Turun yliopisto
University of Turku

FERNS AND LYCOPHYTES IN AMAZONIA: DIVERSITY PATTERNS AND USEFULNESS AS HABITAT INDICATORS

Gabriela Zuquim

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Gabriela Zuquim

University of Turku

Faculty of Mathematics and Natural Sciences
Department of Biology

Supervised by

Doctor Hanna Tuomisto
Department of Biology
University of Turku
Turku, Finland

Doctor Flávia R. C. Costa
Coordination of Biodiversity Research
National Institute of Amazonian Research
Manaus, Brazil

Reviewed by

Doctor Michael Kessler
Institute of Systematic Botany
University of Zurich
Zurich, Switzerland

Professor Jens-Christian Svenning
Department of Biosciences
Aarhus University
Aarhus, Denmark

Opponent

Professor Hans ter Steege
Department of Botany
Naturalis Biodiversity Center
Leiden, The Netherlands

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*For all those who feel the Amazon rivers
running in their veins and are committed to
live, experience, understand and conserve the
enchantment of this forest.*

*Para todos aqueles sentem que tem os rios
da Amazônia correndo em suas veias e estão
comprometidos a habitar, vivenciar, entender e
conservar os encantos dessa floresta.*

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LIST OF ORIGINAL PAPERS

This thesis is based on the following manuscript which are mentioned in numerals:

I.   Zuquim, G., Costa, F.R.C., Prado, J. & Braga-Neto, R. (2009). Distribution of pteridophyte communities along environmental gradients in Central Amazonia, Brazil. *Biodiversity and Conservation* 18: 151-166.

II.   Zuquim, G., Tuomisto, H., Costa, F.R.C., Prado, J., Magnusson, W.E., Pimentel, T., Braga-Neto, R. & Figueiredo, F.O.G. (2012). Broad Scale Distribution of Ferns and Lycophytes along Environmental Gradients in Central and Northern Amazonia, Brazil. *Biotropica* 44: 752-762.

III.   Tuomisto, H., Zuquim, G. & Cárdenas, G. (2014). Species richness and diversity along edaphic and climatic gradients in Amazonia. *Ecography* 11: 1034-1046.

IV.   Zuquim, G., Tuomisto, H., Jones, M., Prado, J., Figueiredo, F.O.G., Moulatlet, G.M., Costa, F.R.C., Quesada, C.A. & Emilio, T. (2014). Predicting environmental gradients with fern species composition in Brazilian Amazonia. *Journal of Vegetation Science* 25: 1195-1207.
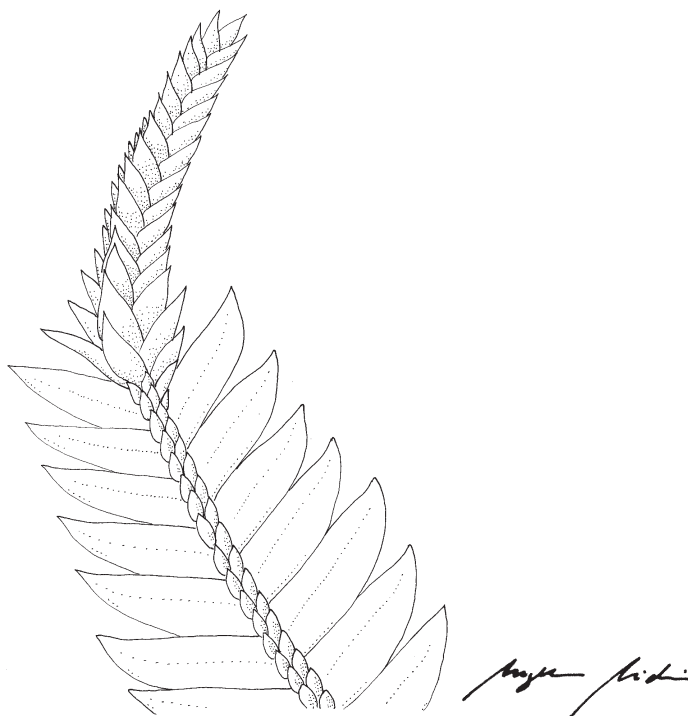
PREFACE

The ultimate purpose of this thesis can be reduced to very simple terms: to know where species are and why they are there. This is important when planning conservation strategies for them. Achieving this is not that simple, especially in Amazonia. Lack of data and the absence of a theoretical background are just two examples of the challenges that make a scientific trajectory even more interesting and demand creativity from the researcher. The need to improve the quality of background data has inspired me to carry out extensive field inventories around Brazilian Amazonia and to access large datasets built by colleagues. The resulting data were made freely available and may also benefit other researchers. While data are still full of gaps, it is definitely the best I could achieve. The next challenge to be faced refers to our incomplete understanding of species-environment relationships. This is addressed in the first three chapters, which among their other aims, report patterns that can be seen as a diagnosis of fern and lycophytes diversity in Amazonia. These patterns provide a possible basic knowledge for the development of ecological and evolutionary theory and an opportunity to test it. Finally, the third – and greatest - challenge is how to use this knowledge towards better conservation strategies in Amazonia; one response is the subject of the last chapter, using ferns as indicators of soil conditions. The knowledge accumulated in this thesis is a small contribution towards better understanding of patterns in Amazonian species distribution.

1.   INTRODUCTION

Amazonia comprises an area of more than six million km^2 and harbours an estimated 16,000 lowland tree species (ter Steege et al., 2013) and 6000 vertebrates (Mittermeier et al., 2002). It is home to some 370 different indigenous groups (1.6 million indigenous people) (RAISG, 2009). In the Brazilian territory alone, 180 languages are spoken (Ricardo and Ricardo, 2011). All this diversity faces alarming deforestation rates. In 2002 and 2003, Brazilian Amazonia lost on average eleven soccer fields of forest every minute (Laurance et al., 2004). In 2014, deforestation destroyed almost 5000 km^2 – or 500,000 soccer fields – of Brazilian Amazonia (INPE/PRODES 2014).

Even under such high pressure, the Brazilian Amazon still contains most of the carbon stock of the world's remaining tropical rainforests (Saatchi et al., 2011), and a conservation plan based on solid scientific information is therefore urgently needed. Scientific understanding does in fact affect conservation planning in Amazonia, but the maps needed by decision-makers to assess biological and habitat diversity are at present too coarse. The purpose of this thesis is to provide information on plant species diversity and distribution patterns in Amazonia, which is part of the background knowledge needed for conservation planning.

1.1   Species distribution and diversity patterns and their importance for conservation

1.1.1   Challenges to mapping species distributions in Amazonia

Amazonia is a mosaic of forest types (Pires, 1984; Salo et al. 1986; Tuomisto et al. 1995; Emilio et al., 2010), and species are non-randomly distributed (Ayres and Clutton-Brock, 1992; Tuomisto et al., 2003c; Ribas et al., 2005; Pitman et al., 2008). A network of conservation units of this biome should contain adequate representation of different habitats, so as to collectively provide viable populations of all occurring species (Margules et al., 2002). Maps of the distribution of the diversity and environmental characteristics of Amazonia are therefore an important tool in evaluating and protecting its heterogeneity. These maps, however, are usually inexistent or made in a resolution that is inadequate for regional planning. For example, the Soil and Terrain Database for Latin America and the Caribbean (Engelen and Dijkshoorn, 2014) is the most complete and recent basin-wide soil map available and divides almost 60% of Amazonian soils into only two categories, Ferrasols and Acrisols (Quesada et al., 2011). Smaller-scale variations are thus overlooked.

Understanding and predicting species distribution in the largest forest in the world in order to strength its conservation is as challenging as it is relevant. The first challenge to ecological studies in tropical forests is the lack of data on species occurrence and environmental conditions. The problem arises from the nature of the Amazonian rainforest: its vastness, inaccessibility, high diversity and complex dynamism. A single hectare of forest can contain more than 300 species of trees (Pitman et al., 2008); more than 900 vascular plant species (Balslev et al., 1998) making fieldwork and specimen identification difficult and time-consuming. The low density of botanical collections compromises biodiversity mapping (Hopkins, 2007). As a result, the basin is floristically poorly known (Hopkins, 2007), and collections are concentrated around research centres (Nelson et al., 1990; Schulman et al., 2007).

Nonetheless, biological theories determine conservation practices even when based in scanty or faulty data. An interesting example of the use of biodiversity distribution maps in planning conservation units was the creation of the Jaú National Park in Amazonas, Brazil. The original proposal for the park was based on a map in which the area was defined as a Pleistocene refuge (Foresta, 1991). Nowadays, the refuge theory has little support (Bush and Oliveira, 2006). It also emerged that the map contained a cartographic error and the region was not even inside the supposed refuge. But the area presented other practical advantages for implementation: low human density, few private areas, exclusive access by boat (facilitating vigilance) etc. and thus the proposed park became true. The Jaú National Park is an important conservation unit but does not contain a known special level of endemism that supports the initially proposed boundaries.

Even when good biotic data are gathered, predicting species distribution is challenging. Not rarely, the proposed predictive models have low predictive power after the inclusion of those variables that the researcher considers relevant (and feasible to measure) and a large part of the compositional variation remains unexplained (Duivenvoorden et al., 2002; Tuomisto et al., 2003a, Jones et al., 2006). This may be due to the absence of some relevant variable, to an inadequate analytical approach, to noise in the data. It can also be simply due to the absence of any strong measurable determinant, e.g. in the case of homogeneous areas. Given that part of the variation in organismal communities can be related stochastic events such as chance of colonization, random extinction and ecological drift (Chase and Myers, 2011), an unexplained part of the variation is always expected in the models.

The availability of light, for example, is among the meaningful but rarely measured variables. Obtaining this data in the field in a tropical forest is not an easy task because of the high spatial and temporal heterogeneity of light conditions. Moreover, not quite 2% of the incident solar light reaches the ground of a tropical forest (Hogan and

Machado, 2002). Therefore, variation in the understory, while minor, is ecologically important (Montgomery and Chazdon, 2002). Its relevance in predictive models might be being underestimated. The inclusion of different variables was one of the approaches adopted towards better predictive power of the species occurrences models.

Another approach is to improve analytical methods. The most commonly applied indices (e.g. Sørensen and Bray-Curtis indices) used to evaluate composition dissimilarity between two plots become saturated at a fixed maximum value when sampling units share few or no species, even if this does not reflect the actual ecological distance (dissimilarity) between the plots. I have therefore applied an alternative statistical index and compared the results to those obtained using the standard ecological procedures.

1.1.2   *Factors determining community composition*

The biogeography of Amazonia is far from understood and species-environment relationships are still under debate. In the 2000s, Hubbell`s neutral theory (Hubbell, 2001) ignited a debate as to whether species distributions were determined by environmental determinism or by stochasticity and dispersal limitation (the niche vs. neutral theory). In Hubbell's seminal book, species relative abundances are explained independently of environmental conditions, as if all species were ecologically identical and thus competitively equivalent. Therefore, in the null-model introduced by Hubbell, species distributions were determined by the dynamics between stochastic dispersal and extinction and not by environmental filtering. It is generally accepted that both spatial and environmental processes act to determine the relative abundances and distribution of species (Chase, 2014) but the relative roles of each in varies among biological groups and on different scales (Karst et al., 2005) and its still an important subject of study. Among ferns and lycophytes, there is strong evidence for dispersal limitation of spores at continental scales (Geiger et al., 2007; Muñoz et al., 2004) but at more local scales, low levels of changes in composition (also called turnover) have been reported in relatively homogeneous environments (Jones et al., 2006; I), probably due to the high dispersal mobility of fern propagules (Tryon, 1989; Page, 2002). A single individual can produce between 100,000 and 30 million of wind-dispersed spores in its life (Kramer 1995 *apud* Ponce et al., 2002).

Within Amazonia, an important contribution of geographic distance to explain variance of fern and lycophyte distribution have been found in some sites (Tuomisto et al., 2003a; c) but not in others (Ruokolainen et al., 2007; II). However, whether the observed effect of geographic distance indicates the importance of dispersal in structuring a biological community (Hubbell, 2001) or if it is related to unmeasured

environmental variables that are spatially autocorrelated is not clear (Tuomisto et al., 2003c). This is a general caveat of variation partitioning analysis.

What is clear is that environmental variables are consistently good predictors of changes in tropical fern and lycophyte species composition among areas (Tuomisto et al., 2003a; Karst et al., 2005; Costa et al., 2005; Jones et al., 2006; Moulatlet et al., 2014; I; II). Among the environmental determinants, edaphic characteristics are an important determinant of fern and lycophyte composition at many scales (e. g., Tuomisto and Poulsen, 1996; Ruokolainen et al., 1997, 2007; Tuomisto et al., 2003a, 2003b; Costa et al., 2005; Jones et al., 2013; I; II). It has been suggested that niche partitioning along soil nutrient gradients is a mechanism promoting speciation and regional coexistence of closely related species in tropical forests (Tuomisto et al., 1998; Schulman et al., 2004; Fine et al., 2005; Tuomisto, 2006; Jones et al., 2007). Generally, studies in larger scales incorporate more heterogeneity. For example, at a large scale, climate is also recognized as an important factor determining plant occurrences (Clinebell et al., 1995; Ter Steege et al., 2003; II). Wet areas tend to be more species-rich (III). At smaller scales, drainage capacity (Moulatlet et al., 2014) and topographic position (Tuomisto et al., 1995; Tuomisto and Poulsen, 1996; Vormisto et al., 2004; Costa, 2006) were often found to be relevant.

1.1.3   *Species richness and diversity*

Another important aspect is an understanding of the diversity patterns based on diversity indices. Species richness and diversity patterns are the framework for numerous evolutionary and ecological hypotheses. Underlying causes of such patterns are a highly complex interaction between geological landscape formation, biological evolution of taxa, present and past environmental conditions, stochasticity, and biotic interactions. The complexity of these processes might be the reason why several patterns in species richness along gradients have been reported in the tropics. The differences are related either to different plant groups or to the same group but in different areas. Several studies have proposed that a common response of vascular plant communities along single gradients worldwide is hump-shaped (Mittlebach et al., 2001; Pausas and Austin, 2001). In agreement with this trend, Ashton (1989) and Tuomisto and Ruokolainen (2005) reported a peak in species density at intermediate levels of soil fertility in tropical forests. Within ferns and lycophytes, on the other hand, most studies have found species density to increase with soil fertility (Tuomisto and Poulsen, 1996; Tuomisto et al., 2003a; Tuomisto and Ruokolainen, 2005; Costa, 2006; Cárdenas et al., 2007; IV) but one found no relationship (Tuomisto et al., 2002). The same study found a negative relationship between species richness and soil fertility for treelets and shrubs from the Melastomataceae family.

In the absence of a clear pattern, at least 120 hypotheses to explain the simple question of why species richness varies among areas have emerged (Palmer 1994). Some of the most relevant hypotheses fall into two groups: 1) hypotheses based on the present-day environment, and 2) hypotheses based on history and space. I have reported the patterns of Amazonian fern and lycophyte species richness and diversity along environmental gradients and compared the obtained results to the predictions of the productivity hypothesis, the age and stability (Fischer, 1960; Baker, 1970)**,** the mid-domain effect (Colwell and Lees, 2000) and others (IV).

1.2 Amazonian landscape evolution and the mosaic of soils

Geological processes are the ultimate cause of many of the habitat properties that are important for plants, such as soil hydrology, texture and nutrient concentration. The evolutionary history of the Amazonia landscape is an important determinant of the present-day mosaic of soils (Sombroek, 2000; Rossetti et al., 2005), which in turn determines forest structure (Sombroek, 2000; Rossetti et al., 2010; Higgins et al., 2011; Quesada et al., 2012) and species distribution (Tuomisto et al., 2002; Tuomisto et al. 2003b; Salovaara et al., 2004; Castilho et al., 2006; Kinupp and Magnusson, 2005; Nogueira et al., 2011). The present day landscape of the Amazon basin is highly determined by the presence of the Precambrian and ultrastable Guyana and Brazilian shields (Kroonenberg and de Roever, 2010) and by the tectonics related to the uplift of the Andes, which caused intense changes in river dynamics and in the input of previously buried sediments (Salo et al., 1986; Räsänen et al., 1987; Mora et al., 2010). These dynamics have a profound effect on the spatial distribution of soil types, which in turn plays an important role in species abundance and distribution.

In simple terms, the Amazon basin can be divided into three huge blocks: the cratonic, the intracratonic, and the Andean foreland (Wesselingh et al., 2010). The oldest block is the Amazonian craton, a more than 4.4 million km^2 Precambrian landmass formed through soft collisions and accretion (Cordani et al., 2009). The Amazon craton is exposed in the in the northeast and southeast of the basin (the Guyanan and Brazilian shields, respectively) but it is continuous below the Amazon drainage (Putzer, 1984; Kroonenberg and Roever, 2010). Before the Cambrian time, the cratonic areas of Amazonia were continuous and part of the supercontinent Pangea (Hoorn et al., 2010a). During the late Ordovician, an E-W orientated fault originated low due to tectonics and the craton was thus divided it into what is nowadays the Guyana and Brazilian shields (Hoorn et al., 2010a). This central and lower part formed between the shields was overlayed due to major tectonic events, forming the Amazon basin (Cordani et al., 2009).

These processes resulted in the formation of another important block: the sedimentary intracratonic zone between the Guyana and Brazilian shields. It corresponds nowadays to the east-central part of the basin, among where the Amazon River flows. The erosion of the Craton is the main source of soil sediments to the intracratonic area (Wanderley–Filho et al., 2010) therefore, intracratonic soils and rivers tend to be geochemically poor (Furch, 1984, Hoorn et al., 2010a). Most of the soils of the sedimentary zone between the Amazonian shields were formed by strongly weathered deposits (Quesada et al 2009). The exceptions are the alluvial soils formed in poorly drained areas, mainly along the present-day or past time margins of the rivers with Andean origin (*várzeas* and *palaeovárzeas*) (Sombroek, 1984). The *várzeas* and *palaeovárzeas* are directly affected by seasonal river flooding and support particular floras (Assis et al., 2015). Their soils are formed by the sedimentation of Andean particles which are typically younger and less lixiviated, and thus richer in nutrients (Junk, 1984).

The third block, the Andean foreland, is located in the western part of Amazonia. The sedimentary evolution is Cenozoic and associated with Andean uplift dynamics that created an elongated region along the Andean East part of the Andean chain where orogenic loading and unloading have occurred (Rodazz et al., 2010). It can be considered the most recent geological feature of the Amazonian basin. Its formation started in the Paleogene period as a consequence of the collision between the Nazca and South American plates that started the uplift of the Andean Mountain chain, more than 65 million years ago (Espurt et al., 2010). The Andean uplift caused deep changes in the landscape (Mora et al., 2010). The tilt in the basin drove a complete reorganization of Amazonian rivers beds and intensified the influx of sediments in the sedimentary zones (Hoorn et al., 2010b). The highly dynamic rivers and their depositional histories are one of the most important causes of the present-day mosaic of soils (Räsänen et al., 1987), which determines the distribution of many plant species (Junk, 1989; Pitman et al., 2008; Higgins et al., 2011; Figueiredo et al., 2014; Assis et al., 2015). An important consequence for biological patterns is that in many regions soil types are distributed as mosaics rather than as broad patches (Quesada et al, 2009).

The consequences of geological evolution for present day plant distributions are manifold. For example, paleochannels in the Marajó island filled with sandy sediments are a suitable substrate for tree growth, while adjacent areas are not because they are slightly lower and experience seasonal flooding (Rossetti et al., 2010). This determines the boundaries between forest and savannah in that region. The evolution of many forest formations in Amazonia occurred mainly during the Tertiary, when Amazonian drainages were undergoing a stage of drastic change due to Andes uplift and intense erosion/depositional dynamics (Hoorn et al., 2010b).

Along the river margins, younger and richer sediments from the Andes started to be deposited, forming the *várzeas*. Due to frequent changes in the riverbed (Salo et al., 1986; Räsänen et al., 1987), some of these areas are today extensive and relatively homogeneous flat areas called *paleovárzeas*, found in white-water interfluves of major tributaries of the Amazon river such as the Jutaí, the Tefé and the Madeira rivers (Assis et al., 2015); the *paleovárzeas* might harbour a particular flora, and the distance from the watershed was found to be one of the important factors determining changes in species composition (Moulatlet et al., 2014).

Sedimentary dynamics also determine the existence of white-sand forests in the Amazon basin (Rossetti et al., 2012). Most of these forests grow on deposits of sediments eroded from the Guyana and Brazilian shield before and during the early stages of the Andean uplift (Hoorn et al., 1995). The soils from these deposits are nutrient-poor and a substrate for the highly endemic white-sand forests (Anderson, 1981) that cover 3% of Amazonia (Pennington and Dick, 2010). White-sand forests are scattered over parts of western and central Amazonia (Frasier et al., 2008) but the largest patches are found in Roraima, Brazil and in upper Rio Negro (IBGE, 2004). At least in Roraima, the accumulation of white-sand sediments is related to the recent reactivation of tectonic faults (Rossetti et al., 2012). Forests over white sands harbour a distinct and less diverse species pool than terra-firme forests (Anderson, 1981; Tuomisto and Poulsen, 1996; Boubli, 2002; Stropp, 2011).

Another recognized geological division with important consequences for edaphic conditions and therefore for floristic composition is the boundary between the Pebas (or Solimões in Brazil) and Nauta formations. Several authors have reported abrupt floristic changes, probably related to the underlying geological formation (Phillips et al., 2003; Tuomisto et al., 2003b; Salovaara et al., 2005; Pitman et al., 2008; Higgins et al., 2011; Figueiredo et al., 2014). The Pebas/Solimões formation originated from the Miocene deposition of Andean sediments, which are young and fertile (Kalliola et al., 1993), into an embayed environment formed by the ongoing Andean uplift on the western side and the Purus Arch on the eastern (Hoorn et al., 1995; Räsänen et al., 1995; Latrubesse et al., 2010). This embayment formed the Pebas system, which has accumulated poorly weathered cation-rich sediment in a mainly freshwater wetland environment with occasional marine incursions (Hovikoski et al., 2007). With the continuous Andean uplift, the Pebas system was drained (Hoorn et al., 1995; Hoorn et al., 2010) and the Pebas formation was covered by coarser sandy cation-poor sediments deposited from a higher energy erosional environment (Rebata et al., 2006). These processes originated the Nauta formation (called Içá in Brazil) (Hoorn et al., 2010). Down to the present day, the increasing erosional fluvial energy and rainwater run-off has led to the removal of these formations and the exposure of buried rich Pebas soils (Higgins et al., 2011). The result is a mosaic of soil types,

with implications for biodiversity distribution in Amazonia. Higgins et al. (2011) has mapped two large boundaries between Nauta and Pebas (or Solimões in Brazil) based on the spectral reflectance of forests growing in each of the geological formations. The larger boundary of the contact between the formations runs in a N/S orientation, nearly parallel to the Brazilian/Colombian border, towards Bolivia. In Equador, the same authors found an E-W orientated boundary (Higgins et al., 2011).

1.3   Usefulness of ferns and lycophytes to predict soil characteristics

Ferns and lycophytes are an informative model group in ecological studies because they are common in the Amazonian understory, relatively easy to collect and identify and can represent up to one third of the terrestrial herbaceous species (Costa, 2004). Their commonness and diversity in the understory may be related to their high photosynthetic capacity under low light conditions and their high resilience to diseases in humid environments (Page, 2002).

It is now well known that most Amazonian fern and lycophyte species display some degree of edaphic specialization (Tuomisto and Poulsen, 1996; Tuomisto et al., 2003b). Throughout the Amazon region, drastic changes in fern and lycophyte species community composition within only 1 km^2 were related to variation of one order of magnitude in plant nutrient concentration or soil texture (Tuomisto et al., 2003a; Costa et al., 2005; Higgins et al., 2011; II). Changes in fern and lycophyte species composition can thus reflect changes in edaphic characteristics in fine spatial resolution.

When information on environmental gradients is needed but measurements of environmental variables cannot be made, biotic communities have been used as predictors of environmental conditions and habitat classification. This is a common situation in the field of palaeontology, where fossil species are used to reconstruct a past climate based on the ecology of the species (Ter Braak and van Dam, 1989; Birks et al., 1990; 2010) The statistical tools developed in the field of palaeontology can potentially be applied to extant species and currently unknown environmental conditions, such as unmonitored areas in Amazonia (Suominen et al., 2013; III). Another approach is the use of indicator plant species in mapping forest types and habitat classification. Indicator species are a powerful tool in conservation biology because of its flexible (Dufrêne and Legendre, 1997) and conceptually straightforward (McGeoch, 1998). Some approaches, like the Ellenberg's indicator values are a standard procedure in non-tropical forests (Kuusipalo, 1985; Ter Braak and Gremmen 1987; Wilson et al., 2001; Gégout et al., 2003; Schaffers and Sýkora, 2009; Häring et al., 2013).

Several specific taxa can also be used as indicators of particular environments or habitat types. In deciding which groups can be used as indicators, certain criteria

should be taken into account. Ferns and lycophytes have been proposed as a suitable indicator group in Amazonia not only because of their close relationship to soil gradients but also because they are relatively easy to observe and identify; they are neither so diverse as to make sampling burdensome nor too rare to be informative; they display broad variation in ecological adaptations, and are relatively common in many different types of habitats; and, they are not often used by human groups, which would cause changes in their natural distribution that would be difficult to measure. All of these are important criteria in choosing a target group for use as an indicator of environmental conditions (Tuomisto and Ruokolainen, 1998).

Finally, fern and lycophyte distribution patterns are to some degree congruent with those of other groups (Ruokolainen et al., 2007; Jones et al., 2013; Pansonato et al., 2013). Ferns can efficiently provide ecological information and therefore I have tested a promising method for using fern data in predicting environmental conditions (IV). I have here used the term "fern" to refer to the monophyletic group Monilophyta that together with the Lycophyta, form an artificial group of seedless vascular plants (also known as pteridophytes; Pryer et al. 2001). Lycophytes were included in papers II and III and excluded from papers I and IV. In old growth Amazonian forests, the only commonly occurring Lycophyta genus is *Selaginella*.

1.4   Aims of the thesis

My general aim in this thesis was to use ferns and lycophytes as model groups enabling a deeper understanding of the biogeography and species distribution patterns in Amazonia, and to link the findings with potential methods for improving diversity mapping. Specifically, Papers I and II report and describe the spatial distribution of fern and lycophyte communities, and its main environmental determinants at different scales. I have attempted to improve the models, using new statistical tools (II) and including less commonly used relevant environmental variables (I, II). Both I and II deal with the concept of species turnover, which is highly and directly relevant for conservation planning, based on the principle of complementarity among areas. Paper III also reports and describes patterns in fern and lycophyte communities along environmental gradients, but using diversity parameters such as species richness. This is an important approach that complement papers I and II, providing more direct insights into the biogeography and evolution of the ecosystem. I also discuss several hypotheses as to why some areas in Amazonia are richer and more diverse than others. Finally, paper IV benefits from the findings of the previous papers, and offers a step towards the application of the new information to biodiversity maps. I quantitatively evaluated methods for using fern data to predict environmental conditions.

2. METHODS

2.1 Sampling strategies and data collection

A well-known challenge in every Amazonian study is the lack of background information. Data on species occurrence in Amazonia are therefore highly valuable *per se*, and should be carefully preserved and preferably shared. In this study, I compiled data collected in four countries harbouring part of the lowland Amazonian forest: Brazil, Colombia, Ecuador and Peru and in addition, I have collected data by myself in the Brazilian Amazon. Most of the areas that I have visited had not been (or were only poorly) explored botanically before.

2.1.1 *Sampling design*

Sampling a representative number of plots and covering a broad enough scale to allow conclusions on a basin-wide basis in a megadiverse forest is not achievable even in a lifetime. That is why collaborative research groups are invaluable. This thesis contributed to and benefited from large datasets available from two well-established Amazonian research groups, one in Brazil, the other in Finland. The thesis made use of data from 540 plots (Figure 1). Plots of two different types, with different background rationales were used. The plots used in papers I, II and IV followed the RAPELD methodology (Magnusson et al., 2005), adopted by the Brazilian Research Program on Biodiversity (PPBio); the plots in paper III followed the methodology adopted in the 90s by the University of Turku Amazon Research Team (UTU-ART) (Table 1). In accordance with PPBio´s data policy, the biotic and environmental data for the 326 PPBio plots (I; II; IV) are freely available at http://ppbio.inpa.gov.br/knb/ style/skins/ppbio/ (only in Portuguese). The remaining data are available by request from Hanna Tuomisto.

I established the first plots in 2004 (I), following the RAPELD method (Magnusson et al., 2005); at the time, this sampling strategy was still used only by a few researchers and Ph.D. students at the Reserva Ducke (Kinupp and Magnusson, 2005; Menin et al., 2007). Following some modifications, the RAPELD has been adopted by the Brazilian Program for Biodiversity Research (PPBio). Today there are more than 800 RAPELD plots in Brazilian Amazonia and another 100 outside Amazonia (http://ppbio.inpa.gov.br/sitios). When data collection for papers II and IV began, establishing the plots and collecting/ processing certain environmental variables were no longer my responsibility.

Moreover, the method was now well established; thus the biotic data could also be collected by colleagues after some training in fern and lycophyte taxonomy. The adoption of the method by a National Program was a turning-point that allowed the first large-scale analysis of patterns of fern and lycophyte species along gradients in Brazilian Amazonia (II).

For the first plots I used a width of 2.5 m (I), but *a posteriori* analysis showed that this could be reduced to 2 m without losing ecological information relevant to the questions proposed (Zuquim et al., 2007). This allowed me to move more rapidly in the forest, and to use the time saved to sample more plots. Another advantage of the RAPELD method (I; II; IV) was that the plots were established following the terrain contour. This minimizes the plot-internal heterogeneity of soil properties and drainage, which often correlate with topographical position in Amazonia (Chauvel et al., 1987). While square or rectangular plots are a more common sampling strategy in Amazonia, plots following the natural shape of the landscape are useful in avoiding environmental variation within the plot that might be detrimental to determining floristic composition-environment relationships (I; II; IV).

A second plot shape used in the thesis (III) was long rectangles 500 x 5 m in size, placed in a straight line, and designed to capture as much of the topographical variation as possible, therefore crossing hills and streams. The rationale of this design is to maximize the representation of habitats in the landscape within a single plot. This sampling strategy increases variability within the plot, which is desirable in representing the richness and diversity of a region; it has been applied by the UTU-ART since the 90s (Tuomisto and Ruokolainen, 1994). The plots are subdivided into smaller units to allow separating sections by topography if a higher degree of local precision is desired (as in Tuomisto and Ruokolainen 1994; Tuomisto et al. 1995; Tuomisto and Poulsen 2000).

Of the 540 plots used in the thesis, some 215 were sampled by myself or with my participation in the field. The remaining were collected by colleagues from the PPBio or UTU group. A vast majority of the plots represent lowland non-flooded Amazonian evergreen dense forest (*terra-firme*), but other forest types, such as semi-deciduous open forest, bamboo forest, white-sand forest with a simpler canopy structure (*campinaranas*) and edaphic savannah (IBGE, 2004), were also included. The variation in environmental conditions covered allows a good representation of the heterogeneity in Amazonia. Average annual rainfall in the plots ranged from 1.633 to 3.561 mm, dry season duration (number of months with less than 100 mm of precipitation) from 0 to 5, and soils from extremely nutrient-poor to rich (sum of bases ranged from 0.06 to 38.11 cmol(+)/kg).
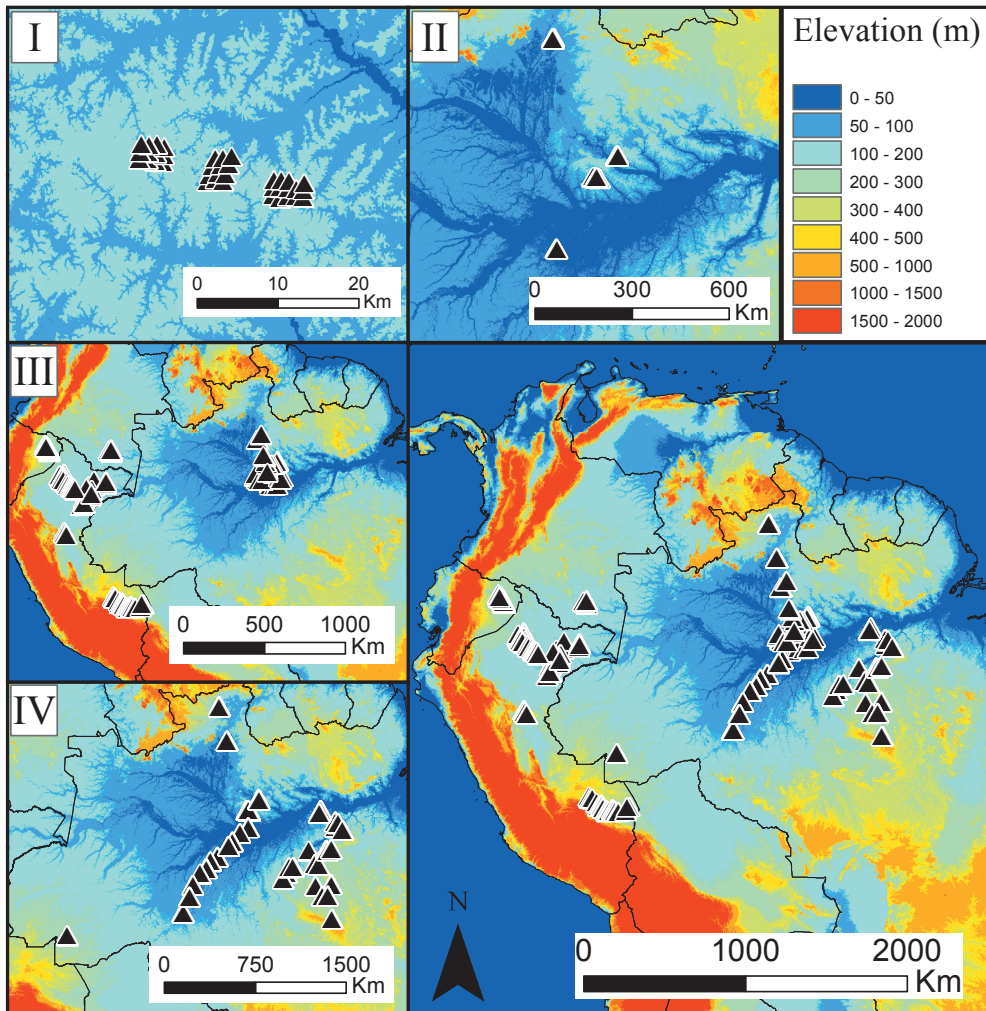
Figure 1. Location of the 540 plots included in the thesis (triangles). Numbered inset maps (I –IV) refers to the plots used in each of the papers.

Table 1. Characteristics of the databases used in each paper.

Paper	Number of plots	Plot dimensions (m)	Maximum distance between plots (km)	Country
I	38	2.5 x 250	21	Brazil
II	109	2 x 250	670	Brazil
III	214	5 x 500	2000	Colombia, Brazil, Ecuador and Peru
IV	326	2 x 250	1800	Brazil

*GZ= Gabriela Zuquim; HT= Hanna Tuomisto; GC= Glenda Cárdenas; GMM=Gabriel M. Moulatlet; FF= Fernando O. G. Figueiredo.

2.1.2 *Biotic data*

For each plot, the number of individuals per morphospecies was counted. All terrestrial fern and lycophyte individuals with at least one leaf longer than 10 cm were counted and identified to species. Voucher specimens were collected to verify species identity, and were deposited in the country of origin. In the case of paper III, duplicates were sent to Finland. The inventories for the PPBio plots (I, II and IV) were carried out between 2004 and 2011. The specimens received preliminary identification by the collector. All identifications were performed or confirmed by me, to ensure taxonomic consistency among data obtained by different researchers. All problematic specimens were also checked by Dr. Jefferson Prado from the Instituto de Botânica de São Paulo. Data for paper III were collected from 1990 to 2010. Brazilian specimens were identified by Hanna Tuomisto and myself; collections from other countries were identified by Hanna Tuomisto. In spite of the careful task of recognizing entities in the field, some species are very similar and differences can only be noticed in the laboratory. There were also cases where a species was split and one or more new species were described to science after the fieldwork. If two or more species were confounded in the field, they had to be combined for the analysis. Aware of this challenge, and hoping to encourage fern and lycophyte inventories in Amazonia, I created an illustrated field guide to ferns and lycophytes for the site sampled in Brazilian Amazonia that was richest in species (Zuquim et al., 2008).

2.1.3 *Environmental data*

The environmental database developed for the purposes of the thesis contained physical-chemical soil characteristics, terrain slope and altitude, geographical coordinates, canopy openness, and climatic data. All these variables were chosen based on the simple idea that plants need water, light and nutrients to grow.

Name of biotic data collectors (initials)*	Research group	Environmental data used
GZ	PPBio	Slope, soil, canopy openness, geographic location
GZ	PPBio	Soil, canopy openness, geographic location
HT, GZ, GC	UTU-ART	Soil, climatic, elevation, geographic location
GZ, GM, FF	PPBio	Soil, climatic, geographic location

The understory light environment is a variable less commonly included in meso to landscape scales. Simple methods are available, for example densiometers or canopy-scope (Brown et al., 2000), but they are too coarse to be applied in rainforest understories where no more than 4% of solar radiation reaches the ground (Chazdon and Fetcher, 1984). These minor differences can be highly relevant for the distribution of understory herbs that are adapted to low levels of light (Chazdon et al. 1996; Page, 2002) but may also be sensitive to degradation in the photosynthetic apparatus (Sonoike, 1996). I used hemispherical photographs to evaluate canopy openness (I; II). The method is reliable (Englund et al., 2000), but obtaining the pictures is demanding because of the short time when sunflecks do not reach the lenses, coupled with the unpredictability of cloud conditions.

Data on terrain slope (I; II) and elevation (III) are easily measured indicators of water availability. But topographic profiles are not causal factors, and their relationship to organism distribution should therefore be interpreted with caution. Direct measures of water availability in Amazonia are difficult to obtain, but there is a growing effort to develop and evaluate better methods that access this important variable in Amazonia (Rennó et al., 2008; Nobre et al., 2011; Moulatlet et al., 2014; Schietti et al., 2014)

Soil chemical components are a direct causal factor influencing plant growth. Surface soil samples were taken along the long axis of each plot, and were carefully stored for laboratory analyses of soil texture and exchangeable bases. The soil analyses were carried out in four different laboratories: the Thematic Laboratory of Soils and Plants at INPA (I; II; IV), MTT Agrifood Finland (vast majority of samples in III), the Geological Survey of Finland, or ISRIC Netherlands (the last two only pertained to a few samples in paper III). The results obtained with different methodologies were not combined in any data analysis.

Climatic data were obtained from freely available literature and databases. Dry season length was based on Sombroek (2001) (II). Other variables were obtained from WorldClim database (http://www.worldclim.org/bioclim) (III; IV). The values for bioclimatic variables (Bioclim - Hijmans et al. 2005) for each plot were extracted using the free software DIVA-GIS (Hijmans et al. 2012) (III; IV). Almost all the plots were georeferenced, using several coordinate readings obtained with a hand-held GPS (I; II; III; IV).

2.1.4   *Data analysis*

It is of interest to determine whether the results are affected by the type of input data. Whenever possible, the analyses were therefore carried out using both presence/absence and quantitative data (I; III; IV).

2.1.4.1 Incorporating new techniques into plant community studies

Studies exploring factors that determine plant communities often result in models with low explanatory power. Part of the problem may lie in the limitations of statistical techniques. In particular, the most widely used indices for calculating floristic distances between two different plots or communities are limited by their saturation. The Sørensen index, for example, quantifies the proportion of species shared by two plots; however, when the dataset as a whole contains numerous plots sharing few species or none at all, the index fails to detect dissimilarities, leading to distortions, such as the arch effect, that complicate the interpretation of ordination results in highly heterogeneous data. This means that floristic relationships cannot be well understood for plots that share few or no species. This is particularly problematic when dealing with long environmental or spatial gradients, where many plots share no species and ordinations may therefore fail (De'ath, 1999). I therefore applied a modified version of the Sørensen index, the extended Sørensen (II; IV). The extended dissimilarities (De'ath, 1999) define a threshold at which ecological distances are saturated, and re-calculate those distances by the shortest path between two plots, using other plots as stepping stones. This approach is becoming more popular nowadays, and simulated data show that extended dissimilarities can in fact solve the problem caused by analyzing long gradients (Tuomisto et al., 2012).

A second innovative approach was to borrow palynological statistical methods; rather than using fossil data to reconstruct environmental past conditions, however, I tested whether current fern data could be used to predict soil conditions in areas without direct environmental measures (IV). I applied and compared the accuracy of predictions for different soil properties using two different statistical procedures (the *k*-Nearest Neighbours and the Weighted Averaging calibration). These techniques assess how well each environmental variable is estimated for each plot, using species-environment relationships as derived from the remaining plots.

2.1.4.2 Understanding community patterns along environmental gradients and the
use of ferns and lycophytes as indicators

Another important contribution is to report trends in communities along gradients in different areas; the repetition of patterns leads to the recognition of more general patterns, which in turn are a mechanism of hypothesis generation (MacKenzie et al. 2006). To understand the general patterns of fern and lycophyte species distribution, and the main environmental factors which determine it in different sites and at different scales (I; II), biotic data from plot inventories were reduced to a few dimensions using multivariate techniques. Multivariate analysis can provide a spatial representation of floristic differences among plots in two, three or more dimensions,

making them easier to interpret. We applied Principal Coordinate Analysis (PCoA) using the Bray-Curtis, Sørensen and Extended Sørensen indices of dissimilarity. The first two floristic axes were then regressed against environmental variables using Multivariate Multiple Regression. Mantel tests were performed to determine the relative contributions of space and environment distances to the floristic variations observed.

Given that fern and lycophyte species occurrences are strongly determined by environment, I also asked which fern species were more strictly related to certain environmental conditions, and could thus be used as indicators of those conditions. The plots were divided into groups with similar environmental conditions. The groups were defined using distance-based multivariate regression tree analysis (db-MRT - De'Ath, 2002) (IV). Indicator species for each group were identified using the IndVal index (Dufrêne and Legendre, 1997; Legendre and Legendre, 1998) (IV). A species is considered a good indicator when it is frequent in one group but rare or absent in the others.

Another approach was to investigate patterns in several components of diversity, such as richness, abundance, diversity and evenness (III). These variables are sensitive to sampling sufficiency; we therefore first tested whether the available data was representative of the local species pool, using estimators of species richness (CHAO1 and ACE). The purpose of these estimators is to quantify how many species are actually present in the local community, even if some of them were missed by the corresponding transect. The smaller the difference between the estimated and observed number of species, the better the sampling. Then, to assess how abundance, species richness, diversity and evenness were related to each other and to edaphic and climatic gradients, we used simple linear, multiple linear and polynomial regressions. Species Richness is a simple and intuitive way to describe the diversity of a community, but it does not give an idea of proportional abundances. I therefore also applied the concept of "effective number of species" (Diversity; ^qD), to describe how equally the species are distributed in a sample. For example: if two communities both have ten species and 100 individuals, community A, where each species is represented by ten individuals, is more diverse than community B, where one species is represented by 91 individuals and the other nine species by only one individual each; nevertheless both A and B share the same value of species richness (10). Diversity (^qD) therefore takes into account both the number of species and its dominance in a given community. The index is flexible, and more or less weight can be assigned to the proportional abundances by controlling the parameter q. If q=0, no weight is given to abundance, and Diversity is thus equal to Species Richness.

3.   RESULTS AND DISCUSSION

In scale, the studies of this thesis ranged from a few kilometres (I; II) to thousands of kilometres (II; III; IV); edaphic conditions varied from soils extremely poor in nutrients (sum of bases = 0.06 cmol(+)/kg) to ones that were very rich (sum of bases = 38.11 cmol(+)/kg); and the number of species observed per plot varied from 0 to 71. This heterogeneity in the dataset allowed a wide range of questions to be addressed. Moreover, some questions could be addressed at different scales and replicated in different areas.

3.1   Patterns in distributions

Observed species occurrences are the outcome of synergetic effects of long-term evolutionary processes and present-day local conditions, such as habitat quality and among-species interactions. Our results support that soil characteristics are an important driver of fern and lycophyte species distribution in Amazonia. Soils are in turn determined by geological history and landform evolution of the area (Rossetti et al., 2010; Higgins et al., 2011). Therefore it is important to take into account both present-day and past conditions to understand the patterns in species distribution.

3.1.1   *Present-day environmental conditions*

Earlier studies in Neotropical rainforests have reached different conclusions as to which factors best explain floristic variation. Several studies have found climate important (Clinebell II et al., 1995; ter Steege et al., 2013), while others have emphasized edaphic characteristics (Tuomisto and Poulsen, 1996; Ruokolainen et al., 1997, 2007; Tuomisto et al., 2003a, b, c; Phillips et al., 2003; Costa et al., 2005; Jones et al., 2006). I found that all these factors were relevant, but that their relative roles differed among sites (II; III). This is probably related to the environmental heterogeneity of a given study area and the spatial scale of the sampling.

Nonetheless, a consistent finding is that fern and lycophyte species in Amazonia are mainly determined by edaphic characteristics (I; II; III; IV), and to a lesser degree by climate (II; III; IV). Climate by its nature varies on a broad scale, and its effect could thus only be tested in studies covering large scales. The combination of different soils with different climates creates a mosaic of habitats, to which ferns and lycophytes have adapted in different ways; different species should thus occupy different types of habitats. Indeed, I found that some species were good indicators of soil quality, and some could also indicate a combination between soil and either drier or wetter climate

(IV). Moreover, plots in Central Amazonia generally had lower species richness (III), probably because these plots combined relatively dry climates with cation-poor soils. Plots with equally poor soils but in wetter climates tended to be richer in species, as did plots with equally dry climates but more cation-rich soils (III).

Edaphic factors have long been recognized as a main driver of fern and lycophyte species diversity and distribution in Amazonia (e. g., Tuomisto and Poulsen, 1996; Ruokolainen et al., 1997, 2007; Tuomisto et al., 2003a, b; Costa et al., 2005). Among-species niche partitioning in relation to soil nutrients has been suggested as a mechanism promoting speciation and the regional coexistence of closely related species in tropical forests (Tuomisto et al., 1998; Schulman et al., 2004; Fine et al., 2005; Tuomisto, 2006; Jones et al., 2007). Soil cation content is the variable most commonly associated with species richness, because it is an indication of the amount of nutrients in the soil. Most species were associated with a particular part of the soil nutrient gradient (I; II; IV). In sites with uniform soil cation concentrations, soil clay content emerged as important (I), lending support to the idea that environmental gradients are hierarchically structured and that gradients occur inside gradients (Costa et al., 2009; IV). Edaphic factors also determined fern and lycophyte richness and diversity; the models including soil chemistry values or heterogeneity had the highest coefficient of explanation (III). The ecological and evolutionary reasons why nutrient-rich soils sustain more species (III) are still to be clarified.

A higher amount of nutrients in the soil is usually associated with resource availability and higher ecosystem productivity. It has been suggested that species richness increases with ecosystem productivity because higher productivity leads to faster demographic traits, such as faster growth, mortality and recruitment rates (Marzluff and Dial, 1991; Nascimento et al., 2005; Allen and Gillooly, 2006; Baker et al., 2014), and shorter generation times (Marzluff and Dial, 1991). Indeed, shorter turnover times were associated with higher diversification rates for Amazonian trees (Baker et al., 2014). If this applies to ferns and lycophytes as well, shorter generation times and faster diversification in richer Amazonian soils could explain the higher observed number of fern and lycophyte species in these kind of soils (Tuomisto and Poulsen, 1996; Tuomisto et al., 2003a; Tuomisto and Ruokolainen, 2005; Costa, 2006; Cárdenas et al., 2007; III). It might also be the reason why the fern species found in richer soils tended to be more closely related to each other than species found in poorer ones (Lehtonen et al., 2015).

3.1.2   *Geological history and dispersal limitations*

It is likely that the evolutionary processes behind the observed patterns are linked to the geological history of Amazonia and to the dispersal ability of the organism. Why

did different species evolve in different habitats? Why did lineages diversify more in certain habitats? How far can they disperse and colonize other areas?

The present-day patterns observed are the first hint towards an answer to such questions. The majority of the Amazonian soils are relatively cation-poor, derived from the highly lixiviated Precambrian rocks of the Guyanan and Brazilian shields (Quesada et al., 2009; Sombroek, 2000). Cation-rich soils are less common, and have become available more recently (Higgins et al., 2011). Amazonian rich-soils are mostly derived from the Pebas Formation or from fresh sediments eroded from the Andean slopes and deposited in the floodplains of white-water Amazonian rivers (Salo et al., 1986; Räsänen et al., 1987). Based on the older age and larger area of poor soils, one might expect that more species would have colonized and diversified in these soils.

However, rich soils tend to have higher species densities and a larger species pool (Tuomisto and Poulsen, 1996; Cárdenas et al., 2007; II; III). In general, the collective species lists of ferns and lycophytes reported in previous studies present smaller species pools in Amazonia for poor soils than for rich ones (Tuomisto and Poulsen, 1996; Tuomisto et al., 2003c; Cárdenas et al., 2007). There are also genera (e.g. *Diplazium*, *Pteris*, *Tectaria*, *Thelypteris*, *Mickelia* and *Bolbitis*) that are restricted to richer soils (Lehtonen et al., 2015; IV). In addition, some genera, such as *Adiantum*, colonize almost the whole gradient of Amazonian soils, but are more diversified towards the richer end of the gradient (Tuomisto et al., 1998; Lehtonen et al., 2015). A few genera, such as *Lindsaea* and *Trichomanes*. are poor-soil specialists (Lehtonen et al., 2015; IV). These findings indicate that evolutionary processes are related to soil characteristics. Net diversification (speciation minus extinction) must have occurred at higher rates on richer soils than on poor ones.

Another factor that may potentially determine species distribution is dispersal. After controlling for environmental conditions, however, I found no clear spatial community structure. The simple Mantel test revealed that at the scale of 90 km^2 floristic similarity did not decrease with increasing geographic distance (I). At broader scales as well, environmental dissimilarity was better than geographical distance at predicting compositional dissimilarities (II). The results support the hypothesis that current environmental conditions are more important than dispersal limitation for fern and lycophyte species distribution in Amazonia (I; II; III). This can be viewed as an indication that the fern spores of Amazonian species are abundant and widespread in this ecosystem, and that species are not limited by dispersal but by habitat suitability. Ferns are wind-dispersed and produce large amounts of spores that can travel thousands of kilometres (Wolf et al., 2001). Frequent windstorms and gap openings may provide opportunities for long dispersal events in closed forests, where turbulent winds are not common in the understory (Kruijt et al., 2000).

3.2   Usefulness of ferns as indicators of environmental conditions

As the general aim of this thesis was to provide background information for modelling predicted species occurrence, I found it useful to systematically assess the extent to which ferns were good indicators of environmental conditions (IV). Ferns and lycophytes are easy to collect and relatively easy to identify, and most species have soil affinities (Tuomisto and Poulsen, 1996). The suggestion that ferns and lycophytes are good indicators is not new but has been applied a number of times (Ruokolainen et al., 1997, 2007; Tuomisto et al., 1998; 2002; 2003c; Salovaara et al., 2004; Tuomisto, 2006; Cárdenas et al., 2007; Higgins et al., 2011; Sirén et al., 2013), usually with a community-level approach. Paper IV, however, is the first to carry out a statistical assessment to evaluate the accuracy of environmental predictions obtained with fern composition data. In addition, species were tested individually and species-unique usefulness could be accessed by the indicator value assigned (IV).

Environmental conditions were classified as habitats using a Multiple Regression Tree. I found that 75% (40 out of the 54) of the species tested were statistically significant indicator species associated with one of the classifications of habitat tested (IV). Around half of the species were indicators of a richer soil habitat, the other half of a poorer one, leading to the conclusion that different fern species do indeed have different soil affinities. This may be relevant for habitat classification, since the groups are present and abundant along the whole gradient of Amazonian soils studied. For example *Adiantum tomentosum* is a common and easily identified species which indicates that the area of its occurrence has relatively poor soil (less than 0.68 cmol/kg of sum of bases) (IV). I then compared the accuracy of the predictions obtained for each of the edaphic variables (sum of bases, sand, silt and clay). The sum of bases (an indication of nutrient availability for plants) was the variable that could be best predicted by fern species composition regardless of the calibration method applied. In fact, the results were very promising: in theoretical terms the different methods have their strengths and weaknesses (Birks et al., 2010), but they all performed well (for example the R^2 values of the regression between predicted x observed soil nutrient content varied between 0.64 and 0.75) (IV).

The other good news was that the prediction accuracies for edaphic variables were similar whether the data used concerned species abundance or presence–absence; thus the latter kind of data are adequate for the purpose (IV). This has two important advantages. First, presence-absence data are considerably faster to collect, thus speeding up the fieldwork. Second, the observed usefulness of data without information of abundance opens a door to the use of already existing species lists and floras available for several Amazonian regions (e.g. Tuomisto and Poulsen, 1996; Edwards 1998; Costa et al., 1999, 2006; Freitas and Prado, 2005;

Costa and Pietrobom, 2007; Maciel et al., 2007; Prado and Moran, 2009; Zuquim et al., 2009).

It is worth noting that the calculated optimum values for the occurrence of a species along the nutrient gradient were congruent with suggestions made in earlier studies, even if the datasets were smaller and represented different Amazonian bioregions (e.g. Tuomisto and Poulsen, 1996; Tuomisto et al., 1998, 2002, 2003b; Cárdenas et al., 2007). Inferences as to the edaphic preferences of ferns thus have good transferability across geographical regions, and the method can be applied to any biogeographical area provided a suitable training dataset is available.

3.3   Improving predictive models

The attempt in this thesis to improve the quality of models by means of new statistical tools (II), and by including less commonly used environmental variables, gave rise to two important findings. First, canopy openness was relevant in explaining differences in fern and lycophytes community composition, from small scales (I; II) to broad ones (II). Even within the narrow range of less than 5% in canopy openness observed at the study site (I), inclusion of this variable increased the percentage of explained variance in fern and lycophyte communities by at least 10%. The effect was stronger when presence-absence data were used (I); many more species were present in the darker plots. On the other hand, at two study sites multiple regression analysis revealed no significant relationship, and in the analysis of variance partitioning, the procedure of backward elimination excluded canopy openness from the models (II).

Second, for datasets dealing with a high degree of compositional heterogeneity, application of the extended Sørensen improved the visual interpretability of the ordination diagrams, increased the variation captured by ordination axes, and increased the total proportion of explained variance in multiple regression on dissimilarity matrices compared to the results obtained using Classical Sørensen (II). At more homogeneous study sites, the use of one or the other index had little effect on the results. I therefore suggest a wide use of extended dissimilarity approach in studies of community ecology.

Insufficient sampling can also add noise to the models. This, however, was not the case, at least for the plots used in papers I (Zuquim et al 2007) and III. I found that the plots contained more than 85% of the actual number of species in the local community as estimated by Chao 1 and ACE estimators (III). The plots thus accurately represented the local pool of fern and lycophyte species.

4.   CONCLUSION

The highly dynamic geological landscape evolution of Amazonia created a mosaic of present-day habitat conditions that drives the observed species diversity and distribution. This causes interesting patterns, posing a challenge to the conservation of such species, and was the inspiration for this thesis.

I found that fern and lycophyte species are strongly determined by the amount of nutrients in the soil (as measured by cation content). Most species are associated with a specific part of the soil nutrient gradient (I; II; IV). Soil nutrient was also important in community level multivariate analysis. Other factors, such as canopy openness and clay content, were important determinants of fern and lycophytes community composition but their relative role varied among study sites (II). Especially in areas where the nutrient content did not vary extensively, other factors played a major role (I). Climatic variables, such as dry season length and annual rainfall, also played a secondary but relevant role in explaining fern and lycophyte species distribution at a broad scale in Amazonia (II; III). From a small scale of 90 km^2 (I) to a broad one of around 140.000 km^2, space played no role (II); this indicates that fern and lycophyte species are not limited by dispersal in Amazonia. The relationship between soils and Amazonian ferns is so strong that in practical terms it can be applied both ways: soil can be used to predict fern species composition, and ferns to predict some aspects of the chemical content of the soil (IV). This also has potential applications in developing maps of probable species occurrence in Amazonia. Models for predicting fern and lycophyte community composition can be improved by using better statistical tools, such as extended indices of floristic dissimilarity (II) and by including other relevant environmental variables (I).

A number of sampling gaps remain to be filled in Amazonia, not only in terms of geographical coverage but also of habitat type, given the heterogeneity of the forests. My results suggest the use of ferns and lycophytes as a model group to understand tropical plants dynamics and distributions. The distribution of ferns and lycophytes reveal informative patterns about the environmental properties and evolutionary processes in Amazonia. Combining the knowledge about the present-day and past characteristics of the landscape can improve habitat diagnosis and mapping in tropical forests.

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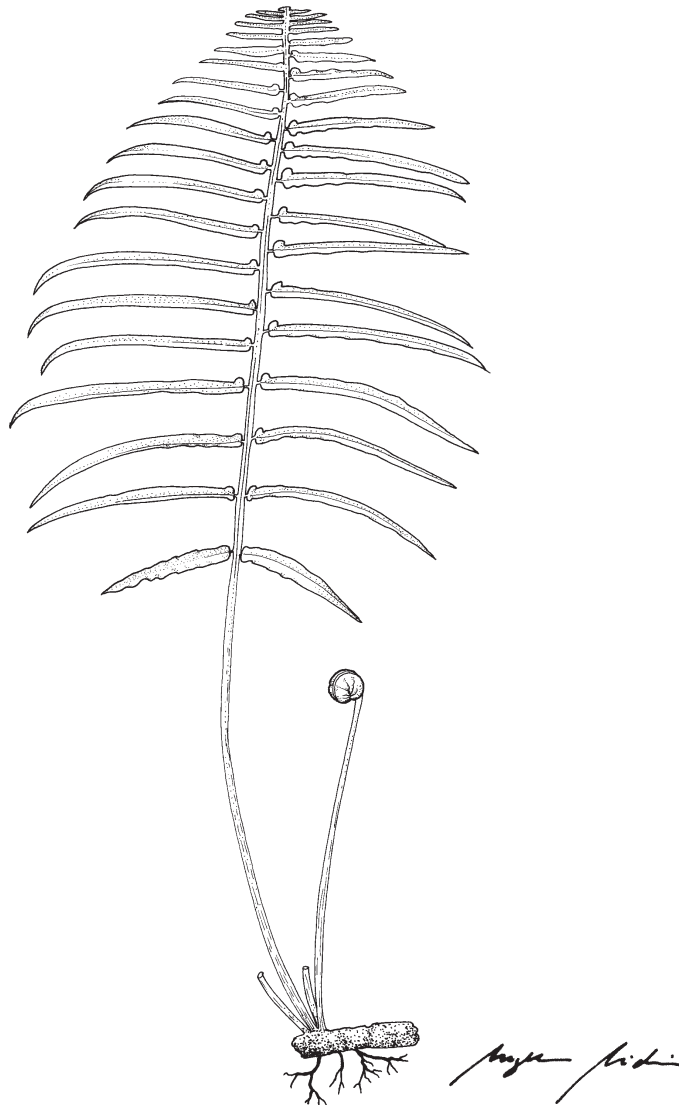
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