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PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Impact of mycorrhization on the abundance, growth and leaf nutrient status of ferns along a tropical elevational gradient

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Abstract Mycorrhizal fungi are crucial for the ecological success of land plants, providing their hosts with nutrients in exchange for organic C. However, not all plants are mycorrhizal, especially ferns, of which about one-third of the species lack this symbiosis. Because the mycorrhizal status is evolutionarily ancestral, this lack of mycorrhizae must have ecological advantages, but what these advantages are and how they affect the competitive ability of non-mycorrhizal plants under natural conditions is currently unknown. To address this uncertainty, we studied terrestrial fern assemblages and species abundances as well as their mycorrhization status, leaf nutrient concentration and relative annual growth along an elevational gradient in the Ecuadorian Andes (500–4,000 m). We surveyed the mycorrhizal status of 375 root samples belonging to 85 species, and found mycorrhizae in 89 % of the samples. The degree of mycorrhization decreased with elevation but was unrelated to soil nutrients. Species with mycorrhizae were significantly more abundant than non-mycorrhizal species, but non-mycorrhizal species had significantly higher relative growth and concentrations of leaf N, P, Mg, and Ca. Our study thus shows that despite lower abundances, non-mycorrhizal fern species did not appear to be limited in their growth or nutrient supply relative to mycorrhizal ones. As a basis for future studies, we hypothesize that non-mycorrhizal fern species may be favoured in special microhabitats of the forest understory with high soil nutrient or water availability, or that the ecological benefit of mycorrhizae is not related to nutrient uptake but rather to, for example, pathogen resistance.

Keywords Altitude · Competition · Ecuador · Mycorrhizae · Nutrients · Phosphorous · Pteridophytes

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Introduction

The colonization of land by plants may never have been possible without mycorrhizal fungi, which provide plants with soil nutrients (especially PO_4^{3-}), water and other benefits (Blackwell 2000; Wilkinson 2001). In exchange, the fungi obtain organic C from the photosynthetic host plants (Smith and Read 2008; Olsson et al. 2010), which allocate up to 20 % of their net photosynthetic C to their fungal partners (Allen et al. 2003). The relative costs of this fungal C use have to be assessed in relation to the benefits derived from increased nutrient uptake, and presumably can be offset partly by higher rates of photosynthesis, if the plants are not light limited (Smith and Smith 2011). In greenhouse experiments with potted plants, mycorrhizal fungi have been shown to increase leaf tissue nutrient concentrations, most importantly those of P (Stribley et al. 1980; Smith and Smith 2011), which especially in tropical ecosystems is

one of the main limiting factors for plant growth (Vitousek 1984; Cleveland et al. 2011). Apart from nutrient supply, mycorrhizal fungi have also been shown to improve the water supply of plants (Allen and Allen 1986; Auge 2001). Further, they increase the resistance of plants to pathogenic fungi, nematodes and insects as well as to diseases, such as those caused by microbial soil-borne pathogens (Gehring and Whitham 2002; Smith and Read 2008; Sikes et al. 2009). Also, mycorrhizal plants have been found to be better colonizers of barren soils and to have higher resistance to soil toxins such as heavy metals (Jeffries et al. 2003).

All these potential benefits to the host plants are interlinked, so that it can be difficult to disentangle if, for example, resistance to a pathogen or toxin is a direct effect of the mycorrhizae or the indirect result of increased plant health (Simard et al. 2012). Most experimental studies show enhanced growth of mycorrhizal plants, but neutral or even negative growth effects of mycorrhiza have also been reported on occasion (Janos 1980; Johnson et al. 1997; Smith and Read 2008; Veiga et al. 2011).

Despite these well-documented ecological advantages of mycorrhizae, not all land plants are mycorrhizal. Of the flora present today, mycorrhizae have been found in 68 % of the studied fern and lycophyte species, 86 % of angiosperms and 100 % of gymnosperms (Wang and Qiu 2006). Mycorrhizae are known to be scarce among many epiphytic plant groups because the most common fungal partners (Glomeromycota) require stable soil conditions for growth and development (Janos 1993; Zubek et al. 2010), although epiphytic orchids are characterized by specialized mycorrhizae (Yukawa et al. 2009). Along environmental gradients, the degree of mycorrhization tends to decrease with increasing elevation and latitude, presumably indicating that fungal growth is reduced at low temperatures (Read and Haselwandter 1981; Olsson et al. 2004; Schmidt et al. 2008). Furthermore, mycorrhizal species are less common in humid habitats and on acidic or fertile soils (Compant et al. 2010; Hempel et al. 2013).

Ferns and lycophytes have the lowest occurrence of mycorrhiza among vascular plants, and typically only about 75 % of all soil-rooting species found at a given site have mycorrhizae (Berch and Kendrick 1982; Kessler et al. 2009, 2010). A previous study on the island of La Réunion found that the degree of mycorrhization of fern assemblages decreases with increasing soil fertility and that fern species with mycorrhizae are more abundant than non-mycorrhizal species (Kessler et al. 2010). These results suggest that mycorrhization provides ecological advantages to fern species. In turn, this raises the question why is it that not all fern species have mycorrhizal symbioses? This is particularly puzzling since the mycorrhizal state is ancestral among ferns (Wang et al. 2010), so that the non-mycorrhizal state is the result of an evolutionary loss, suggesting that there may be a selective advantage to loose mycorrhizal associations. One likely explanation would be that fern photosynthesis in the dark forest understory is so limited that the cost of supplying the fungi with carbohydrates does not offset the advantage of increased nutrient acquisition. Alternatively, it could be that the advantage of mycorrhization is not related to nutrient supply, but rather, for example, protection against pathogenic fungi. This hypothesis requires comparing nutrient levels within the plants as well as growth rates between mycorrhizal and non-mycorrhizal species, something that has previously not been undertaken for ferns along natural environmental gradients.

To address the poorly known role of mycorrhization in tropical ferns, we studied terrestrial fern assemblages and species abundances as well as their mycorrhization status, leaf nutrient concentration, and relative annual growth along an elevational gradient in the Ecuadorian Andes. Specifically, we aimed to assess whether mycorrhization provided ecological advantages relative to nutrient uptake. If this was the case, we would expect the following relationships:

1. The degree of mycorrhization at assemblage level increases with decreasing soil fertility.
2. Leaf nutrient concentrations, growth, and species abundances are higher in fern species with mycorrhizae than in those without mycorrhizae.

As an alternative hypothesis, we may assume that the benefits of mycorrhization are related to other factors, especially protection against pathogens. In this case, we could develop the following predictions:

1. The degree of mycorrhization at assemblage level is not related to soil fertility.
2. Growth, and species abundances are higher in fern species with mycorrhizae than in those without mycorrhizae but leaf nutrient concentrations do not differ.

Materials and methods

Study sites and sampling

Our study was carried out along an elevational gradient from 500 to 4,000 m in steps of 500 m on the eastern Andean slope of Ecuador in the province of Napo at sites off the road from Quito to Tena (Fig. 1). All sites consisted of primary or near-primary humid to perhumid forest. Study sites are described in detail in Salazar et al. (2013). At each elevation, we established three permanent plots of 20 × 20 m^2. To assess biomass production, all terrestrial fern individuals in these plots were permanently marked in

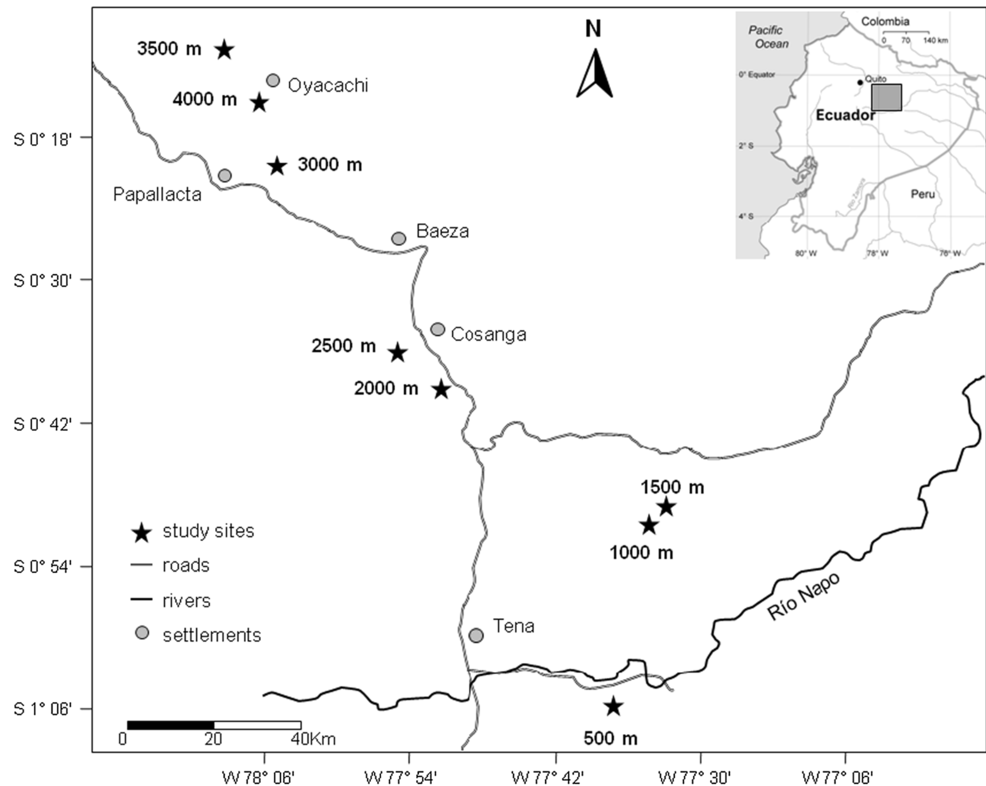

Fig. 1 Location of the study sites on the humid eastern Andean slope in Ecuador

2009, and the number of fronds and their size, as well as rhizome length and diameter, were recorded. At intervals of 1 year, the plots were revisited to mark newly grown individuals and to measure the growth of pre-marked individuals.

To characterize the nutrient status of the study plots, we took four soil samples per plot using a soil corer of 5-cm diameter and 25-cm length. The plots were divided into four quarters of 10 × 10 m^2 and the samples taken in the centre of each quarter. 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 substrate for estimating organic matter content. The depth of the organic layer was recorded. In the laboratory at the University of Göttingen, the following parameters were measured for the upper mineral soil: total C and N (gas chromatography), resin-extractable P (resin-bag method; Dowex 1×8-50) and soil pH (in KCl). The analytical methods are described in detail in Unger et al. (2010).

To estimate biomass production for each species growing at an elevation step, leaves and rhizomes were collected from three individuals per species from the periphery of each plot and dried to later evaluate dry weight. Total biomass was extrapolated by using the counts of fronds and rhizome measurements, and their corresponding density values. Relative productivity for each species-elevation record was calculated as mean of percentage increment of absolute biomass of aboveground and rhizome productivity from one year to the next. Further details on biomass estimation are provided in Kessler et al. (submitted).

Root samples of ferns were collected between April and June 2010. Samples were not taken from the marked individuals in the plots but from conspecific plants found in the direct vicinity of the plots in order to allow establishment of the correlation between mycorrhization and biomass allocation without interfering with the measurements of the latter parameter. Whenever available, three individuals of different size (small, intermediate and large) were sampled for each species. For smaller species, the entire plant was carefully removed from the soil including the fine roots and cleaned mechanically from substrate and other plant material. For larger species, parts of the root systems were excavated. Roots were rinsed several times with water until cleared of soil particles. At least 10 cm of young roots from the tips were cut and preserved in 70 % ethanol.

To evaluate leaf nutrient contents, leaf parts of about 10 cm^2 were collected from three individuals in the periphery of the plots (to avoid damage to the marked plants) and quick dried in silica for laboratory analyses. The samples were dried and chemical analyses were carried out at the University of Göttingen. The total concentrations of foliar C and N were determined with a C/N elemental analyser (Vario EL III; Elementar, Hanau, Germany). Total

concentrations of Ca, K, Mg and P were analysed using an inductively coupled plasma analyser (Optima 5300DV ICP-OES; Perkin Elmer, Waltham, MA) after the samples were digested with concentrated HNO_3.

Mycorrhizal survey

Preparation of the root samples for light microscopy largely followed the protocols of Grace and Stribley (1991) and Haug et al. (2004). The stored root material was taken out of the ethanol and rinsed with water to clean it of remaining soil particles. The specimen were cleared in 10 % KOH for at least 24 h at 60 °C with replacement of the bleaching lye after ca. 12 h. If the roots were still dark at this point, the sample was kept at 60 °C for another 12–24 h in the bleaching solution, which was replaced approximately every 12 h. The roots were then rinsed twice with water before acidifying them with 1 M HCl. Roots were stained using a solution of 0.1 % methyl blue in lactic acid for 3 h at 60 °C. The roots were then placed in a petri dish and cleared with lactic acid. Promising root sections were cut into pieces of approximately 1-cm length and about ten such pieces were arranged on object plates and the cover glass carefully pressed down. The stained roots were examined with a dissecting microscope first at 40× magnification to get an overall impression. Promising portions were then examined at 100–400× magnification for a more precise quantification and identification of the type of colonizing fungus. If roots were too hard to be flattened or when mounted roots turned out to be still too dark to see mycorrhizal colonization, pieces were bleached in a solution containing 3 % H_2O_2 and 25 % ammoniac (10:1) for 2–5 min. The cleared roots were then covered again with the staining solution and heated over a small flame for 1–3 min. After staining, roots were cleared of excess staining solution with lactic acid and prepared in the same matter as before to examine the roots under the microscope.

We quantified the colonization of single roots based on examination of a minimum length of 10 cm of root tips. We categorized the extent of colonization following the approach of Gemma et al. (1992): 0 = no colonization (<5 % of root length with mycorrhizae), 1 = slight colonization (5–25 %), 2 = moderate colonization (25–75 %), 3 = intense colonization (>75 %). The threshold of <5 % root length fungal colonization is commonly used to distinguish between mycorrhizal and non-mycorrhizal plants and represents a compromise between the risks of including erroneous colonization and missing real colonization (Kessler et al. 2009, 2010; Lehnert et al. 2009).

We distinguished two types of colonizing fungi, arbuscular mycorrhizal fungi (AMF) and dark-septate endophytes (DSE). AMF were recognized as relatively strong, aseptate hyphae of irregular diameter forming lateral and terminal vesicles and arbuscules. The colonizations of the roots were classified as AMF when internal hyphae or arbuscules were visible in the cortex. DSE are dark-coloured, septate fungi. In comparison to AMF fungi, DSE form thinner and more regular hyphae that are often arranged in dense coils. Roots were counted as colonized by DSE when septate hyphae were seen to infiltrate the cortex. Dark-septate endophytes often do not stain properly when using the described method and were thus harder to detect. Some infections might thus have been overlooked. Record photographs of root specimens were taken using the digital microscope camera Axio Cam HRc.

For eight of the 88 study species, no samples were taken because the species could not be located outside of the plots. For *Elaphoglossum atropunctatum* at 4,000 m, we obtained mycorrhizal data from roots of three herbarium samples collected in the same region. We coded *Asplenium harpeodes* and *Serpocaulon subandinum* as non-mycorrhizal, *Botrychium virginianum* as strongly AMF mycorrhizal, and *Hypolepis bogotensis* as AMF mycorrhizal of medium intensity, based on literature data provided by M. Lehnert (Bonn). For another three species, *Cyathea* cf. *microdonta* at 2,500 m, *Elaphoglossum albescens* at 3,500 m, and *Megalastrum* sp. at 1,500 m, no literature values were available and these species were excluded from the analyses.

For the three samples of every species at each elevation, we calculated the median of the colonization categories for further analyses. The first series of analyses were run using the four colonization categories as well as a simple distinction between mycorrhizal (combining categories 1–3) and non-mycorrhizal species (i.e., category 0). Since the results of the latter analyses were qualitatively identical to those obtained when considering the four categories, and since the meta-analysis of Karst et al. (2008) has shown that the presence/absence of mycorrhizae appears to be more important than their abundance, we here mostly only report on the contrast of mycorrhizal vs. non-mycorrhizal species. We also conducted analyses separately for AMF and DSE fungi, but because all DSE infections occurred in specimens that also had AMF fungi, this analysis did not provide significant additional insight. Hence, we mostly report on mycorrhization in a general sense, combining both types of fungi.

Statistical analysis

Frequencies of species in different mycorrhizal categories were compared using *G*-tests. For further statistical analyses, the mycorrhizal status of fern species was compared with their respective abundance, relative productivity, and tissue nutrient levels. Because many parameters showed elevational trends, we used analyses of covariance with the respective factor as the dependent and elevation

as the independent metric and status of mycorrhization as the independent categorical variable. Statistical tests were carried out using the statistical platform R (R Core Team 2012).

Results

Mycorrhization of the surveyed fern community

In total, in the 24 study plots we recorded 88 species of terrestrial ferns belonging to 18 families (Table 1). Of the 85 surveyed species, 71 had not previously been surveyed for mycorrhizal associations and the genus *Maxonia* was surveyed for the first time.

Species richness showed a humped pattern with elevation and varied between four species at 4,000 m and 27 species at 2,000 m. Because numerous species occurred at several elevations, in total we had 128 species records. Of these, we obtained and screened 375 root samples for mycorrhizal infections. For 119 of the 128 species records, three individuals were collected, for two records two, for two records only one, and for a further five species herbarium and literature data were used. Three species were excluded because no data on mycorrhizae were available. Among those species for which more than one sample was analysed, all samples were assigned to the same colonization category in 35 (28 %) cases, but in 89 (72 %) at least one sample deviated from the others. However, this usually involved adjacent colonization categories and strong variation was rare. Overall, assignation to colonization categories differed significantly from randomness (*G*-test, $G = 124.2$, $P < 0.01$) and shows that our observations reflect a reasonably high species specificity of mycorrhizal colonization.

In total, we found mycorrhizal infections in 335 (89 %) of the individual fern samples (Table 2). In the remaining 40 (11 %) no or only minimal mycorrhizal colonization could be detected. Split into the four colonization categories, 40 (11 %) samples showed no, 67 (18 %) low, 153 (41 %) medium and 115 (31 %) strong mycorrhizal colonization. In the majority of colonized samples (275, 81 %), only AMF were found. DSE were found in 60 (19 %) of the 335 samples with mycorrhizal colonization. In all observed samples with DSE, the surveyed roots were co-colonized by AMF.

At the species level, 114 (89 %) of all 128 species records revealed mycorrhizal infections and 14 (11 %) were non-mycorrhizal. Separated into the four colonization categories, 14 (11 %) species-elevation records were non-mycorrhizal, 16 (13 %) showed low, 67 (52 %) medium and 31 (24 %) strong levels of mycorrhizal colonization. Of the 114 mycorrhizal species, 100 (88 %) species-elevation records had only AMF while 14 (12 %) had mixed DSE and AMF colonization.

Mycorrhization along the elevation gradient and in relation to soil parameters

On the lower three elevational steps, all species–elevation records were mycorrhizal (Fig. 2). From 2,000 to 3,500 m, the proportion of non-mycorrhizal species increased from 11.1 to 36.4 %, but this trend was not significant due to the low sample size (*G*-test, $G = 4.78$, $P > 0.1$). At 4,000 m, the non-mycorrhizal proportion disappeared because all three species found were mycorrhizal, albeit with low to medium colonization intensity only.

The depth of the organic layer increased linearly with elevation, whereas values of pH, C, N, and Mg in the mineral soil showed hump-shaped patterns with highest concentrations around 2,500 m (Table 3). The remaining soil nutrients (P, K, Ca) as well as Al did not show significant elevational trends. Concentrations of soil nutrients were not related to those of leaf nutrients for any of the six studied nutrients (Table 3). Neither was the percentage of mycorrhizal species per plot related to any of the studied soil parameters.

Relations between mycorrhization and fern species abundances, productivity, and leaf nutrient contents

Species with mycorrhizae were significantly more abundant than those lacking the association with the fungal partners (Fig. 3). However, species without mycorrhizae had significantly higher relative productivity than those with mycorrhizae. Nutrient leaf concentrations showed significantly higher values in non-mycorrhizal species for N, P, Mg and Ca. Ratios between C and other leaf nutrients revealed no difference between mycorrhizal and non-mycorrhizal species except for lower C/Mg ratios in non-mycorrhizal species.

Discussion

General patterns

We found that 89 % of all species had mycorrhizal associations. This percentage is higher than the values of 65–70 % typically reported for ferns both in general (Wang and Qiu 2006) and in local surveys (Fernandez et al. 2008; Kessler et al. 2009, 2010; Lehnert et al. 2009; Zubek et al. 2010). Even if epiphytic species, which often lack mycorrhizae, are excluded, previous surveys found only about 75 % of all soil-rooting species to be mycorrhizal (Berch and Kendrick 1982; Kessler et al. 2009, 2010). We cannot offer any

Table 1 The degree of mycorrhizal colonization [<5 % = no (*0*), 5–25 % = low (*1*), 25–75 % = medium (*2*), >75 % = strong (*3*)] and colonizing types [arbuscular mycorrhizal fungi (*AMF*), dark-septate endophytes (*DSE*)] of all the sampled fern species at a specific elevation

Family	Species	Elevation	Colonization		
			Level	AMF	DSE
Aspleniaceae	*Asplenium flabellatum* Kunze[a]	2,500	0	–	–
	Asplenium harpeodes Kunze [b]	3,000	0	–	–
	Asplenium laetum Sw.[a]	2,000	2	+	–
		2,500	3	+	–
	Asplenium rutaceum (Willd.) Mett.[a]	2,000	0	–	–
		2,500	0	–	–
	Asplenium serra Langsd. and Fisch.[a]	3,000	0	–	–
	Asplenium sp.	3,500	0	–	–
Athyriaceae	*Diplazium alienum* (Mett.) Hieron.[a]	1,500	3	+	+
	Diplazium costale (Sw.) C. Presl[a]	2,000	1	+	–
		2,500	2	+	+
	Diplazium expansum Willd.[a]	1,000	2	+	–
	Diplazium hians Kunze ex Klotzsch[a]	2,000	2	+	–
		2,500	1	+	–
	Diplazium longisorum (Baker) C. Chr.[a]	1,000	3	+	–
	Diplazium macrophyllum Desv.[a]	1,500	1	+	–
		2,000	2	+	–
	Diplazium pinnatifidum Kunze[a]	500	1	+	–
		1,000	3	+	–
	Diplazium tungurahuae (Sodiro) C. Chr.[a]	2,000	2	+	–
Blechnaceae	*Blechnum chilense* (Kaulf.) Mett.[a]	3,000	3	+	+
		3,500	2	+	–
	Blechnum cordatum (Desv.) Hieron.[a]	2,500	3	+	+
	Blechnum divergens (Kunze) Mett.[a]	2,000	1	+	–
		2,500	2	+	+
	Blechnum sprucei C. Chr.[a]	2,500	2	+	+
	Salpichlaena hookeriana Alston[a]	2,000	2	+	–
	Salpichlaena volubilis (Kaulf.) J. Sm.[a]	1,000	3	+	–
Cyatheaceae	*Alsophila erinacea* (H. Karst.) D.S. Conant[a]	2,000	2	+	–
	Alsophila paucifolia Baker[a]	1,000	2	+	–
	Cyathea aemula Lehnert[a]	1,500	2	+	–
	Cyathea bipinnatifida (Baker) Domin[a]	1,500	2	+	–
	Cyathea ewanii Alston[a]	1,500	2	+	–
	Cyathea cf. *fulva* (M. Martens and Galeotti) Fée	3,000	2	+	–
	Cyathea guentheriana Lehnert[a]	3,000	2	+	–
	Cyathea lasiosora (Mett. ex Kuhn) Domin[a]	2,000	3	+	–
	Cyathea quitensis Domin[a]	2,000	2	+	–
	Cyathea tortuosa R.C. Moran[a]	500	1	+	–
		1,000	3	+	–
		2,000	2	+	–
		2,500	2	+	–
	Cyathea tungurahuae Sodiro[a]	3,000	2	+	–
	Cyathea xenoxyla Lehnert[a]	2,500	3	+	–
Dennstaedtiaceae	*Dennstaedtia auriculata* H. Navarrete and B. Øllg.[a]	2,500	2	+	–
	Dennstaedtia dissecta (Sw.) T. Moore[a]	2,000	2	+	–
		2,500	2	+	–

Table 1 continued

Family	Species	Elevation	Colonization		
			Level	AMF	DSE
	Hypolepis bogotensis H. Karst.[a]	3,000	2	+	–
		3,500	2	+	–
		4,000	2	+	–
	Hypolepis crassa Maxon[a]	3,500	1	+	–
		4,000	1	+	+
	Hypolepis hostilis (Kunze) C. Presl[a]	2,000	2	+	–
		2,500	2	+	–
	Saccoloma elegans Kaulf.	500	3	+	–
	Saccoloma inaequale (Kunze) Mett.[a]	2,000	2	+	+
Dicksoniaceae	*Dicksonia sellowiana* Hook.[a]	2,000	1	+	–
	Lophosoria quadripinnata (J.F. Gmel.) C. Chr.[a]	2,500	2	+	–
		3,000	2	+	–
Dryopteridaceae	*Bolbitis lindigii* (Mett.) C. Chr.[a]	1,000	2	+	–
	Bolbitis sp.	1,000	2	+	–
	Ctenitis microchlaena (Fée) Stolze[a]	1,000	2	+	–
	Cyclodium meniscioides (Willd.) C. Presl[a]	500	2	+	–
		1,000	3	+	–
		1,500	2	+	+
	Cyclodium trianae (Mett.) A.R. Sm.[a]	500	3	+	–
	Elaphoglossum antisanae (Sodiro) C. Chr.	3,500	0	–	–
	Elaphoglossum atropunctatum Mickel[a]	3,500	1	+	–
		4,000	1	+	+
	Elaphoglossum castaneum (Baker) Diels[a]	2,000	0	–	–
		3,000	1	+	–
	Maxonia apiifolia (Sw.) C. Chr.[a]	1,000	3	+	–
		1,500	2	+	–
		2,000	2	+	–
	Megalastrum andicola (Sw.) C. Chr.[a]	2,000	2	+	+
		2,500	1	+	–
		3,000	1	+	–
	Polybotrya crassirhizoma Lellinger[a]	500	2	+	–
	Polystichum lehmannii Hieron.[a]	2,500	2	+	–
		3,500	2	+	–
	Polystichum muricatum (L.) Fée[a]	2,000	2	+	–
Hymenophyllaceae	*Trichomanes elegans* Rich.	1,500	2	+	–
	Trichomanes pinnatum Hedw.	500	3	+	–
	Trichomanes plumosum Kunze[a]	1,500	2	+	–
Lindsaeaceae	*Lindsaea divaricata* Klotzsch[a]	500	3	+	–
	Lindsaea taeniata K.U. Kramer[a]	500	2	+	–
Marattiaceae	*Danaea elliptica* Sm.	500	2	+	–
		1,000	2	+	–
	Danaea humilis T. Moore	500	2	+	–
		1,000	2	+	–
	Danaea moritziana C. Presl[a]	1,500	3	+	–
		2,000	3	+	–
		2,500	3	+	–

Table 1 continued

Family	Species	Elevation	Colonization		
			Level	AMF	DSE
	Marattia laevis Sm.[a]	2,000	3	+	–
		2,500	3	+	–
Metaxyaceae	*Metaxya rostrata* (Kunth) C. Presl	500	2	+	–
Ophioglossaceae	*Botrychium virginianum* (L.) Sw.[b]	3,000	3	+	–
Polypodiaceae	*Campyloneurum amphostenon* (Kunze ex Klotzsch) Fée	3,000	0	–	–
	Serpocaulon fraxinifolium (Jacq.) A.R. Sm.	2,000	0	–	–
		2,500	0	–	–
	Serpocaulon subandinum (Sodiro) A.R. Sm.[b]	3,000	0	–	–
		3,500	0	–	–
	Serpocaulon sp.	1,500	1	+	–
Pteridaceae	*Adiantum humile* Kunze[a]	500	3	+	–
		1,000	3	+	–
		1,500	2	+	–
	Pteris altissima Poir.[a]	1,500	3	+	–
	Pteris coriacea Desv.[a]	2,000	2	+	–
		2,500	2	+	–
	Pteris livida Mett.[a]	2,000	2	+	–
		2,500	2	+	–
	Pteris muricata Hook.	3,000	1	+	–
	Pteris podophylla Sw.[a]	2,500	2	+	+
Schizaeaceae	*Schizaea elegans* (Vahl) Sw.	1,500	3	+	–
Tectariaceae	*Tectaria antioquoiana* (Baker) C. Chr.[a]	500	2	+	–
		1,000	3	+	–
Thelypteridaceae	*Thelypteris biformata* (Rosenst.) R.M. Tryon[a]	1,000	2	+	–
		1,500	3	+	+
		2,000	2	+	–
	Thelypteris caucaensis (Hieron.) Alston[a]	3,500	2	+	–
		4,000	2	+	–
	Thelypteris funckii (Mett.) Alston[a]	2,000	3	+	–
	Thelypteris gardneriana (Baker) C.F. Reed[a]	500	2	+	–
	Thelypteris glandulosa (Desv.) Proctor[a]	500	2	+	–
	Thelypteris glandulosolanosa (C. Chr.) R.M. Tryon[a]	3,000	2	+	–
	Thelypteris macrophylla (Kunze) C.V. Morton[a]	500	2	+	–
		1,000	3	+	–
	Thelypteris rudis (Kunze) Proctor[a]	2,500	2	+	–
Woodsiaceae	*Cystopteris fragilis* (L.) Bernh.	3,500	0	–	–

[a] First survey of this species

[b] No samples taken, substituted by literature values provided by M. Lehnert (personal communication)

explanation for this high degree of mycorrhization in our study region, especially considering that the soils there are mostly derived from young volcanic substrates and generally fairly nutrient rich. The previously documented high incidence of fern mycorrhization on nutrient-poor soils (Kessler et al. 2010) is therefore unlikely to play a role in our study region.

Mycorrhization along the elevation gradient and in relation to soil parameters

Omitting the highest site which only had three species, we observed the expected trend for a decrease in overall mycorrhization with increasing elevation. The same trend has also been reported for flowering plants both with increasing

Table 2 Degree of colonization at sample and species level, and type of colonization at sample and species level summarized for all elevations

	No (<5 %)		Low (5–25 %)		Medium (25–75 %)		Strong (>75 %)		Total
	n	%	*n*	%	*n*	%	*n*	%	*n*
Degree of colonization									
Samples	40	10.7	67	17.8	153	40.8	115	30.7	375
Species	14	11.0	16	12.5	67	52.3	31	24.2	128

	No		AMF		AMF + DSE		Total
	n	%	*n*	%	*n*	%	*n*
Colonization type							
Samples	40	10.7	275	73.3	60	16	375
Species	14	11.0	100	78.1	14	10.9	128

For abbreviations, see Table 1

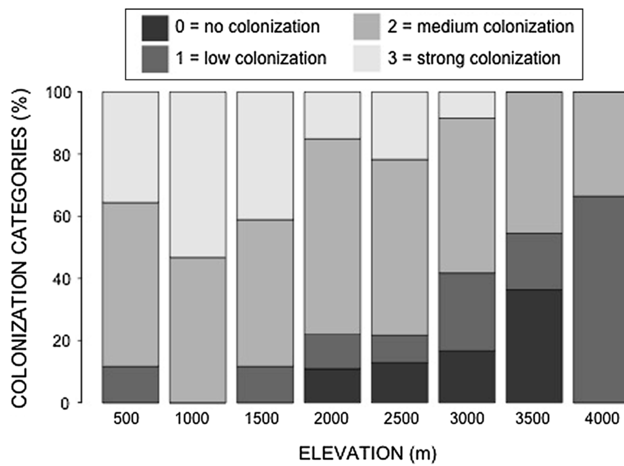

Fig. 2 Relative frequencies (%) of the categories of degree of colonization for all species-elevation records along the elevational gradient, showing the overall decrease of mycorrhization with elevation

elevation (Read and Haselwandter 1981; Wu et al. 2004; Schmidt et al. 2008) and latitude (Olsson et al. 2004; Newsham et al. 2008). The most common explanation for this pattern is linked to lower temperatures that slow down physiological processes including growth, which in turn affect the mutual relationship between both partners (Gardes and Dahlberg 1996; Averill and Finzi 2011; Liu et al. 2011). Hyphal growth of internal and external mycelia of AMF and fungal P contribution are reduced at lower temperatures (Heinemeyer and Fitter 2004; Kytoviita and Ruotsalainen 2007). Since the partial pressure of CO_2 in air decreases with increasing altitude, alpine plants are more CO_2 limited than those in the lowlands, but Gale (1972) argued that this difference is compensated by increased rates of diffusion and plant CO_2 uptake. More likely, plant photosynthesis is limited as a result of low temperatures, persistent leaf wetness and reduced irradiation inputs due to cloud and fog cover (Brunijnzeel and Beneklaas 1998). While we do not have data on photosynthesis, biomass allocation or respiratory C losses in our study plants, the above patterns are so general that we feel safe to propose that mycorrhization might decrease because the relative costs of allocating C to the fungal partner increase with elevation and possibly exceed the benefits of the fungal nutrient supply.

We found no relationship between the percentage of mycorrhizal species and the soil parameters that we

Table 3 Trends of soil nutrients related to elevation and leaf nutrients

Soil parameter	Elevation			Leaf nutrients		% Mycorrhizal species	
	R^2	*P*	Model	R^2	*P*	R^2	*P*
Organic layer depth	*0.76*	*<0.001*	Linear			0.10	0.64
pH (KCl)	*0.62*	*0.001*	Polynomial			0.39	0.06
C	*0.65*	*0.001*	Polynomial	0.32	0.13	0.14	0.52
N	*0.79*	*<0.001*	Polynomial	0.15	0.49	0.29	0.17
C/N	0.24	0.26	Linear			0.19	0.37
P	0.28	0.19	Polynomial	0.08	0.73	0.05	0.81
K	0.06	0.77	Linear	0.09	0.68	0.09	0.69
Mg	*0.71*	*<0.001*	Polynomial	0.15	0.50	0.23	0.29
Ca	0.24	0.26	Linear	0.15	0.48	0.22	0.31
Al	0.17	0.42	Linear			0.18	0.41

All soil parameters except the first are for the top layer of the mineral soil, i.e. from the rooting substrate of the ferns. Polynomial models reflect hump-shaped elevational patterns with highest values at mid-elevations. All models between soil and leaf nutrients are linear. Significant relationships are highlighted in *italic*

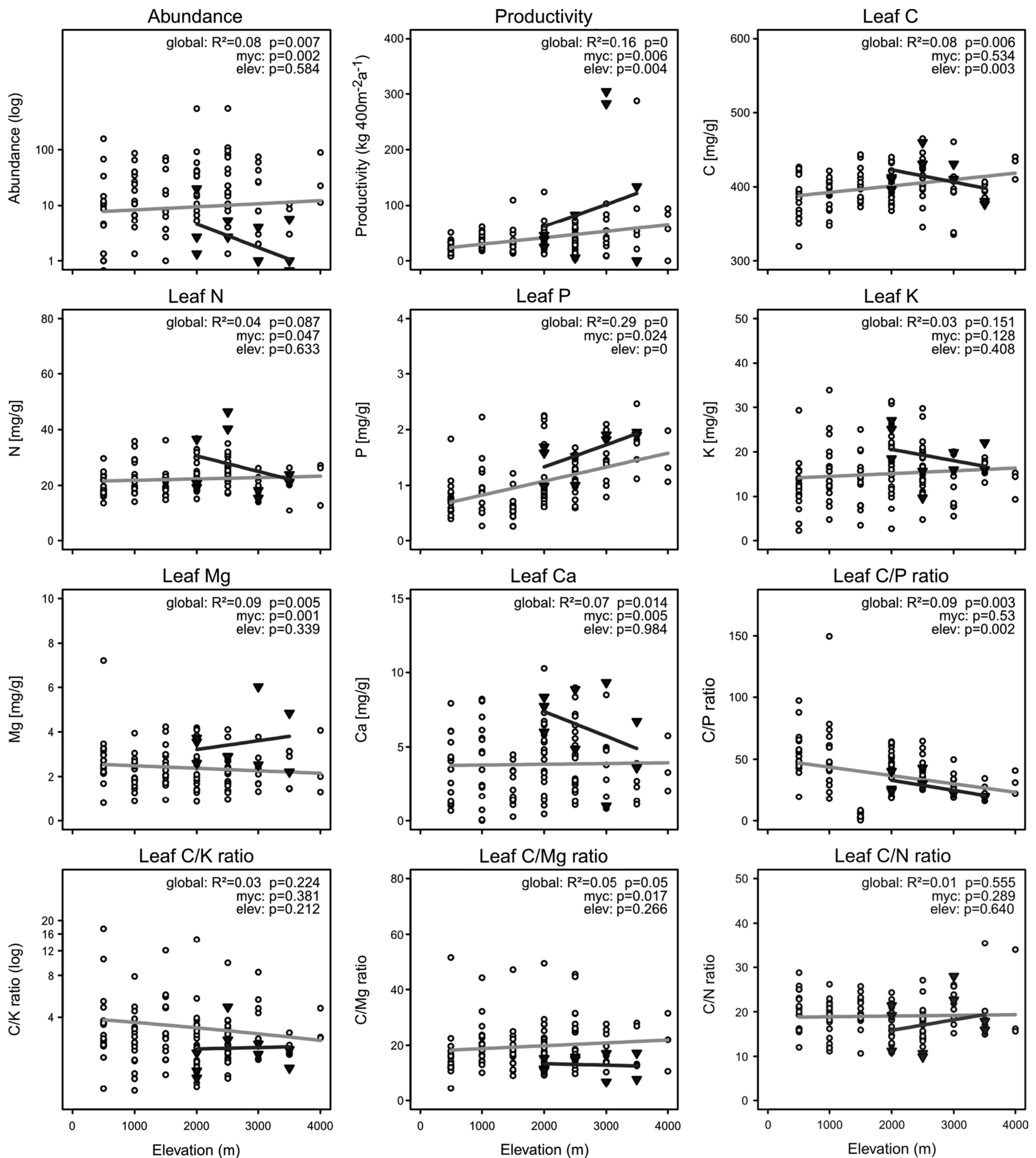

Fig. 3 Elevational patterns of abundances, relative productivity and leaf nutrient concentrations and ratios of mycorrhizal (*open circles*) and non-mycorrhizal (*black triangles*) species along an elevational gradient in Ecuador. *Lines* show linear trends. Results of analysis of covariance are provided in each graph, testing for differences between mycorrhizal and non-mycorrhizal species (*myc*) and for elevational trends (*elev*). For reasons of space, we do not show the non-significant pattern for leaf C/Ca ratios (global $R^2 = 0.01$, $P = 0.53$; myc, $P = 0.926$; elev, $P = 0.287$)

measured. This result contrasts with a previous study on the island of La Réunion (Kessler et al. 2010), and suggests that elevational trends of mycorrhization of ferns in our study region are not closely linked to availability of the studied soil nutrients and may rather be driven by climatic factors such as decreasing temperatures, as discussed above. We believe that the difference between these two studies is due to length of the environmental gradients covered, with the study on La Réunion involving a much more pronounced edaphic gradient (raw lava to peaty soils vs. only well-developed zonal soils in Ecuador) but a much narrower climatic gradient (2,000-m elevational range vs. 4,000 m).

Relations between mycorrhization and fern species abundances, productivity, and leaf nutrient contents

As expected, mycorrhizal fern species had significantly higher abundances compared to non-mycorrhizal species. These findings are consistent with the prediction that mycorrhizal plants have an ecological advantage over non-mycorrhizal individuals and agree with previous studies on ferns (Kessler et al. 2010) and angiosperms (Genney et al. 2001). Various experiments assessing the influence of AMF on the outcome of interspecific competition support the concept that mycorrhization is beneficial in competition between species (Fitter 1977; Bever et al. 1997; Facelli et al. 2010).

However, in contrast to abundance, we found higher relative biomass productivity of non-mycorrhizal fern species. Furthermore, in contrast to our expectations and to previous experimental results with flowering plants (Stribley et al. 1980; Smith and Read 2008; Smith et al. 2011), we found that non-mycorrhizal fern species had significantly higher concentrations of N, P, Mg, and Ca in their leaves. It is generally considered that AMF can increase plant growth, especially under infertile soil conditions (Hayman and Mosse 1972; Schubert and Hayman 1986). Yet, although positive effects of mycorrhizal colonization on growth are commonly highlighted, negative effects have also been reported (Facelli et al. 1999; Smith et al. 2009; Veiga et al. 2011). Our study also provides field evidence that the ecological advantages of mycorrhization may not be as simple as commonly portrayed, and raises the question under which conditions do ferns have or lack their fungal root partners?

The mycorrhizal condition is the common situation for the majority of plants in natural ecosystems (Smith et al. 2011) and the ancestral state for vascular plants and ferns in an evolutionary context (Blackwell 2000; Wilkinson 2001; Wang et al. 2010). Considering the obvious ecological advantages of mycorrhizal partners (Brundrett 2002, 2004), the loss of this symbiosis demands an explanation. Our study shows that non-mycorrhizal ferns grow faster and have higher leaf nutrient concentrations than mycorrhizal species, suggesting that the lack of mycorrhizae might not be limiting to these species with respect to growth and nutrient supply. On the other hand, mycorrhizal species are significantly more abundant than non-mycorrhizal ones, revealing an ecological advantage of mycorrhization.

An interpretation of these conflicting results must by necessity be somewhat speculative. Most importantly, the challenge is to deduce whether the differences between the mycorrhizal and non-mycorrhizal species are due to advantages or disadvantages of their respective conditions. For example, the higher productivity of non-mycorrhizal ferns may be due to disadvantages of the mycorrhizal species or due to advantages of the species lacking the symbiosis. Negative growth effects of mycorrhization have previously been documented in a number of cases (e.g., Johnson et al. 1997; Smith and Read 2008; Veiga et al. 2011). These often reflect the parasitic nature of mycorrhizal fungi in situations in which the nutritional benefits for the plant do not outweigh the C loss to the fungi (Johnson et al. 1997; Karst et al. 2008). Whether such a situation occurs among the ferns in our study cannot be assessed with the data available, since our comparisons are between species rather than between inoculated and non-inoculated individuals of the same species.

Our study does not support the hypothesis that mycorrhizae provide their host fern species with an increased nutrient supply. On the contrary, non-mycorrhizal species had higher leaf nutrient concentrations. The good nutrient supply of non-mycorrhizal ferns could reflect taxon-specific trends in leaf-nutrient concentrations, but since the 11 non-mycorrhizal species found by us belong to five different fern families, we do not consider that this is likely. An alternative explanation would be that non-mycorrhizal fern species grow under ecological conditions where nutrients are not limiting while C uptake is limited. This could, for example, be the case in densely shaded forest microhabitats where low light availability limits photosynthesis. In such a situation, plants would accumulate nutrients in the course of their normal water uptake while being unable to grow very fast. However, the higher productivity of non-mycorrhizal species contradicts this assumption. Alternatively, special microsites where non-mycorrhizal species are favoured might consist of soil patches with high nutrient concentrations, e.g. near dead wood or in depressions where nutrients accumulate. Soil nutrients are known to be exceedingly variable in their spatial distribution (Bruelheide and Udelhoven 2005) and non-mycorrhizal ferns might take advantage of such heterogeneity. Unger et al. (2010) showed strong spatial heterogeneity of soil properties within our study plots at 500–2,000 m. For several important parameters (pH, exchangeable cation

concentrations and N mineralization) variability within plots was higher than between different plots at the same elevation or between different elevations. We currently lack the necessary small-scale (within-plot) environmental data at the actual growth sites of the ferns to test the idea that mycorrhization is linked to local soil parameters, and propose this here mainly in the hope of inspiring future research in this direction.

Alternatively, it may be that the ecological advantages of mycorrhizae in our study species do not primarily influence growth and nutrient acquisition, but rather other aspects such as the water supply of the plants (Allen and Allen 1986; Auge 2001) or, considering the humid climate in our study region, more likely their resistance to pathogenic fungi, nematodes, insects or bacteria (Gehring and Whitham 2002; Smith and Read 2008; Sikes et al. 2009). This hypothesis is consistent with the observation of the lower frequency of non-mycorrhizal ferns, which might reduce the infection risk between conspecific individuals. Or, stated the other way round, non-mycorrhizal fern species may not attain high densities because under such conditions, pests might easily spread amongst them. The higher growth of the non-mycorrhizal species would be in accordance with this interpretation, as these species do not suffer from a loss of C to their fungal partners. However, the higher leaf nutrient concentrations of the non-mycorrhizal fern species found by us are not consistent with the pathogen-resistance hypothesis.

In conclusion, our study documented significant ecological differences between mycorrhizal and non-mycorrhizal fern species that are difficult to interpret. We found no direct evidence that mycorrhizal ferns have better nutrient supply than non-mycorrhizal ones, suggesting that the latter either favour nutrient-rich microhabitats, or a different ecological benefit of mycorrhizae, e.g. in pathogen resistance. What becomes apparent is that the relatively straightforward results obtained in many pot and greenhouse experiments cannot be simply translated to field conditions, probably because artificial systems lack the complex interactions of plant performance and the variety of abiotic and biotic environmental factors occurring in natural ecosystems. In particular, many experimental studies have compared mycorrhizal and non-mycorrhizal individuals of the same plant species. Thus, the non-mycorrhizal plants may often correspond to stressed individuals of species adapted to be mycorrhizal. Cross-species comparisons are much rarer but are biologically more relevant (Veiga et al. 2011).

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