

THE ROLE OF SOILS FOR PTERIDOPHYTE DISTRIBUTION IN TROPICAL AMERICAN FORESTS

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ABSTRACT

The distributions of plant species are affected by characteristics of their environment, most importantly climate and soils. Ferns and lycophytes (hereafter pteridophytes) are no exception to this general ecological principle. However, until relatively recently, little information has been available about pteridophyte-soil relationships in the tropics. Here we review literature that sheds light on the impact of soil conditions on pteridophyte distribution in the lowland forests of tropical America. We provide examples of both soil-related community-level patterns in species turnover and distributions of individual species and genera along soil gradients. We then discuss the relevance of these patterns for the evolution and diversification of pteridophyte lineages and for practical applications, such as the use of pteridophytes as indicators in classification and mapping of soil-related habitats. Finally, we discuss challenges in filling the gaps of knowledge in pteridophyte-soil relationships and suggest possible solutions for them.

INTRODUCTION

Globally, vegetation is classified into biomes according to regionally dominant physiognomy and life-forms. These mostly reflect the prevailing climatic conditions, especially precipitation and temperature, which generally vary gradually over long distances and large extents (e.g., Woodward et al., 2004). In contrast, soil factors can vary sharply over short distances, and are therefore considered important mostly at finer scales. Extreme soil conditions can give rise to azonal vegetation, i.e. to physiognomy that is considered atypical for the climatic zone (e.g., Walter & Breckle, 1986). Although it is in many cases obvious that structural changes in vegetation are related to changes in floristic composition, floristic variation related to soils can take place also within structurally uniform vegetation, which is not obvious at first glance.

Early quantitative attempts to determine fern species occurrences along soil gradients were made by Wherry (Wherry, 1917, 1920), who observed species on different rock types in the Appalachian mountains and carried out chemical analyses to assess fern species occurrences along a gradient of soil calcium concentration and acidity. Petersen (1985) provided a review on what was known of edaphic (i.e. soil-related) niche requirements of ferns at the time, mostly based on studies in North America. More recently, a study in Norway applied rigorous statistical methods to model how the abundances of three fern species varied along several environmental gradients, including soil pH, cation exchange capacity and base saturation (Odland et al., 1995).

In the American tropics, Tryon (1944) observed that the genus *Doryopteris* predominantly occurs in rocky sites above 300 m elevation. He speculated that the centre of origin of the genus was in the southern end of the Brazilian rocky highlands, where the environmental conditions have been relatively stable and available for plants since the Mesozoic. For the subsequent five decades after Tryon's paper, most studies focused on how pteridophyte species distributions relate to geographical regions, elevation, climate or structurally defined vegetation or habitat types (e.g., forest, scrub, cliff), but ignored soil properties (Tryon, 1960; 1972; Smith, 1972; Tryon & Conant, 1975; Parris, 1985; Moran, 1995). Other studies mentioned specific aspects of the soils (e.g., if they were rocky or sandy) when describing the preferred habitats of pteridophyte species, but without including quantitative data on physical or chemical soil properties (Kramer, 1974; Parris, 1976; Cremers, 1991; van der Werff, 1992).

Floristic gradients are especially challenging to observe and document in lowland tropical rain forests, which combine a complex multi-layered vegetation with high species richness and poorly resolved species taxonomy. Detailed information on the soil relationships of any plants in the rain forests of tropical America has started to accumulate only relatively recently. With few exceptions (e.g., Gentry, 1981) researchers in the 1980s paid little attention to local site conditions. The quantitative documenting of soil chemistry in connection with floristic studies started in the 1990s (Duivenvoorden, 1995; Tuomisto et al., 1995; Ruokolainen et al., 1997) but only became routine in the 2000s (e.g., Tuomisto et al., 2003a; 2003b; 2003c; 2016; Ruokolainen et al., 2007; Phillips et al., 2003; Schulman et al., 2004; Baltzer et al., 2005; Fine et al., 2005; Higgins et al., 2011; 2012; Baldeck et al., 2013; 2016).

Quantifying and mapping exact soil characteristics is laborious and expensive, as it requires measurements to be made in laboratories. Nevertheless, there is potential for useful information relevant for species distributions to emerge. The soils in tropical America have various origins and histories (Chauvel et al., 1987; Lips & Duivenvoorden, 1996; Vitousek et al., 2003; Rossetti et al., 2005; Quesada et al., 2011; Quesada & Lloyd, 2016). As a result, soils in some areas are formed by *in situ* weathering of base rock and in other areas by weathering of fluvial or marine sedimentary deposits; differences in texture (the relative contents of sand, silt and clay in a soil sample) and chemical composition (concentration of macro and micronutrients) that are relevant for plants can emerge due to differences in the mineralogical composition of the original parent material and through sorting processes during sedimentation. In addition, climate and the amount of time that has been available for surface erosion and weathering are important, because the weathering process causes leaching of nutrients, which gradually impoverishes the soils.

In addition, plants are affected by hydrological conditions, which vary with climate, topography and soil texture. Some combinations between these three factors can lead to anoxic conditions due to permanent waterlogging or seasonal flooding (Wittmann et al., 2002; Engelbrecht et al., 2007; Parolin, 2009). Overall, climate and edaphic conditions can be considered to be filters for species establishment.

Here we provide an overview of field studies focusing on pteridophyte–soil relationships in lowland forests of tropical America. We address both community-level patterns and the edaphic niches of some pteridophyte species. We also discuss the broader relevance of these relationships for the biogeography and evolutionary history of pteridophytes, and possible applications of the current knowledge

COMMUNITY-LEVEL PATTERNS ALONG EDAPHIC GRADIENTS

Soil chemistry and texture

Historical overview

Early studies on pteridophyte–soil relationships in the American tropics focused on pteridophyte species lists from sites with contrasting soil types. For example, Cremers (1991) compared fern communities between rocky and clayey substrates in French Guiana. Peruvian Amazonian ferns were compared by Young and León (1989) between clay soil and loamy sand soil and by van der Werff (1992) among inundated sites, swamps and white-sand soils. Tuomisto and Ruokolainen (1994) documented quantitatively how species composition and abundances change in the transition from loamy soils to white sand soils in Peruvian Amazonia. All of these studies found many species restricted to only one of the observed substrates, and concluded that the overall species richness was fostered by environmental heterogeneity and substrate specificity of most pteridophyte species.

To obtain a more general view of compositional variation across moist forests in tropical America, Tuomisto and Poulsen (1996) compiled the locality-specific species lists published until then into a sites by species table. They then carried out community-level ecological analyses on the data set, which contained many localities from Amazonia and some from the Guianas and Central America. In spite of the broad geographical coverage and differences in climate among the sites, ordinations revealed that the most important compositional variation could be associated with a gradient from extremely nutrient-poor white sand soils to nutrient-rich, often clayey soils.

Since then, many studies have made quantitative inventories of pteridophytes and collected surface soil samples for chemical and textural analyses to test the pteridophyte-soil relationships in more detail. These studies have both documented patterns of species turnover and assessed how this turnover is related to different edaphic gradients. Some studies have simplified the soil information to one or a few synthetic variables (e.g. PCA ordination axes), which allows assessing the importance of general soil gradients but does not clarify the relative importance of the different soil properties (e.g., Costa et al., 2005; Jones et al., 2008; 2016).

Exchangeable base cations and aluminium

In those studies that have assessed soil variables separately, the most consistent pattern that has emerged is that pteridophyte species turnover is strongly related to variation in the concentration of exchangeable base cations (Ca, K, Mg, Na). In all the studies, the sum of bases has emerged as one of the most important factors in data analyses. One or more of the individual base cations have invariably been found significant as well. This has been the situation in lowland forests both in Amazonia (figure 1; Tuomisto et al., 1995; 2003a; 2003b; 2003c; 2016; Ruokolainen et al., 2007; Higgins et al., 2011; Zuquim et al., 2012; Moulatlet et al., 2014) and in Central America (Jones et al., 2006, 2013). The importance of base cations conforms with expectation, as all of them except Na are essential plant nutrients that play important roles in physiological processes such as photosynthesis, water uptake and intracellular transportation of solutes (Jackson et al., 2000).

Studies made in Hawaii found that leaf Ca, K and Mg contents varied both within and among species, but no clear relationship with the concentration of the corresponding

elements in the soil was found (Amatangelo & Vitousek, 2008; Richardson & Walker, 2010). The clearest result was a phylogenetic signal: polypod ferns had systematically higher leaf Ca, K and Mg contents than non-polypod ferns. When compared to angiosperms, both polypod and non-polypod ferns had lower leaf Ca contents, but K contents were higher in polypods than angiosperms and Mg contents were similar. It has been hypothesized that fern leaves have low Ca content because ferns evolved in soils with low Ca concentration (Amatangelo & Vitousek, 2008), but whether extant ferns with different soil Ca preferences differ in leaf Ca content is not known. Furthermore, the studies carried out in Hawaii included only 15 pteridophyte and six angiosperm species, and since we do not know similar studies in continental tropical America, it is unclear how general the observed pattern is.

The contribution of other chemical variables to explain pteridophyte species turnover has been more erratic. Aluminium, for example, can be toxic in high concentrations and potentially constrain fern growth by limiting nutrient uptake and root development (Schmitt et al., 2017). Many pteridophytes have developed evolutionary strategies to tolerate aluminium (Olivares et al., 2009), and aluminium accumulation seems to be more common in terrestrial ferns than in angiosperms (Schmitt et al., 2017). Epiphytic species show lower levels of aluminium accumulation than terrestrial species, which is not surprising given that epiphytes do not have a direct connection with the soil.

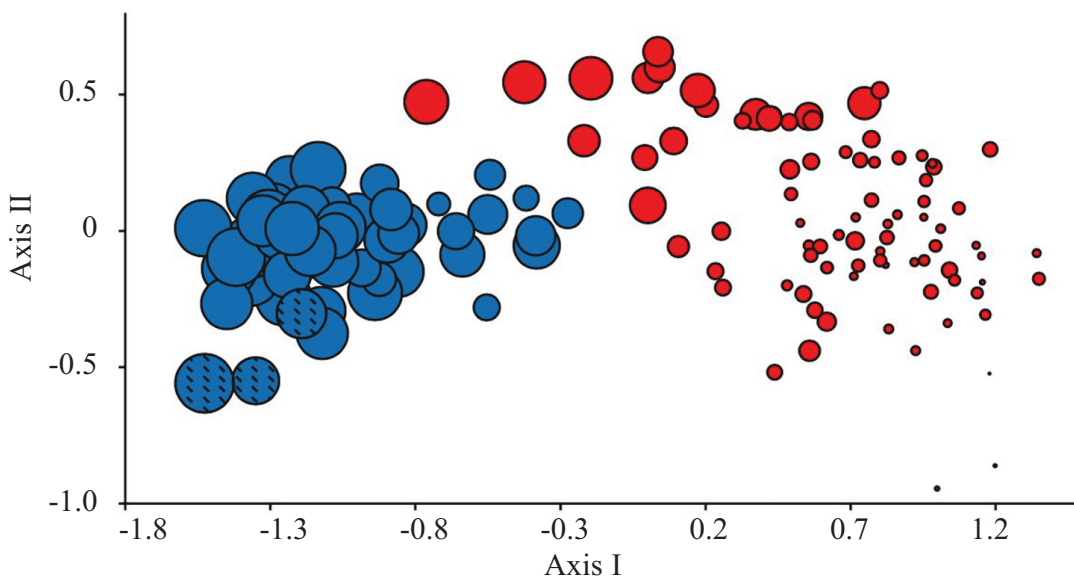


Figure 1. Ordination (NMDS optimised for two dimensions) of 138 transects of 500 m x 5 m in northern Peruvian Amazonia based on their pteridophyte species composition (floristic similarities between two transects calculated with the Jaccard index, i.e. as a proportion of species shared out of the total number of species found in both transects). The transects are plotted such that similar ones are closer together than more dissimilar ones (numeric values on the axes are unimportant). Point size is proportional to the concentration of exchangeable base cations in the soil (Ca+Mg+K+Na, log-transformed) and colours correspond to the two most distinct classes in a cluster analysis based on the floristic similarities. The same division exactly corresponds to the dichotomy between cation-rich clay soils proposed to be of semi-marine origin (in blue) and relatively cation-poor sandy-loamy soils of fluvial origin (in red). Reprinted from figure 2 of Higgins et al. 2011 (the source article is OnlineOpen).

However, aluminium accumulation has been observed in at least two epiphytic species, an *Elaphoglossum* and a *Didymoglossum* (Schmitt et al., 2017). Further studies including more species are needed to clarify if this is actually a phylogenetic effect, since most of the fern epiphytes belong to just a few genera.

Phosphorus and nitrogen

Other soil properties such as phosphorus (P) concentration, loss-on-ignition (LOI) and pH have also been investigated both in the lowlands (Tuomisto et al., 2003a; 2003c; 2016; Costa et al., 2005, Jones et al., 2006; 2013; Moulatlet et al. 2014) and in montane areas (Homeier et al., 2010; Unger et al., 2012). LOI has often had relatively low explanatory power. Phosphorus is among the important plant macronutrients, and some studies have indeed found P to be one of the most important explanatory variables in numerical analyses (Jones et al., 2013; Tuomisto et al., 2016). Other studies have found P to have little explanatory power, however (Tuomisto et al., 2003a; 2003c). This is probably because the Bray method used in these earlier studies to analyse P concentration in the soil samples does not succeed in representing plant-accessible P as well as do the methods used in the more recent studies (e.g., Mehlich III).

Nitrogen is another important plant nutrient that is technically difficult to analyse reliably from soil samples. Furthermore, N concentration in a soil sample can change during storage due to the activity of soil bacteria, unless samples are immediately frozen. Therefore, soil N concentration has not been reported in any of the studies that were carried out in remote rain forest areas. In one study that did report N, it was not among the most important soil variables (Jones et al., 2013). Whether this is because nitrogen is not limiting in the soils of the American tropics (Quesada et al., 2010) or is due to methodological problems remains to be clarified.

In a Hawaiian study (Amatangelo & Vitousek, 2008), leaf N content was found not to vary much among ferns growing on soils with different natural N concentrations. In contrast, leaf P did vary along a soil P gradient and also increased clearly in response to P fertilization. In the Andes, leaf N content was found to be essentially constant within a species along an elevational gradient (Wegner et al., 2003). However, the community-level mean leaf C:N ratio decreased with elevation, even though the C:N ratio in the soil increased.

Texture

Documenting chemical soil properties requires laboratory analyses, but gross soil texture is a characteristic that is easy to observe already in the field. Texture is often related to soil cation concentration, although this relationship is context-specific.

In northern Peruvian Amazonia, the cation-richest soils are heavy clays, intermediate soils are loamy, and the poorest soils consist of coarse white sand (Ruokolainen & Tuomisto, 1998; Higgins et al., 2011). However, in the Yasuni area of Ecuadorian Amazonia, the sandiest soils are not white sands but actually have a higher cation concentration than the loamy soils (Tuomisto et al., 2003a). In central Amazonia, the situation is yet different, because clay soils can there be almost as cation-poor as the white sands (Quesada & Lloyd, 2016). Consequently, it is important to be aware of the local conditions determining soil texture in order to avoid erroneous conclusions. In general, further investigation is still needed to obtain a complete picture of the contributions of different soil variables to explaining pteridophyte species turnover.

Species richness

Not only species composition but also species richness varies along edaphic gradients. Amazonia has relatively low species richness and endemism compared to the montane areas surrounding it, which is probably related to the relatively uniform environment (Tryon, 1985). However, clear species richness gradients have been identified also within Amazonian lowland forests. The highest local species richness seems to be found on the cation-rich soils both at the local (Costa, 2006) and at broader scales (figure 2; Tuomisto & Ruokolainen, 2005; Tuomisto et al., 2014). The broad-scale studies found that also

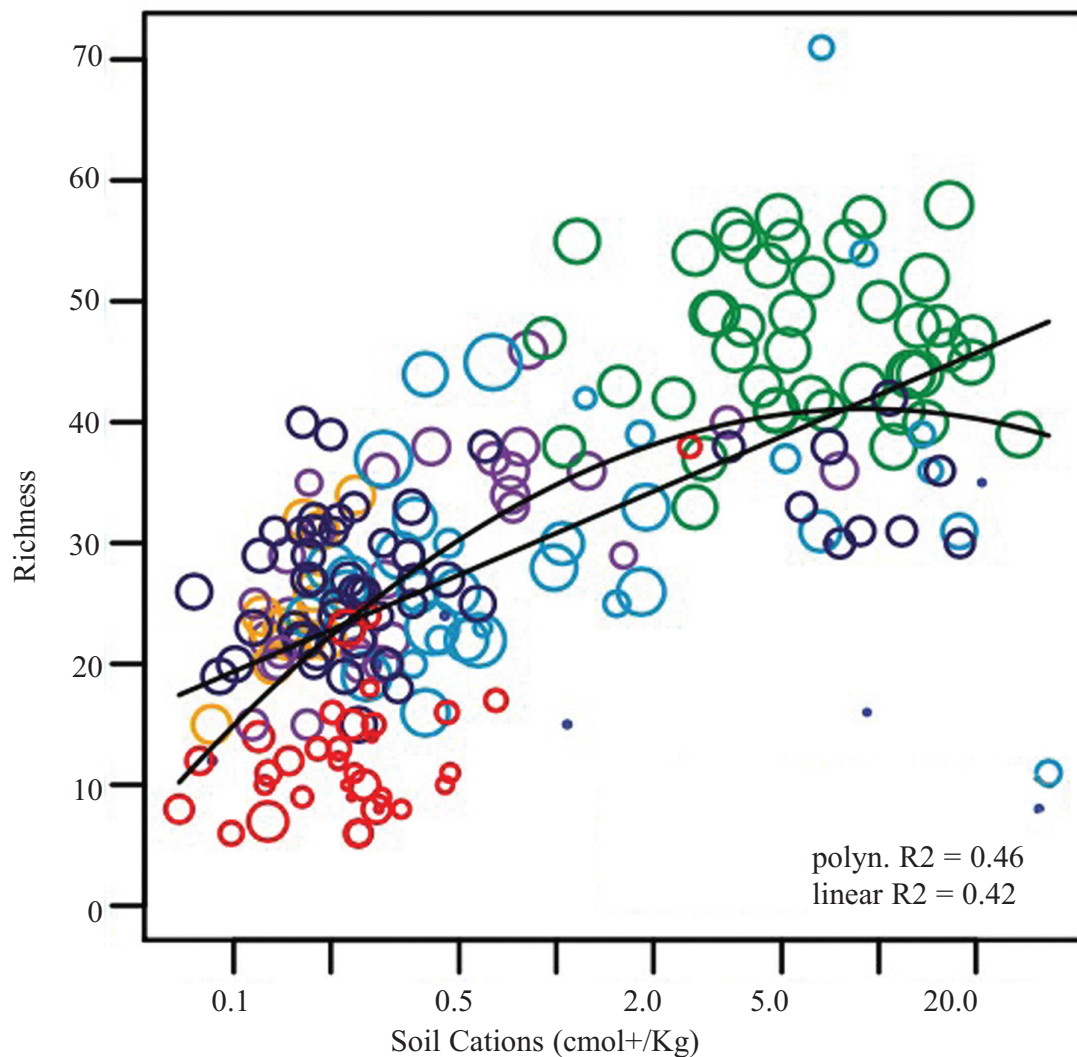


Figure 2. Trends in species richness (i.e. the number of species) of pteridophytes in 214 transects of 500 m x 5 min Amazonian non-inundated forests as a function of measured concentration of exchangeable base cations in the soil. Colours refer to geographical regions: green, Ecuador; orange, Colombia; red, central Amazonia; dark blue, NW Peruvian Amazonia; purple, NE Peru; mid blue, central Peru; light blue, S Peru. The most distant sites are more than 2000 km apart. Symbols are sized in relation to annual rainfall (extracted from WorldClim v. 1.4), which is only weakly correlated with soil cation concentration ($r = 0.21$). Reprinted, with permission, from figure 5 of Tuomisto et al. (2014).

aluminium concentration and the local variability in both Al and base cations correlate with pteridophyte species richness. Moreover, the species pool of pteridophytes seems to be larger on cation-rich than cation-poor soils (Tuomisto & Poulsen, 1996; Tuomisto et al., 2014). High pteridophyte species richness is also related to high annual rainfall, so highest average species richness is found on fertile soils in wet climates (Tuomisto et al., 2014).

Topography and hydrology

In addition to soil nutrients, water availability and soil drainage are important determinants of plant species distributions. Soil moisture varies with local topography, such that low-lying sites are generally moister and more prone to waterlogging than sites at higher topographic positions, which in turn may be susceptible to drought. In Amazonia, seasonality in rainfall causes considerable fluctuation in the water level of rivers (from a few to more than 10 m), which causes extensive areas of forest in the river floodplains to become seasonally inundated. Along the margins of the floodplains there are often swamp forests, which have waterlogged soils even during the low-water season.

A prolonged period of inundation is stressful for plants because it causes hypoxia in the soil and prevents photosynthesis in the submerged parts of the plant (e.g., Pires & Prance, 1985; Parolin, 2009). Specific adaptations are needed for plants to tolerate such conditions, which is reflected in dissimilar species composition between the inundated and non-inundated (the latter is known as ‘terra firme’) forests (Balslev et al., 1987; Kahn, 1987). These contrasting habitats are clearly distinct also in terms of pteridophyte species composition (Tuomisto et al., 2003c; Salovaara et al., 2004), and pteridophyte species richness in the inundated forests seems to be relatively low (Tuomisto & Ruokolainen, 2005). Most species that have been reported to be typical of seasonally inundated forests are epiphytic or hemiepiphytic, which allows them to at least partly escape the inundation (e.g. *Campyloneurum fuscusquamatum* Lellinger, *Lomagramma guianensis* (Aubl.) Ching, *Polybotrya caudata* Kunze, *P. glandulosa* Mett. ex Kuhn and *Salpichlaena hookeriana* (Kuntze) Alston) (van der Werff, 1992; Salovaara et al., 2004). Although non-inundated forests are not affected by floods from rivers, they, too, contain a hydrological gradient from the wet valley bottoms and creeksides to the drier hill tops and ridges. Corresponding gradients in pteridophyte species composition have been reported in several studies both for Amazonia (Tuomisto & Ruokolainen, 1994; Tuomisto et al., 1995; Tuomisto & Poulsen, 2000; Tuomisto et al., 2000; Costa, 2006; Poulsen et al., 2006; Drucker et al., 2008; Moulatlet et al., 2014) and for Central America (Jones et al., 2006; 2007; 2016). Although most pteridophytes seem to avoid waterlogged areas, moist and even sporadically inundated sites along creeks have often had high pteridophyte species richness in western Amazonia (Tuomisto & Ruokolainen, 1994; Tuomisto et al., 1995; Tuomisto & Poulsen, 2000; Poulsen et al., 2006). Slopes have been found to have high species richness and abundance in a central Amazonian study (Costa, 2005).

Often it is difficult to disentangle the possible causal factors behind observed pteridophyte species distribution patterns along topographical gradients. This is because local topographic variation can be related to factors other than soil moisture, in particular soil nutrient concentration, soil texture and light intensity at the forest floor. How such factors interact is always somewhat idiosyncratic, as it depends on the geological history of the area: the sources and mineralogy of the soil parent material as well as the different sedimentation, erosion and weathering processes that have affected it (Chauvel et al.,

1987; Vormisto et al., 2004; Chadwick & Asner, 2016). For example, white sand soils are not only nutrient-poor, but they have a low water holding capacity (which causes them to dry out quickly during dry spells) and may have a hard pan as well (which makes them even more drought-prone but in addition causes them to become waterlogged when it rains). Ridges are the most exposed part of the local topography and receive more light than do slopes and valleys. However, the amount of light that reaches the understory, where data on pteridophytes have predominantly been collected, depends also on vegetation structure and especially the presence of canopy gaps. In western Amazonia, white sands tend to be situated on the hill tops or upper plateaus, which renders them more prone to drought than in central Amazonia, where the white sands are usually found along creeks (Tuomisto & Ruokolainen 1994; Vormisto et al., 2004; Costa et al., 2005; Chadwick & Asner, 2016).

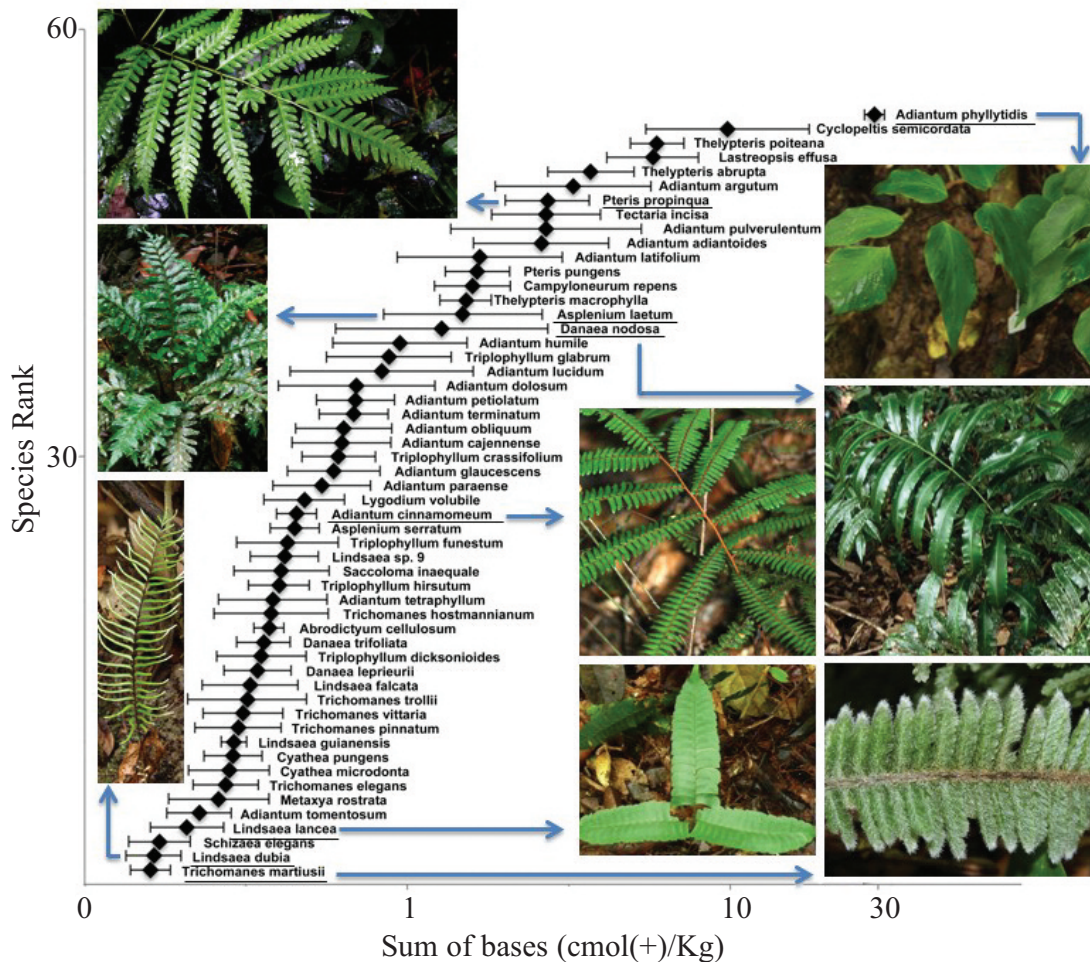


Figure 3. Optima and tolerances of fern species along a gradient of soil exchangeable base cation concentration (sum of bases) as estimated using data from 305 plots in Brazilian Amazonia. The most distant sites are more than 2000 km apart. The x axis is in logarithmic scale. Example of white-sand species is *Trichomanes martusii*, which typically grows in low-nutrient white-sand patches. Rich-soil species, like *Adiantum phyllitidis* J.Sm., typically grow on clay soils. Reprinted, with permission, from figure 3 of Zuquim et al. 2014.

SPECIES DISTRIBUTIONS ALONG EDAPHIC GRADIENTS

As discussed above, pteridophyte species present general and clear species turnover along a soil cation concentration gradient. This emerges from the behaviour of the individual species, many of which are specialised to just a limited part of the soil cation concentration gradient (figure 3) (e.g., Tuomisto & Poulsen, 1996; Tuomisto et al., 2002; Cárdenas et al., 2007; Zuquim et al., 2014; Moulatlet et al., 2017).

It has been documented that different species within the same genus can present specialisation to different parts of edaphic gradients, suggesting niche partitioning within genera. For example, six species of the terrestrial genus *Adiantum* in Peruvian and Ecuadorian Amazonia could be grouped into three distribution types (Tuomisto et al., 1998): one species (*A. tomentosum* Klotzsch) was found only in relatively cation-poor loamy to sandy soils, four (*A. humile* Kunze, *A. obliquum* Willd., *A. terminatum* Kunze ex Miq., *A. tetraphyllum* Humb. & Bonpl. ex Willd.) were relatively broadly distributed on intermediate soils, and one (*A. pulverulentum* L.) was exclusively found on the most cation-rich soils. This pattern has remained consistent in other studies that have looked at the distributions of the same *Adiantum* species along the soil cation concentration gradient (Tuomisto & Poulsen, 1996; Tuomisto et al., 2002; 2016; Cárdenas et al., 2007; Higgins et al., 2011; Zuquim et al., 2014; Moulatlet et al., 2017). *Adiantum pulverulentum* has also been found in the nutrient-rich anthropogenic dark-earth soils in Bolivia (Quintero-Vallejo et al., 2015). These examples from areas more than 1000 km apart suggest that the soil preferences are consistent across the Amazon basin.

Another genus whose species have been found to be clearly differentiated along edaphic gradients in Amazonia is the hemiepiphyte genus *Polybotrya* (Tuomisto, 2006). This genus has two species restricted to cation-rich soils (*P. crassirhizoma* Lellinger and *P. fractiserialis* (Baker) J.Sm.), two found on intermediate soils (*P. caudata* and *P. osmundacea* Humb. & Bonpl. ex Willd.), one on relatively cation-poor soils (*P. pubens* Mart.) and two on very cation-poor soils (*P. sessilisora* R.C.Moran and *P. glandulosa*). In addition, the species segregate along a hydrological gradient: *P. caudata* and *P. glandulosa* occur in swamps and in seasonally inundated areas along streams, *P. sessilisora* occurs mainly on hill tops, and the other species are intermediate.

It has been found that even within the relatively local scale of La Selva biological station in Costa Rica, different species of ferns show different distributional patterns along gradients of soil chemistry and topography (Jones et al. 2007; 2008).

Our understanding of edaphic specialisation in pteridophytes is advancing in parallel with taxonomic progress and data accumulation. For example, the terrestrial genus *Metaxya* was thought to be monotypic, but now it is known to include at least six species. One of these is specialised to very nutrient-poor white sand soils, and its edaphic distribution is therefore clearly segregated from the other species, even though its geographical distribution overlaps with two of them (Cárdenas et al., 2016).

A similar case was found for two species of the mainly terrestrial genus *Lindsaea*. *Lindsaea divaricata* Klotzsch has traditionally been considered a widespread generalist species, but ecological field work in Amazonia revealed that the populations on edaphically different sites have subtle morphological differences, especially at the juvenile stage. It turned out that *L. divaricata* itself only occurs on very nutrient-poor sites, such as white sand soils and peat bogs, and the form growing on loamy soils is a different species, *Lindsaea digitata* Lehtonen & Tuomisto (Lehtonen & Tuomisto, 2007). Several fern genera show strong edaphic niche conservatism to either poor or rich soils, whereas many other genera have radiated to span a rather broad edaphic range (Lehtonen

et al., 2015). Both *Adiantum* and *Trichomanes* have species on various kinds of soils, but their overall distributions have been found to be biased such that *Adiantum* is mostly a rich-soil lineage and *Trichomanes* mostly a poor-soil lineage (Lehtonen et al., 2015). Some other genera are more uniform in their edaphic distribution. For example, all species of the genera *Bolbitis*, *Pteris* and *Tectaria* seem to be restricted to rich soils in Amazonia, whereas in the mostly rich-soil *Thelypteris* s.l. there are a few exceptions (with the most notable one being *Thelypteris (Meniscium) macrophylla* (Kunze) C.V.Morton on intermediate soils). In contrast, all species of *Triplophyllum* and *Schizaea* and almost all species of *Lindsaea* are restricted to poor soils (Tuomisto & Poulsen, 1996; Tuomisto, 1998; León et al., 2005; Lehtonen et al., 2015). For a long time, *Tectaria brauniana* (H. Karst.) C.Chr. seemed to be an odd *Triplophyllum*-like poor-soil species within an otherwise rich-soil genus, but eventually molecular phylogenies showed that it belongs to the genus *Hypoderris*, which is sister to *Triplophyllum* (Moran et al., 2014; Wang et al., 2014).

BIOGEOGRAPHICAL AND EVOLUTIONARY CONSEQUENCES

Strong soil specificity restricts the occurrences of a pteridophyte species to sites representing its favoured kinds of soil. When the soil properties themselves are regionally distributed such that different areas are geochemically different, this may lead to patterns of biogeographical magnitude, with different regions having different pteridophyte species pools (Tuomisto et al., 2016). Tryon and Conant (1975) observed that Brazilian Amazonia has a lower diversity of the terrestrial genera *Thelypteris* and *Pteris* than do surrounding areas. This is consistent with these genera being mostly found on cation-rich soils, which in turn are rather rare and restricted to small patches in central Amazonia (Tuomisto & Poulsen, 1996; Zuquim et al., 2009).

In both Peruvian and western Brazilian Amazonia, a steep turnover of pteridophyte species has been documented across the limit between two geological formations, one of which consists of relatively cation-rich clays and the other one of cation-poor loamy soils (Higgins et al., 2011 in Peru; Tuomisto et al., 2016 in Brazil). In the Peruvian area, the borderline between the two formations is identifiable in satellite imagery for a distance of more than 200 km, and in the Brazilian area, for about 1000 km. In each area, the species turnover patterns were similar, and a larger number of pteridophyte species and genera was found on the formation with the higher concentration of base cations. Although such boundaries between soil types do not form physical dispersal barriers, they may nevertheless effectively function as such and restrict the distributions of specialist species.

Furthermore, such an edaphic barrier can cause differential selection pressures on the two contrasting surfaces. The observed edaphic segregation among congeneric fern species has indeed inspired the suggestion that speciation in Amazonia may have been driven in part by mechanisms of geographic isolation (allopatric speciation) but also by reproductive isolation caused by abrupt discontinuities of soil conditions (i.e. parapatric or sympatric speciation; Tuomisto et al., 1998; Tuomisto, 2006; 2007). This hypothesis has not yet been tested for pteridophytes using well-resolved phylogenies, but results from analyses involving other Amazonian plant groups have supported the idea (Schulman et al., 2004; Fine et al., 2005; Fine & Kembel, 2011).

PRACTICAL APPLICATIONS OF PTERIDOPHYTE-SOIL RELATIONSHIPS

An important practical application emerging from the edaphic specificity of pteridophyte

species is that they can be used as indicator species for habitat classification and mapping, which are essential for conservation planning. Soil heterogeneity causes variation in the floristic composition of forests that is not necessarily reflected in easily detectable changes in forest structure (Suominen et al., 2015). For example, Amazonia is mostly covered in dense terra firme rainforests, the classification of which into more accurately defined forest types is not a trivial task (Pires & Prance, 1985; Duivenvoorden & Lips, 1995). To some extent, habitat classification can be done solely on the basis of differences in soil conditions (Duivenvoorden & Lips, 1995), but taking into account also floristic information may give ecologically more meaningful results (Ferrier, 2002).

Although habitat specificity is common in other plant groups as well (e.g., trees, palms and Melastomataceae; Ruokolainen et al., 1997, 2007; Vormisto et al., 2000, 2004; Phillips et al., 2003; Tuomisto et al., 2003a; 2003b; 2003c; 2016; Baldeck et al., 2013; 2016), pteridophytes have advantages that make them an especially good indicator group. Most importantly, pteridophytes are relatively easy and quick to sample, especially compared to trees: the individuals are of a convenient size and easily accessible in the forest understorey (if canopy epiphytes are ignored), the number of species is manageable, and most genera and species are easy to identify on the basis of gross morphology (Ruokolainen et al., 1997; 2007; Kessler & Bach, 1999; Tuomisto et al., 2003c; Duque et al., 2005; Zuquim et al., 2009; 2017).

Given that many tropical forest areas are difficult to access, remote sensing has been used to identify patterns in vegetation and soil heterogeneity. The interpretation of satellite images needs to be supported by field verification, and several studies have used pteridophytes for the purpose of validating observations based on Landsat TM/ETM+ images (Tuomisto et al., 1995; 2003a, 2003b; Salovaara et al., 2005; Higgins et al., 2011; 2012) and LiDAR data (Higgins et al., 2015). Combining information on pteridophyte-soil relationships with remote sensing opens a large set of applications. Rajaniemi et al. (2005) used satellite images to produce predictive maps of the species richness of pteridophytes and Melastomataceae, including maps for subsets with different edaphic preferences. Salovaara et al. (2005) used pteridophyte inventories and satellite imagery to produce a habitat map for mammal surveys. Zuquim et al. (2014) tested the use of pteridophytes as indicators of different soil properties, and found that their predictive power was best for the concentration of exchangeable base cations. Sirén et al. (2013) used known pteridophyte optima for soil cation concentration to produce a map indicating variation in potential site productivity, which can be expected to be related with game animal population density and carrying capacity, to support local decision-making on where to apply hunting restrictions to ensure sustainability of hunting.

Several digital soil maps have been published that can be used in species distribution modeling and other applications (SOTERLAC [FAO 2006], SoilGrids [Hengl et al. 2007], HWSD [Nachtergaele et al. 2012]). Although these have been found to improve the performance of fern species distribution models above that of models based on climatic data only (Figueiredo et al., 2018), they are based on scant field data, so their accuracy at fine scales varies considerably. Moulatlet et al. (2017) used field data on soils and pteridophytes to test the accuracy of these maps, and found that they had only limited capacity to reconstruct the known edaphic preferences of thirteen fern species (*Adiantum pulverulentum*, *Adiantum tomentosum*, *Cyathea pungens* (Willd.) Domin, *Cyclopeltis semicordata* (Sw.) J. Sm., *Lindsaea guianensis* (Aubl.) Dryand., *Pteris pungens* Willd., *Saccoloma inaequale* (Kunze) Mett., *Schizaea elegans* (Vahl) Sw.,

Thelypteris macrophylla, *Trichomanes elegans* Rich., and *Trichomanes martusii* C.Presl).

FUTURE PROSPECTS AND RECOMMENDATIONS

Our knowledge of species–soil relationship has significantly increased in the past few decades. However, the tropical American forests cover a vast area, and the distribution of both pteridophyte and soil diversity is still largely unknown. In particular, there is need for more collections to fill the existing data gaps (figure 4; Feeley, 2015). The digital revolution of the past 10 years has also affected soil and plant sciences (Hartemink & McBratney, 2008; Peterson et al., 2010; Hardisty & Roberts, 2013): species records and taxonomic information have been compiled into online databases, herbarium collections have been digitalised and made available online, and mapping techniques have been developed.

Access to plant records has improved dramatically. Many herbaria have made their collections available online, and almost one million geo-referenced pteridophyte observations are accessible through the Global Biodiversity Information Facility (www.gbif.org), which provides an interface to the digital databases of herbaria worldwide. Currently, nearly 50,000 pteridophyte observations from South America are accessible through GBIF (figure 4). These data can give valuable information on pteridophyte occurrences at the broad scale, and thereby facilitate biogeographical and macroecological inferences. In addition, the increasing access to fern data in online

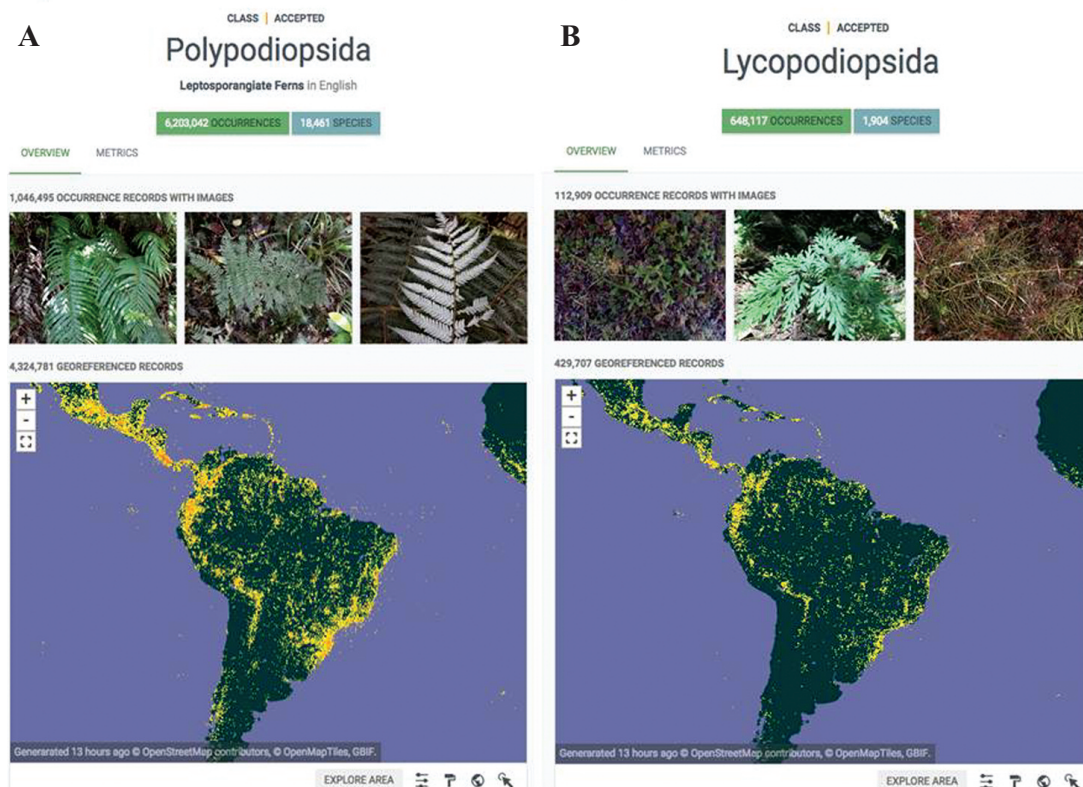


Figure 4. Density of **A:** Polypodiopsida and **B:** Lycopodiopsida records available in the Global Information Facility (GBIF - www.gbif.org). Dark green indicates that there are no collections available, shades from yellow to red indicate increasing density of collections. Retrieved on the 30th of May 2018.

portals helps to identify the data voids and to target the collection of new field data to unsampled areas (Feeley, 2015). Unfortunately, the accuracy of the geographic coordinates provided with the observations is variable. Even when a careful data-cleaning step is implemented, one cannot count on high geo-referencing accuracy in the GBIF data.

Individual researchers and other interested persons can share their digital collections (photographs) and taxonomic information globally through the Ferns and Lycophytes of the World portal (www.ferns-of-the-world.com). Currently, this portal contains photographs of nearly 1000 species. However, the total area inventoried still represents a very small portion of the American tropics. The impact of collection density on the observed pteridophyte species richness has been documented in Bolivia, where the number of known species has increased dramatically during a project aiming to document the pteridophyte flora of the country (Soria-Auza & Kessler, 2008). Such trends have an impact on the global species richness estimates as well: while ca. 9,000 fern species are currently known worldwide, it has been estimated that 15,000 may exist (Kessler, 2010). Indeed, compilations of fern richness show that the number of species keeps increasing (Prado et al., 2015).

It seems that the relationships between pteridophytes and soils in the American tropics have mostly been studied in Amazonia, and to some degree in Central America. We did not find studies explicitly addressing soil characteristics in other rainforest areas in the American tropics, such as the Atlantic rainforest of Brazil or montane forests in the Andes. Although collecting and transporting soil samples takes some effort, and laboratory analyses are expensive, the existence of soil data significantly adds value to the pteridophyte data as well. In particular, following already used protocols would allow data to be combined across studies in order to build a broader view of community ecology and biogeography not only of pteridophytes themselves but of tropical forests in general. One possible strategy to improve our knowledge on pteridophyte distributions is to crowdsource data collection by involving non-scientists. Citizen science is emerging as an important way not only to increase the number of observations but also to engage the society and to raise public awareness of nature. This approach is facilitated by the existence of online platforms, such as iNaturalist (inaturalist.org), which allows easy uploading and curation of data by any interested person. We have recently started a campaign to collect data on pteridophytes in Amazonia (<https://www.inaturalist.org/projects/samambaias-helechos-ferns-amazonia>), and encourage everyone who visits the area to participate, or to start their own campaigns in other areas.

The forests in tropical America face high deforestation rates (Watson et al., 2018), and some areas, soil types and forest types may be more at risk than others (Laurance et al., 2002). A broad picture of both species distributions and species–soil associations is needed to understand the ecology, biogeography and evolution of pteridophytes in the tropics. Such information can help conservation and the planning of sustainable use of forest resources.

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SHORT BIOGRAPHIES OF THE AUTHORS

Gabriel M. Moulatlet was born in São Paulo, Brazil on 20 April 1987 and spent his childhood in the countryside town of Itapeva. He studied biology at the University of the State of São Paulo (UNESP) and then moved to Manaus to obtain his master's degree from the Brazilian National Institute of Amazonian Research (INPA). It was at INPA where he started to study ferns, inspired by his supervisor Flavia Costa. He graduated with a thesis that investigated the spatial distribution of understory herbs along hydrological gradients in Central Amazonia. After finishing his thesis he was invited by Hanna Tuomisto to participate in a 3-month boat expedition along the Juruá River in Brazilian western Amazonia. The successful trip resulted in an



invitation to go to Finland for a year to work with the Amazon Research Team of the University of Turku. His stay in Finland was extended to five years, during which he was involved in several scientific publications, participated in field expeditions to the Amazon and did a PhD degree. Currently, he is back to the Amazon, living in Ecuador, teaching and researching and supervising students at the Universidad Regional Amazónica Ikiam. His interests are in biogeographical and ecological aspects of ferns and other plant groups of tropical forests and their relationship with soil and hydrological conditions.

Gabriela Zuquim was born in São Paulo, Brazil on 22 July 1981. After obtaining a



degree in Biology at the University of São Paulo in 2003, she moved to Manaus, Brazil, to enroll in a master degree program in Ecology at the National Institute of Amazonian Research (INPA). She completed her degree in 2006. Between 2006 and 2010, she collected fern data over five states of the Brazilian Amazonia, in research sites established by the Brazilian Research Program on Biodiversity Research (PPBio). She made a comprehensive sampling of the, until then, widely unknown pteridoflora of Uatumã region, central Amazonia that resulted in a richly illustrated field guide published in 2008. In 2011, she moved to Finland to carry out PhD studies in ecology at the University of Turku. Her doctoral thesis was on the diversity patterns and usefulness of ferns and lycophytes as habitat indicators in Amazonia. During her PhD, she also produced an online key to Amazonian ferns. She completed her PhD in 2015 and continues as a post-doctoral researcher at the University of Turku. She is interested in modelling Amazonian species distribution in the present and in the future.

Hanna Tuomisto was born in Helsinki, Finland, on 4 May 1965. She studied botany at the University of Helsinki, and interrupted the studies for half a year to set off with fellow student Kalle Ruokolainen to explore the biological wonders of Peru. Both were fascinated by Amazonian rain forests, and went on to study tropical ecology for a year at Aarhus University, Denmark. After finishing their MSc degrees in 1990, they joined the Amazon Research Team at the University of Turku to pursue PhD studies in the heterogeneity of

Amazonian forests and how geological history and soil properties might be linked to plant species distributions and speciation. Since she obtained her PhD in 1994, her research has included not only floristic studies but also taxonomy, molecular phylogeny and biogeography of ferns, as

well as remote sensing and conceptual studies related to beta diversity. She enjoys field work and has carried out numerous expeditions to remote parts of Amazonia.

