohde, 1992; Ferrer-Castán and Vetaas, 2005).

Recently, energy input into ecosystems (productivity) has been suggested to be one of the dominant predictors of species richness pattern (e.g. Abrams, 1995; Rosenzweig, 1995; Evans *et al.*, 2005). For instance, actual evapotranspiration (AET), a measure of energy availability that combines temperature and rainfall, is often positively related to species richness. This is in accordance with the ‘species-energy theory’, originated from the species-area theory, that proposes species richness in a given area to be limited by the quantity of energy available (Wright, 1983). According to the species energy theory, variation in species richness may be explained by the effect of factors such as food resources levels, habitat diversity and biomass levels on overall diversity (MacArthur and MacArthur, 1961; Cody, 1981; Braithwaite *et al.*, 1989) However, there are uncertainties and shortcomings in assessing the productivity of assemblages of organisms. First, often only surrogates of productivity are measured, namely climatic variables as a combination of temperature and water (AET) and standing biomass. Concerning the latter, this is not a direct measure of the turnover (gain and loss) of carbon, so productivity should be directly measured through the increase of biomass per temporal unit (Chase and Leibold, 2002; Whittaker and Heegaard, 2003). Second, the richness pattern of a certain plant group (i.e. ferns) does not necessarily use or have access to the total energy present in the ecosystem, so it is desirable to measure the fraction of productivity exclusively captured by that species group (Mittelbach *et al.,* 2001).

The species-richness relationship generally shows a hump-shaped (unimodal) pattern (e.g. Rozensweig and Abramsky, 1993; Waide *et al.,* 1999; Mittelbach *et al.,* 2001), but there is other type of species richness-productivity relationship, where diversity increases monotonically with productivity (e.g. Currie, 1991; Weide, 1999; Gaston, 2000). According to Evans *et al.* (2005) there are nine mechanisms that may influence the species richness-productivity relationship of which four are relevant to ferns and the study area.

Sampling hypothesis: In this hypothesis, the number of individuals plays an important role because their abundance is the determining connection between energy availability and species richness (Srivastava and Lawton, 1998). An increase inenergy availability may raise the number of individuals that an area can support (Evans *et al.,* 2005) and consequently, assemblages may be comprised of individuals randomly selected from a regional species pool. In high-energy areas, more individuals are selected, which increases the number of novel species that are added to an assemblage (Evans *et al.,* 2005).

Population size hypothesis: This hypothesis states that **"**areas with more productive energy can support more individuals, (Wright, 1983) which allows, species to obtain higher population sizes, reduce extinction rates and elevate species richness" (Evans *et al.,* 2005).

Both the sampling hypothesis and the population size hypotheses make the same prediction: an increase in energy availability may generate positive correlations between total abundance and species richness (Evans *et al.,* 2005). However, the sampling hypothesis describes how an increase in abundance 'captures' available species from the surrounding pool, whereas the population size hypothesis explain how abundance governs the structure of an assemblage (Kaspari *et al.,* 2003).

Niche position: This hypothesis states that "high productive energy increases the abundance of the relatively rare resources that are exploited by niche position specialists" (Evans *et al.,* 2005). "In high-energy areas more species of niche-position specialists can maintain viable populations, thus increasing species richness" (Evans *et al.,* 2005).

Niche breath: This hypothesis states that **"**high productive energy elevates the abundance of individual resource types, which enables species to switch patterns of resource use away from less preferred resources" (Evans *et al.*, 2005). "This reduced niche breath leads and reduces niche overlap, reducing rates of competitive exclusion, thus elevating species richness in high-energy areas" (Evans *et al.*, 2005).

1.2 Research focus 2: Nutrient availability

Even though, information about possible drivers of species richness patterns and species-productivity relationships is available, additional drivers such as soil conditions and nutrient availability may need to be considered. In tropical mountain forests, tree height and above-ground net primary productivity (NPP) decline with increasing elevation (Whitmore, 1984; Stadmüller, 1987; Moser *et al.*, 2011), which has been attributed to reductions in temperature (Kitayama and Aiba, 2002; Hoch and Körner, 2003) and nutrient supply rate (Grubb, 1977; Tanner *et al.*, 1998; Moser *et al.*, 2011) or other potentially limiting factors. While altitudinal gradients in above ground biomass (AGB), above ground biomass increment (AGBI) and foliar characteristics have been studied for trees and vascular and non-vascular epiphytes in a number of transects in neotropical and paleotropical mountains (e.g. Unger *et al.*, 2012, Werner *et al.*, 2012), much less is known about elevational change in other groups of primary producers such as terrestrial ferns and herbaceous plants along tropical mountain slopes. Terrestrial ferns may contribute to < 10% of total biomass in woody ecosystems (Tanner, 1985; Scatena *et al.*, 1993; Raich *et al.*, 1997; Crews *et al.*, 2001), but reach a high percentage of the understory biomass (Raich *et al.*, 1997) and according to the limited information available, it is possible that "terrestrial ferns make the greatest proportional contribution to biomass on nutrients-poor soils" (Richardson and Walker, 2010). For instance, some species of the family Lycopodiaceae are common in poor nutrient rain forest (e.g. Cullen, 1987; Aplet and Vitousek, 1994).

Foliar nitrogen (N) and phosphorus (P) content and specific leaf area (SLA) are key functional traits with an indicator value for light availability, photosynthetic capacity, leaf longevity, and also exposure to drought in plants (Wright *et al.*, 2004, 2005). In general, fast-growing species have higher foliar N concentrations and higher SLA values than slower growing species. Altitudinal changes in foliar nutrients and leaf morphology in trees along tropical mountain transects have been studied (i.e. van de Weg *et al.*, 2009) to search for indications of N or P limitations of tree growth at low and high elevations (Tanner *et al.*, 1998; Vitousek *et al.*, 1988, 1993). In trees, foliar N and P concentrations have been found to either decrease or remain unchanged as elevation increases (Letts *et al.*, 2011; Moser *et al.*, 2011; Soethe *et al.*, 2008; van de Weg *et al.*; 2009) depending on the geology of the mountains. Much less is known about altitudinal change in leaf chemistry and leaf morphology of ferns. In contrast to trees, Wegner *et al.* (2003) found an increase in leaf N concentration with elevation for ferns in the Bolivian Andes. Epiphytic ferns had significantly lower N concentrations than terrestrial ferns in Bolivian and Costa Rican mountain forests (Wegner *et al.*, 2003; Watkins *et al.*, 2007). However, whether terrestrial ferns have higher or lower foliar N concentrations than trees at the same site remains unclear. An important indicator of the relative importance of N and P availability for plant growth is the foliar N/P ratio which has been found to decrease with elevation in terrestrial ferns (Wegner *et al.*, 2003) and suggests a relative shift from prevailing P limitation of growth at low elevation to N limitation at high elevation. A similar altitudinal pattern has been reported for trees in tropical mountains (e.g. Wittich *et al.*, 2012), but such gradients have never been compared among co-occurring trees and terrestrial ferns. A widely reported trend is the altitudinal decrease in SLA that was demonstrated for tropical trees and ferns (e.g. Körner, 1989; Moser *et al.*, 2007).

Terrestrial ferns might differ in their soil fertility-productivity relationship from trees growing at the same site because ferns and trees in the canopy layer are exposed to largely different light regimes. This may result in contrasting nutrient use efficiencies of productivity and differences in nutrient demand. Further, ferns seem to have a lower degree of mycorrhization than trees (e.g. Alexander and Lee, 2005; Kessler *et al.*, 2010) which could affect nutrient acquisition. Finally, trees with their deep-reaching roots may have access to much larger soil nutrient pools than terrestrial ferns with their main root system located in the organic layer and mineral topsoil.

1.3 Specific research objectives and hypotheses

The main objective of this investigation is to study the levels of ecosystem and fern community productivity along an elevational gradient in Ecuador to unravel the causal mechanisms that determine the relationship between energy input of ecosystem and fern richness patterns.

To develop this investigation we set up the following objectives and hypotheses:

1) To evaluate the changes in species richness of ferns along the elevational gradient and relate these changes to climatic variables in order to assess their relative importance in driving fern richness patterns (Chapter 3).

2) To evaluate the productivity at three levels along the elevational gradient (Chapter 4):
    - Total energy input, driven by climatic variables (AET assessment).
    - Productivity of the ecosystem as a whole in relation to the amount of energy available (tree biomass increment assessment).
    - The partial use of this productivity by the focal plant-group (terrestrial fern biomass increment assessment).

    These three levels of productivity are required because of the current uncertainties and shortcomings in assessing energy input (productivity) into an assemblage of organisms.

3) To determine the relationship between terrestrial fern species richness and the above mentioned productivity levels along the elevational gradient. From this objective emerged the following hypotheses (Chapter 4):

    H1: A positive relationship exists between terrestrial fern richness and ecosystem productivity.

    H2: A positive relationship exists between terrestrial fern richness and fern assemblage productivity.

4) To determine the causal mechanisms of the relationship between terrestrial species richness and productivity. From this objective emerged the following hypotheses Evans *et al.* (2005) (Chapter 4):

   H3a: The relationship between terrestrial fern richness and ecosystem productivity is determined by the sampling effect.

   H3b: The relationship between terrestrial fern richness and fern assemblage productivity is determined by the sampling effect.

   H4: The species richness-productivity relationship of terrestrial ferns is determined by the increased population size mechanism.

   H5: The species richness-productivity relationship of terrestrial ferns is determined by the niche position mechanism.

   H6: The species richness-productivity relationship of terrestrial ferns along the elevational gradient is influenced by source-sink effects.

5) To compare indicators of plant nutrition, biomass and productivity between trees and terrestrial ferns and to analyze their dependence on elevation. From this objective emerged the following hypotheses (Chapter 5).

   H7: Trees and terrestrial ferns growing in the same stand display similar elevational patterns in their leaf functional traits (in this study: foliar N and P concentration, and SLA)**.**

   H8: Terrestrial ferns growing in the deep shade have lower foliar N and P concentrations than trees` sun leaves.

6) To evaluate the influence of soil chemical properties on leaf functional traits, biomass and productivity of terrestrial ferns and trees along the elevational gradient. From this objective emerged the following hypotheses (chapter 5).

   H9: The foliar N and P concentrations are correlated with indicators of soil N and P availability in both plant groups.

H10: Elevational gradients in soil N and P availability influence the biomass and productivity of ferns and trees in a similar way.

1.1 Study area

Field work was carried out in 24 plots within eight elevational steps of about 500 m in elevational distance each on the eastern Andean slope in Napo province, Ecuador (Fig. 1.1, Table 1.1). This gradient spans localities from lowland forests in the vicinity of Rio Napo (Reserva Jatun Sacha) at 400 m via 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 timberline at 4,000 m (Fig. 1.1). These sites were selected because they harbour well preserved forest habitats along the whole gradient from lowlands up to the treeline ecotone. According to the most recent vegetation classification for Ecuador (Palacios *et al.*, 1999), the studied sites at 400 m correspond to evergreen lowland forests, at 1,000 m to evergreen premontane forests, between 1,500 and 2,000 m to evergreen lower montane forests, between 2,000 and 2,900 m to montane cloud forest, between 2,900 and 3,600 to evergreen upper montane forest. But in our area of study at about 3,500 and 4,000 m we established the plots in Polylepis patches.

Temperature data were measured between October 2009 until June 2011 with 3 HOBO Pro loggers at each elevational step of 500 m. The mean annual temperature decreases from 22.17°C at 420 m (Jatun Sacha) to 5.8°C at 3900 m (Oyacachi). Exact data on the annual precipitation of the study are lacking, therefore, we used data from the WorldClim data bank (Hijmans *et al.*, 2004).

With regard to soil characteristics, the depth of the organic layer and plant-available P concentration increase with elevation, whereas N availability tends to decrease with elevation. In addition, Ca, Mg and K in the organic layers increase with elevation as well, the acidity of the organic layer is moderately to high (data from 500 m to 2,000 m came from Unger *et al.*, 2010, 2012). In regards to the forest structure (up to 2,000 m), the aboveground biomass is not decreasing with elevation (Unger, 2012).

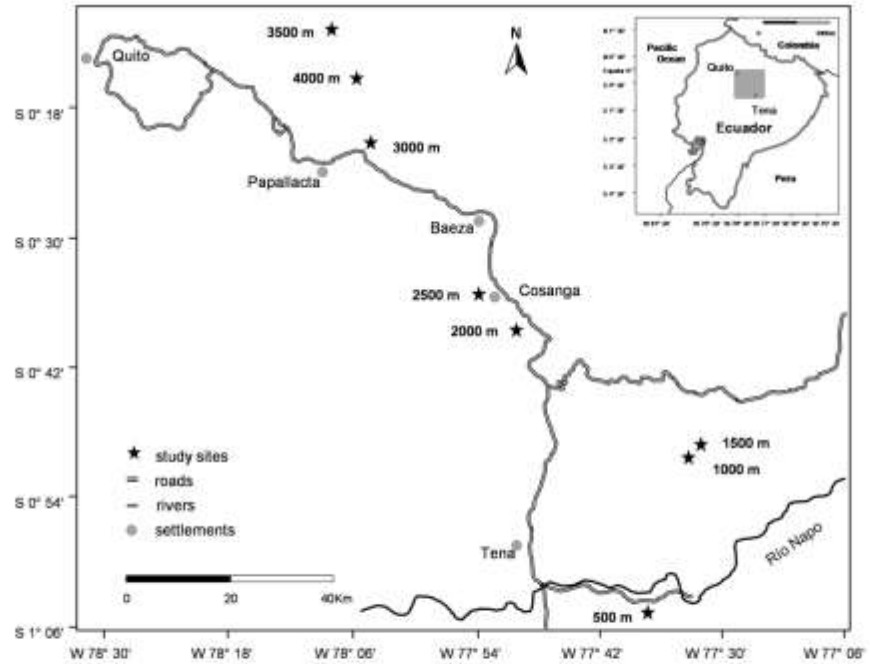

Fig. 1.1 *Study sites and their locations in Ecuador (insets). Positions of all study locations long the altitudinal transect are given with elevation.*

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Chapter 2

Bryophyte cover on trees as proxy for air humidity in the tropics

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2.1 Abstract

Climatic conditions are a prime candidate to explain local patterns of biodiversity and consequently there is great need of on-site climatic measurements. Among them, however, air humidity is notoriously difficult and time-consuming to measure, and it has been proposed that the epiphytic bryophyte cover can be used as an indicator of long-term air humidity conditions. Here we explore the utility of visually estimated epiphytic bryophyte cover on large canopy branches as a proxy for air humidity at 26 study sites in tropical forests where we measured microclimate for at least 12 months. Across all sites, bryophyte cover was weakly related to relative air humidity (R2 = 0.17), but when we separated highland (1,800–3,500 m elevation) from lowland (<1800 m) sites, relative air humidity showed significant and distinct relations to bryophyte cover (R2 = 0.36–0.62), whereas temperature was related to bryophyte cover only in the lowlands (R2 = 0.36). We conclude that epiphytic bryophyte cover can be used as a proxy for air humidity if temperature and elevation are taken into account within a circumscribed study region, but might not be applicable for comparisons across extensive elevational gradients or wide differences in temperature.

2.2 Introduction

Air humidity plays a central role in determination of plant morphology and physiology (via control of transpiration) and con-sequently for plant productivity (e.g. Kozlowski and Pallardy, 1997; Lendzion and Leuschner, 2009; Leuschner, 2002). Accordingly, air humidity is commonly considered to be crucial in influencing the distribution of species and the structuring of plant communities (Lendzion and Leuschner, 2009; Leuschner and Lendzion, 2009). Despite this ecological importance, quantitative data on air humidity are often hard to obtain, especially in tropical regions. Air humidity cannot be derived from climate models and its measurement in the field requires considerable effort. For these reasons, measures of air humidity are often limited to short time periods or few localities, restricting the inclusion of this important factor in many ecological studies. Therefore, estimating the bryophyte cover on trees as a proxy for air humidity has become increasingly popular in ecological studies (e.g. Frahm and Gradstein, 1991; Kessler *et al.*, 2011; Kluge *et al.*, 2006; Wolf, 1993). While the relation between air humidity and bryophyte cover is intuitively appealing and supported by observational reports (Gehrig Downie *et al.*, 2011; Kluge *et al.*, 2006; Obregon *et al.*, 2009; Sporn *et al.*, 2009; Wolf, 1993), a quantitative study on this relationship is still lacking. In humid tropical forests bryophytes are most abundant at high elevations in mountains above the level of cloud formation, where air humidity is generally high (Frahm and Gradstein, 1991), in contrast they are almost absent on low-land trees, except in valleys with early morning fog accumulation (Gehrig Downie *et al.*, 2011; Obregon *et al.*, 2009). Various expla-nations have been suggested for these patterns. One relates to the fact that bryophytes are poikilohydric, i.e., they are unable to balance their water potential on their own (León Vargas *et al.*, 2006; Sporn *et al.*, 2009). Therefore, air humidity has a direct effect on bryophytes by stopping their photosynthesis below approximately 95% relative air humidity (RH) (León Vargas *et al.*, 2006). Low levels of air humidity can, however, be easily tolerated by bryophytes due to their desiccation tolerance. After remaining dormant during periods of low air humidity, they can return to their normal metabolism within a few hours (Proctor *et al.*, 2007). Alternatively, it has been suggested that high temperatures limit the growth of bryophytes due to elevated respiration rates, especially during the night when there is no photosynthetic activity (Frahm, 1990a, b; Zotz *et al.*, 1996). Furthermore, the survival rate of desiccated bryophytes declines steeply with increasing temperatures, limiting the ability to recover from periods of low air humidity (Proctor, 1984).

Fig. 2.1. *Examples of estimates of bryophyte cover on trees in tropical forests. The percentage reefers to the area covered by bryophytes in relation to the whole area. To estimate the bryophyte cover in a 20 m × 20 m plot, the whole area of all branches within the plot was used.*

In the present study, assess the performance of epiphytic bryophyte cover as proxy for air humidity using microclimatic data recorded over the last decade in a series of field studies at 26 tropical forest sites.

2.3 Material and methods

2.3.1 Data acquisition

Climatic variables (air temperature, RH) were measured using Hobo Pro v2 temp/RH and Hobo Pro temp/RH data loggers (Onset Corp., MA, USA) at 14 sites in Ecuador, 6 in Costa Rica, and 6 in the Philippines at different elevations ranging from 40 m to 3500 m above sea level (Table 2.1). Data loggers were placed at 1.5–2 m height in the forest understorey for a measuring period of at least 12 months. Measuring interval was 1 h. Bryophyte cover was estimated visually by assessing the mean percentage of bryophyte cover on all larger canopy branches (minimum size: 5 cm branch diameter) of all trees within a plot of 20 m × 20 m surrounding the sites of the placement of the data loggers. As measure for the bryophyte cover, the percentage of area covered with bryophytes in relation to the uncovered area was used (Fig. 2.1). If necessary, binoculars were used to estimate bryophyte cover and to distinguish between bryophytes and vascular epiphytes. Canopy branches were used to estimate bryophyte cover, because bryophyte cover in the forest understorey is generally sparse and does not vary as conspicuously as in the canopy (Frahm and Gradstein, 1991; Wolf, 1993). On the other hand, we did not place the data loggers in the canopy due to problems of accessibility. However, at one of our locations (Costa Rica), we measured RH both in the understorey and in the canopy and found that both were strongly correlated across elevational and habitat gradients (6 plots, mean correlation $r = 0.92$, range $r = 0.83–0.96$, $p \leq 0.001$ across all plots) (Appendix 1), although RH tended to decrease more pronouncedly during sunny weather in the canopy.

2.3.2 Data analysis

Aside from air temperature and relative humidity we also incorporated the vapour pressure deficit (VPD), which was calculated using the Magnus equation (Magnus, 1844):

$$\mathrm{VPD} = e - ea\ [\mathrm{kPa}] \qquad (1)$$

with:

$$e=0.6108*\mathrm{EXP}(17.27*T[°\mathrm{C}]/(T[°\mathrm{C}]+237.3)) \qquad (2)$$

León Vargas *et al.* (2006) stated that mean annual values are of little significance in determining bryophyte distribution. Therefore, we used 28 different approaches to determine the influence of air temperature and air humidity on bryophyte cover. The basic parameters considered were elevation above sea level, mean daily temperature, mean daily RH, mean daily VPD, minimum daily temperature, minimum daily RH, maximum daily temperature, and maximum daily VPD. Because it has previously been recognized that high night time temperatures influence bryophyte physiology due to high respiration (Frahm, 1990a, b; Zotz *et al.*, 1996), we further conducted all measurements mentioned above separately for daylight hours and night times. Aside from these measurements, we also assessed the potential influence of mean daily maximum temperature, mean daily minimum RH, and mean daily maximum VPD which also could be potential limiting factors for bryophyte growth. In addition, we calculated the number of days per year in

Table 2.1 *Data sources and detailed description of the surveyed locations. Bryophyte cover estimation has been conducted at the beginning of the time period measured.*

Location	Elevation	Time period measured	Forest type	Coordinates	Source
Costa Rica					Kluge et al., 2006
La Selva	40 m	24.07.2002–23.07.2003	Lowland rainforest	N10°25'36.12" W84°0'42.84"	
Ceibo	650 m	24.07.2002–23.07.2003	Lowland rainforest, border zone to lower montane rainforest	N10°18'46.08" W84°4'26.04"	
San Rafael (3 Plots)	1800 m	24.07.2002–23.07.2003	Lower montane rainforest	N10°12'12.6" W84°5'35.88"	
Barva	2800 m	24.07.2002–23.07.2003	Upper montane rainforest	N10°8'9.24" W84°6'21.6"	
Ecuador					Unpubl. data
San Francisco	2545 m	01.11.2004–30.10.2005	Upper montane rainforest, Purdiaea	S03°59'28" W79°04'15"	
San Francisco	2455 m	01.11.2004–30.10.2005	Upper montane rainforest, Purdiaea	S03°59'23.0" W79°04'20.8"	
San Francisco	2500 m	01.11.2004–30.10.2005	Upper montane rainforest, Purdiaea	S03°59'33.6" W79°04'14.5"	
Tapichalca	2550 m	01.11.2004–30.10.2005	Upper montane rainforesT	S4°29'1.2" W79°8'16.2"	
Tapichalca	2650 m	01.11.2004–30.10.2005	Upper montane rainforest	S4°29'21" W79°7'4.8"	
Tapichalca	2650 m	01.11.2004–30.10.2005	upper montane rainforest	S4°29'21" W79°7'4.8"	
Tapichalca	2400 m	01.11.2004–30.10.2005	Upper montane rainforest	S4°29'21" W79°7'4.8"	
El Tiro	2575 m	01.11.2004–30.10.2005	upper montane rainforest	S3°59'22.2" W79°7'47.4"	
Jatun Sacha	500 m	13.04.2010–12.04.2011	Lowland rainforest	S1°4'2.28" W77°37'0.12"	
Jatun Sacha	1000 m	13.04.2010–12.04.2011	Pre-montane rainforest	S0°48'51.84" W77°34'39.36"	
Cordillera Galeras	1500 m	13.04.2010–12.04.2011	Lower montane rainforest	S0°49'40.08" W77°32'21.12"	
Cordillera Guacamayos	2000 m	13.04.2010–12.04.2011	Upper montane rainforest	S0°38'17.88" W77°50'23.64"	
Yanayacu	2500 m	13.04.2010–12.04.2011	Upper montane rainforest	S0°35'22.92" W77°53'53.88"	
Oyachachi	3500 m	13.04.2010–12.04.2011	Upper montane rainforest,	S0°11'35.88" W78°7'35.04"	
Philippines					Unpubl. data
Luzon, Mingan Mountains	1100 m, 1200 m	29.10.2009–28.10.2010	Lower montane rainforest	N15°25'31.15" E121°24'18.16"	
Mindanao, Mt. Kitanglad	1200 m	29.10.2009–28.10.2010	Lower montane rainforest	N8°8'37.63" E124°55'9.26"	
Mindanao, Mt. Hamiguitan	1100 m, 1200 m	29.10.2009–28.10.2010	Lower montane rainforest	N6°44'9.41" E126°10'1.51"	
Camiguin, Mt. Timpoong	1200 m	29.10.2009–28.10.2010	Lower montane rainforest	N9°11'1.73" E124°42'56.30"	

which the mean RH dropped below 95%, and in which the mini-mum RH dropped below 95%, to identify how many days per year the bryophytes experienced water stress. To check for an influence of the length of dry periods, we calculated the mean length of dry periods (given by the hours < 95% RH/year). We used linear regression analysis to access the effects of the climate variables on bryophyte cover. Additionally, we performed a Mixed Effects Linear Model with locality and elevation as random factors controlling for observer bias, local environmental conditions and time inconsistencies. Elevational level was included to take into account possible differences between lowland and high-land forests. Since the boundary between these two levels is rather arbitrary and varies from one site to another (Frahm and Gradstein, 1991; Kessler, 2000), we considered all sites above 1500 m asl as highlands. At this elevation, cloud condensation regularly occurs at all our study locations. All analyses were conducted using R (R Development Core Team, 2011) and the package “nlme” (Pinheiro *et al.*, 2011).

2.4 Results

The different measures of air humidity and temperature all yielded qualitatively identical results. For the sake of clarity we only report here in detail on the mean annual RH and temperature values, but this does not imply that we believe that these variables may be ecologically more important than others. Data on the other variables can be found in the supplementary materials (Appendix 2 and Appendix 3). RH showed a barely significant relationship with bryophyte cover for all study sites and all measured humidity variables (Fig.2.2), VPD also only showed a weak relationship with bryophyte cover (Appendix 2). Maximum temperature during the night, during daylight and within 24 h, showed moderate relationships with bryophyte cover. When we considered lowland and highland sites separately, RH and VPD showed strong relationships with bryophyte cover both in the lowlands and the highlands whereas mean annual temperature showed only a significant relationship with bryophyte cover in the lowlands and maximum temperature only in the highlands (Fig. 2.2, Appendix 2). For lowland sites, minimum daily RH showed the highest relationship with bryophyte cover ($R2 = 0.80$, $p < 0.001$), whereas in the highlands mean daily VPD and mean VPD during daylight (both: $R2 = 0.76$, $p < 0.001$) showed the highest relationships (Appendix 2). The Mixed Effects Linear Model, taking locality as random factor into account, also showed significant relationships of bryophyte cover to mean annual RH and temperature (Table 2.2). There was a slightly significant interaction between mean annual temperature and mean annual RH but both variables were not significantly correlated, neither across the entire dataset (r = 0.12, p = 0.55) nor when lowland (r = 0.48, p = 0.13) and highland (r = 0.13, p = 0.66) sites were separated. The Mixed Effects Linear Models using elevational level as random factor to test for differences in the intercept of the two models showed a significant difference of 5.6% RH in the intercept of both models (p < 0.001), with the highland sites having the lower intercept.

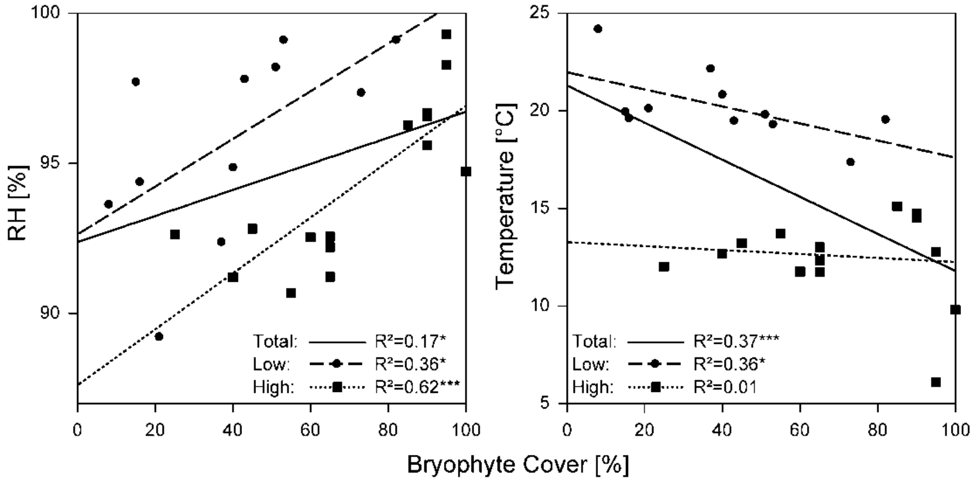

Fig. 2.2 *Relationship of visually estimated bryophyte cover on canopy tree branches with mean annual relative air humidity (RH) and mean annual temperature at 26 sample sites in tropical forests. The solid lines represent the linear fit for the entire dataset (Total), the dashed lines (circles) the fit for the lowland sites (Low) only and the dotted lines (squares) that for the highland sites (High) only (significance codes: *p < 0.05, ***p < 0.001).*

Table 2.2 *Mixed effects linear model relating visually estimated bryophyte cover on canopy tree branches to mean annual temperature and mean annual relative air humidity, with Locality as random factor.*

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
meanRH	1	3096.3	3096.3	16.7945	<0.001
meantemp	1	4496.7	4496.7	24.3899	<0.001
meanRH:meantemp	1	1177.0	1177.0	6.3842	<0.05
Residuals	19	3503.0	184.4		

2.5 Discussion

Our study confirms the intuitively appealing relationship of bryophyte cover on canopy branches and RH, as predicted e.g. by Frahm and Gradstein (1991), Gehrig Downie *et al.*

(2011), Kluge *et al.* (2006), Obregon *et al.* (2009), Sporn *et al.* (2009), and Wolf (1993). It also suggests that the visual estimation of bryophyte cover on branches can be used as a proxy for air humidity when detailed measurements are unfeasible. While the visual estimation may appear to be a rough, non-quantitative method, we consider that it is superior to almost any quantitative approach because of the high spatial variability of bryophyte cover in the tree canopy, with differences between tree species, tree individuals, different positions in the crown as well as in relation to branch diameter, inclination, and age (Wolf, 1993; Gehrig Downie *et al.*, 2011). To adequately sample this variability by climbing into the tree crowns to collect samples would require dozens if not hundreds of individual samples which is too time consuming to be useful as a proxy method. In such a situation, a visual estimation can average and integrate this variability. The only caveat with this method is observer bias and we suggest that within a study estimates should always be performed by the same person. We found that different measures of air humidity involving both RH as well as VPD showed similar patterns which is unsurprising because the calculation of VPD is mainly based on RH and both factors are strongly correlated ($r = -0.95$, $p < 0.001$). Our study is therefore unsuitable to discern which aspect of air humidity, e.g. mean values against maxima or minima, is ecological more meaningful. Disentangling this situation will require detailed eco-physiological studies. In the following, we therefore talk about air humidity in general, without any assumption as to which individual factors may be crucial. Perhaps the most important result of our study is that the relationship between bryophyte cover and air humidity was only evident when we separated the data by elevational levels. Same bryophyte covers in lowland sites on average showed ca. 5.6% higher mean annual RH than highland sites (Fig.2.2). In addition, mean annual temperature showed a significant relationship with bryophyte cover only in the lowlands and maximum temperature only in the highlands. While ecophysiological studies are needed to confirm our conclusions, we interpret these results as follows. We believe that while air humidity influences bryophyte growth everywhere, in the lowlands high temperatures pose an additional stress factor by increasing desiccation even at high levels of air humidity and by increasing nocturnal respiration (Frahm, 1990a, b; Zotz *et al.*, 1996). Accordingly, higher levels of air humidity are required to obtain similar levels of bryophyte cover in the low-lands than in the highlands. In the highlands, low temperatures are likely to be a limiting factor for plant growth. Short times of high temperatures therefore may have a positive effect of bryophyte growth by promoting plant growth as long as high humidity is sustained. We further found that measurements of air humidity considering only diurnal values showed higher correlations with bryophyte cover than nocturnal values. This suggests that air humidity has a stronger effect on bryophyte growth when the plants are photosynthetically active than during the night when they are dormant. Overall, determination coefficients of RH and VPD (R2 values) were reasonably high (0.36–0.80), showing that much variation of bryophyte cover could be accounted for by air humidity. Other factors might play a role here, for example the fact that bryophyte cover was estimated by different people, or differences in vegetation structure. The data was collected during different years at the different locations, and climatic anomalies like the El Niño effect might have altered the observed pattern to some degree. In any case, this effect would be taken into account by our mixed effects model, in with locality–and hence measurement year–as a random factor. But even taking these effects into account, relative humidity and temperature still showed a significant impact on the bryophyte cover. Another factor, especially in the highlands, might be that our estimation of bryophyte cover only took into account the branch surface area covered by bryophytes, but not the thickness of the bryophyte layer or pendulous live forms, which can be quite abundant at high elevations (León Vargas *et al.*, 2006). Therefore, total bryophyte biomass might be strikingly different especially at high levels of bryophyte cover (>90%) when pendulous life forms are present and when liverworts have grown into thick carpets (Mandl *et al.*, 2010; Wolf, 1993).

2.6 Conclusions

Bryophyte cover can be used as a reasonably reliable proxy for air humidity for studies, where levels of air humidity vary considerably, where approximate assessments of air humidity are sufficient, and where microclimatic measurements cannot be con-ducted due to financial or logistical limitations. We caution against comparing bryophyte cover estimates across extensive elevational gradients, between different geographical regions, and obtained by different field workers. We finally suggest that the estimation approach might be improved by including estimates of the thickness of bryophyte mats and the abundance of pendulous bryophytes.

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Chapter 3

Is fern diversity highest at the equator? Diversity patterns of ferns along two elevational gradients in Ecuador

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3.1 Abstract

We document the first elevational fern transects at two locations in Ecuador (Napo and Pichincha) close to the Equator. The hump-shaped species richness patterns confirm the notion that fern diversity is primarily driven by energy-related variables (temperature and humidity), and that especially a low annual variability of these factors favors species rich fern communities. These findings are set into context of numerous elevational gradients known so far from the Neotropical mountain range between Bolivia and Mexico. We analyzed whether elevational species richness pattern change from the equator towards subtropical regions to test the hypotheses that (a) species composition patterns should be similar between gradients despite different species pools, and that (b) due to gradually changing climatic conditions with increasing distance from the equator species richness of whole gradients should gradually decline, and (c) the elevation ranges of highest species richness should gradually decline. We find that the taxonomic composition is strikingly similar between regions, and that elevational richness patterns and overall richness are virtually equal along the latitudinal gradient, except for abrupt declines at the transitions from tropical to subtropical climates. This may suggest that within tropical habitats species richness of ferns is bounded by the number of species that can co-occur and that the available niche space is saturated.

Key words: elevational gradient, Neotropical mountain range, ferns, species richness, equator, climatic variables.

3.2 Introduction

The latitudinal gradient of increasing species richness from the boreal regions towards the tropics is among of the best documented richness pattern in ecology, but the causes determining the observed patterns are still discussed controversially (Rohde, 1992; Rosenzweig, 1995; Gaston and Blackburn, 2000; Hillebrand, 2004; Ricklefs, 2007). In addition to this classical richness gradient, patterns of species richness along elevational gradients have also received considerable attention in the last decade (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 relative short distances (few tens of km). Relative to the latitudinal gradients from the equator to the poles, they have the advantage not to be as strongly influenced by dispersal limitation (due to shorter distances) and that they are frequently replicated (Lomolino, 2001).

Trees are the main structural component of tropical forests (Gentry, 1988, 1995). However, the majority of plant species in tropical forests belong to herbaceous (both terrestrial and epiphytic) life forms (Gentry and Dodson, 1987; Ibisch, 1996; Balslev *et al.*, 1998). Additionally, due to the large size of trees, often low population densities, and difficulties of species identifications, trees present methodological sampling problems and are not suitable for answering many questions in tropical ecology (e.g. Jones *et al.,* 2008). As a result, numerous researchers have focused on non-tree life forms to study the diversity patterns, ecology and biogeography of tropical forests (e.g. Poulsen and Pendry, 1995; Tuomisto *et al.,* 1995; Kluge *et al.,* 2008; Kessler *et al.,* 2011; Willinghöfer *et al.*, 2012).

In humid tropical forests, ferns and lycophytes (henceforth called ferns for simplicity) 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; Ibisch, 1996; Balslev *et al.,* 1998; Linares-Palomino *et al.,* 2009). Ferns are widely distributed across the world with about 11.000 species (Smith *et al.*, 2006), but their diversity varies between regions (Kessler *et al.,* 2011). Ferns are most diverse in tropical forests, especially in montane habitats (Moran, 2004; Kreft *et al.,* 2010; Kessler *et al.,* 2011). Numerous studies have shown that fern species richness commonly shows a hump-shaped richness pattern with a peak at mid-elevations (Hemp, 2001, 2002; Kessler, 2000, 2001a, 2001b; Bhattarai *et al.*, 2004; Krömer *et al.,* 2005; Kluge *et al.*, 2006, 2008). A global comparative analysis recently showed that this is 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 is roughly 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 so far. On a national scale, Ecuador harbors about 1400 fern species, although with an area of approximately 283.000 km² it is the smallest of the Andean countries (Jørgensen and León-Yánez, 1999; Ulloa Ulloa and Neill, 2005; Neil and Ulloa Ulloa, 2011). A comparison to other Andean countries shows that this overall richness is exceptionally high (Peru: 1200 species: Smith *et al.,* 2005; Bolivia: 1163 species: Soria-Auza and Kessler, 2007). As a result, one might expect that local fern diversity should peak in Ecuador.

For Ecuador, the highest concentration of fern species is assumed to be in cloud forests between 1500 m and 3000 m (Navarrete, 2001). However, the few detailed studies in Ecuador concerning Oyacachi, Quijos and Alto Aguarico (Øllgaard and Navarrete, 2000) used an exceptional transect method which cannot be compared to other quantitative studies of ferns diversity, and an only partly published transect in Pichincha (Kessler *et al.,* 2011). Another detailed study in Podocarpus National Park (Kessler and Lehnert, 2009a, b; Mandl *et al.,* 2010), where species richness declines more or less linearly with elevation between 1000 m and 3000 m is not comparable with other regions due to the unique geology and ecology of that area.

In the present study, we establish the first suitable fern transects on the equator, in Napo on the eastern (Amazonian) slope of the Andes, and in Pichincha on the western (Pacific) slope. The Napo transect presents entirely new data, whereas the Pichincha transect was already included in a comparative analysis by Kessler *et al.* (2011), but is reported here for the first time as a whole. In this study, we first evaluate the elevational patterns of species richness of terrestrial and epiphytic ferns species along both elevational gradients and relate these patterns to climatic variables (temperature, relative humidity, and rainfall) in order to assess their relative importance in driving fern richness patterns. Second, we set our results in context to comparable data from other Neotropical elevational gradients along a latitudinal gradient spanning from Mexico to Bolivia. Specifically, we set out to test the hypothesis that, in common with many other groups of organisms, species richness of ferns in the Andes peaks at the equator and declines with increasing distance. Specifically, we test hypotheses that (a) species composition patterns should be similar between gradients despite different species pools, and that due to gradually changing climatic with increasing distance from the equator (b) species richness of whole gradients should gradually decline, and (c) the elevation of highest richness should gradually decline.

3.3 Material and Methods

3.3.1 Study areas

The Napo transect was studied in 24 plots within eight elevational steps of about 500 m in elevational distance each on the eastern Andean slope in Napo province, Ecuador (Fig. 3.1, Table 2.1). This gradient spans localities from lowland forests in the vicinity of Rio Napo (Reserva Jatun Sacha) at 400 m via 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 timberline at 4000 m. These sites were selected because they harbour well preserved forest habitats along the whole gradient from lowlands up to the treeline ecotone.

The depth of the organic layer and plant-available P concentration are increasing with elevation, whereas N availability tends to decrease with elevation. Also, Ca, Mg and K in the organic layers increase with elevation as well, the acidity of the organic layer is moderately to high (data from 500 m to 2000 m came from Unger *et al.*, 2010, 2012). Concerning to the forest structure (up to 2000 m), the aboveground biomass is not decreasing with elevation (Unger, 2012).

The Pichincha transect covers 22 plots between 450 m and 3600 m on the western Andean slope in Pichincha province (Fig. 3.1, Table 3.1).

Data from studies realized in Mexico (one transect), Costa Rica (one transect) and Bolivia (three transects) were used to compare several elevational gradients at different latitudes in the Neotropics (for sources of data see Table 1).

3.3.2 Climatic measurements

Along both gradients we collected data on temperature and precipitation as well as their respective variability (seasonality: variation coefficient). Additionally, we assessed ambient humidity. Temperature and its variability in Napo were measured between October 2009 until June 2011with 3 HOBO Pro loggers at each elevational step of 500 m. The loggers were positioned at 2 m height on tree trunks and covered by a plastic cap to avoid direct rain and sunlight. Measuring frequency was set to a high temporal resolution (every 30 minutes) to account for unusual outliers (minimum measuring duration was 12

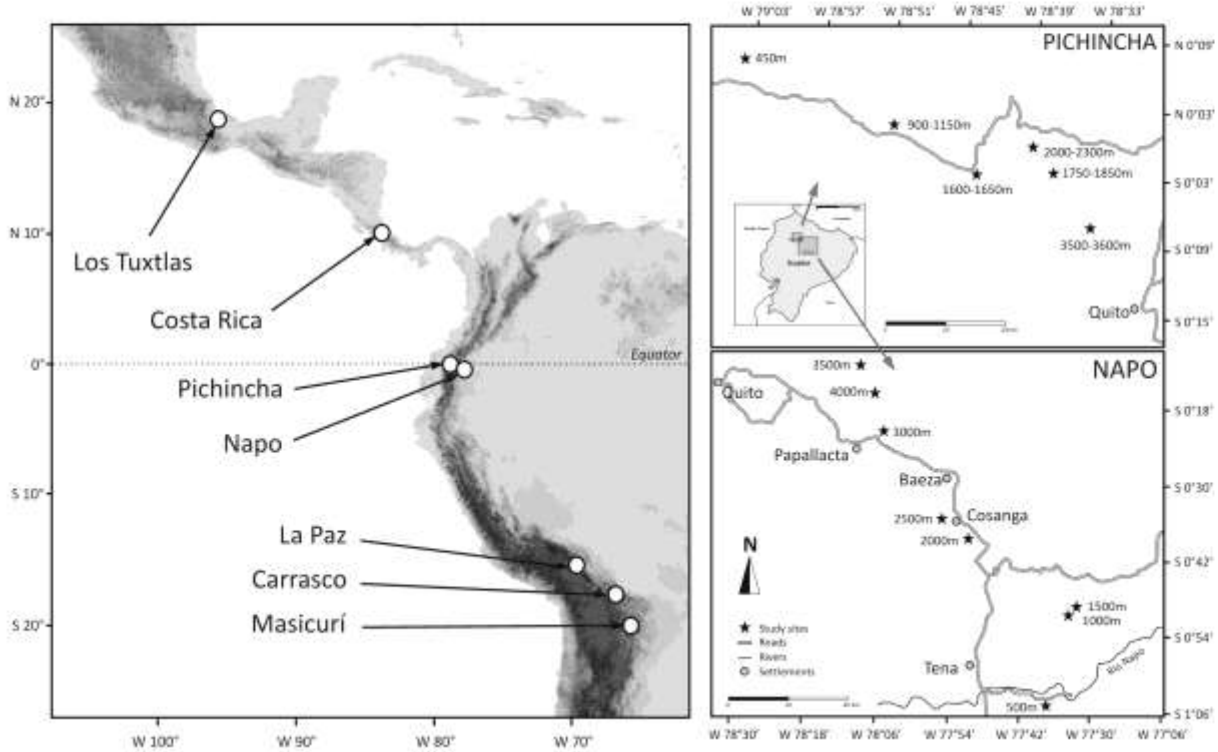


Fig. 3.1 *Study regions in the Neotropics (circles in continental map) and the study sites at the Equator (detailed maps): Pichincha and Napo province and their locations in Ecuador (insets). Positions of all study locations along the Ecuadorian transects are given with elevation.*

Table 3.1 *Location and data source of the seven elevational gradients along the latitudinal gradient in the New World included in this study.*

Locality	Abbreviation used in this study	Elevation sampling range (m)	Coordinates	Data source and time of collection
Mexico, Los Tuxtlas, Veracruz	TUXT	140 - 1675	95° 12' - 95° 04' W 18° 32' - 18° 35' N	T.K. 2005-2006 (unpubl.)
Costa Rica, Braulio Carrillo National Park and Cerro de la Muerte	CR	100 - 3400	83° 41' - 67° 55' W 9° 33' - 10° 24' N	J.K. 2001-2002; Kluge and Kessler (2005)
NE Ecuador, Jatun Sacha to Oyacachi, Napo	NAPO	400 - 4000	78° 05' - 77° 36' W 0° 14' - 1° 04' S	This study
NW Ecuador, Felipe Carrillo Puerto to Volcán Pichincha, Pichincha	PICH	450 - 3600	78° 35' - 79° 05' W 0° 07' N - 0° 08' S	This study
N Bolivia, Pilón Lajas to Cotapata, La Paz	LAPAZ	350 - 3500	67° 07' - 67° 54' W 15° 05' - 16° 18' S	M.K. et al., Jun-Nov 1997 (unpubl.)
C Bolivia, Carrasco National Park, Cochabamba	CARR	200 - 3750	83° 44' - 83° 41' W 16° 11' - 16° 17' S	M.K. et al. 1996-1997; Kessler (2001c)
C Bolivia, Masicurí Valley, Santa Cruz	MASI	500 - 2450	63° 42' - 63° 54' W 18° 40' - 19° 03' S	M.K. et al. May-Jun 1996; Kessler (2000)

month). We compared our measured data with data for the same localities extracted from the WorldClim data bank (Hijmans *et al.*, 2004) using a correlation analysis. No data loggers were used along the Pichincha transect. Here we used data from the WorldClim data bank (Hijmans *et al.*, 2004). For assessing the ambient humidity at each elevational belt in Napo, we used the on-site measured relative air humidity logger values by processing the original data as follows: since the daily mean values from Hobo data loggers in tropical forest are almost 100%, the amount of dry spells is for hygrophilous organisms like many ferns more informative, because these short-time dry spells may cause severe damages for example to thin-structured filmy ferns (Hymenophyllaceae). Therefore, instead of taking daily averages, we expressed the relative frequency of values below 60%, 70%, and 80% relative humidity as a Humidity Index (HI). For Pichincha no such data are available, so that as in other comparable studies before (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 data bank (Hijmans *et al.*, 2004), since there are no climate stations in the vicinity of the study gradients.

3.3.3 Vegetation sampling

Along the Napo transect, fern diversity was sampled on three permanent plots of 400 m^2 at each elevational step, resulting in a total of 24 study plots, whereas along the Pichincha transect, we inventoried 22 plots of the same size at more irregular intervals between 450 m and 3600 m. This plots size has previously been used for surveys of local fern diversity (e.g, Kessler, 2001b; Kluge *et al.*, 2006), because it is large enough to be representative, but also small enough to be ecologically homogeneous and to allow rapid and efficient surveys (Kessler and Bach, 1999). All plots were placed in zonal forest avoiding special geomorphological features like deep valleys and exposed ridges, as well as special forest structures like canopy gaps. Within these plots, we separated species lists for both major fern life forms, terrestrials and epiphytes. 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 for each life form. All species were collected for identification at the herbarium of the Pontificia Universidad Católica del Ecuador (QCA) and by specialists for difficult groups.

3.3.4 Data analyses

To assess the relative impact of climatic variables on the distribution of species richness, we used multiple linear regression models. The best model was chosen by inspection of 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):

$$AICc = AIC + (2k(k + 1))/(n - k - 1)$$

with n as the number of observations and k 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 as ‘best model’. However, often differences of the AICc values (Δ_i) between nested models are small, and the sole acceptance of a single model may lead to wrong conclusions about the performance of the parameters (Wagenmakers and Farrell, 2004). Models with $\Delta_i < 2$ are supported to have substantial support, models with $\Delta_i > 4$ should definitely be excluded (Burnham and Anderson, 2002). Based on Δ_i, the Akaike weight w_i quantifies the plausibility that a given model i being actual better than the next model within the set of all models. With these weights we assess the relative importance of all variable across all models by summing the weights of all competing models including the respective variables (Burnham and Anderson, 2002), and the sums for the variables can then be compared. We report on the best models for all species and separated for life forms, as well as on the sums of w_i of all parameters within significant models with $\Delta_i < 4$ (‘model averaging’; see Burnham and Anderson, 2002). For all models, we report on the standardized coefficients and their *p*-value of all variables which entered the respective model, because they inform about the influence of each variable within the model, as well on adjusted R^2, p, AICc, ΔAICc, and model weight w_i.

Multimodel inference and model averaging were performed with the R package ‘MuMIn’ (Barton, 2010) within the statistical platform R (R Development Core Team, 2011).

To assess the floristic and compositional similarity between all pairs of elevational transects along the latitudinal gradient on the basis of family richness and distribution, we (i) compared the numbers of species in each family in every pair of gradient by applying

Pearson's R ("R is high when the same fern families are species rich and species poor respectively in both compared transects"), and (ii) compared the elevations of maximum species richness likewise ("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 applying loess models to elevational distribution of species numbers of families.

3.4 Results

3.4.1 Climate variables

Along the Napo transect, temperature regularly declined with elevation, the lapse rate was 0.56°C per 100 m elevational distance (Fig. 3.2a, c), which fits well to the data of the *WorldClim* databank ($R = 0.98$, $p<0.001$). 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 (Fig. 3.2c). Likewise, relative air humidity showed the strongest influence of dry spells towards both ends of the gradient (Fig. 3.2b). Accordingly, our Humidity Index showed a unimodal relation with elevation (Fig. 3.2d). Highest rainfall values occurred between 1000 m and 2000 m, just below the condensation layer (Fig. 3.2e).

Along the Pichincha transect, temperature showed virtually the same pattern as on the Napo transect (Fig. 3.2c), whereas rainfall values were considerably lower and lacked a pronounced hump at low elevation compared to the Napo gradient (Fig. 3.2e).

3.4.2 Species richness

Along the Napo transect, we found a total of 91 of terrestrial fern species in 34 genera and 20 families (Appendix 4). The most abundant species were *Diplazium costale* (Sw.) C. Presl, *Cyclodium trianae* (Mett.) A.R. Sm. and *Maxonia apiifolia* (Sw.) C. Chr. (Appendix 4). For terrestrial taxa, the families with highest numbers of species were Dryopteridaceae with 16 species, Cyatheaceae with 13 and Woodsiaceae with 8 (Appendix 5). The largest fern genus was *Cyathea* with 11 species, followed by *Thelypteris* and *Diplazium* with 8 species each. Dryopteridaceae and Thelypteridaceae were found along the entire elevational gradient from 500 m to 4000 m (Appendix 4), while most of the other families showed an elevation preference. This was especially the case for Lindsaeaceae, Metaxyaceae, Ophiglossaceae, and Schizaeaceae. Among the epiphytic species, we found about 259 species of epiphytes distributed in 49 genera and 21 families based on preliminary identifications and sorting to morphospecies (Appendix 5). The most species rich families were Polypodiaceae (90 spp., mainly from the former family Grammitidaceae) and Dryopteridaceae (77 spp., mainly *Elaphoglossum* with 68 spp.).

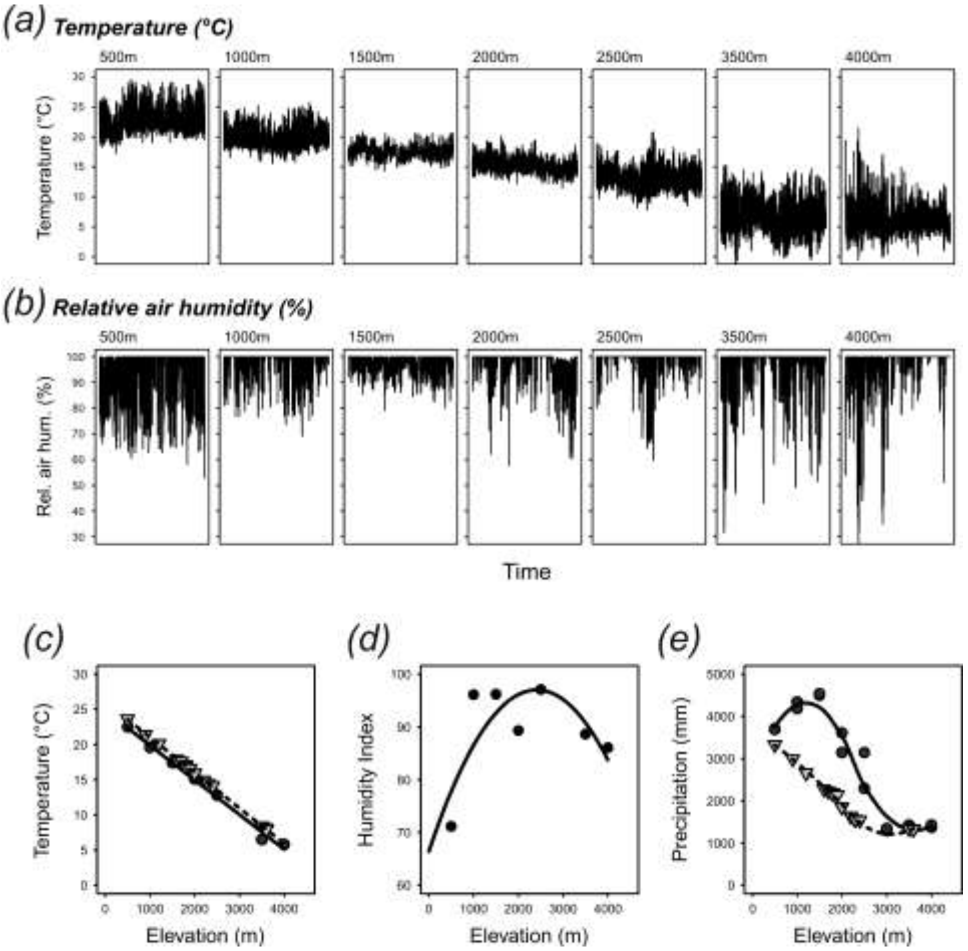


Fig. 3.2 *Environmental variables along the Napo and Pichincha elevational gradients. Course of (a) temperature and (b) relative air humidity from selected data loggers at each elevational step, based on values from 30-minute-intervalls. (c) Elevational lapse of mean annual temperature, lapse rate is 0.56°C/100m (circles and continuous line: Napo; triangles and dashed line: Pichincha). (d) Humidity Index based on values for relative air humidity (%) shown in (b); for further details of calculation see text. (e) Mean annual precipitation (mm) along the elevational gradient for each plot obtained from the WorldClim data bank (Hijmans et al. 2004). For (c) and (e): circles and continuous line: Napo; triangles and dashed line: Pichincha.*

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 (Appendix 5). 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 (Appendix 5).

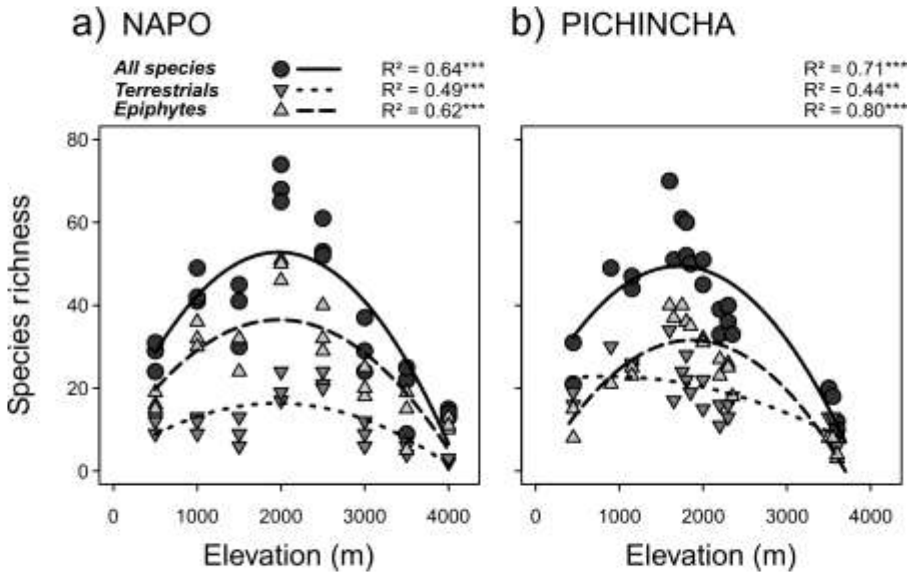


Fig. 3.3 *(a) Species richness along the study elevational gradient in the Napo province. (b) Species richness along the elevational gradients in Pichincha province based on data from Kessler et al. (2011). Different symbols and trend lines (quadratic models) as well as* R^2*-values of model fit are given for all species and major life forms (terrestrials and epiphytes).*

Along the Napo transect, species richness of all, terrestrial, and epiphytic species showed clear hump-shaped patterns with elevation (Fig. 3.3a) 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 (Fig. 3.3b).

Table 3.2a *Results of multiple regression analyses and Multi-Model Inference of the relationship between climatic variables and fern species richness along the elevational gradient in Napo. 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 considered models; all models are given with delta AICc <4; var.imp: variable importances 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.*

		Beta coefficients (standardized)					**Model results**			
Dependent variable	**Model**	**hum.index**	**prec**	**var(prec)**	**temp**	**var(temp)**	**R^2-adj**	**AICc**	**Δ AICc**	**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***		–0.26	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	–0.34*	0.78***	124.9	3.92	0.11
	var.imp	*1.00*	*1.00*	*1.00*	*0.12*	*1.00*				
EPIPYHTES	1	0.21		0.64**			0.51***	160.8	0.00	0.30
	2	0.30		0.58**		–0.26	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*				

Table 3.2b *Same as Table 3a for elevational gradient in Pichincha.*

		Beta coefficients (standardized)					**Model results**			
Dependent variable	**Model**	**hum.index**	**prec**	**var(prec)**	**temp**	**var(temp)**	**R²-adj**	**AICc**	**deltaAICc**	**weight**
ALL SPECIES	1		0.93	-2.20	2.67	-1.19	0.83***	157.5	0.00	0.26
	2			-3.14	3.98	-0.52	0.81***	157.9	0.45	0.21
	3		2.06			-2.04	0.78***	158.5	1.05	0.15
	4	0.15		-2.99	3.84	-0.55	0.82***	158.6	1.13	0.15
	5		1.53		0.33	-1.76	0.79***	159.9	2.37	0.08
	6		1.78	0.19		-1.91	0.78***	161.1	3.64	0.04
	7	0.08	0.69	-2.36	2.93	-1.03	0.83***	161.2	3.73	0.04
	var.imp	*0.20*	*0.62*	*0.75*	*0.79*	*1.00*				
TERRESTRIALS	1		1.70			-1.34	0.52***	139.7	0.00	0.37
	2			-2.83	3.42		0.48***	141.5	1.73	0.15
	3	-0.03	1.72			-1.36	0.49**	143.1	3.35	0.07
	4		1.63		0.05	-1.30	0.49**	143.1	3.38	0.07
	5		1.73	-0.02		-1.36	0.49**	143.1	3.39	0.07
	var.imp	*0.09*	*0.79*	*0.31*	*0.31*	*0.79*				
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	-0.97	0.93***	126.8	3.19	0.09
	var.imp	*0.55*	*0.36*	*1.00*	*1.00*	*1.00*				

3.4.3 Species richness and climate variables

Relating the patterns of species richness of both the Napo (Table 3.2a) and the Pichincha transect (Table 3.2b) to climate variables, we found that all climatic variables were important to a variable extent. 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, along both gradients the variability of temperature and precipitation performed better than the respective raw values (variable importance due to model averaging equal or close to 1), and in Napo moreover humidity considerably added explanatory power to the models. With respect to life form, in Napo the terrestrials and in Pichincha the epiphytes showed clearer patterns than the respective other life forms.

3.4.4 Comparison of elevational transects

The elevational richness patterns of the seven transects in our comparative study showed similar hump-shaped patterns along the five central transects and also hump-shaped but noticeably lower richness curves along the southern- and northernmost transects (Fig. 3.4). The residuals of species richness between the individual transects and the overall richness trend derived from all transects in combination (bold regression line) 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 not distinguishable (Fig. 3.5). Only the Bolivian transects close to the southern limit of tropical cloud forests had slightly lower values than the other four transects (Fig. 3.5).

The number of species per family was highly correlated among the transects (R-values of pairwise 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 (Masicurí or Los Tuxtlas) were involved (Fig.3.6).

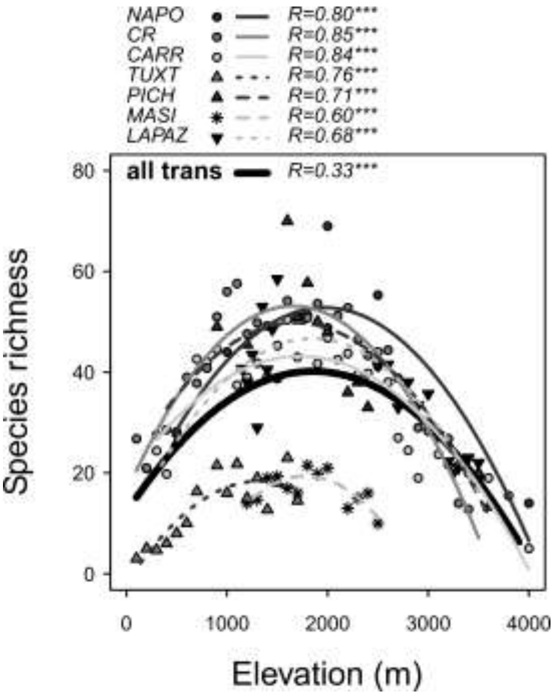


Fig. 3.4 *Patterns of species richness of seven elevational gradients in Napo and Pichincha (NAPO, PICH, Ecuador), Costa Rica (CR), Carrasco and Masicuri (CARR, MASI, LAPAZ Bolivia) and Los Tuxtlas (TUXT, Mexico). Different symbols and trendlines (quadratic models) as well as R^2-values of model fit are given (**p < 0.01; ***p < 0.001). Bold line represents regression line of all gradients pooled.*

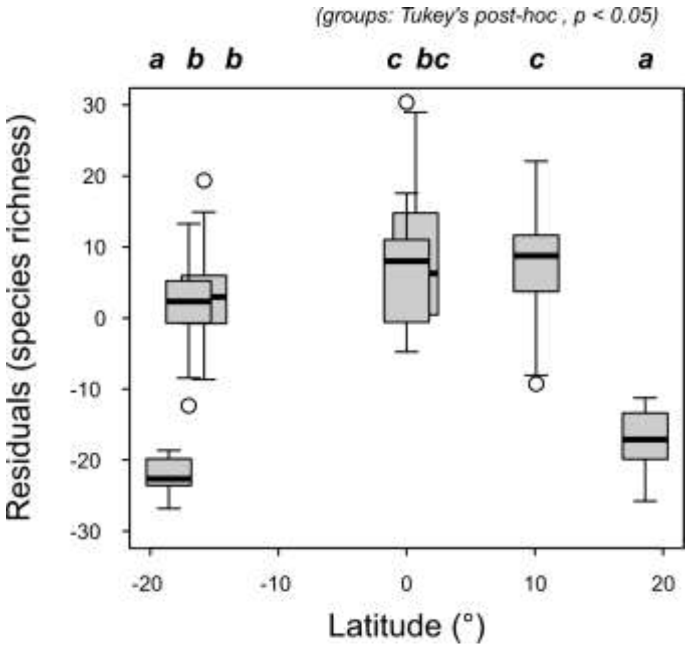
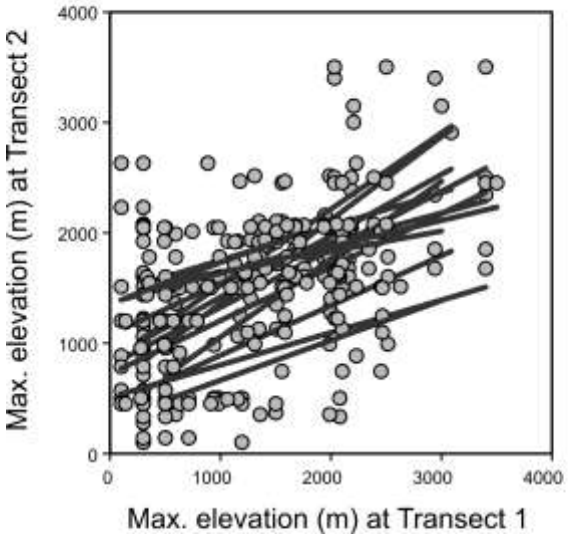


Fig. 3.5 *Boxplots of residuals of species richness of ferns along all seven gradients with respect to model fit of all gradient pooled (bold line in Fig. 3.4). Boxplots are arranged along latitudinal gradient with southernmost transect (Masicurí) on the left and northernmost transect (Los Tuxtlas) on the right side.. Letters above the plot indicate significant different groups following ANOVA and Tukey posthoc test (p < 0.05).*



Trans 1	Trans 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*

Fig. 3.6 *Pairwise Pearson correlations of gradients with respect to elevations of highest species richness within families for six elevational gradients; each dot represents a family for a pairwise comparison. Gradient La Paz was excluded because of gaps in the elevational coverage. Trend lines with R and p-values are given.*

3.5 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 for both major life forms. With our on-site climatic measurements of temperature and ambient humidity, and precipitation data from global climatic models (Hijmans *et al.*, 2004), we were able to simultaneously characterize the elevational climatic conditions for the gradients, and the relations of both patterns fit very well to general hypotheses about climatically driven species richness distributions, including ferns.

3.5.1 Climatic conditions and fern diversity

As in other mountain ecosystems, temperature declines linearly with elevation whereas annual sums of precipitation shows a pattern typical for tropical mountains with highest values between 1000 m and 2000 m, just below the mayor 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-time drought events may cause irreversible damage to ferns since these are not able to actively control their water balance in the manner of 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 certain absolute level. Thus, the variability of humidity and temperature may provide more information to characterize the relation of 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 turn, in this study region around 1500 m to 2000 m, harbored 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 elevation has often been interpreted as reflecting these ambient conditions of a balanced climate without extremes like drought at low elevations and frost at high elevations (Kessler, 2001b; Hemp, 2002; Battarai *et al.*, 2004; Krömer *et al.*, 2005; Kluge and Kessler, 2007; Kessler *et al.*, 2011). Consequently, all regression models, the resulting averaged models and variable importance in our study showed that balance-related climatic parameters (variability of temperature and rainfall as well as our humidity index) had a better performance than the averaged parameters. However, the congruence of a climatic setting and species richness distributions is appealing and expectable (Moran, 2004), but does not explain any mechanism. There are two mechanistic possibilities. First, the influence of climate may be indirect, as it is possibly related to ecosystem productivity, which in turn is supposed to drive 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.

3.5.2 Comparison of the elevational transects

In general, we found a surprising similarity of the richness and taxonomic composition of the seven elevational transects spanning the latitudinal range between 18°N and 18°S. Only the northernmost and southernmost transects, located at or even slightly beyond the transition from tropical to subtropical conditions showed significantly reduced species numbers, which might be caused by drier, colder and harsher climatic conditions of these areas. However, these two transects show similar trends of species richness as well as comparable taxonomic composition.

Excluding these marginally tropical transects, we found that within the tropics there is basically no latitudinal diversity gradient at the local scale. At the regional scale, Ecuador has a higher species density of ferns than Peru and Bolivia. Thus, Ecuador has about 1400 fern species on 283.000 km² (Jørgensen and León-Yánez, 1999; Ulloa Ulloa and Neill, 2005; Neil and Ulloa Ulloa, 2011), whereas the other two countries have about 1200 species on well over 1 million km² each (Smith *et al.*, 2005; Soria-Auza and Kessler, 2007). The latitudinal decrease of 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 the high regional diversity of ferns in Ecuador does not translate to the local scale studied here. This may suggest that within the tropical habitats studied by us, species richness of ferns is bounded by the number of species that can co-occur and that communities are saturated, perhaps due to a preemption of available niche space. On the other hand, the discrepancy of regional and local richness patterns of ferns suggests that spatial species turnover (i.e., beta diversity), for example between different habitats (Kessler and Lehnert, 2009a, b; 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 is currently not available.

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. Thus, on all transects the most species rich families are Polypodiaceae and Dyropteridaceae, that together comprise roughly half of the total species richness along each study gradient, usually followed the by filmy ferns (Hymenophyllaceae). Given that all these groups display distinct morphological features, which reflect certain ecological adaptations (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 forest. These commonalities extend even 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).

In conclusion, we found that at the local scale fern assemblages along tropical elevational gradients show a high degree of similarity within mountains 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 only 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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Chapter 4

Species richness-productivity relationships of ferns along a tropical elevational gradient

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4.1 Abstract

The species richness-productivity relationship (SRPR), by which habitats or ecosystems with higher productivity harbour more species, has been documented both on regional and local scales. Yet, its generality and biological meaning continue to be debated, partly because of methodological problems in documenting the SRPR and in unravelling the underlying mechanisms. In the present study, we evaluated the SRPR and four mechanistic hypotheses using terrestrial ferns along an elevational gradient (500-4000 m) in Ecuador. In 18 study plots, we measured aboveground biomass increment of 6175 fern individuals from 91 species over two years. In addition, we estimated ecosystem productivity by calculating actual evapotranspiration from climatic data as well as from aboveground biomass increment measures of 560 trees. Overall, we found that fern diversity was related to the productivity of the fern assemblages, but only marginally to that of the ecosystems. Along the elevational gradient, we found a positive SRPR that appears to be determined by an increase in the number of fern individuals and by niche availability. When comparing plots within elevational belts, we found a negative SRPR that is likely driven by interspecific competition. We thus argue that at both spatial scales of our study, fern diversity appears to be limited by the number of available niches and competition to occupy these niches. Our study presents the first evidence that energy availability and competition affect the diversity of tropical herb assemblages at the local scale.

Key words: abundance; actual evapotranspiration; altitude; Andes; diversity; ecosystem productivity; energy availability, interspecific competition.

4.2 Introduction

Biologists have long been intrigued by the relationship between species richness and productivity (the rate of generation of biomass in an ecosystem) within ecological communities. Already Charles Darwin (1859) stated that “it has been experimentally proved, that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater weight of dry herbage can be raised in the latter than in the former case”. This positive relationship has since been confirmed by numerous experimental and observational studies. Today, is generally accepted that, all else being equal, communities of higher species richness tend to have higher levels of biomass production, i.e., higher productivity (Balvanera *et al.*, 2006, Cardinale *et al.*, 2006).

The causality of the species richness-productivity relationship can, however, also be assessed from the opposite perspective. Since the pioneering insights of Wallace (1878), an increasing number of researchers have proposed and documented that habitats or geographical areas with high levels of ecosystem productivity or energy input, i.e., with high temperatures and high levels of solar radiation, tend to have higher levels of species richness, if not limited by other factors such as water or nutrient availability (e.g. Hutchinson, 1959; Pianka, 1966; Odum, 1969; Wright, 1983; Wilson and Keddy, 1988; Mittelbach *et al.*, 2001). Although this species richness-productivity relationship (SRPR) has been documented both on regional and local scales, and has been considered to be one of the few universal ecological laws (Huston, 1994; Rosenzweig, 1995), its validity and biological meaning continue to be debated, partly due to the following reasons:

(i) The documentation of the SRPR is challenging. One aspect is obtaining the appropriate measure for productivity. In theoretical considerations, net primary productivity (NPP), i.e., in terrestrial and most aquatic ecosystems the energy assimilated by the plants and made available to themselves as well as to consumers at higher trophic levels, is most often considered to be the driving variable. However, in field studies productivity measures are mostly restricted to surrogates of NPP (Waide *et al.*, 1999). This includes indirect variables such as, e.g. rainfall and Actual Evapotranspiration (AET), or direct variables such as biomass or foliage area. Yet, even measures of standing aboveground biomass are not an unambiguous measure of NPP, as, e.g. forests can have the same standing biomass at very different levels of energy input and biomass turnover (Phillips *et al.*, 1994, Whittaker and Heegaard, 2003; Keeling and Phillips, 2007). Thus, biomass increment within a given time period is a more realistic measure of energy availability within an ecosystem (Gaston, 2000; Chase and Leibold, 2002; Whittaker and Heegaard, 2003), but this approach is rarely followed due to the difficulty of obtaining such data. Accordingly, coupled measures of NPP and richness at the same scale are rare (Waide *et al.*, 1999, Whittaker, 2010).

(ii) The majority of studies to date have used productivity measures at ecosystem level and related these to the species richness of some group of organisms, i.e., of only a (usually minor) part of the diversity of the ecosystem's biota (Groner and Novoplansky, 2003). This approach implicitly assumes that the focal group of organisms of a given study uses (or has access to) an equal amount of total energy along the whole productivity range (Gaston, 2000; Chase and Leibold, 2002). If this assumption is not valid, relating total energy to a fraction of the whole biota is misleading (Mittelbach *et al.,* 2001). It is thus desirable to either assess both productivity and species richness at the ecosystem level or, alternatively, measure the fraction of energy exclusively used by the organism of interest (Oberle *et al.,* 2009, Axmanová *et al.,* 2012). Since neither approach is commonly followed, Waide *et al.* (1999) concluded that when productivity and species richness are measured at different scales, there might arise a "tangle of cause and effect", and that there are no studies "relating diversity directly to productivity (...) to unravel this tangle".

(iii) The assessment of the SRPR is further complicated by issues of spatial scale. Local scales, where species interact so that factors such as competition or facilitation play a role, might show different relationships than regional scales, where species richness may be more related to aspects such as habitat diversity (Whittaker, 2010). These problems have created a situation where currently there is no consensus as to how the generalized SRPR looks like (monotonically increasing or hump-shaped) or even whether such a general relationship exists (Rosenzweig and Abramsky, 1993; Waide *et al.,* 1999; Mittelbach *et al.,* 2001; Gillman and Wright, 2006; Whittaker, 2010).

(iv) The SRPR can also be influenced by population level processes, e.g. when non-self-sustaining populations from a regional species pool inflate local species richness (Grytnes *et al.,* 2008; Kessler, 2009; Kessler *et al.,* 2011). The contribution of such sink populations to productivity is likely to be small, although it has so far not been quantified. Yet, if sink populations alter species richness or productivity patterns, the observed SRPR may conceivably also be modified.

(v) The final complication arises because little is known about the mechanisms that may answer the question "how can increasing energy materialize into more species?" (Willig *et al.,* 2003; Mönkkönen *et al.,* 2006). Literature on the SRPR refers only in very few cases to such causal mechanisms, probably because of the belief that they were understood. For example, Rosenzweig and Abramsky (1993) stated that the relation of richness and energy "troubles no one": a poor environment does not provide many resources for rare species, and they become extinct. This simplistic view has proven to be misleading, as the few studies addressing the SRPR reported conflicting results (Willig *et al.*, 2003; Evans *et al.*, 2005). Evans *et al.* (2005) reviewed the set of potential mechanisms that may explain the causality of richness and energy and evaluated a total of nine mechanisms, as well as their underlying predictions. They concluded that none of the mechanisms has been adequately evaluated to date, largely because the lack of specific mechanistic hypotheses has led researchers to focus on documenting the SRPR as such while ignoring additional data that would be necessary to discriminate between different mechanisms.

In the present project, we evaluated the SRPR by focussing on an elevational gradient as a presumed productivity gradient and using terrestrial ferns and lycophytes (for simplicity henceforth called ferns) as the study group. Elevational gradients are suitable for this kind of study because they represent strong, directional climatic gradients that can be studied in concise geographical region with limited biogeographical influences (Lomolino, 2001; Körner, 2007). Ferns in turn are a suitable study group because they are the dominant herbaceous forest plants in tropical forests (Willinghöfer *et al.*, 2012), have a high but manageable species number, and typically show pronounced hump-shaped species richness curves in humid montane habitats with maximum richness at about 1500-2500 m elevation, both at the local (Kessler *et al.*, 2011) and the regional scale (Jacobsen and Jacobsen, 1989; Bhattarai *et al.*, 2004; Karger *et al.*, 2011). Accordingly, fern diversity declines towards hot tropical lowland habitats where water stress presumably becomes limiting for many fern species as well as towards cold environments, where low temperatures become limiting, especially for epiphytes (Krömer *et al.*, 2005). Along elevational gradients, ferns thus allow to contrast assemblages of high diversity at mid-elevations with those of low diversity both at low and high elevations where environmental conditions are very different (Kluge and Kessler, 2011). At the same time, very little is known about the SRPR in ferns, except at the global scale (Kreft *et al.*, 2010).

Despite the well-documented climate-richness relationships among ferns (Bhattarai *et al.*, 2004; Kluge *et al.*, 2006; Kreft *et al.*, 2010; Kessler *et al.*, 2011), the mechanisms underlying these relationships remain unexplored. Simply put, if a certain number of fern species can survive in a given environment, why should not more species be able to do so, even if the habitat is physiologically stressful to ferns? There are probably dozens of possible explanations, but we consider that two main groups of factors are currently actively discussed in the research community. First, local species richness may be constrained by the number of species that can co-occur in a given habitat due to the amount and variability of resources that are available (Karst *et al.*, 2005; Sedio *et al.*, 2012; Urgenson *et al.*, 2012). In this case productivity, i.e., the energy available to the ferns, may limit the number of species. Second, species richness may be limited by evolutionary constraints and historical factors that have led to differently sized species pools in different habitats (Wiens and Donoghue, 2004; Condamine *et al.*, 2012). Such patterns may result from different rates of speciation or extinction, or from differences in the time available for a certain group to diversify in a given habitat (Jablonski *et al.*, 2006; Kissling *et al.*, 2012; Soria-Carrasco and Castresana, 2012). In the present study, we focus exclusively on the first of these potential processes while acknowledging that the other may also be relevant to our situation, and further that both are not mutually exclusive.

Table 4.1. *Overview of the hypotheses addressed in this study regarding the species richness productivity relationship (SRPR) of terrestrial ferns in Ecuador. H1 and H2 establish the presence of the SRPR, H3 and H4 refer to two possible mechanisms leading to the SRPR, and H5 addresses the impact of source-sink dynamics on the SRPR.*
***SR{raw}** = number of species of terrestrial fern species per plot; **SR{Fisher}** = species richness of terrestrial ferns per plot measured using Fisher's Alpha; **N{fern}** = total number of fern individuals per plot; **N{mean}** = mean number of fern individuals per species per plot; **Evenness{fern}** = evenness of fern assemblages per plot; **P{eco}** = ecosystem productivitiy measured via AET and tree biomass increment; **P{fern}** = productivitiy of fern assemblages.*

Hypothesis	**Assertion**	**Supported if**
H1	*general relationship*: there is a SRPR	
H1a	there is a SRPR considering P{eco}	SR{raw} ~ P{eco} is *positive*
H1b	there is a SRPR considering P{fern}	SR{raw} ~ P{fern} is *positive*
H2	*sampling effect*: at higher levels of productivity, there are more individuals and hence a higher probability to include more species from the regional species pool	
H2a	the SRPR considering P{eco} is determined by the *sampling effect*	SR{Fisher} ~ P{eco} is *not significant* or *negative*
H2b	the SRPR considering P{fern} is determined by the *sampling effect*	SR{Fisher} ~ P{fern} is *not significant* or *negative*
H3	*population size mechanism*: at higher levels of productivity, more species are able to increase their abundances and thus to maintain viable populations	SR{Fisher} ~ N{fern} is *positive*

H4	*niche position mechanism*: at higher levels of productivity, species using rare resources are more likely to persist	
H4a	at higher levels of productivity, rare species (niche specialists) increase	Evenness{fern} ~ P{eco} is *negative*
H4b	the mean number of individuals per species remains constant along the productivity gradient	SR{Fisher} ~ N{mean}is *not significant or negative*
H5	*source-sink-effects*: SRPRs are affected by the presence of sink populations	results of H1-H4 are affected when including only source populations

In order to address the methodological challenges outlined above in documenting and understanding the SRPR, we selected the following approaches. First, we conducted the analyses at two spatial extents (Whittaker, 2010): *along the entire elevational gradient* and *within elevational belts*. Second, we used three measures of productivity, two at ecosystem level (indirect: AET; direct: tree aboveground biomass increment) and one at the level of the fern assemblages (fern aboveground biomass increment). Third, we took sink populations into account to assess whether they influence the observed SRPR. Fourth, based on these approaches, we tested the following five hypotheses, largely based on Evans *et al.* (2005) (Tab. 4.1).

H1: There is a *positive SRPR* among terrestrial fern assemblages.

This hypothesis has two sub-hypotheses:

H1a: There is a positive relationship of terrestrial fern richness to *ecosystem productivity* measured via AET and tree biomass increment.

H1b: There is a positive relationship of terrestrial fern richness to the *productivity of the fern assemblages* measured via aboveground fern biomass increment.

H2: The SRPR of terrestrial ferns is determined by the *sampling effect* which predicts that the higher richness of ferns on more productive plots is determined by a higher number of individuals.

Just as H1, this hypothesis has two subhypotheses:

H2a: The SRPR of terrestrial fern richness to *ecosystem productivity* measured via AET and tree biomass increment is determined by the *sampling effect.* There is a positive relationship.

H2b: The SRPR of terrestrial fern richness to the *productivity of the fern assemblages* measured via aboveground fern biomass increment is determined by the *sampling effect*.

H3: The SRPR of terrestrial ferns is determined by the *increased population size* mechanism which predicts that as productivity increases, more species are able to increase their abundances and thus to maintain viable populations.

H4: The SRPR of terrestrial ferns is determined by the *niche position* mechanism which postulates that at higher levels of productivity, species using rare resources are more likely to persist.

Because no direct measures of niche position are available, this hypothesis is addressed indirectly by two sub-hypotheses:

H4a: Increased productivity results in a disproportionately *stronger increase of rare species* (niche specialists).

H4b: Across the productivity gradient the *mean number of individuals* per species remains constant.

H5: The SRPR of terrestrial ferns along the elevational gradient is influenced by *source-sink effects*.

We did not include all nine mechanisms listed by Evans *et al.* (2005) through which a positive SRPR may arise, for a number of reasons. The *more trophic levels mechanism* is only applicable to organisms of higher trophic levels (Evans *et al.*, 2005). We did not test the *niche breadth mechanism* because it requires specific data on resource use by the species that was unavailable in our study, and because Evans *et al.* (2005) considered that this mechanism is unlikely to operate in nature. Likewise, assessing the *consumer pressure mechanism* requires data on consumption rates that are not available in our case. The *dynamic equilibrium mechanism* of Evans *et al.* (2005) assumes that high species richness in habitats of high productivity is determined by faster recovery rates from disturbance and predicts that recovery rates from disturbance are positively correlated with energy. This mechanism is unlikely to apply to our situation as we studied fern assemblages in mature forest habitats without signs of recent major disturbance. Finally, the *range limitation* and *diversification rate mechanisms* place richness-productivity in an evolutionary context that will be the focus of a different publication.

4.3 Materials and Methods

4.3.1 Study sites and plots

The original study design included 24 permanent study plots with 3 replicate plots at 8 elevational steps about every 500 m in elevational distance on the eastern Andean slope in Napo province, Ecuador (Salazar *et al.,* submitted manuscript). This gradient spans localities from lowland forests in the vicinity of Río Napo (Reserva Jatun Sacha) at 500 m via Reserva Biósfera Sumaco, Reserva Ecológica Antisana, Estación Biológica Yanayacu, and Guango Lodge up to highest elevations at Reserva Ecológica Cayambe-Coca close to timberline at 4000 m (Unger *et al.,* 2010; Salazar *et al.,* submitted manuscript). Plots were located in natural slope forests, avoiding anthropogenically or naturally disturbed habitats as well as special microhabitats such as ravines or ridges. However, at 1500 m and 3000 m, single plots were atypical and these elevations were therefore excluded from the present study.

Study plots were of 20 m x 20 m (400 m^2), a plot size that has previously been used for surveys of local tree (Homeier *et al.,* 2010*a*) and fern diversity (e.g, Kessler 2001; Kluge *et al.,* 2006) because it is large enough to be representative but also small enough to be ecologically homogeneous (Kessler and Bach, 1999). At those elevational levels where the abundance of terrestrial ferns was very high, the measurements of biomass and productivity of the most abundant species were restricted to a subplot of 10 m x 10 m embedded in the main plot and afterwards recalculated to the original plot size. This was the case in single plots at 1000 m, 2000 m, and 2500 m. Destructive sampling (herbarium specimens, leaves and rhizomes for biomass measurements) was conducted on fern individuals outside of the study plots. All species were collected for identification at the herbarium of the Pontificia Universidad Católica del Ecuador (QCA) and by specialists for difficult groups. We excluded epiphytic ferns from the study because the inaccessibility of the canopy implied that most individuals could be accessed, tagged, and remeasured.

Plots at 500-2000 m were established in 2005-2008 for studies of trees (Homeier *et al.*, 2010*b*; Unger *et al.*, 2010, 2012) while plots at 2500-4000 m were established for the present study in 2009 and 2010. Field sampling campaigns took place in 2009 (May-August), 2010 (April-July), and 2011 (April-July). One plot each at 3500 m and 4000 m suffered human disturbance in the first study year and had to be relocated.

4.3.2 Diversity measurements

Species richness was expressed as the number of terrestrial fern species per 400 m^2 plot. To test H2 we needed a richness measure that was independent of the number of fern individuals in a plot. We used Fisher's Alpha, a scalar that accounts for differences in numbers of individuals and hence removes the sampling effect (Fisher *et al.*, 1943; Hubbell, 2001; Kaspari *et al.,* 2003). We did not use individual-based rarefaction for this purpose because the lowest number of individuals in some plots (N = 11) was below that of the number of species in some other plots and would have led to the exclusion of 96% of the data points. Evenness of species abundances per plot was calculated using Simpsons (1949) evenness index $E_{1/D}$ (Magurran, 2004; Tuomisto, 2012).

Source populations were defined as species records in a given plot that included at least one mature and fertile individual or, in a few species, a mature individual that showed vegetative reproduction, e.g. via buds (Grytnes *et al.*, 2008; Kessler *et al.,* 2011). Accordingly, sink species were all those not able to reproduce in a given plot during the observation period.

4.3.3 Productivity measurements

Actual evapotranspiration (AET) was calculated using Turc's formula (Turc 1954, González-Espinosa *et al.,* 2004), where $AET = P / [0.9 + (P/L)^2]^{1/2}$ with $L = 300 + 25\,T + 0.05\,T^3$, P = mean annual precipitation, and T = mean annual temperature. Precipitation and temperature values were compiled from the WorldClim data bank (Hijmans *et al.*, 2005), since there are no climate stations in the vicinity of the study sites.

Aboveground Biomass Increment of Trees ($AGBI_{trees}$) was measured as stem increment measurements. In all plots, all stems with dbh ≥10 cm were equipped with dendrometer tapes (type D1; UMS, Munich, Germany) that were monitored at least once per year for stem diameter growth. Tree height was measured with a Vertex IV height meter and a T3 transponder (Haglöf, Langsele, Sweden) in April/ May 2011. $AGBI_{trees}$ was calculated as the sum of all individual tree increments applying the allometric equation of Chave *et al.* (2005) for tropical wet forests, with stem diameter, wood specific gravity (WSG) and tree height as parameters. WSG data for the tree species were obtained from Chave *et al.* (2006) or, in cases of missing information on species, genera or family means of WSG were calculated from the same source and applied to the respective species. Growth monitoring started in 2005 in the plots at 500-2000m and data on $ABGI_{trees}$ of these plots were taken from Unger *et al.* (2012). $ABGI_{trees}$ of the plots at 2500-4000m was calculated over the period 2009-2012. A more detailed description of the $ABGI_{trees}$ calculation is given in Unger *et al.* (2012).

Aboveground Biomass Increment of Ferns ($AGBI_{ferns}$) was measured as the sum of annual leaf and rhizome biomass increment of all terrestrial fern individuals in each plot over two consecutive years (2009-2010, 2010-2011). At the beginning of the study, we marked the rhizomes of all fern individuals in the study plots with numbered plastic tags, measured rhizome length and frond length with a tape measure, and counted the number of fronds. Each petiole was marked with non-corrosive wire so that in the consecutive field phases turnover of leaves and productivity could be unambiguously assessed. In subsequent field campaigns, newly developed fern individuals and leaves were marked and measured in similar ways.

To relate leaf length to leaf biomass, three healthy mature fronds with few or no epiphylls were sampled for each species at each elevational level . Leaves were scanned and their leaf-area and length were measured from the digital image using WinFolia (Regent Instruments Inc. Quebec, Canada) and ImageJ (Rasband, 1997–2009). After leaves were dried at 65°C, their mean tissue density was evaluated by weighting (accuracy 0.1 g). Individual level leaf length (x) and foliar tissue density (y) were related by averaging values of the fronds collected for all species at all elevations using the linear regression equation $y = 0.0002*x^{2.2854}$ ($R^2=0.87$, $p<0.001$). Number of fronds and leaf-length were combined with the tissue density values to calculate total biomass and biomass increment, respectively.

A similar procedure was applied to rhizomes, with three specimens collected, weighted, and used to relate field measurements of rhizome length. For partly subterranean rhizomes, biomass increment was quantified by measuring the distance between the petioles of the old and newly formed leaves.

Overall, biomass values were obtained from 399 vouchers of 82 species. Nine rare species (1-3 individuals per plot) were only found within the plots and the values for these species were taken from species of the same genus that were the most comparable in size and texture.

Because productivity measures were unavailable for two plots for the first year of the study, we conducted all analyses with the data from the second year only. However, for the remaining 16 plots, productivity values were highly correlated between the two study years (Spearman's Rank Correlation, $r = 0.98$, $p < 0.001$), showing that our data are representative for the respective plots.

4.3.4 Data analyses

Prior to analyses, $AGBI_{ferns}$ was log-transformed to approach normality. To assess if this affected our results, we also conducted the analyses with untransformed data using non-parametric statistics and obtained qualitatively similar results (data not shown).

For analyses *along the elevational transect*, we used the raw values of species richness, productivity, etc. per plot.

For analyses *within elevational belts*, we calculated the mean value of each parameter from the three plots at each elevation and then expressed the values of each plot relative to that mean. In this way, we were able to combine plots from different elevations (which had different absolute values) by using a common relative measure, resulting in $n=18$ for the analyses. AET was excluded from this analysis because it was calculated as a standard value for each elevation based on climatic data and hence provided no information on variability at a given elevation.

To test H1, we used ordinary least-squares (OLS) regression with Species Richness as dependent variable and AET, $AGBI_{trees}$, and $\log(AGBI_{ferns})$ as explanatory variables.

To test H2, we used ordinary least-squares (OLS) regression with Fisher's Alpha as dependent variable and AET, $AGBI_{trees}$, and $\log(AGBI_{ferns})$ as explanatory variables. H2 is supported if there is no or a negative relationship of a productivity measure (using only those measures not rejected in H1) to fern diversity as measured by Fisher's Alpha, a diversity index that accounts for differences in numbers of individuals (Kaspari *et al.,* 2000, 2003; Beck *et al.,* 2011).

To test H3, we used ordinary least-squares (OLS) regression with Fisher's Alpha as dependent variable and Total Number of Fern Individuals as explanatory variable. Further, because this hypothesis predicts that productivity increases species richness via an increase in the number of individuals, we tested for a covariance between Number of Fern Individuals and $\log(AGBI_{ferns})$ using Spearman's Rank Correlation.

To test H4a, we used ordinary least-squares (OLS) regression with Evenness as dependent variable and $\log(AGBI_{ferns})$ as explanatory variable. We also assessed whether Evenness was correlated to Fisher's Alpha using Spearman's Rank Correlation. To test H4b, we conducted ordinary least-squares (OLS) regression using Fisher's Alpha as dependent variable and Mean Number of Individuals per species and plot as explanatory variable.

To test H5, we re-ran all analyses for H1-H4 after excluding sink species from each plot. The hypothesis is supported if results of the analyses regarding H1-H4 are affected when sink populations are excluded.

Analyses were run with the statistical platform R (R Development Core Team 2012).

4.4 Results and Discussion

For clarity's sake, in the following we separately present the results of the test of each hypothesis and discuss these in the context of previous research on each of them. In the conclusions, we then draw all lines of evidence together to assess the importance of productivity in determining local patterns of fern species richness.

General Patterns

In total, in the 18 study plots we encountered and measured 6175 individuals of terrestrial ferns belonging to 91 species in 34 genera and 20 families (Salazar *et al.,* submitted manuscript). Overall, we measured 13945 fern leaves in the two years of the study. Values of $AGBI_{trees}$ were based on measurements of 560 tree stems.

Species Richness, Fisher's Alpha, and Number of Fern Individuals all showed hump-shaped patterns relative to elevation, with intermediate values at low elevations (500-1000 m), high values in the middle of the gradient (2000-2500 m), and low values at high elevations (3500-4000 m) (Fig. 4.1A-C). These patterns are typical for fern assemblages along extensive elevational gradients in the tropics (Bhattarai *et al.*, 2004; Kessler *et al.*, 2011; Kluge and Kessler, 2011) and show that our study sites are representative of a general pattern.

Considering the productivity measures, log($AGBI_{ferns}$) showed a hump-shaped pattern (Fig. 4.1F) whereas values of AET and $AGBI_{trees}$ declined roughly linearly with elevation (Fig. 4.1D, E). While no previous studies exist on the productivity of fern assemblages, the patterns for AET and $AGBI_{trees}$ correspond to the general trends in humid tropical mountains (Girardin *et al.*, 2010; Moser *et al.*, 2011).

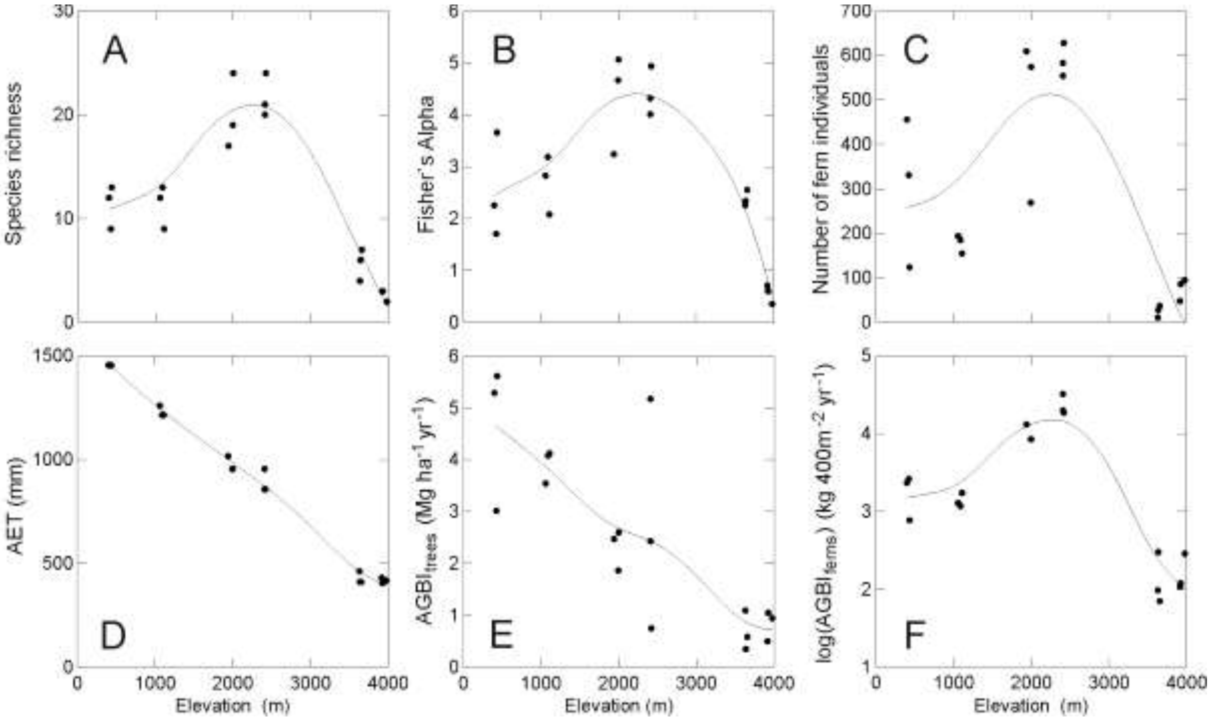

Fig 4.1 *Patterns of fern diversity (top) and productivity (bottom) along the elevational study gradient in Ecuador. Lines are trend lines drawn with Distance-Weighted Least-Squares Smoothing (DWLS) with tension 0.5.*

H1 (Presence of a SRPR)

Along the elevational gradient

Species richness of terrestrial ferns per plot was strongly positively related to $AGBI_{ferns}$ (OLS, $R^2 = 0.82$, $P < 0.001$) but marginally not to AET ($R^2 = 0.20$, $P = 0.07$) and clearly not to $AGBI_{trees}$ ($R^2 = 0.12$, $P = 0.17$) (Fig. 4.2A-C).

We thus found that local fern diversity along the elevational gradient was only weakly related to ecosystem productivity, here measured as AET and $AGBI_{trees}$. This result contrasts with those of numerous previous studies were animal (Currie, 1991; Hawkins *et al.*, 2003; Morales-Castilla *et al.*, 2012) and plant (Venesky and Venskaia, 2003; Kreft and Jetz, 2007) diversity, and also fern diversity (Kreft *et al.*, 2010), have been found to be closely correlated especially to AET. These differences are presumably based on differences in geographical scale and scope (Gillman and Wright, 2006; Whittaker, 2010), with most previous studies considering continental to global scales. Furthermore, in previous studies, species richness was mostly considered at a regional rather than at the local scale. However, regional fern diversity along elevational gradients is closely correlated to local diversity (Karger *et al.*, 2011). In consequence, it is unlikely that regional fern diversity would have been found to be strongly correlated to AET in our study system. AET has also not been found to be a good predictor of fern diversity along other elevational gradients (Kluge *et al.*, 2006; Kessler *et al.*, 2011).

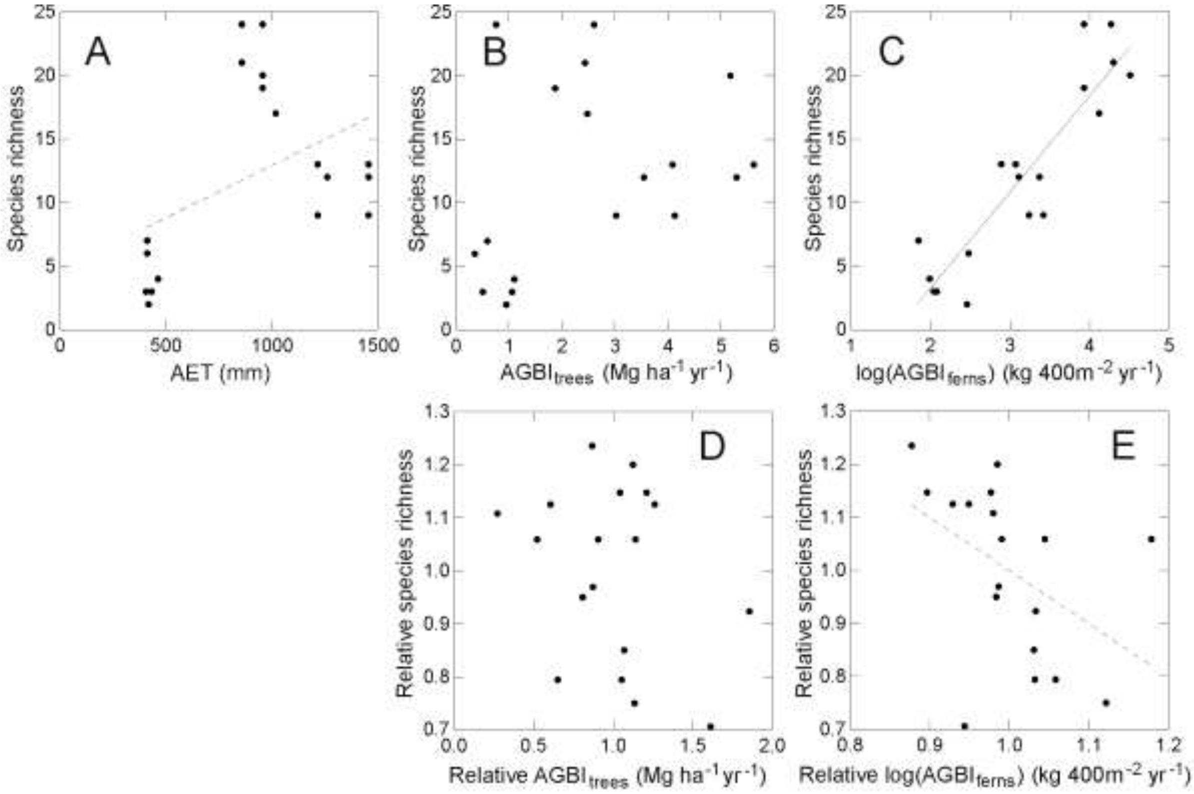

Fig. 4.2 *Relationships of absolute (A-C) and relative (D-E) fern species richness per plot relative to three productivity measures. Continuous trend lines denote relationships significant at P < 0.05, dashed ones at P < 0.10.*

Most likely, the lack of a close relationship of local fern richness and ecosystem productivity in our study is due to the fact that the contribution of ferns to the local floras varies strongly with elevation. The percentage of ferns relative to total vascular plant richness in Napo province increases from 9.8% at 0-500 m to 18.7% at 1500-2000 m, and then declines to 4.5% at 3500-4000 m (based on data from Jørgensen and León-Yánez, 1999). The abundance of ferns also follows a similar trend, with low contributions of individuals (and presumably biomass) to total terrestrial herb assemblages at low elevations and high values at mid-elevations (Willinghöfer *et al.*, 2012). We thus consider that the relative contribution of ferns to Net Primary Productivity (NPP) at ecosystem level varies along elevational gradients and peaks at mid-elevations. Partly, this may be driven by an increase of photosynthetically active radiation in the forest understory from the lowlands to mid-elevations (Unger *et al.*, 2012). Accordingly, ecosystem productivity cannot to be a suitable measure of the energy availability for ferns which explains why we found a much stronger relationship of fern richness to $\log(\mathrm{AGBI}_{\mathrm{ferns}})$.

Within elevational belts

Relative species richness of terrestrial ferns per plot was marginally negatively related to relative $\log(\mathrm{AGBI}_{\mathrm{ferns}})$ (OLS, $R^2 = 0.21$, $P = 0.059$) but not to relative $\mathrm{AGBI}_{\mathrm{trees}}$ ($R^2 = 0.09$, $P = 0.24$) (Fig. 4.2D-E).

This shows a tendency towards a negative SRPR within elevational belts that counters our original assumption of a positive SRPR (Tab. 4.1). However, negative SRPRs have been previously documented (Gillman and Wright, 2006). The shape of SRPRs has been the focus of contentious arguments and it is still uncertain if general patterns can be identified (Mittelbach *et al.*, 2001; Whittaker and Haegaard, 2003; Whittaker, 2010). In any case, there is consensus that SRPRs are scale dependent that negative relationships are most likely to be determined by interspecific competition, and that such relationships should be most influential at small spatial scales (Evans *et al.*, 2005; Whittaker, 2010). This was indeed the case in our study.

This suggests that at this spatial scale, the SRPR is determined by different factors than along the overall elevational gradient where environmental conditions are more variable.

H2 (Sampling hypothesis)

Along the elevational gradient and within elevational belts

Fisher's Alpha of the terrestrial fern assemblages was less strongly related to log($AGBI_{ferns}$) than species richness, but still highly significantly so (OLS, $R^2 = 0.57$, $P < 0.001$) (Fig. 4.3A). Fisher's Alpha was not related to either AET ($R^2 = 0.13$, $P = 0.14$) nor to $AGBI_{trees}$ ($R^2 = 0.07$, $P = 0.28$). Within elevational belts, relative Fisher's Alpha of the terrestrial fern assemblages was negatively related to relative log($AGBI_{ferns}$) (OLS, $R^2 = 0.44$, $P = 0.003$) (Fig. 4.3B) but not to relative $AGBI_{trees}$ ($R^2 = 0.01$, $P = 0.64$). Thus, in both cases H2a was supported while H2b was rejected.

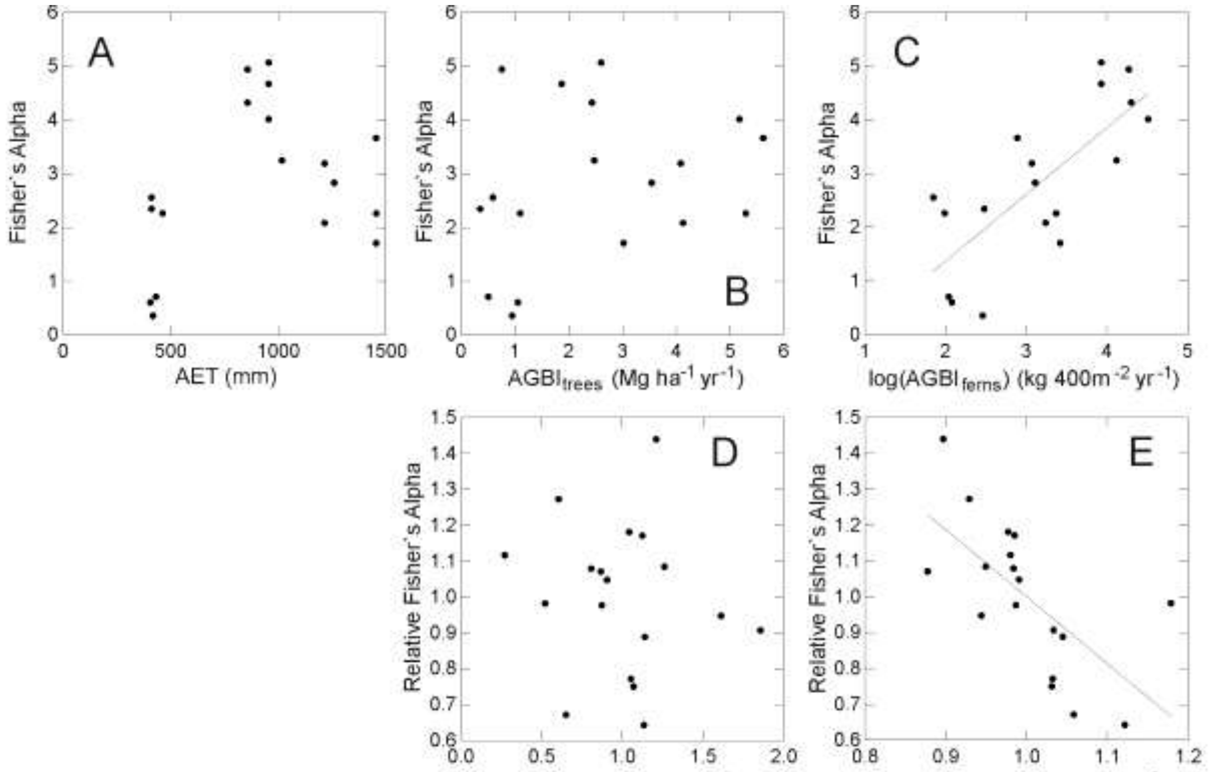

Fig.4.3 *Relationships of absolute (A-C) and relative (D-E) Fisher's Alpha relative to three productivity measures. Continuous trend lines denote relationships significant at P < 0.05.*

The sampling effect occurs when higher productivity increases the number of individuals in a sampling unit and hence stochastically increases the probability of including more species from the local species pool (Kaspari *et al.*, 2000, 2003; Evans *et al.*, 2005). In our analyses, we accounted for the differences in numbers of individuals by using Fisher's Alpha as measure of species richness. The fact that a SRPR when using $AGBI_{ferns}$ as productivity measure was still visible after accounting for this effect implies that the observed SRPRs cannot be solely explained by the sampling effect. Conversely, the observed richness-productivity relationship using AET as productivity measure could be accounted for by the sampling effect.

H3 (Increased population size hypothesis)

Along the elevational gradient

Fisher's Alpha of the terrestrial fern assemblages was significantly related to the total Number of Fern Individuals per plot (OLS, $R^2 = 0.45$, $P = 0.003$) (Fig. 4.4A). Furthermore, the Number of Fern Individuals and $\log(AGBI_{ferns})$ were significantly correlated (Spearman's Rank Correlation, $r = 0.92$, $P < 0.001$).

Thus, we found support for the increased population size mechanism, which assumes that a higher number of individuals allows more species to coexist because population sizes can increase, reducing extinction rates (Wright, 1983). This is probably the most basic requirement to observe positive SRPRs (Evans *et al.,* 2005). However, most previous studies of mechanisms of SRPRs have not differentiated between the sampling and increased population size effects (Evans *et al.,* 2005). In consequence, this is one of few studies to actually document the increased population size effects (Kaspari *et al.,* 2000, 2003; Acharya *et al.,* 2011; Bienhold *et al.,* 2012).

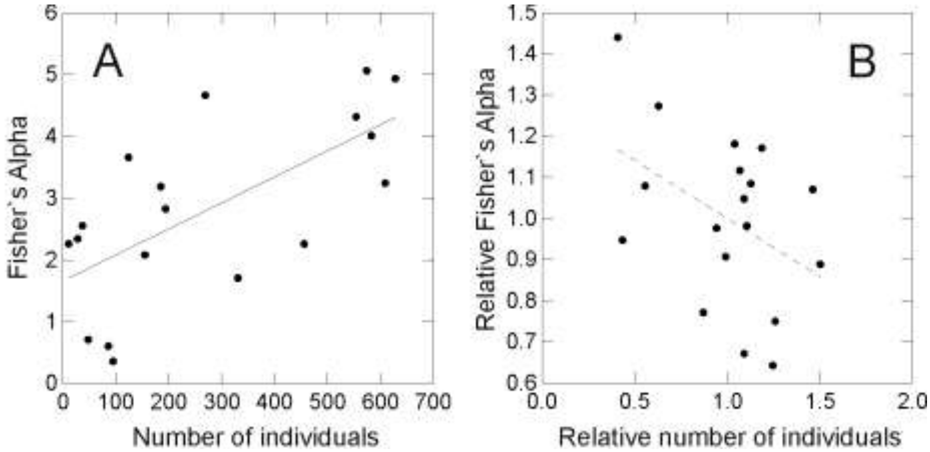

Fig. 4.4 *Relationships of Fisher's Alpha to Number of Fern Individuals along the elevational gradient (A) and considering relative values within elevational belts (B). The continuous trend lines denotes a relationship significant at P < 0.05, the dashed one at P < 0.10.*

Within elevational belts

Relative Fisher's Alpha of the terrestrial fern assemblages was marginally negatively related to the relative total Number of Fern Individuals per plot (OLS, $R^2 = 0.18$, $P = 0.08$) (Fig. 4.4B). Furthermore, there was no significant relationship between relative Number of Fern Individuals and relative log($AGBI_{ferns}$) (Spearman's Rank Correlation, $r = 0.12$, $P = 0.16$).

Thus, this hypothesis was rejected within elevational belts, again suggesting that SRPRs are determined by different factors at the two spatial scales of our study.

H4 (Niche position hypothesis)

Along the elevational gradient

There was a significant decline of Evenness with log($AGBI_{ferns}$) (OLS, $R^2 = 0.57$, $P < 0.001$) (Fig. 4.5A). Evenness was also correlated with Fisher's Alpha (Spearman's Rank Correlation, $r = 0.58$, $P = 0.013$). There was no significant relationship between Fisher's Alpha and the Mean Number of Individuals per species and plot (OLS, $R^2 = 0.03$, $P = 0.47$). Neither did the Mean Number of Individuals change significantly with elevation ($R^2 = 0.02$, $P = 0.56$) or log($AGBI_{ferns}$) ($R^2 = 0.16$, $P = 0.10$).

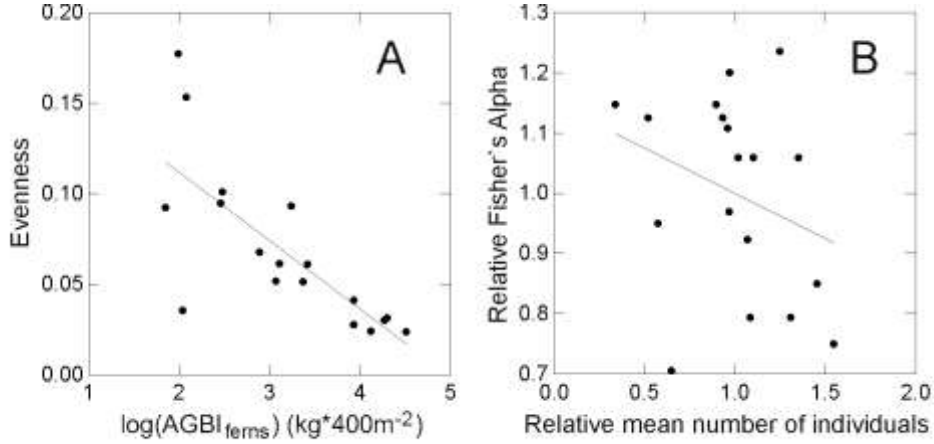

Fig. 4.5. *Relationship of (A) evenness to the productivity of the fern assemblages along the elevational gradient, and (B) of relative Fisher's Alpha to relative Mean Number of Individuals per Species within elevational belts.*

We thus obtained circumstantial support for the niche position hypothesis (Evans *et al.*, 2005) which assumes that increased energy availability results in higher resource availability in specialized ecological niches, allowing specialized species to exploit them.

This was based on our observation that evenness of the fern assemblages declined with increasing productivity, indicating that the increase of species richness in highly productive plots was mainly driven by the increase of rare species. Furthermore, the mean number of individuals per species was unrelated to productivity or fern diversity, suggesting that in more productive assemblages resources were not monopolized by a few species. We are not aware of any previous assessments of the niche position hypothesis, except for some indirect support outlined by Evans *et al.* (2005). However, we would be careful to claim that our study provides direct evidence for the niche position hypothesis since we were unable to test alternative hypotheses that might lead to similar patterns, such as the niche breadth hypothesis or even the influence of habitat heterogeneity.

Within elevational belts

There were no significant relationships of relative Evenness with relative log($AGBI_{ferns}$) (OLS, $R^2 = 0.01$, $P = 0.73$) nor with relative Fisher's Alpha (Spearman's Rank Correlation, r = -0.13, P = 0.61). In contrast, there was a strong negative relationship between relative Fisher's Alpha and the relative Mean Number of Individuals per species and plot (OLS, $R^2 = 0.65$, $P < 0.001$) (Fig. 4.5B). Relative Mean Number of Individuals was also significantly positively related to relative log($AGBI_{ferns}$) ($R^2 = 0.59$, $P = 0.01$).

Within elevational belts, we thus found no support for the niche position hypothesis.

H5 (Source-sink hypothesis)

General patterns

The number of species, defined as source species per plot, showed a hump-shaped pattern with elevation (Fig. 4.6A) being highly correlated with the overall pattern of species richness (Spearman Rank Correlation, r = 0.93, $P < 0.001$). The percentage of source species per plot varied between 37% and 100 % and showed a tendency towards a U-shaped pattern with lowest values at mid elevations (Fig. 4.6B). This pattern was marginally non-significant (polynomial regression, $R^2_{adj} = 0.19$, $P = 0.07$).

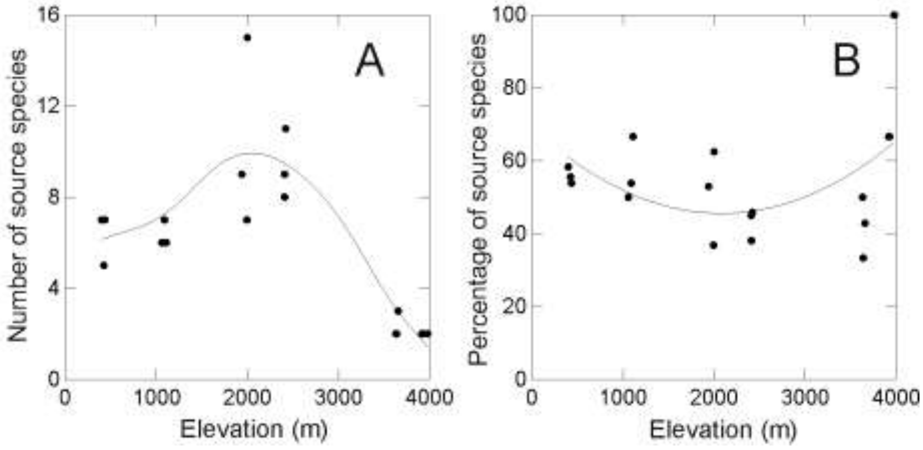

Fig. 4.6. *Number (A) and percentage (B) of source species along the elevational gradient. Lines are trend lines drawn with Distance-Weighted Least-Squares Smoothing (DWLS) with tension 0.5.*

Hump-shaped diversity patterns along elevational gradients have been hypothesized to be at least partly determined by source-sink dynamics. Here, non-self-sustaining sink populations accumulate at the center of the gradient because species disperse there from both low and high elevations (Kessler, 2000; Grytnes *et al.*, 2008; Kessler *et al.*, 2011). In our study, we indeed found a trend towards such a process, with slightly higher percentages of sink species at mid-elevations. Previous studies on alpine plants in Norway (Grytnes *et al.*, 2008) as well as on ferns along a range of elevational transects (Kessler *et al.*, 2011) have found mixed support for this hypothesis. In consequence, the factors leading to the variation of sink species proportions along elevational gradients remain to be explored in more detail.

In the following, we recalculated all the major analyses of H1 to H4 considering only source species, and compared the results to those obtained considering all species.

Along the elevational gradient

Relative to H1, source species richness of terrestrial ferns per plot was strongly significantly positively related to log($AGBI_{ferns}$) (OLS, $R^2 = 0.70$, $P < 0.001$) and less clearly so to AET ($R^2 = 0.27$, $P = 0.03$) as well as to $AGBI_{trees}$ ($R^2 = 0.18$, $P = 0.08$). Results of H1 were thus affected by source-sink dynamics in that H1a is now partly supported (results including all species: H1a: rejected).

Relative to H2, Fisher's Alpha of the source terrestrial fern assemblages was significantly related to AET (OLS, $R^2 = 0.23$, $P = 0.04$), marginally not to $AGBI_{trees}$ ($R^2 =$

0.18, $P = 0.08$), and strongly so to log($AGBI_{ferns}$) ($R^2 = 0.46$, $P = 0.002$). These relationships are weaker than those considering all species, suggesting that sink populations somewhat affect this relationship. However, H2b is still rejected.

Relative to H3, Fisher's Alpha of the source terrestrial fern assemblages was significantly related to the Number of Fern Individuals per plot of the source species (OLS, $R^2 = 0.42$, $P = 0.004$). Among source species, Number of Fern Individuals and log($AGBI_{ferns}$) were significantly correlated (Spearman's Rank Correlation, $r = 0.91$, $P < 0.001$). These values are higher than those obtained when considering all species. Hence, exclusion of sink species increased the support for this hypothesis.

Concerning H4, there was no significant relationship between the Evenness and log($AGBI_{ferns}$) of the source species (OLS, $R^2 = 0.07$, $P = 0.29$), contrasting with the results obtained considering all species. However, this pattern was driven by two outlier plots at 4000 m that had only two species each, in both cases with one fairly common species (35 and 59 individuals, respectively) and the other species only represented by a single individual. When these two plots were excluded from the analysis, there was a highly significant relationship between the Evenness and log($AGBI_{ferns}$) of the source species ($R^2 = 0.63$, $P < 0.001$). Evenness was not correlated with Fisher's Alpha (Spearman's Rank Correlation, $r = 0.12$, $P = 0.65$). Neither was there a significant relationship between Fisher's Alpha and the Mean Number of Individuals per species and plot for the source assemblages (OLS, $R^2 = 0.15$, $P = 0.11$). Also, there was no significant relationship of Mean Number of Individuals with elevation ($R^2 = 0.10$, $P = 0.19$) but with log($AGBI_{ferns}$) ($R^2 = 0.53$, $P = 0.001$).

In summary, the changes of species richness patterns led to slightly different SRPRs along the elevational gradient when only source populations were considered. In particular, species richness was only related to log($AGBI_{ferns}$) when considering all species, but relationships were also found to AET and (marginally) to $AGBI_{trees}$ when we only considered source species. This may be interpreted as suggesting that the core richness of the fern assemblages may indeed be related to some degree to ecosystem productivity. However, these relationships were lost when fern diversity was quantified as Fisher's Alpha, so that if a relationship exists between fern diversity and ecosystem productivity, this is likely to be driven by the sampling effect. Furthermore, none of the other analyses were affected by considering only source species. We therefore conclude that the influence of source-sink dynamics on richness-productivity relationships along our study transect is rather weak overall.

Within elevational belts

Relative to H1, relative source species richness of terrestrial ferns per plot was not related to relative $AGBI_{trees}$ ($R^2 = 0.01$, $P = 0.93$) nor to relative $\log(AGBI_{ferns})$ (OLS, $R^2 = 0.13$, $P = 0.15$). As H1 was now rejected, results of H1 were markedly affected by source-sink dynamics in that.

Relative to H2, relative Fisher’s Alpha of the source terrestrial fern assemblages was not related to relative $AGBI_{trees}$ ($R^2 = 0.07$, $P = 0.29$) but markedly so to relative $\log(AGBI_{ferns})$ ($R^2 = 0.34$, $P = 0.01$). H2 is thus still rejected, but R^2 values are lower.

Relative to H3, relative Fisher’s Alpha of the source terrestrial fern assemblages was negatively related to the relative Number of Fern Individuals per plot belonging to the source species (OLS, $R^2 = 0.47$, $P = 0.002$). Among source species, relative Number of Fern Individuals and relative $\log(AGBI_{ferns})$ were not significantly correlated (Spearman’s Rank Correlation, $r = 0.36$, $P = 0.15$). These values are higher than those obtained when considering all species. Hence, exclusion of sink species increased the support for this hypothesis.

Concerning H4, there was no significant relationship between the relative Evenness and the relative $\log(AGBI_{ferns})$ of the source species (OLS, $R^2 = 0.11$, $P = 0.18$) nor with relative Fisher’s Alpha (Spearman’s Rank Correlation, $r = 0.24$, $P = 0.34$). However, there was a significant relationship of relative Mean Number of Individuals per species and plot to relative Fisher’s Alpha for the source assemblages (OLS, $R^2 = 0.47$, $P = 0.002$), and to relative $\log(AGBI_{ferns})$ ($R^2 = 0.36$, $P = 0.01$). These values were slightly lower than those obtained when all species were considered. H4 was thus not markedly affected.

Source-sink effects are most likely to affect assemblage composition at small spatial scales, since dispersal beyond the suitable habitat of a species is more likely over short distances (Gilpin and Hanski, 1991; Hubbell, 2001). Indeed, we found that within elevational belts, SRPRs were markedly different when all species were included. This suggests that the trend towards a negative SRPR detected when including all species was mainly driven by sink species represented by scattered, juvenile individuals that accumulate in assemblages of low productivity where competition is presumably lower. Indeed, when fern diversity was quantified via Fisher's Alpha, which reduces the influence of infrequent species on the diversity measure, source-sink effects disappeared. We thus argue that the influence of source-sink effects is mainly driven by the sampling effect (Evans *et al.,* 2005) by which sink species are randomly drawn from a species pool.

4.5 Conclusions

This is the first study to assess the SRPR in ferns and more generally one of very few to address this topic for plants at the local scale (Oberle *et al.,* 2009; Axmanová *et al.,* 2012; Reich *et al.,* 2012). Perhaps the most informative result of our study is that we found strikingly contrasting patterns along the elevational gradient and within elevational belts.

Along the elevational gradient, the positive SRPR appears to be determined by an increase in the number of fern individuals that allows more species to coexist. Although the actual mechanisms determining this relationship remain to be elucidated, it is likely that light (Unger *et al.,* 2012) and niche availability play an important role and hence, by extension, also interspecific competition. Indeed, a previous study of ferns along an elevational gradient in Costa Rica also found indirect evidence for interspecific competition based on morphological trait diversity, especially in the species rich assemblages at mid-elevations (Kluge and Kessler, 2011).

Within elevational belts, we found the opposite pattern, namely a trend towards a negative SRPR. We were unable to explain this pattern by the increased population size or niche position hypotheses, which is not surprising considering that these effects are regarded to determine positive SRPRs (Evans *et al.,* 2005). However, we found a fairly strong impact of sink populations on the SRPR within elevational belts, with sink species accumulating in plots of low productivity. This suggests that the negative SRPR may be driven by interspecific competition. It would mean that in plots of high productivity relatively few strong competitors occupy the available niche space, whereas in plots of low productivity there are open spaces that can be colonized by competitively inferior sink species which then increase the species counts. This situation is analogous to the competitive exclusion of inferior competitors in eutrophied ecosystems such as strongly fertilized grasslands (Zobel and Liira, 1997).

Interspecific competition is commonly considered to limit local plant diversity in grasslands (Al-Mufti *et al.,* 1977; Moore and Keddy, 1989; Zobel and Liira, 1997) and among forest trees (Oberle *et al.*, 2009). However, to our knowledge this is the first study to suggest that competition may limit terrestrial herb diversity in a tropical forest. This result is not as trivial as it may appear at first glance, since forest herb assemblages are commonly characterized by an open structure with much apparently open space between plants (Reich *et al.,* 2012; Axmanová *et al.,* 2012). In such a situation, competition for light, space, or nutrients is less easy to conceive than in densely packed assemblages (e.g. grasslands, closed forests) where every available space is occupied. Additionally, competition has been considered not to be important in structuring herb assemblages in temperate forests (Hart and Chen, 2006, 2008; Reich *et al.*, 2012; Axmanová *et al.*, 2012). Based on our field experience, we believe that the density of individuals within fern assemblages may largely be determined by suitable germination sites, and that competition therefore plays role at the gametophytic and early sporophytic life stages. Clearly, the role of competition in structuring tropical herb assemblages deserves closer examination beyond the limitations imposed by a correlative study such as ours.

In any case, we found that at both spatial scales of our study, fern diversity appears to be limited by the number of available niche space and competition to occupy this space. Along the elevational gradient, variation in the number of niches result in a positive SRPR, whereas within elevational belts, the limited number of available niches emphasizes the role of competition and results in a negative SRPR.

Our study presents the first evidence that the amount of energy available to fern assemblages as well as interspecific competition within the assemblages affect the local diversity of ferns in tropical mountain ecosystems. However, many of our conclusions are based on circumstantial evidence and call to be tested by additional approaches. For example, to better understand the role of competition in structuring fern assemblages, it might be instructive to compare assemblages with similar abiotic conditions but different species pools (e.g. mainland assemblages and depauperate assemblages on isolated islands, Keppel *et al.,* 2010). In such a comparison, species poor assemblages would be expected to have less interspecific competition, leading to broader realized niches and increasing abundances of the individual species. Perhaps more importantly, experimental approaches would be appropriate to confirm the structuring roles of niche availability and competition.

Finally, current patterns of diversity and species interactions should be considered in an evolutionary and historical context by linking phylogenetic studies with ecological data.

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Chapter 5

Altitudinal change in biomass, productivity and leaf functional traits in the Ecuadorian Andes: Comparing terrestrial ferns with trees

Laura Salazar, Jürgen Homeier, Christoph Leuschner, Michael Kessler and Jürgen Kluge

5.1 Abstract

We studied leaf properties, biomass and biomass increment of terrestrial ferns and trees along an elevational transect from 400 m to 4000 m on the eastern slope of the Ecuadorian Andes. The aim of our study is to compare both life forms regarding their performance in relation to elevation and soil properties.

We found a systematic difference in specific leaf area (SLA) between fern and tree leaves (fern SLA being c. 40 cm² g^{-1} < than tree SLA) along the elevational gradient, reflecting the different light regimes of both life forms. The linear SLA decreases with elevation point to the production of thicker (and smaller but longer-living) leaves and fronds in the uppermost forests.

Since the foliar N concentration remained invariant and foliar P increased with elevation in our transect, one would assume that the SLA reduction was mainly caused by other factors than nutrient shortage such as the unfavourable thermal regime at high elevations which demands for more robust leaves with extended longevity. However, we found a significant SLA decrease with increasing soil C/N ratio for the trees (but not the ferns) which makes it likely that N shortage is at least an additional factor causing tree leaf SLA to decrease with elevation in this transect.

We found a striking difference between ferns and trees with respect to the patterns of altitudinal change in biomass and productivity which is clear evidence in support of the hypothesis that both plant groups are growth-limited by different factors. While biomass and productivity of trees decreased with elevation, in ferns it peaked at 2000-2500 m, suggesting that factors (soil and air humidity, light availability) other than nutrient availability should play a key role for terrestrial ferns

Key words: Andes, leaf properties, elevational gradients, biomass, productivity.

5.2 Introduction

With increasing elevation in mountains, climate, soil and vegetation change rapidly over short distances (e.g. Bruijnzeel *et al.*, 2010; van de Weg *et al.*, 2009). In tropical mountain forests, tree height and above-ground net primary productivity (NPP) decline with increasing elevation (Whitmore, 1984; Stadmüller, 1987; Moser *et al.*, 2011), which has been attributed to reductions in temperature (Kitayama and Aiba, 2002; Hoch and Körner, 2003) and nutrient supply rate (Grubb, 1977; Tanner *et al.*, 1998; Moser *et al.*, 2011) or other potentially limiting factors. While altitudinal gradients in biomass, productivity and foliar characteristics have been studied for trees and vascular and non-vascular epiphytes in a number of transects in neotropical and paleotropical mountains (e.g. Unger *et al.*, 2012; Werner *et al.*, 2012), much less is known about elevational change in other groups of primary producers such as terrestrial ferns and herbaceous plants along tropical mountain slopes. Epigaeic (non-epiphytic) ferns may contribute with only a small percentage (typically much less than 10 %) to the total biomass of tropical mountain forests (Tanner, 1985; Scatena *et al.*, 1993; Raich *et al.*, 1997; Crews *et al.*, 2001), but they may represent a large fraction of understory biomass (Raich *et al.*, 1997). The relative importance of terrestrial pteridophytes in terms of biomass seems to be largest in mountain forests on nutrient-poor soils (Richardson and Walker, 2010). Examples for tropical forests with particularly high abundance of terrestrial pteridophytes are certain forests on infertile soils that harbor a rich flora of Lycopodiaceae (e.g. Cullen, 1987; Aplet and Vitousek, 1994).

While it is generally assumed that ferns increase in abundance with increasing atmospheric moisture along mountain transects, precise quantitative data on terrestrial fern biomass across long tropical elevation transects from lowland to timberline do not exist. No study has yet examined the elevation-dependence of the productivity of terrestrial ferns in tropical mountain transect. Because ferns and canopy-reaching trees experience different microclimates within the stand and thus may have developed different adaptations to the environment in tropical mountains, both plant groups may reveal different altitudinal biomass and productivity patterns.

Foliar nitrogen (N) and phosphorus (P) content and specific leaf area (SLA) are key functional traits with an indicator value for light availability, photosynthetic capacity, leaf longevity, and also exposure to drought in plants (Wright *et al.*, 2004, 2005). In general, fast-growing species have higher foliar N concentrations and higher SLA values than slower growing species. Various authors have studied altitudinal changes in foliar nutrients and leaf morphology in trees along tropical mountain transects (e.g. van de Weg *et al.*, 2009) searching for indications of N or P limitation of tree growth at low and high elevations (Tanner *et al.*, 1998; Vitousek *et al.*, 1988, 1993). In trees, foliar N and P concentrations have been found either to decrease of to remain unchanged with increasing elevation (Letts *et al.,* 2010; Moser *et al.,* 2011; Soethe *et al.,* 2008; van de Weg *et al.,* 2009) depending on the geology of the mountains. Much less is known about altitudinal change in leaf chemistry and leaf morphology of ferns. In contrast to trees, Wegner *et al.* (2003) found an increase in leaf N concentration with elevation for ferns in the Bolivian Andes. Epiphytic ferns had significantly lower N concentrations than terrestrial ferns in Bolivian and Costa Rican mountain forests (Wegner *et al.,* 2003; Watkins *et al.,* 2007). However, it is not known whether terrestrial ferns have higher or lower foliar N concentrations than trees at the same site. An important indicator of the relative importance of nitrogen and phosphorus availability for plant growth is the foliar N/P ratio which has been found to decrease with elevation in terrestrial ferns (Wegner *et al.*, 2003) indicating a relative shift from prevailing P limitation of growth at low elevation to N limitation at high elevation. A similar altitudinal pattern has been reported for trees in tropical mountains (e.g. Wittich *et al.,* 2012) but such gradients have never been compared among co-occurring trees and terrestrial ferns. A widely reported trend is the altitudinal decrease in SLA that was demonstrated for tropical trees and also for ferns (e.g. Körner, 1989; Moser *et al.,* 2007).

Whether plant productivity is limited by nutrient shortage in tropical mountain forests, can be tested only by nutrient addition experiments as they were conducted, for example, by Homeier *et al.* (2012) at different elevations in the Ecuadorian Andes. However, valuable information on the possible role of soil nutrient availability for productivity can also be obtained from altitudinal transect studies when plant biomass and productivity are related to different parameters of nutrient availability and soil chemistry (e.g. Unger *et al.,* 2012). However, the results of experimental and observational studies on the role of nutrient limitation for the productivity of tropical mountain forests are partly contradictory (e.g. Ashton and Hall, 1992) and they do only provide information about trees but not on other groups of primary producers which could behave differently**.**

Terrestrial ferns might differ in their soil fertility – productivity relationship from trees growing at the same site because ferns and trees in the canopy layer are exposed to largely different light regimes which may result in contrasting nutrient use efficiencies of productivity and thus differences in nutrient demand. Further, ferns seem to have a lower degree of mycorrhization than trees (e.g. Alexander and Lee, 2005; Kessler *et al.,* 2010) which could affect nutrient acquisition. Finally, trees with their deep-reaching roots may have access to much larger soil nutrient pools than terrestrial ferns with their main root system located in the organic layer and mineral topsoil.

In this study across a long altitudinal transect on the eastern slope of the Ecuadorian Andes, we aimed at comparing indicators of plant nutrition between two primary producer groups, trees and terrestrial ferns, and to analyze their dependence on elevation. In a network of 22 plots in undisturbed forest between 400 m and 4000 m a.s.l., we measured not only the standing aboveground biomass of terrestrial ferns and trees, but also estimated aboveground productivity, which has rarely been done for tropical epigaeic ferns. Finally, three key leaf functional traits, foliar N and P concentration and SLA, were examined as proxies of plant nutrient status; we analyzed the influence of soil chemical properties on these traits and on biomass and productivity. We tested the hypotheses that a) trees and terrestrial ferns growing in the same stand display similar altitudinal patterns in their leaf traits, b) terrestrial ferns growing in the deep shade have lower foliar N and P concentrations than the trees' sun leaves, c) the foliar N and P concentrations are correlated with indicators of soil N and P availability in both plant groups, and d) altitudinal gradients in soil N and P availability influence the biomass and productivity of ferns and trees in a similar way.

5.3 Materials and Methods

5.3.1 Study area and plot selection

Field work was carried out in an elevation transect from 400 m to 4000 m a.s.l. on the slope of the eastern Andes in Central Ecuador. Twenty-four plots were established at eight elevation levels at steps of about 500 m with each three replicate plots per elevation level selected (Figure 5.1, Table 5.1). This gradient spans localities from lowland forests in the vicinity of the Napo River (Jatun Sacha biological station) at 400 m up to the highest sites located in the Cayambe-Coca ecological reserve at 4000 m close to the timberline. The sites were selected because they still harbor intact and well preserved forests along a continuous gradient from the lowlands up to the treeline ecotone.

At each elevation step, three permanent plots of 20 m x 20 m were demarcated. A plot size of 400 m^2 has previously been used for surveys of local tree and fern communities in the region (e.g. Homeier *et al.,* 2010a, Kessler, 2001; Kluge *et al.,* 2006), because it is large enough to be representative, but also small enough to guarantee a sufficiently homogeneous forest structure and to allow for rapid but precise surveys (Kessler and Bach, 1999). All plots were placed in the characteristic altitudinal forest belts on moderately steep slopes avoiding specific geomorphological conditions such as deep valleys or exposed ridges and anthropogenically or naturally disturbed habitats.

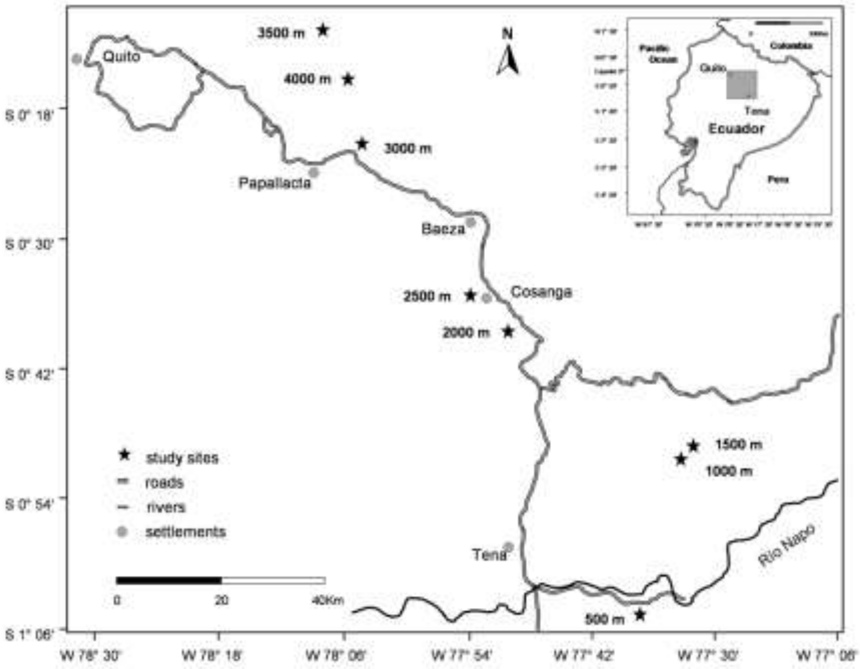

Fig. 5.1. *Study sites and their locations in Ecuador (insets). Positions of all study locations long the altitudinal transect are given with elevation.*

The plots at 500-2000 m were established in 2005-2008 for studying the tree layer (Homeier *et al.*, 2010b; Unger *et al.*, 2010, 2012) while the plots at 2500-4000 m were selected for the present study in 2009 and 2010. Field sampling campaigns took place in 2009 (May-August), 2010 (April-July), and 2011 (April-July) in all 24 plots.

5.3.2 Leaf traits

For measuring the specific leaf area (SLA) and leaf length of fern leaves, at least three healthy mature fronds of every fern species present we collected from different individuals that had few or no epiphylls on the foliage. The samples were dried at 65°C and transported to the lab, where the fronds were scanned and their leaf area and leaf length determined with Winfolia software (V. 5.1a, Régent Instruments Inc., Quebec, Canada).

Table 5.1 *The study sites in north-eastern Ecuador at the eight elevation levels.*

Elevational level (m a.s.l.)	**Study site**	**Elevational range (m)**	**Vegetation type**
500	Jatun Sacha biological station	400-435	Evergreen lowland forest
1000	Cordillera Galeras	1060-1110	Evergreen premontane forest
1500	Cordillera Galeras	1450-1570	Evergreen lower montane forest
2000	Cordillera Guacamayos	1940-2000	Evergreen lower montane forest
2500	Yanayacu biological station	2410-2420	Evergreen lower montane forest
3000	Guango biological station	2900-3098	Evergreen upper montane forest
3500	Oyacachi	3631-3656	Polylepis forest
4000	Oyacachi	3916-3978	Polylepis forest

Tree leaves were collected from each five to ten randomly chosen tree individuals per plot to obtain plot-level means of foliage characteristics. Ten to 30 fully developed, sun-exposed leaves from two different branches were collected from every sampled tree. The fresh leaves were scanned and SLA was determined with WinFolia software and subsequently samples were dried at 65°C.

The total concentrations of foliar N were determined in the fern and tree leaves with a C/N elemental analyzer (Vario EL III, Elementar, Hanau, Germany). Total P concentrations were analyzed using an Inductively Coupled Plasma Analyzer (Optima 5300DV ICP-OES, Perkin Elmer, Waltham, Massachusetts, USA) after digesting the samples with concentrated HNO_3.

5.3.3 Fern biomass and productivity

Fern productivity was measured over two consecutive years (2009-2010, 2010-2011) as the sum of annual leaf production and rhizome biomass increment of all terrestrial fern individuals present in the plots. At the beginning of the study, we placed numbered tags with plastic wire around the rhizomes of all fern individuals in the study plots, measured rhizome length and frond length with a measuring tape and counted the number of fronds per plant. Each petiole was marked with non-corrosive wire so that the turnover of the fronds and thus foliage productivity could be quantified unambiguously during the subsequent plot inspections. In subsequent field campaigns, newly developed fern individuals and leaves were marked and measured in a similar way.

After averaging the data over all fronds of a species, and over all species of an elevation, we regressed leaf dry mass (y) on leaf length (x) and obtained the linear regression equation $y = 0.0002*x^{2.2854}$ ($R^2=0.87$, $p<0.001$) which was used to calculate fern leaf dry mass from leaf length across the whole transect. The data on the number of fronds present and on leaf length from the consecutive measurements in the field were then multiplied with the leaf dry mass data and extrapolated to total fern biomass, or cumulative annual fern biomass increment, per plot.

A similar procedure was applied to the fern rhizomes, with three rhizome segments per species and plot collected and weighed. The resulting regression equation was used to calculate dry mass from field measurements of rhizome length. Although some species had partly subterranean rhizomes, this was not problematic because rhizome biomass increment was quantified by measuring the distance between the insertion of the petioles of the old and newly formed leaves.

Overall, biomass data were obtained for 399 vouchers from 82 fern species. Nine rare species (1-3 individuals per plot) were found only within the plots (no specimens have been collected to not disturb the ongoing productivity measurements) and the values for these species were taken from species of the same genus that were the most comparable in size and frond structure.

We conducted all analyses with the average productivity values of the two study years with the exception of two plots where only data from the second year were available.

At those elevation levels where the abundance of terrestrial ferns was very high, the measurements of biomass and productivity of the most abundant species were restricted to subplots of 10 m x 10 m nested in the respective main plots. This was the case for single plots at 1000 m, 2000 m, and 2500 m elevation. Destructive sampling (herbarium specimens, leaves and rhizomes for biomass measurements) was conducted on individuals outside of the study plots. Specimens of all species were deposited at the herbarium of the Pontificia Universidad Católica del Ecuador (QCA).

5.3.4 Tree biomass and productivity

In all plots, we conducted stem increment measurements by equipping all stems of a dbh ≥10 cm with dendrometer tapes (type D1; UMS, Munich, Germany) that were monitored at least once per year for stem diameter growth. Annual diameter increment was calculated by relating the diameter difference between the first and last reading to a full year. To calculate annual aboveground live woody biomass (AGB) and AGB increment (AGBI), we applied the allometric equation of Chave *et al.* (2005) which was derived for tropical wet forests, with stem diameter, wood specific gravity (WSG) and tree height as parameters. Plot-level AGB was calculated as the sum of the tree biomass of all individuals and AGBI as the sum of the related annual increments. WSG data for the tree species were obtained from Chave *et al.* (2006) or, in cases of missing information on species, genera or family means of WSG, were calculated from the same source and applied to the respective species. Tree height was measured with a Vertex IV height meter and a T3 transponder (Haglöf, Langsele, Sweden) in April/ May 2011. Growth monitoring started in 2005 in the plots at 500-2000m and data on AGB and AGBI of these plots were taken from Unger *et al.* (2012). Mean AGBI of the plots at 2500-4000 m was calculated over the period from 2009 to 2012. A more detailed description of the AGBI calculation is given in Unger *et al.* (2012).

5.3.5 Temperature measurements

Temperature was measured with three HOBO Pro loggers at each elevation level. The loggers were positioned at 2 m height on tree trunks and covered by a plastic cap to avoid direct sunlight and access of rain water. Measuring frequency was set to a high temporal resolution (every 30 min) to register temperature extremes; the minimum duration of measurement was 12 months.

5.3.6 Soil sampling

In order to characterize the study plots in terms of their soil chemistry and nutrient availability, we conducted a set of analyses in all 22 plots. Briefly, we extracted each four soil samples per plot. The plots were divided into four equally-sized quadrates of 10 m x 10 m size and the samples were taken in the centre of each quadrate using a soil corer of 5 cm diameter and 25 cm length. The soil core was split into two subsamples (organic layer material and upper 10 cm of mineral soil). The organic layer included the L, F, and H horizons of variable depth; the transition from the organic H horizon to the mineral soil Ah horizon was arbitrarily set at about 30 % organic matter content using morphological criteria of the substratum for estimating organic matter content. The upper mineral soil consisted of A- and B-horizons with much lower organic matter content than the organic layers themselves. In the laboratory at the University of Göttingen, the following parameters were measured: total carbon and nitrogen (gas chromatography), resin-extractable phosphorus (resin-bag method; Dowex 1 x 8–50) and soil pH (in KCl). The analytical methods are described in detail in Unger *et al.* (2010).

Since we assumed a strong influence of the vegetation on the chemical composition of the organic soil layers, all subsequent correlation analyses focused on the mineral topsoil and its importance for the vegetation.

5.3.7 Statistical analyses

Regression analyses (first or second order polynomial models) were applied to examine the relationships between leaf properties, biomass and productivity, and elevation. These regressions were calculated using Xact software (version 8.0; SciLab, Hamburg, Germany).

To investigate the influence of soil properties and temperature on biomass, productivity and SLA of ferns and trees, multiple linear regression models were fitted with R (R Development Core Team, 2012). The best model for each target parameter was chosen by inspection of the Akaike Information Criterion (AIC).

5.4 Results

5.4.1 Leaf traits, biomass and productivity along the elevation gradient

The analysis of leaf samples of 183 terrestrial ferns and of 220 trees for their nutrient concentrations showed diverging altitudinal trends for the different nutrient species (Fig. 5.2). However, ferns and trees showed congruent elevation gradients for a given element. For foliar N in fern and tree leaves, no significant change with elevation was detected. In contrast, the P concentration showed a significant increase with elevation in both groups (from 0.8 mg g^{-1} at 400m to 1.53 mg g^{-1} at c. 4000 m in ferns, and from 0.8 mg g^{-1} to 1.7 mg g^{-1} in trees; Fig 5.2a, b). No altitudinal trend was visible for the foliar C/N ratio, while the N/P ratio declined with increasing elevation in terrestrial ferns as well trees (Fig. 5.2c and d).

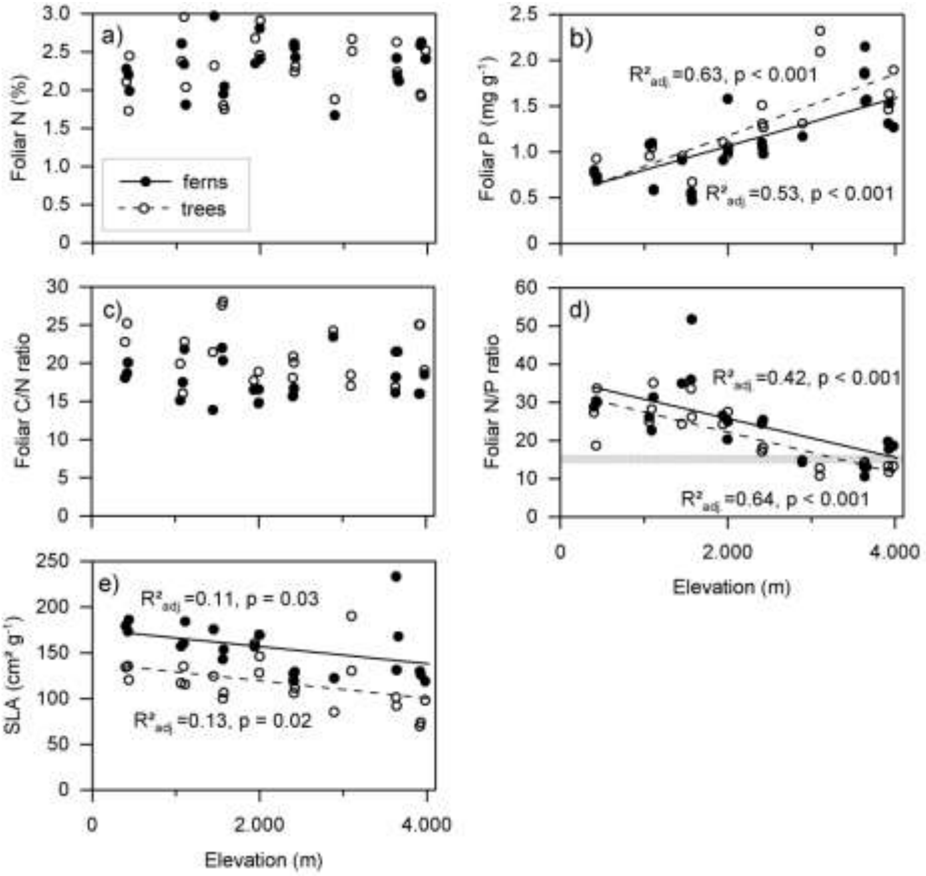

Figure 5.2. *Some chemical and morphological oliar traits of ferns and trees along the elvational gradient.* ***(a)*** *Foliar nitrogen and* ***(b)*** *phosphorus concentrations.* ***(c)*** *Foliar C/N ratio.* ***(d)*** *Foliar N/P ratio, the gray bar represents the transition zone between N limitation (N/P ratio < 14) and P limitation (N/P ratio > 16) (Townsend et al., 2007).* ***(e)*** *Specific leaf area. Shown are plot means for 22 plots (ferns) and 24 plots (trees).*

Specific leaf area (SLA) differed not significantly between fern fronds and tree leaves according to our analyses (Fig. 5.2e). Nevertheless, the SLA means of fern fronds were by c. 40 cm^2 g^{-1} higher than the tree leaf means throughout the whole transect reflecting the contrasting light exposure. Fern and tree leaves showed a similar linear SLA decrease from 400 to 4000m, even though the between-plot variation was considerable (ferns: adj. R^2 = 0.11, p = 0.03; trees: adj. R^2 = 0.13, p = 0.02; Fig. 5.2e). A particularly high SLA value was recorded for a plot at 3500 m, caused by the presence of the fern Cystopteris fragilis (L.) Bernh. with very thin pinnae (Appendix 6).

In contrast to the leaf trait variation along the slope, aboveground live biomass (AGB) and productivity (aboveground biomass increment, AGBI) followed markedly different altitudinal trends in terrestrial ferns and in trees. Fern biomass showed a clear hump-shaped curve with a peak at ~2500 m and very low values at highest (3500 – 4000 m) but also lowest elevation, while tree AGB decrease linearly from c. 350 Mg DM ha^{-1} at 400m to <100 Mg ha^{-1} at 4000 m (Fig. 5.3a). Aboveground productivity (production of fern fronds and rhizomes or tree stem wood production) mirrored the altitudinal biomass patterns with a mid-elevation peak of fern productivity at about 2000 – 2500 m and a continuous AGB decrease from c. 4.5 Mg DM ha^{-1} yr^{-1} at 400 m to <1 Mg ha^{-1} yr^{-1} at 4000 m in the trees (Fig. 5.3b).

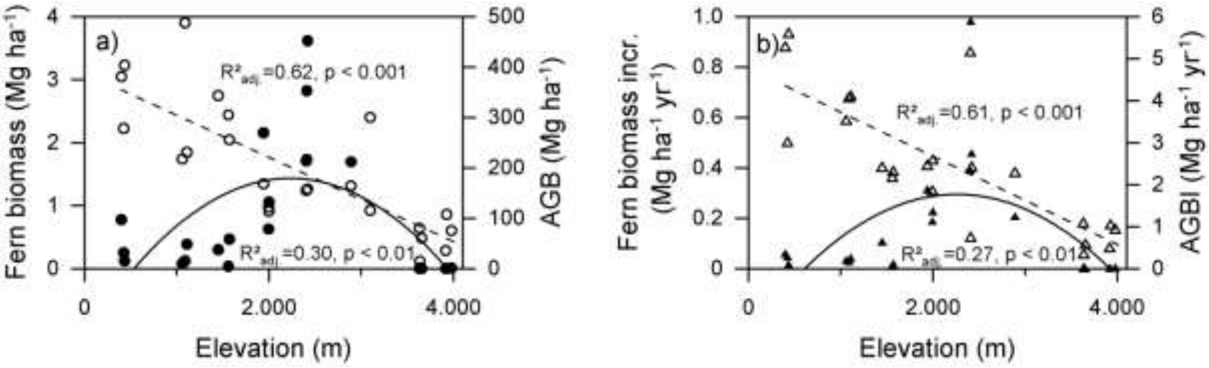

Fig. 5.3 ***(a)*** *Aboveground biomass (in Mg DM ha^{-}1) and* ***(b)*** *productivity (increment and AGBI, in Mg DM ha^{-1} yr^{-1}) of terrestrial ferns and trees along the elevation gradient (ferns: production of fronds and rhizomes; trees: wood production). Filled circles and triangles: ferns, unfilled circles and triangles: trees.*

5.4.2 Influence of soil chemistry and temperature on leaf traits, biomass and productivity

The regression analyses show that no significant relation existed between chemical and morphological leaf traits of terrestrial ferns and soil chemical conditions along the elevation transect. In fact, neither foliar N nor foliar P of the fern fronds revealed a dependence on soil C/N ratio or available P (P_a) in the soil (Fig. 5.4a and b). Similarly, the relations between SLA and soil C/N ratio or soil P_a were not significant in the ferns (Figs. 5.4c and d). Tree foliage differed from this pattern with significant negative relationships between foliar N and soil C/N and SLA and C/N (Figs. 5.4a and c); however, the scatter of the data was large.

Simple linear regression analyses indicated for fern AGB a significant negative relation to soil C/N ratio but no relation to organic layer depth (Figs. 5.5a and b). Similarly, tree AGB showed close negative relationships to these two soil parameters (Figs. 5.6a and b). For fern aboveground productivity, the dependence on soil C/N ratio was best described by a second order polynomial model with a maximum at a C/N ratio of ~12 (Fig. 5.5a) while no relation to organic layer depth appeared (Fig. 5.5b). None of these two soil parameters showed a significant relation to aboveground tree productivity (Figs. 5.6a and b). Neither pH nor available P (P_a) in the soil showed significant relations with biomass or productivity of fern or trees.

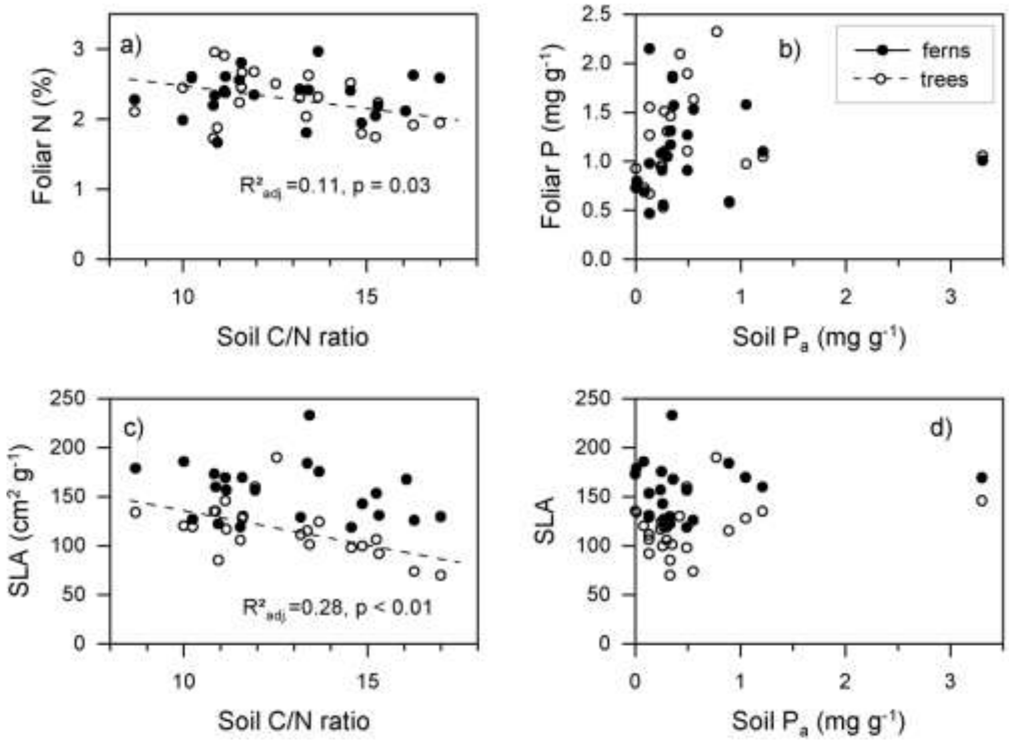

Fig. 5.4 *Variation of foliar N **(a)**, foliar P **(b)**, and SLA (**c** and **d**) in terrestrial fern fronds and sun-exposed tree leaves as a function of soil C/N ratio or available P in the soil (P_a). The regression equations of the significant relationships between N or SLA and soil C/N are given for tree leaves.*

According to multiple regression analyses, the biomass and productivity of ferns and trees along the transect is determined by different environmental factors (Table 5.2). The best models according to their AIC values suggest that fern biomass was primarily influenced by soil pH and temperature, while tree biomass was only influenced by temperature, but not by pH (Table 5.2). The aboveground productivity of ferns and trees was determined by both temperature and soil C/N ratio, but in addition showed a strong pH influence in the case of the ferns; the pH effect was absent in the trees. Specific leaf area was found to be influenced mainly by pH (and additionally by the depth of the organic layer, temperature and available P) in the trees, while no significant influencing factor was found for fern SLA.

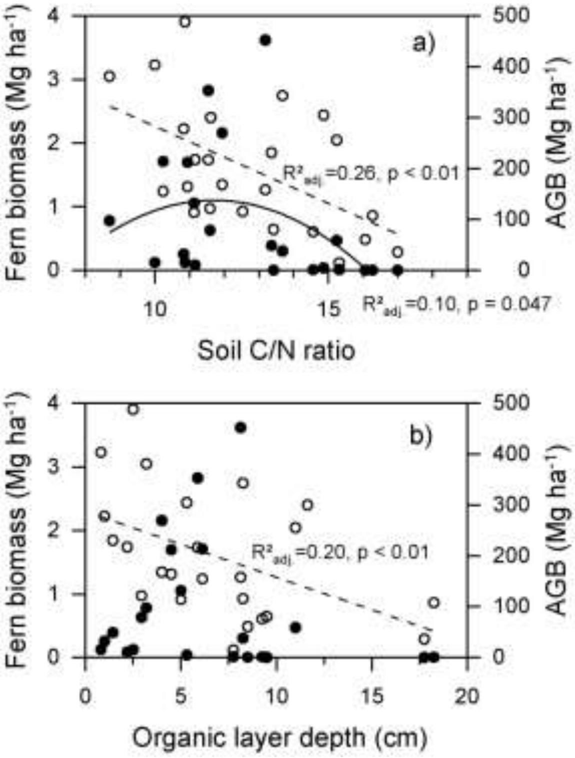

Fig. 5.5 *Dependence of fern and tree biomass on soil C/N ratio (a) and organic layer depth (b). Filled circles: ferns, open circles: trees.*

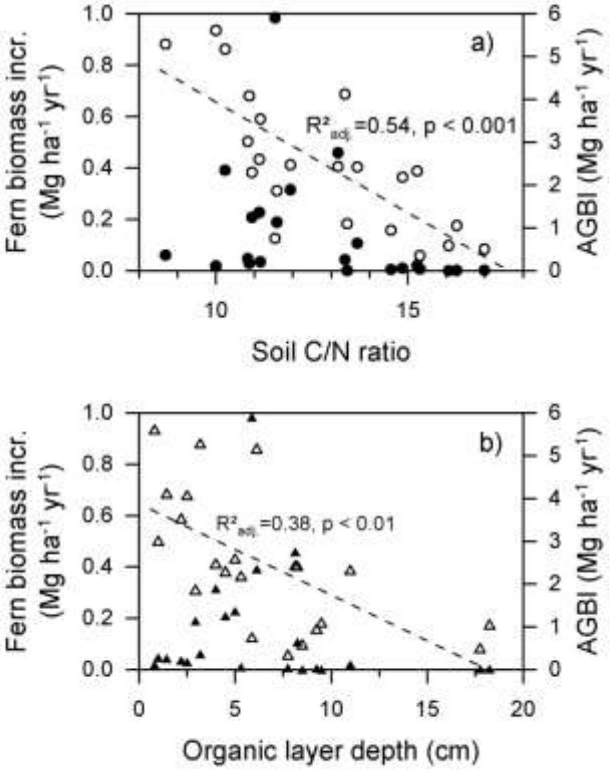

Fig. 5.6 *Dependence of fern and tree aboveground productivity on soil C/N ratio (a) and organic layer depth (b). Filled circles: ferns, open circles: trees*

Table 5.2 *Results of multiple regression analyses on the effects of soil C/N ratio, depth of the organic layer, pH, available phosphorus (P_a) and temperature on fern and trees biomass, productivity and SLA in the 24 studied plots. Presented are the best models with the lowest AIC value and with a minimum R^2 of 0.4.*

Dependent variable	Model P	Model R^2 (adjusted)	Independent variable	Parameter estimate	Standard error	P
Fern biomass	<0.001	0.54	pH	2.26	0.95	0.0286
			temperature	0.12	0.02	<0.001
Fern productivity	<0.001	0.61	C/N	-0.17	0.07	0.02379
			pH	2.31	0.69	<0.001
			temperature	0.04	0.02	0.10857
Tree biomass	<0.001	0.56	temperature	13.98	2.52	<0.001
Tree productivity	<0.001	0.64	C/N	-0.28	0.12	0.0353
			temperature	0.11	0.04	0.0155
Tree SLA	0.003	0.45	depth org. layer	-2.42	1.41	0.10328
			pH	65.65	21.07	<0.001
			Ppa	3.28	6.82	0.63599
			temperature	1.15	1.01	0.26879

Table 5.3 *Average mineral soil properties of the eight study sites.*

Elevational level (m a.s.l.)	Organic layer depth (cm)	pH(KCl)	C/N ratio	P_a (mg g^{-1})
500	1.67	4.02	9.84	1.61
1000	2.04	4.18	11.80	0.78
1500	8.19	4.28	14.59	0.17
2000	3.98	4.44	11.55	0.07
2500	6.71	4.34	11.66	0.46
3000	8.13	4.60	11.69	0.28
3500	8.58	4.28	14.93	0.23
4000	15.08	4.21	15.94	0.51

5.5 Discussion

Both nitrogen and phosphorus shortage have been found to limit the productivity of terrestrial ecosystem in large regions of the globe (Elser *et al.*, 2007; LeBauer and Treseder, 2008). In both terrestrial ferns and trees, we found foliar N concentration to remain more or less invariant across the 3600 m-long elevation gradient in Ecuador. This finding contrasts with the only other study in neotropical mountain forests reporting foliar nutrient concentrations in ferns to increase at the community level along an elevation gradient in Bolivia (Wegner, *et al.*, 2003). For tree leaves, in contrast, many studies reported decreases of foliar N concentration with elevation (Vitousek *et al.*, 1988; Tanner *et al.*, 1998; Raich *et al.*, 1997; Soethe *et al.*, 2008; van de Weg *et al.*, 2009**)** while invariant N concentrations are the exception. Our results indicate that the terrestrial ferns and also the trees accumulated N in their foliage in apparent independence from the thermal regime across the transect, even though mean annual temperature decreased by about 20 °C from 400 to 4000 m a.s.l.

Aboveground tree biomass decreased by a factor of three or four from lowland to upper montane elevation in Ecuador suggesting that leaf biomass was greatly reduced along the transect as well. A leaf biomass and leaf area reduction of the canopy trees has been shown to occur in tropical mountain forests according to a global literature review conducted by Moser *et al.* (2007). Thus, constant leaf N concentrations in the trees from 400 to 4000 m could well be the consequence of simultaneous reductions in the amount of carbon available for leaf production due to lowered canopy C gain and in the amount of N taken up by the plants which may result from reduced soil N supply with increasing elevation and decreasing temperature.

The situation is different in the terrestrial ferns which maintained a constant foliar N concentration along the transect despite large biomass and productivity decreases at both low and high elevation. The remarkable invariance of foliar N concentration and foliar C/N ratio despite a biomass variation by a magnitude suggests that the terrestrial ferns in this transect were supplied with sufficient amounts of soil N from the lowlands to the timberline. The absence of significant differences between the plant life forms (trees vs. ferns) in foliar N and P concentrations in our study is partly in agreement with the literature where no clear trend toward higher or lower foliar nutrient concentrations in ferns compared to angiosperms is visible (e.g. Quested *et al.*, 2003; Wright *et al.*, 2004).

In contrast to N, the altitude (temperature) effect on foliar P concentration was strong in both plant groups suggesting a progressive release from P limitation of growth with increasing elevation. A similar altitudinal increase in foliar P concentration in ferns was reported from the Bolivian transect (Wegner *et al.*, 2003) while for trees, deviating altitudinal P concentration trends (decreases or mid-elevation peaks) have been reported from tropical wet mountains (Raich *et al.*, 1997; Tanner *et al.*, 1998; Soethe *et al.*, 2008). The large reduction in foliar N/P ratio with elevation in both plant groups is strong support for the hypothesis that, in this transect, an assumed growth limitation of the trees and ferns manifests in a shift from P limitation at low elevation to N limitation at high elevation as was suggested by Vitousek and Farrington (1997). The highly significant negative correlation between soil C/N ratio (as a rough estimate of N availability) and aboveground productivity of the trees (but not the ferns) indicates that the N limitation of growth at higher elevation, if it is relevant, must be stronger in the trees than the ferns. A remarkable result of our study is that terrestrial ferns and the sun-exposed tree leaves trees were so similar with respect to their foliar N/P ratio. This can be interpreted in the sense that neither the light regime (understorey vs. overstorey) nor the growth form is an important determinant of this element ratio in this environment.

While the systematic (though non-significant) SLA difference between fern and tree leaves is a reflection of the different light regimes, the linear SLA decreases with elevation point to the production of thicker (and smaller but longer-living) leaves and fronds in the montane and upper montane forest. Moser *et al.* (2007) were able to quantify the negative SLA – leaf lifespan relation for tropical mountain forest trees in southern Ecuador in a study of leaf survivorship across an elevation gradient. Since the foliar N concentration remained invariant and foliar P increased with elevation in our transect, one would assume that the SLA reduction was mainly caused by other factors than nutrient shortage such as the unfavourable thermal regime at high elevations which demands for more robust leaves with extended longevity. However, we found a significant SLA decrease with increasing soil C/N ratio for the trees (but not the ferns) which makes it likely that N shortage is at least an additional factor causing tree leaf SLA to decrease with elevation in this transect.

A role for N availability as a determinant of high-elevation SLA was also assumed for an altitudinal transect in southern Ecuador (Moser *et al.*, 2011).

We found a striking difference between ferns and trees with respect to the patterns of altitudinal change in biomass and productivity which is clear evidence in support of the hypothesis that both plant groups are growth-limited by different factors. The biomass and productivity peak in the ferns at 2500 m suggests that air humidity (possibly in combination with soil moisture) should play a key role since this maximum corresponds to the cloud condensation level in the Ecuadorian Andes. Nutrient availability can only be of secondary importance for fern productivity, if it plays a role at all.

No significant relationship was detected between the three key leaf functional traits and soil chemical properties in the case of the ferns, while foliar N (and SLA) showed a dependence on soil C/N in the trees. This discrepancy between the plant life forms may be explained by the fact that foliar nutrient concentrations are dependent on both plant uptake and carbon gain which dilutes the nutrient in the biomass. Factors other than nutrients (such as air humidity or light availability in the understorey) must be the main determinants of fern productivity, thereby decoupling foliar nutrient concentration from soil nutrient availability and plant uptake, while these factors seem to be less important for tree growth.

A dominant positive effect of soil pH on fern productivity was identified which is not easy to explain. While a direct harm of high concentrations of H+ to fern roots is not very likely, a possible explanation could be that an increase in pH most likely will improve the plant-availability of P in the soils of the transect. Along the transect, soil pH was mostly below 4.5 (table 5.3) where P is increasingly immobilized by the presence of Al and Fe oxides and hydroxides. P fertilization experiments with ferns could help to understand the apparent pH dependency of fern productivity.

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Chapter 6

General conclusions

6.1 A summary of the findings

In this chapter, the results of this study are summarized and assessed with the objectives and hypotheses as presented in the first chapter.

6.1.1 Diversity of ferns and its relationship with productivity

The first objective of this study was to evaluate the changes in species richness of terrestrial ferns along the elevational gradient and to relate these changes to climatic variables in order to assess their relative importance in driving fern richness patterns.

Although terrestrial ferns are the main group of plants for this study, we included epiphytic fern species to obtain a more comprehensive overview of total species richness (Chapter 3). We found a total of 91 terrestrial fern species in 34 genera and 20 families (Appendix 4). Based on morphospecies characteristics, we found 259 species of epiphytes distributed in 49 genera and 21 families. Along our elevational gradient in Ecuador, terrestrial and epiphytic fern species richness showed a hump-shaped pattern with the highest values at about 2,000 m which is the common pattern along tropical elevation gradients for ferns (e.g. Bhattarai *et al.*, 2004; Kluge and Kessler, 2011; Kessler *et al.*, 2011). In addition, we found that all climatic variables (temperature, air humidity and precipitation) were related to species richness. However, the variability of temperature and precipitation performed better than the respective raw values, which suggests that fern diversity is primarily driven by energy-related variables (temperature and humidity) and that a low annual variability of these factors favors species rich fern communities. This coincides with other studies that reported the highest values of species richness at mid elevation and reflected balanced climate without extremes like drought at low elevations and frost at high elevations (Kessler, 2001; Hemp, 2002; Battarai *et al.*, 2004; Krömer *et al.*, 2005; Kluge and Kessler, 2007; Kessler *et al.*, 2011).

As we showed in Chapter 3, climatic conditions may influence the local species richness patterns. However, on-site climatic measurements have been proven difficult to obtain and alternatively the epiphytic bryophyte cover has been proposed that can be used as an indicator of air humidity conditions. In Chapter 2 the intuitively appealing relationship of bryophyte cover on canopy branches and relative humidity was demonstrated as predicted by e.g. Frahm and Gradstein (1991), Gehrig Downie *et al.* (2011), Kluge *et al.* (2006), Obregon *et al.* (2009), Sporn et al. (2009), and Wolf (1993). In addition, the visual estimation of bryophyte cover on branches can be used as a proxy for air humidity, on the condition that temperature and elevation are taken into account within a restricted study region. However, these results might not be applicable for comparisons across extensive elevational gradients or wide differences in temperature.

To understand the findings of Chapter 4, the following general information is relevant: we conducted the analyses at two spatial extents: across the entire elevational gradient and within elevational belts.

Objectives 2 and 3 were to evaluate the productivity at the level of the fern assemblages (terrestrial fern above ground increment $ABGI_{ferns}$) and at two ecosystem levels: Actual evapotranspiration (AET) and tree aboveground biomass increment ($ABGI_{trees}$) along the elevational gradient, and to determine the relationship between terrestrial fern species richness and these three productivity levels. Along the elevational gradient, the relationship between species richness and both levels of ecosystem productive was non-significant because of the strong variation in the contribution of ferns to the local floras, which is reflected in higher values of terrestrial species richness, number of individuals, and biomass of terrestrial ferns at mid elevations of the gradient (Willinghöfer *et al.,* 2012). With this result, we reject our *H1* hypothesis regarding a positive relationship between terrestrial fern richness and ecosystem productivity.

In contrast, we found a significant relationship between species richness and fern productivity ($AGBI_{ferns}$), which confirmed our *H2* hypothesis regarding a positive relationship between terrestrial fern richness and fern assemblage productivity. This latter pattern is due to an increase in the number of fern individuals, which allows more species to coexist. Our results suggest that ecosystem productivity is not a proper measure of the energy available to ferns, which is in accordance with previous studies (Kluge *et al.,* 2006; Kessler *et al.,* 2011).

On the other hand, within elevational belts, the fern relative species richness per plot was marginally negatively related to $AGBI_{ferns}$, but not to $AGBI_{trees}$. These findings suggest that the richness-productivity relationship (SPRP) is scale dependant, that negative relationships are most likely to be determined by interspecific competition, and that such relationships should be most influential at small spatial scales (Evans *et al.,* 2005;

Whittaker, 2010). According to these results, the influencing factors on SRPR at this special scale are not the comparable to those along the elevational gradient.

After we established the fern richness - AGBI$_{\text{ferns}}$ relationship, the causal mechanisms of the relationship between terrestrial species richness and productivity were asseses by Objective 4. Based on Evans *et al*. (2005), testing the following hypotheses, which are presented with their respective results:

H3a: The relationship between terrestrial fern richness and ecosystem productivity is determined by the sampling effect. *H3b*: The relationship between terrestrial fern richness and fern assemblage productivity is determined by the sampling effect. Along the elevational gradient, we found that Fisher´s Alpha of the terrestrial fern assemblages was significantly related to AGBI$_{\text{ferns}}$, but not to AET or AGBI$_{\text{trees}}$, which suggested that SPRPs could not be entirely explained by the sampling effect when AGBI$_{\text{ferns}}$ was used as a measure of productivity. Thus, hypothesis *H3a* was rejected and *H3b* supported at this scale. In contrast, within elevational belts, fern relative Fisher´s Alpha was negatively related to relative AGBI$_{\text{ferns}}$, but not related to AGBI$_{\text{trees}}$, which supported hypotheses *3a* and b at this scale.

H4: The species richness-productivity relationship of terrestrial ferns is determined by the increased population size mechanism. Along the elevational gradient, Fisher´s Alpha of the terrestrial ferns assemblage was significantly correlated to the total number of fern individuals per plot, and the number of fern individuals per plot and AGBI$_{\text{ferns}}$ were significantly correlated. These findings, supported the increased population size mechanism (Wright, 1983), therefore, supporting hypothesis *H4* at this scale. However, within elevational belts, relative Fisher´s Alpha of ferns was marginally negatively related to the relative number of fern individuals per plot and there was no relationship between relative number of fern individuals and AGBI$_{\text{ferns}}$, which rejected the increased population size mechanism at this scale. Different factors may determine SRPRs at the two special scales of our study.

H5: The species richness-productivity relationship of terrestrial ferns is determined by the niche position mechanism. Along the elevational gradients, there was: i) a significant decline of Evenness with AGBI$_{\text{ferns}}$, ii) a correlation between Evenness and Fisher´s Alpha, iii) no significant relationship between Fisher´s Alpha and the mean number of individuals per species and plot, and iv) a significant change with elevation on the mean number of individuals. These results supported the niche position mechanism (Evans *et al*., 2005), and therefore confirmed hypothesis *H5* at this scale. However, it is important to clarify that this support is circumstantial because we were unable to test alternative hypotheses that might confirm the niche position mechanism. In contrast, within elevational belts, we found no significant relationship between relative Evenness and $AGBI_{ferns}$, and no significant relationship between relative Evenness and relative Fisher´s Alpha. However, we found a strong negative relationship between relative Fisher´s Alpha and the relative mean number of individuals per species and plot and also a significant relationship between the relative mean number of individuals and $AGBI_{ferns}$, thus rejecting hypothesis *H5* at this small scale.

H6: The species richness-productivity relationship of terrestrial ferns along the elevational gradient is influenced by source-sink effects. We found that along the elevational gradient, the influence of source-sink dynamics on SRPRs is rather weak overall, which rejected hypothesis *H6* at this scale. However, within elevational belts, source-sink effects might modify the SRPR, partially supporting hypothesis *H6* at this scale.

In summary, we found that fern diversity was related to the productivity of the fern assemblages, but only marginally to that of the ecosystems. Along the elevational gradient, we found a positive SRPR that appeared to be determined by an increase in the number of fern individuals and by niche availability. When comparing plots within elevational belts, we found a negative SRPR that was likely driven by interspecific competition. We thus argue that at both spatial scales of our study, fern diversity appears to be limited by the number of available niches and competition to occupy these niches.

6.1.2 Nutrient availability

Although terrestrial ferns are the main group of plants for this study, we included trees in order to compare indicators of plant nutrition, biomass and productivity of two primary producer groups, trees and terrestrial ferns (Objectives 5 and 6) because of the interesting contribution to the nutrient ecology.

6.1.2.1 Leaf traits, biomass and productivity along the elevation gradient

We found that ferns and trees display similar elevational patterns on the foliar functional traits evaluated in this study, namely foliar N and P concentrations, and SLA supporting *H7*, but rejecting *H8* hypothesis. P concentration showed a significant increase with elevation in both groups, while for foliar N, no significant change with elevation was detected; these findings were not in agreement with previous studies (for ferns: Wegner *et al*., 2003; for trees: Vitousek *et al*., 1988; Tanner *et al*., 1998; Raich *et al*., 1997; Soethe *et al*., 2008; van de Weg *et al*., 2009). In addition, these results suggested that in our study area, altitude or temperature had no effect on the availability of N.

Specific leaf area (SLA) of ferns and trees showed a similar decrease with increasing elevation. However, it is intriguing that values of SLA of trees are about 40 cm^2 g^{-1} lower than fern values along the entire elevational gradient, possibly due to the contrasting light exposure (Moser *et al*., 2007).

On the other hand, AGB and AGBI followed different trends in terrestrial ferns and trees. AGB_{ferns} and $AGBI_{ferns}$ showed a hump-shaped pattern with a peak at mid elevations, while AGB_{trees} and $AGBI_{trees}$ drecreased linearly with elevation. A monotonic pattern has been shown to occur in trees in tropical mountain forests according to a global literature review conducted by Moser *et al.* (2007). However, this is the first study to evaluate AGB_{ferns} and $AGBI_{ferns}$ in ferns at local scale along an elevational gradient.

6.1.2.2 Influence of soil chemistry and temperature on leaf traits, biomass and productivity

Chemical and morphological leaf traits of terrestrial ferns were not influenced by soil chemical conditions along the elevation transect following linear regression analysis. In contrast, significant negative relationships between foliar N and soil C/N, and SLA and C/N were showed for trees. Thus, our *H9* hypothesis was rejected for ferns and partially supported for trees. These findings may be explained by the fact that foliar nutrient concentrations are dependent on both plant uptake and carbon gain which dilutes the nutrient in the biomass. Other possible factors, such as air humidity or light availability in the understory, may be the main determinants of fern productivity.

Simple linear regression analyses indicated a significant negative relation between AGB_{fern} and soil C/N ratio. AGB_{trees} showed close negative relationships to C/N ratio and organic layer depth. For $AGBI_{fern}$, the dependence on soil C/N ratio was best described by a second order polynomial model, while no relation to organic layer depth appeared and none of these two soil parameters showed a significant relation to $AGBI_{trees.}$

According to multiple regression analyses, the biomass and productivity of ferns and trees along the transect was determined by different environmental factors. AGB_{ferns} biomass was primarily influenced by soil pH and temperature, while AGB_{trees} was only influenced by temperature, but not by pH. The $AGBI_{ferns}$ and $AGBI_{trees}$ were determined by both temperature and soil C/N ratio, whereas pH had a strong influence for ferns only. The specific leaf area was influenced mainly by pH (and additionally by the depth of the organic layer, temperature and available P) in trees, while no significant influencing factor was found for fern SLA. According to these results, *H9* hypothesis is partially supported for $AGBI_{ferns}$ and $AGBI_{trees}$; however, a dominant positive effect of soil pH on fern productivity was identified. A possible explanation could be that an increase in pH will most likely improve the plant-availability of P in the soils of the transect.

6.2 The most significant remarks of this study

While it is generally assumed that ferns increase in abundance with increasing atmospheric moisture along mountain transects, precise quantitative data on terrestrial fern biomass across long tropical elevation transects from lowland to timberline do not exist. Thus, this is the first study in which the elevation-dependence of the productivity of terrestrial ferns in tropical mountain transect is examined. Furthermore, this is the first study to assess the SRPR in ferns and more generally one of very few to address this topic for plants at the local scale (Oberle *et al.*, 2009, Axmanová *et al*., 2012, Reich *et al*., 2012).

Our study also presents the first evidence that energy availability and competition affect the diversity of tropical herb assemblages at the local scale.

It is not known whether terrestrial ferns have higher or lower foliar N concentrations than trees at the same site, thus in our study we compared for first time indicators of plant nutrition, biomass and productivity among co-occurring trees and terrestrial ferns.

6.3 Suggestions for further studies

Many of our conclusions on Chapter 4 are based on circumstantial evidence and call to be tested by additional approaches. For example, to better understand the role of competition in structuring fern assemblages, it might be instructive to compare assemblages with similar abiotic conditions but different species pools (e.g. mainland assemblages and depauperate assemblages on isolated islands, Keppel *et al*., 2010). In such a comparison, species poor assemblages would be expected to have less interspecific competition, which leads to broader realized niches and increasing abundances of the individual species. Perhaps more importantly, experimental approaches would be appropriate to confirm the structuring roles of niche availability and competition.

We made a comparison of foliar functional traits, biomass and productivity between terrestrial ferns and trees; however, a comparison between terrestrial ferns and herbaceous angiosperm that share the same light condition may offer new insights.

A dominant positive effect of soil pH on fern productivity was not easy to explain, for this reason we think that P fertilization experiments with ferns could help to understand the apparent pH dependency of fern productivity.

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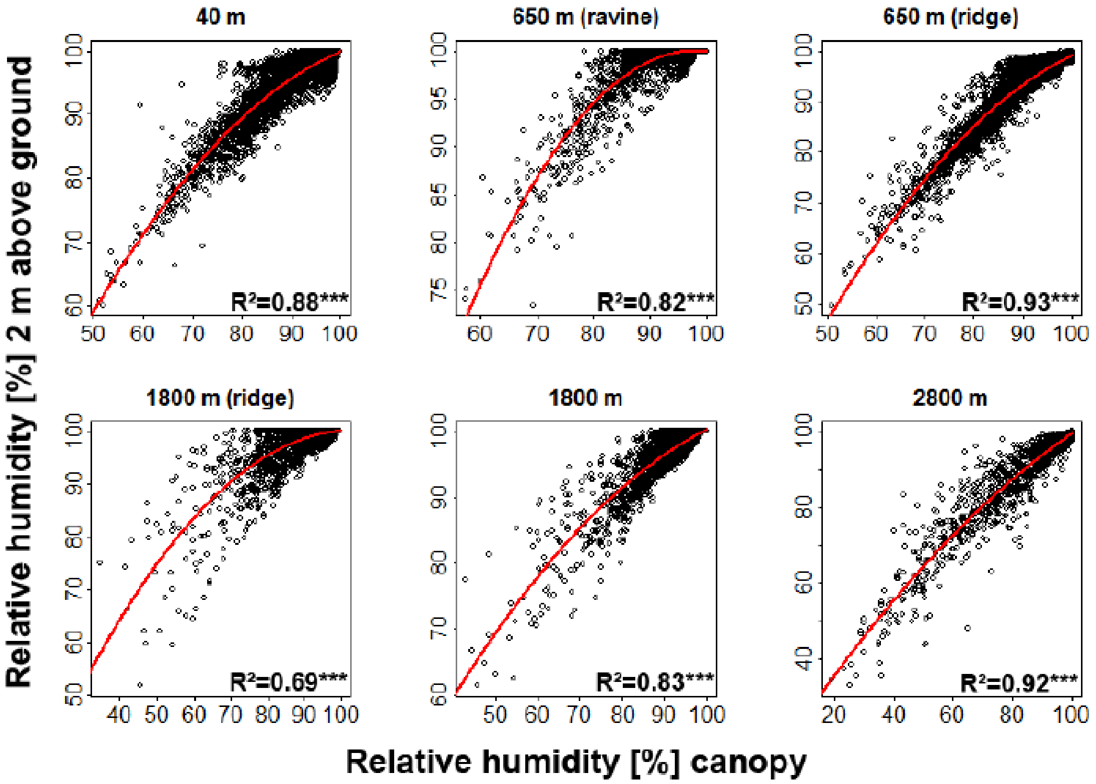
Appendices

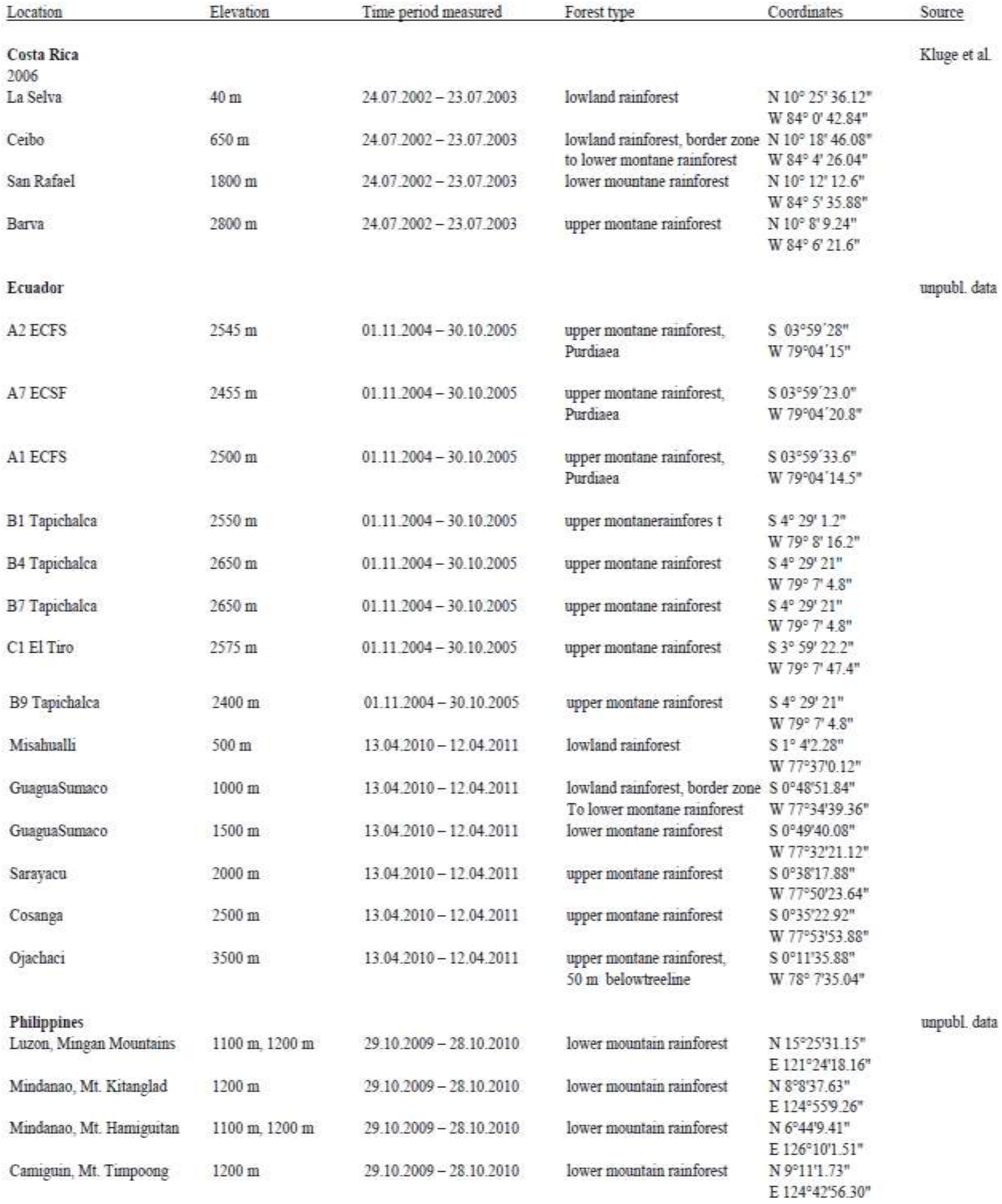
Appendix 1 to Chapter 2

Relationship of relative humidity [%] measured 2 m above the ground with relative humidity [%] measured in the canopy at four different elevations. Ravine refers to measuring sites located in a ravine within the forest, ridge to a measuring site located on a mountain ridge. Red lines show the quadratic regressions. p<0.05*,p<0.01**,p<0.001***.



Appendix 2 to Chapter 2

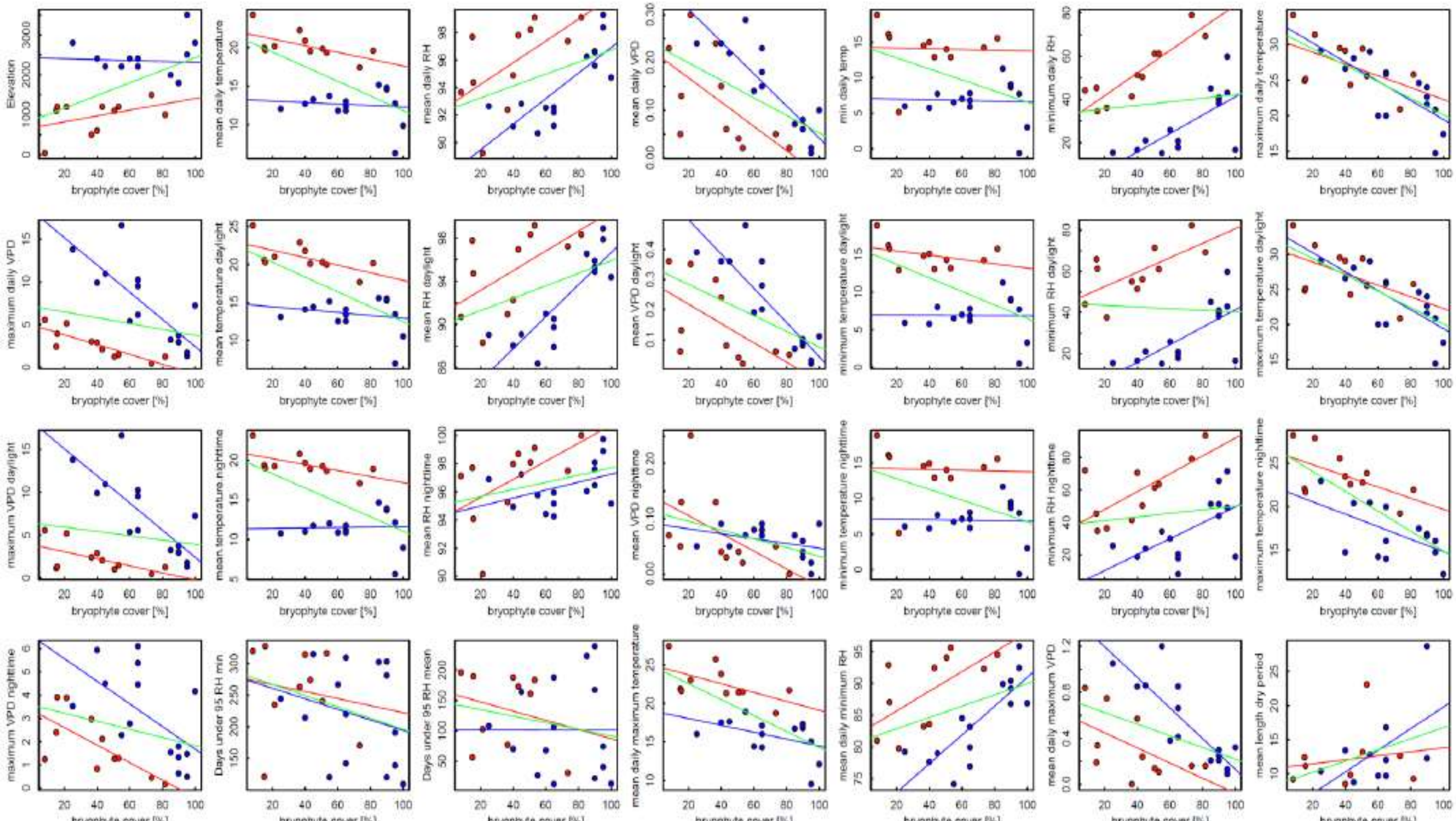
Data source



Location	Elevation	Time period measured	Forest type	Coordinates	Source
Costa Rica					Kluge et al.
2006					
La Selva	40 m	24.07.2002 – 23.07.2003	lowland rainforest	N 10° 25' 36.12" W 84° 0' 42.84"	
Ceibo	650 m	24.07.2002 – 23.07.2003	lowland rainforest, border zone to lower montane rainforest	N 10° 18' 46.08" W 84° 4' 26.04"	
San Rafael	1800 m	24.07.2002 – 23.07.2003	lower mountane rainforest	N 10° 12' 12.6" W 84° 5' 35.88"	
Barva	2800 m	24.07.2002 – 23.07.2003	upper montane rainforest	N 10° 8' 9.24" W 84° 6' 21.6"	
Ecuador					unpubl. data
A2 ECFS	2545 m	01.11.2004 – 30.10.2005	upper montane rainforest, Purdiaea	S 03°59´28" W 79°04´15"	
A7 ECSF	2455 m	01.11.2004 – 30.10.2005	upper montane rainforest, Purdiaea	S 03°59´23.0" W 79°04´20.8"	
A1 ECFS	2500 m	01.11.2004 – 30.10.2005	upper montane rainforest, Purdiaea	S 03°59´33.6" W 79°04´14.5"	
B1 Tapichalca	2550 m	01.11.2004 – 30.10.2005	upper montanerainfores t	S 4° 29' 1.2" W 79° 8' 16.2"	
B4 Tapichalca	2650 m	01.11.2004 – 30.10.2005	upper montane rainforest	S 4° 29' 21" W 79° 7' 4.8"	
B7 Tapichalca	2650 m	01.11.2004 – 30.10.2005	upper montane rainforest	S 4° 29' 21" W 79° 7' 4.8"	
C1 El Tiro	2575 m	01.11.2004 – 30.10.2005	upper montane rainforest	S 3° 59' 22.2" W 79° 7' 47.4"	
B9 Tapichalca	2400 m	01.11.2004 – 30.10.2005	upper montane rainforest	S 4° 29' 21" W 79° 7' 4.8"	
Misahualli	500 m	13.04.2010 – 12.04.2011	lowland rainforest	S 1° 4'2.28" W 77°37'0.12"	
GuaguaSumaco	1000 m	13.04.2010 – 12.04.2011	lowland rainforest, border zone To lower montane rainforest	S 0°48'51.84" W 77°34'39.36"	
GuaguaSumaco	1500 m	13.04.2010 – 12.04.2011	lower montane rainforest	S 0°49'40.08" W 77°32'21.12"	
Sarayacu	2000 m	13.04.2010 – 12.04.2011	upper montane rainforest	S 0°38'17.88" W 77°50'23.64"	
Cosanga	2500 m	13.04.2010 – 12.04.2011	upper montane rainforest	S 0°35'22.92" W 77°53'53.88"	
Ojachaci	3500 m	13.04.2010 – 12.04.2011	upper montane rainforest, 50 m belowtreeline	S 0°11'35.88" W 78° 7'35.04"	
Philippines					unpubl. data
Luzon, Mingan Mountains	1100 m, 1200 m	29.10.2009 – 28.10.2010	lower mountain rainforest	N 15°25'31.15" E 121°24'18.16"	
Mindanao, Mt. Kitanglad	1200 m	29.10.2009 – 28.10.2010	lower mountain rainforest	N 8°8'37.63" E 124°55'9.26"	
Mindanao, Mt. Hamiguitan	1100 m, 1200 m	29.10.2009 – 28.10.2010	lower mountain rainforest	N 6°44'9.41" E 126°10'1.51"	
Camiguin, Mt. Timpoong	1200 m	29.10.2009 – 28.10.2010	lower mountain rainforest	N 9°11'1.73" E 124°42'56.30"	

Appendix 3 to chapter 2

Different measurements of air humidity and temperature in comparison to bryophyte cover.


Elevation
mean daily temperature
mean daily RH
mean daily VPD
min daily temp
minimum daily RH
maximum daily temperature
maximum daily VPD
mean temperature daylight
mean RH daylight
mean VPD daylight
minimum temperature daylight
minimum RH daylight
maximum temperature daylight
maximum VPD daylight
mean temperature nighttime
mean RH nighttime
mean VPD nighttime
minimum temperature nighttime
minimum RH nighttime
maximum temperature nighttime
maximum VPD nighttime
Days under 95 RH min
Days under 95 RH mean
mean daily maximum temperature
mean daily minimum RH
mean daily maximum VPD
mean length dry period
bryophyte cover [%]

Appendix 4 to Chapter 3

Full species list and general information about terrestrial fern species along the elevational gradient in Napo, Ecuador. Minimum (Min) and maximum (Max) observed elevation, number of plots (N) in which the species were recorded (total 24 plots) and mean number of individuals per plot (ind) is given.

Species	**Min**	**Max**	**N**	**ind**
Aspleniaceae				
Asplenium flabellatum Kunze	2500	2500	3	2
Asplenium harpeodes Kunze	3000	3000	2	10
Asplenium laetum Sw.	2000	2500	6	2.16
Asplenium rutaceum (Willd.) Mett.	2000	2500	4	1
Asplenium serra Langsd. & Fisch.	3000	3000	1	7
Asplenium sp.	3500	3500	1	1
Blechnaceae				
Blechnum chilense (Kaulf.) Mett.	3000	3500	3	8.6
Blechnum cordatum (Desv.) Hieron.	2500	2500	2	8
Blechnum divergens (Kunze) Mett.	2000	2500	6	17.16
Blechnum sprucei C.Chr.	2500	2500	3	33.6
Salpichlaena hookeriana Alston	2000	2000	1	10
Salpichlaena volubilis J.Sm.in Hk.	1000	1000	3	11.6
Cyatheaceae				
Alsophila erinacea (H.Karst.) D.S.Conant	2000	2000	3	2.6
Alsophila paucifolia Baker	1000	1500	3	3.3
Cyathea aemula Lehnert	1500	1500	3	14
Cyathea bipinnatifida (Baker) Domin	1500	1500	2	4
Cyathea cf. fulva (M. Martens & Galeotti) Fée	3000	3000	1	8
Cyathea cf. microdonta (Desv.) Domin	2500	2500	2	2.5
Cyathea guentheriana Lehnert	3000	3000	1	2
Cyathea quitensis (Domin) R.M.Tryon	2000	2000	1	2
Cyathea lasiosora (Mett. ex Kuhn) Domin	2000	2000	2	8
Cyathea tortuosa R.C. Moran	500	2500	10	32.3
Cyathea tungurahuae Sodiro	3000	3000	2	14
Cyathea xenoxyla Lehnert	2500	2500	3	12.3

Cystopteridaceae				
Cystopteris fragilis (L.) Bernh.	3500	3500	1	5
Dennstaedtiaceae				
Dennstaedtia auriculata H. Navarrete & B. Øllg.	2500	2500	3	7.3
Dennstaedtia dissecta (Sw.) T. Moore	2000	2500	6	12.16
Hypolepis crassa Maxon	3500	4000	6	35.3
Hypolepis hostilis (Kunze) C. Presl	2000	2500	5	6.6
Hypolepis bogotense H. Karst.	3000	4000	4	17.25
Dicksoniaceae				
Dicksonia sellowiana Hook.	2000	2000	2	1
Lophosoria quadripinnata (J.F. Gmel.) C. Chr.	2500	3000	2	3.5
Dryopteridaceae				
Bolbitis lindigii (Mett.) C. Chr.	1000	1000	1	4
Bolbitis sp.	1000	1000	2	5
Ctenitis microchlaena (Fée) Stolze	1000	1000	1	102
Cyclodium meniscioides (Willd.) C. Presl	500	1500	6	13.5
Cyclodium trianae (Mett.) A.R. Sm.	500	500	3	149
Elaphoglossum albescens (Sodiro) H. Christ	3500	3500	1	1
Elaphoglossum antisanae (Sodiro) C. Chr.	3500	3500	1	2
Elaphoglossum atropunctatum Mickel	3500	4000	2	5
Elaphoglossum castaneum (Baker) Diels	2000	3000	4	4.75
Maxonia apiifolia (Sw.) C. Chr.	1000	2000	9	27.6
Megalastrum andicola (C. Chr.) A.R. Sm. & R.C. Moran	2000	3000	6	10.8
Megalastrum sp.	1500	1500	1	2
Polybotrya crassirhizoma Lellinger	500	500	2	2
Polystichum lehmannii Hieron.	2500	3500	6	24
Polystichum muricatum (L.) Fée	2000	2000	1	18
Polystichum orbiculatum (Desv.) J. Rémy & Fée	3500	3500	1	1
Equisetaceae				
Equisetum bogotense Kunth	3000	3000	1	35
Hymenophyllaceae				
Trichomanes pinnatum Hedw.	500	500	2	11.5
Trichomanes elegans Rich.	1500	1500	1	18
Trichomanes plumosum Kunze	1500	1500	1	3

Lindsaeacea				
Lindsaea divaricata Klotzsch	500	500	2	36
Lindsaea taeniata K.U. Kramer	500	500	2	2
Marattiaceae				
Danaea elliptica Sm.	500	1000	4	4.25
Danaea humilis T. Moore	500	1000	2	1.5
Danaea moritziana C. Presl	1500	2500	8	130.6
Marattia laevis Sm.	2000	2500	5	10
Metaxyaceae				
Metaxya rostrata (Kunth) C. Presl	500	500	2	5
Ophioglossaceae				
Botrychium virginianum (L.) Sw.	3000	3000	2	18
Polypodiaceae				
Campyloneurum amphostenon (Kunze ex Klotzsch) Fée	3000	3000	1	2
Serpocaulon fraxinifolium (Jacq.) A.R. Sm.	2000	2500	4	4
Serpocaulon subandinum (Sodiro) A.R. Sm.	3000	3500	3	1.3
Serpocaulon sp.	1500	1500	1	1
Pteridaceae				
Adiantum humile Kunze	500	1500	8	11.8
Pteris altissima Poir.	1500	1500	1	1
Pteris coriacea Desv.	2000	2500	6	21.6
Pteris livida Mett.	2000	2500	5	4.6
Pteris muricata Hook.	3000	3000	3	27.3
Pteris podophylla Sw.	2500	2500	3	3.3
Saccolomataceae				
Saccoloma elegans Kaulf.	500	500	1	2
Saccoloma inaequale (Kunze) Mett.	2000	2000	1	2
Schizaeaceae				
Schizaea sp.	1500	1500	1	15
Tectariaceae				

Tectaria antioquiana (Baker) C. Chr.	500	1000	5	46.8
Thelypteridaceae				
Thelypteris biformata (Rosenst.) R.M. Tryon	1000	2000	7	10.8
Thelypteris caucaensis (Hieron.) Alston	3500	4000	5	7
Thelypteris funckii (Mett.) Alston	2000	2000	2	2.5
Thelypteris gardneriana (Baker) C.F. Reed	500	500	2	6.5
Thelypteris glandulosa (Desv.) G. R. Proctor	500	500	2	15
Thelypteris glandulosolanosa (C. Chr.) R.M. Tryon	3000	3000	3	23.3
Thelypteris macrophylla (Kunze) C.V. Morton	500	1000	2	6
Thelypteris rudis (Kunze) G. R. Proctor	2500	2500	2	12
Woodsiaceae				
Diplazium alienum (Mett.) Hieron.	1500	1500	1	167
Diplazium costale (Sw.) C. Presl	2000	2500	6	174.1
Diplazium expansum Willd.	1000	1000	2	41
Diplazium hians Kunze ex Klotzsch	2000	2500	5	232
Diplazium longisorum (Baker) C. Chr.	1000	1000	1	4
Diplazium macrophyllum Desv.	1500	2000	5	13.2
Diplazium pinnatifidum Kunze	500	1500	3	29
Diplazium tungurahue (Sodiro) C. Chr.	2000	2000	3	14.3

Appendix 5 to Chapter 3

Families and genera with number of species per genera (absolute and % of all species) for terrestrial and epiphytic fern taxa along elevational gradients in Napo and Pichincha.

TERRESTRIALS		**NAPO**		**PICHINCHA**	
Familiy	Genus	No. of species	% of species	No. of species	% of species
ASPLENIACEAE	*Asplenium*	6	6.6	10	6.1
ATHYRIACEAE	*Athyrium*			1	0.6
BLECHNACEAE	*Blechnum*	4	4.4	11	6.7
	Salpichlaena	2	2.2	1	0.6
CYATHEACEAE	*Alsophila*	2	2.2	2	1.2
	Cyathea	11	12.1	15	9.1
	Sphaeropteris			2	1.2
CYSTOPTERIDACEAE	*Cystopteris*	1	1.1		
DENNSTAEDTIACEAE	*Blotiella*			1	0.6
	Dennstaedtia	2	2.2	2	1.2
	Histiopteris			1	0.6
	Hypolepis	3	3.3		
DICKSONIACEAE	*Dicksonia*	1	1.1	1	0.6
	Lophosoria	1	1.1	1	0.6
DRYOPTERIDACEAE	*Arachniodes*	1	0.6		
	Bolbitis	2	2.2	1	0.6
	Ctenitis	1	1.1		
	Cyclodium	2	2.2		
	Dryopteris	2	1.2		
	Elaphoglossum	4	4.4	20	12.2
	Lastreopsis	2	1.2		
	Maxonia	1	1.1		
	Megalastrum	2	2.2	4	2.4
	Polybotrya	1	1.1	4	2.4
	Polystichum	3	3.3	4	2.4
EQUISETACEAE	*Equisetum*	1	1.1	1	0.6
GLEICHENIACEAE	*Sticherus*			3	1.8
HYMENOPHYLLACEAE	*Hymenophyllum*			4	2.4
	Trichomanes	3	3.3	4	2.4
HYPODEMATIACEAE	*Didymochlaena*			1	0.6
LINDSAEACEAE	*Lindsaea*	2	2.2	1	0.6
LOMARIOPSIDACEAE	*Lomariopsis*			1	0.6
LYCOPODIACEAE	*Huperzia*			1	0.6
MARATTIACEAE	*Danaea*	3	3.3	2	1.2
	Marattia	1	1.1	1	0.6

METAXYACEAE	*Metaxya*	1	1.1		
NEPHROLEPIDACEAE	*Nephrolepis*			1	0.6
OPHIOGLOSSACEAE	*Botrychium*	1	1.1	1	0.6
POLYPODIACEAE	*Alansmia*			8	4.9
	Campyloneurum	1	1.1	2	1.2
	Melpomene			1	0.6
	Serpocaulon	3	3.3	3	1.8
OPHIOGLOSSACEAE	*Botrychium*				
PTERIDACEAE	*Adiantum*	1	1.1	3	1.8
	Eriosorus			1	0.6
	Pteris	5	5.5	5	3.0
SACCOLOMATACEAE	*Saccoloma*	2	2.2	1	0.6
SCHIZAEACEAE	*Schizaea*	1	1.1		
SELAGINELLACEAE	*Selaginella*			8	4.9
TECTARIACEAE	*Tectaria*	1	1.1	3	1.8
THELYPTERIDACEAE	*Thelypteris*	8	8.8	10	6.1
WOODSIACEAE	*Diplazium*	8	8.8	12	7.3
EPIPHYTES					
(INDET)	*(indet)*	8	3.3		
ASPLENIACEAE	*Asplenium*	13	5.3	18	11.6
BLECHNACEAE	*Blechnum*	6	2.5	6	3.9
	Salpichlaena			1	0.6
CYATHEACEAE	*Cyathea*	2	0.8		
CYSTOPTERIDACEAE	*Cystopteris*	1	0.4		
DENNSTAEDTIACEAE	*Dennstaedtia*	1	0.4		
	Hypolepis	2	0.8		
DRYOPTERIDACAEAE	*Ctenitis*	2	0.8		
	Elaphoglossum	68	27.9	35	22.6
	Megalastrum	2	0.8		
	Polybotrya	6	2.5	4	2.6
	Polystichum	2	0.8		
	Stigmatopteris	1	0.4		
EQUISETACEAE	*Equisetum*	1	0.4		
GLEICHENIACEAE	*Sticherus*	1	0.4		
HYMENOPHYLLACEAE	*Hymenophyllum*	11	4.5	12	7.7
	Trichomanes	8	3.3	4	2.6
LINDSAEACEAE	*Lindsaea*	1	0.4		
LOMARIOPSIDACEAE	*Lomariopsis*	2	0.8		
LYCOPODIACEAE	*Huperzia*	8	3.3	3	1.9
NEPHROLEPIDACEAE	*Nephrolepis*	4	1.6	2	1.3
OLEANDRACEAE	*Oleandra*	2	0.8	1	0.6
OPHIOGLOSSACEAE	*Botrychium*	1	0.4		
	Ophioglossum	1	0.4		

POLYPODIACEAE	*Alansmia*	10	4.1	7	4.5
	Ascogrammitis	1	0.4		
	Campyloneurum	15	6.1	10	6.5
	Ceradenia	2	0.8	2	1.3
	Cochlidium	1	0.4	1	0.6
	Enterosora	1	0.4	1	0.6
	Grammit indet.	18	7.4		
	Grammitis	2	0.8	1	0.6
	Lellingeria	1	0.4	4	2.6
	Melpomene	8	3.3	6	3.9
	Microgramma	2	0.8	2	1.3
	Moranopteris	3	1.2	1	0.6
	Niphidium	1	0.4	2	1.3
	Pecluma	6	2.5	5	3.2
	Phlebodium			1	0.6
	Pleopeltis	4	1.6	5	3.2
	Serpocaulon	11	4.5	7	4.5
PTERIDACEAE	*Ananthacorus*			2	1.3
	Anetium	1	0.4		
	Antrophyum	3	1.2	2	1.3
	Pteris	3	1.2		
	Radiovittaria	3	1.2	2	1.3
	Vittaria	1	0.4	1	0.6
SCHIZAEACEAE	*Schizaea*	1	0.4		
SELAGINELLACEAE	*Selaginella*	4	1.6		
THELYPTERIDACEAE	*Thelypteris*	2	0.8		
WOODSIACEAE	*Diplazium*	1	0.4		

Appendix 6 to Chapter 5

Average foliar traits of terrestrial fern species in each elevational level.

Elevational level (m a.s.l.)	Species	N total(%)	C/N	P mg/g	N/P	LA (cm2)	SLA (cm2/g)
500	*Danaea elliptica Sm.*	1.60	23.06	0.79	20.36	2382.57	99.18
	Danaea humilis T. Moore	1.97	16.25	0.74	26.44	32.12	122.16
	Cyathea tortuosa R.C. Moran	1.86	20.78	0.60	31.19	4497.84	134.03
	Metaxya rostrata (Kunth) C. Presl	1.67	25.02	0.86	19.44	1179.31	136.66
	Thelypteris macrophylla (Kunze) C.V. Morton	1.74	22.81	0.69	25.35	846.22	140.55
	Lindsaea taeniata K.U. Kramer	1.82	20.79	0.31	58.49	362.63	157.09
	Cyclodium trianae (Mett.) A.R. Sm.	2.21	19.32	0.76	29.19	1181.89	158.34
	Cyclodium meniscioides (Willd.) C. Presl	1.68	25.01	0.98	17.09	544.45	167.33
	Polybotrya crassirhizoma Lellinger	1.65	25.79	1.08	15.21	441.20	183.30
	Saccoloma elegans Kaulf.	2.38	16.20	0.70	34.11	1633.50	188.96
	Trichomanes pinnatum Hedw.	1.85	21.16	0.75	24.71	85.09	193.37
	Thelypteris glandulosa (Desv.) G. R. Proctor	1.82	20.03	0.55	32.82	664.22	200.45
	Tectaria antioquiana (Baker) C. Chr.	2.49	15.86	0.89	28.06	635.03	201.71
	Diplazium pinnatifidum Kunze	2.97	12.04	1.83	16.20	573.59	203.59
	Thelypteris gardneriana (Baker) C.F. Reed	1.37	28.78	0.45	30.51	431.95	207.02
	Lindsaea divaricata Klotzsch	2.41	15.12	0.61	39.77	86.90	219.86
	Adiantum humile Kunze	2.19	16.03	0.72	30.25	44.14	259.09
1000	*Danaea humilis T. Moore*	2.93	12.84	1.29	22.67	37.90	114.50
	Diplazium pinnatifidum Kunze	2.92	11.90	1.49	19.64	301.09	135.62
	Tectaria antioquiana (Baker) C. Chr.	2.25	18.17	0.69	32.74	258.73	139.84
	Danaea elliptica Sm.	1.88	20.81	0.50	37.68	710.28	140.29
	Cyclodium meniscioides (Willd.) C. Presl	2.00	21.35	0.66	30.02	517.80	142.07
	Diplazium longisorum (Baker) C. Chr.	3.58	11.17	2.23	16.10	513.13	143.86
	Maxonia apiifolia (Sw.) C. Chr.	3.40	12.00	1.24	27.45	989.67	156.47
	Diplazium expansum Willd.	2.82	14.14	0.96	29.50	299.47	161.26
	Ctenitis microchlaena (Fée) Stolze	2.28	17.72	1.23	18.53	198.12	165.93
	Alsophila paucifolia Baker	1.74	21.19	0.89	19.50	3703.36	169.36
	Salpichlaena volubilis J.Sm.in Hk.	1.73	20.36	0.58	30.08	407.65	185.96
	Adiantum humile Kunze	1.71	22.96	0.26	65.16	46.02	195.93
	Cyathea tortuosa R.C. Moran	1.76	22.12	0.57	30.89	917.37	196.78
	Thelypteris biformata (Rosenst.) R.M. Tryon	1.42	26.17	0.50	28.20	223.81	197.33
	Bolbitis sp.	1.98	19.84	0.96	20.48	631.53	214.73
	Bolbitis lindigii (Mett.) C. Chr.	2.40	16.21	0.88	27.25	198.18	224.72
	Thelypteris macrophylla (Kunze) C.V. Morton	2.13	19.40	0.86	24.75	266.44	261.22
1500	*Schizaea elegans (Vahl) Sw.*	2.31	19.18	0.72	32.28	53.34	131.90
	Maxonia apiifolia (Sw.) C. Chr.	1.89	23.24	0.58	32.49	513.73	137.20
	Trichomanes elegans Rich.	1.90	21.97	0.26	74.02	72.56	138.88
	Danaea moritziana C. Presl	2.41	15.95	0.63	38.59	163.27	148.58
	Cyathea bipinnatifida (Baker) Domin	2.29	18.02	1.02	22.34	400.47	151.45
	Cyclodium meniscioides (Willd.) C. Presl	2.12	18.82	0.50	42.10	403.99	153.47

	Trichomanes plumosum Kunze	1.62	24.54	0.53	30.72	52.29	160.19
	Cyathea aemula Lehnert	1.96	19.60	0.43	45.76	1605.18	160.49
	Thelypteris biformata (Rosenst.) R.M. Tryon	1.48	25.72	0.43	34.13	309.75	162.25
	Pteris altissima Poir.	1.83	20.74	0.61	30.06	981.32	162.71
	Alsophila paucifolia Baker	1.65	22.58	0.65	25.38	2941.77	165.69
	Cyathea ewanii Alston	1.93	22.08	0.61	31.33	110.85	176.51
	Adiantum humile Kunze	2.19	18.40	0.26	85.67	69.52	183.78
	Diplazium macrophyllum Desv.	2.19	18.57	0.53	41.40	424.49	185.61
	Diplazium alienum (Mett.) Hieron.	3.62	10.67	1.22	29.79	1431.85	197.63
2000	*Polystichum muricatum (L.) Fée*	2.33	18.93	0.83	28.05	636.22	127.38
	Salpichlaena hookeriana Alston	1.78	20.99	0.62	28.67	264.84	129.70
	Maxonia apiifolia (Sw.) C. Chr.	1.85	22.77	0.82	22.72	326.22	131.09
	Diplazium hians Kunze ex Klotzsch	3.18	13.01	2.24	14.21	2111.68	131.85
	Cyathea lasiosora (Mett. ex Kuhn) Domin	2.01	19.49	0.77	26.10	2143.02	137.45
	Dicksonia sellowiana Hook.	2.81	14.73	1.74	16.18	2858.64	140.41
	Hypolepis hostilis (Kunze) C. Presl	2.20	19.83	0.93	23.57	320.69	140.97
	Cyathea tortuosa R.C. Moran	2.18	18.92	0.73	29.79	1636.14	149.65
	Danaea moritziana C. Presl	2.42	15.71	0.87	27.83	321.98	152.48
	Blechnum divergens (Kunze) Mett.	1.51	24.31	0.77	19.61	110.96	158.68
	Diplazium macrophyllum Desv.	2.17	18.11	1.69	12.89	601.12	159.16
	Marattia laevis Sm.	3.30	12.54	2.07	15.95	1871.90	164.17
	Saccoloma inaequale (Kunze) Mett.	1.96	22.04	0.67	29.14	1817.23	167.61
	Dennstaedtia dissecta (Sw.) T. Moore	2.43	16.68	1.00	24.40	684.92	177.47
	Elaphoglossum castaneum (Baker) Diels	2.07	19.17	0.98	21.00	69.98	188.24
	Cyathea quitensis (Domin) R.M.Tryon	2.02	18.45	0.79	25.72	924.51	190.03
	Alsophila erinacea (H.Karst.) D.S.Conant	1.96	19.29	0.93	21.08	2563.54	197.51
	Pteris coriacea Desv.	1.95	19.99	1.22	15.89	465.85	198.02
	Thelypteris biformata (Rosenst.) R.M. Tryon	1.81	21.32	0.61	29.79	129.62	199.58
	Thelypteris funckii (Mett.) Alston	1.87	21.83	0.90	20.85	98.03	211.86
	Pteris livida Mett.	3.28	12.84	2.25	14.57	2104.75	225.61
	Diplazium costale (Sw.) C. Presl	3.01	12.82	0.97	30.86	583.17	230.85
	Megalastrum andicola (C. Chr.) A.R. Sm. & R.C. Moran	3.01	14.43	2.18	13.82	216.78	259.56
	Diplazium tungurahue (Sodiro) C. Chr.	3.68	10.88	1.14	32.20	178.64	265.04
	Serpocaulon fraxinifolium (Jacq.) A.R. Sm.	1.93	21.39	1.69	11.41	160.74	295.08
	Asplenium laetum Sw.	2.51	15.95	1.05	23.86	42.88	328.80
	Asplenium rutaceum (Willd.) Mett.	3.65	11.23	1.58	23.10	48.49	338.34
2500	*Lophosoria quadripinnata (J.F. Gmel.) C. Chr.*	1.72	27.09	0.99	17.41	3848.37	101.39
	Diplazium costale (Sw.) C. Presl	2.53	15.72	0.97	25.99	1971.83	105.59
	Polystichum lehmannii Hieron.	2.53	17.66	1.25	20.15	1477.41	107.23
	Pteris coriacea Desv.	1.97	20.38	0.74	26.64	731.11	110.20
	Cyathea xenoxyla Lehnert	2.27	18.67	1.46	15.52	5610.78	126.50
	Megalastrum andicola (C. Chr.) A.R. Sm. & R.C. Moran	1.76	24.57	1.03	17.04	255.81	130.24
	Danaea moritziana C. Presl	2.35	17.09	0.62	37.84	121.88	137.89

	Blechnum divergens (Kunze) Mett.	2.64	14.08	0.88	30.03	646.89	138.09
	Cyathea tortuosa R.C. Moran	2.50	17.38	1.10	22.71	5441.94	140.24
	Marattia laevis Sm.	3.11	13.83	1.40	22.15	1955.02	146.99
	Dennstaedtia dissecta (Sw.) T. Moore	2.43	18.03	1.28	18.94	603.65	147.80
	Diplazium hians Kunze ex Klotzsch	2.86	14.55	1.56	18.33	1995.17	150.78
	Dennstaedtia auriculata H. Navarrete & B. Øllg.	2.65	14.63	1.25	21.23	646.62	152.34
	Cyathea bipinnatifida (Baker) Domin	2.40	18.48	0.91	26.43	814.40	153.66
	Blechnum cordatum (Desv.) Hieron.	1.73	19.99	0.58	29.56	574.36	161.66
	Asplenium flabellatum Kunze	4.03	10.70	1.00	40.17	289.10	168.16
	Asplenium laetum Sw.	3.02	14.18	1.27	23.81	135.56	169.86
	Asplenium rutaceum (Willd.) Mett.	4.64	9.91	1.52	30.49	85.27	169.99
	Pteris livida Mett.	3.20	13.44	1.29	24.77	4748.36	171.73
	Blechnum sprucei C.Chr.	2.21	18.21	1.11	19.92	216.70	179.87
	Pteris podophylla Sw.	2.12	18.71	1.07	19.84	1423.79	180.65
	Hypolepis hostilis (Kunze) C. Presl	2.76	15.44	1.68	16.46	216.68	180.68
	Serpocaulon fraxinifolium (Jacq.) A.R. Sm.	3.50	12.16	1.31	26.77	311.49	204.52
	Thelypteris rudis (Kunze) G. R. Proctor	2.20	18.58	1.07	20.58	155.05	250.86
3000	*Cyathea tungurahuae Sodiro*	2.17	18.81	1.57	13.78	3653.20	81.77
	Blechnum chilense (Kaulf.) Mett.	1.41	23.86	1.46	9.65	1439.78	83.70
	Campyloneurum amphostenon (Kunze ex Klotzsch) Fée	1.54	27.97	1.90	8.09	73.64	88.94
	Pteris muricata Hook.	1.55	21.85	1.00	15.54	1160.33	110.11
	Cyathea cf. fulva (M. Martens & Galeotti) Fée	2.61	15.21	2.00	13.09	4245.64	120.70
	Hypolepis bogotense H. Karst.	1.61	25.69	1.08	14.91	1174.33	126.99
	Megalastrum andicola (C. Chr.) A.R. Sm. & R.C. Moran	2.29	17.15	2.10	10.92	187.32	130.87
	Cyathea guentheriana Lehnert	1.99	20.54	1.43	13.91	4219.30	135.42
	Thelypteris glandulosolanosa (C. Chr.) R.M. Tryon	1.53	25.70	0.79	19.37	320.64	141.85
	Lophosoria quadripinnata (J.F. Gmel.) C. Chr.	1.77	26.03	1.38	12.83	1767.36	150.74
	Serpocaulon subandinum (Sodiro) A.R. Sm.	1.81	22.63	1.82	9.97	61.39	153.97
3500	*Elaphoglossum atropunctatum Mickel*	1.09	35.42	1.12	9.74	78.45	60.76
	Elaphoglossum albescens (Sodiro) H. Christ	0.82	42.35	0.97	8.45	38.43	97.90
	Blechnum chilense (Kaulf.) Mett.	2.37	17.02	1.82	13.05	473.80	114.99
	Thelypteris caucaensis (Hieron.) Alston	2.16	18.28	2.46	8.79	614.78	116.90
	Hypolepis bogotense H. Karst.	2.02	20.19	1.47	13.75	1118.41	117.86
	Hypolepis crassa Maxon	2.63	14.96	1.76	14.98	21.78	212.87
	Serpocaulon subandinum (Sodiro) A.R. Sm.	2.11	17.88	1.95	10.80	48.73	213.37
	Cystopteris fragilis (L.) Bernh.	2.39	15.92	1.90	12.60	45.25	295.89
4000	*Thelypteris caucaensis (Hieron.) Alston*	1.28	33.95	1.06	12.03	154.59	51.75
	Hypolepis bogotense H. Karst.	2.72	16.20	1.98	13.73	1118.41	117.86
	Hypolepis crassa Maxon	2.62	15.64	1.32	19.91	76.75	131.51

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