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**MAPPING SPECIES-HABITAT
ASSOCIATIONS IN LOWLAND AMAZONIA:
AN ACROSS-SCALE PERSPECTIVE WITH
BIOGEOGRAPHICAL IMPLICATIONS**

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ABSTRACT

Amazonia is the largest continuous forest in the world, and is a terrestrial ecosystem with one of the highest estimated number of plant species globally. Even with the accumulated knowledge on species distributions in lowland Amazonia, long-standing questions as to species-habitat associations remain unanswered. This is because for most parts of Amazonia the associations between species and environmental conditions are still unknown. In this thesis, I investigated species-habitat associations from multiple perspectives. In the first paper I evaluated evidence of community assembly arising from soil vs. hydrological niche partitioning. I found that when soil cation concentrations were relatively uniform, communities of understorey plant species were strongly associated with local hydrological conditions as determined by topography. In the second paper I found that when soil cation concentrations ranged more widely, floristic patterns were strongly associated with soils. Single-species models showed that species' realized niches are to a large degree defined by soil nutrients and hydrological conditions. In the third paper, species-habitat associations were quantified across potential zones of species turnover. Turnover zones have been hypothesized to be associated with the main rivers of the Amazon basin, if these represent dispersal barriers that trigger vicariance. I showed that a previously mapped, ca. 1000-km-long geological limit in western Amazonia is a biotic boundary associated with high species turnover. Species composition on the western side of the boundary was very different to that on the eastern side. This barrier runs in a north-south direction perpendicularly to the Juruá River. No barrier effect across the Juruá River was found. It has been assumed that the current positions of rivers in central Amazonia became established in the Pliocene, promoting speciation on both sides of the rivers by vicariance. In the fourth paper, however, I present evidence that central Amazonian river channels and floodplains have continued to be highly dynamic during the Quaternary. This means that current biogeographical models will need to be revised. Lastly, knowledge of species-habitat associations makes spatial predictions of species distributions possible if appropriate environmental data layers are available. In final paper, I used species associations with soil cation concentrations, as measured from soil samples taken in the field, to test whether digital soil maps allow reconstruction of these associations. The correspondence between field and digital data was low, indicating that the mapping of Amazonian diversity needs better digital environmental data. In sum, the results of this thesis suggest that species-habitat associations in Amazonia are strongly related to habitat heterogeneity at different scales. Floristic patterns therefore need to be investigated from different perspectives, to provide a broad picture of how species are currently distributed. This is crucial in an ecosystem that is highly affected by diversity loss.

TIIVISTELMÄ

Amazonia on maailman laajin yhtenäinen metsäalue, jonka kasvilajisto kuuluu maailman monimuotoisimpiin. Vaikka eri kasvilajien levinneisyydestä Amazoniassa on jo kertynyt melko runsaasti tietoa, kasvilajiston ja elinympäristön välisiin suhteisiin liittyy edelleen paljon ratkaisemattomia kysymyksiä. Tässä väitöstutkimuksessa selvitän kasvilajien suhdetta ympäristöön monesta eri näkökulmasta. Väitöstutkimuksen ensimmäisessä osatyössä tutkin, liittyvätkö erot kasviyhteisön lajikoostumuksessa maaperän ravinnepitoisuuden tai kosteuden vaihteluun. Selvisi, että jos ravinnekationipitoisuus oli kasvupaikkojen välillä samankaltainen, kenttäkerroksen kasviyhteisön koostumus riippui voimakkaasti maaperän kosteusolosuhteista, joihin puolestaan vaikuttivat maaston pinnanmuodot ja korkeuserot. Jos taas kationipitoisuuksissa oli enemmän vaihtelua, kasviyhteisön koostumus riippui enemmänkin maaperästä kuin kosteudesta. Lajikohtaiset mallinnukset osoittivat, että maaperän ravinnepitoisuus ja kosteusolot ovat tärkeimmät kasvilajien ekologisia lokeroita rajaavat tekijät. Toisessa osatyössä mitattiin lajien suhdetta ympäristöön lajiston vaihettumavyöhykkeen molemmin puolin. Vaihettumavyöhykkeiden on arveltu olevan yhteydessä Amazonian altaan pääjoki-uomiin, jotka saattaisivat muodostaa lajeille leviämiseiteitä, ja siten johtaa lajiutumiseen jokien vastakkaisilla puolilla. Osoitimme, että Amazonian länsiosassa jo aiemmin havaittu 1000 kilometrin pituinen geologinen rajapinta on myös bioottinen rajapinta. Rajapinnan länsipuolella lajisto on hyvin erilaista kuin itäpuolella. Tämä rajapinta ylittää Amazonin suuren sivujoen, Juruán, kohtisuoraan pohjois-eteläsuunnassa. Juruá-joella itsellään ei havaittu olevan minkäänlaista rajapintavaikutusta. On oletettu, että keskisen Amazonian suuret joet vakiintuivat nykyisiin uomiinsa jo plioseenikaudella, minkä jälkeen lajiutumista olisi tapahtunut niillä metsäalueilla, joiden välille joet muodostavat leviämiseiteen. Tässä työssä osoitamme kuitenkin, että Amazonian jokiuomat ja tulvatasangot ovat olleet erittäin dynaamisia systeemejä vielä kvartaarikaudellakin. Tämä merkitsee sitä, että Amazonian eliömaantieteen perusteita tulee päivittää. Lajien ympäristövasteiden tunteminen mahdollistaa lajien levinneisyyden mallintamisen, jos sopivaa aineistoa ympäristön vaihtelusta on tarjolla. Viimeisessä osatyössä tutkin, ovatko kasvilajien ympäristövasteet samanlaisia maastonäytteiden ja digitaalisten maaperäkarttojen perusteella määritettynä. Niissä oli samankaltaisuutta vain vähän, mikä viittaa siihen, että Amazonian biodiversiteetin kartoittamiseen tarvitaan nykyistä parempaa digitaalista ympäristöaineistoa. Yhteenvedo väitöstutkimuksen tuloksista on, että Amazoniassa kasvilajiston ja elinympäristön väliset suhteet ovat vahvasti kytköksissä ympäristöolosuhteiden vaihteluun useassa eri mittakaavassa. Tarvitaan kasvilajiston tutkimusta monista eri näkökulmista, jotta olisi mahdollista saada kattava käsitys siitä, miten lajit ovat nykyään jakautuneet Amazoniassa. Tämä on ensiarvoisen tärkeää, kun kyse on ekosysteemistä, jonka monimuotoisuus hupenee kaiken aikaa.

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications and manuscripts, hereafter referred to in the text by their Roman numerals:

- I. Moulatlet, G.M., Costa, F.R.C., Rennó, C.D., Emilio, T., & Schietti, J. (2014) Local Hydrological Conditions Explain Floristic Composition in Lowland Amazonian Forests. *Biotropica*, **46**, 395–403.
- II. Moulatlet, G.M., Rennó, C.D., Figueiredo, F., Ruokolainen, K., Banon, L., Emilio, T., Balslev, H., & Tuomisto, H. Mapping the association between floristic composition, hydrological conditions and soil fertility in a complex Amazonian landscape. *Manuscript*.
- III. Tuomisto, H., Moulatlet, G.M., Balslev, H., Emilio, T., Figueiredo, F.O.G., Pedersen, D., & Ruokolainen, K. (2016) A compositional turnover zone of biogeographical magnitude within lowland Amazonia. *Journal of Biogeography*, **43**, 2400–2411.
- IV. Ruokolainen, K., Moulatlet, G.M., Zuquim, G., Hoorn, C., Tuomisto, H. A mobile river network shaped central amazonian biogeography. *Manuscript*.
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AUTHOR CONTRIBUTIONS

	I	II	III	IV	V
Original idea	FC, GM, TE, CR, JS	GM, HT, CR	HT, KR	KR, HT, GM	GZ, GM, HT
Data collection	GM, TE, JS	HT, KR, GM, TE, FF, HB	HT, KR, GM, TE, FF, HB, DP	KR, GM, GZ, HT	HT, GM, GZ, FF, TE, KR, SL
Statistical Analysis	GM, CR, FC	GM, CR, LB	HT, GM	-	GM
Lead writing	GM	GM	HT, GM	KR, GM, GZ	GM, GZ, HT
Writing and commenting	FC, CR, TE, JS	HT, FF, HB, CR, LB, KR	KR, HB, TE, FF	HT, CH	FF, SL, KR, TE

Authors are listed in decreasing order of contribution for each paper.

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1. INTRODUCTION

The Amazon forest is the largest continuous tropical forest in the world, and most of its diversity in plant species is still unknown (ter Steege *et al.*, 2013; Zappi *et al.*, 2015; Cardoso *et al.*, 2017). In parallel to increasing efforts to fill the gaps of knowledge on species ecology and distribution (Hopkins, 2007; Feeley, 2015), environmental threats caused by unsustainable economic activities and inefficient legislation have increased as well (Nolte *et al.*, 2013; Azevedo *et al.*, 2017). The consequences of the alarming rates of forest loss due to deforestation can already be seen in changing local climatic regimes, as unusual climatic events have become more frequent (Lewis *et al.*, 2011; Coe *et al.*, 2016; Boers *et al.*, 2017). More than ever, forest resilience to major climate changes has been questioned (Levine *et al.*, 2016). The effect of both climate change and human-induced deforestation on species distributions is still under debate (Feeley & Silman, 2010), but there is a consensus that mapping environmental heterogeneity and species distributions is fundamental for an understanding of the changes that Amazonia is facing both now and in the long term.

The mapping of species distribution and environmental heterogeneity has been approached in a number of different ways. The niche approach is based on the assumptions of the niche theory (Leibold, 1995), applied at local to regional scales. According to this theory, species are expected to occupy a niche defined by a set of environmental conditions and biotic interactions. The combination of environmental conditions and biotic interactions that has been observed to be optimal for species occurrences in one area can be used to predict the potential occurrence of the same species elsewhere. An underlying assumption of the niche theory is that spatial patterns of species distribution fully reflect underlying biotic and abiotic conditions. However, a species may be absent from a portion of its optimal environmental conditions at one site, and success in predicting its distribution at another site will therefore be limited. A substantial number of studies in different parts of Amazonia have been devoted to investigating the relationships between species and environmental conditions. At the local scale, species are reported to segregate across environmental gradients defined by soil texture (Gentry, 1988; Tuomisto & Ruokolainen, 1994; Costa *et al.*, 2005; **I**), soil fertility (Tuomisto *et al.*, 2003; Poulsen *et al.*, 2006; Zuquim *et al.*, 2012; **II**), topography and microtopography (Kahn & de Castro, 1985; Svenning, 1999; Tuomisto & Poulsen, 2000; Valencia *et al.*, 2004; Vormisto *et al.*, 2004; **I**; **II**) and light (Webb & Peart, 2000). At the regional scale, the most important determinants of species occurrences are climate and soil conditions

(Clinebell *et al.*, 1995; ter Steege *et al.*, 2006; Stropp *et al.*, 2009; Zuquim *et al.*, 2012). Annual precipitation decreases and becomes more seasonal from the foothills of the Andes towards the border between the Amazon Biome and the Cerrado Biome in central Brazil (Davidson *et al.*, 2012), and community composition is expected to change along this gradient (Clinebell *et al.*, 1995; Toledo *et al.*, 2011). This turnover is partly related to species tolerances to drought conditions caused by climate seasonality (Esquivel-Muelbert *et al.*, 2017a, 2017b).

The dispersal approach to mapping species distributions is based on the detection of dispersal barriers within a biome. Dispersal barriers are landscape features that prevent the free movement of individuals, and are therefore zones of species turnover. They also define the borders of areas where similar historical processes of colonization, extinction and environmental changes have taken place (Antonelli *et al.*, 2009; Wesselingh *et al.*, 2009), although dispersal barriers may also define borders between areas that have experienced different events of colonization and speciation or even environmental changes, even if nowadays these areas present similar environmental conditions. The vicariance theory in turn suggests that the onset of a physical barrier triggers vicariance processes, in which two populations become isolated from each other. As the genetic flux between them ceases, they start gradually diverging into different species. Thus dispersal barriers define biogeographical units, among which the connectivity between populations is null or very low (Cracraft, 1985).

A hypothesis regarding the presence of physical dispersal barriers was first proposed by Wallace (Wallace, 1852), during his expedition along the Amazon River and its tributaries. Following the riverine barrier hypothesis, several other biogeographical hypotheses have been proposed and tested (Haffer, 1969, 2008; Cracraft, 1985; Tuomisto & Ruokolainen, 1997; Antonelli *et al.*, 2009; Higgins *et al.*, 2011; III). Even now there is still uncertainty as to the location and relative importance of biogeographical barriers in Amazonia. The mapping of dispersal barriers will therefore promote a more complete picture concerning changes in species composition across Amazonia.

The mapping approach is based on species distribution models (SDMs). The investigation of species-habitat associations at regional and broader scales requires species occurrence data (abundances or presence/absence), regional maps of environmental conditions (e.g. soil maps, digital elevation models), and methods for building spatial models. Predictive spatial models are perhaps among the most powerful tools for mapping species distributions at regional to continental scales (Franklin, 1995). Over the last decades the field of modeling species distributions has

seen great advances, thanks to the increasing capacity of computers to process complex models, the advance of remote sensing information, and the increasing amount of data on species occurrences available through database projects such as the Global Biodiversity Information Facility (GBIF). The applications of species distribution models (SDMs) are numerous, since they can be oriented towards conservation policies, climate change, dispersal limitations and biogeographical assessments (Barbosa & Schneck, 2015). In comparison with other, more densely sampled areas, SDMs are rarely used in research and conservation planning in Amazonia because of the lack of both species and environmental data to input into the models (Mod *et al.*, 2016). Despite these limitations, SMDs have recently been used to map trees (Saatchi *et al.*, 2008; Thomas *et al.*, 2014; Figueiredo *et al.*, 2017; Levis *et al.*, 2017), palms (Bush & McMichael, 2016), bamboos (McMichael *et al.*, 2014), non-seed plants (McPherson, 2014), and understorey plants (Figueiredo *et al.*, 2017).

This thesis investigates understorey plant species distributions and habitat heterogeneity in the light of the three approaches mentioned above. The niche approach is applied in **I**, **II**, **III** and **IV**. The dispersal approach is used in **III** and **IV**, and the mapping approach in **V**. All of these include discussion and suggestions for a more accurate mapping of Amazonian forests.

2. BACKGROUND AND AIMS

2.1 Topography and community composition at the local scale

At local scales, plant species are expected to segregate along gradients of environmental conditions, which often follow local topographic variation. Environmental classes of edaphic variation can be defined in terms of a combination of drainage conditions and soil fertility. Drainage conditions range from well-drained to water-logged soils according to topographical position, while soil fertility varies from a low to a high nutrient concentration according to the local mineralogy (Kahn & de Castro, 1985; Becker *et al.*, 1988; Vormisto *et al.*, 2004). As general environmental differences associated with topography can be identified in the field, the role of topography in explaining the distribution of floristic composition and its habitat association in the tropics has been the subject of numerous studies (Clark *et al.*, 1999; Svenning, 1999; Tuomisto & Poulsen, 2000; Webb & Peart, 2000; Harms *et al.*, 2001; Vormisto *et al.*, 2004; Normand *et al.*, 2006; Poulsen *et al.*, 2006; Costa *et al.*, 2009). Many species were found to be non-randomly distributed along the topographic profile (Valencia *et al.*, 2004; Jones *et al.*, 2016). For several parts of Amazonia, however, species associations with the environmental heterogeneity found at the local scale is uncertain. This is because large areas in central and western Amazonia suffer from gaps in data collection (Hopkins, 2007; Feeley, 2015). Certainly, data from these areas would help in composing a more complete picture of species–habitat associations (I; II; III).

All species depend on water for their primary physiological functions (Jackson *et al.*, 1995, 2000), and water availability is thus a crucial factor for plants to establish in specific areas. The tolerances of different plant groups to water conditions along topographic gradients are expected to be variable (Jones *et al.*, 2016). Trees, for example, are expected to be more tolerant to drought than understorey species, because the former have deeper root systems. Conversely, understorey plants are expected to be more closely associated with the moist areas of the terrain, due to their shorter root systems and higher likelihood of wilting in areas with strong seasonality. Areas immediately adjacent to creeks and ponds have been shown to harbor different understorey species than slopes and high plateaus (Vormisto *et al.*, 2004; Costa *et al.*, 2005, 2009; Jirka *et al.*, 2007; Drucker *et al.*, 2008; Schiatti *et al.*, 2014). Lower topographic areas hold more water, due to their proximity to the water table and to water runoff from higher topographic parts. These characteristics make topography a practical surrogate for water availability in the terrain (Haitjema & Mitchell-Bruker,

2005; Rennó *et al.*, 2008). Aside from the documentation on species preferences for habitats defined by topography, this information is still missing for large areas in central and western Amazonia.

Soil fertility also varies with topography as a consequence of local erosional processes during the formation of the catena (Chauvel *et al.*, 1987; Osher & Buol, 1998; Vitousek *et al.*, 2003; Luizão *et al.*, 2004; Chadwick & Asner, 2016). Several nutrients, including Ca, Mg and P, tend to accumulate in the surface and subsurface soil of hill slopes, as they flow from higher to lower zones (Chadwick & Asner, 2016). Topographical differences in nutrient concentrations are formed by erosional processes in areas with a homogeneous base material when a catena is formed. In areas with a heterogeneous base material, such as the intersection of sedimentary deposits formed in different environments, surface erosion can cause variation of nutrients along the topographical gradient. In both cases mentioned above, local valleys and high topographical areas will have different nutrient concentrations. Accordingly, species edaphic specialization is expected to be found along the nutrient gradient provided by topography (Tuomisto & Ruokolainen, 1994). The mechanisms that explain species distribution along gradients of environmental heterogeneity driven by topographic variation are not fully understood. What is most likely is that environmental heterogeneity leads to species edaphic adaptations (Fine *et al.*, 2005; Tuomisto, 2006).

In Amazonian lowland *terra firme* forests (non-inundated forests), in both a local and a regional context the mapping of species-habitat associations is a complex task. Local hydrological conditions are complex to measure at all scales, due the difficulty of quantifying the potential water availability in the soil. Locally, a qualitative mapping of hydrological conditions can be done using descriptors of edaphic conditions that differ clearly (e.g. well-drained vs. occasionally inundated soils) (Svenning, 1999; Drucker *et al.*, 2008), or by means of topographic measurements in the field using hand-held clinometers. Regional mapping, on the other hand, depends on remote sensing coupled with field data for validation (Moulatlet *et al.*, 2015); this is the bottleneck of several algorithms for deriving hydrological features from digital elevation models (Moore *et al.*, 1991; Rennó *et al.*, 2008). In order to obtain surrogates of hydrological conditions that can be applied at different scales, both local environmental descriptors and remote sensing techniques for deriving hydrological features from digital elevation models are required (**I**; **II**).

Data on soil nutrients are derived from locally collected soil samples, but soil collection is mostly restricted to relatively easily accessible areas, either by road or by fluvial connections. Methods for inferring edaphic conditions across the whole

Amazon basin based on legacy data still need to be improved (V). In order to scale up species affinities to edaphic and hydrological conditions from a local to a regional scale, better representation of environmental conditions coupled with more species observations are needed.

2.2 Geologically driven environmental conditions and community composition at the regional scale

Amazonia has a complex geological history (Hoorn *et al.*, 1995; Rossetti, 2014). One of the most important events occurred during the Miocene, when the Andean uplift that had started in the Eocene changed the Amazonian drainage system and the rates of sedimentation in the Andean foreland basin (Räsänen *et al.*, 1992; Hoorn *et al.*, 2010). The foreland basin was abruptly filled with sediments eroded from these young mountains and transported by newly established fluvial connections in the area (Hoorn *et al.*, 1995). The transportation of sediments is an ongoing process, carried out by white-water rivers such as the Amazon, Purus, Juruá and Madeira, whose headwaters drain the eastern flanks of the Andes. All these changes gradually modified the environmental structure of the area, its physical characteristics, and consequently its biota (Salo *et al.*, 1986; Räsänen *et al.*, 1987; Antonelli *et al.*, 2009; Rossetti *et al.*, 2010; Ribas *et al.*, 2012).

During the Miocene, western lowland Amazonia was dominated by large swamps and shallow lakes constituting the Pebas system (Hoorn *et al.*, 2010). Marine incursions during that period have also been discussed (Hoorn, 1993; Räsänen *et al.*, 1995; Hoorn & Wesselingh, 2011). In this lacustrine/semi-marine environment, cation-rich clay sediments were deposited, giving rise to the Pebas Formation (known in Brazil as the Solimões Formation). After the draining of the Pebas system fluvial coarse-grained and relatively cation-poor sediments covered the Pebas Formation. This sedimentation gave rise to the Nauta Formation (known in Brazil as the Içá Formation). Subsequently, the sediments of the Nauta Formation were exposed to rainfall denudation. Unlike the sediments of the Pebas and Nauta Formations, derived from the Andes, the intracratonic basin was filled by sediments derived from the Brazilian and Guiana Shield. These sediments originated from pre-weathered material, which explains the lower nutrient concentration in the soils of this area (Quesada & Lloyd, 2016). These events have led to the formation of a general east-west gradient of soil fertility in Amazonia (Quesada & Lloyd, 2016). The edaphic differences produced by variations in mineralogy, sedimentation processes and time available for weathering (Fittkau *et al.*, 1975; Quesada *et al.*, 2011) may have had a profound

impact on species diversification (Hoorn *et al.*, 2010) and current distributions (Higgins *et al.*, 2011).

The mapping of Amazonian geology is not yet complete (Rossetti *et al.*, 2005). Some of the limits between geological formations can be seen in the current landscape, being characterized by abrupt changes in environmental conditions or topography. These limits are associated with differences in vegetation. For example, the Brazilian vegetation map associates vegetation differences in western Brazilian Amazonia with a zone of environmental changes (IBGE, 2004), which acts as a limit between *Florestas abertas* (open forests) and *Florestas densas* (dense forests). Figueiredo *et al.* (2014) mapped floristic differences between the boundaries of the Trombetas, Alter do Chão and Iricouré formations in central Amazonia. Using remote sensing imagery, (Higgins *et al.*, 2011) investigated an erosional zone in Peru where the nutrient-rich Pebas Formation was exposed by the erosion of the nutrient-poor Nauta Formation. The area showed a great turnover of species. On the basis of satellite image interpretation, Higgins *et al.* (2011) predicted that a similar erosional front as seen in Peru would be found to extend across more than 1000 km of Brazilian Amazonia, and would be associated with similar species turnover. In order to investigate the magnitude of this turnover zone and its potential biogeographical implications, a field expedition to the area was organized in 2012 (II; III).

2.3 Amazonian biogeographical barriers

Among the hypotheses postulated to explain Amazonian biogeography, the riverine barrier hypothesis, suggested by Wallace (1852), deserves special attention. As he noted with regard to monkey species ranges in the Amazon basin: "*I soon found that the Amazon, the Rio Negro and the Madeira formed the limits beyond which certain species never passed*". Wallace also noticed that towards a river's headwaters, species ranges expand to occupy both sides of the river. He classified Amazonia into four 'districts', which he referred to as Brazil, Guiana, Ecuador and Peru, whose boundaries were determined by major rivers. Wallace, however, did not speculate as to possible mechanisms which might explain differences among species distributions. Currently, allopatric speciation is considered one of the main results of vicariance, i.e. when two continuous populations become disjunct because of the formation of a geographical barrier between them. Lowland Amazonia lacks other obvious geographical barriers, such as mountains or deserts. Instead, as observed by Wallace, the most likely physical barriers to dispersal of *terra firme* species are formed by the major rivers of the Amazon basin.

While evidence of rivers acting as barriers for understory birds and primates has accumulated (Ayres & Clutton-Brock, 1992; Hayes & Sewlal, 2004; Ribas *et al.*, 2012; Boubli *et al.*, 2015), little evidence has been found for plants (Nazareno *et al.*, 2017), termites (Dambros *et al.*, 2017), rodents (da Silva & Patton, 1998) or lizards (Souza *et al.*, 2013). Different dispersal strategies may affect the way species perceive the rivers. While plants have a broad range of dispersal strategies (seeds and spores, for example, may traverse long distances by wind), animals may be reluctant to cross large floodplains. Another factor that may influence species distribution is habitat specialization. Plant species that have evolved under certain edaphic conditions may simply be physiologically intolerant to other kinds of edaphic conditions (Gentry, 1988; Tuomisto *et al.*, 1995; Fine *et al.*, 2005). Animal distributions, in turn, may be related to the productivity of forests, as determined by soils, or the distribution of the plant species they feed on (Peres, 2008; Pomara *et al.*, 2012), and may not be limited by rivers as such (Tuomisto & Ruokolainen, 1997; Tuomisto, 2007). In addition, many species are adapted to floodplain conditions, and for them rivers are dispersal corridors and wetlands can be considered more as biogeographical refuges during evolutionary history than as dispersal barriers (Kubitzki, 1989; Wittmann *et al.*, 2013; Assis *et al.*, 2015).

For a river to act as a dispersal barrier, it is necessary for enough time to have passed since the river has been established in its current location. The dating of the formation of the Amazon Basin Rivers, however, is a topic of intense debate (Räsänen *et al.*, 1987; Campbell *et al.*, 2006; Figueiredo *et al.*, 2009; Hoorn *et al.*, 2010, 2017; Latrubesse *et al.*, 2010). The main Amazon channel has followed the same course at least since the late Miocene (Figueiredo *et al.*, 2009; Hoorn *et al.*, 2017; van Soelen *et al.*, 2017), and Pliocene dates have been given for the stabilization of its main tributaries (Latrubesse *et al.* 2010). In addition to sedimentological evidence, biological information has also been used to estimate the times when the rivers established their courses (Ribas *et al.* 2012). Based on phylogenetic divergences among birds of the genus *Psophia*, a Pliocene-Pleistocene date is attributed to the stabilization of the rivers Madeira, Tapajós, Rio Negro and Xingu. Within this time-frame, allopatric speciation is possible. However, intense modifications of the river network associated with tectonism are still ongoing in the Quaternary (Rossetti 2014), with evidence that rivers were captured by fault reactivations (Hayakawa & Rossetti, 2015).

River channels can be easily identified in the Digital Elevation Model from the Shuttle Radar Topographic Mission (SRTM). These data provide a core variable in all chapters of this thesis. Old marks of previous channels and floodplains gradually

disappear due to more recent river dynamism and associated erosion in the landscape (Salo et al. 1986). However, some of these marks can still be identified in the SRTM (IV). The marks provide evidence of rivers dynamism in the past 50,000 years, i.e., much more recently than is generally thought for central Amazonia. There are still many uncertainties about the impact of rivers as dispersal barriers for the biota (Tuomisto 2007). In the light of the new evidence of unexpectedly recent dynamism (IV), the mechanisms proposed to explain current biogeographical patterns based on river stability over time (Ribas et al. 2012) will need to be reassessed.

2.4 Soil heterogeneity across Amazonia: an assessment of available soil maps and datasets

Soil conditions are known to be important determinants of plant distribution patterns at the local and regional scales, as well as highly relevant to biogeographical patterns in Amazonia (Tuomisto *et al.*, 2003b; Poulsen *et al.*, 2006; ter Steege *et al.*, 2006; Pitman *et al.*, 2008; Higgins *et al.*, 2011; Zuquim *et al.*, 2012; II; III). Despite this importance, few attempts have been made to apply soil data from digital soil maps in species distribution modeling (Figueiredo et al. 2007, Thomas et al. 2014, McPherson 2014, McMichael et al. 2014, Levis et al. 2017). Much wider use is made of climatic layers, partly because climate is thought to be more relevant at broad scales (Pearson & Dawson, 2003), but also because ecologically relevant climatic data are easily available (Hijmans *et al.*, 2005).

The improvement of digital soil data through such projects as SoilGrids (www.soilgrids.org) has benefited the use of soil information in SDMs in Amazonia. Other soil maps have already been available for some time (e.g. SOTERLAC, HWSD), but the edaphic properties derived from these digital soil maps have usually played only a secondary or non-significant role in SDMs (McMichael et al. 2014, Levis et al. 2017). The discrepancy between the strong observed association between species and edaphic conditions, as measured from field data, and the low predictive and explanatory power of edaphic conditions derived from soil maps is intriguing. In order to understand why soil conditions perform poorly in SDMs, I compared the correspondence between species tolerances and edaphic conditions as measured in the field to that derived from soil maps (V), and examined the reliability of the picture of soil properties themselves provided by soil maps. Species distribution models (SDMs) may expand our comprehension of species occurrences at large scales, but the reliability of the input data for the models first needs to be assessed.

2.5 Aims and ecological questions

I first studied patterns of species composition of ground understorey herbs in terms of the relationship between species occurrences and edaphic, climatic and hydrological conditions in the Purus-Madeira interfluvium in central Amazonia (**I**). I asked what are the main determinants of understorey species composition and I hypothesized that in the absence of prominent variation in soil fertility, species composition of understorey herbs, would mainly be structured by hydrological gradients.

I also investigated patterns of floristic composition (at both community and species levels) within each 500-meter long transect in the Juruá River region (**II**). My purpose was to explain patterns of species distribution along gradients of soil fertility and hydrological conditions across two geological formations. I asked the following two questions: 1) whether the importance of hydrological and edaphic conditions differ among plant groups and species, and 2) whether the importance of these environmental conditions for floristic composition is variable in different geological settings.

In **III** I asked what are the relative roles of geologically defined terrain types (environmental heterogeneity) and a major river (physical dispersal barrier) as predictors of ecological structuring and biogeographical differentiation of plants within Amazonian forests. I tested species turnover across a geological boundary in Brazilian western Amazonia, as predicted by Higgins et al. (2011). I measured the degree of environmental heterogeneity across the border, and tested its effect on species turnover. The results were compared to those obtained across a similar border in Peruvian Amazonia. I also tested species turnover on both sides of the Juruá River, as postulated by the riverine hypothesis.

In **IV** I show the evidence that the biogeography of central Amazonia is shaped by a dynamic river network (**IV**). I asked what is the role of central Amazonia Rivers as biogeographical barriers for species dispersal. Using the largest identifications of river marks left in the terrain, coupled with documentation of river connections bequeathed by eighteenth-century naturalists and geological dating found in the literature, I discuss the implications of river dynamism for central Amazonian biogeography.

Finally, given the higher relevance of soil conditions found in the other studies, I assessed the importance of three available digital soil maps (SOTERLAC, HWSD, and SoilGrids) (**V**). As species distribution models are becoming essential tools for an understanding of the biogeography and macroecology of Amazonian species, I assessed whether the soil classes mapped by these soil maps can be used as surrogates of local soil cation concentrations within the Amazon rain forest biome; how closely

the information extracted from digital soil maps reflects species edaphic affinities, as inferred from field data; and the nature of current problems in using digital soil maps to determine plant species niches across Amazonia. I specifically ask 1) if soil classes can be used as surrogates of local soil cation concentration within the Amazon rain forest biome; 2) how well the information extracted from digital soil maps reflects species edaphic affinities as inferred from field data; and 3) what are the current caveats when using digital soil maps to determine plant species niches across Amazonia.

3. METHODS

3.1 Study area

Amazonia comprises an area of approximately 5,000,000 km², of which some 75% is covered by rainforests. Average annual rainfall is 2200 mm year⁻¹ (Coe et al. 2016), but the margins of the basin are marked by strong seasonality; precipitation varies from <1600 mm year⁻¹ in the southeast areas to more than 2800 mm year⁻¹ in the northeast. The number of months with less than 100 mm of rainfall varies from one to seven (Sombroek, 2000). With regard to soil diversity, Amazonia contains 19 of 32 soil types of the World Reference Base (Quesada and Lloyd 2016), with high local variation in nutrient concentrations and texture (Lips & Duivenvoorden, 1996; Luizão *et al.*, 2004; Quesada *et al.*, 2011).

This thesis combines data collected by myself and by several colleagues. I carried out field campaigns in two areas (Fig. 1). In 2010 I worked along the Purus-Madeira interfluvium (Fig. 1-I). The climate is predominantly hot and moist, with temperatures in the coldest month above 18° C. The number of months with less than 100 mm of precipitation varies from one to five (Sombroek, 2001). The topography is generally flat, with low plateaus with poorly-drained soils, slopes with well-drained soils, and riverine terraces close to primary rivers (Brasil 1978). The main soil types in the area are Plinthosols in the low plateaus and slopes and Fluvisols on riverine terraces (Dijkshoorn *et al.*, 2005).

In 2012, I worked along the Juruá River (Fig. 1, II, III). Average annual rainfall in the area is ca. 2200 mm. the mean annual temperature is 27 °C, but temperatures as low as 15 °C can occur from June to August (Marengo *et al.*, 1997). The limit between the Nauta (Içá) Formation and the Pebas (Solimões) Formation runs north-south across the study area. Both are sedimentary deposits that have a wide distribution in western Amazonia. The Nauta Formation consists of relatively nutrient-poor and loamy to sandy sediments deposited during the Plio-Pleistocene, and the terrain is typically steeply hilly. The Pebas Formation consists of nutrient-rich clay sediments deposited under semi-marine or lacustrine conditions during the Miocene (Hoorn and Wesseling 2011). The topography is generally flat or undulating, but steep slopes can occur. In addition, the area contained alluvial terraces along both rivers. These are relatively flat, and consist of sediments of varying texture deposited in the river floodplains that have subsequently been abandoned (Salo *et al.*, 1986; Toivonen *et al.*, 2007). Soil types in alluvial terraces have been mapped as Acrisols, the Solimões formation as Acrisols or Cambisols, and the Içá formation as Plinthosols (Dijkshoorn *et al.* 2005).

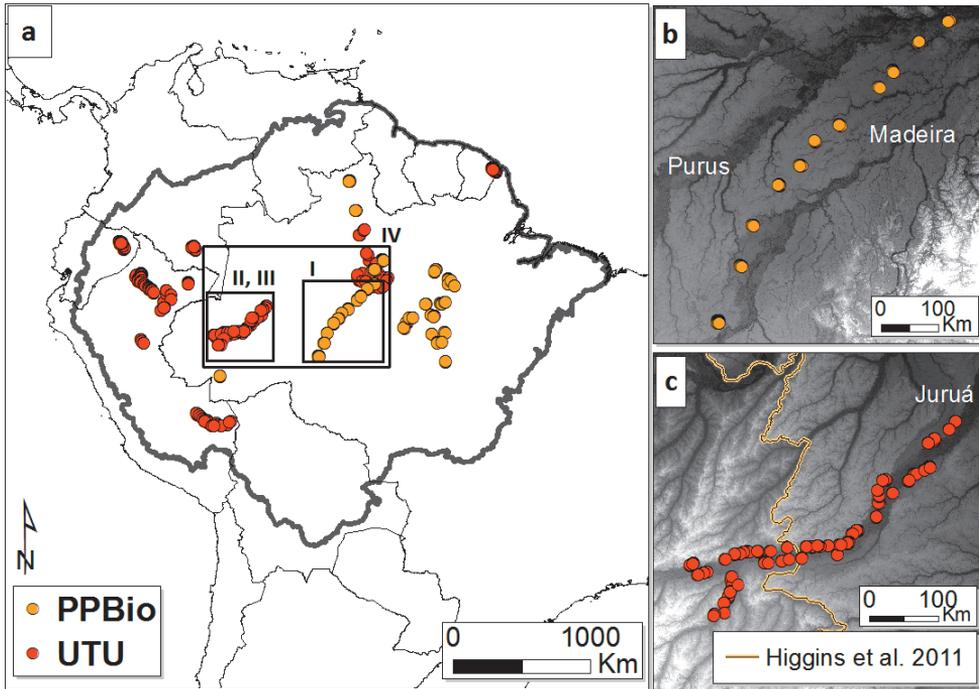


Figure 1. Study area and distributions of all plots used in the thesis. Plots were collected in the context of two research projects (PPBio and UTU), shown as orange and red respectively. SRTM image is shown as background in the smaller panels, where darker colors indicate lower elevation values. (a) Distribution of all transects used in V, with the study area of V limited by the thick gray line. Rectangles in panel (a) indicate extensions of areas used in each of the studies. (b) Location of transects in Purus-Madeira interfluve used in I. (c) Location of transects along the Juruá River used in II and III, with the limit between the Nauta and Pebas Formations shown in light orange according to Higgins *et al.* (2011).

3.2 Field data

Field data were collected according to two sampling designs. The RAPELD method (Magnusson *et al.*, 2005) was used to sample 326 permanent transects (88 sampled by myself) of 250 m by 2 m (orange dots in Fig. 1a). These transects are part of the PPBio research program (Brazilian Research Program on Biodiversity). All transects followed the isoclines of the terrain in order to minimize environmental heterogeneity within a transect. The methods used by the Amazon Team of the University of Turku (UTU) are fully described in (Tuomisto *et al.*, 2003a). The UTU method was used to sample 311 transects (red dots in Fig. 1a) of 500 m by 5 m, of which I participated in the sampling of 71. In contrast to PPBio transects, UTU transects try to maximize environmental heterogeneity within a transect by sampling local topographic

variation. The number of transects and sampling method used in each study can be found in Table 1.

Table 1. Characteristics of the floristic datasets used in each study. The limits of Amazonia *sensu lato* were defined according to (Eva & Huber, 2005) and Quesada et al. (2011). The term ‘pteridophyte’ refers to both ferns and lycophytes.

Chapter	Number of plots	Database	Method	Country/Region	Botanical groups sampled
I	88	PPBio	RAPELD	Brazil	pteridophytes and monocots (except palms)
II	71	UTU	UTU	Brazil	pteridophytes, Zingiberales, Melastomataceae and palms
III	71	UTU	UTU	Brazil	pteridophytes, Zingiberales, Melastomataceae and palms
IV	-	-	-	central Amazonia	-
V	637	PPBio, UTU	RAPELD, UTU	Amazonia <i>sensu lato</i>	ferns

In each transect, the number of individuals belonging to pre-selected plant groups was counted (Table 1). For transects inventoried in the context of the PPBio research program, all obligate understory herbs (*sensu* Poulsen, 1996) taller than 5 cm and rooted within the transect were counted, but epiphytic ferns fallen to the ground were not included. In UTU transects located in the Juruá River region we inventoried four plant groups: pteridophytes, Melastomataceae, palms and Zingiberales. All terrestrial ferns and epiphytes with the largest leaf longer than 10 cm were included. Epiphytes found up to 2 m above ground were also sampled. All Melastomataceae individuals with post-cotyledon leaves were sampled, as were all Zingiberales individuals with a minimum height of 5 cm. Bunches of leaves of clonal species were considered as separate individuals when more than 20 cm apart. All palm individuals higher than 5 cm were sampled, but palm seedlings that could not be identified were not included. Ramets of clonal individuals were counted as individuals.

Vouchers of the specimens collected in the 2010 expedition are deposited in herbaria of TUR (pteridophytes and monocots) and SP (pteridophytes). Vouchers from the 2012 expedition are deposited in the herbaria of TUR (pteridophytes and Melastomataceae), AAU (palms), INPA (palms, Zingiberales) and SP (pteridophytes and Melastomataceae).

A major effort to combine the UTU and PPBio datasets was made in **V**, as the two projects have used different sampling designs. I developed an R routine to subset the transects of UTU, so as to obtain subunits of the same surface area as the PPBio transects. We then selected thirteen fern species that are relatively easy to identify, making it possible to combine the PPBio and UTU data without having cross-checked voucher specimens. These species were also well represented in both datasets, and collectively span the soil gradients of the data.

Soil samples of the sub-surface mineral soil (0-5 cm depth) were taken along the main transect axes of all plots. In PPBio transects, six samples were taken and combined in a single composite sample. In UTU transects, three composite samples were taken in order to document the local topographic variation. All PPBio samples were analyzed at the Thematic Laboratory of Soils and Plants at the National Institute for Amazonian Research (INPA) in Manaus. PPBio samples were air-dried and sieved through a 2 mm mesh. The soil texture content was determined by the hydrometer method after treatment with physical and chemical dispersal of the particles (Donagena *et al.*, 1997). Cations were extracted by the KCl method (Ca and Mg) or by Mehlich's I extraction solution (K). Cation concentrations were determined by atomic spectrometry. UTU samples were analyzed at the Agricultural Research Center of Finland (MTT). Analyses used standard methods (van Reeuwijk, 1993) for pH (1M KCl), cations (Ca, K, Mg, Na and Al; extraction by 1M ammonium acetate at pH 7), LOI (loss on ignition at 420°) and total phosphorus (according to (Quesada *et al.*, 2010).

Coordinates from all transects were taken with hand-held GPS in the field. In the PPBio transects, coordinates were taken every 10 m along the 250 m line. In the UTU transects coordinates were taken every 100 m.

3.3 Digital data

Topography-derived proxies for water availability in the soil were used to assess the hydrological conditions of transects in **I** and **II**. Along a topographic profile, valleys tend to be drier compared to slopes and plateaus. The water table is located more or less parallel to the terrain, so in the valleys it gets closer to the surface (Cuartas *et al.*, 2012). The height above the nearest drainage (HAND) can therefore be used as a practical proxy of the water availability for each part of the topographic profile (Rennó *et al.* 2008). HAND values, calculated as the vertical distance of any part of the terrain to the estimated water table, are derived using the Shuttle Radar Topographic Mission (SRTM) digital elevation model. These values allow environments that are hydrologically similar to be compared, once elevational differences are normalized according to the inferred drainage level (all valleys are

assigned the value zero). The main limitation of HAND is in dealing with deforestation features in the SRTM. That issue is not assessed in this thesis, but Moulatlet et al. (2015) discuss how HAND values are affected by deforestation, as well as possible ways to overcome this problem.

A flooding index was used in combination with HAND (**I**). Some of the transects were located in areas subjected to seasonal flooding. In those areas we installed level loggers and piezometers to estimate the level of flooding and its duration. Observations concerning water marks on trees and on the terrain were also taken into account in the composition of the index.

Apart from HAND, slope declivity and drainage order (Strahler, 1957) were also derived from the SRTM and used in the analysis in **II**. In a much more complex landscape, HAND values on their own may not be enough to describe species-water availability relationships at the local scale: two or more local valleys may have the same HAND values, even though one of them is located near a large river and another near the spring of a small one.

Climate was one of the variables used in **I**. Precipitation data for each transect were downloaded from the WorldClim database (Hijmans et al. 2005) at 30 arc-sec (approximately 1 km) resolution. The bioclimatic variable ‘Precipitation of driest quarter’ (bioclim17) was used as a proxy for water stress.

In **IV**, soil data from digital soil maps and soil databases were used as datasets. Of the soil maps available for Amazonia, three have been used in species distribution assessments. The SOTER map, including its version for Latin America (SOTERLAC; Dijkshoorn et al., 2005), is a polygon-based map at a minimum scale of 1:1 million, showing soil information that has been collected over several decades. The Harmonized World Soil Database (HWSD; Nachtergaele *et al.*, 2012) is a raster map with 1 km resolution, based on information from national databases and giving a coverage probability of soil types for each pixel. The SoilGrids (Hengl *et al.*, 2014, 2017) are raster layers with 250 m resolution modeling several soil properties, based on remote sensing covariates and validated with soil samples taken in the field.

Associated with these maps are databases of soil samples taken in the field in different contexts and with different methodologies. A total of 300 soil profiles from the SOTERLAC database (Batjes, 2005), containing data on soil exchangeable cations from the top 30 cm, were used in assessing the correspondence between soil maps and species-soil affinities.

3.4 Data analysis

Community patterns along environmental gradients were assessed in **I**, **II** and **III**. In these cases, plant community data were used as the response variable in the analyses.

Simple and multiple linear regression were performed in **I**. Models that included only hydrological variables (soil texture, HAND and climate) were compared to ones that also included soil cation concentration, in order to assess the relative importance of each variable through a Pillai-Trace test (Legendre & Legendre, 2012).

In **II**, Linear Mixed Models (LMMs) and Generalized Linear Mixed Models (GLMMs) were used to test the effects of soil cation concentration and HAND, slope and drainage order (Strahler 1957) in explaining floristic patterns. In **I** and **III**, entire transects were used as observation units, but **II** made use of subunits within transects. This is why models suitable for hierarchical sampling design were chosen. Both LMM and GLMM allow for random terms in the models (Bolker *et al.*, 2009; Zuur, 2009). In both cases, transect identity was used as the random term. Model selection was performed based on the lowest AIC (Akaike Information Criterion). LMMs were applied to the community data, while GLMMs were used for single-species models.

Most of the analyses in **I**, **II** and **III** were based on dissimilarity matrices. This approach is preferred in analyzing species turnover along environmental and spatial gradients (Ruokolainen *et al.* 2007). Dissimilarity matrices were calculated independently for each plant group, using the Bray-Curtis index. For each environmental variable, a distance matrix was calculated using Euclidian distances. The correlation between floristic and environmental dissimilarity matrices was assessed by simple and partial Mantel tests (Legendre and Legendre 2012).

Transects were then ordered by the dissimilarities in their species composition using Nonmetric Multidimensional Scaling (NMDS). The NMDS was set for a weak treatment of ties to recover the long floristic gradient and avoid the arch effect (De'Ath, 1999). Both species abundances and species presence/absence were analyzed. The Kuleczynski (**I**) and Bray-Curtis (**II**, **III**) indices were used to calculate pairwise dissimilarities in floristic compositions between plots. In **I** and **II** the first and second axes of the NMDS were used as response variables in regression models, while in **III** both axes were used to illustrate the main floristic patterns.

Distance-based multivariate regression trees (De'Ath, 2002) were constructed to evaluate the predictability of floristic dissimilarities (presence-absence data only) on the basis of the environmental variables (**II** and **III**). This method produces a hierarchical classification of sites on the basis of their positions along one or more of

the environmental gradients measured. In the first step, the sites (e.g. transects or subunits) are divided into two subgroups along each environmental gradient, at a point that minimizes floristic differences among sites within the same subgroup. The environmental variable with the lowest cross-validation error criterion is then selected, and the process is repeated for each previously obtained subgroup until further divisions no longer meet the cross-validation criterion.

To determine whether any taxa could be considered indicators of specific edaphic classes, indicator species analyses were carried out in **III**, using the IndVal.g index (De Cáceres & Legendre, 2009). This index defines indicator values based on the multiplication of two species properties: specificity and fidelity of the species to the class.

The analyses in **IV** were based on visual interpretation of the SRTM for fluvial marks and on information collected from the available literature. No statistical test was included in this study.

In **V** we investigated the correspondence of species tolerances as obtained from soil maps, in comparison to species tolerances as obtained from field data. We calculated, for every taxon separately, the soil cation concentration optimum (*sensu* ter Braak & van Dam, 1989). This equals the weighted average of the soil cation concentration values in those plots where the taxon occurred, with the taxon's abundance used as the weight. In addition, the root mean squared error (RMSE) around the optimum was used to calculate tolerances for each taxon.

Multiple linear regression models were applied to assess the predictive power of soil layers derived from digital soil maps, in comparison to soil cation concentration values obtained in the field. Models were built combining several soil classes from HWSD and SoilGrids and the SoilGrids-CEC (Cation Exchange Capacity) layer. We performed a backward-forward selection of the models and compared them using AIC. Finally, we calculated the species optimum and tolerances using the predicted values from each model, and checked the correspondence of these values to species optima and tolerances obtained using field data. This correspondence was quantified using Kendall's tau.

All statistical analyses were performed in R (R Core Team, 2015), using several packages to perform data analysis, data manipulation and plotting; this was supplemented with ad hoc codes written by myself. Remote sensing analyses were performed in R, ArcGIS (v.10.3.1) and ENVI (v 4.7 and 5.0).

4. RESULTS AND DISCUSSION

4.1 Floristic patterns along environmental gradients

The field campaigns of 2010 and 2012 involved the sampling of a number of plant groups. In the field campaign of 2010 along the Purus-Madeira interfluve, I sampled 31,362 individuals, belonging to pteridophytes or to any of seven monocot families. These individuals belonged to 148 species: 39 pteridophytes, 4 Bromeliaceae, 55 Zingiberales, 21 Cyperaceae, 2 Cyclanthaceae, 21 Poaceae, 4 Rapateaceae and 2 Orchidaceae (I). In the campaign of 2012 in the Juruá River region, our team sampled 112,700 individuals belonging to pteridophytes (154 species), palms (62 species), Melastomataceae (128 species) and Zingiberales (114 species) (II; III). I was a member of the pteridophyte team. The sampling effort covered ca. 44,000 m² of the Purus-Madeira interfluve and 192,500 m² of the middle Juruá River region.

We found that plant community composition in the Purus-Madeira interfluve can be predicted by gradients of edaphic and hydrological conditions (I). The soils of the area have low cation concentration values (range of 0.09 – 2.28 cmol(+)/kg) and the terrains are relatively flat. These conditions contrast with many studies performed in western Amazonia, where the gradient of soil cations can be an order of magnitude longer (Vormisto *et al.*, 2004; Ruokolainen *et al.*, 2007). The reason for such differences can be attributed to the origin of the sediments deposited in each area (their pedogenesis), and to the degree of exposure to erosional processes (Quesada *et al.* 2011, Quesada and Lloyd 2016). In the relatively short gradient of soil cation concentration in the Purus-Madeira interfluve, local drainage explained the largest part of the variation in understorey herb composition (I). We showed that hydrologically similar environments could be identified along the topographic gradient yielded by the height above the nearest drainage (HAND). Other studies that have assessed the role played by topography in floristic patterns in areas of a short range of soil nutrient conditions have found results similar to ours (Svenning 1999, Valencia *et al.* 2004). In those studies, however, topography was classified into three to five habitats rather than being associated with a continuous range of values. Hydrology has been shown to be an important variable for understorey herbs, as has been shown for palms (Svenning 1999, Vormisto *et al.* 2004), trees (Valencia *et al.* 1994), ferns and Melastomataceae (Tuomisto *et al.* 1995, Tuomisto and Poulsen 2000). The hydrological effect on floristic composition seems to be transferable across areas and plant groups. The general conclusion can be drawn that when the soil cation

concentration is not variable, hydrological variables associated with topography may explain most of the variation on species distribution.

In the Juruá region, the variation of soil cation concentration ranged from 0.09 to 53.56 cmol(+)/kg. In this very long gradient we found that the soil cation concentration explained most of the variation in the species composition of pteridophytes, palms, Zingiberales and Melastomataceae (II; III). In II we compiled data on soil cation concentration, HAND, slope, drainage and species occurrences at the same scale (25-m to 30-m resolution). This also allowed us to investigate single-species occurrences along these gradients. The community patterns were explained by soil cation concentration for all plant groups. HAND had a weaker effect as an explanatory variable, but was still significant for palms and Zingiberales. Single-species models showed that species consistently segregate into niches defined by soil cation concentration and HAND. Most species occupied the extremes of these gradients; few species were significantly related to the intermediate parts. These results are in agreement with previous studies suggesting a niche partitioning for palms (Vormisto *et al.*, 2004; Cámara-Leret *et al.*, 2017), as well as for pteridophytes and Melastomataceae (Tuomisto *et al.*, 2003c).

Part of the unexplained variation in the species composition in our models may be due to other environmental variables that were not taken into account in the studies conducted in the Purus-Madeira interfluve and in the Juruá region. Actual measurements of soil moisture during long periods of time would certainly elucidate the role of hydrological conditions in the area better than topographical variables. However, given logistic problems of long term monitoring of environmental conditions in remote areas of Amazonia, this type of assessment is still not realistic. Similar problems can explain why nitrogen concentration is not often measured in Amazonian soils. Soil samples are exposed to microbial activity that, during the transportation, could affect the measured nitrogen content. Canopy conditions are known to be an important causal driver of understorey species composition. Canopy light conditions are associated with forest structure and the dynamics of tree stem turnover. In relatively nutrient-rich sites, turnover is faster because the environmental conditions favor faster growth and lower wood density. The opposite situation is found in nutrient-poor sites (Quesada *et al.*, 2012; Phillips *et al.*, 2016). Therefore, western Amazonian transects would be more affected by canopy disturbances and consequently by variation in light incidence. However, given the high spatio-temporal variability in the canopy opening, it is difficult to extrapolate its effects to regional scale studies. Local-scale variation due to gap dynamics adds noise to the results when explicitly measured light conditions are not included in the models. Instead, they get

averaged when the sampling grain is 250 to 500-m transect. At the regional scale, the average dynamic conditions are dependent on soil conditions and therefore their explanatory power may be nested within the soil effect. Detailed assessments of canopy structure in shaping understorey are thus needed. Recent studies have given opposite results. Structural differences between Pebas and Nauta Formations were not found in the field assessment made by Suominen *et al.* (2015), but the LiDAR assessment in the same Formation did find a difference (Higgins *et al.*, 2015).

4.2 Biogeographical patterns of species distribution

In the Juruá region, we tested the effect of the Juruá River as a barrier to species dispersal. A comparison of the two sides of the Juruá River showed that the presence of the river did not increase the turnover among transects on opposite sides of it. Instead, we found consistent species turnover across a boundary defined by two geological formations running perpendicularly to the Juruá River. Mantel tests confirmed a strong correlation between species turnover and differences in soil properties; this is in agreement with previous studies showing high species turnover related to changes in edaphic conditions elsewhere in Amazonia (Phillips *et al.*, 2003; Ruokolainen *et al.*, 2007). We thus found no support for the riverine barrier hypothesis.

Higgins *et al.* (2011) identified an erosional front in Amazonia advancing from west to east, exposing the Pebas Formation that underlies the Nauta Formation. These authors predicted that soils on the two sides of the front would differ in terms of nutrient concentration. Accordingly, species turnover was also expected in the area. Our results confirmed these predictions, as shown by the large differences in cation concentration in the soils of the Pebas and Nauta Formations (II; III). Soil cation concentrations in the Pebas transects differ by up to two orders of magnitude from those in the Nauta Formation transects. Floristic classifications established by regression trees showed that transects with similar floristic composition were grouped, and revealed a clear separation of transects between geological formations. Higgins *et al.* (2011) has mapped this geological limit across more than 1000 km in Brazilian Amazonia, and our findings confirm that it constitutes a species turnover zone of biogeographical magnitude. Our results showed that floristic differences between the two sides of the barrier are due to strong variation in soil properties. This explains why earlier studies conducted in the area (da Silva and Patton 1998) did not find differences in rodent haplotypes between forests on different sides of the river, but did find them between forests in the lower vs. middle reaches along the main river channel.

Rivers in the Amazon basin, such as the Rio Negro, Madeira, Purus, Xingu and Tapajós, have been suggested to form barriers for species dispersal (Cracraft 1985, Ribas *et al.* 2012). This assumption, however, depends on the age and stability of the river and its floodplains (Irion *et al.*, 1997; Junk *et al.*, 2011). We found that there are many fluvial marks in central Amazonia that can be associated with the rivers dynamics of the past 50.000 years (IV). Major tributaries of the Amazon basin would have shifted across the landscape until they reached their current locations. Perhaps the most emblematic case is the connection between the river Japurá and the Amazon River. We found in the SRTM that the Japurá River, which is currently a tributary of the Amazon River, was earlier connected to the Rio Negro. Both the Japurá and the Amazon are white water rivers, meaning that they have relatively high suspension loads and nutrient concentrations. The Rio Negro, on the other hand, is a black water river, with a low suspension load. The disconnection of the Japurá from the Rio Negro and its new connection with the Amazon may have had a profound impact on the local terrestrial and aquatic fauna and flora, and also in the river's flooding pulses (Junk *et al.*, 1989, 2015). In addition to the remote sensing evidence, reports from eighteenth-century naturalists indicate a fluvial passage from the Japurá to the Rio Negro by way of the Urubaxi, a tributary of the Rio Negro. The disconnection between the Japurá and the Rio Negro is likely to be younger than 1,000 years, as indicated by the decrease in sedimentation of material carried by the Rio Negro. There are other cases of recent fluvial connections between the rivers Madeira, Purus and Juruá. Our investigations strongly suggest that rivers have migrated dynamically in central Amazonia, contrary to the common view that the central Amazonian river network was stabilized a long time ago (Latrubesse *et al.* 2010).

Our interpretation that rivers have been highly dynamic in the landscape will have several implications for Amazonian biogeography (IV). The mechanisms associated with current patterns of *terra firme* species distribution as delimited by rivers (Ayres and Clutton-Brock 1992, Ribas *et al.* 2012) and endemism zones (Prance, 1982; Cracraft, 1985; Da Silva *et al.*, 2005) will have to be revised.

4.3 Correspondence between soil maps and species-edaphic affiliations

There are currently three digital soil maps available for Amazonia. The use of information derived from these maps is fundamental for the application of SDMs at a basin-wide scale, especially for areas where data on local edaphic conditions are not available. When these soil maps have been used in SDMs, they played a non-significant or weak role as a predictive variable (McMichael *et al.* 2014, Levis *et al.*

2017). We found that the tolerances of 13 fern species for soil cation concentrations derived from soil maps corresponded poorly with tolerances measured from field data (V). Due to edaphic specialization (Tuomisto & Poulsen, 1996; Zuquim *et al.*, 2014), species can be restricted to high, low or intermediate cation concentrations. This gradient, however, was poorly recovered from data derived from the soil maps.

Soil classes are often used in species distribution models as surrogates for soil fertility (Poorter *et al.*, 2015), because it is thought that soil nutrient concentrations vary among them. We found, however, that within each soil class the cation concentration was quite variable on all the soil maps (SOTERLAC, HWSD and SoilGrids) (V), showing that they may be poor surrogates of soil variation in analyses at a local to regional scale. Soil maps do not currently provide soil cation concentration layers, but SoilGrids and HWSD provide CEC. The problem is that CEC has been shown to be a poor surrogate for soil nutrient concentrations in species distribution assessments (McMichael *et al.* 2014, Levis *et al.* 2017; V). This is because CEC quantifies the soil's potential to bind cations in general (including aluminum), not the concentrations of base cations that are actually present in the soil and available to plants. CEC has a very low correlation with the soil cation concentration, and in our results species tolerances based on CEC represented poorly the edaphic segregation obtained from field-measured cation concentration values.

We also identified several areas in the soil maps that had georeferencing problems. Polygons of fluvial soil classes such as Fluvisols and Plinthosols in SOTERLAC and HWSD were displaced by up to 20 km in relation to the current floodplains. Georeferencing errors between soil classes with contrasting soil conditions can promote artefactual associations between taxa and soil conditions. Taxa may appear to be less specialized to certain soil conditions than they actually are. Errors in the predictions based on species-soil type associations can have a major impact when the results are used in conservation or other ecological assessments. This issue is quite serious; plots located by the river margins represent a large part of the inventory plots in Amazonia (Nelson *et al.*, 1990; ter Steege *et al.*, 2013; McMichael *et al.*, 2017).

All these issues may be resolved as more soil data are added to soil databases and high-resolution, more soil data is collected and more accurate covariates are used in soil modeling. Given the importance of species modeling for an understanding of broad patterns of species distribution, is it important for researchers to be aware of the problems and limitations of the input data, and how these can affect the prediction of species occurrences.

5. CONCLUSIONS

Multiple investigation approaches are needed in order to understand the distribution of species in Amazonia. The results of this thesis suggest that species-habitat associations in Amazonia are strongly related to soil heterogeneity at different scales. At local to regional scale, topographic variation and soil cation concentration were determinant to explain variation in species composition, which indicated clear niche preferences of species along gradients determined by both of these environmental conditions. Environmental heterogeneity was found to be associated with biogeographical patterns of species distribution. Differences in soil conditions of one order of magnitude are associated to turnover zones. This refuted the hypothesis that the Juruá River is a barrier for dispersion of plant species of pteridophytes, Palms, Zingiberales and Melastomataceae. I provide evidences suggesting that rivers in central Amazonia have been less stable than is generally believed. Rivers that have been hypothesized as dispersal barriers and triggers of vicariance processes may have moved laterally for hundreds of kilometers, drastically changing the river network patterns in the past 50,000 years. The biogeographic assumptions based on the river's stability need to be re-discussed. Lastly, I question the use of existing soil maps as environmental layers in species distribution models, presenting their problems and prospects. At continental scale, the mapping of species distributions has become a powerful tool to predict species distributions under known environmental conditions. However, species affinities to soil conditions as deduced from soil maps resembled those measured in the field only weakly. In sum, floristic patterns need to be investigated from multiple perspectives in order to provide a broad picture of how species are currently distributed and what are the main factors that explain the distribution patterns.

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