Integrating molecular biogeography and community ecology to understand the evolution of habitat specialization in Amazonian forests

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Declaration

I hereby declare that the work contained in this thesis is my own, unless otherwise acknowledged and cited. This thesis has not in whole or in part been previously presented for any degree.

Roosevelt García-Villacorta

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Abstract

I investigated the origin of western Amazonian white-sand vegetation and the evolution of plant habitat specialization to different edaphic conditions in Neotropical lowland forests. In order to address these goals I used complementary ecological as well as molecular phylogenetic approaches. Amazonian white-sand forests harbour a flora specialized to nutrient-poor sandy soils, which is distributed as habitat-islands across the Amazon and Guiana Shield regions. This flora has been suggested to have many local and regional endemics, therefore making an important contribution to overall Neotropical plant diversity. The role of habitat specialization in the origin of this flora and its relationships with other floras within the Amazon-Guiana regions is not well understood. To shed light onto these questions, this thesis studies the floristic composition of these forests as well as molecular phylogenetic patterns of selected plant lineages containing white-sand species. The floristic study focused on the white-sand forests of the western Amazon region, which contained 1180 species of vascular plants whereas the non-white-sand Amazon and Guiana Shield dataset consisted of 26,887 vascular plant species. 77% of these species occurred outside white-sand habitats, in other habitat types of the Amazon region, while 23% were white-sand specialists. This demonstrates lower endemism in western Amazonian white-sand forests than previously estimated. 88% of the total westen Amazon white-sand specialist occur within the limits of the Guiana Shield region with the remaining 12% being endemics to the white-sand forests of the western Amazon. Within the Guiana-Shield region, Caquetá Moist Forests (56%), Guayanan Highlands (55%), and Negro-Branco Moist Forests (53%) were the biogeographic regions with the highest proportions of western Amazonian white-sand specialists. Cluster analysis of province level floristic checklists across the Amazon and Guiana regions showed that western Amazonian white-sand forests are nested within floras of the western Guiana-Shield region compared to other floras in the Amazon. Molecular phylogenetic analyses were carried out for the widespread and species-rich families Sapotaceae and Chrysobalanaceae, which display an uneven number of white-sand specialists. Sapotaceae had only three white-sand specialists but Chrysobalanaceae had a larger number of white-sand specialists (14 species). Phylogenetic analysis showed that white-sand specialist species in both studied families were scattered across the phylogenies. Both families show a marked absence of edaphic niche conservatism, suggesting that evolutionary switching amongst habitat types has been frequent. Ancestral state reconstruction of habitat specialization under a maximum likelihood approach suggests that preference for poor soils may be ancestral in these clades, especially in Chrysobalanaceae, but that the evolution of species entirely restricted to white-sand soils is in general much more recent and has multiple origins. For the white-sand flora of the western Amazon in particular, there is little evidence that it comprises ancient lineages as previously hypothesized. The historical construction of the Amazonian white sand flora is more likely to be the result of a gradual accumulation of species with different degrees of edaphic specialization, both by on-going speciation driven via habitat switching from non-white-sand specialists and via regional dispersal events after these habitats became available in regions such as the western Amazon. Edaphic transitions between different habitat types were not evolutionary constrained, which may have favoured edaphic niche evolution and the accumulation of plant species diversity in Neotropical lowland forests.

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Table of Contents

List of figures

List of tables

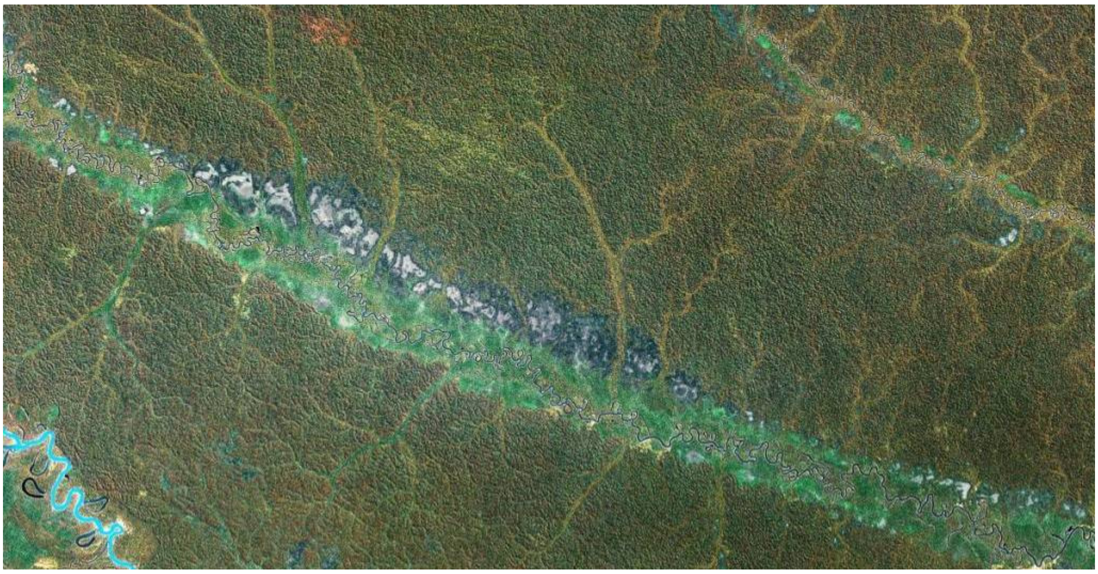
Chapter 1: Introduction

1.1. Overview

Throughout Amazonia and the Guiana Shield region two major environmental gradients related to edaphic conditions define plant species distributions and habitat types. One is related to flooding and the other, which is the focus of this thesis, concerns the level of nutrients in the soil (Ducke & Black 1953, Gentry 1982, 1988, Keel & Prance 1979, Kubitzki 1989, Duivenvoorden & Lips 1995, Terborgh & Andresen 1998, ter Steege *et al.* 2013). There is a wide range of soil nutrient and hydromorphic variations in Amazonia, with western Amazonia having in general more cation rich soils compared to eastern Amazonia and the Guiana Shield (Sombroek 1984, Quesada *et al.* 2011). Among the soil substrates that form the nutrient-poor end of the spectrum of Amazonian soils, white-sand soils combine the most extreme edaphic conditions for a plant. This is because besides its nutrient-poor status these soils also experience different levels of water-logging and drought (Damasco *et al.* 2013, Proctor 1999). Phosphorous and especially Nitrogen are the most limiting nutrients in these habitats compared to soils on non-white-sand *terra firme* forests (Grubb & Coomes 1997, Mardegan *et al.* 2008).

White-sand soils are classified as Arenosol or Podzol in the soil literature (FAO 1988, Buol *et al.* 2011) and in Amazonia and the Guianas support a very distinctive forest type, with many endemic plants and animals, variously known as *campina*, *campinarana*, *varillal*, *chamizal*, *bana*, *Amazon caatinga* or *wallaba* forests depending on the country where they occur (Lisboa 1975, Ducke & Black 1953, Encarnacion 1985, García-Villacorta *et al.* 2003). These forests are extensive in the Guiana Shield, a well-defined biogeographic region in northern South America, and are distributed as habitat-islands (Prance 1996) elsewhere in the rest of Amazonia (Prance & Schubart 1978, Berry *et al.* 1995, Arbeláez & Duivenvoorden 2004) (Figure 1).

Figure 1 Archipelago of white-sand habitats in northern Peruvian Amazon along the upper Nanay River as interpreted from a Landsat satellite image. Bright green = swamps, dark green = terra firme forest on clayey soils, yellow lines = streams, blue and sky blue = rivers, white patches = white-sand habitats.



White-sand forest is characterized by densely packed slender trees, high light penetration into the forest floor, sclerophyllous leaves, and low canopy, which varies from stunted forests (3-6 m height) to medium-tall forest (10-25 m) (Figure 2b). In extreme cases, especially in forests growing on isolated sandstone outcrops near the Andean range and the Brazilian and Guiana shield (Chapter 2), the vegetation may consist of low xeromorphic scrubs (Prance & Johnson 1992, Estrada & Fuertes 1993, Arbeláez & Duivenvoorden 2004, Neill 2008).

About 27% of seed plant species (ca. 115,000 species) exist within the Neotropics, almost ten times the estimate for Europe (Govaerts 2001), and within Amazonia itself an estimated 16,000 different tree species occur (ter Steege *et al.* 2013), with the majority of them rare (69%, ~11,000 species) and most of the dominant species habitat specialists. In order for these species to occupy and successfully establish populations along major soil and water environmental gradients, they have to possess or develop several adaptations that allow them to tolerate hydro-edaphic variations in the landscape.

Figure 2. White-sand soils covered by non-white-sand soils (clayey soils) at the Iquitos-Nauta road, Peruvian Amazon. b) View of the characteristic forest structure of a poorly-drained white-sand forest with densely packed, thin trees.

a)

b)

The evolution of tolerance to white-sand soils in Amazonia and the Guiana Shield region could have happened either rarely or frequently. Phylogenetic niche conservatism is a model of low evolutionary change; it describes the tendency of species and lineages to retain their ancestral predilection (Wiens & Donoghue 2004, Donoghue 2008), in this case, to track a particular edaphic preference. An alternative, though not mutually exclusive scenario is habitat-switching, is that every species specialized to white-sand soils has originated from a species found on other soil types. The role of niche conservatism in the evolution of lineages has been investigated using a biome-level approach (e.g. Crisp *et al.* 2009, reviewed in Donoghue & Edwards 2014), whereas the role of habitat specialization and edaphic niche conservatism has been largely unexplored, especially in the Neotropics. There have been few studies that specifically attempted to uncover the origin of Amazonian white-sand taxa and their relationship to those of the Guiana Shield using modern phylogenetic approaches (Fine *et al.* 2005, Frasier *et al.* 2008, Fortunel *et al.* 2014). In this dissertation I investigated these questions by focusing on Amazonian white-sand forests and taxa, which represent the most extreme nutrient-poor soil and hydromorphic conditions in the Neotropics.

Because tolerance to extreme hydro-edaphic conditions may be expected to exert a strong influence on community composition and species evolution, an analysis of floristic relationships and the evolution of tolerance to nutrient-poor conditions of its constituent taxa may provide us with important insights on the role of habitat specialization and edaphic niche evolution in Neotropical forests. Both floristic and molecular phylogenetic approaches are used in this thesis, which represents an attempt to integrate ecological and historical (phylogenetic) biogeography insights in studying the evolution and large scale biogeographic patterns of regions (Ricklefs & Schluter 1993, Wiens & Donoghue 2004, Ricklefs 2007). Understanding the ecological and evolutionary specialization of species to edaphic variation as well as their degree of tolerance is a necessary step to interpret the role of habitat specialization in creating and maintaining the high biotic diversity in Amazonia and the Neotropics in general. This is important if only because an understanding of the ecological and evolutionary processes that gave rise to this outstanding diversity may help us to address its conservation in relation to on-going and future changes in Neotropical environments.

1.2. Aims and structure of the doctoral thesis

This doctoral thesis aimed to understand the origin of western Amazonian white-sand forests and the evolution of habitat specialization to different edaphic conditions using a combination of ecological and phylogenetic comparative methods. Below I provide a description of the main questions addressed in each chapter and some reasons why they are considered important components in this dissertation.

Chapter 2: What are the main processes involved in the origin of white-sand soils across Amazonia and how old are they?

This chapter presents a review of the geological and soil science literature on Amazonian white-sand soils. It addresses the main processes involved in the origin of these soils in different parts of the basin, why they occur as an archipelago of islands in certain regions, and their estimated range of ages across the study region. It also presents a discussion of the role of regional tectonic forces involved in creating edaphic heterogeneity in Amazonia and the association of white-sand soils with other soil types in the study region. It has been largely assumed that white-sand soils in the Amazon outside the Guiana Shield region have been an ancestral soil in terms of their temporal exposure to the soil surface and their availability for plant taxa. However, no previous study has looked at the spatial and temporal origin of these soils across Amazonia. The extension, estimated ages, and relationships of white-sand soils to other soils types in Amazonia is an important background because it helps us to put into context the ecological and evolutionary research questions addressed in Chapters 3 and 4.

Chapter 3: What are the phytogeographic relationships of western Amazonian white-sand forests and what is the proportion of white-sand specialists?

While several studies have suggested phytogeographic affinities between north-western Amazonian white-sand forests and white-sand forests of the Guiana Shield (Prance & Schubart 1978, Cleef & Duivenvoorden 1994, Cortés *et al.* 1998, Giraldo-Cañas 2001, Arbeláez & Duivenvoorden 2004), this topic has not yet been thoroughly evaluated by including white-sand forests (but see Ferreira 2009) and non-white-sand forests outside of the Guiana Shield region (Chapter 3). In order to understand the origin and maintenance of a flora an analysis of its floristic composition and similarities with other regions may provide us with important insights that can help us to discern and hypothesize biogeographic and evolutionary scenarios (Chapter 4, and 5). In order to address these questions I employed two related approaches that use the species composition and distribution of habitat specialist and generalist species across the study region. This chapter helps us to understand better the relationships amongst the white-sand forests of the western Amazon region, the Guiana Shield region and the rest of Amazonia.

Chapter 4: What is the role of edaphic niche conservatism in the evolution of habitat specialization in the Neotropical lowlands?

Taxonomic and ecological studies in the Neotropical lowlands have highlighted the potential role of habitat specialization to different edaphic conditions as an important component in the evolution of species diversity. The role of niche conservatism, or alternatively niche shift due to habitat differences, has been suggested as important components of species diversification that can be expressed in plant phylogenetic patterns. However, no previous study has evaluated specifically their relative roles using well sampled molecular phylogenies and phylogenetic comparative methods. In this chapter I study the evolution of habitat specialization through time by analysing the phylogenetic signal for nutrient-poor tolerance across the range of hydro-edaphic conditions present in Neotropical forests. To address these questions I use two species-rich families—Sapotaceae, and Chrysobalanaceae—which are distributed in a variety of habitat types in the Neotropics. Studying the evolution of tolerance to nutrient-poor substrates and habitat specialization in a range of edaphic conditions can help to put into context the origin of white-sand specialists across the Neotropics and the role of edaphic niche conservatism in facilitating the accumulation of diversity of species in this biogeographic region.

Chapter 5: General conclusions and future prospects

In this chapter I summarize the main conclusions of this dissertation, and expand on several ideas intended as future research questions. An assessment of the conservation status of white-sand forests across the study region will only be attainable by developing a habitat map that includes the full variation in soil conditions on which they occur. I expand on several phylogenetic and phylogeographic hypotheses based on an extension of this doctoral research. Addressing these questions will give us a better understating of the evolution and maintenance of plant species diversity in Amazonia.

Chapter 2: Edaphic heterogeneity and the origin of white-sand soils in Amazonia

> "Overlying the shales there has been a soft white sandstone, in thick strata, great part of which has been decomposed and carried into the hollows, and even into the plain below, by the torrential rains leaving only a few scattered blocks of more tenacious material than the rest."
>
> —R. Spruce (1908)

2.1 Introduction

With approximately 744 million hectares, the Amazon and Guiana region encompasses a diversity of soil types that are just starting to be appreciated (Dijkshoorn *et al.* 2005, Quesada *et al.* 2010). The range of soil types has a complex spatial distribution, but in general the soils are predictable according to their level of pedogenic development, from intensely weathered soils mostly located towards central and eastern Amazonia, to soils in the western Amazon that tend to be more cation-rich and less developed (Sombroek 1966, Irion 1978, Quesada *et al.* 2010). Soil development is a dynamic process driven by a variety of pedogenic processes, starting with the rock or parent material from which a particular soil type is derived (Quesada *et al.* 2011). An understanding of the changing geo-morphological settings predominant in the past is therefore essential for interpreting current soil differences, which in turn may have affected biotic diversity, evolution and biogeography in these regions through variations in habitat heterogeneity. Insights into the age differences of white-sand patches, their spatial configuration and associations with other less extreme nutrient-poor soils, and proximity to putative parent material, may have implications for our understanding of the evolution of the Amazonian flora via habitat specialization.

Given the complex geological and soil formation history of the Amazon landscape (Sombroek 1984, Räsänen *et al.* 1987, 1990, 1992, Hoorn 1993, 1994, Räsänen *et al.* 1995, Wesselingh *et al.* 2002, Hoorn 2006, Roddaz, Viers, *et al.* 2005, Wesselingh & Salo 2006, Hoorn, Wesselingh, *et al.* 2009), the origin of white-sand soils, and hence the white-sand vegetation they support, is still debated. A review of the geology, palinostratigraphy, and soil studies of quartz-rich sandy soils in the Amazon and Guiana region suggest that they can have at least four origins: (i) the product of deep *in situ* weathering of quartzitic sandstones (Gansser 1974, Kubitzki 1989, Hammond 2005); (ii) deposition by eolian (wind) transport (Horbe *et al.* 2004); (iii) as fluvial deposits of paleo-channels (Klinge 1965, Hoorn 1994, Räsänen & Linna 1998, Roddaz, Baby, *et al.* 2005, Rossetti *et al.* 2012); and (iv) the final product of on-going Ferralsol/Acrisol to Podzol transformation (Lucas *et al.* 1984, Dubroeucq & Volkoff 1998, Lucas *et al.* 2012, Mendonça *et al.* 2014).

In this chapter I review the origin and development of white-sand soils in the Amazon and Guiana region. I start with a general review of the geological events that provided the parent material and sediments over which the Amazon and Guiana biota evolved. Second, I give a general background on white-sand soils in relation to current classification systems and discuss other relevant aspects of white-sand soil associations. I continue with a discussion of the four models of white-sand soil formation proposed above, with special emphasis on providing evidence for each of them and its applicability across the whole study area in Amazonia. The spatial configuration of white-sand patches in Amazonia and how some of the models may account for it is also reviewed. Finally, I discuss examples of white-sand soils that have been dated by different field studies in both the Amazon and Guiana Shield region.

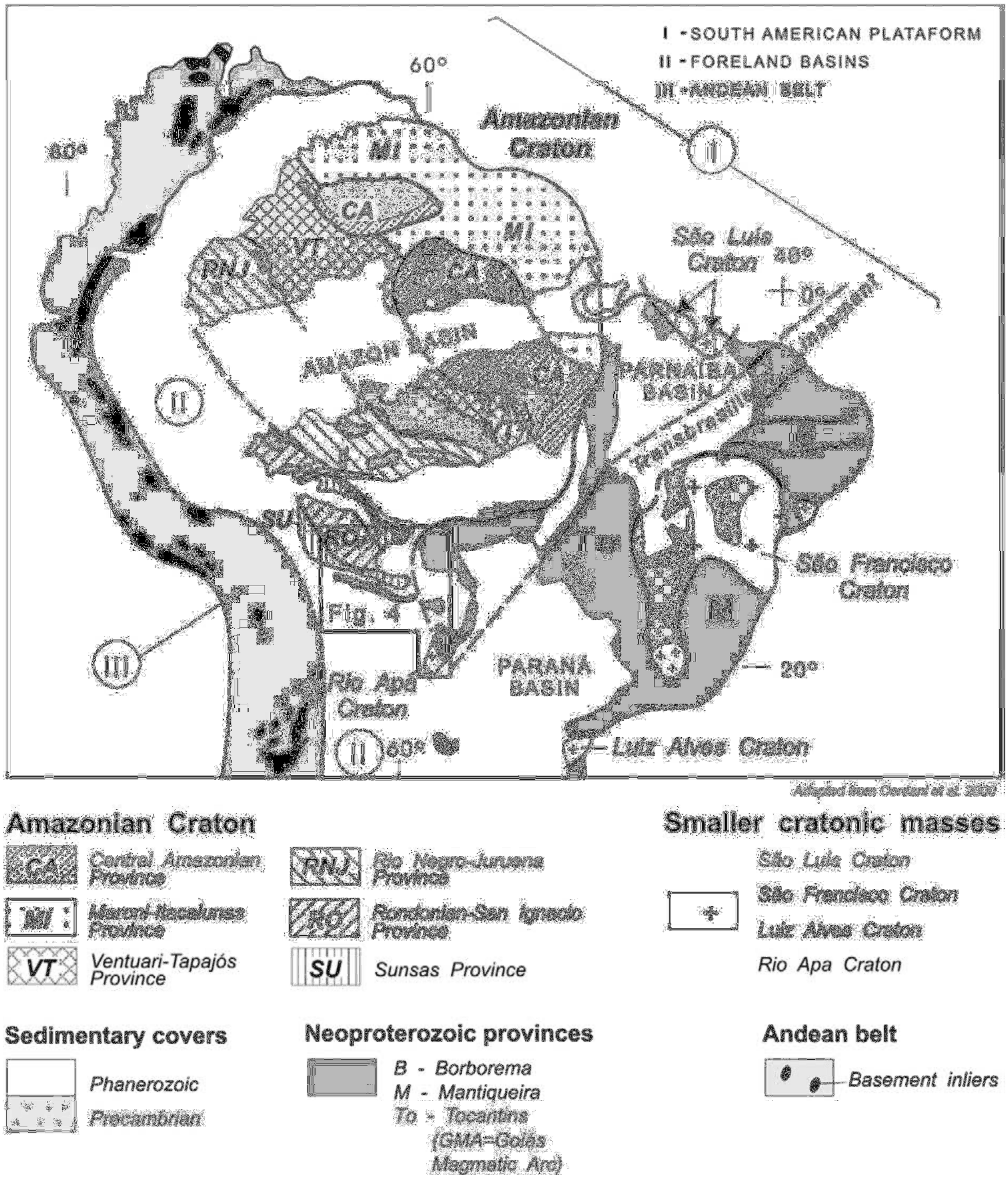
The aim of this review is to develop a geological and soil framework on which to base further biogeographical analysis and interpretation of plant habitat evolution and specialization. Understanding which processes are mainly responsible for the development of these extremely nutrient-poor soils, and their close association with other soil types, can help us to put into a wider context how they may have influenced plant evolution through habitat specialization in this biodiverse region.

2.2. Geological settings

After its split from Africa and North America (ca. 100-90 Mya.), South America was essentially an island continent, with two emerging lands, the Brazilian and Guiana Shields (also known as the Amazonian craton, Figure 3), inhabited by angiosperm families which evolved in West Gondwana (South America plus Africa) about 135 Mya (Graham 2010). These two regions are mainly built of Precambrian rocks (2.4-0.57 Byr) which have been eroded for most of their history (Hammond 2005), depositing massive amounts of sandy soils in the lowlands north and south, especially on the western fringe of lowland Guiana (Kubitzki 1990). Before the rise of the Andean chain, during a period of about 85 million years, a proto-Amazon drainage system discharged to the Pacific and Caribbean and these quartz-rich cratonic Shields were the main source of sediments deposited on the western side of South America (Kubitzki 1989, Potter 1997, Wong *et al.* 2009).

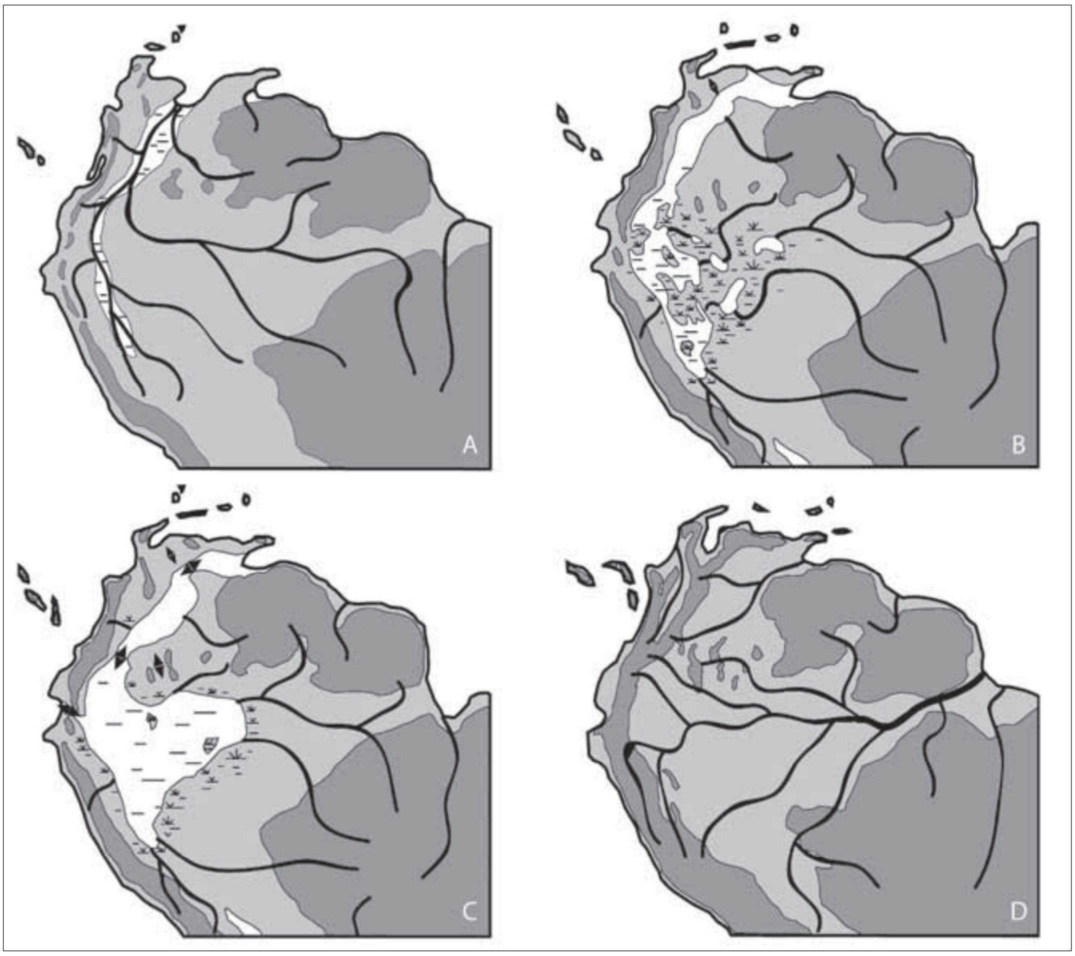
During the rise of the Andes mountains, multiple lines of evidence suggest that the western Amazon region was submerged between 18 and 9 Mya (middle Miocene), under a huge fluvio-marine wetland system (>1 Million km^2) known as the Pebas system (Figure 4) (Wesselingh *et al.* 2002, Wesselingh & Salo 2006). During this period, a proto-Amazon continued to drain towards the west, with connections to the Pacific and the Caribbean Ocean in a monsoon tropical environment (Wesselingh & Salo 2006). At its south-west margin the Pebas system was in contact with developing floodplains of Andean rivers (Hermoza *et al.* 2005), whereas towards the north and northeast, it received black water influx and sedimentation from the Guiana Shield craton (Hoorn 1994).

Figure 3 Amazonian craton (Guiana and Brazilian Shields) and its tectonic provinces (after Cordani *et al.* 2009).



Adapted from Cordani et al. 2009

Figure 4. Paleo-geographic reconstruction of western Amazonia in the past 34 million years. A) 34-23 Mya: proto-Amazon ran east to west and drained to the Caribbean, B) 23-17 Mya: A fluvial-lacustrine system started to develop in western Amazonia (the Pebas system), C) 17-9 Mya: The Pebas system dominated the region, marine conditions were also present, D) ca. 8 Mya: the modern eastward Amazon system became established (after Wesselingh & Salo 2006).



The demise of the Pebas system, and the origin of the modern Amazon system, was influenced by the Andean orogeny (Hoorn 1993) and the westward motion of the South American continent (Shephard *et al.* 2010). The initiation of the Andean orogeny gradually closed the proto-western Amazon with its Pacific and Caribbean connections (Wesselingh & Salo 2006). The fluvio-lacustrine period of Pebas ended about 6-10 Mya (late Miocene) when the rise of the western Guiana Shield blocked the Caribbean connection of the Pebas system (Wesselingh & Salo 2006, Shephard *et al.* 2010). It was during this period that newly formed habitats in the western Amazon, with varied soils, may have been gradually occupied by plants.

2.3. Amazon and Guiana white-sand soils

White-sand vegetation in the Amazon and Guiana regions occurs on soils classified as Podzols (Spodosols in the US Soil Taxonomy) or Arenosols (Psamments and Psammaquents in the US Soil Taxonomy) in the WRB classification (World Reference Base for Soils Resources) (Driessen *et al.* 2000, Quesada *et al.* 2011). Arenosols are soils with little or no profile differentiation and cover approximately 10% of the world's land surface, with the largest expanses representing eolian sands found in arid and semi-arid regions. In the Neotropics they are found in coastal areas and within the Amazon tropical biome, on top of both very old surfaces and more recent landforms (IUSS Working Group 2014).

Badly drained white-sands (hydromorphic white-sands) are also known as Ortsteinic Podzols in the World Reference Base soil classification (IUSS Working Group WRB, 2014) due to their capacity to develop a cemented spodic horizon (composed generally of iron, aluminum, and organic matter) close to the soil surface, with consequences for drainage conditions. This spodic horizon exerts an influence on the vegetation structure and composition through hydro-edaphic interactions (Anderson 1981, Chauvel *et al.* 1987, Jirka *et al.* 2007, Damasco *et al.* 2013). Podzols are classified as Giant Podzols if they have a spodic horizon located > 200 cm or more from the soil surface (FAO 1988, IUSS Working Group 2014). If this spodic horizon is located <200 cm depth they are classified as Podzols (FAO 1988, Dubroeucq & Volkoff 1998).

Podzols are soils with profile differentiation and usually with a thick (>1m thickness) organic horizon (Bh) in the topsoil (Chauvel *et al.* 1996) which has been recently found to store large amounts of carbon (Montes *et al.* 2011). They are more common in boreal and temperate regions, and in Amazonia they occur locally in areas rich in siliceous rock sediments (Klinge 1965, do Nascimento *et al.* 2004, Quesada *et al.* 2011, IUSS Working Group 2014), or closely associated with Low Activity Clay soils (i.e. low in CEC, Cation Exchange Capacity, due to strong weathering) like Ferralsols and Acrisols (do Nascimento *et al.* 2004, Bardy *et al.* 2010).

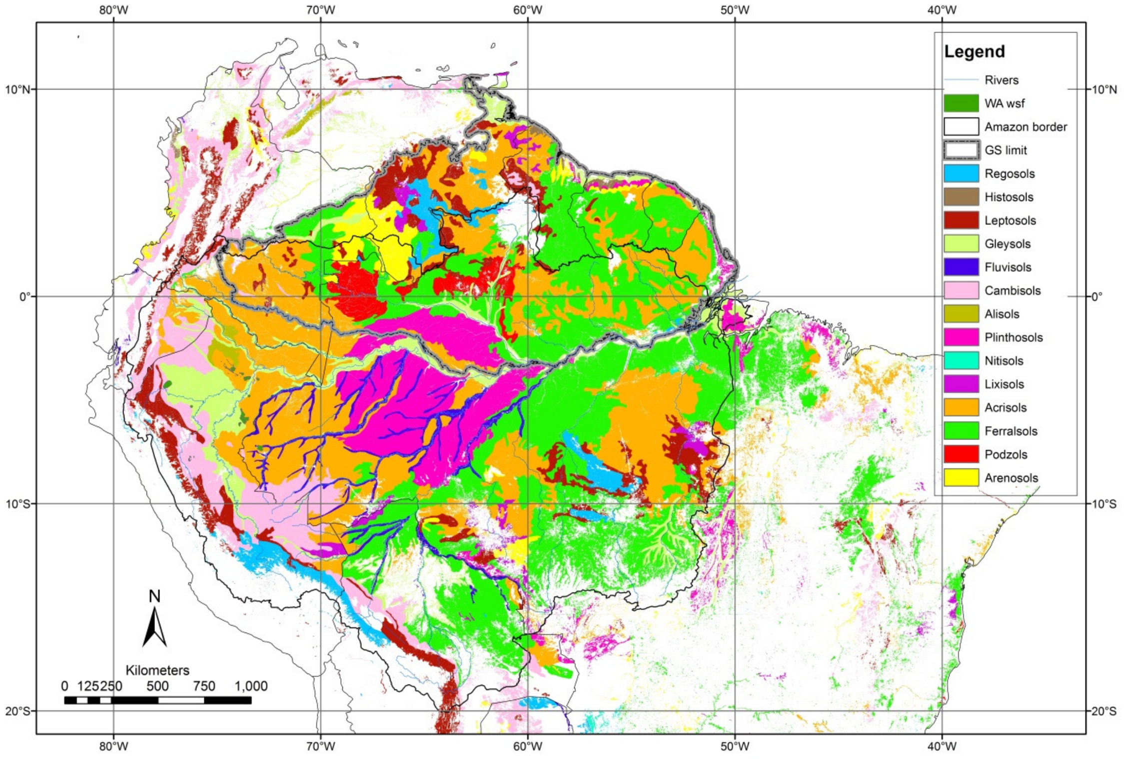
Well drained white-sand soils support generally taller and slightly more diverse vegetation than poorly-drained white sands (García-Villacorta *et al.* 2003, Vicentini 2004). Both Podzols and Arenosols are especially abundant in the upper Rio Negro, Brazil, (Figure 2) with some of them thought to represent the last stage of soil evolution in the Amazon, through podzolization of previously clay-rich Ferralsols and Acrisols (Dubroeucq & Volkoff 1998, Lucas *et al.* 2012, do Nascimento *et al.* 2004).

Ferralsols (Oxisols in the US Soil Taxonomy) are mainly found in central and eastern Amazonia, as soil mantle of old geomorphic surfaces and they are less common on the younger Andean sediments of the western Amazon (Quesada *et al.* 2012, Duivenvoorden & Lips 1995, Veillon & Soria-Solano 1988). They include most of what in the past were called laterites or Latosols (Carneiro-Filho *et al.* 2002). They consist of strongly weathered iron-rich (reddish-yellow coloured) low activity clays with an advanced pedogenic development. Compared to Acrisols (below), Ferralsols have a ferralic B horizon between 25-200 cm of the soil surface and in the central and eastern Amazonia (mostly Brazilian Amazon) they occur in the upper part of the *terra firme* clayey soil mantle (Figure 5).

Acrisols (Ultisols in the US Soil Taxonomy) are also low activity clay soils and the second most common soil in Amazonia, after Ferralsols (Quesada *et al.* 2012). They are devoid of a ferralic horizon and are especially prevalent in the Amazon region of

Colombia, northern Peru, and western Brazil (Figure 5). Podzols can develop from Ferralsols and Acrisols both centripetally (from the lower part of the terrain) and centrifugally (from the central part of the terrain) (Montes *et al.* 2011). In tropical waterlogged environments these soils are conductive to podzolization of clay with sandy soils as residuals (Lucas *et al.* 1984, Chauvel *et al.* 1987, do Nascimento *et al.* 2004).

Figure 5. Soil map of the Amazon and Guiana region. Legend ordered by age gradient, from younger to older pedogenic development. Note greater extension of Arenosol and Podzol in the Guiana Shield in yellow and red. Small patches of western Amazon white-sand forests (WA wsf) in dark green. Acrisol (Orange) and Ferralsols (bright green) are discussed in the text. White areas in the map are non-forested areas. GS limit = Guiana Shield limit (adapted from Quesada *et al.* 2011).



Quesada et al. (2011) using soil data compiled by the project SOTERLAC for Latin America and the Caribbean (Dijkshoorn *et al.* 2005) along with a vegetation map for the the Amazon basin (Saatchi *et al.* 2008) developed an updated version of soil map for the Amazon and Guiana Shield region (Figure 5). Although this map shows soil classes as discrete units it is important to emphasize that transitions between soil types exist, Ferralsol/Acrisol-Podzol being one of them (see below), that remain still unmapped. In the same vein, Podzols and Arenosols have been described as the final stage of soil development in the Amazon and Guiana region (Quesada *et al.* 2010) and shortcuts for the formation of these soils can occur depending on their proximity to the sandstone/crystalline rock parent material. Likewise, Arenosols and Podzols occur in geographic close proximity to Regosols and Leptosols, which are shallow mineral soils associated with rocky sandstone areas, in the Andes, Guianan and Brazilian Shields (Figure 5).

White-sand vegetation outside the Guiana Shield area is associated with, or occurs in relatively close proximity to, rocky sandstone formations, as has been reported in several mountainous areas of the Neotropics such as cordillera Cahuapanas (Dietz 2002, Treidel 2004), Cordillera del Condor (Neill 2008), Serra do Cachimbo (Lleras & Kirkbride 1978, Zappi *et al.* 2011), Serra do Moa, Serra do Divisor (Whitney *et al.* 2004), Cordillera Azul, Sierra Divisor, and Cerro Escalera (Neill *et al.* 2014). It is thus plausible that areas with Leptosols and Regosols, as currently classified (Figure 5), contain not yet mapped Arenosols and Podzols. Alternatively, Regosols and Leptosol may have hydro-edaphic characteristics similar to the Podzols and Arenosols of the lowlands, which makes them suitable for the establishment and nutrient-poor edaphic specialist plant species.

Another caveat to consider is the level of uncertainty in areas not well studied or not yet incorporated into maps. For instance, Veillon & Soriano (1988) described white-sand soils in Jenaro-Herrera, northern Peruvian Amazon, that they suggest were the product of podzolisation, in which Ferralsol/Acrisol soils were transformed into Podzols. In a second example from the western Amazon, Lips & Duivenvoorden

(1996) reported the presence of sandy-clay Ferralsols, with incipient podzolisation in the Caquetá region of Colombia. Both studies are not represented in the current soil map of the Amazon and Guiana regions (Figure 5). It is possible that the small size of areas of white-sand soils outside the Guiana Shield region makes it difficult to represent them at continental scale, thus masking the edaphic heterogeneity at the local scale.

The question is whether edaphic variation important to study the ecology, evolution and biogeography of plants and other organisms is represented in enough detail to answer relevant questions in each of these fields. In addition, soil mapping techniques and classification systems do not necessarily translate into data that is useful to study plant species distribution and functional properties, especially for patchy soil distributions (Sollins 1998). Along these lines, a quick glimpse of the recent soil map for Amazonia (Figure 5) might suggest that edaphic heterogeneity is high outside western Amazonia. However, relatively high levels of habitat heterogeneity has been documented for north-western Amazonia (Tuomisto *et al.* 1995, Duivenvoorden 1995, Pitman *et al.* 2008) which may be associated with its overall species diversity (Steege *et al.* 2003, Bjorholm *et al.* 2005, Barthlott *et al.* 2007, Kreft & Jetz 2007).

The exact extension of tropical Podzols and Arenosols in the Amazon and Guiana region is still unknown, but a recent estimation suggests that Arenosols and Podzols may account for 20 (2.7%) and 14.1 (1.9%) million hectares respectively (Table 1). This means that white-sand soils in Amazonia may have roughly an extension of 34.1 million hectares (4.6% of the soil surface in the whole region). This is in a sense an underestimate since some white-sand taxa may occur on Regosols and Leptosols as discussed above. At a regional level, Arenosols account for 17% of the Zanderij Formation in Surinam and approximately 26% of Guyana's Berbice Formation (FAO 1988, Hammond 2005). It has been estimated that white-sand Arenosols and Podzols occupy 17% and 26% of the current sedimentary plains of Suriname, and Guyana respectively (Schulz *et al.* 1960, FAO 1965).

In the Amazon and Guiana regions, estimates suggest that Ferralsols and Acrisols (and to a lesser extent, Cambisols) represent the largest soil mantle in the species-rich *terra firme* forests (Figure 5), with 235 (32%) and 215 (29%) million hectares of soil cover respectively (Table 1). It has been estimated that Ferralsol-Podzol associations cover approximately 18% of the Brazilian Amazon (Radambrasil 1978), and can occur within the same spatial unit and geological formation from Precambrian, Tertiary to Quaternary (de Almeida *et al.* 1976, Chauvel *et al.* 1987, Veillon 1990, Hammond 2005).

Table 1. Soil extension of the white-sand soils (Arenosols and Podzols), Ferralsols, and Acrisols in the Amazon and Guiana regions (modified from Quesada *et al.* 2011).

Soil type	**Area (mill. has)**	**%**
Ferralsols	235.0	32
Acrisol	215.4	29
Arenosol	20.0	2.7
Podzol	14.1	1.9
Others (n=10)	259.7	34.4
Total	744.2	100

2.4. Processes involved in the origin of Amazonian white-sand soils

(i) Deep in situ weathering of quartzitic sandstones

Of the original ca. one million km^2 of estimated Roraima sandstone extension in the Pre-Cambrian, three quarters have been eroded (Gansser 1974). Given the importance of the Guiana and Brazilian shield as the source of sand material in South America it was thus believed that most of the white-sand soils in the western Amazon were derived from erosion from these Pre-Cambrian sandstone formations and subsequent deposition in this region by fluvial transportation when the proto-Amazon region was drained in an east-west direction before the rising of the Andes in the Miocene (Kubitzki 1989, Räsänen *et al.* 1993, Hoorn 1994, Potter 1997, Frasier *et al.* 2008). Potter (1994) estimated that 62% of all quartzitic sands in South America, including coastal and inland, have a cratonic provenance (i.e. originated in the Guiana and Brazilian Shield regions). Most of the eroded sands were deposited north or south of the Guiana Shield area, within the now coastal savannas of Guyana, French Guiana, and Surinam; and between the Upper Orinoco and Rio Negro in the Amazon (Kubitzki 1989, Potter 1997).

Because of the abundance of white-sand soils in the Guiana Shield region as a whole (Klinge 1965, Hammond 2005, Quesada *et al.* 2012), early interpretations attributed this region as the main source of white-sand soils in the Amazon. A distinction was made, however, when discussing the potential origin of white-sand soils depending on the presence of sandstone parent materials nearby white-sands. Thus, white-sand forests of the upper and lower Rio Negro, specifically the ones located between the upper Rio Negro and Rio Branco, were postulated to have their origin on sands eroded from sandstone outcrops of the Guiana Shield region. The existence of white-sands occurring in other areas of Amazonia was attributed to be the result of ancient fluvial depositions on abandoned river beaches (Prance 1996).

Given that white-sands in the upper and lower Rio Negro are located in geographical proximity to quartz-rich rocky outcrops of the Guiana Shield; it is plausible that eroded sediments were transported by paleo-rivers to this area (Prance & Schubart 1978). A good example of *in-situ* white-sand soil developed by deep weathering and erosion of quartzitic sandstones is the white-sand soils of Serra do Aracá, which is the southernmost extension of the Roraima Formation in the Upper Rio Negro, Brazilian Amazon (Prance & Johnson 1992). However, not all white-sand soils in the Guiana Shield lowlands may have their origin from in-situ erosion of sandstone outcrops.

Lucas *et al.* (1984) studied a representative toposequence in the Manaus region and found that Podzols developed by weathering of clayey Ferralsols/Oxisols, a finding later corroborated by other studies (do Nascimento *et al.* 2004 and references therein).

In the western Amazon lowlands, white-sand soils generally occur isolated from any sandstone formations. However, there exist some areas that may have provided the parent material for their origin and these include Palaeozoic sandstone table-mountains in Colombia, which are geologically related to the Guiana Shield (Teixeira *et al.* 1989, Tassinari & Macambira 1999, Cordani *et al.* 2009, Hammond 2005), and Cretaceous sandstone rocks in the northwest of the Peruvian Amazon (Stallard & Lindell 2014). It is possible that at least some of the white-sand soils found in the northwest of the Peruvian Amazon may have their origin from similar quartzitic sandstone transported down the lower watershead areas by now extinct paleo-rivers.

(ii) White-sands deposited by eolian transport

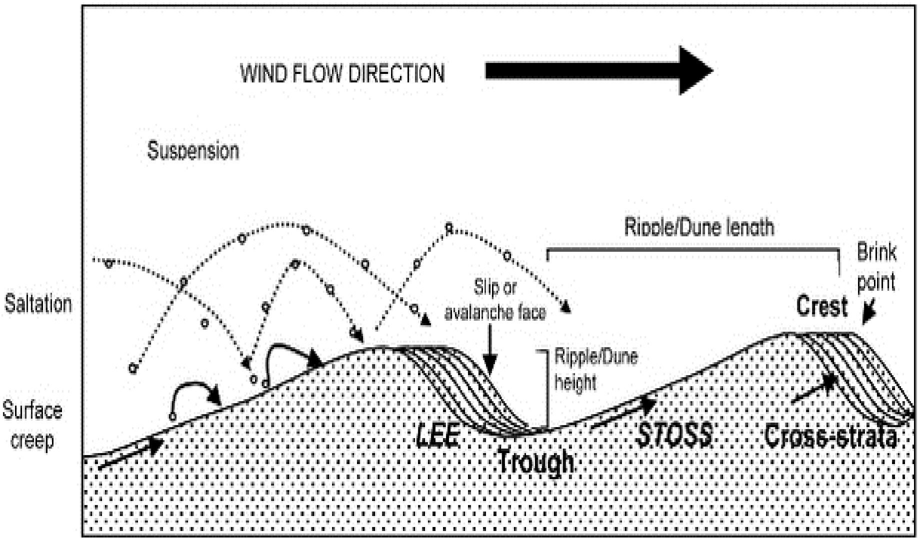
The formation of sand dunes in any geographic region requires certain wind conditions (speed and direction; see above) and open areas, like the ones present in deserts, or coastal areas such as the *restinga* forests found from northeastern to southeastern Brazil (Bigarella *et al.* 1969, Clapperton 1993). Some authors have presented relict sand formations (paleo-dunes) now covered by savanna vegetation in northeast South America as evidence for drier climates in the past (Ab'Saber 1977, Clapperton 1993, Latrubesse & Nelson 2001).

Clapperton (1993), in particular, hypothesized that white-sands in the Amazon may have an eolian origin based on interpretation of Ab'Saber's soil studies in the region of Amapa, northeast Brazil (Ab'Saber 1982). He suggested that white-sand soils may have been transported first across the Amazon by wind, during dry periods, after having been eroded from sandstone outcrops in the Guiana-Shield region.

The orientation of putative paleo-dune ridges covered with campina and campinarana vegetation south of Serra de Aracá (Borges *et al.* 2014) coincides with modern dominant wind direction (Teeuw & Rhodes 2004). These white-sand soils may have been deposited during a dry phase preceding the Last Glacial Maximum (LGM), during the late Pleistocene and early Holocene, 32,000-8,000 yrs B.P. (Carneiro-Filho *et al.* 2002). In the Upper Rio Negro in Brazil, thermoluminescence dating of white-sand soils has suggested eolian activity during dry periods before the LGM, with sand deposition until at least 7800 yr BP when a more humid climate fixed the soil with vegetation cover (Carneiro-Filho *et al.* 2002).

Dune formations present a particular manner of sand grain deposition known as cross-bedding, in which sand grains blown by wind from one direction are deposited at the top of the dunes and then eventually fall towards the lee part of the dune ("avalanche phase", Figure 6). Likewise, grain bedding of sand deposited in eolian conditions exhibit *inverse grading*, a systematic change in grain size with coarser sand grains at the top and fine grains at the bottom of the sediment layer.

Figure 6. Sand dune formation by eolian action. In contrast to fluvial dunes, eolian dunes deposit fine sand grains at the bottom and coarse grains at the top (after Sloss *et al.* 2012).



Although there has been a suggestion that white-sand soils in the upper Rio Negro, Brazil have been transported by wind (Santos 1993 cited in Latrubesse & Nelson 2001) this process may not be as important as previously thought for the deposition of sandy soils in other regions of the Amazon. Current sedimentary records, as well as ocean and climatic models, suggest that most of tropical South America and the Amazon landscape did not develop an arid environment during the LGM (Last Glacial Maximum) (Baker *et al.* 2001, Mayle *et al.* 2004, Bush *et al.* 2007, Clark *et al.* 2012, Maslin *et al.* 2012). Most of Amazonia may have remained covered by tropical rainforests during this period and only at its margins may have transitioned to savannas or seasonal dry forests (Beerling & Mayle 2006, Cruz *et al.* 2009, Cheng *et al.* 2013).

In the Guyana-Brazil border, in the Rio Branco-Rupununi savannas, optical dating of the onset of eolian activity was estimated in the range of 15,000-17,000 yrs ago (late

Pleistocene), suggesting that eolian deposition has been relatively stable since soon after the LGM, with a constant deposition rate of 13 cm per 1,000 years, and is now fixed by savanna vegetation (Teeuw & Rhodes 2004). Finally, it is not clear what has been the relative importance of wind in the origin of white-sand soils in north-eastern Amazonia, south of Serra de Aracá (Figure 1 in Borges *et al.* 2014), given that they occur in close proximity to areas recently hypothesized of being the result of sedimentation processes due to paleo-channel abandonment by fault reactivation (Rossetti *et al.* 2012).

(iii) Fluvial deposit of paleo-channels

Abandonment of fluvial channels since the late Miocene-Pliocene (6-5 Ma), and especially during the Pleistocene-Holocene, due to tectonic events (fault reactivation), may have created depositional systems over which sediments of different types, including sandy soils, were deposited in massive quantities (Rosetti et al. 2012). In the region of Iquitos, white-sand soils occur parallel to a former cratonic river, a proto-Nanay River, which, along with the horizontal zonation of sand grains was used as evidence to infer that they were deposited as sand by a now extinct paleo-river which left its sandy sediments in the uplands between 8-1 Ma (Räsänen & Linna 1998).

A further comparison of the white-sands of Iquitos with sediments from Andean sources pointed to a cratonic origin (Hoorn, Wesselingh, *et al.* 2009) and an estimated range age of one outcrop, via cosmogenic dating, in the range of 600,000-800,000 years old (M. Roddaz, pers. com.). White-sand outcrops are common around the Iquitos region and we cannot be sure that this age is representative for other areas until more studies are carried out. If further studies confirm that this age is representative of white-sand soils in this area, it will provide support for the idea that its flora was building up relatively recently, in the middle Pleistocene, by the arrival of white-sand specialists from other areas or by adaptation of non-white-sand specialists from less oligotrophic soils nearby.

Fluvial perturbation of the Amazon landscape may have been a recurrent pattern in recent geological time in eastern Amazonia, in areas influenced by sandy sediments from pre-Cambrian rocks. Latrubesse & Franzinelli (2005) established that the Rio Negro fluvial system, Brazil, has left Late Pleistocene floodplain terraces composed of abundant quartz sand deposited by the river during its aggradational phase (ca. 65 kyr to 25 kyr ago B.P.).

Sedimentary evolution due to fault reactivation that affected fluvial systems shows that sedimentary dynamism in the Rio Branco area (Amazonian Brazil) was high, with constant rearrangement of fluvial tributaries in the landscape (Rossetti *et al.* 2012). These events may have been especially pronounced during the Pleistocene-Holocene, with fluvial rearrangements due to local tectonics. The result may have been the abandonment of paleo-channels carrying sandy sediments, providing the conditions necessary for the development of white-sand vegetation of various types surrounded by the typical Amazon rainforest (Rossetti *et al.* 2012).

In the Viruá National Park of Roraima and the Demini region, north east Brazil, multiple paleo-channels exist within subsiding areas which were filled up with sandy sediments from pre-Cambrian rocks present in the area. The age of these sandy sediments have been C^{14} dated up to 38,161 yrs BP, and they have a grain size from coarse to fine, with finer grains deposited at the bottom of the paleo-channels. Interestingly, as with the Iquitos white-sand areas of the western Amazon, some parts of the forests on white-sand soils in Viruá occur on sandy hills, several meters above the landscape, which might represent exposed fluvial bars (Rossetti *et al.* 2012).

Palynological and sedimentological studies in the Amazon region of Colombia suggest that the Mariñame and Apaporis sand units have been deposited from the Guiana Shield by a former river that ran from east to west during the Miocene, 23-5 Ma (Hoorn 1993, 1994). In the northern Peruvian Amazon, the depositional phase of a marine mega-lake deposited cation-rich sediments known today as the Pebas Formation during the Middle Miocene to Upper Miocene (17 Ma to 11 Ma) (Hoorn 1994). River dynamics of incision and denudation have exposed the buried cation-rich Pebas formation in many areas of western and central Amazonia (from ca. 5 Ma to present) (Räsänen *et al.* 1990, Roddaz, Baby, *et al.* 2005, Roddaz, Viers, *et al.* 2005).

Sandy-clay soils in the Peruvian Amazon were deposited between 10-5 Ma (late Miocene), as part of the Nauta formation, above the clay-rich Pebas formation (equivalent to the Solimões formation in Brazil) during a period that coincided with the closing of a mega-lake that occupied much of the Amazon basin (the Pebas system) (Wesselingh & Salo 2006). Likewise, the white-sand unit of the Iquitos area has been interpreted as fluvial in origin and dated between 8-1 Ma (Räsänen et al. 1998). The composition of Iquitos white-sand indicates that the most probable source for these soils was metamorphic basement (not Andean sediment) and located probably not far away from the Iquitos area (Roddaz, Viers, *et al.* 2005). Accordingly, western Amazon white-sand floras and mega-diverse upland forests on clay may have assembled only after the Pebas mega-lake dried up in the late Miocene (ca. 11-9 Ma BP). There is sedimentological, and palinostratigraphic evidence that a river originating in the Guiana Shield discharged its sediments in the Caquetá region, Colombian Amazon (Hoorn 1994) whereas the Vaupés formation, that extends between the Vaupés and Caquetá Rivers developed within an epicontinental environment (Priem *et al.* 1982).

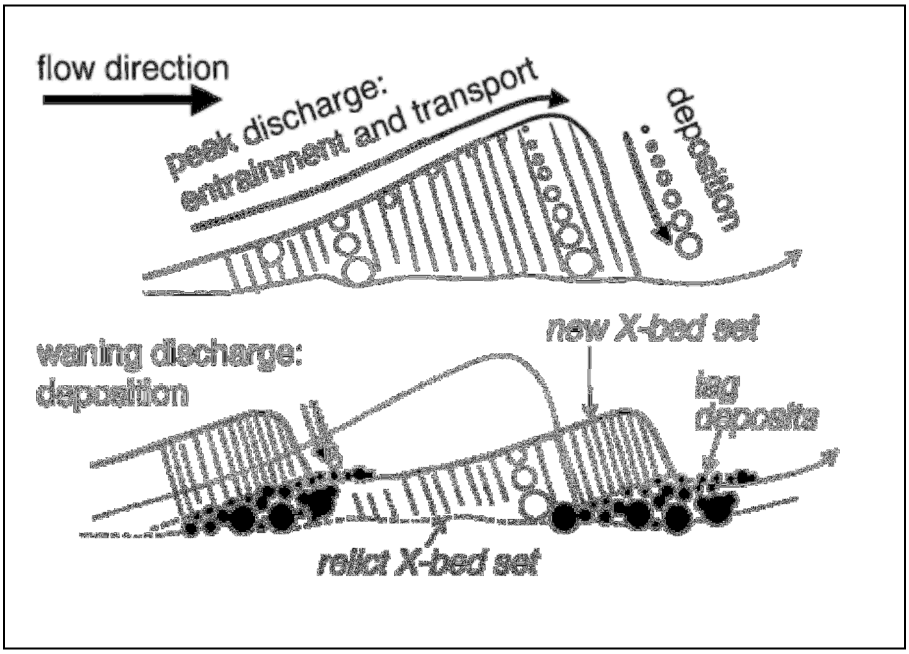
Given that the Nauta sandy-clay Formation, and the Iquitos white-sand Formation were exposed to the same weathering conditions and considering that the Nauta formation does not show signs of quartz enrichment (podzolisation), Roddaz *et al.* (2005) inferred that Iquitos white-sands might have been deposited as such by an extinct cratonic river, not by Andean rivers. Because of its location only on the eastern part of the Iquitos arch, they also suggested that the Iquitos white-sand formation may have been deposited by an eastern fluvial system draining the Amazonian craton (Roddaz, Baby, *et al.* 2005).

A review of absolute dating by stratigraphy puts the white-sand formations in the Caquetá region between 23-5 Ma B.P. (Hoorn 1993, Hoorn, Wesselingh, *et al.* 2009). Considering that the western lowlands of the Guiana Shield may have had, up to this time, a flora pre-adapted to sandy nutrient-poor soils, their constituent taxa were the natural candidates for occupying these newly created habitats in northern Amazonia (Kubitzki 1989).

Fluvial paleo-dunes

Sand dunes resulting from fluvial deposits can be characterized as such by depositional patterns, grain size distribution, and stratification types (Visher 1969, Hunter 1977, Kocurek & Dott Jr 1981, Kocurek 1991). Dunes formed by fluvial (or eolian) activity exhibit a cross-bedding deposit (i.e. inclined layer deposition), which results from the "avalanche phase" during dune propagation (Figure 7). In contrast to eolian dunes, dunes formed by fluvial dynamics generally deposit coarser grains (or gravel) at the lower part of the dune and finer grains occupy the upper half (Figure 7).

Figure 7. Fluvial dune formation process in which larger sand grains (or gravels) are deposited at the bottom and finer grains at the top (after Kleinhans 2001).



This sedimentation pattern of fluvial dunes is due to a combination of an intrinsic physical process of fluvial transport (coarser grains or gravels are deposited in the dunes during river discharge while finer grains remain in transport longer) helped by the "avalanche phase" (Kleinhans 2001, 2004). These two processes of dune formation by eolian and fluvial systems are, however, not mutually exclusive and they can interact to shape the geomorphology of landscapes (Bullard & Livingstone 2002, Field *et al.* 2009).

Fluvial deposition on the Iquitos paleoarch

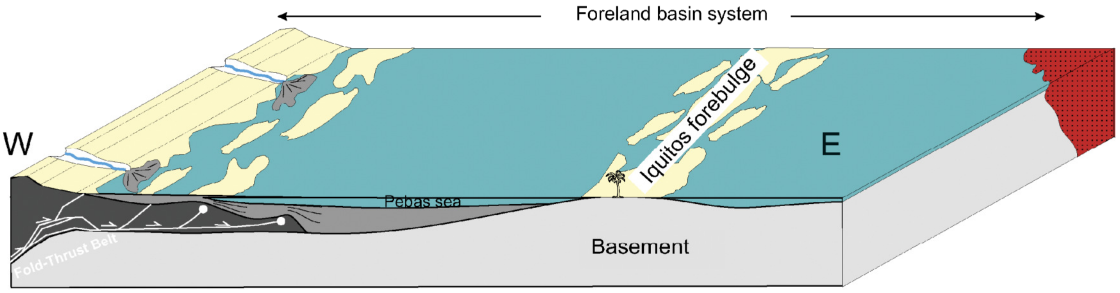
The vast extension of the Amazon basin can be sub-divided into smaller sub-basins by structural highs in the terrain called forebulge arches (Figure 8). In a geo-morphological context, the rising of a massive geological fault system in the northern

Peruvian Amazon—the Iquitos Arch—has been associated with deposition of fluvial white-sand soils as well as their prevalent location on hilltops along this Arch (Roddaz, Baby, *et al.* 2005, Roddaz, Viers, *et al.* 2005, Stallard 2006). Roddaz, Baby, *et al.* (2005) proposed that the forebulge depozone induced the retreat of the Pebas system and accumulated Andean fluvial sediments of the Nauta formation (late Miocene), whereas the backbulge depozone of the arch received white-sand sediments (Figure 8).

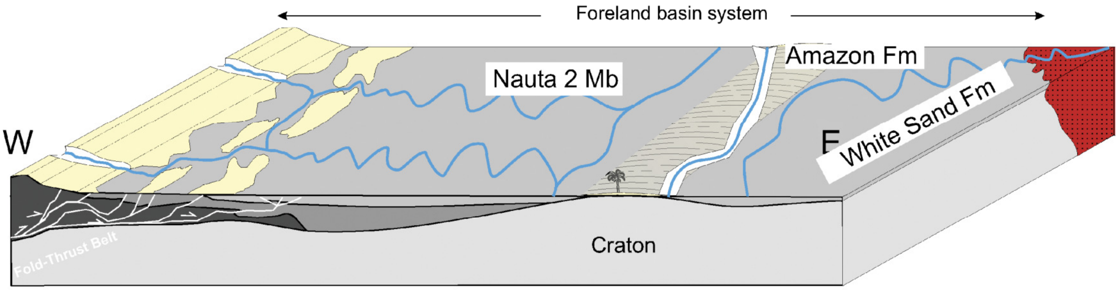
Since the modern Amazon drainage system have been active since 6-8 Ma (Roddaz, Viers, *et al.* 2005), and considering that white sand deposits around Iquitos occur at some localities covered by the Pebas Formation that are dated from the Middle Miocene (16.3-10.4 Ma) (Kauffman *et al.* 1998), Roddaz, Baby, *et al.* (2005) estimated the age of the Iquitos white-sand soils at 6-8 Ma (late Miocene). In the same geological context of the Iquitos Arch, southwest of the Iquitos white-sands, an extensive area of white-sand forests has been reported (Vriesendorp *et al.* 2006). Soils in this area occupy mostly flat hilltops and were interpreted as belonging to remnants of a former fluvial landscape (Pliocene, 5-3 Ma) that may have been alluvial in origin or derived from more complex sediments via strong weathering of sandy-clay soils (Stallard 2006).

Figure 8. Schematic representation of the Iquitos forebulge arch evolution (a, b, and c) and the deposition of white-sand soils on the backbuge depozone of the arch since the middle Miocene to present (after Roddaz, Baby, *et al.* 2005).

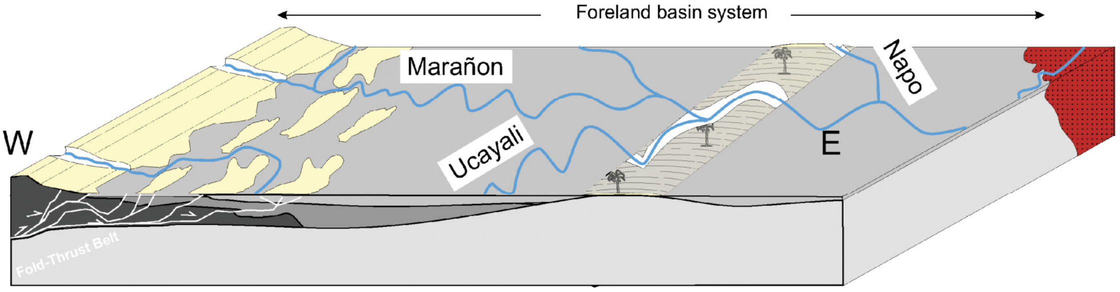
a) **Middle-Late Miocene**



b) **Late Miocene Pliocene**



c) **Present-day**



So far, there has not been another claim for the role of arches as white-sand sediment beds in other parts of Amazonia and the Iquitos arch's circumstantial function for trapping white-sand sediments in the western Amazon seems unique. In addition to receiving cratonic sediments from the east of Amazonia, the accumulation of new sediments in its forebulge depozone (Roddaz, Viers, *et al.* 2005) and subsequent and continuous uplifting may have increased the erosion rates, exposing diachronically deposited sediments. The upper hills on tropical conditions may have favoured leaching of soil nutrients at the top which may be reflected in the presence of nutrient-poor associated plant species (García-Villacorta *et al.* 2010, 2011). The accumulation of sediments from different ages and origin with subsequent erosion may have had a profound effect on creating the edaphic heterogeneity in the terra firme forests of the western Amazon.

Räsänen & Linna (1998) worked in the same Iquitos area as Roddaz, Baby, *et al.* (2005) and classified the sediments that outcrop in the Iquitos arch into five groups: the Pebas unit, Nauta C, Nauta B, White-sand unit, and fluvial terraces. The Pebas unit is interpreted as the legacy of the early-middle Miocene (17-11 Mya) mega-lake system with the same name. It is rich in cations due to the presence of marine deposits and it outcrops intermittently in the terra firme (e.g. salt-lick areas) and more commonly exposed along some river banks. The two Nauta units (C, and B) are interpreted as Andean fluvial deposits (12-8 Mya) (Räsänen & Linna 1998) and overlay the Pebas unit for the most part. The white-sand unit was interpreted as a fluvial deposit from the late Miocene (8-1 Mya) by an extinct cratonic river. Fluvial terraces ages are assigned to middle to late Quaternary age (ca. 1 Mya) (Räsänen & Linna 1998).

The use of paleo-arches to interpret biogeographic patterns in the Amazon (Da Silva & Patton 1998, Patton *et al.* 2000) has been criticized by Rossetti *et al.* (2005) on the grounds that they no longer represent physical barriers that isolate populations (see also Wesselingh & Salo 2006). For example, the Purus arch, west of Manaus, has been buried >1000 m under Cretaceous rock of the Alter do Chão Formation (Rossetti *et al.* 2005). Considering that other arches, like the Iquitos arch, are still growing and active today (Roddaz, Baby, *et al.* 2005), this observation does not preclude the effect paleo-arches may exert on topographic variation, their effect on erosion rates (Stallard 1988), and exposure of different sediments, including white-sands, which may affect the level of edaphic heterogeneity of entire watersheds at local and regional scales (Roddaz, Baby, *et al.* 2005, Stallard 2006, 2011). The few phylogeographic studies on plants and animals along areas influenced by paleo-arches suggest that these terrain structures may have an important effect on creating strong edaphic variations that may separate species distributions (e.g. Da Silva & Patton 1998, Lougheed *et al.* 1999, Dexter *et al.* 2012) or create abrupt changes over entire plant communities (Pitman *et al.* 2008, Higgins *et al.* 2011).

(i) Ferralsol/Acrisol-Podzol transformation

Deposition of sand by cratonic (non-Andean) paleo-rivers or lakes competes with the possibility that white-sand soils may develop *in situ* by the transformation of low activity clay soils like Ferralsols (Oxisols) and Acrisols (Ultisols) into white-sand soils, over thousands to millions of years of strong weathering (Dubroeucq & Volkoff 1998, Lucas *et al.* 1996, Horbe *et al.* 2004, Hoorn, Wesselingh, *et al.* 2009). These two types of soil are widely distributed in the *terra firme* forests of the Amazon basin representing in total 61% of the soil mantle in the Amazon and Guiana Shield regions (Quesada *et al.* 2012) and more than 65% in the Guiana Shield alone (Hammond 2005) (Figure 5, Table 1). Ferralsols are more strongly weathered than Acrisols and together they occupy different extensions and distributions, with Acrisols more extended in the western Amazon, while Ferralsols are more widespread in the Brazilian Amazon (Figure 5).

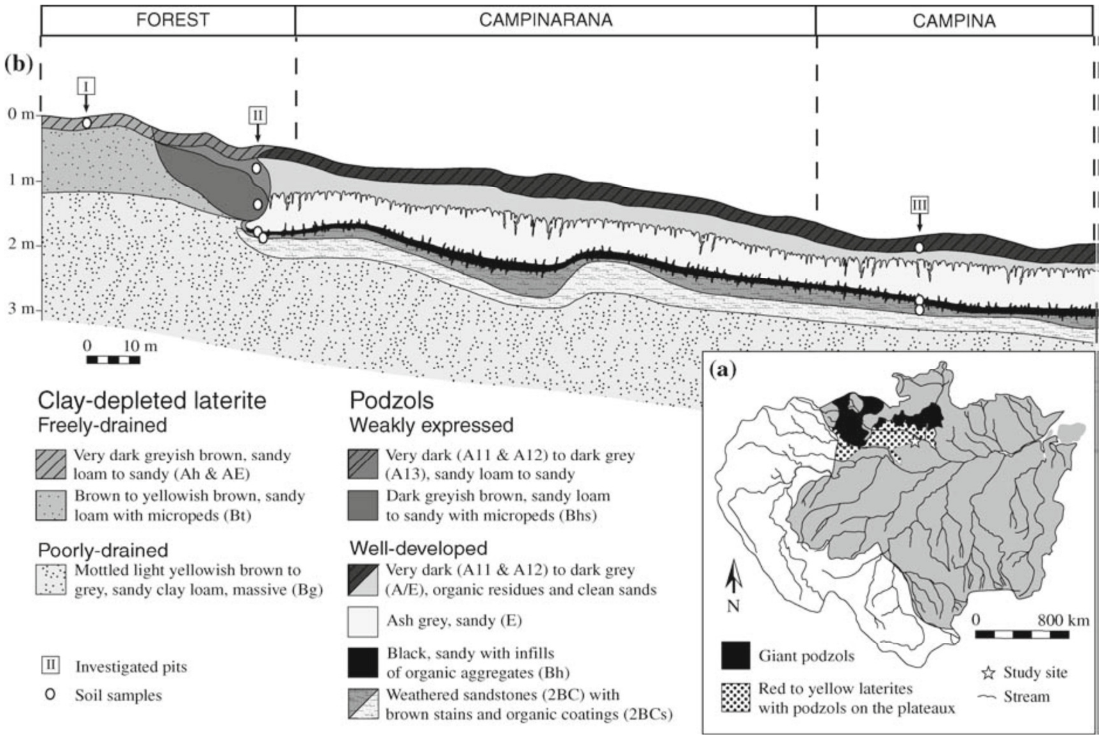
White-sand soils in the Guiana Shield area exist alongside Ferralsols and Acrisols and occupy the same geo-morphological units, this being Tertiary sediments (66-2.6 Ma) in the central Amazon (Lucas et al. 1989) and Quaternary sediments in coastal Guyana (Bleackley & Khan 1963, Hammond 2005) and Precambrian Guiana Shield areas (de Almeida *et al.* 1976, Veillon 1990, Hammond 2005). White-sand soils therefore would be the final product of tropical weathering in the pedogenic process of soil development in the Amazon and Guiana regions (Quesada *et al.* 2012). The enormous extensions of white-sand soils (Arenosols and Podzols) in the Guiana Shield region, including the Upper Rio Negro, might testify to the longer period of weathering the soil mantle in this area has passed through compared to the scattered nature of white-sands in the western Amazon region.

Pedogenic evidence from the eastern and western Amazon suggests that white-sand soils and low activity clay soils (Ferralsol/Acrisol) can co-exist in the same spatial matrix. In the Manaus and Rio Negro region, white-sand soils develop as the final product of podzolization in which sandy-enriched sediments like Ferralsols/Acrisols develop into podzols over thousands or millions of years of strong weathering (Lucas *et al.* 1984, p.84, Chauvel *et al.* 1987, Bravard & Righi 1988, Kubitzki 1989, Lucas *et al.* 1996, Cornu *et al.* 1998, Dubroeucq & Volkoff 1998, Lucas 2001, Horbe *et al.* 2004).

For example, the geological unit upon which white-sand soils occur in Manaus is known as the Alter do Chão Formation, which has been dated to the Cretaceous (100 Ma) through palynological and stratigraphical studies (Putzer 1984). ^{14}C dating of Podzols 30 km north of Manaus shows that they have developed from sandy to sandy-clayey horiozons in less than 3,000 years under current forest and climatic conditions (Horbe *et al.* 2004).

Supporting the view of an *in-situ* origin of white-sand soils is the work of Veillon & Soria-Solano (Veillon & Soria-Solano 1988) who studied white-sand soils on the tropical uplands of French Guiana and found a dynamic Ferralsol to Podzol formation of white-sands. Figure 9 presents a simplified representation of how this process works and the associated white-sand vegetation.

Figure 9. Podzol development from Ferralsols with associated vegetation types in a soil catena of the eastern Amazon, Brazil. Inset map shows approximate distribution of Giant Podzols along with Podzol-Ferralsol associations (after Bardy *et al.* 2010).



2.5. Models for the spatial arrangement of white-sand soils as island-habitats

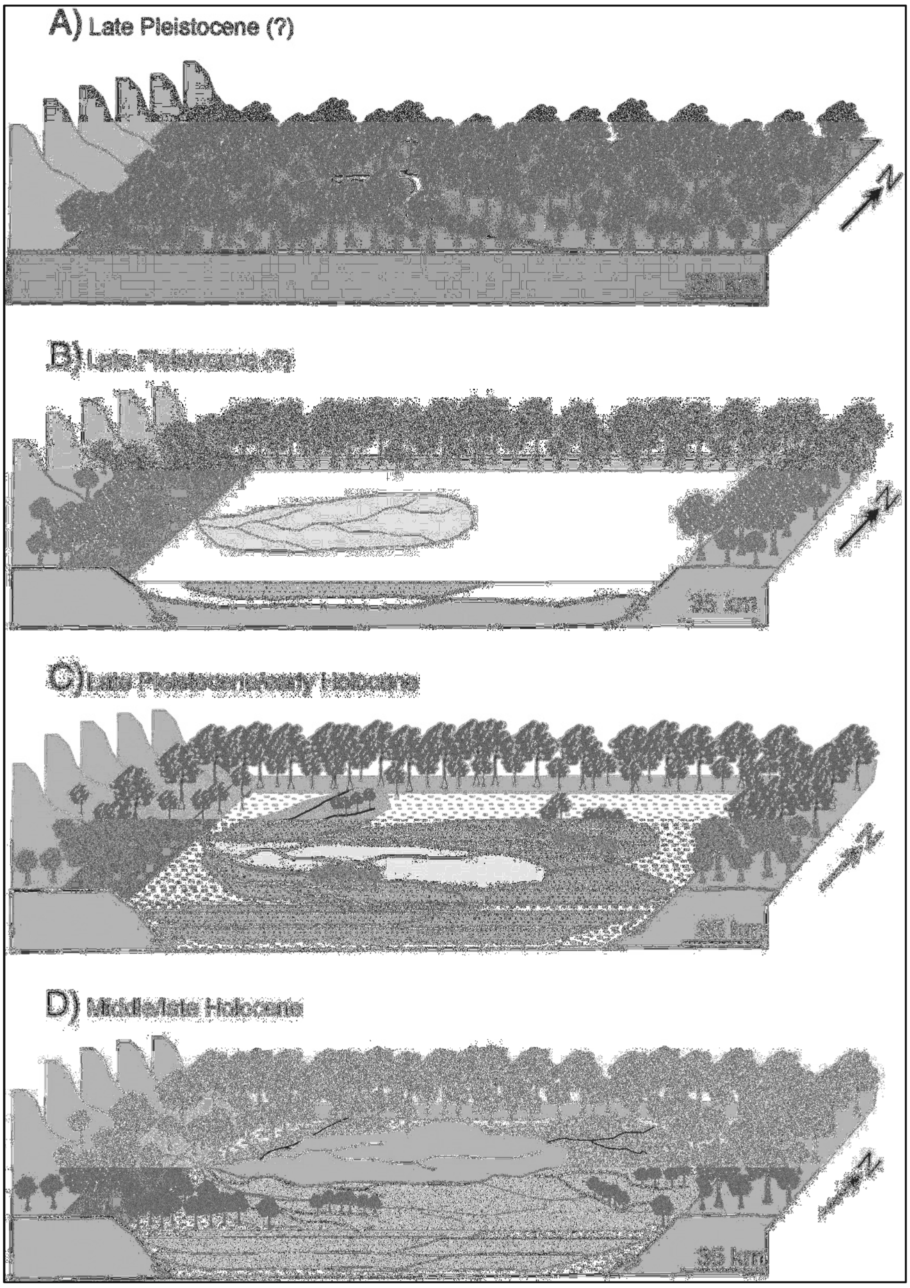
Of the four proposed models for the origin of white-sand soils presented above, only two of them have been interpreted in the light of their peculiar spatial distribution, as habitat-islands in a sea of rain forests (Figure 1, Prance 1996). The first one is related to the origin of white-sand soils via Ferralsol/Acrisol-Podzol transformation. According to Legros (2012), based on the work of Veillon & Soria-Solano (1988), three different spatial patterns may occur through the podzolization process: a) white-sand podzols that occur only in the centre of a plateau, b) white-sands occur in the centre as well as on the edges of the plateau, and c) a mature stage where patches of white-sands at the slope and plateau combine to form an archipelago of patches affecting an entire landscape (cf. do Nascimento *et al.* 2004).

A second model for patchy distribution of white-sand soils (and vegetation) in the Amazon has been recently proposed by Rossetti *et al.* (2012). In their tectonic model, a paleo-channel carrying sandy sediments and surrounded by rain forests is forced to abandonment by fault reactivation. This newly created depression in the terrain forms a wetland that is filled by sandy-clay or almost pure quartz sand sediments depending on the existence of rocky parent material in the area. Using a combination of satellite imagery, digital elevation maps, and field verification they identified several of these paleo-channels in the Viruá and Demini areas, Roraima, Brazil, which has characteristically fan-shape sedimentation. Over time, this area becomes suitable for the development of open and semi-open white-sand forests, distributed like islands, surrounded by the typical rain forest (Figure 10).

The on-going podzolization both in western Amazonia (Veillon & Soria-Solano 1988, Lips & Duivenvoorden 1996) and eastern Brazilian Amazonia (e.g. Lucas *et al.* 1984) provides some support for this model. If so, the fact that white-sand soils in the eastern Amazon are more extensive may only reflect the age of the weathering process compared to the western Amazon. However, given that podzolisation has been demonstrated to occur gradually according to soil age, this model might be more important in the Guiana Shield area where Ferralsols are more widely distributed than in the rest of the region (Quesada *et al.* 2011).

It will be expected that the tectonic model will be more predominant in the Guiana and Brazilian Shield regions where sandy sources are extensive. With this caveat in mind both models can work in complemen to create the peculiar archipelago-like distribution of white-sand habitats. Only more soil studies in different areas where white-sand habitats occur will tell us which model explains better their spatial distribution.

Figure 10. Tectonic model for the origin and spatial configuration of Amazonian white-sand vegetation and soils (Rossetti *et al.* 2012).



2.6. White-sand soil ages

As with many other soil types in the Amazon, the determination of white-sand soil ages is still for the most part a work in progress. There have been advancements from different fields, especially geology, using relative age dating, in which the relative order of soil layers are interpreted as younger (usually on top) or older (usually below) according to their position in the stratigraphic column. Absolute dating has been also playing a role more recently to estimate the ages of younger sediments. A review of ages of some white-sand soil formations in the Amazon shows that they can range from 3,000 yrs to 23 Ma old, with several eastern Amazonian white-sands dated relatively recently, <60 yrs B.P (Table 2).

White-sand formations from the Mariñame Sand Units, in the Colombian Amazon, are estimated to be 23-12 Ma old (Hoorn 1993). Within the same region, the Apaporis Sand Unit has been dated to belong to the middle Miocene-early Pliocene (12-5 Ma) in age. Both sand formations are rich in quartz and were deposited by a now extinct river. This river drained a pre-Cambrian basement, which outcrops in some parts of the landscape, and are part of the south-west margin of the Guiana Shield (Hoorn 1994).

The Rio Tapiche basin has recently been found to concentrate the largest extension of white-sand archipelagos in the Peruvian Amazon (Stallard 2006). They are mostly poorly drained white-sand forests (hydromorphic soils) and extends towards the south to include edaphic savanna-like formations and extensive black water forests (*igapo* forests). Using relative dating from geological formations and sediments in an area northeast of Tapiche, Stallard (2006) has suggested that white-sand soils in this area date from the Pliocene (5-3 Ma) and are probably the product of fluvial deposition followed by weathering.

The region of Iquitos contains another collection of white-sand formations, with Arenosols situated on the hills and Podzols situated on the lower part of the terrain, ca. 140 m a.s.l. (Räsänen & Linna 1998). These sands were interpreted to have been deposited in a fluvial system by a paleo-river with a wide floodplain area. Alternatively they may have developed by strong podzolisation after deposition of quartz-rich fluvial sediments (Räsänen & Linna 1998). Supporting a fluvial deposition origin of these white-sands is the decreasing sand grain on the deposits, which resemble similar deposition of extant rivers in the area.

Geological and geomorphological studies in this area have established that the Iquitos white-sand formation was deposited on top of the Pebas Formation, which is dated from 18-10 Ma, suggesting that these sands cannot be older than 18 Ma. Roddaz, Baby, *et al.* (2005) further studied the same white-sand outcrops of the Iquitos area and concluded that they were deposited by a now extinct cratonic river after the Amazon system was created as such, and constrained its age to be 8-1 Ma. Preliminary cosmogenic dating results of a white-sand outcrop of this area suggest that some can be even younger, from the late Pleistocene (600-800 kyr) (M. Roddaz, pers. comm.).

In the Brazilian Amazon, north of Manaus, Horbe *et al.* (2004) studied a Ferralsol-Podzol system and using C^{14} radiocarbon dating estimated the age of the Podzol as 3,000 yrs. As a point of reference, in temperate regions, time of Podzol formation varies, with incipient podzolisation visible between 100 and 500 years, whereas mature Podzols develop between 1,000 – 6,000 years (Sauer *et al.* 2007).

On the other hand, white-sand fluvial terraces from the upper Rio Negro—which outcrops along the along the Vaupés, Tiquié, and Curicuriarí rivers—were found to be from the late Pleistocene (60-28 kys) (Latrubesse 2000). In the same area, Carneiro-Filho et al. (2002) interpreted some dunes as eolian in origin, a bit younger than the fluvial deposits, at 32,000-8,000 yrs. White-sands interpreted as eolian in origin were also reported by Teew & Rhodes (2004) for the Rio Branco-Rupununi savanna, with an estimated age of 7,000-5,000 yrs (Holocene).

Using a combination of satellite imagery, digital elevation models and field work, Rossetti et al. (2012) studied several paleo-channels in a vast area of the Brazilian Amazon, including one that may have been the origin of some white-sand soils in the Roraima region, northeast of Brazil. They determined that the *campinas* and open savannas in this area grow over an abandoned paleo-channel. This paleo-channel was left behind by fault activation in the area with subsequent filling by sandy sediments from surrounding Pre-Cambrian quartz-rich sandstones. The sandy soil-cover from this area is recent in age, c. 37-38 kys BP.

Finally, the coastal Guiana white-sand areas of the Berbice Formation were studied by Bleackley & Khan (1963). They interpreted that these sands were not deposited as such in these areas but instead developed by podzolisation of sandy-clay soils. The presences of transitional areas in which loss of iron and clay occur support their findings. It is assigned a Pleistocene age (c. 2 Mya) (Hammond 2005). Table 2 summarizes some examples of white-sand soils in the Amazon and Guiana region along with estimated ages, dating method used, and suggested white-sand formation process.

Table 2. Estimated ages of some Amazonian white-sand soils, ordered by decreasing age, and models of soil origin. Models: (i) product of deeply *in situ* weathering of quartzitic sandstones; (ii) fluvial deposits after paleo-channel abandonment, (iii) final product of on-going Ferralsol/Acrisol to Podzol transformation, (iv) deposited by eolian transport, and (v) outcrop exposure by regional tectonics (paleo-arches)

Site	**Age**	**Dating method**	**Soil process formation (model)**	**Locality (country)**	**Source**
Mariñame Sand Unit	23-12 Ma (early Miocene-middle Miocene)	Relative dating by stratigraphy	Fluvial deposits (ii)	Western Amazon (Colombia)	Hoorn *et al.* (1993); Hoorn *et al.* (2009)
Apaporis Sand Unit	12-5 Ma (middle Miocene-early Pliocene)	Relative dating by stratigraphy	Fluvial deposits (ii)	Western Amazon (Colombia)	Hoorn *et al.* (1993); Hoorn et al. (2009)
Iquitos white-sands	8-1 Ma	Relative dating by stratigraphy	Fluvial deposits (ii)	Iquitos (Peru)	Räsänen *et al.* 1998

Iquitos white-sands	8-6 Ma (late Miocene-Pliocene)	Relative dating by stratigraphy	Fluvial deposits (ii)	Iquitos (Peru)	Roddaz *et al.* 2005
Tapiche white-sands	5-3 Ma (Pliocene)	Relative dating by stratigraphy	Fluvial deposits or Podzolisation (ii, iii)	Rio Tapiche (Peru)	Stallard (2006)
Berbice Formation (Coastal Guyana)	c. 2.5 Ma (Pleistocene)	na	Ferralsol-Podzol transformation (podzolisation) (iii)	Guiana-Shield coastal	Bleackley & Khan (1963)
Iquitos white-sands	600 kyr-800 kry B.P. (mid-Pleistocene)	Cosmogenic dating	Fluvial deposits (ii)	Iquitos (Peru)	Roddaz & Regard (per. com.)
Tiquié Formation,	60 to 28 kyr B.P. (late Pleistocene)	C^{14} Radiocarbon dating	Fluvial deposits (ii)	Brazilian Amazon (Upper Rio Negro)	Latrubesse & Franzinelli (2005)

Upper Rio Negro paleo-dunes (00 35 N, 63 14 W)	32,000-8,000 yr B.P. (late Pleistocene-early Holocene)	Thermoluminiscence dating	Eolian deposits (iv)	Brazilian Amazon	Carneiro-Filho *et al.* (2002)
Viruá (Roraima)	36,607-38,161 yr B.P.	C^{14} Radiocarbon dating	Fluvial deposits	Brazilian Amazon	Rossetti *et al.* (2012)
Rio Branco-Rupununi Savanna	7,000-5,000 yr B.P. (middle Holocene)	Optically Stimulated Luminescence dating	Eolian deposits (iv)	Brazilian Amazon	Teeuw & Rhodes (2004)
Manaus white-sands/Brazil	3,000 yr B.P.	C^{14} Radiocarbon dating	Ferralsol-Podzol transformation (podzolisation) (iii)	Manaus (Brazil)	Horbe *et al.* (2004)
Jenaro-Herrera white-sands	NA	NA	Ferralsol-Podzol transformation (podzolisation) (iii)	Jenaro Herrera (Peru)	Veillon & Soria-Solano (1988)

In general, the Guiana Shield region contains both the oldest and the youngest white-sand soils (3,000 yrs to 23 Mya), whereas in the rest of Amazonia the age of these soils age ranged from 600,000 to 5 Mys. These age ranges have to be taken with caution since few absolute dates have been carried out in western Amazonian white-sands soil. Nevertheless, the current evidence indicates that these habitats ages is very heterogeneous perhaps reflecting their complex evolution and origins.

2.7. Conclusions

The Amazon basin has passed through different phases of development during which sedimentation, erosion and climatic processes have created the soil mantle over which evolutionary and ecological processes gave origin to its outstanding present day diversity. Within the basin, white-sand soils are more likely to be the result of multiple origins, depending on their peculiar geology, pedogenic development, and hydro-tectonic dynamism of the area in which they occur. This multiple origin of Amazonian white-sand soils is further inferred by their occurrence over a wide range of geo-morphological situations: as cover sands on interfluves, as terraces in uplands, and as former river beds or paleo-channels (Sombroek 1966, Ab'Saber 1982, Clapperton 1993, Horbe *et al.* 2004). Based on the reviewed geological and soil research studies in the Amazon and Guiana regions, white-sand soils in this region may have originated by least four processes: (i) the product of deep *in situ* weathering of quartzitic sandstones (Kubitzki 1989, Hammond 2005); (ii) deposition by eolian (wind) transport (Horbe *et al.* 2004); (iii) as fluvial deposits of paleo-channels (Klinge 1965, Hoorn 1994, Räsänen & Linna 1998, Roddaz, Baby, *et al.* 2005, Rossetti *et al.* 2012); and (iv) the final product of on-going Ferralsol/Acrisol to Podzol transformation (Lucas *et al.* 1984, Dubroeucq & Volkoff 1998, Lucas *et al.* 2012, Mendonça *et al.* 2014).

Current geological and soil studies in the western Amazon (Loreto, Peru) date white-sand soils from the early Pliocene to the late Quaternary (from 5 Ma to 600,000) which is well after the Pebas system disappeared (Wesselingh & Salo 2006). This strongly implies that the flora of these habitats, at least in the western Amazon south of Colombia, is of recent origin, receiving immigrants from pre-adapted lineages capable of coping with challenges of plant life on these extreme substrates. There are, however, at least 39 endemic species just on the white-sand of northern Peruvian Amazon (Pitman *et al.* 2013) which represent 24% of the total endemics for this region. If these habitats are of recent origin, white-sand endemics from the Amazon lowlands may have evolved relatively recently and may represent neo-endemics. On the other hand, the upper age limit in both estimated ages is based on the relative position of other sediment layers (relative dating by stratigraphy) and hence it is possible that these upper limits are overestimated. For example, cosmogenic dating of a white-sand outcrop from the Peruvian Amazon assigns it an age within 600,000-800,000 yrs (M. Roddaz, pers. comm.), which corresponds to the mid-Pleistocene.

Of the four processes suggested for the existence of these extremely poor-soils in the Amazon and Guiana regions, fluvial deposition by paleo-channels along structural highs on the terrain (i.e. the Iquitos Arch) may be the most likely source of some white-sand soils in the western Amazon, especially the ones occurring within the area of the Iquitos Arch influence. Erosion of in situ Palaeozoic or pre-Cambrian cratonic outcrops (e.g. tepuis, serranias) might be more prevalent in the areas where they are more common, the Guiana and Brazilian Shield region (e.g. Serra do Cachimbo) and some outliers at the margins of the Amazon like Serra do Moa, Sierra del Divisor, Cerro de Contamana, Cordillera del Condor. They might also have sourced extinct paleo-rivers which deposited their sandy sediments later covered by the younger Andean soils. Transformation of Ferralsol/Acrisol soils to Podzols may also be an important process for the origin of white sands, especially in the eastern Amazon and the Guiana Shield which contains relatively older clay soils compared to western Amazonia. In general, eolian activity may have been of minor importance for white-sand soil formation in the Amazon but with some importance in coastal areas of the Guiana and Brazilian Shields, nearby sandstone tepuis, and at the margin of northeast Amazonia. In these marginal regions, seasonal climatic conditions and millennial stable paleo-winds may have provided optimal conditions for the formation of paleo-dunes now fixed by savanna vegetation (Teeuw & Rhodes 2004).

Deposition of sandy soils on ancient paleo-channels, and progressive transformation from Ferralsol/Acrisol to Podzol do not have to be mutually exclusive to account for the origin of white sands in the lowlands of Amazonia. Fluvial deposition can occur first, depositing a mixture of sediments on a given terrain that further weathering can transform to Podzol by leaching of clay and other minerals. In cases where these terrain depressions and channel abandonments occur in relatively close proximity to sandy sources, like sandstones or tepui-like formations, these areas are readily filled up with white-sand soils (and do not need to pass through any transformation) as may have occurred during the Pleistocene/Holocene in the Viruá and Demini areas of northern Brazilian Amazon (Rossetti *et al.* 2012).

The presence of paleo-arches in general might have be important in creating edaphic heterogeneity by differential erosion rates on hilly areas and exposure of buried sediments. Regional tectonics through the effect of the Iquitos paleo-arch exerts an important effect on the exposure of sediments in a vast trench of the western Amazon (from the south of the Colombian Amazon to the northern Peruvian Amazon) (Hoorn 1994, Räsänen & Linna 1998, Roddaz, Baby, *et al.* 2005). The frequency and intensity of paleo-channel abandonment and sedimentation by local and regional tectonics during recent times, along with on-going podzolisation processes of sandy-clay soils may have increased the range of soil and habitat types in the Amazon basin on which plant lineages evolved. Taken together, these processes have been largely underappreciated thus far by the students of evolution, ecology and biogeography of the Amazon biota in relation to their importance for creating the variations in edaphic heterogeneity in these regions. All these factors, acting together in space and time, may have been an important force to create the current variation in soil and habitat heterogeneity currently observed in the Amazon and Guiana regions.

Chapter 3: Phytogeographic patterns and habitat specialization in western Amazonian white-sand forests

> "… it is scarcely necessary to add that many species of
> plants which grow down to the very coast in Guayana
> exist also in the Peruvian province of Maynas that is,
> at the eastern foot of the Andes"
> —R. Spruce (1908)

3.1. Introduction

Quartz-rich sandy soils are patchily distributed in the Amazon basin, embedded within the more widely distributed clayey red soils that house the archetypical species-rich *terra firme* forests (see chapter 2). These soils support a specialized vegetation type known as Amazonian white-sand forests in the botanical literature that occupy relatively large extensions in the Guiana Shield region, one of the oldest geological regions in northern South America (Hammond 2005). In Amazonia, however, they occur scattered patchily, like island-habitats within a matrix of upland rainforests, varying in size from a few to hundreds of hectares (Prance & Schubart 1978, Anderson 1981, Prance 1996).

There is a sharp physiognomic contrast when one crosses from a multi-layered cathedral-like *terra firme* forest to white-sand forests; a decline in forest stature, a burst in pole-like high stem density, and a relatively open canopy, with large amount of sunlight reaching into the understory (Coomes & Grubb 1996, García-Villacorta *et al.* 2003). Likewise, white-sand forests are substantially distinct floristically from the typical *terra firme* forest, with many local and regional habitat specialists and even endemic species (Anderson 1981, Prance 1996, Gentry 1986, Fine *et al.* 2010).

Given their distinctive structure and floristic composition, is not surprising that white-sand forests across the Amazon have received distinct local designations such as: *varillal*, *chamizal* (Peru, Colombia), *Amazon caatinga*, *campina*, *campinarana* (Brazil), *caatinga*, *bana* (Venezuela), *wallaba* forest, *muri bush* (Guyana, French Guiana, Surinam) (Richards 1941, Revilla 1974, Klinge *et al.* 1977, Cooper 1979, Anderson 1981).

Fundamental to the existence of these forests is the presence of sandy soils in a given region of the Amazon. A review of the pedological and geological evidence on the origin of these soils in this region has found that they may have at least four different origins: (i) the product of deep *in situ* weathering of quartzitic sandstones (Kubitzki 1989, Potter 1994, Hammond 2005); (ii) deposition by eolian transport (Ab'Saber 1982, Clapperton 1993, Horbe *et al.* 2004); (iii) as fluvial deposits of paleo-channels (Klinge 1965, Anderson 1981, Ab'Saber 1982, Hoorn 1994, Räsänen & Linna 1998, Roddaz, Viers, *et al.* 2005, Rossetti *et al.* 2012), (iv) the final product of on-going Ferralsol/Acrisol to Podzol transformation (Lucas *et al.* 1984, Dubroeucq & Volkoff 1998, Lucas *et al.* 2012, Mendonça *et al.* 2014) (see Chapter 2).

Briefly, the Precambrian Roraima Formation (ca. 1,600 Mys old) is a massive sandstone mountain deposited in a shallow marine, fluvial, deltaic, lacustrine, or epicontinental (areas of ocean overlying the continental shelf) environment (Sidder *et al.* 1995) which overlies the western part of the Guiana Shield region (Priem *et al.* 1973). These mountains were uplifted after the separation of South America from Africa was completed (ca. 100 Mya) followed by erosion and fragmentation that ended 90-70 Mya with the creation of table-like mountains (500-3,000 m height) known as "tepuis" (Briceño *et al.* 1990). For 85 million years, the interval after the breakup from Africa until the formation of the Andean mountains in the mid-Miocene, the drainage systems in South America were dominated by Guiana Shield sediments (Potter 1997). Enormous amounts of quartz-rich sandy sediments were deposited in what is the current coast of the Guiana Shield (Guyana, French Guiana, Surinam, Northern coastal Brazil) as well as its western fringe: the adjacent lowlands of the Solimões, Rio Negro, Japurá/Caquetá and Orinoco basins (Amazon regions of Brazil, Venezuela, and Colombia) (Kubitzki 1989, 1990).

A good starting point for beginning to understand the origin of a flora is by assessing how much of its current floristic composition is shared with other regions, including assessment of distributional patterns of individual species. Taxonomic revisions and local floristic studies in Amazonian white-sand forests have stressed the existence of plant species and genera disjunctly distributed between the Guiana Shield region and western Amazonian white-sand forests (e.g. Spruce 1908, Gentry & Ortiz 1993, Berry *et al.* 1995, Cortés & Franco 1997, Silveira 2003, Arbeláez & Duivenvoorden 2004, García-Villacorta & Hammel 2004, Struwe & Albert 2004, Fine *et al.* 2010). However, there has been no attempt so far to study species distribution and compositional patterns of these floras at the entire Amazon-Guiana scale. To shed light into the phytogeographic connections of western Amazon white-sand forests, I asked three main questions: 1) What are the distributional patterns of western Amazon white-sand species?; 2) Are white-sand forests of the western Amazon floristically more similar to nearby floras than to floras of the Guiana Shield region?; and 3) Are white-sand forests clearly-defined floristic units compared to other floras in the Amazon and Guiana Shield region?

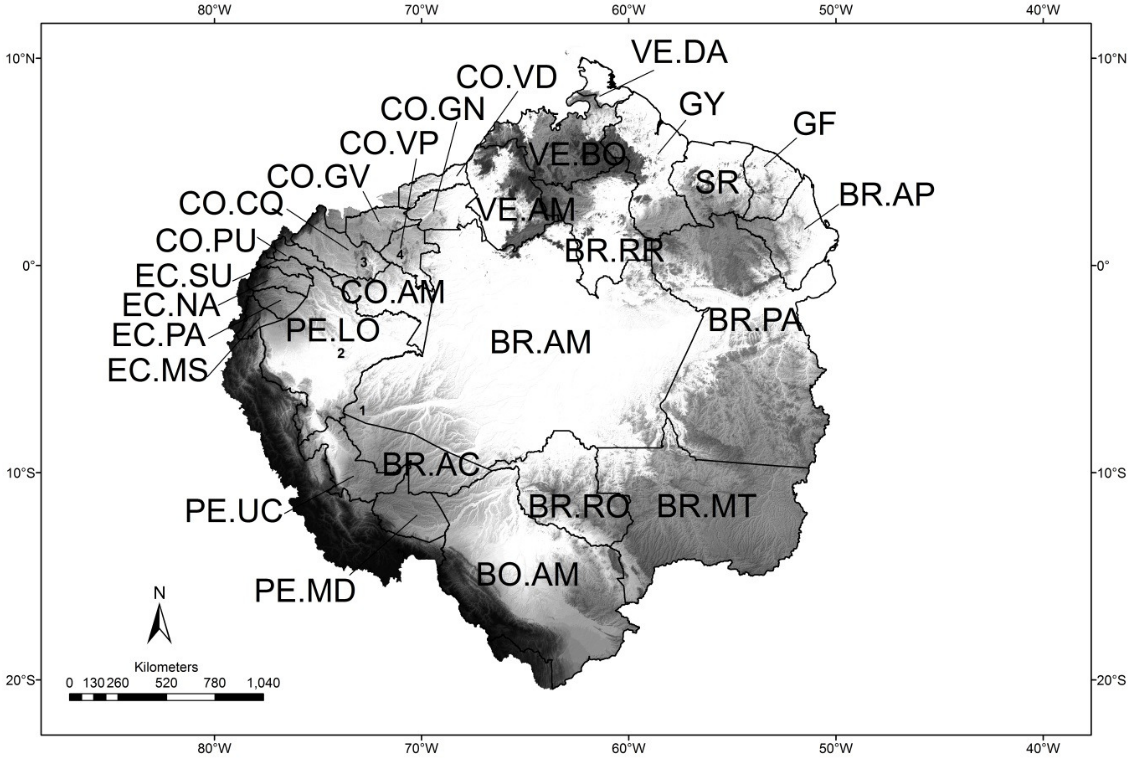
Because forests on white-sand soils are extensive in the Guiana Shield region I hypothesized that a high proportion of western Amazon white-sand species will occur within this region. Similarly, I predicted that floras from the western Amazon white-sand forests will be floristically closer to Guiana Shield floras compared to other floras in the Amazon. Given the position of white sand forests at one extreme of the soil gradient continuum I expected to find some floristic distinctiveness in them. Finally, given their patchy spatial distribution, I predicted that geographic distance between the studied white-sand forests will exert a significant influence on floristic similarity patterns among both non-white-sand forests and white-sand forests.

3.2. Methods

3.2.1. Study area

The study area encompasses the Amazon and Guiana Shield region (Figure 11). The border of the Amazon and Guiana regions was extracted from the Olson et al. (2002) ecoregions of the world, following closely Hammond (2005) and HYBAM's Amazon basin watershed limits (Seyler *et al.* 2009) respectively.

Figure 11. Map of Amazon-Guiana region with political division acronyms used in the floristic analysis. Numbers 1 to 4 indicate approximate locations of studied white-sand forests: 1 = acre.wsf.BR, 2 = lore.wsf.PE, 3 = caqu.wsf.CO, 4 = guai.wsf.CO. Acronyms in Table 7.



3.2.2. Data analysis

The study of phytogeographic patterns was carried out using two approaches. First, I conducted a "geographical affinity analysis" of western Amazonian white-sand species and calculated how much of the western Amazonian white-sand flora is shared with other regions at two geographical levels: biomes, and ecoregions. A second approach consisted of developing presence-absence floristic checklists for each political province in the Amazon-Guiana regions (27 provinces) to perform a "floristic similarity analysis" of species composition using hierarchical clustering and NMDS ordination (Non-Metric Multidimensional Scaling).

Both analytical approaches allow us to extract or visualize, albeit with different assumptions and methods, any floristic pattern inherent in a matrix of species versus sites (Keough & Quinn 2002, Legendre & Legendre 2012). Recovering similar floristic patterns by these different methods would reassure us that these patterns may reflect a real ecological phenomenon that exists in nature.

3.2.3. Dataset compilation

I compiled 27 province-level floristic lists from the botanical literature (Appendix I: Table AI 1: 1) for the entire Amazon and Guiana Shield region as well as four vascular plant checklists from the white-sand forests of Peru (Loreto), south-western Brazil (Acre), and Colombia (Caquetá, and Guainía) (Cortés *et al.* 1998, Arbeláez 2003, García-Villacorta *et al.* 2003, Silveira 2003, Cárdenas-Lopez 2007, Ferreira 2009, Fine *et al.* 2010). Although political unit definitions vary depending on the country (e.g. state in Brazil, department in Peru and Colombia) I use the name "provinces" throughout the chapter.

White-sand forests from Colombia (guai.wsf.CO, and caqu.wsf.CO), occur at the margin of the western Guiana Shield (Chapter 2) and previous studies have shown they have phytogeographic connections with this region (Cortés & Franco 1997, Cortés *et al.* 1998, Arbeláez 2003). In order to properly evaluate the phytogeographic relationship of western Amazon white-sand forests outside of the Guiana Shield region these Colombian white-sand datasets were not considered when performing the distributional analysis to avoid biasing the results in favour of a Guiana Shield connection. For similar reasons, species from all four white-sand forests were excluded from their respective provinces before performing the floristic analysis (i.e. white-sand areas are embedded geographically within provinces). In addition to a systematic method of taxonomic standardization of checklists (see below), voucher specimens of most of the species in the white-sand dataset were checked at the Missouri Botanical Garden herbarium (MO) to confirm identifications.

3.2.4. Biome and ecoregion affinities in western Amazon white-sand forests

To study the distributional patterns of white-sand taxa, I searched for specimens of each taxon with geographical coordinates from the Missouri Botanical Garden herbarium online database Tropicos. To investigate which proportion of this white sand flora was shared because of species habitat preferences, I classified each species in the white-sand dataset into one of three categories: white-sand specialist, poor-soil specialist, or habitat generalist. The assignment of species to each category was based on field knowledge of species habitat preferences supplemented by review of herbarium label descriptions citing the habitat where specimens were collected (e.g. white-sand forest, "*varillal*", "*campina forest*", "*campinarana*", "*suelo arenoso*", "*Amazon caatinga*", "*suelo de arenisca*"). For this study, white-sand specialists are defined as species occurring exclusively on white-sand soils, poor-soil specialists are species that can be found in both white-sand soils as well as other similar nutrient-poor soils, and generalist species refer to those occurring on white-sand soils, other nutrient-poor soils and any other habitats of the Neotropical region (e.g. clay-rich upland forests, flooded forests, swamp forests, montane forests, savanna, dry forests). The distributional analysis was done for the three groups separately (white-sand specialist, poor-soil specialist, and habitat generalist) as well as together (full dataset) at the level of species, exploring taxa shared at two biogeographical levels: biomes, and ecoregions. Delimitation of biomes and ecoregions in the analysis follows Olson *et al*. (2001).

3.2.5. Floristic relationships of western Amazon white-sand forests

Until very recently, plant taxonomic treatments for each country in the Amazon and the Guiana Shield region were not available. The recent publication of major taxonomic treatments has started to fill this gap. Despite differences in completeness, up-to-date plant checklists in each of these countries represent the best of our present botanical knowledge that can start to provide important contributions to our understanding of Neotropical plant diversity and biogeography.

To carry out the floristic relationship analysis, province-level plant checklists were compiled for each of the countries with territories in the Amazon and Guiana Shield region which include: Bolivia, Brazil, Colombia, Ecuador, Peru, Venezuela, Guyana, French Guiana, and Surinam (Figure 1). For developing this database the following taxonomic treatments were used: checklist of Peru (Brako & Zarucchi 1993, Tropicos-Peru 2013), checklist of Ecuador (Jorgensen & León-Yánez 1999, Tropicos-Ecuador 2013), checklist of Bolivia (Tropicos-Bolivia 2013), checklist of Brazil (Forzza *et al.* 2010a, b), checklist of the Colombian Amazon (SINCHI 2013), and checklist of the Guiana Shield region (Funk *et al.* 2007) (Appendix I: Table 11). These compiled checklists and floras were used to create a presence-absence matrix on which I conducted the study of floristic patterns. To restrict the analysis to lowland floras in the Amazon and Guiana region, some political provinces which are part of the Amazon based on a hydrographic criterion were left out of the analysis because they mainly include Andean regions that in a preliminary analysis clustered together and obscured patterns of lowland Amazon and Guiana floras.

3.2.6. Taxonomic standardization

To have a standardized database, all checklists and flora treatments were checked for synonyms and illegitimate names using the Taxonomic Name Resolution Service v3.0 (Boyle *et al.* 2013, TNRS 2013), which is an online tool that matches a plant checklist against agreed plant taxonomies. Only native vascular plants (gymnosperms, angiosperms, and ferns) were included in the database, and all cultivated, naturalized and hybrid species were excluded. The Missouri Botanical Garden Tropicos database was the chosen source for taxonomic matching. Intraspecific names (sub-species, varieties, forms) were maintained as much as possible in the database because they may represent taxonomic variation confined to white-sand habitats (e.g. white-sand specialists, cryptic undescribed species), and also because taxonomic revisions tend to find new species when revising taxa occurring in these habitats (e.g. Cuatrecasas 1961, Struwe & Albert 2004, Daly & Fine 2011). Therefore, including subspecific taxa may be useful for a better understanding of floristic patterns in relation to white-sand forests.

In very few cases, especially for recently described species that are still in the process of inclusion in taxonomic databases, resolving species names was done manually by consulting The Plant List website (The Plant List 2013). Prior to the analysis, plant families or genera with strictly aquatic habit, or not well represented in forested habitats, were excluded from the database, including: Elatinaceae, Nymphaeaceae, Pontederiaceae, Alismataceae, Salviniaceae, Onagraceae, Poaceae, Ceratophyllaceae, Cyperaceae, Hydrocharitaceae, Hydroleaceae, Mayacaceae, Potamogetonaceae, Typhaceae, Lentibularaceae, Cabombaceae, *Pista*, *Montrichardia*, and *Lemna* (Araceae). The taxonomy at the family level follows the Angiosperm Phylogeny Group III system (The Angiosperm Phylogeny Group 2009).

3.2.7. Dissimilarity index

A critical aspect in uncovering biogeographic patterns via cluster and ordination analysis is the choice of an appropriate dissimilarity index to construct the pairwise dissimilarity matrix of species composition between sites. Some indices are more appropriate for presence/absence data whereas others are affected by differences in species richness of the compared sites and hence do not represent true differences in species composition. Differences in species composition can be generated by two phenomena: one is the replacement of some species by others from site to site (spatial turnover), and the other occurs when the poorest site is a strict subset of the richest site (i.e. nestedness in Baselga 2012). The latter case is problematic because it means that even in the absence of species replacement differences in species richness can affect dissimilarity values between sites (Baselga 2012) and distort the resulting floristic pattern. Given the extreme difference in species richness between the floristic lists in the present dataset (Table 7), an approach was needed to account for these differences.

Lennon *et al.* (2001) recovered an original observation by Simpson (1943), who highlighted the need to account for the effect of species richness differences on dissimilarity values calculated when using the Sørensen dissimilarity index. To avoid this problem, and to focus the comparison in the species composition between sites instead of richness, I used here an adjusted-Sørensen dissimilarity index which uses the smallest diversity value of any two compared pair of sites in the denominator to decrease the influence that differences in local species richness may have on floristic similarity analyses (Lennon *et al.* 2001, Koleff & Gaston 2002, Koleff *et al.* 2003):

$$\beta_{sim} = 1 - \frac{a}{\min(b,c) + a}$$

Where *a* is the total number of species present in both sites; *b* is the number of species present in one site but not in the focal site; and *c* is the number of species that occur in the focal site but not in the other compared site (Koleff *et al.* 2003). The site with the lowest number of species (*b* or *c*) is used when making the calculations and represented by the term *min* in the formula. Although still not commonly applied in standard ecological analysis, the effect of species richness on the calculation of dissimilarity index between sites has been increasingly recognized as important in floristic and biogeographic analysis (Lennon *et al.* 2001, Pitman *et al.* 2005, Fine *et al.* 2010, Kreft & Jetz 2010).

3.2.8. Cluster analysis

Classical cluster analysis looks for discontinuities in a dataset, in this case floristic discontinuities expressed by species composition between sites. After constructing a dissimilarity matrix with the Sørensen-adjusted index, each site in the dataset was clustered hierarchically using five clustering algorithms: Ward, Average linkage (UPGMA), Single linkage, Complete linkage, and Neighbour joining algorithms. Each algorithm was then evaluated in their performance of representing the original dissimilarity matrix by calculating a cophenetic correlation index. Finally, I assessed cluster validity via multi-scale bootstrap resampling procedures, calculated the optimum number of clusters, and evaluated how well each site was classified in their respective cluster using the Silhouette plot method. All these methods are described in detail below.

3.2.8.1. Cluster algorithms

There are multitudes of cluster algorithms for different kinds of datasets and applications. Yet, evaluations to support favouring one algorithm over another are seldom carried out in ecological or biogeographical applications. A comparative analysis of three hierarchical agglomerative clustering algorithms, for instance, found

Ward's algorithm to be the most robust compared to average linkage (UPGMA) and complete linkage algorithms (Singh 2008). Other studies working with different datasets reached similar conclusions (Blashfield 1976, Hands & Everitt 1987, Kuiper & Fisher 1975, Ferreira & Hitchcock 2009). More recently, Kreft & Jetz (2010) evaluated the performance of nine clustering algorithms on different groups of organisms and taxonomic levels by correlating the distances on the resulting dendrograms with their original distance matrices. Contrary to the above studies they found that Average linkage (UPGMA) was the best performing cluster algorithm (Kreft & Jetz 2010). Rather than being prescriptive, they suggested that the appropriate clustering algorithm may differ from dataset to dataset, with geographical extent, and with the scale of the study.

Assessment of dendrograms is possible by correlating the original dissimilarity matrix with a cophenetic matrix obtained from a dendrogram (Sokal & Rohlf 1962). The algorithm with the highest Pearson cophenetic correlation value will be the one that best represents the original dissimilarity matrix in the topology of the resulting dendrogram (Sokal & Sneath 1963). I evaluated the performance of five clustering algorithms (Ward, Average linkage (UPGMA), Single linkage, Complete linkage, and Neighbour joining's algorithms) with the present dataset by first building a cophenetic matrix from each resulting cluster dendrogram and calculating their correlation with the original dissimilarity matrix obtained with the adjusted-Sørensen index.

Briefly, Single linkage clustering requires that at least one object in two different clusters have the shortest distance in order to be combined. In Complete linkage clustering one object joins a cluster only when it is linked to all the objects already member of that cluster. The goal of Average linkage clustering is to join objects based on the average dissimilarity of each cluster's member. The Ward's clustering algorithm tries to minimize at each agglomeration step the sum of the squared distance between objects and cluster centroids (Legendre & Legendre 2012). Unlike the above methods, which are agglomerative, the Neighbour joining algorithm starts with a dendrogram in which one node connects two objects that have the smallest branch lengths, and the other node is linked to all remaining objects. This process is repeated until the tree is completely dichotomous (Paradis *et al.* 2004).

To observe the main trends in the cophenetic correlations I performed a LOWESS non-parametric regression (Borcard *et al.* 2011), which uses a smoother parameter to fit a model to localized subsets of the dataset point by point.

3.2.10. Assessment of cluster stability

Several methods have been developed recently that allow a statistical assessment of cluster analysis which relies on permutation procedures. One of these calculates p-values via multiscale bootstrap resampling for each group and is implemented in the R statistical package *pvclust* (Suzuki & Shimodaira 2006, 2014). In this method, the number of species in each site is altered at each resampling scale and by doing this, changes the probability of each species being included in the permuted matrix (Suzuki & Shimodaira 2014). The resampling is done with replacement and the position of the sites is maintained as constant in the whole permutation procedure. The frequency of sites that matches the original cluster is counted and classical bootstrap permutation (BP), and approximately unbiased bootstrap p-values (AU) are scored at each node for each cluster of sites. A part of this method has been criticized by Dapporto *et al.* (2013) who demonstrated that when a high frequency of ties and zero-values is present in dissimilarity matrices, and the site order is kept unchanged, it yields strong support for clusters that are affected by the order of the sites in the original matrix. They implemented their solution in another R statistical package called *recluster*, which re-samples both species and sites to obtain a consensus tree and a value of the frequency of times a node is replicated after shuffling the dissimilarity matrix (Dapporto *et al.* 2013).

Given that I did not know beforehand the effect that row-order of sites may influence dendrogram topology due to the proportion of ties and zero-values generated by the dissimilarity matrices, I assessed cluster stability by using both *pvclust* and *recluster* methods. Both methods evaluate the consistency of recovering similar floristic patterns via resampling and randomization of the dataset and assign relative support value to clusters. The main value of both approaches is that instead of relying on a single cluster dendrogram for inferring biogeographic relationships (as typically done in biogeographic studies), support values obtained by sub-sampling the original dataset create alternative dendrograms which are used to calculate the level of concordance with the original dendrogram.

A consensus tree based on 100 trees that sampled the dissimilarity matrix with the sites in different order was obtained with the recluster function 'recluster.cons'. The frequency of times a node is replicated out of five bootstrap levels (levels = 5), obtained separately from 100 trees (t = 100), was calculated with the function 'recluster.boot'. One thousand trees (boot = 100) were sub-sampled at each level and only nodes that re-occurred in all 100 trees (p = 1) were accepted in the consensus tree.

The number of bootstrap replications in *pvclust* analysis was set to 100 at 10 different re-sampling levels. The AU p-values obtained by multi-scale bootstrap resampling is superior to the classical BP bootstrap values because it is a better approximation to unbiased p-values (Suzuki & Shimodaira 2006). The former is used here in the interpretation of *pvclust* results. For interpreting *recluster* I used the frequency of times a node is replicated after permuting the original matrix. Both analyses in *recluster* and *pvclust* were performed using the Average linkage clustering algorithm.

3.2.11. Assessment of the optimal number of clusters

After obtaining clusters of sites with different levels of floristic similarities it becomes necessary to decide how many clusters best represent the floristic patterns. I used a correlational matrix approach that correlates the original distance matrix and several binary dissimilarity matrices calculated from the original matrix at different cut levels (Borcard *et al.* 2011). The optimal number of clusters is the one where the Mantel correlation between the two matrices is the highest. In this analysis the Mantel correlation is in its simplest form and equivalent to the Pearson r correlation and was calculated as such.

3.2.12. Cluster membership evaluation

Once the optimal number of clusters has been determined I examined if the group membership of each site was appropriately assigned by using the Silhouette plot method (Rousseeuw 1987). This is especially useful to interpret some clusters with poor bootstrap support values obtained with the previous analyses. The Silhouette plot method uses a dissimilarity matrix and a specified number of k clusters to put each site into each group according to its average dissimilarity in relation to all other sites of the cluster to which it belongs. It computes a Silhouette width score (s) for each site or object.

Sites with large Silhouette width values (towards 1) are well clustered, sites with small values (around zero) means that the site lies between two groups, and sites with negative values are probably in the wrong cluster and would be better assigned to a neighbouring cluster. Silhouette plots only depend on the cluster partition of the objects and are independent of the clustering algorithm used to construct it (Rousseeuw 1987). Comparing the individual and average Silhouette score widths can help in the interpretation and validation of the clustering result. As determined in the previous analysis I used five clusters as the optimum number of groups on which I ran the membership evaluation. The s score for each cluster element i is calculated with the formula:

$$s(i) = \frac{b(i) - a(i)}{max\,\{a(i), b(i)\}}$$

Where $a(i)$ is the average dissimilarity of an element i with all other data in the same cluster, and $b(i)$ is the lowest average dissimilarity of element i to any other cluster in which i is not a member. A lower $a(i)$ value indicates a good assignment of the object to the cluster. The average $s(i)$ over the entire dataset is a measure of how well the data have been clustered.

3.2.13. Ordination

As a complement to the floristic patterns studied by the clustering analysis I performed Non-metric Multidimensional Scaling (NMDS) which extracts the main trends of the floristic composition among sites by summarizing it in a few orthogonal (independent) axes (Minchin 1987, Borcard *et al.* 2011). The goal of the iteration procedure in the NMDS ordination analysis is to find the lowest possible stress between the original distances and the distances in the ordination space. This means that if a given pair of sites has a lower similarity value than some other pair, then the first pair of sites will be closer than the other pair of sites in the NMDS ordination space.

NMDS analysis is done by first specifying the number of axes (dimensions) to be sought and constructing an initial configuration of the objects (sites) in these dimensions. The initial configuration of the sites starts usually at random and from then an iterative process tries to position the sites in the number of specified dimensions in a way that the original distances between sites in the dissimilarity matrix are monotonic to the distances in the reduced ordination space (Borcard *et al.* 2011). Fitting a monotonic regression step line on a scatterplot of the resultant ordination distances versus the original dissimilarity distances is known as a Sheppard diagram and provides a measurement of the goodness of fit of this iteration. The fitting procedure measure a stress function (“badness of fit”) that goes from 0 to 1 (a stress value ≥0.20 indicates a poor NMDS analysis (Kruskal 1964)).

I used the R package *vegan* (Oksanen *et al.* 2015) which implements NMDS as recommended by Minchin (1987) using the function *metaMDS* with different random start configurations and a final scaling of the results, with the function *postMDS*, along the first dimension for a better interpretation. To avoid reaching an unstable solution where a local optimum of stress is found even though there is still a lower stress (global optimum) I ran the analysis from different random spatial configurations up to 500 times. Convergence to the same stress value from these random spatial configurations can give a hint that it reached a global optimum. The dissimilarity matrix for the NMDS analysis was constructed using the adjusted-Sørensen dissimilarity index.

3.2.14. Effect of distance on white-sand floristic patterns

To test whether geographical distance between the studied floras had an influence on the floristic patterns recovered by the ordination and cluster analysis, I performed a Mantel test (Mantel 1967, Rossi 1996, Dutilleul *et al.* 2000, Legendre & Legendre 2012). A Mantel test calculates the correlation between two distance matrices to test the null hypothesis that the geographic and floristic distances between pair of sites are not correlated (i.e. are sites closer to each other also floristically closer and vice versa?). The correlation value ranges from -1 (negative correlation) to 1 (positive correlation). Because the elements from each matrix are not independent of each other, the significance of the correlation is estimated by permuting the floristic matrix a large number of times to calculate new correlation values creating as a result a statistical distribution against which the original *r* correlation is compared (Mantel 1967, Legendre & Legendre 2012). To create the distance matrix I extracted the geographical coordinates of each province by using its polygon centroid in a GIS that were then used to calculate geographical (Euclidean) distances between floras. I ran 999 permutations on the floristic dissimilarity matrix at a significance p-value of 0.05.

All the analyses described above were done in the statistical program R (R Core Team 2015) using the packages *vegan* (Oksanen *et al.* 2015), *cluster* (Maechler *et al.* 2015), *recluster* (Dapporto *et al.* 2013), *ape* (Paradis *et al.* 2014), and *pvclust* (Suzuki & Shimodaira 2006).

3.3. Results

3.3.1. Patterns in habitat specialization

Overall, a total of 1,180 vascular plant species comprising 133 families, and 491 genera were compiled from four western Amazon white-sand forest sites: Colombian white-sand forests (caqu.wsf.CO, and guai.wsf.CO), Peruvian white-sand forests (lore.wsf.PE), and western Brazil white-sand forests (acre.wsf.BR). The species distributional dataset resulted in 69,986 unique plant records representing all these species. Of the total 69,986 records in the dataset 74% (51,790 records) corresponded to “habitat generalist” species, 21% to “poor-soil specialists” (14,723 records), and 5% to “white-sand specialists” (3,473 records). In terms of species, 43% of the total vascular flora occurring on white-sand forests was found to be habitat generalist, 34% poor-soil specialist, and 23% white-sand specialist. Table 3 summarizes the richness of families, genera, and species found in the three designated habitat preference categories.

Table 3. Summary statistics and ecological preferences of 1,180 species found in four western Amazonia white-sand forests.

Ecological preference	**No. families**	**No. genera**	**No. species (%)**	**Records**
habitat generalist	103	295	509 (43)	51,790
poor-soil specialist	89	208	406 (34)	14,723
white-sand specialist	65	160	277 (23)	3,473
Total general	133	491	1,180 (100)	69,986

3.3.2. Distribution of species in biomes

Of the total number of vascular plant species found in the white-sand forests of the western Amazon, two biomes outside of wet and moist forests had the highest number of shared species: Tropical and Subtropical Grasslands, Savannas and Shrublands (48%), and Tropical and Subtropical Dry Broadleaf Forests (34%) (Table 4).

Table 4. Percent of families, genera, and species distribution found in each biome using the total dataset

Biome code	Biome name	No. families	No. genera	No. species (%)	Records
1	Tropical and Subtropical Moist Broadleaf Forests	133	490	1,180 (100)	5,9267
2	Tropical and Subtropical Dry Broadleaf Forests	104	250	403 (34)	3,848
3	Tropical and Subtropical Coniferous Forests	66	104	128 (11)	1,671
4	Temperate Broadleaf and Mixed Forests	3	3	3 (0)	6
5	Temperate Conifer Forests	8	8	8 (1)	44
7	Tropical and Subtropical Grasslands, Savannas and Shrublands	105	298	570 (48)	3,728

8	Temperate Grasslands, Savannas and Shrublands	1	1	1(0)	1
9	Flooded Grasslands and Savannas	36	48	51 (4)	80
10	Montane Grasslands and Shrublands	53	89	111 (9)	168
12	Mediterranean Forests, Woodlands and Scrub	1	1	1 (0)	1
13	Deserts and Xeric Shrublands	66	113	152 (13)	378
14	Mangroves	81	153	207 (18)	794
Total general		133	491	1,180 (100)	69,986

When restricting the analysis to the white-sand specialist dataset, the largest proportion of species was shared with the Tropical and Subtropical Grasslands, Savannas and Shrublands (28%) (Table 5). However, the number of species shared with Tropical and Subtropical Dry Broadleaf Forests dropped to only 4% (Table 5).

Table 5. Percent of families, genera, and species of white-sand specialists found in each biome using only the white-sand specialist dataset.

Biome code	**Biome name**	**No. families**	**No. genera**	**No. species (%)**	**Records**
1	Tropical and Subtropical Moist Broadleaf Forests	65	160	277 (100)	3180
2	Tropical and Subtropical Dry Broadleaf Forests	8	9	11 (4)	17
7	Tropical and Subtropical Grasslands, Savannas and Shrublands	37	60	79 (29)	267
9	Flooded Grasslands and Savannas	1	1	1 (0)	1
13	Deserts and Xeric Shrublands	1	1	1 (0)	1

14	Mangroves	4	4	4 (1)	7
Total general		65	160	277 (100)	3473

3.3.3. Distribution patterns in ecoregions

White-sand forests of the western Amazon had a large proportion of their species occurring within ecoregions of the Guiana Shield area. When using the white-sand specialists from the four white-sand forests, 88% of the total (247 white-sand specialists species out of 279 species) occur within the limits of the Guiana Shield region with the remaining being endemics to the western Amazon. When confining the analysis to white-sand forests outside of the Guiana Shield region (acre.wsf.BR (Brazil), lore.wsf.PE (Peru)), 59% of white-sand specialist species were found to be distributed in the Guiana Shield while the rest (41%) would represent endemics of the western Amazon. When looking at which ecoregion had more than 10% of western Amazon white-sand specialists, the majority (seven to eight out of ten) were ecoregions from the Guiana Shield region.

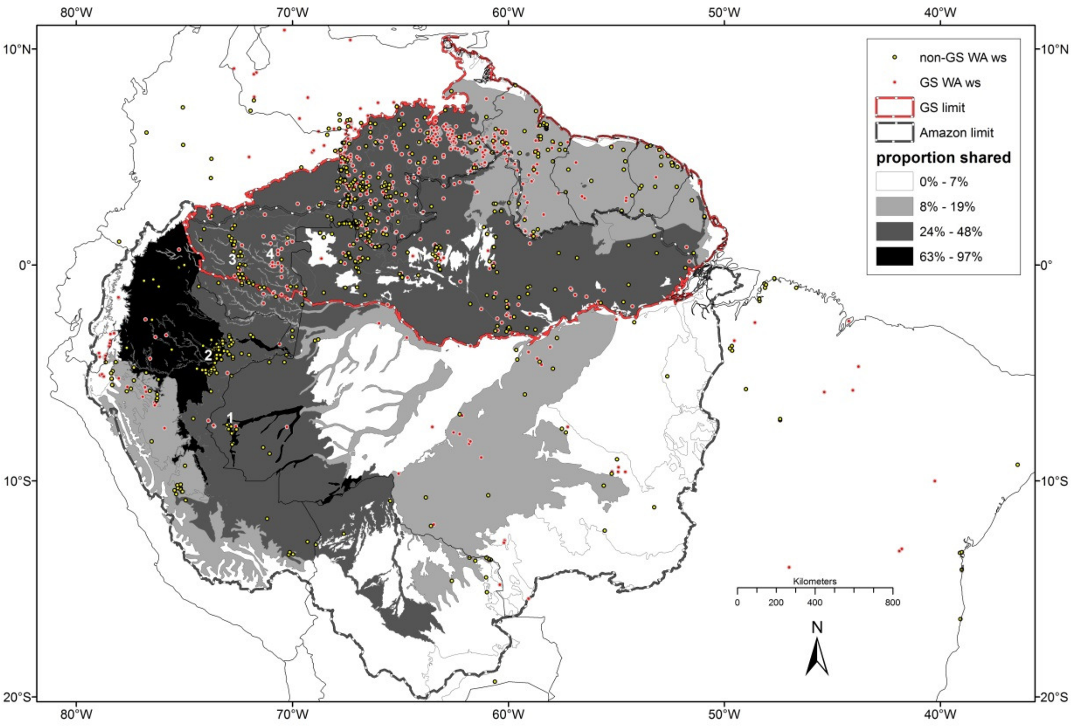
There were differences in the ecoregion that shared most of the species depending on the inclusion of white-sand forests of Colombia (caqu.wsf.CO, guai.wsf.CO). In general, when using only the non-Guiana Shield white-sand forests (acre.wsf.BR, lore.wsf.PE), the proportion of species shared with different Guiana Shield ecoregions dropped. The three ecoregions from the Guiana Shield with the highest percentage of species also distributed in the western Amazon were: Caquetá Moist Forests (69-30%), Guayanan Highlands Moist Forests (51-33%), Negro-Branco Moist Forests (49-43%). Table 12, and 13 (Appendix I) list statistics for each ecoregion and white-sand species representation.

Table 6. Ecoregions with at least 20% of white-sand specialists using the (a) whole white-sand specialist dataset compared to using only the (b) non-Guiana Shield white-sand dataset. Note changes in the proportions and ecoregions according to the dataset used.

a) **Whole white-sand dataset:** caqu.wsf.CO (Colombia), guai.wsf.CO (Colombia), acre.wsf.BR (Brazil), lore.wsf.PE (Peru)			b) **non-Guiana Shield white-sand dataset:** acre.wsf.BR (Brazil), lore.wsf.PE (Peru)		
Ecoregions	**No. species**	**% species**	**Ecoregions**	**No. species**	**% species**
Caquetá moist forests	191	69%	Iquitos varzea	86	97%
Guayanan Highlands moist forests	142	51%	Napo moist forests	56	63%
Negro-Branco moist forests	137	49%	Southwest Amazon moist forests	43	48%
Iquitos varzea	95	34%	Negro-Branco moist forests	38	43%
Tepuis	93	34%	Guayanan Highlands moist forests	29	33%

Japurá-Solimoes-Negro moist forests	64	23%	Caquetá moist forests	27	30%
Guianan moist forests	61	22%	Japurá-Solimoes-Negro moist forests	25	28%
Napo moist forests	59	21%	Uatuma-Trombetas moist forests	25	28%
Uatuma-Trombetas moist forests	56	20%	Solimoes-Japurá moist forest	22	25%
Solimoes-Japurá moist forest	55	20%	Tepuis	21	24%

Figure 12. Proportion of western Amazon white-sand specialists shared among different ecoregions within Amazonia. White sand areas: (1) acre.wsf.BR (Brazil), (2) lore.wsf.PE (Peru), (3) caqu.wsf.CO (Colombia), (4) guai.wsf.CO (Colombia). 1 and 2 = non-Guiana-Shield western Amazon white-sand areas, 3 and 4 = GuianaShield western Amazon white-sand areas. GS limit = Guiana Shield limit.



3.3.4. Floristic similarity analysis

3.3.4.1. Floristic dataset

A total of 31 floristic datasets at the level of provinces were compiled which included four western Amazon white-sand forests (Figure 11; Table 7). There were a total of 26,887 vascular plant species in the floristic dataset grouped in 2,865 genera, and 268 APG III families. Table 5 gives a summary of the area and number of vascular plant species found at each evaluated site. The number of species in the white-sand forest dataset ranged from 363 (acre.wsf.BR) to 955 species (guai.wsf.CO). The number of species in the province checklists ranged from 607 (Vichada, Colombia) to 8,355 species (Amazonas, Brazil).

Table 7. Number of vascular plant species found at each study site ordered by ascending number of species. Studied western Amazon white-sand forests in bold: acre.wsf.BR (Brazil), caqu.wsf.CO (Colombia), lore.wsf.PE (Peru), guai.wsf.CO (Colombia).

Site	**Province**	**Area (km^2)**	**Country**	**No. spp.**
acre.wsf.BR	Acre	-	Brazil	363
CO.VD	Vichada	38734.93	Colombia	607
caqu.wsf.CO	Caquetá	-	Colombia	657
lore.wsf.PE	Loreto	-	Peru	731
guai.wsf.CO	Guainía	-	Colombia	955
PE.UC	Ucayali	105078.38	Peru	1,148
CO.GN	Guainía	68819.14	Colombia	1,289
CO.VP	Vaupés	53242.63	Colombia	1,738
VE.DA	Delta Amacuro	38230.4	Venezuela	1,765

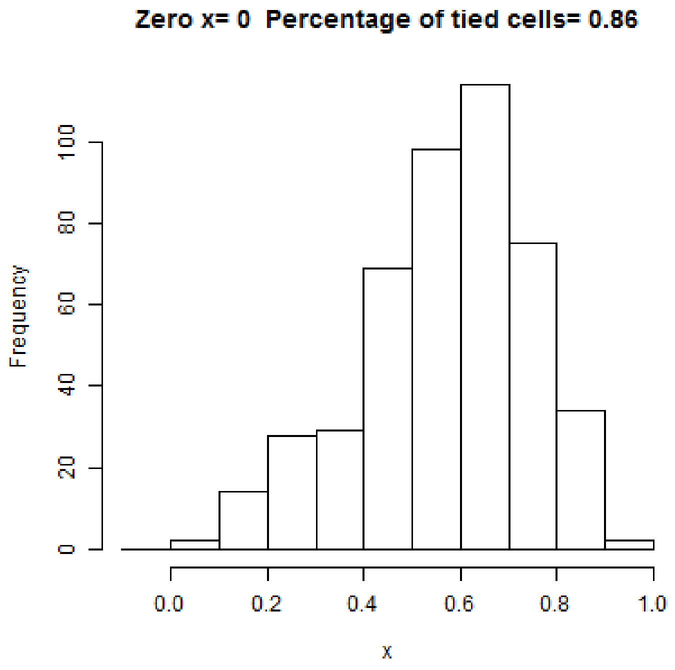
CO.GV	Guaviare	55570.16	Colombia	1,769
EC.SU	Sucumbios	18041.41	Ecuador	1,959
PE.MD	Madre de Dios	84420.81	Peru	2,088
BR.AP	Amapá	141105.57	Brazil	2,523
BR.RR	Roraima	224384.08	Brazil	2,688
BR.RO	Rondonia	236376.67	Brazil	2,882
CO.CQ	Caquetá	90029.75	Colombia	3,021
EC.PA	Pastaza	29723.82	Ecuador	3,154
BR.MT	Mato Grosso	599681.47	Brazil	3,247
EC.MS	Morona-Santiago	24055.22	Ecuador	3,384
CO.AM	Amazonas	107462.42	Colombia	3431
BR.AC	Acre	152729.51	Brazil	4,214
SR	Surinam	146011.49	Surinam	4,886
GF	French Guiana	83014.98	French Guiana	5,166
PE.LO	Loreto	375550.2	Perú	5,271
BO.AM	Amazon	681909.86	Bolivia	5,378

	region			
EC.NA	Napo	33833.15	Ecuador	5,765
BR.PA	Pará	892481.47	Brazil	6,098
GY	Guyana	209549.47	Guyana	6,938
VE.BO	Bolivar	193997.81	Venezuela	6,941
VE.AM	Amazonas	179579.86	Venezuela	7,146
BR.AM	Amazonas	1570659.01	Brazil	8,355

3.3.4.2. Cluster analysis

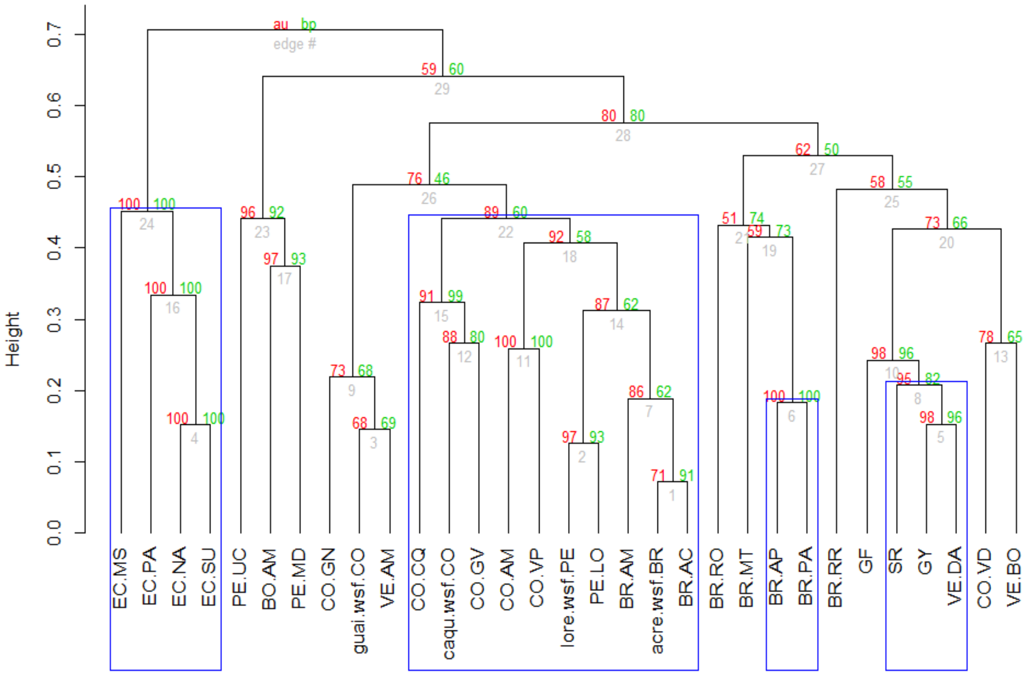
The proportion of tied values in the dissimilarity matrix constructed with the Sørensen-adjusted index was very low (0.86 %) with no zero values (Figure 13).

Figure 13. Frequency distribution of dissimilary values present in the species per site dissimilarity matrix built using the adjusted-Sørensen index.



Cluster topologies created by both *recluster* and *pvclust* differed in the proportion of support value given to each node of the dendrogram: *recluster* analysis gave 100% bootstrap values to all recovered nodes at all levels of analysis (Appendix I: Figure 30) whereas *pvclust* assigned a more conservative AU support value that ranged from 50 to 100% (Figure 14). Given that *recluster* assigned to all nodes 100% support, and to err on the side of caution, further discussion and interpretation will be based only on the results from *pvclust*.

Figure 14. Cluster analysis of floristic checklists based on Multi-scale bootstrap results from *pvclust* with Average linkage as clustering algorithm. AU bootstrap p-values at each node (left). Standard bootstrap probability (BP) to the right (right). Cluster numbers in grey. Dashed rectangles enclose clusters with AU support p-values ≥ 85. Western Amazon white-sand forests: acre.wsf.BR (Brazil), caqu.wsf.CO (Colombia), lore.wsf.PE (Peru), guai.wsf.CO (Colombia).



The analysis of cophenetic correlation among the five algorithms ranged from 0.47 to 0.83 (Figure 31: in Appendix I). The best performing clustering algorithm was Neighbour joining with an r cophenetic correlation of 0.83 followed by Average Linkage with r = 0.70, and Complete Linkage clustering (r = 0.63). The Ward clustering algorithm had the second lowest cophenetic correlation (r = 0.58) after the Single linkage clustering algorithm (r = 0.47). Hereafter I only discuss the biogeographical patterns recovered by the Neighbour joining and Average linkage (UPGMA) algorithms.

3.3.4.3. Neighbour joining vs. Average linkage floristic patterns

Overall, the cluster analysis using the two best performing algorithms (Neighbour Joining, and Average linkage) recovered similar floristic clusters with respect to western Amazonian white-sand forests (Figure 14; Appendix I: Figure 31). Peruvian (lore.wsf.PE) and western Brazilian (acre.wsf.BR) white-sand forests were joined in the same floristic group by both algorithms along with the floras of Acre (BR.AC), Amazonas (BR.AM), and Loreto (PE.LO). Colombian white-sand forests (guai.wsf.CO, and caqu.wsf.CO) on the other hand were floristically distinct and placed in their own clusters by both Neighbour joining and Average linkage algorithms. Both algorithms, however, showed that caque.wsf.CO was closer floristically to other Colombian floras in the area (CO.GV, CO.CQ, CO.AM, CO.VP), whereas guai.wsf.CO was most similar floristically to the floras of Vichada (CO.VD), Guainía (CO.GN), and Amazonas in Venezuela (VE.AM).

The Neighbour joining algorithm clustered the northern Peruvian Amazon flora (PE.LO) with the floras of the southern Peruvian Amazon (Ucayali (PE.UC), Madre de Dios (PE.MD)) and the Amazonas province of Bolivia (BO.AM) without including the Peruvian white-sand forests (lore.wsf.PE) (Appendix: Figure 32). In contrast to this result, Average linkage clustered the PE.LO flora with the Peruvian white-sand flora (lore.wsf.PE) located in the same region (AU p-value = 97) (Figure 14).

Finally, the white-sand forests of Caquetá (caqu.wsf.CO) were clustered with the flora of Guaviare (CO.GV) by both the Average linkage and the Neighbour joining algorithms, only differing in that Neighbour joining put this cluster in a different agglomeration, apart from the other three western Amazonian white-sand forests (Appendix I: Figure 32), which remained in the same cluster region defined by Average linkage clustering (Figure 14).

In a wider geographical context, white-sand forests of Peru (lore.wsf.PE) and western Brazil (acre.wsf.BR) are more closely related floristically to the white-sand forests of Colombia (guai.wsf.CO, and caqu.wsf.CO) than to forests of the core Guiana Shield area: VE.DA, GF, SU, GY, VE.BO, BR.RR (Figure 14). The only exception may be the forests of the Brazilian province of Amazonas (BR.AM), which in the cluster analysis using the Average linkage clustered with the forests of Acre (BR.AC) including the white-sand forests of this region (acre.wsf.BR) (Figure 5). In the Neighbour Joining clustering, the flora of the Amazonas province of Brazil grouped with the flora of Rondonia (BR.RO), apart from western Amazon white-sand forests (Appendix I: Figure 32).

3.3.4.4. Cluster bootstrap support values

Relatively high levels of unbiased bootstrap support values (AU) were found by the *pvclust* randomization procedure for all clusters with white-sand forests sites, which suggest that these clusters are well supported by the analysed data (Figure 14). In particular, the cluster grouping the four western Amazonian white-sand floras along with other non-white-sand floras had an AU pv-value of 76 (Figure 14). It is, however, clear from the *pvclust* analysis that guai.wsf.CO is nested within two floras more representative of the western lowlands of the Guiana Shield area (CO.GN, and VE.AM (AU p-value = 73)) than to the other three western Amazonian white-sand sites.

A first division of the dendrogram generated by Average linkage occurs at approximately 0.70 where all Ecuadorian western Amazon floras clustered with a very high AU p-value = 100. A second division occurs at 0.64 height with two big agglomerations of sites, one containing only western Amazon floras (PE.UC, BO.AM, PE.MD), and another big cluster with a mix of white-sand forests and other floras of the Amazon-Guiana regions. At 0.57 of dendrogram height, all south-western Amazon floras form a single group with 96% AU bootstrap support value.

At 0.52 dendrogram height, all western Amazon white-sand forests are clustered in the same group, and always mixed with other floras within the same province, with AU p-value = 76. At the same height, a second group clustered sites representative of the Guiana (GF, SU, GY, VE.BO, VE.DA, CO.VD) and Brazilian Shield regions (BR.RO, BR.AP, BR.PA, BR.MT, BR.RR).

At approximately 0.48 of dendrogram height, four different clusters are formed: one containing guai.wsf.CO along with CO.GN, and VE.AM (AU P-value = 73), another one containing all other three western Amazon white-sand sites (caqu.wsf.CO, lore.wsf.PE, acre.wsf.BR) with mostly Colombian floras (CO.CQ, CO.GV, CO.AM, CO.VP) (AU p-value = 89), a third cluster with Brazilian shield floras (BR.RO, BR.MT, BR.AP, BR.PA) (AU p-value = 51), and a final cluster containing Guiana Shield sites (BR.RR, GF, SR, GY, VE.DA, CO.VD, VE.BO) (AU p-value = 58). At a dendrogram height of 0.44, the white-sand forest of Caquetá (caqu.wsf.CO) is grouped only with Caquetá (CO.CQ), and Vaupés (CO.VP) (AU p-value = 91).

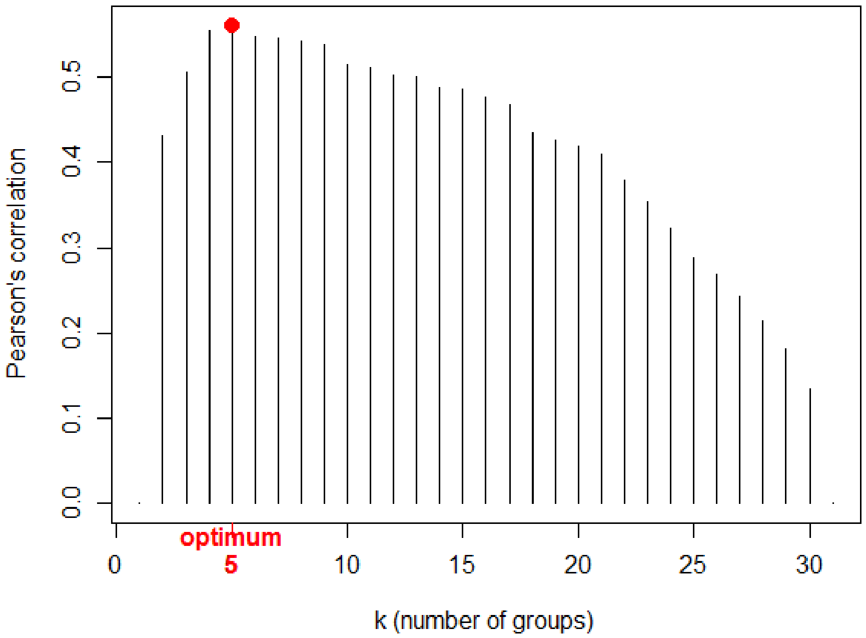
At this same height of 0.44, the white-sand forest of Peru (lore.wsf.PE), and western Brazil (acre.wsf.BR) form a single cluster along with the floras of Amazonas Colombia (CO.AM), Vaupés (CO.VP), the northern Peruvian Amazon (PE.LO), Amazonas Brazil (BR.AM), and the flora of the Brazilian province of Acre (BR.AC) (AU p-value = 87). At 0.31 dendrogram height, caqu.wsf.CO only clusters with the flora of Guaviare (CO.GV) (AU p-value = 80), and lore.wsf.PE clusters only with the flora of Loreto (PE.LO) (AU p-value = 97). At the same height, the white-sand forests of western Brazil (acre.wsf.BR) form a cluster with BR.AM, and BR.AC (AU p-value = 86). Finally, at 0.19 dendrogram height, Guainía white-sand forests (guai.wsf.CO) is clustered only with the flora of the Amazonas province of Venezuela (VE.AM), whereas Acre white-sand forests (acre.wsf.BR) is clustered only with the flora of Acre (BR.AC) (Figure 14).

The standard error of the majority AU bootstrap values in *pvclust* was close to 0.1 or below (Figure 14) which gives confidence that the existence of these phytogeographic clusters is supported by data. Only clusters 1 (formed by acre.wsf.BR and Acre) and 15 (formed by Caquetá's white-sand forests (caqu.wsf.CO) with Caquetá (CO.CQ) and Guaviare (CO.GV)) had the highest standard errors in the bootstrap procedure. The observed AU p-values for both cluster 1 and 15 however, fell within their expected ranges and provide confidence of their existence (Appendix I: Table 14).

3.3.4.5. Optimal number of clusters

The optimal number of clusters as defined by the highest Mantel (Pearson) correlation between the original dissimilarity matrix and pre-defined binary dissimilarity matrices cut at various *k* levels was found to be five (Figure 15).

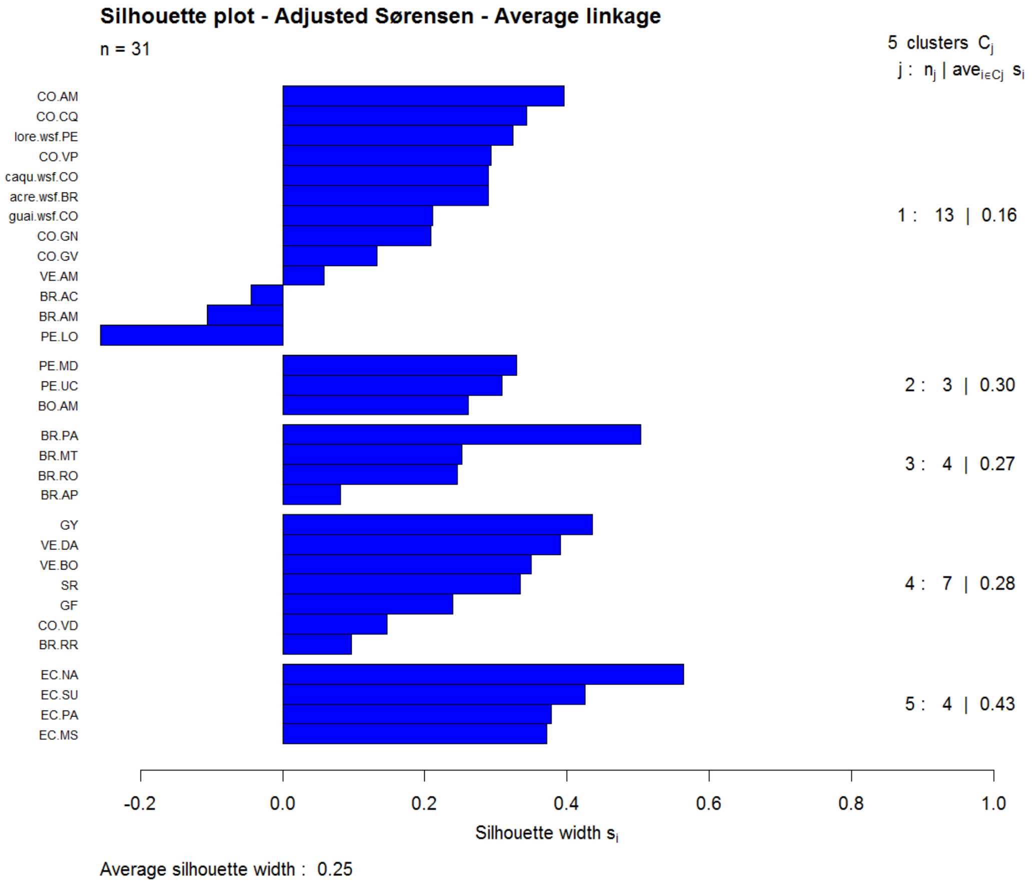
Figure 15. Matrix correlations between the original distance matrix and binary dissimilarity matrices computed from the dendrogram segmented at various *k* levels.



3.3.4.6. Cluster membership evaluation

The cluster membership evaluation confirmed previous results from *recluster* and *pvclust* in which all western Amazonian white-sand forests were agglomerated within the same cluster along with some floras of the Colombian Amazon, Venezuela, and Brazil (Figure 16). According to this analysis, three sites, BR.AC, BRA.AM, PE.LO, were misclassified within cluster 1 as interpreted by their negative Silhouette width values (Appendix I: Table 15).

Figure 16. Silhouette plot of the 31 analysed floras from the Amazon-Guiana regions. Negative Silhouette values indicate misclassified sites. BR.AC, and PE.LO would be better placed in cluster 2. BR.AM would be better placed in cluster 4. j = cluster number, n_j = number of sites in cluster j. Average Silhouette values per cluster to the right.

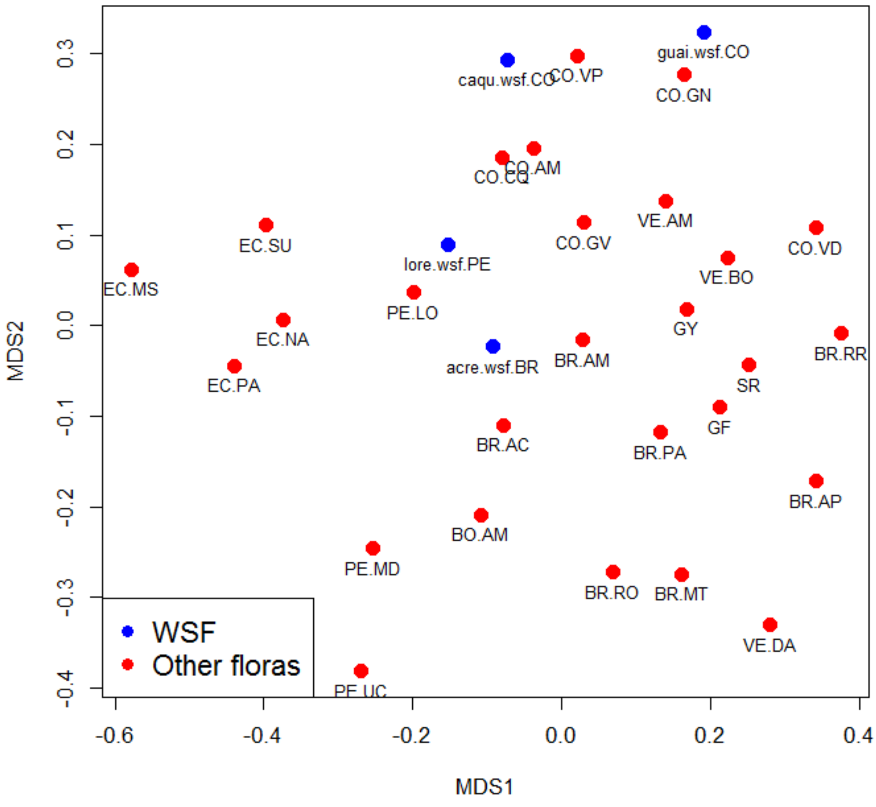


Both BR.AC and PE.LO may be better placed in the neighbour cluster 2, along with most western Amazon floras (PE.MD, PE.UC, BO.AM). The misclassified flora of Amazonas Brazil (BR.AM) may be better placed in cluster 3, along with the Brazilian Shield floras of Pará (BR.PA), Mato Grosso (BR.MG), Rondonia (BR.RO), and Amapá (BR.AP).

3.3.4.7. Ordination

The NMDS ordination analysis recovered similar phytogeographic patterns to cluster analysis results as interpreted by the relative distances between floras and white-sand forests portrayed by this analysis in the ordination space (Figure 17).

Figure 17. Relationships of western Amazon white-sand forests with provinces (political units) in the Amazon and Guiana regions as represented by non-metric Multidimensional Scaling (NMDS) ordination. WSF = western Amazon white-sand forests. Province names as in Table 6.



In this analysis, all four western Amazonian white-sand floras were relatively closer to each other and more similar to Colombian floras compared to other floras in the Amazon-Guiana region. Furthermore, these white-sand forests were more similar floristically to other Colombian floras than to other floras in the Guianan-Amazon region (Figure 17).

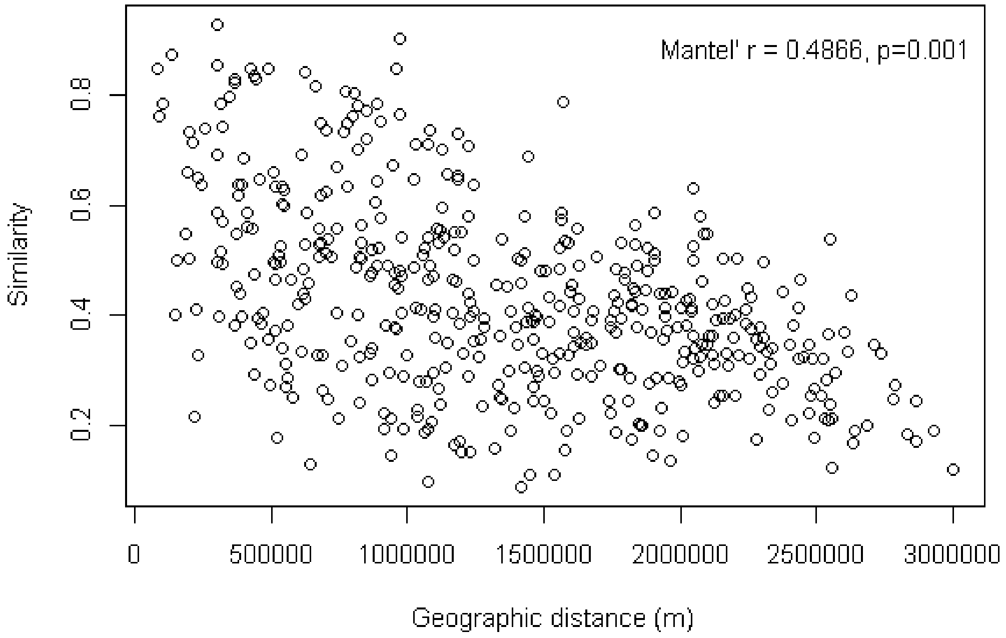
White-sand forests of Acre (acre.wsf.BR), Loreto (lore.wsf.PE), and Caquetá (caqu.wsf.CO) are closer to each other floristically than they are to the white-sand forests of Guainía (guai.wsf.CO). These results mirror similar patterns found by Neighbour joining and Average linkage clustering, providing further confidence in the phytogeographical patterns revealed by cluster analysis.

The Sheppard plot indicates that there is a good fit of the ordination distance among sites against the original dissimilarity distance which is expressed in the relatively low stress value (stress = 0.12) (Appendix I: Figure 34).

3.3.4.8. Spatial distance and floristic similarity

I found a significant positive Mantel correlation between the floristic distance and geographical distance matrices (Mantel's $r = 0.4866$, $p<0.001$). Based on this result I reject the null hypothesis that these two matrices are not related and hence the geographical separation of sites may explain a portion of the observed floristic dissimilarities (Figure 9).

Figure 18. Floristic similarity as a function of geographic distance between pairs of floras in the Andes-Guiana Shield region. Statistical significance from Mantel test.



3.4. Discussion

3.4.1. Patterns in habitat specialization

Viewed from the air and explored on the ground, Amazonian white-sand forests are no doubt distinctive in physiognomy and structure compared to neighbouring upland forests on clay soils (Anderson 1981, Prance 1996, Coomes & Grubb 1996, Bongers *et al.* 1985, Duivenvoorden 1995, García-Villacorta *et al.* 2003, Fine *et al.* 2010, Silveira 2003, Vicentini 2004, Ferreira 2009). In terms of species composition, however, my results shows that only about a quarter (23%) of the total 1,183 vascular plant species inhabiting western Amazonian white-sand forests are specialized to these forests while the vast majority (77%) also occur on non-white-sand habitats (Table 3). This finding contradicts the idea that this unique vegetation type is inhabited mainly by white-sand specialists. I suggest that the combination of soil nutrient factors along with their variable drainage conditions opens these habitats to members from other habitat types. This species distributional pattern only becomes evident when the analysis is done at large geographical scale as this study has attempted to do. The finding that only a small proportion of species is specialized to certain environmental conditions of emblematic Amazonian vegetation types has also being documented recently for Amazonian swamps. In these habitats less than 10% of species were found to be swamp specialists whereas more than 80% of the species also occur in neighbouring well-drained forest types (Pitman *et al.* 2014).

In contrast to this result, previous work on white-sand floristics and phytogeography have looked at taxonomic sub-sets of floras or taken a sub-regional geographic approach in their analyses, which despite showing the influence of plants also found in other habitats, they may have overestimated the proportion of true white-sand soil specialists. For instance, a floristic study of the white-sand forests of the Brazilian Amazon found that the majority of the species (54.5%) were restricted to this vegetation type, whereas 23.6% occurred in non-white-sand *terra firme* forests, 20% in *igapo* forests, and 2.6% in *varzea* forests (Anderson 1978, cited in Anderson 1981). Similarly, a previous analysis of the Peruvian white-sand tree flora found that 52% of them were white-sand specialists, while the rest were facultative specialists (9%), and habitat generalists (39%) (Fine *et al.* 2010). Considering the local to regional scope of both Anderson (1981), and Fine *et al.* (2010) studies, my results highlight the importance of taking a wider taxonomic and geographic approach when studying the distributional patterns of species in relation to habitat specialization.

Studies of plant communities in north-western Peruvian Amazonia have documented the existence of high edaphic heterogeneity closely matched with distinct plant communities (Tuomisto & Ruokolainen 1994, Tuomisto *et al.* 1995, Ruokolainen & Tuomisto 1998, Tuomisto *et al.* 2003). Likewise, tree plot inventories in the western Amazonian forests close to the Andean piedmont have documented that most of the species are rare in the landscape while the majority of trees belong to a small set of abundant species apparently indifferent to edaphic conditions (Pitman *et al.* 2001, 2002). Despite the high proportion of species not restricted to white-sand forests found in this study, none of these generalists reaches dominance in terms of biomass or stem numbers in white-sand forests. Dominance in these forests is exerted by a selected number of white-sand specialist (Fine *et al.* 2010, Stropp *et al.* 2011) or species with tolerance to water-logged soils conditions (Freitas Alvarado 1996, García-Villacorta *et al.* 2003, Vicentini 2004, Fine *et al.* 2010). Within these hydro-edaphic stressed forests, community dominance can only be achieved by a suite of taxa possessing particular trait combinations to outperform less adapted competitors. Candidate traits for conferring community dominance include relatively high levels of anti-herbivore toxins (Janzen 1974, Fine *et al.* 2006), slow growth (Fine *et al.* 2006), tolerance to flooding and drought (ter Steege 1994, Damasco *et al.* 2013, Aymard-C *et al.* 2014), high wood density (Baker *et al.* 2004, Baraloto *et al.* 2011), large seed size (Hammond & Brown 1995, ter Steege & Hammond 2001, Baraloto & Forget 2007), multi-stemmed growth (Vormisto *et al.* 2000), mast-fruiting (Janzen 1974), and ectomycorrizal associations (Henkel 2003, McGuire 2007, Smith *et al.* 2013).

3.4.2. Distributional patterns

Of the total Western Amazonian white-sand specialists, 88% of them occurred in floras within the Guiana Shield region, whereas approximately 12% would represent endemics to the western Amazon region. This pattern of phytogeographic connection was still high when only non-Guiana Shield white-sand forests were considered (59%). Caquetá moist forests, Guayanan Highlands Moist Forests, and Negro-Branco Moist Forests had the highest proportions of western Amazon white-sand specialists. These ecoregions are located at the southwestern fringe of the Guiana Shield region (Figure 12) which may explain why, when including the Colombian white-sand forests (caqu.wsf.CO, and guai.wsf.CO), the proportion of shared phytogeographic patterns increased substantially (30% to 69% in Caquetá Moist Forests, 33% to 51% in Guayanan Highlands Moist Forests, and 43% to 49% in Negro-Branco Moist Forests). This suggests that white-sand forests of the western Amazon, not only white-sand forest from the Colombian Amazon, have their stronger phytogeographic links with the western fringe of the Guiana Shield lowland floras (Table 6).

The fact that the three top ecoregions with the highest percentage of non-Guiana Shield western Amazon white-sand forest species are located in the western Amazon (Iquitos varzea, Napo moist forests, and Southwest Amazon moist forests; Table 6) indicate that white-sand forests in this region share a lesser number of white-sand species with the Guiana Shield flora compared to Colombian white-sand forests. The phytogeographic connection between Colombian white-sand forests and the Guiana Shield flora has been demonstrated before (Cortés *et al.* 1998). Interestingly, the most important taxa in these Colombian white-sand forests of Chiribiquete were mainly shrubs and herbs in the families Rubiaceae, Melastomataceae, Orchidaceae, and Bromeliaceae (Cortés *et al.* 1998). These plant groups are favoured in open white-sand areas with a rocky substrate common not only in the Chiribiquete area of Colombia but also in the Pantepui mountain summits of the Guiana Shield (Berry & Riina 2005). Similar rocky outcrops are for the most part absent in the white-sand forests of Loreto (Perú) and Acre (Brazil) (see Chapter 2 for more details).

The high proportion of species not specialized to white-sand habitats that occur on the western Amazon white-sand habitats may result from: (i) the combined mechanisms of mass-effect dispersal of species present in neighbouring habitats, which may have the ability to survive and reproduce in both white-sand and non-white-sand habitats (true generalists); (ii) widespread species that occur on poor-nutrient soils, including white-sands, which may be in the process of ecological parapatric adaptation or on-going speciation; and (iii) cryptic undescribed species – i.e., the populations found on white sand may be different species, but are not morphologically characterisable and therefore not recognised as such. The distribution of generalist species over poor-nutrients soils in Amazonia, including white-sands, suggests that (ii) and (iii) may be complementary. The few taxonomic revisions and phylogenetic analyses including species and populations inhabiting white-sand forests tend to find cryptic, undescribed species restricted to white-sand habitats within taxa previously thought to represent widespread habitat generalists (see *Humiria* in Cuatrecasas (1961); *Potalia* in Struwe & Albert (2004); *Pagamea* in Steyermark (1965), and Vicentini (2007); and *Protium* in Daly & Fine (2011), for some examples).

Revision of some plant groups has highlighted the existence of cryptic species within these taxonomic complexes when more collections, ecological, genetic, and/or reproductive biology data have been gathered. For instance, studying the distributional patterns of the *Passiflora vitifolia* complex (Passifloraceae) in the Peruvian Amazon, Gentry (1981) observed the segregation of four different species within this complex among four habitat types: one on seasonally inundated forests, another on non-inundated clay-rich soils, a third on non-inundated alluvial soils, and a fourth on non-inundated white-sand soils. This last species was previously lumped within a more wide-ranging species and was described as new by Gentry (1981).

Likewise, a cryptic species in the genus *Protium* (Burseraceae) was found under the name of a species that occurred both on white-sand and non-white sand soils (Daly & Fine 2011). Molecular phylogenetics has shown that this species was in actuality two species, with subtle morphological cues only discerned after careful cross-habitat checking (Daly & Fine 2011). Similarly, a recent study on reproductive biology, phenotypic differences, and ecological preferences within the *Pagamea coriaceae* complex (Rubiaceae) identified two different species distributed in sympatry and exploiting different gradient combinations of light and drainage within white-sand forests (Esteves & Vicentini 2013). Elucidating what proportion of non-specialist white-sand species are simply the outcome of mass-effect seed dispersal from non-white sand species from neighbouring habitats, true habitat generalists, cryptic undescribed species, or potentially incipient species undergoing ecological adaptation, will remain uncertain until more taxonomic, field, and molecular-based studies are done on these taxa.

3.4.3. Floristic patterns

All studied white-sand forests clustered with the flora of the province where they belong geographically (Figure 14). Given the overall dominance of non-white-sand specialists in western Amazon white-sand floras, this result suggests that the floristic patterns are driven by the overwhelming number of non-white-sand specialist species; this is, by the interaction of local and especially regional historical processes (Ricklefs 1987, Cornell & Lawton 1992, Holt 1993, Latham & Ricklefs 1993, Cottenie 2005, Ricklefs 2008). This result supports the hypothesis of a flora constructed via long-distance dispersal or stepping-stone dispersal from nearby white-sand habitats as well as well as taxa from other less oligotrophic habitats of the Amazon, on which these forests are embedded (poor-soil specialists, and generalists).

Current estimates of the extent of Arenosols and Podzols soils in the Amazon region suggests that these soils may account for a small proportion of the soil cover: 2.7% (20 million ha), and 1.9% (14.1 million ha) respectively (Chapter 2). This estimation is based on the presence of these soils in different parts of the Guiana Shield and the Amazon, which more probably developed diachronically by several physical, biological and chemical processes (Chapter 2). Fine *et al.* (2010) studied the floristic composition of white-sand forests of Peru and found that patterns of dominance were less predictable compared to non-white-sand forests (i.e. different patches were largely dominated by a different set of species). They interpreted this finding as a result of the dispersal capacity of plants and the variable size of white-sand habitat patches (Fine *et al.* 2010).

Alternatively, pedogenic processes of white-sand soil formation in association with the most widespread soils in the Amazon, Ferralsols and Acrisols, have been demonstrated by several studies in both the Amazon and Guiana Shield region (Chapter 2). Podzolisation processes are local phenomena occurring on other oligotrophic (sandy-clay) substrates over time, which raises the possibility that oligotrophic soils on clay substrates (not the extremely poor white-sands) represent habitats that can be used by oligotrophic-loving species that are common in the eastern Amazon and the Guiana Shield region. These "oligotrophic families" may include: Lecithydaceae, Chrysobalanaceae, Ochnaceae, Clusiaceae, Malpighiaceae, Myrtaceae, and Sapotaceae (Terborgh & Andresen 1998, Berry *et al.* 1995). Indeed, biogeographical patterns of plant species distribution in Amazonia have been related to the regional variation in soil fertility (ter Steege *et al.* 2000, Quesada *et al.* 2011). The hypothesis that species from these families can endure white-sand soil conditions may explain the abundance of non-white-sand specialists on Amazonian white-sand habitats; even though they are not restricted to white-sand soils, species in these families may be adapted to occupy a part in the Amazon soil gradient towards nutrient-poor soils.

In connection with this, the great majority of western Amazonian white-sand species (77%) occur widely distributed on different vegetation types, including other less extreme, oligotrophic soils (Figura 12; Table 6). The clustering of white-sand forests with nearby floras indicates that dispersal processes from other white-sand areas and from water-logged stressed habitats may be the main process shaping the evolution and community assembly of these forests. In this regard, peat-accumulating palm swamps (Tuomisto *et al.* 1994, Lähteenoja *et al.* 2009), and old terraces of *terra firme* forests on sandy-clay soils (García-Villacorta *et al.* 2010) may provide adequate environmental stress (i.e. poor drainage, or slightly nutrient-poor soils respectively) that may be used by poor-soil plant specialists as dispersal corridors to reach isolated white-sand forests (García-Villacorta *et al.* 2011).

Ancient hilly terraces on poor oligotrophic clay soils were found to be a common feature at certain drainage divides of the western Amazon (Stallard 2011). These eroded hilly terraces are extensive in these areas and several taxa commonly occurring as white-sand poor-soil specialists have been found on them (García-Villacorta *et al.* 2010, 2011). Similarly, some non-specialist white-sand species have been found on swamp habitats of the Amazon flood-plain (Tuomisto *et al.* 1994, Lähteenoja *et al.* 2009, Lähteenoja & Page 2011, García-Villacorta *et al.* 2011, Dávila *et al.* 2013, Draper *et al.* 2014), which suggest that edaphic conditions on these habitats may facilitate their species range distribution. Habitat heterogeneity in these areas is high and the top areas of the hills are composed of nutrient-poor Plio-Pleistocene alluvial sediments (2 Mya), whereas middle and lower areas can have outcrops of Pebas formation soils (6 Mya), higher in nutrients, or most commonly covered with younger poor fluvial sediments like Nauta sandy-clay formations (Räsänen & Linna 1998, Stallard 2011).

Previous studies of plant species distributional data across a broad range of edaphic gradients have reported that species are often found associated with certain edaphic and topographical characteristics which imply that they may have played a role in plant evolution in the Amazon. For instance, Schulman (2003) described the ecological restriction of the shrub *Adelobotrys ruokolainenii* (Melastomaceae) to nutrient-poor hills on sandy-clay soils which correspond to the geological formation known as Nauta C in northern Peruvian Amazonia. Similarly, two species of *Clidemia* (Melastomataceae) that occur sympatrically, but on different habitat types with contrasting soil cation concentrations, were proposed to have evolved by ecological speciation in response to environmental variation (Schulman *et al.* 2004). Likewise, Tuomisto (2006) studied the geographic and ecological distribution of seven *Polybotrya* fern species across a large swathe of the western Amazon (Colombia, Ecuador, and northern Peru). She found that each species occurred in a unique set of hydro-edaphic conditions. A single study site encompassed only a small proportion of their preferred edaphic gradient, with complete absence of certain species from some sites when the proportion of sand in the soil exceeded 60% (Tuomisto 2006). Similar explanations have been invoked for palm species in the western and eastern Amazon regions (Roncal 2006, Gomes de Freitas *et al.* 2014).

Most of the species shared with other biomes in the western Amazon white-sand forests come from areas with rainfall or edaphic constraints like seasonally dry forests or savanna forests (Table 3). The patterns revealed by the distributional analysis using the whole dataset by biomes suggest a connection with Tropical and Subtropical Grasslands, Savannas and Shrublands (48%) followed by Tropical and Subtropical Dry Broadleaf Forests (34%). Species restricted to white-sand soils in the western Amazon have a lesser connection with these biomes: the proportion of white-sand species found in Tropical and Subtropical Grasslands, Savannas and Shrublands dropped to around quarter (25%) whereas Tropical and Subtropical Dry Broadleaf Forests dropped to an almost insignificant 4% of shared species. This sharp drop in shared species when using the white-sand specialist dataset may be related to the intrinsic differences in soil nutrient levels between these two biomes, savannas being more nutrient-poor habitats, and usually found on sandy soils compared to relatively cation-rich seasonally dry forests (Beard 1953, Prance 1996, Huber 2006, Pennington *et al.* 2006).

I found that western Amazonian white-sand forests are floristically more related to each other and to floras of the western edge of the Guiana Shield region than to other floras in the Amazon-Guiana region (Figure 11-12). Specifically the Colombian lowland floras of Caquetá (CO.CQ), Guaviare (CO.GV), Vaupés (CO.VP), and Guanía (CO.GN), which are part of the western Guiana Shield region (Figure 3), were found to be floristically close to western Amazonian white-sand forests in both cluster and NMDS analysis (Figures 8, and12). The two other lowland floras of the western side of the Guiana Shield region with similarities to the studied white-sand forests were the floras of the Brazilian provinces of Amazonas (BR.AM) and Acre (BR.AC), and Amazonas in Venezuela (VE.AM). Furthermore, a massive number of western Amazonian white-sand specialists were found to occur within the Guiana Shield region (88%). Within this region, Caquetá moist forests, Guayanan Highland moist forests, and Negro-Branco moist-forests sub-biomes had the highest proportion of shared species. Previous studies in the Caquetá region have reported the presence of white-sand taxa with geographical affinities with the Guiana Shield region (Duivenvoorden 1995, Cortés *et al.* 1998, Arbeláez & Duivenvoorden 2004) and my results confirm these findings.

Geographical proximity among studied floras and white-sand forests may help explain the observed phytogeographical affinities. Both BR.AM, and VE.AM provinces are geographically adjacent to each other as well as to the Colombian sites described above to have close links to western Amazonian white-sand forests. This may help explain why acre.wsf.BR (Brazil) and lore.wsf.PE (Peru) are more similar to each other and to caqu.wsf.CO (Colombia) than to guai.wsf.CO (Colombia), the latter being closer in geographic distance to the core Guiana Shield region (Figure 12). A correlation analysis of the geographic distance and floristic matrices (Mantel test) in the dataset found a significant association between them, implying that spatially closer sites are also floristically more similar.

It has been hypothesized that the species occurring on Amazonian white-sand forests were part of a historical, mostly continuous, landscape of sandy soils that were later fragmented as the Amazon biome developed during the Miocene (Struwe & Albert 2004). This hypothesis implies a mostly uniform white-sand forest floristic composition across the Amazon, and given its old relative age compared to other habitat types, the existence of endemic relict species (paleo-endemics) in white-sand forest patches is possible (Struwe & Albert 2004). If some white-sand forests in the Amazon are younger than others, as suggested by the relative age of soils (Chapter 2), their floristic composition might be biased towards well dispersed members of the Amazonian white-sand species pool. If this is the case, the existence of local endemics in the white-sand forests of the western Amazon will be somewhat puzzling because it implies that these species diverged relatively recently.

Several studies of plant dispersal syndromes in Amazonian white-sand forests have suggested that long-distance dispersal may be an important ecological process in the maintenance, and perhaps origin, of Amazonian white-sand forests. In an “open campina” white-sand forest in Manaus, Brazil, the proportion of plant species with hypothesised capability for long-distance dispersal was relatively high in the studied plant community (76%), with 59% of the plants being bird-dispersed species (Macedo & Prance 1978). Prance & Schubart (1978) also reported that long-distance dispersal might be an important factor shaping the similarity of white-sand forests near Manaus in the lower Rio Negro basin of Brazil. Finally, Arbeláez & Parrado-Roselli (2005) characterized the dispersal syndromes of different sandstone vegetation types in the Colombian Amazon. They found that anemochorous (40.2%) and zoochorous (37.8%) were the dominant dispersal syndromes in the forest-scrub vegetation whereas autochory (60%) was the main dispersal syndrome in the open-herbaceous vegetation. Overall birds were the most important dispersal agents (58.9%). Geographic distance, the connectivity of white-sand forests with less oligotrophic soils, and the spatial distribution of the white-sand forest archipelagos, all together may have some influence in the origin, community structuring and maintenance of this Amazonian plant community.

3.4.4. Conclusions

In returning to my initial questions, I found that about a quarter (23%) of the western Amazon white-sand flora is specialized to white-sand substrates whereas the great majority (77%) also occur in other habitat types in the Amazon. This finding contradicts the general idea that white-sand forests are mainly inhabited by specialized species as has been usually described in the botanical, ecological and taxonomic literature. Because of adaptations to stressing hydro-edaphic conditions, white-sand forests of the Amazon are physiognomically well defined. Floristically, however, they receive a large number of species that possess similar physiological and ecological preferences but that are not restricted to white-sand habitats. Some of these non-specialist white-sand species may represent species that preferentially disperse from nearby less oligotrophic soils and water-stressed habitats of the Amazon basin. 88% of the white-sand specialist species are shared with the Guiana Shield region, whereas 12% would represent local endemics. The distributional analysis shows that white-sand forests share a substantial number of species with extra-Amazonian biomes like savanna forests, and seasonally dry forests, especially amongst their non-specialist representatives.

Cluster analysis and NMDS ordination concurred that the white-sand forests of the western Amazon are floristically more similar to floras of the geographic region to which they belong. In general, the composition of white-sand forests of the western Amazon is more similar to floras of the western side of the Guiana Shield than to the rest of floras in Amazonia. There was significant distance decay in similarity of overall floristic composition, which implies that dispersal processes are playing an important role in driving current floristic assemblage patterns. Also, both the floristic and distributional analysis point to the western oligotrophic floras of the Guiana Shield as their closest floristic affinities. Geographical distance seems to explain an unmeasured fraction of the floristic similarity between white-sand floras and other floras in the Amazon. Therefore, regional dispersal processes may have more importance than local species interactions in structuring Amazonian white-sand plant communities. Taken as whole, my results suggest the western Amazon white-sand forests are relatively recent assembled floras of different ages, structured mainly by dispersal processes from other, geographically proximate white-sand forests and with a large component of non-white-sand specialist taxa immigrating from less extreme oligotrophic habitats nearby. Nevertheless, at the local and regional level white-sand forests possess a significant number of endemics that add up to the regional and beta diversity in the Amazon. Additionally, they represent a unique combination of Amazonian hydro-edaphic conditions that can serve as natural laboratories to understand the evolution of habitat specialization, plant-animal interactions and physiological adaptations to drought and flooding. The existence of a variety of soils and habitats, from extreme-poor to relatively-rich in close proximity of the same geographic space, may provide the evolutionary arena for habitat specialization, which may be essential for the generation and maintenance of the plant biodiversity across the Amazon and Guiana regions.

Chapter 4: Pervasive habitat switching and the evolution of habitat specialization in lowland Neotropical forests

> "And yet, when the constituent plants of the different classes
> of forest come to be compared together, they are found to
> correspond to a degree quite unexpected; for although the
> species are almost entirely diverse, the differences are
> rarely more than specific. It is only in the caatingas
> that a few genera, each including several species,
> seem to have taken up their exclusive abode"
> —R. Spruce (1908)

4.2. Introduction

Edaphic diversity across Amazonia is greater than previously appreciated (Quesada *et al.* 2011; Chapter 2). The length of the soil gradient varies at local and regional scales, with some areas having a concentration of extremely nutrient-poor habitats (ter Steege 1993, Stropp *et al.* 2011), others having more cation-rich soils, at least by Amazonian standards (Gentry 1986, 1988), and others having a mixture of both extremes within the same geographical area (e.g. Tuomisto *et al.* 1995, Ruokolainen & Tuomisto 1998, Pitman *et al.* 2008). This asymmetrical variation in edaphic conditions across Amazonia (Quesada *et al.* 2010, 2011) may have its roots in the unique geomorphological histories that each sub-region experienced in the past (Salo *et al.* 1986, Rossetti *et al.* 2005, Higgins *et al.* 2011; Chapter 2). This variation of edaphic characteristics that creates differences in habitat types—from various types of terra firme non-inundated forests to seasonally flooded forests—was recognized early on by Amazonian naturalists (Bates 1863, Spruce 1908) and it is represented in contemporary classification of habitats and vegetation types in this region (Macedo &

Prance 1978, Encarnacion 1985, Kalliola *et al.* 1991, Duivenvoorden & Lips 1995, Kvist & Nebel 2001, Salovaara *et al.* 2005, Huber 2005, Josse *et al.* 2007, Gond *et al.* 2011, Junk *et al.* 2011).

Amazonian white-sand soils are found at one extreme of this edaphic gradient in terms of soil nutrients and water availability. These quartz-rich sandy soils are classified as Arenosol or Spodosol in the soil literature (Chapter 2; FAO 1988, Buol *et al.* 2011) and support a physiognomically distinctive forest type, with many endemic plants and animals, which is variously known as *campina*, *campinarana*, *varillal*, *chamizal*, *bana*, *Amazon caatinga* or *wallaba forest* depending on the country where it occurs (Davis & Richards 1933, Ducke & Black 1953, Lisboa 1975). For a casual observer, the transition from a typical rainforest to a white-sand forest can be quite dramatic: from a multi-layered, tall and exuberant rainforest to a stunted forest with voluminous stem density and high levels of sunlight reaching the forest floor. It has been shown that inhabiting these nutrient-poor habitats require certain physiological adaptations that have a genetic component and that trade-off with plant growth (Proctor 1999, Fine *et al.* 2004, Lamarre *et al.* 2012). Leaves are characteristically leathery and well protected (rich in lignin and secondary compounds), and the forest floor is sometimes covered with an irregular and thick tapestry of organic layer, both of which are an indication of its nutrient-poor soil condition (Duivenvoorden & Lips 1995, Cuevas 2001). The drainage system is characterized by black-water rivers and streams which result from the high levels of tannins and other secondary compounds leaching vertically and laterally from the slowly-decomposing leaves and organic matter (Janzen 1974, Proctor 1999, Lucas *et al.* 2012).

The study of the evolution of tolerance to nutrient-poor habitats and specialization to different edaphic conditions may help us to explain extant diversity patterns in Neotropical plants. In this context, two basic models of edaphic niche evolution have been advanced in the Amazon. Firstly, Gentry (1981) proposed that divergent specialization to different edaphic conditions may have been important in the diversification of the Amazonian flora. Using field and herbarium studies of the distributional patterns of the *Passiflora vitifolia* complex (Passifloraceae) in which four different species occupied four different edaphically-determined habitat types in the Peruvian Amazon—seasonally inundated forests, non-inundated clay-rich soils, non-inundated alluvial soils, and non-inundated white-sand soils—he proposed that habitat specialization may have been an important driver in the diversification of Neotropical plants. This mechanism of species habitat sorting through evolutionary time could be expressed by lineages showing high levels of edaphic niche lability that facilitate niche evolution by habitat switching.

On the other hand, Kubitzki (1990) put forward the hypothesis of a younger evolutionary origin of the lowland flora of Amazonia compared to a hypothesized mainly Cretaceous-age radiation of the Guiana Shield flora. According to this hypothesis the evolution of a proto-Amazonian flora found on nutrient-poor substrates may have taken place at the southern margin of the Guiana Shield before the availability of younger and richer soils in the Miocene (Kubitzki 1989). This implies niche conservatism of Guianan-centered lineages that were exposed for millions of years to infertile substrates on the Guiana-Shield region, from the time the South American plate drifted from Africa ca. 100 Mya until the emergence of the northern Andes, extinction of the Pebas lake-system and establishment of the modern Amazon biome (ca. 8 Mya) (Chapter 2). As new habitats were created, these basal lineages may have tracked and diversified in their “preferred” nutrient-poor niches across the Amazon (Kubitzki 1989, 1990), including white-sands substrates (Frasier *et al.* 2008). This interpretation suggests that niche conservatism for ancestral edaphic preferences might have influenced speciation patterns in Neotropical plants or alternatively, the opportunity for habitat switching with the advent of new habitats and soils may have increased as at no other time before, giving rise to new species via habitat specialization.

Along these lines, in studying the biogeography of *Potalia* (Gentianaceae), Frasier *et al.* (2008) hypothesized that white-sand soils were widespread in the proto-Amazon before the rising of the Andes in the Miocene, but were later fragmented and replaced by the more cation-rich Andean derived soils. Early branching lineages would preferentially occupy white-sand substrates in this genus, whereas plants lineages on clayey soils are sister to white-sand lineages. Using a combined molecular-morphology dataset they tested the hypothesis that white-sand species of *Potalia* were early branching lineages compared to species occurring on other soil types in the Amazon. Species known to be restricted to the Guiana Shield and Amazonian white-sands were found to be early branching lineages in relation to to the rest of the members in the phylogeny, thus implying that non-white-sand species in other regions of the Neotropics were derived from them (Frasier *et al.* 2008).

Several studies in the tribe *Protieae* (Burseraceae), along with other white-sand species, are among the few that have addressed the role of habitat heterogeneity in the evolution of ecological specialization using a combination of molecular phylogenies, natural transplant experiments, and measurements of phenotypic variations of species ecotypes (e.g. Fine *et al.* 2004, 2005, Lamarre *et al.* 2012, Fine *et al.* 2013). Studying the evolution of ancestral soil associations, Fine *et al.* (2005) used species distributional data from floristic plots located in three different soil types of the Peruvian Amazon and Ecuador (clay, terrace, and white-sand) to classify species by their soil preference. Twenty six species out of 35 showed habitat specialization to one of the soil types, with terrace (sandy-clay) soil inferred as probably being the ancestral state with subsequent speciation on clay and white-sand soils (Fine *et al.* 2005). Using a molecular biogeographic approach, Fine *et al.* (2014) also investigated, among other questions, the habitat evolution of *Protieae* in the Neotropics. They found the terra firme forests were the most probable ancestral habitat of *Protieae* with multiple transitions to other habitats, especially in western Amazonia and towards white-sand habitats (Fine *et al.* 2014).

In Chapter 3 I showed that a large proportion of species inhabiting the white-sand forests of the western Amazon also occur on other habitat types somewhere in their overall distributional range. This result suggests that the ecological conditions prevalent on white-sand soils are tolerated by various species that are not white-sand specialists, highlighting the importance of looking at the overall species distribution in order to properly evaluate habitat preference and associations. Given the complex geo-climatic history of the Amazonian biome, with a flora relatively rich in local and regional endemics, it is at present not clear whether edaphic niche conservatism or evolutionary habitat switching of ancestral habitat preferences has played a major role in speciation via habitat specialization.

Variation of habitat diversity in space and time during the formation of the Amazon biome, and the Neotropics in general, may have influenced profoundly the current levels of plant taxonomic diversity in this region. For this reason, the study of phylogenetic niche conservatism may give us insights into how it may have influenced extant diversity patterns. Furthermore, because of their different physiological requirements, studying the degrees of tolerance to edaphic conditions may give us some clues about their influence on the general patterns of plant species diversification in the Neotropics. I used a molecular phylogenetic approach in two diverse Neotropical plant families, Sapotaceae and Chrysobalanaceae, to investigate the phylogenetic patterns of tolerance to extremely nutrient-poor soils and the evolution of edaphic niches via habitat switching from and into other habitat types. In particular I asked the following questions:

(i) are Amazonian white-sand specialists early branching taxa relative to non-white-sand habitats across the Neotropical forests?

(ii) are white-sand specialist species clustered in certain clades of the phylogenetic trees?

(iii) does tolerance to extremely nutrient-poor soils in the Neotropics show signs of edaphic niche conservatism over evolutionary time?

(iv) what were the most likely ancestral edaphic preferences among different species in Neotropical Sapotaceae and Chrysobalanaceae?

(v) what is the role of niche conservatism and/or habitat switching in generating the extant species diversity in these two Neotropical clades?

If species on early branches of the phylogenies are found in white-sand habitats then this suggests that white-sand specialism could be the ancestral habitat type, regardless of where they occur geographically in the Neotropics (i.e. Amazon white-sand specialists clustering with Guiana-Shield specialists). If tolerance to extremely nutrient-poor white-sand soils is a conserved trait, I would expect that this trait may have evolved early in the history of a clade (i.e. deeper in the phylogeny) and has remained conserved (i.e. not shifted to other habitat types) over evolutionary time. This result would support a role for edaphic niche conservatism in the evolution of habitat specialization. On the other hand, if tolerance to stressful hydro-edaphic conditions is a labile trait, I will not expect to find any large clade composed exclusively of white-sand specialists, but instead they will be scattered across the phylogenies. This latter result will support a role of habitat specialization through habitat switching in the evolution of species diversity in these Neotropical clades.

4.3. Methods

4.3.1. Clade selection

Clades were selected using the following criteria: (a) they have species occurring on both white-sand and non-white-sand forests, (b) they have taxa distributed in both the Amazon and the Guiana Shield regions, and (c) they have a well revised taxonomy which included molecular phylogenies that could be expanded upon with additional white-sand and non-white-sand species in this project. Among the candidate groups, two well-defined Neotropical monophyletic clades were selected to study the evolution of habitat specialization: Chysophylloideae (Sapotaceae), and the *Licania/Hirtella/Couepia/Gaulettia* (Chrysobalanaceae) clades (Swenson *et al.* 2008, Bardon *et al.* 2013). Species in both clades are important components of Amazonian tree diversity and density (Terborgh & Andresen 1998, ter Steege *et al.* 2000, Pitman *et al.* 2001, ter Steege *et al.* 2013), inhabiting a wide range of habitat types (Prance 1972, Pennington 1990, Prance & White 1988).

Chysophylloideae, with ca. 600 species, is one of the three sub-families in Sapotaceae (the other two being *Sapotoideae* and *Sarcospermatoideae*) and like the family is distributed pantropically (Bartish *et al.* 2011). Using a robust, fossil-calibrated phylogeny it was estimated that *Chrysophylloideae* first diversified in Africa (73-83 Mya) after splitting from Asian *Xantholis*, with subsequent colonization of South America via long-distance trans-oceanic dispersal 54–64 Mya (Bartish *et al.* 2011). The Neotropical species of *Chrysophylloideae* fall into 'clade G' as defined by Swenson et al. (2008), and include species assigned to *Pouteria*, *Chrysophyllum*, *Pradosia* (minus *P. spinosa*), *Micropholis*, *Ecclinusa*, *Elaeoluma*, plus *Sarcaulus brasiliensis* and *Diploon cuspidatum*. This clade G is the subject for the Sapotaceae analysis and newly generated sequences were added and aligned for Bayesian phylogenetic and molecular dating analysis (see phylogenetic reconstruction and dating section).

Chrysobalanaceae is also a pantropical family with the vast majority of its species restricted to the Neotropics (ca. 423 species, 80%). Using a Bayesian and Maximum likelihood approach to phylogenetic reconstruction the family was inferred to have originated in the Paleotropics about 80 Mya with subsequent repeated dispersal to the Neotropics ca. 40-60 Mya (Bardon et al. 2012). Clade N in the recently derived molecular phylogeny of the family includes only Neotropical species (species in the genus *Hirtella*, *Licania*, *Couepia* and *Gaulettia*) (Bardon *et al.* 2013) and forms the backbone for the habitat reconstruction analysis here. Species identities included in the analysis follow recent taxonomic rearrangements in this clade in which some *Couepia* taxa were transferred to the genus *Gaulettia* (Sothers *et al.* 2014). Molecular phylogenetics has also provided support for the transfer of some Asian *Licania* into their own genera (*Angelesia*) and the re-circumscription of *Licania* as entirely Neotropical (Sothers & Prance 2014).

4.3.2. Field work

Fieldwork to collect white-sand and non-white-sand species for phylogenetic analysis was conducted in the Peruvian Amazon and the rainforests of Guyana. I made a total of 118 collections of Chrysobalanaceae (42 species total: 17 in Guyana and 31 in Peru) and 140 of Sapotaceae (43 species total: seven in Guyana and 39 in Peru) in both regions. Differences in the number of species per region and the total samples collected result from widespread species collected in both regions (six species in Chrysobalanaceae, three species in Sapotaceae). All collections were dried in the field using silica gel and duplicate vouchers for herbarium specimens were prepared following standard botanical practices. Botanical vouchers are stored at the MOL (Universidad Agraria La Molina, Peru) and RBGE (Royal Botanic Garden of Edinburgh) herbaria. I visited six sites in the Peruvian Amazon, from the lowlands (Allpahuayo-Mishana, Puerto Almendras, Tamshiyacu, and Jenaro-Herrera; elevational range: 129-162 m a.s.l.) to areas closer and within the Andes (Davicillo and Aguas Verdes; elevational range: 189-1,155 m a.s.l.). In Guyana I collected at three sites: Soesdyke-Linden Highway (38-58 m a.s.l.), Bartica-Potaro road (73-85 m a.s.l.), and Mabura-Hill (105-127 m a.s.l.). Specimens were preliminarily identified in the field and subjected to further work at the RBGE herbarium using taxonomic keys, exsiccatae previously identified by taxonomic experts and digital resources available in online databases.

4.3.3. Taxon sampling

A total of 147 species (24.5% of total species in the family, 369 accessions) of *Chrysophylloideae* (Sapotaceae) were used in the phylogenetic reconstruction and molecular dating analysis. Sapotaceae samples were subject to molecular work in the lab facilities of the RBGE. Chrysobalanaceae samples were sent in collaboration for DNA extraction and sequencing to the research lab of Dr. Jérôme Chave (Université Paul Sabatier, France) where Léa Bardon is working on the phylogenetic systematics and biogeography of the family as her PhD project. 167 species (39.5% of total species in the family) were used in reconstructing the molecular phylogeny of Chrysobalanaceae of which 36 species were collected in fieldwork carried out during this project (21% of species in the phylogeny).

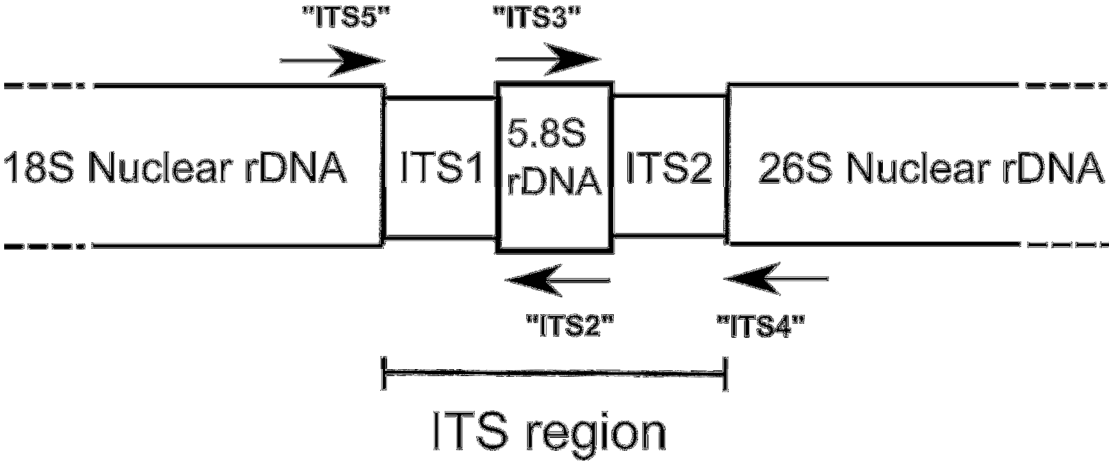
4.3.4. DNA extraction, PCR amplification and sequencing

I worked on 49 accessions representing 40 Sapotaceae species from Peru and Guyana, extracting total genomic DNA from field-collected silica-dried samples using Qiagen DNeasy Plant Mini Kit spin columns following their standard protocol (Qiagen Inc., Valencia, California). The nuclear ribosomal ITS region was amplified and sequenced for the collected samples using the primers ITS5p (forward) and ITS4 (reverse) following Swenson *et al.* (2008).

The ITS region is composed of two sub-regions (ITS1 and ITS2) flanking the sub-units of the nuclear ribosomal RNA genes: 18S, 5.8S, 26S (Figure 19). Due to its high copy number and easy of amplification by standard PCR technology it has been proven to be an important tool in molecular plant phylogenetics (Baldwin 1992, Baldwin *et al.* 1995). A number of genetic processes may impact the utility of the ITS region in phylogenetic inference, including the presence of pseudogenes, evolutionary constraints to maintain rRNA secondary structure, extensive ancient or recent duplication events and lack of complete concerted evolution (Álvarez & Wendel 2003, Small *et al.* 2004). Also, the presence of multiple arrays of divergent rRNA due to organismal processes of hybridization and polyploidization add another layer of complexity for resolving phylogenetic relationships using the ITS region. All of these processes can manifest in a network of paralogous/orthologous events that can affect phylogenetic reconstruction (Álvarez & Wendel 2003).

Countering these proceses, the ITS region undergoes an homogenization process known as concerted evolution, in which if a mutation occurs in one copy of the region it is generally corrected to match the other lead copy. Concerted evolution then would in theory eliminate or minimize paralogous sequences in the multiple copies of ITS region within the individual cell, thereby facilitating the recovering of true homology and phylogenetic relationships between taxa. However, this homogenization process is not always completed and the ITS region can be polymorphic within the individual plants due to incomplete concerted evolution (Álvarez & Wendel 2003, Bailey *et al.* 2003).

Figure 19. Organization of the ITS region within the nuclear ribosomal DNA (rDNA). Arrows indicate the direction and approximate location of primer sites to amplify the region. ITS5 and ITS4 primers were used in this study. Conventional name for primers follows White *et al.* (1990)(1990). Adapted from Baldwin *et al.* (1995).



Despite these potential drawbacks for phylogenetic reconstructions, the ITS region has proven useful for inferring the phylogenetic relationships in Sapotaceae. Swenson *et al.* (2008) studied the molecular phylogenetics in the family and sub-families and found that the combined nuclear ribosomal Internal Transcribed Spacer (ITS)/chalcone synthase gene intron (ChsI) resulted in a similar topology compared to a gene tree topology generated by combining seven chloroplast loci (Swenson *et al.* 2008). Additionally, the ITS region has been found to be the most informative genetic marker compared to other molecular markers in helping discriminate among Neotropical Sapotaceae species (Vivas *et al.* 2014).

PCR products of each targeted taxon were purified with ExoSAP-IT® following the manufacturer's instructions. Sequencing reactions were analyzed on the ABI 3730 at the Genepool facilities of the University of Edinburgh. In both selected clades the phylogenetic and molecular dating estimation was done *de novo*.

4.3.5. Phylogenetic reconstruction and molecular dating

In the following section, I describe how the Sapotaceae and Chrysobalanaceae trees were built along with their associated divergence date estimates.

4.3.5.1. Sapotaceae phylogeny

Raw sequences for each newly generated taxon were imported into the program Sequencher® v4.3 where they were edited and combined into consensus sequences. These consensus sequences were then imported into the program Mesquite® for manual alignment with sequences previously obtained in other studies of the same taxa. Additional ITS accessions from French Guiana (65 species) generated by Julien Vieu (Dr. J. Chave lab) were aligned manually to the original matrix before performing the phylogenetic analysis. To obtain a hypothesis of the evolutionary relationships in Neotropical Chrysophylloideae (Sapotaceae) a phylogenetic tree estimation and concurrent molecular dating was performed under a Bayesian approach using the program BEAST v1.8.0 (Drummond *et al.* 2012) in the CIPRES computer cluster gateway (https://www.phylo.org/).

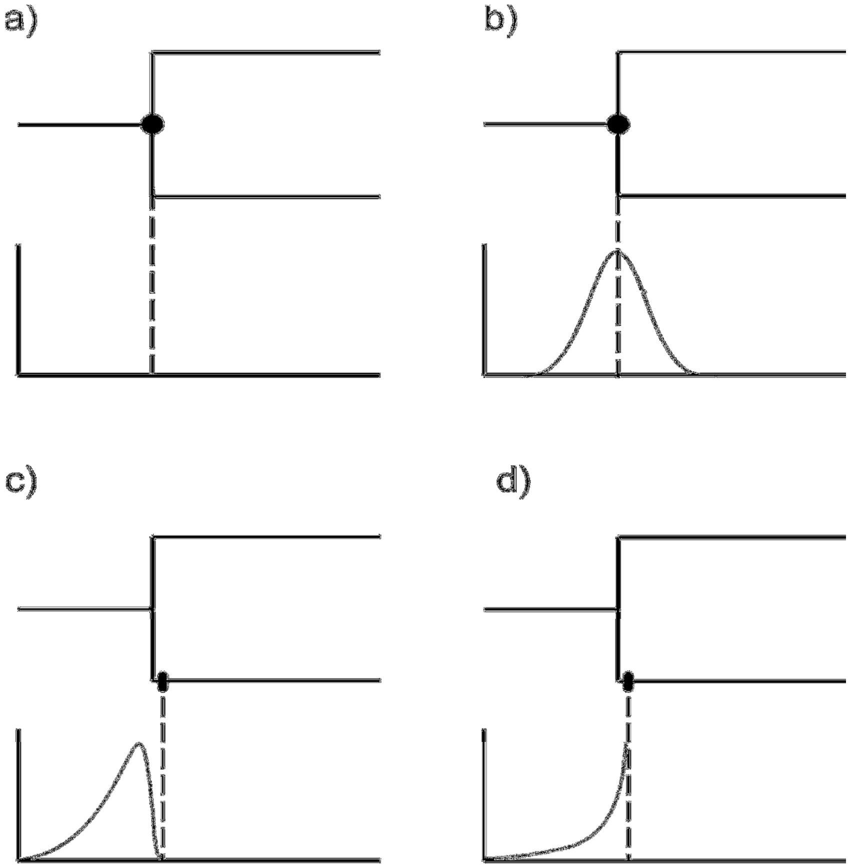
Bayesian phylogenetic analysis uses the Markov Chain Monte Carlo (MCMC) method to sample the posterior probability distribution to generate multiple phylogenetic tree topologies and divergence times, along with their associated parameter values (Drummond *et al.* 2006). It is called posterior probability because the probability is assigned after taking into account the prior evidence given by the data at hand. Bayesian inference of phylogenetic trees and divergence times in BEAST requires, among other data, a model of sequence evolution, a prior probability on the fossil and a prior on the phylogeny (the tree prior). Below I describe briefly some one of the most critical elements.

It has been widely recognized that molecular rate variation is largely heterogeneous among and within lineages (Welch & Bromham 2005) and that in order to estimate absolute species divergence time across the tree this needs to be calibrated with external temporal data, usually a fossil with known estimated age. Fossil data can only provide reliable minimum age constraints on lineage divergence events (Donoghue & Benton 2007) because there is no guarantee that the lineage we are trying to calibrate has not been in existence well before the appearance of the fossil (Ho & Phillips 2009). In accordance with the criterion of the use of safe minimum ages, and because the exact age of a fossil within a stratigraphic deposit is uncertain, it is advisable to use the upper limit (i.e. the most recent) of the oldest geologic deposit in which the fossil has been recovered (Ho 2007, Sauquet 2013).

In the case of Chrysophylloideae, the oldest geological deposit of fossils is pollen of Paleocene/early Eocene age (59-47 Ma) from the Maracaibo basin, western Venezuela. This pollen fossil was identified as *Psilatricolporites maculosus* Regali, an extinct species associated with Neotropical *Chrysophyllum* (Sapotaceae) (Rull 2000). This fossil represents a minimum age for the presence of Chrysophylloideae in the New World.

In a Bayesian phylogenetic analysis this fossil is assigned to calibrate a node in the phylogenetic tree and is assumed to be distributed in the form of a parametric distribution to model calibration uncertainty. Assuming that the ages on the actual calibration nodes follow parametric distributions incorporates the intrinsic uncertainty of dating a molecular phylogeny (Drummond *et al.* 2006). This prior information in the form of parametric distributions (known as prior probability distribution) can take different shapes (e.g. normal, lognormal, exponential, Figure 20) which are chosen based on a comprehensive analysis of the fossil record of the clade of interest (Nowak *et al.* 2013).

Figure 20. Some methods for calibrating estimates of substitution rates and divergent times: a) point calibration: fixing the node age to a specific value, b) normal distribution, c) lognormal distribution with a rigid minimum bound, d) exponential distribution with a rigid minimum bound. Adapted from Ho (2007).



For instance, exponential priors are useful when our preliminary assessment of the calibration node with the available fossil information indicates that the internal nodes are more likely to have smaller values than larger ones and there is no expectation for what the mode of the distribution might be (Ho & Phillips 2009). In other words, there is a long tail in the probability distribution towards higher ages (there is a higher probability of a nodal age being equivalent to the oldest fossil and unlikely to be much older) and the mode of the exponential distribution is set at the hard minimum age or offset value. Consequently, an exponential prior age estimate of 55 Ma (mean = 1.0, offset = 55, in BEAST) was assigned to the stem node which included all Neotropical Sapotaceae in the dataset. Two non-Neotropical Chrysophylloideae members, the Southeast Asian species *Xantolis siamensis* and the African *Omphalocarpum strombocarpum*, were assigned as outgroups.

The branching pattern in the tree was constrained to follow a Yule process (Yule tree prior in BEAST), a simple uniform probability speciation process in which symmetrical trees are more likely than asymmetrical trees (Yule 1925, Huelsenbeck & Kirkpatrick 1996, Mooers & Heard 1997, Aldous 2001). I chose the General Time Reversible (GTR) model with the option “Estimated” base frequencies and site heterogeneity model set as “Gamma” with four categories as the model parameters of nucleotide substitution for the analysis. Under the GTR model the rate of change of each nucleotide state is the same in any direction and the Gamma distribution approximates the rate variation across sites (Salemi *et al.* 2009).

The information necessary for the phylogenetic analysis in BEAST requires a specific formatting of the data which is facilitated using the program BEAUti. This program saves the data file in XML (Extensible Markup Language) format, a text-based format to handle, store, and transport data. Thus, an XML file was prepared in the program BEAUti v1.8.0 with chain length set to 600,000,000 generations. The length of the chain was determined after previous runs to determine the most appropriate number of generations based on parameter convergences.

The Bayesian phylogenetic tree search reconstruction and dating was done in two independent runs. Results from each simulation were screen-logged every 1,000 generations, saving the results and estimated trees each 10,000 generations for a total 120,000 estimated trees (60,000 per run). I used Tracer v1.6 to explore the convergence of the estimated parameters. The majority of estimated parameters obtained by the combined MCMC runs reached Effective Sample Size (ESS) larger than 200 which means that the estimated model parameters converged (Drummond et al. 2006). Parameter values with ESS less than 100 means that the MCMC chain has not run long enough to get a valid estimate of the parameters because it may contain a large number of correlated samples and may not represent well the posterior distribution of the estimated parameters (Drummond *et al.* 2007). The likelihood, coefficient of variation and tree likelihood parameters had ESS values in the range of 184-194.

I used LogCombiner v1.8.0 to combine into one file the log and tree file data generated in the two independent Bayesian analyses by BEAST. I then used TreeAnotator v1.8.0 to find the best supported tree (the tree with the highest posterior probability, known as the Maximum Clade Credibility Tree) from the 120,000 trees obtained by BEAST. 12,000 trees were used as burnin (10% of total trees obtained) leaving the posterior probability limit to zero in order to annotate all nodes. Node heights were set to mean heights (estimated ages).

4.4.5.2. Chrysobalanaceae phylogeny

For Chrysobalanaceae, a preliminary phylogenetic tree was first produced based on combining 49 cpDNA genomes developed by using a whole genome "shotgun sequencing" methodology described in Malé *et al.* (2014) (see also Cronn *et al.* 2008, Straub *et al.* 2012, McPherson *et al.* 2013). Using this tree, new primers were designed and 120 more individuals (including samples from Peru and Guyana) were sequenced using standard Sanger sequencing methodology, similar to that described for

Sapotaceae above. Using both molecular datasets a new phylogeny was produced by RAxML (Randomized Axelerated Maximum Likelihood) methodology, in which nodes resolved by the whole cpDNA genomes were used to constrain well supported groups in the combined molecular phylogeny. RAxML uses maximum likelihood with tree search optimizations to evaluate tree topologies in distributed and parallel computer systems, which allows it to explore phylogenies with thousands of species (Stamatakis *et al.* 2005). All the lab work and analysis described above was done at the research lab of Dr. Jérôme Chave (Université Paul Sabatier, France).

I edited this resulting phylogeny by pruning all non-Neotropical species (i.e. species from Africa, Madagascar, and Asia), species without full taxonomic names, and species with no habitat classification. To focus the analysis on the Neotropical region, two genera with known Palaeotropical as well as Neotropical distribution, *Parinari* and *Chrysobalanus*, were also pruned from the original tree. Of the total 167 species, 62 species were pruned from the tree including the outgroup *Euphronia guianensis*, leaving 105 species for further analysis. This phylogenetic tree contained the monophyletic Neotropical clade of *Hirtella/Coupia/Licania/Gaulettia* which was dated using secondary calibration (Bardon *et al.* 2013) via relaxed penalized likelihood (Sanderson 2002). Secondary calibration uses ages dated in a previous study to calibrate the node ages and species divergence in another non-calibrated phylogenetic tree. Similar to Bayesian phylogenetic dating, penalized likelihood attempts to incorporate the intrinsic rate variation of different lineages in a phylogenetic tree (i.e. rate variation is minimized in neighbor branches). Instead of using statistical prior distributions on which to center the tree nodes and search for posterior probabilities as in Bayesian molecular dating, penalized likelihood uses a semi-parametric approach within a maximum likelihood framework with a smoothing parameter that penalizes rapid changes on the tree (Sanderson 2002).

The smoothing parameter was set to zero, which means that rate variation was allowed to vary as much as possible (Paradis *et al.* 2014). Minimum and maximum age constraints were specified on two nodes of the tree using dates reported in a previous study dealing with the whole family (Bardon *et al.* 2013). A hard minimum age bound was set to 54 Mys to represent the minimum age for the presence of Chrysobalanaceae in the New World as recovered by Bayesian phylogenetic dating (Bardon *et al.* 2013). A leaf fossil assigned to Hirtella found in Minas Gerais, Brazil, and dated from the Eocene (54-34 Mys), provided the minimum age (34 Mys) for the Hirtella clade. Therefore, the node containing *L. alba* and *L. michauxii* was set to bounds within 40-54 Mys, and the node containing *Hirtella davisii* and *Licania licaniiflora* was set to be constrained within 34-54 Mys. Bardon et al. (in prep.) have recently reviewed the fossil evidence for Chrysobalanaceae and concluded that most of the fossil data used in Bardon *et al.* (2013) is not reliable. This decision pushes the age constrain for the presence of the Neotropical clade in the New World to ca. 40 Mya. Because of the inherent uncertainty in fossil calibrations I kept the calibration process as in Bardon *et al.* (2013), which do not affect the ancestral reconstruction of edaphic preferences as would tree topology or the distribution of characters among the tips (Mooers & Schluter 1999). The Chrysobalanaceae chronogram was created using functions of the R statistical packages *phytools* (Revell 2015) and *ape* (Paradis *et al.* 2014).

4.3.6. Defining and classifying habitat specialists

Habitat selection can promote habitat specialization (Holt 1987) which in turn can be associated with tolerances to certain edaphic characteristics. In addition, there is a strong relationship between physiological tolerance and plant species distribution (Ackerly 2003). Therefore, the study of the evolution of physiological tolerance can provide important insights to understand the processes in species evolution. I classified habitat specialization of each species in the Sapotaceae and Chrysobalanaceae phylogenies according to their degree of tolerance or intolerance to white-sand soils in the Neotropics. Tolerance to nutrient-poor soils for each species in the phylogenies was based on the evidence of species occurrences on different habitat types as described in taxonomic monographs (Prance 1972, Pennington 1990) and habitat descriptions from herbarium labels available at the Missouri Botanical Garden (MBG) online database Tropicos (www.tropicos.org) supplemented with field experience for species occurring in the western Amazon region and Guyana.

An estimated 3,500 herbarium label specimens were checked in Tropicos to classify species in both families. In an attempt to be as comprehensive as possible and to reduce the possibility of white-sand false positives (i.e. species classified as a white-sand specialist when in reality it has a broader soil preference) the classification looked at the entire species distribution and associated habitat preferences across as many sources as possible. For related reasons, species with only one field collection record, or records ambiguously describing the habitat types where they were collected, were pruned from the phylogenetic trees before conducting the analysis.

I defined white-sand tolerant species as species reaching white-sand habitats across the Amazon, and Guiana regions but not restricted to them. White-sand intolerant species are species never found or reported from white-sand habitats. The white-sand tolerant species category was sub-divided according to their degree of habitat specialization to white-sand soils as: (1) white-sand specialist (WS-S): species restricted to white-sand soils, igapo/sandy beaches, coastal sand dunes or sandstone areas; (2) white-sand poor-soil specialist (WS-PSS): species occurring on white-sand soils but also on other less nutrient-poor soils like old clay terraces or sandy-clay soils; and (3) white-sand generalist (WS-G): species occurring in a variety of soils and habitat types including white-sand, clay, sandy-clay, flooded varzea forests, riparian forests, montane forests, roads and open areas. The definitions of the different sub-sets of white-sand tolerant species are in accord with the ones used in the phytogeographic analysis of Chapter 3. Two additional categories were included to accommodate the distribution of species never found on white-sands, namely: (4) non-white-sand-poor-soil specialist (NWS-PSS) and (5) non-white-sand generalist (NWS-G). These two latter categories constitute white-sand intolerant species as defined above.

4.3.7. Defining phylogenetic niche conservatism

Most species and clades only occupy certain environmental conditions which are determined by their intrinsic biological traits (e.g. physiological tolerances) and biotic interactions. The concept of the “niche” has been widely reviewed in the ecological literature (e.g. Whittaker *et al.* 1973, Chase & Leibold 2003, Peterson 2011). Here it is defined as a set of biotic or abiotic conditions that allow the persistence of species, which is Hutchinson’s “fundamental niche” (Holt & Gaines 1992, Pulliam 2000, Colwell & Rangel 2009). Because physiological tolerances are heritable traits shared by common ancestry they can provide important insights from analysis of patterns of trait evolution and speciation using phylogenetic trees. Harvey & Purvis (1991) coined the term “phylogenetic niche conservatism” to refer to one of the three components affecting the similarity of related species in a phylogeny; the two others being phylogenetic time lags and adaptive responses. If phylogenetic niche conservatism for tolerance to certain edaphic factors is important in the evolution of a clade, its ancestral condition will determine the range of habitats it can occupy. On the other hand, niche evolution (i.e. the expansion of niche breath or specialization to new habitats) is what allows invasion of new habitats and climatic regimes (Wiens & Donoghue 2004). Because species within a clade may have different distributional ranges, comparing the dynamics between niche conservatism and niche evolution within a clade may give us important insights into their biogeographic and diversification patterns (Wiens & Donoghue 2004). For the purposes of this study I define edaphic niche conservatism as the tendency of closely related species to retain their ancestral edaphic preferences over evolutionary time. This tendency can be studied by evaluating evolutionary outcomes reflected in well resolved phylogenetic trees. In this sense phylogenetic niche conservatism for edaphic conditions is studied here as an evolutionary pattern (Losos 2008, Crisp & Cook 2012, cf. Pyron *et al.* 2014) which can be the product of several evolutionary processes over time (Wiens 2004, Revell *et al.* 2008, Crisp & Cook 2012).

4.3.8. Studying the evolution of nutrient-poor soil tolerance

I studied the evolution of nutrient-poor soil tolerance by mapping the distribution of white-sand tolerant and intolerant species on the time-calibrated phylogenetic trees. In order to quantify the level of convergent evolution for edaphic niche conservatism across the trees I measured phylogenetic signal for nutrient-poor soil tolerance.

4.3.8.1. Measuring phylogenetic signal

One way to approach the study of evolutionary lability of a trait is by measuring how much of the traits shared by species in the phylogeny are explained by their evolutionary relatedness. Species traits, like tolerance to nutrient-poor soils or waterlogged soils, are not statistically independent because shared evolutionary history leads to shared phenotypic similarity (Felsenstein 1981, Harvey & Pagel 1991). In comparative studies of trait evolution among species we need to take into account this intrinsic property of molecular phylogenies in order to make sound evolutionary inferences.

Measurement of trait similarity patterns due to phylogenetic relatedness across a tree (e.g., correlated evolution due to edaphic niche conservatism) can be accomplished by estimating the “phylogenetic signal” for a trait in the dataset (Revell *et al.* 2008). Phylogenetic signal, also called phylogenetic constraint or phylogenetic inertia (but see Blomberg & Garland 2002 for reasons to avoid the use of these terms), is the tendency for related species to resemble each other more than they resemble species drawn at random from a phylogenetic tree (Freckleton *et al.* 2002, Losos 2008). There are several methods used to measure phylogenetic signal depending on the trait data at hand being continuous or discrete.

To measure phylogenetic signal in both datasets I used the phylogenetic D statistic developed by Fritz & Purvis (2010) for discrete binary characters as implanted in the *caper* R package (Orme *et al.* 2013). The D statistic tests for a significant association between the observed sum of sister clade differences across the entire phylogeny compared to (1) sum of sister-clade difference in phylogenies where the traits have been shuffled randomly a large number of times (e.g. 1,000 times) and (2) sum of sister-clade differences expected from a random phylogenetic pattern that follows a Brownian motion model of evolution (Fritz & Purvis 2010). This is the appropriate null model for testing phylogenetic signal of a character because we are interested in the evolution of the character state and the phylogenetic tree is fixed (Maddison & Slatkin 1991).

If the D statistic of phylogenetic signal is equal to “1” the trait across the phylogeny has a phylogenetically random distribution (lack of phylogenetic signal). If D is equal to “0”, the observed traits are clumped across the phylogeny (presence of phylogenetic signal) as if it followed a Brownian motion model during its evolution (Fritz & Purvis 2010). Because of the goal to explore the influence of habitat specialization through edaphic niche conservatism, the convergent evolution of tolerance to white-sand habitats was examined in two ways in both Sapotaceae and Chrysobalanaceae datasets: for white-sand specialists only (WS-S) and for any species inhabiting white-sands (WS-S+WS-PSS+WS-G).

4.3.9. Studying the evolution of habitat specialization to edaphic niches

4.3.9.1. Reconstructing edaphic trait evolution

I studied the evolution of habitat specialization by reconstructing the evolution of edaphic preferences into the five different edaphic substrates of each species in the phylogenies of Neotropical Sapotaceae and Chrysobalanaceae. Before starting the analysis, each phylogeny was pruned to be represented with only one accession per species. This was a necessary step because the assignment to different edaphic types was done per species and not per each accession in the phylogeny. A per species assignment was better suited to the purpose of studying edaphic niche evolution because it helps to include the edaphic preference over the entire species distribution in the coding of species habitat preferences as explained above.

From an initial 369 accessions (147 species) used in the phylogenetic reconstruction of Sapotaceae, 219 accessions were dropped from the phylogeny in order to have only one accession per species, full taxonomic identifications, only Neotropical species, and unambiguous habitat classification. The Chrysobalanaceae phylogeny had originally 167 accessions (154 species) with mostly one accession per species. As with Sapotaceae, 62 accessions, which included undetermined taxa, non-Neotropical species, and species with uncertain habitat classification, were pruned from the tree to leave only the Neotropical *Hirtella*/*Licania*/*Couepia*/*Gaulettia* clade. Accordingly, the study of tolerance and avoidance to nutrient-poor soils evolution in the Neotropics was conducted in 99 Sapotaceae and 105 Chrysobalanaceae species.

I used different levels of tolerance to nutrient-poor soils of each species as a discrete trait to differentiate five edaphic conditions which correspond to five states, as explained above: (1) white-sand specialist (WS-S), white-sand poor-soil specialist (WS-PSS), (3) white-sand generalist (WS-G), (4) non-white-sand-poor-soil specialist (NWS-PSS), and (5) non-white-sand generalist (NWS-G).

Ancestral character reconstruction (also known as character mapping or character optimization) (Omland 1999) is an important tool for understanding the evolution of traits in molecular phylogenies. Two general approaches have been developed which rely upon parsimony (Swofford & Maddison 1992), Bayesian (Bollback 2006) or maximum likelihood criteria (Schluter *et al.* 1997). Maximum parsimony reconstruction (MPR) attempts to reconstruct ancestral histories of character states at internal nodes of the tree in a way that minimizes the number of character changes of the observed character states (Paradis *et al.* 2004). MPR assumes that along any tree branch only a single character change has occurred and does not accommodate uncertainty in character state estimation. It may also perform poorly when the opportunity for character change is high and time elapsed is long (Mooers & Schluter 1999). It has also been shown that rapid evolution of a trait may mislead parsimony character reconstruction (Schultz *et al.* 1996, Omland 1999, Cunningham 1999). Only maximum likelihood reconstructions are presented and discussed in this study.

Pagel (1994) was the first to develop a method for tracing the evolutionary history of a discrete character along the branches of a phylogeny using maximum likelihood (Felsenstein 2004). For a discrete binary character, there will be two likelihoods of fixing a character, one when fixing the state at “1” and another when fixing the character state at “0” (Pagel 1997). The probability of moving from one character state to another is determined by a transition rate with integer values taken as indices of the parameters (Paradis *et al.* 2004).

Transition rates of characters states can be represented in unordered or ordered matrices with the “from” states on the rows, the “to” states in the columns and the diagonal containing the negative of the sum of the row rates, which are often simply represented by the symbol “-“ (O’Meara 2012). In a phylogenetic context, maximum likelihood estimates of character reconstruction represent the estimation of the parameter values (i.e. the transition probability between character states) that makes the observed data more likely given a model of evolution (Pagel 1997). Figure 21 contains the unordered transition rates of the five character states used here representing edaphic substrates in the Neotropics. In unordered matrices the order of character states in the transition matrix has no effect on how evolution modeling proceeds (i.e. a white-sand specialist can evolve to be a non-white-sand generalist in one step).

In the context of character evolution, model-based reconstruction means reconstructing the observed character states in a way that makes it most likely given a model of how the evolution of character may have proceeded (Pagel 1999). An important difference between parsimony and maximum likelihood reconstruction of character states is that maximum likelihood, unlike parsimony, takes into account tree branch lengths, thus when some part of the tree has shorter branch lengths it will adjust for this and not assume that they will have a similar amount of change as larger branch lengths of the tree (Felsenstein 2004).

For three or more character states the number of possible models is very large but character evolution can be approximated by assessing three general models: "ER" for the equal-rates model (a single parameter for all transitions), "SYM" for the symmetrical model (a forward and reverse transition share the same parameter but each transition has a different probability), and "ARD" for the all-rates-different model (different parameters for forward and reverse for all transitions) (Paradis 2004). This character matrix of indices (e.g. white-sand specialist = 1, white-sand poor-soil specialist = 2) is used to fit a Continuous Time Markov Chain Finite State Space (CTMC-FSS) model with maximum likelihood methods.

Figure 21. Unordered transition rate matrices with the five character states used in maximum likelihood ancestral character reconstruction. a) ER = equal rates, b) SYM = symmetrical rates, c) ARD = all rates different. 1 = WS-S (white-sand specialist), 2 = WS-PSS (white-sand poor-soil specialist), 3 = NWS-PSS (non-white-sand poor-soil specialist), 4 = NWS-G (non-white-sand generalist), 5 = WS-G (white-sand generalist).

a)	To:					
		1	**2**	**3**	**4**	**5**
From:	**1**	-	1	1	1	1
	2	1	-	1	1	1
	3	1	1	-	1	1
	4	1	1	1	-	1
	5	1	1	1	1	-

b)	To:					
		1	**2**	**3**	**4**	**5**
From:	**1**	-	1	2	3	4
	2	1	-	5	6	7
	3	2	5	-	8	9
	4	3	6	8	-	10
	5	4	7	9	10	-

c)	To:					
		1	**2**	**3**	**4**	**5**
From:	**1**	-	5	9	13	17
	2	1	-	10	14	18
	3	2	6	-	15	19
	4	3	7	11	-	20
	5	4	8	12	16	-

CTMC-FSS is a random simulation process in which the probability to change into the next state depends only on the present state—the Markov property (O'Meara 2012). The Markov process is used to model state transitions of discrete data, with random walks in continuous time as the explicit evolutionary model (Schluter et al. 1997). The random nature of the Markov model is known to capture many of the complexities of the evolutionary process (Schluter *et al.* 1997, Pagel 1999, Ronquist 2004).

To specialize into white-sand soils (or to be white-sand tolerant) may require certain physiological pre-adaptations, trade-offs, or genetic backgrounds (Fine *et al.* 2006; Lamarre *et al.* 2012) that may prove fruitful to be incorporated into models of edaphic character evolution. For example, we can assume that evolving from a white-sand generalist (or from a white-sand poor-soil specialist) into a white-sand specialist is easier (i.e. require less steps) than evolving from a non-white-sand generalist. On the other hand, in order for a non-white-sand generalist to become a white-sand specialist it has to pass alternate states before it can evolve into a white-sand specialist.

I investigated these possibilities by using an ordered transition matrix where consecutive states are assumed to be neighbouring states (i.e. one state has to pass a neighbouring intermediate state in order to change to a subsequent state) and certain transitions between states were not allowed (Figure 2). Given that both Neotropical Sapotaceae and Chrysobalanaceae arrived into the New World at least 54 Mya (Bartish *et al.* 2011; Bardon *et al.* 2013), when edaphic conditions were dominated by nutrient-poor Guiana-Shield sediments (Chapter 2), the assumption of gradual changes among nutrient-poor conditions and weights against certain transitions may hold for studying their habitat evolution.

In the context of this study this means that transitions from certain edaphic states were allowed to occur in the simulations whereas others were prohibited (i.e. transitions from white-sand specialist state to any non-white-sand state were not allowed; transitions from white-sand poor-soil specialist to non-white-sand generalist were not allowed; any states were allowed to transition to a white-sand generalist state). This rationale for coding and weighting of character states has a biological and biogeographical basis and was represented by the order of the character code in the transition matrices (Figure 22).

In order to evaluate which model of character evolution (each with its own transition matrix) in each family was more appropriate for evolutionary inference based on current species edaphic preference, they were model-fitted using maximum likelihood. This analysis was done for both the ordered and unordered matrices. Fitted models are usually evaluated by comparing metrics that balance the likelihood of models with the number of estimated parameters, including: lnL (log-likelihood), AIC (Akaike Information Criterion), and AICc (Akaike Information Criterion corrected for small sample sizes).

Figure 22. Ordered transition rate matrices with the five character states used in maximum likelihood ancestral character reconstruction. a) ER = equal rates, b) SYM = symmetrical rates, c) ARD = all rates different. 1 = WS-S (white-sand specialist), 2 = WS-PSS (white-sand poor-soil specialist), 3 = NWS-PSS (non-white-sand poor-soil specialist), 4 = NWS-G (non-white-sand generalist), 5 = WS-G (white-sand generalist). “0” scores in the transition rates matrices mean corresponding transitions are prohibited.

a)	To:					
From:		**1**	**2**	**3**	**4**	**5**
	1	-	1	0	0	1
	2	1	-	1	0	1
	3	0	1	-	1	1
	4	0	0	1	-	1
	5	1	1	1	1	-

b)	To:					
From:		**1**	**2**	**3**	**4**	**5**
	1	-	1	0	0	4
	2	1	-	2	0	5
	3	0	2	-	3	6
	4	0	0	3	-	7
	5	4	5	6	7	-

c)	To:					
From:		**1**	**2**	**3**	**4**	**5**
	1	-	3	0	0	11
	2	1	-	6	0	12
	3	0	4	-	9	13
	4	0	0	7	-	14
	5	2	5	8	10	-

In general, adding complexity to a model will increase its likelihood (lnL), but choosing the model with the highest lnL does not guarantee it is the best model for the data. On the other hand, AIC favors less complex models to avoid over-fitting; models with lower AIC (or AICc) values are preferred because they are a good approximation of the information in the data (Anderson 2007). Since the number of samples (species number) in both studied families was much larger (i.e. each family had around 100 species) than parameters in all evaluated models, AIC scores converged to AICc scores. Thus only AIC scores were used here for model evaluation.

I plotted the resulting marginal likelihoods of character change obtained from the five states at each node in the phylogeny using pie diagrams. The analyses of character state estimations with maximum likelihood, and the fitting of the six models (ER, SYM, ARD, unordered ER, unordered SYM, unordered ARD) to the transition probabilities of the different species groups was executed in the R package *geiger* (Harmon *et al.* 2014). Ancestral state reconstructions at nodes onto the phylogenies under the different models were implemented in the R package APE (Paradis *et al.* 2004).

4.4. Results

4.4.1. Phylogenetic patterns

Tolerance to white-sand soils has evolved repeatedly in the evolutionary history of Neotropical Sapotaceae and Chrysobalanaceae as shown by the scatter of white-sand species across the phylogenetic trees. Even though both Sapotaceae and Chrysobalanaceae can be classified as nutrient-poor tolerant families due to their number of white-sand tolerant species, there were a larger number of white-sand specialists in Chrysobalanaceae compared to Sapotaceae (Figure 23, and 24).

Figure 23. Distribution of nutrient-poor tolerant taxa (red branches) in the phylogeny of Neotropical Sapotaceae. Asterisks indicate white-sand specialist species (WS-S). Clades in red, with their subtending stem branch, are those that are comprised entirely of species that are tolerant of white sand soils. Scale in millions of years.

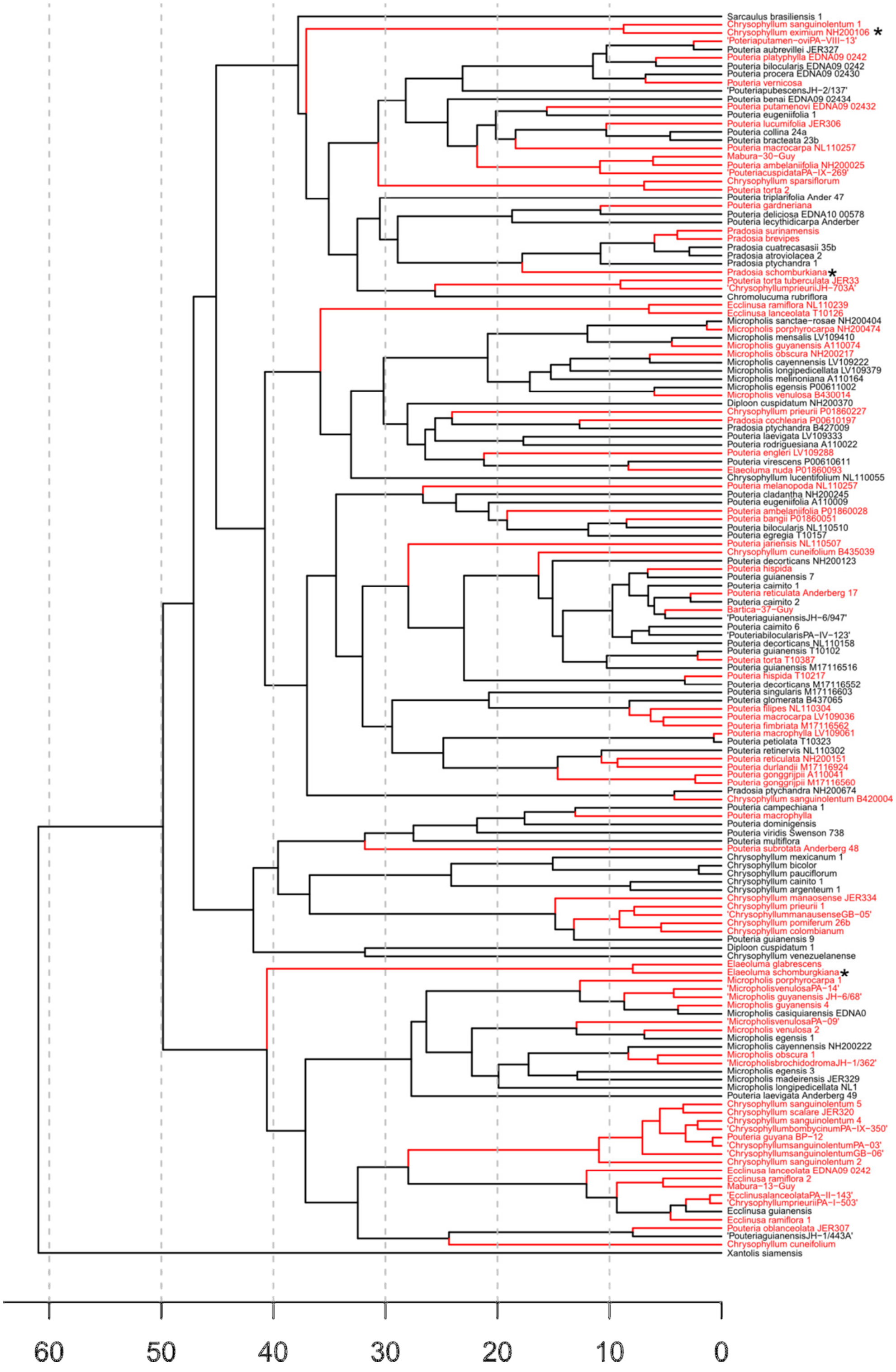


Figure 24. Distribution of nutrient-poor tolerant taxa (red branches) in the phylogeny of Neotropical Chrysobalanaceae. Asterisks indicate white-sand specialist species (WS-S). Clades in red, with their subtending stem branch, are those that are comprised entirely of species that are tolerant of white sand soils. Scale in millions of years.

A total of 80 white-sand tolerant species was found in Sapotaceae (out of 99 species analyzed) with only three found to be white-sand specialists compared to 59 white-sand tolerant species in Chrysobalanaceae (out of 105 species analyzed) with 14 species classified as white-sand specialists. No white-sand specialists in both families were found to be early branching divergent taxa in the phylogenetic trees (Figure 23, and 24).

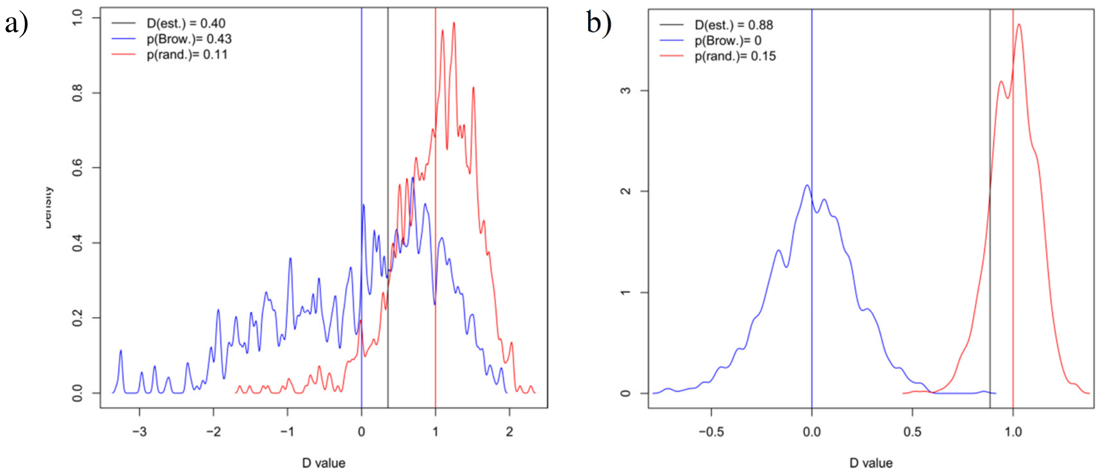
4.4.2. Phylogenetic signal

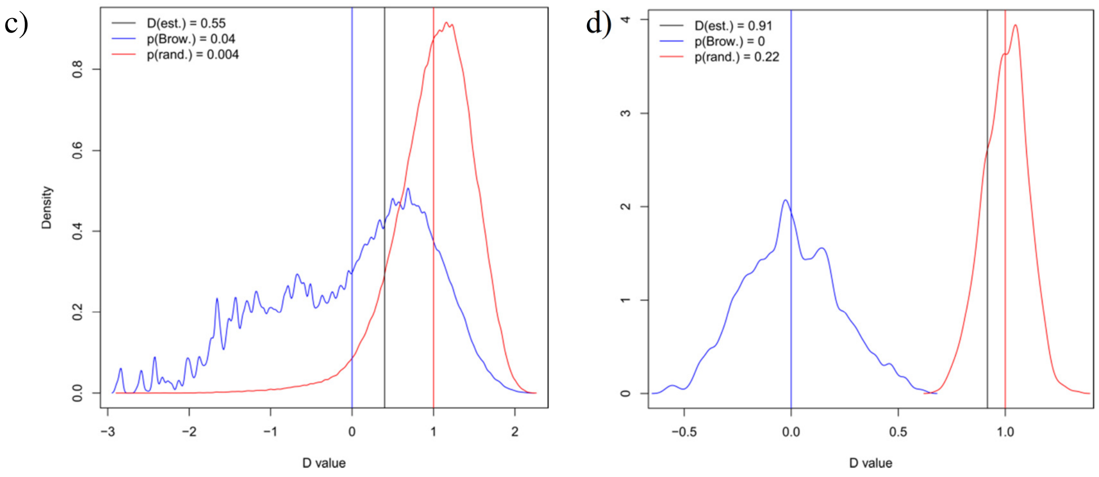
I found that tolerance to nutrient-poor soils was not correlated with phylogenetic history in both Sapotaceae and Chrysobalanaceae (Figure 5, and 6). Nutrient-poor soil tolerance was found to be a highly labile trait in both families as measured by the D statistic, which tended strongly towards a lack of phylogenetic signal (Sapotaceae estimated D = 0.88, p(Brownian) = 0, p(random) = 0.15; Chrysobalanaceae estimated D = 0.91, p(Brownian) = 0, p(random) = 0.22).

There was a lack of phylogenetic signal for white-sand specialism in Sapotaceae (D estimated = 0.40; p(Brownian) = 0.43; p(random) = 0.11. There was a significant strength for randomness in the evolution of phylogenetic signal for white-sand specialization in Chrysobalanaceae (D estimated = 0.55; p(Brownian) =0.04, p(random) = 0.004). The scatter in the phylogenetic distribution of white-sand specialists due to low number of species in this category made the frequency of the density plots in both expected models (Brownian and random) less clear cut and noisy than the frequency distribution for nutrient-poor soil tolerance in both families (Figure 25a, and 25c).

The lack of phylogenetic signal was found at the three sub-sets of the datasets representing distinct levels of habitat specialization in each family: with only white-sand specialists, with all white-sand tolerant species, or white-sand intolerant species (only the first two are shown in Figure 25). Given the differences in tolerant and specialist species in both Sapotaceae and Chrysobalanaceae, the finding of lack of phylogenetic signal in both families further strengthens the result that niche conservatism to edaphic conditions in Neotropical trees is a highly labile trait.

Figure 25. Density plots of the distribution of the simulations of the nutrient-poor soil tolerance trait under Brownian and random models for both Sapotaceae (a-b) and Chrysobalanaceae (c-d). a) Sapotaceae WS-S, b) Sapotaceae WS-tolerant, c) Chrysobalanaceae WS-S, d) Chrysobalanaceae WS-tolerant. D(est.) = D estimated, p(Brow.) = probability of estimated D resulting from a Brownian process (presence of phylogenetic signal), p(rand.) = probability of estimated D resulting from random phylogenetic structure (lack of phylogenetic signal).





4.4.3. Ancestral edaphic reconstruction

Model selection of edaphic trait evolution under different evolutionary models favored the ordered rate matrices, with a symmetrical rate model (ordered SYM) favored in Sapotaceae and an all-rates-different model (ordered ARD) favored in Chrysobalanaceae as measured by the AIC scores (Table 8). Accordingly, the character state reconstruction of these two models are presented and discussed below.

Table 8. AIC scores in ascending order of the evaluated ancestral habitat reconstruction models. ER = equal rates, SYM = symmetrical, ARD = all rates different, ord. = ordered model, unord. = unordered model. Lowest AIC scores suggest the preferred model according to the data.

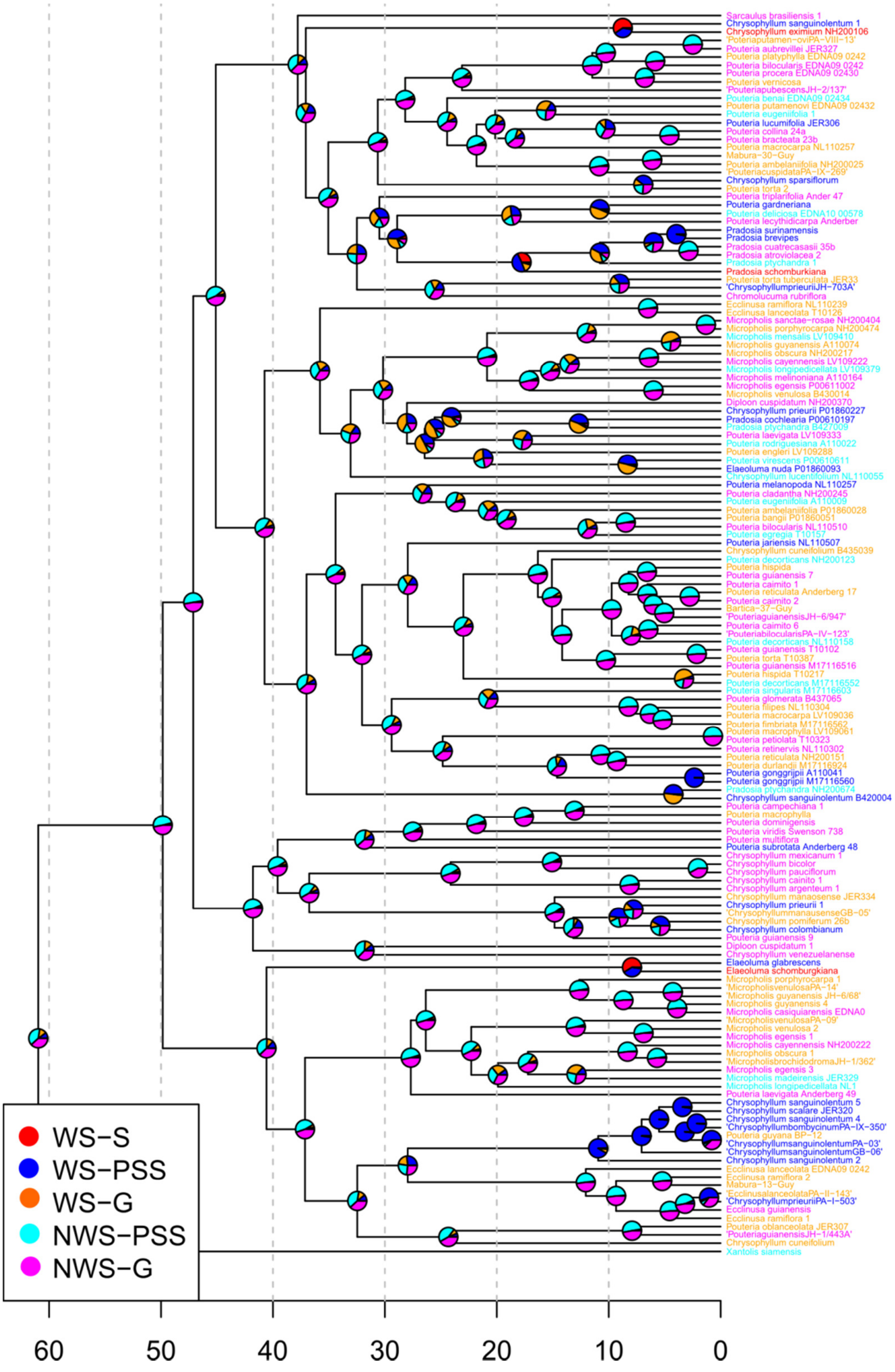
Sapotaceae		**Chrysobalanaceae**	
Model	**AIC**	**Model**	**AIC**
ord. SYM	415.5439	ord. ARD	339.7559
unord. SYM	421.5439	unord. ER	339.9851
ord. ARD	424.2028	ord. ER	340.2486
unord. ARD	436.1816	ord. SYM	341.1941
ord. ER	452.2659	unord. SYM	344.6436
ER	475.9077	unord. ARD	348.5013

4.4.3.1. Sapotaceae ancestral edaphic character reconstruction

Maximum likelihood reconstruction of white-sand species tolerance across the phylogeny of Sapotaceae using an ordered symmetric model (ord. SYM) shows that a non-white-sand condition was the most likely ancestral state in the family (Figure 8). This non-white-sand condition appears to have shifted towards nutrient-poor soil tolerance around 32 Mya and with the first appearance of white-sand poor-soil specialists 28-25 Mya (Figure 26).

The ancestral reconstruction for two Sapotaceae white-sand specialists (*Chrysophyllum eximium*, *Elaeoluma schomburgkiana*) shows that their most likely recent ancestor was a white-sand specialist whereas the ancestral state for *Pradosia schomburgkiana* was recovered to be white-sand tolerant, with no clear certainty whether its most recent ancestor was a white-sand generalist or a white-sand poor-soil specialist. As with other species in the family, deeper in the tree all three white-sand specialists likely evolved from non-white-sand ancestors (Figure 26). In Sapotaceae, the ancestral reconstruction of white-sand specialism shows that it probably evolved in the last 18-8 Mys whereas the non-white-sand condition is much older, going back to the arrival of the family into the New World (ca. 55 Mya) (Figure 26).

Figure 26. Maximum likelihood ancestral reconstruction of edaphic preferences in Neotropical Sapotaceae (ordered SYM model). Areas of pies indicate the relative support for different ancestors. Color of pies and taxa coded as in Figure 3. Scale in millions of years.

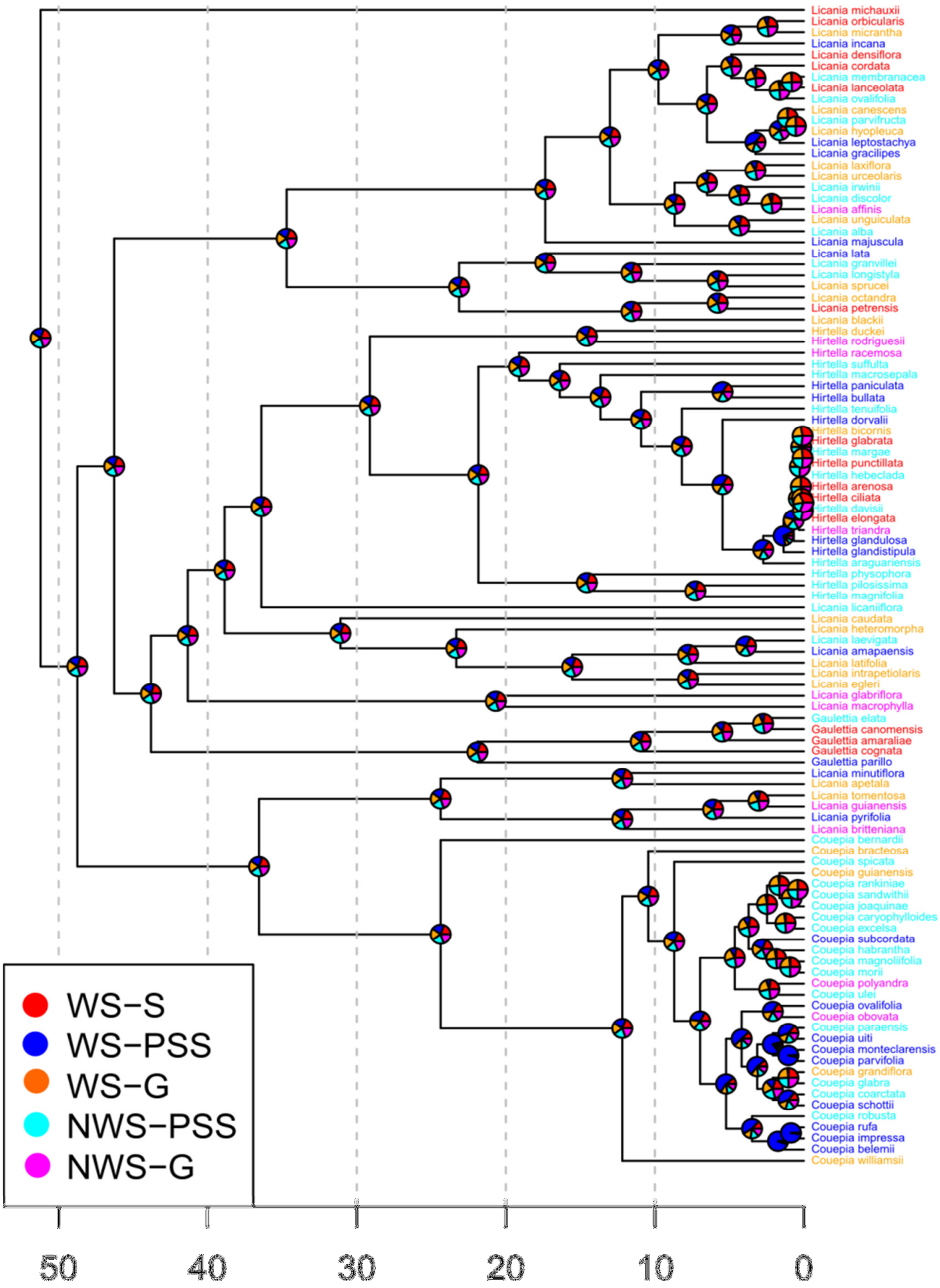


4.4.3.2. Chrysobalanaceae ancestral edaphic character reconstruction

In contrast to Sapotaceae, the overall pattern of ancestral edaphic reconstruction in Chrysobalanaceae shows that white-sand tolerance has been the norm across the evolution in the family (Figure 27). Although it is not clear which edaphic group within the white-sand tolerance is more likely, the summation of marginal likelihoods in the supported ARD model shows that white-sand tolerant states (WS-S + WS-PSS + WS-G) are always higher compared to non-white-sand tolerant states (NWS-PSS + NWS + G) across all nodes in the phylogeny (Figure 27).

The edaphic ancestral state reconstruction in Chrysobalanaceae indicates that there is a high likelihood that white-sand specialists and non-white-sand species in this family have evolved from any of the white-sand tolerant groups (WS-S, WS-PSS, or WS-G). The origin of white-sand specialist species in Neotropical Chrysobalanaceae seems to be a recent event compared to Sapotaceae, occurring mostly toward the tips of the phylogeny, within the last 11 Mys or younger (ca. 2 Mya) in the case of a subset of the *Hirtella* clade (Figure 27).

Figure 27. Maximum likelihood ancestral reconstruction of edaphic preferences in Neotropical Chrysobalanaceae (ordered ARD model). Areas of pies indicate the relative support for different ancestors. Color of pies and taxa coded as in Figure 3. Scale in millions of years.



4.5. Discussion

4.5.1. Phylogenetic signal for nutrient-poor soil tolerance and niche evolution

In studying the evolution of habitat specialization in closely related species of Neotropical Sapotaceae and Chrysobalanaceae I measured the strength of the phylogenetic signal for nutrient-poor soil tolerance. This tolerance was based on the species occurrence on white-sand or non-white-sand soils. Phylogenetic signal for this complex trait was generally weak or absent, which suggest that species evolution in these families has not been constrained by their habitat preferences or edaphic tolerances. My results are therefore not in accord with the idea that species niche conservatism for ancestral ecological conditions has been fundamental in the accumulation of species diversity in Neotropical lowland plant lineages (cf. Ackerly 2003, Wiens & Donoghue 2004).

The reconstruction of the ancestral edaphic preferences within these families gives us a better indication of how it may have influenced its present diversity and biogeographic patterns. In order for a species to diverge from its ancestral edaphic preference (i.e. niche evolution) edaphic niche lability may be a requirement. However, most of these speciation events promoted by habitat switching in a clade may occur when clades invade geographies that possess habitats not too extreme from their ancestral habitat preferences. This is because when gradual spatial gradients in space and time in the environment deviate only slightly from the ancestral niches of species, it allows species populations to evolve (and avoid extinction) compared to sharp habitats transitions (Holt & Gaines 1992). My results of the evolution of ancestral edaphic preferences (Table 1, Figures 8, and 9) in both families support this theoretical expectation and suggest that whilst there has been a lot of habitat switching, this tend to be amongst similar edaphic conditions, towards poor-nutrient edaphic preferences for Chrysobalanaceae, and towards non-poor-nutrient edaphic preferences for Sapotaceae.

4.5.2. The origin and evolution of white-sand specialists and white-sand tolerant lineages

The phylogenetic pattern for nutrient-poor tolerance is widespread in both studied families (Figure 23 and 24). In this context, Arenosol and Podzol soils represent only 4.7% (34.1 million of hectares) of the Amazon and Guiana Shield regions, whereas less nutrient-poor soils like Ferralsol accounts for about 235 million hectares (32% of the Amazon and Guiana Shield combined), and distributed mostly in the eastern Amazon (Chapter 2). In essence, Arenosol-, Podzol-, and Ferralsol-dominated habitats may constitute the fundamental edaphic niche for Guiana-centered taxa, with the two first soil classes representing the most extreme edaphic classes. Previous floristic and phytogeographic analyses have shown that both Sapotaceae and Chrysobalanaceae have their abundance, endemism and most of their diversity biased towards the Guiana Shield region (Prance & White 1988, Terborgh & Andresen 1998, ter Steege *et al.* 2000, Hopkins 2007). This would suggest that the large extension of oligotrophic habitats in this region may have favored the evolution of these families within the range of their fundamental edaphic niche.

On the other hand Chrysobalanaceae had more white-sand specialists than Sapotaceae. The fact that some lineages have more white-sand specialists suggest that within Neotropical lineages, some clades are more likely to evolve specialist species than others (Futuyma & Moreno 1988). Alternatively, extinction rates may be higher in white-sand specialists or that once this complex trait is lost in the evolution of a lineage it is difficult to be regained. Both Sapotaceae and Chrysobalanaceae chronograms show that white-sand specialists in these Neotropical clades evolved relatively recently (18-8 Mya and 8-2 Ma respectively) (Figures 26 and 27). This is a period within the range of the rising of Amazon and the extinction of Pebas mega-lake (Chapter 2). Studies in Amazonian Protieae trees (Burseraceae) have also found that white-sand specialism is a derived trait in *Protium*, with white-sand specialists nested within non-white-sand clades (Fine *et al.* 2005). White-sand specialism on the other hand may have evolved early or later in the history of Neotropical plant groups, and only a more inclusive ancestral edaphic reconstruction—sampling very widely taxonomically—may help us clarify further deep in its evolutionary history.

The Neotropical region has been enriched by plant lineages that penetrated it at different times in history and arriving from various regions using different biogeographical routes. These historical contingencies may have affected species adaptive diversification, with certain clades being more successful than others in diversifying on different habitat types including oligotrophic habitats. For instance, Lauraceae eco-geographical diversification in the Neotropics may provide one example of this pattern. This family is a temperate plant group that has at least 11 species endemic to western Amazonian white-sand forests belonging to six different genera (R. García-Villacorta, unpub.). Lauraceae was not part of the Guiana-Shield flora stock that reached towards white-sand habitats in the Amazon after they developed (Kubitzki 1989). With more than 1,000 extant species, Lauraceae reached South America from the North and radiated there both in the lowlands and highlands since the early Miocene, 20 Mya (Rohwer & Kubitzki 1993, Chanderbali *et al.* 2001).

On the other hand it is also possible that specialization to nutrient-poor soils may be an evolutionary dead end (Simpson 1943), not spurring the same level of species proliferation as other oligotrophic tolerant species that can switch between habitats more frequently as conditions change. *Potalia* (Gentianaceae) and *Lissocarpa* (Ebenaceae) represent two interesting cases of small clades with white-sand specialists that diversified preferentially on nutrient-poor substrates. Frasier *et al.* (2008) studied the phylogenetic relationships in *Potalia* and found that white-sand Amazonian lowland *Potalia* were early branching members in the phylogeny along with western Guiana Shield species, whereas non-white-sand species were sister lineages that diversified in younger Andean-sourced soils. The minimum age for the presence of *Potalia* in the Neotropics is the middle Eocene (ca. 48-37 Mya) (Frasier *et al.* 2008) well before Lauraceae reached South America; the *Potalia* clade, however, did not reach anything near the level of species diversity as Lauraceae. The small clade in the mono-generic sub-family *Lissocarpoideae* (eight species, Ebenaceae) provides a similar phylogenetic pattern of a clade that occurs preferentially on white-sand substrates in the Neotropics that has not diversified at similar pace as its sister clade *Diospyros*. This genus is endemic to South America (Duangjai *et al.* 2009) and speciated mainly on extremely nutrient-poor substrates (i.e. white-sand soils, Andean sandstones) with few species occurring on clayey soils (Wallnöfer & Halbritter 2003) (Chapter 5). Similar to *Potalia*, *Lissocarpa* is an early branching clade within the Ebenaceae family that did not reached the level of diversity as its sister pantropical clade *Diospyros* (~500 species) despite being hypothesized to have a Gondwanan origin (Raven & Axelrod 1974, Duangjai *et al.* 2009). The timing and route taken to reach South America between these three nutrient-poor tolerant lineages (Lauraceae, *Potalia*, and *Lissocarpa*) may have impacted their diversification patterns and influenced their extant species diversity.

In any case, because of their small size *Potalia* (nine species total), *Lissocarpa* (8 species total) and similar white-sand specialist lineages may not be representative of Amazonian species diversification related to habitat specialization to different edaphic conditions. They instead may prove useful to understand how certain clades diversify from an ancestral preference for extreme nutrient-poor soils to less oligotrophic habitats. These taxa are also important in terms of local endemism in the areas where they occur (e.g. Frasier *et al.* 2008; Wallnöfer & Halbritter 2003).

In this study white-sand specialists were not clustered, but scattered across the phylogenies, which indicates that white-sand specialists evolved multiple times from different edaphic ancestors within the two studied families. Also, white-sand tolerance was a widespread and evolutionary labile trait in both families. Together, these results give support to the hypothesis of ecological speciation by filling different edaphic niches (Gentry 1981) which may be facilitated by edaphic niche lability. Consequently, there is weak support for the idea that closely related species diversified confined to their preferred habitat type (Kubitzki 1989, 1990). The Guiana Shield however may have been an important source area for Amazonian plant taxa after the extinction of the Pebas mega-lake and the formation of modern Amazonia (Antonelli *et al.* 2009, Roncal *et al.* 2013), only that adaptive diversification was largely not constrained by their ancestral specific habitat preferences.

In general, I suggest that tolerance to nutrient-poor habitats has evolved repeatedly in other Neotropical plants groups that had a genetic background for nutrient-poor tolerance. Few early branching, nutrient-poor clades (e.g. *Potalia*) may have retaining this ancestral condition (i.e. may show higher levels of edaphic niche conservatism). In the majority of cases, like in Sapotaceae and Chrysobalanaceae, white-sand specialists evolved early or at later stages from poor-soil tolerant or relatively intolerant Neotropical ancestors. Tolerance to stressed hydro-edaphic conditions may be ancestral or derived trait within a bigger clade, like Chrysobalanaceae, which has allowed them to occupy and speciate whithin their range of ancestral habitat conditions in tropical environments. The latter is shown in some members of the the *Hirtella* clade that includes *H. arenosa* which represents a transition from a non-white-specialist (Figure 27).

An analysis at higher phylogenetic levels (e.g. genera) may prove fruitful to assess this deeper level effect that edaphic niche conservatism may have in certain clades. I would predict that within lowland Neotropical clades tolerance to nutrient-poor soils has evolved multiple times (i.e. it is highly labile trait) but it is not randomly distributed, with some clades being more prone to evolve white-sand tolerant and white-sand specialist taxa while other clades tracking more tightly their ancestral edaphic conditions.

4.5.3. Phylogenetic signal in complex traits and functional trade-offs

Lack of phylogenetic signal in a trait does not mean that species will not exhibit phylogenetic signal for other characters that may be related to the trait. This is especially true for a complex trait like tolerance to nutrient-poor habitats in which taxa must have developed (or had in their ancestral genetic background) physical, physiological, and chemical adaptations to inhabit these habitats. These adaptations may affect each other and include: adaptations to drought (Brunig 1969, Sobrado 2009), adaptations to growth on nutrient-poor soils (Jordan 1985, Cuevas & Medina 1988, Medina *et al.* 1990), adaptation to waterlogged soils (Bongers *et al.* 1985, Coomes & Grubb 1996, Proctor 1999); and adaptation to germinating on extremely phyto-toxic and acidic soils (Janzen 1974, Proctor 1999, Luizão *et al.* 2007). Even though these adaptive traits are listed individually above, several studies in controlled and natural populations have documented that a few genes can be responsible for changes associated with habitat switching and other ecological transitions (Schemske & Bradshaw 1999, Bradshaw & Schemske 2003, Levin 2009).

On this line, the acquisition of certain ecological traits may favor ecological transitions towards habitat specialization. For instance, the acquisition of ecological traits for tolerance to drought or flooding in plants may favor habitat specialization in these habitats. Using a combination of field measurements coupled with ancestral state reconstructions of species soil transitions in molecular phylogenies, Cacho & Strauss (2014) showed that adaptation to open habitats was the evolutionary precursor towards specialization to California ultramafic soils (i.e. tolerance to open areas evolved before tolerance to soils). Similar results of pre-adaptive traits that enhanced diversification are inferred in the evolution of C_4 photosynthesis from C_3 photosynthesis in flowering plants and grasses (Osborne & Freckleton 2009, Christin *et al.* 2013). In the case of the Neotropical taxa studied here, it would be interesting to investigate whether the evolution of habitat specialization to certain habitat types was facilitated by first acquiring certain traits, especially traits that confer tolerance to drought and flooding. It will also be important to test whether habitat shift has preceded the evolution of traits that confer tolerance to different habitat types (cf. Huttunen *et al.* 2012).

Phylogenetic signal may be low when the evolutionary history of a group has filled all niches due to the long time since its evolution. Alternatively, a trait may lack phylogenetic signal if it has recently evolved as has been suggested for chemical defenses in *Inga* (Kursar *et al.* 2009), and habitat preferences in *Quercus* (Cavender-Bares *et al.* 2004). Plant defenses (different chemical combinations as well as physical defenses) in several Amazonian genera in which species pairs occupied nutrient-poor or richer soils were found to be phylogenetically constrained with white-sand species having higher total defense investment compared to clay specialists (Fine *et al.* 2006). However, since the studied genera had a variety of defensive options to choose from, protection effect or growth were found to be phylogenetically labile which result in species not constrained to a particular soil type (Fine *et al.* 2006).

A variety of ecological traits may trade-off amongst each other in order to allow growth on different habitat types. Tolerance for nutrient poor-soils in particular may work in association with traits that confer tolerance to flooding (or anoxic conditions) and drought conditions. The presence of a hardpan layer close to the soil surface makes some white-sand habitats prone to have waterlogged conditions, whereas the existence of well-drained Arenosols makes water-stress a permanent feature in others (Chapter 2). Given that most of the South American oligotrophic flora may have originated in the Guiana and Brazilian Shield regions, its associated black-water seasonally flooded habitats (i.e. igapo forests) may have also been a permanent feature in the evolution of this oligotrophic flora (Kubitzki 1989). Other functional and ecological traits that may be important in trading-off among each other to occupy and speciate on these environments include flowering time (Savolainen *et al.* 2006), seed size (Hammond & Brown 1995, Coomes & Grubb 1996, ter Steege & Hammond 2001), dispersal syndrome (Macedo & Prance 1978, Arbeláez & Parrado-Rosselli 2005), plant height (Brunbjerg *et al.* 2014), root, stem and leaf tissue (Fortunel *et al.* 2012), and wood density (Chave *et al.* 2006, Swenson & Enquist 2007, Wright *et al.* 2007, Fortunel *et al.* 2012, Quesada *et al.* 2012).

Ecological studies of functional traits have shown that white-sand forest in Amazonia are functionally distinct compared to terra firme and flooded forests (e.g. Fortunel *et al.* 2014) and in this study I have shown that white-sand tolerant and white-sand specialists of the western Amazon region are phytogeographically closer to seasonally dry forests, savanna habitats, and Guiana Shield ecoregions containing black-water ecosystems compared to other regions (Chapter 3). In this regard, the western side of the Amazon holds more fertile soils than eastern Amazonia (e.g. Quesada *et al.* 2010, 2011) which may have an effect on eco-physiological traits with regional consequences for species evolution.

These functional and ecological traits may contain important phylogenetic information related to adaptations to different habitat conditions that may be correlated with their evolution and diversification. For instance, slow growth in Amazonian and Guiana Shield oligotrophic habitats correlates well with high wood density in Amazonian trees (Baker *et al.* 2004, ter Steege *et al.* 2006, Quesada *et al.* 2012) and there is an association between diversification rates and high generation times in some western Amazon tree lineages (Baker *et al.* 2014). Also, because deep clay soils with higher water-holding capacity are common in eastern and southern Amazonia compared to western Amazonia, species in these regions are able to extract water during the dry season which favors a semi-evergreen or deciduous habit (Lloyd *et al.* 2009). The spatial and temporal distribution of these eco-geographical factors may have had an important effect in the evolution of plant habitat specialization and hence in the evolution of clades distributed in certain geographic regions and habitat types.

4.5.4. Evolutionary processes and habitat switching

Lack of phylogenetic signal for edaphic preferences detected in both phylogenies suggest that this complex trait has been subject to some kind of selection pressure (different conditions of stabilizing selection or divergent selection) or lineages experiencing environments that increased their rates of niche shifts initially with a later slowdown, or with initial high rates of genetic drift; all of which are conducive to low phylogenetic signal over time (Revell *et al.* 2008, Crisp & Cook 2012). For these reasons it would be difficult to infer evolutionary processes responsible for the phylogenetic lability to nutrient-poor conditions by only measuring phylogenetic signal. However, the reconstruction of the phylogenetic history of the five edaphic conditions studied under different evolutionary models provides additional insights, along with phylogenetic signal, to suggest that niche lability may have facilitated niche evolution via habitat switching and other associated ecological shifts. The pervasive presence of niche lability for edaphic preferences may have promoted species accumulation via ecological speciation in these clades.

From an evolutionary standpoint it is appropriate to ask why edaphic niche lability would be so pervasive in the studied Neotropical plants. Due to the vastness of the Amazonian biome with no apparent physical barrier to split species populations to promote allopatric speciation, the lability for edaphic preference may help to take advantage of ecological opportunities in terms of habitat occupation and speciation when opportunities arise. Phylogenetic niche lability of Neotropical plant species may be a reflection of the geological dynamism that has prevailed since the Miocene in the Neotropical region, when new, cation-rich sediments and the expansion of riparian and seasonally flooded habitats created new ecological opportunities for species adaptive diversification. In the studied families, tolerance to nutrient-poor edaphic conditions is found in a large number of their component species (Figure 23, and 24). Unlike phylogenetic structuring usually found when studying diversification patterns due to climatic niche conservatism induced by physiographic heterogeneity (Pennington *et al.* 2010, Särkinen *et al.* 2012) or biome shifting (Crisp *et al.* 2009, De-Nova *et al.* 2012, Dick & Toby Pennington 2012, Donoghue & Edwards 2014) the lack of phylogenetic niche conservatism and lack of geographical structuring for edaphic preferences in the studied phylogenies points to a role of habitat switching in the accumulation of species within the Neotropics. Changes in habitat heterogeneity in space and time in the Neotropical lowlands may have provided opportunities to different plant lineages for habitat switching facilitated by niche lability for edaphic preferences.

Ecological speciation occurs when ecological differences between populations arise due to biotic or abiotic environmental factors conducive to independent genetic pools in the presence of gene flow (Schluter 2000, Nosil 2012). The mapped habitat preferences and switching patterns in the studied phylogenies provide important insights into the evolution of Neotropical plants. In order for a lineage to enter or invade new adaptive zones or niches, the ability to switch habitats without strong physiological constraints, at least within a certain range of their fundamental niche, may be a requirement for subsequent lineage diversification. Invasion of new edaphic conditions may result in the formation of new adaptive genotypes, perhaps via hybridization (Rieseberg *et al.* 2003, Nosil 2008, Papadopulos *et al.* 2013, Misiewicz & Fine 2014). Lineage diversification in Neotropical lowland regions then would not result from the classical adaptive radiation documented for oceanic islands (e.g. Baldwin & Sanderson 1998) or high elevation systems (Hughes & Eastwood 2006, Madriñán *et al.* 2013) in which closely related species diversify by occupying different niches within a certain shared temporal frame, but instead be the product of species accumulation by continuous habitat shift over evolutionary time.

4.5.5. Ancestral edaphic state reconstructions models

There will always be uncertainty in the estimation of character evolution in phylogenetic trees. Given a phylogenetic tree and a transition matrix with character states different than zero, any transition state can be possible only that some are more likely (Harvey & Pagel 1991). According to AIC scores the preferred models of edaphic trait evolution with the analyzed phylogenetic datasets were transitions matrices with ordered SYM and ARD models in both Sapotaceae and Chrysobalanaceae respectively. If character states are coded consistently and correctly, selected models should reflect how trait evolution was likely to have proceeded in the studied families. The selection of ordered models as best models supports the notion that incorporation of informed biological and biogeographic assumptions provides important information in the analysis of trait evolution. The selection of the ARD ordered model for Chrysobalanaceae implies that within this family certain directions of change are more frequent compared to the selected SYM ordered model in Sapotaceae. The *Gaulettia* and *Hirtella* clade that includes *H. arenosa* are examples of this, with both groups exhibiting a tendency to have white-sand specialists derived from an ancestor that had a trait for white-sand tolerance (Figure 27).

Overall, maximum likelihood reconstruction shows that ancestral conditions for both Sapotaceae and Chrysobalanaceae are somewhat different in terms of nutrient-poor tolerance, with white-sand tolerance recovered as most likely for the ancestor in Chrysobalanaceae, and non-white-sand tolerance as the most likely ancestor in Sapotaceae. Both Chrysobalanaceae and Sapotaceae are eastern Amazon (Guiana-Shield/Brazilian-Shield) families in terms of diversity and abundance (Prance & White 1988, Terborgh & Andresen 1998, ter Steege *et al.* 2000, Hopkins 2007). However, the Andean flank of the Andes rivals the Guiana Shield region in Sapotaceae diversity (J. Richardson, pers. comm.) which is in accord with the finding of ancestral condition for non-white-sand soil in this family. Both Sapotaceae and Chrysobalanaceae do not have western Amazon white-sand specialists, while white-sand specialists distributed in the eastern and central Amazon.

4.5.6. The interplay between niche conservatism and niche evolution

The phylogenetic signal and character evolution patterns found in this study support the idea that the niche lability for edaphic preferences allows the studied families to speciate in different habitat types. In terms of niche conservatism both families can exploit a range of nutrient-poor soils in the Amazon-Guiana region (coastal sandy areas, igapo forests, savanna on sandy soils, serranias, Andean sandstones, or old-clay terrace soils) whereas white-sand soils in the western Amazon may have different ages of origin, from recent to very old (Chapter 2). As these substrates developed in the lowlands they may have been colonized by nutrient-poor tolerant families from different biogeographic origins. Similar conditions for high levels of ecological transitions may have occurred with western Amazon plant families like Moraceae/Myristicaceae, or some genera like *Inga* that diversified mostly on more fertile soils (Richardson *et al.* 2001). If the idea that edaphic niche lability facilitates niche evolution and related ecological transitions, it would be expected that western Amazon-centred taxa will show similar levels of lack of phylogenetic signal for habitat preferences. On this point, the existence of nutrient-poor tolerant species (but not white-sand specialists) in western Amazon taxa (e.g. *Inga*, *Guarea*, *Virola*) has been documented by floristic studies on white-sand forests (e.g. García-Villacorta *et al.* 2003, Fine *et al.* 2010, Stropp *et al.* 2011). Yet, even in these taxa with preference for cation rich soils, like *Inga*, adaptive responses to edaphic gradients may have been important in the evolution of their extant diversity patterns (Palow *et al.* 2012). Neotropical palm lineages with different clades restricted to the Andes and lowland habitats provides another example of the interplay of niche conservatism and evolution (Eiserhardt *et al.* 2013). In this case both edaphic and climatic niche conservatism appears to have been important in the evolution in this family.

The failure to invade new habitats or climatic niches that are adjacent to the geographic range of a species or clade can be taken as evidence for niche conservatism; at a broad global scale one expression of this is the tropical conservatism hypothesis (Wiens & Donoghue 2004). *Licania michauxii* is sister to South American Chrysobalanaceae and represent a good example to illustrate the influence niche conservatism can exert in the evolution and diversification of Chrysobalanaceae. This species is a nutrient-poor specialist and it is endemic to the Sand Hills of Florida, coastal Mississippi and Georgia (USA) (Prance 1970, GBIF 2013). In relation to the Neotropical clade and other members in the family (i.e. non-Neotropical clades), the node leading to *L. michauxii* is closer to the root of the tree and hence can be interpreted as an early branching taxon (Crisp & Cook 2005).

Given that both *L. michauxii* and the Neotropical clade studied here (*Licania*/*Couepia*/*Hirtella*/*Gaullettia* clade) have the same age (i.e. they are sister clades) the failure for *L. michauxii* to diversify in the North American temperate environments suggest that climatic niche conservatism for tropical climates and edaphic niche conservatism for nutrient-poor soils may have played an important role in its evolution and biogeographic history. On the contrary, the invasion of tropical

South America by its sister clade ca. 49 Mya (Bardon *et al.* 2013) coupled with trait lability for habitat/edaphic niche conservatism may have provided ample ecological opportunities to evolve in different habitat niches and to reach its outstanding species diversity: 80% of the whole family or about 531 species (Bardon *et al.* 2013). Whereas the interplay of niche conservatism and niche evolution may have influenced the biogeographic history and species generation within particular clades, several biogeographic patterns suggest that edaphic niche evolution has been more important in the accumulation of species diversity in Neotropical lowland forests compared to edaphic niche conservatism. First, Arenosol, Podzol and similar sandy/rocky soil conditions exist in other parts of North America (Schwendiman 1977, Anderson *et al.* 2007, Chesworth 2008), but *L. michauxii* has not extended its current distribution more than 33° latitude north (GBIF 2013). Second, as showed by several biogeographic and ecological studies, some plants groups, like Chrysobalanacae and to some extent Sapotaceae, are more diverse in the Guiana Shield region (Gentry 1982, Prance & White 1988, Terborgh & Andresen 1998, ter Steege *et al.* 2000, Hopkins 2007), which has been shown to be towards the nutrient-poor spectrum of the Amazonian edaphic gradient (ter Steege *et al.* 2000, Hammond 2005, Quesada *et al.* 2011; Chapter 2). It thus seems clear that niche conservatism for tropical climates has impeded species divergence of Chrysobalanaceae in temperate and cold climates, whereas edaphic niche evolution through habitat switching may have facilitated their diversification in the Neotropical region.

Furthermore, as discussed above, conservatism for white-sand soils—which it would be expected to impose stronger selection pressures to taxa compared to most benign habitats—has not generated large diversity in clades (e.g. in Ebenaceae, Gentianaceae). Together, these patterns suggest that edaphic niche evolution has been more important than climatic niche conservatism for Neotropical lowland taxa. Edaphic niche lability may have facilitated habitat switching (i.e. edaphic niche evolution), invasion of different habitat types—mostly within a clade's ancestral fundamental edaphic niche—and subsequent niche divergence and speciation. This series of evolutionary transitions may have developed the outstanding plant diversity of the Neotropical lowland region.

4.5.7. Habitat switching, plant-animal interactions, and ecological speciation

A discussion of the evolution of the Neotropical lowland flora would be incomplete without considering the influence that its rich fauna may have had on the different diversification paths of plant lineages. The evolutionary flexibility to adapt to particular hydro-edaphic conditions in the terra firme (from relatively nutrient-rich clay to nutrient-poor sand/sandstone), flooded (igapo and varzea forests) and swamp habitats of the Neotropics may facilitate speciation in correlation with other ecological traits. Habitat switching may indeed precede other ecological switches like pollinator switching or disparity in flowering times, both of which promote genetic isolation between populations (Levin 2004, 2009). It has been shown that flowering disparity indeed facilitates habitat tolerance to new conditions (Rice 1987, Brady *et al.* 2005, Wright *et al.* 2006, Sambatti & Rice 2007, Levin 2009) which in turn may promote assortative mating within habitats as a by-product and hence ecological speciation in the presence of gene flow (Paterniani 1969, Rice & Salt 1988, 1990, Dieckmann & Doebeli 1999).

On the other hand, it has been repeatedly shown that (animal) behavioral traits are more labile compared to morphological or physiological traits (Gittleman *et al.* 1996, Blomberg & Garland 2002). Because a substantial number of rainforest plants rely on animals for seed dispersal (Howe & Smallwood 1982, Fleming *et al.* 1987), plant lability for edaphic preference over evolutionary time may have also been influenced by their seed dispersers in their quest to exploit new habitat types or while responding to changing environmental conditions. On this line, different animal frugivorous guilds evolved at different times in the Neotropics (Fleming & John Kress 2011, Correa *et al.* 2015). For example, fish frugivore families in the Neotropics arose ca.70 Mya whereas frugivorous families in birds, bats and primates originated much later, between 36-10 Mya (Fleming & John Kress 2011, Correa *et al.* 2015, Bond *et al.* 2015). A wide variety of dispersal agents move the seeds of both Sapotaceae and Chrysobalanaceae including fish, water current, primates, bats, birds, and rodents (Prance & White 1988, Pennington 1990). Plant-animal evolutionary associations may have certainly influenced the evolution and diversification of plant lineages in association with differential seed dispersal, pollinator shifts and other ecological transitions across habitat types.

All in all, the existence of different edaphic conditions and the spatio-temporal variation in habitat heterogeneity that the Neotropics has passed through (Chapter 2) may have facilitated ecological speciation by jointly amplifying the effect of (i) herbivory pressure in the allocation of differential growth and defense resources (Fine *et al.* 2004, 2005, 2006, Lamarre *et al.* 2012), (ii) contrasting flowering-time phenologies (Savolainen *et al.* 2006, Hall & Willis 2006, Levin 2009), (iii) pollinator shifting (van der Niet *et al.* 2006, Whittall & Hodges 2007, Kay & Sargent 2009, Johnson 2010, van der Niet & Johnson 2012), and (iv) differential seed dispersal along topographic and hydro-edaphic gradients (Gomes de Freitas *et al.* 2012, Barbosa *et al.* 2013, Britton *et al.* 2014).

In closing, it is only fair to mention that by using a phylogenetic pattern approach to study the evolution of ancestral habitat preferences and plant diversity in the Neotropical lowlands, this study has not addressed the specific processes that operate at population levels that translate in species evolution. However, analyzing the evolution of ecological traits using molecular phylogenies is useful if we are attempting to gain insights into the build-up of species diversity (Pagel 1997, Mooers & Heard 1997) by means of integrating certain aspects of ecology, evolution, and biogeography (Ricklefs & Schluter 1993, Losos 1994, Moritz *et al.* 2000, Silvertown & Antonovics 2001, Wiens & Donoghue 2004, Ricklefs & Jenkins 2011).

Additional studies may certainly provide further insights of the factors responsible for species divergences in Neotropical habitats, especially by addressing the specific processes at the population levels (e.g. Da Silva & Patton 1998, Dick *et al.* 2003, Capurucho *et al.* 2013, Fine *et al.* 2013, Misiewicz & Fine 2014) and with field experiments (e.g. ter Steege 1994, Coomes & Grubb 1998, Parolin 2002, Fine *et al.* 2004, Baraloto *et al.* 2007, Lamarre *et al.* 2012, Stropp *et al.* 2014). Likewise, exploring the evolution or conservatism of other ecological traits, especially the ones that confer tolerance to drought, water-logging, and flooding conditions, may give us a deeper understanding of the order in the evolutionary transitions that gave origin to the Neotropical lowland plant diversity. They can also serve as a basis to inform us about the ability of different plant groups to adapt to on-going and future environmental changes.

Meanwhile, the results of this study support the idea that edaphic niche lability has facilitated niche evolution by allowing habitat switching over evolutionary time due probably to ecological opportunities arising from spatio-temporal changes in habitat heterogeneity over time, playing thus a fundamental role in species formation in the Neotropics.

4.6. Conclusions

Habitat specialization through continuous habitat switching has occurred multiple times in the evolution of Neotropical plant lineages. Edaphic niche conservatism, as measured by phylogenetic signal, was found to be weak or absent. In general, edaphic switching among closely related species appears to be pervasive. White-sand tolerant species were not biased to any particular clade within Sapotaceae and Chrysobalanaceae; instead they were distributed randomly across the phylogenies. It thus appears that a large number of species in these two species-rich Neotropical families have the capacity to tolerate nutrient-poor water-stressed habitats. Chrysobalanaceae showed a weak signal for convergent evolution of tolerance to extreme nutrient-poor soils (white-sand specialism) and white-sand specialists were found scattered and usually nested within white-sand tolerant taxa. Chrysobalanaceae had more white-sand specialists than Sapotaceae but overall tolerance to nutrient-poor soils has not resulted in a particular species radiation towards white-sand specialists or any other edaphic condition. Yet, phylogenetic patterns in some genera indicate that edaphic niche conservatism may be stronger in some Neotropical clades (e.g. *Lissocarpa*) but they cannot explain alone the overall species diversity in the Neotropical lowlands.

Although the interplay between tropical niche conservatism (Wiens & Donoghue 2004) and edaphic niche conservatism (Kubitzki 1990) may have influenced the biogeography and speciation of some lowland Neotropical clades, edaphic niche evolution may have been more important overall. The restricted distribution of *Licania michauxii* (the sole species sister to the Neotropical Chrysobalanaceae clade) confided to the sandy soils of Florida, and its lack of expansion and diversification further north since splitting from its sister Neotropical clade (ca. 49 Mya), implies niche conservatism for both (sub)tropical climates and edaphic conditions. Contrary to this phylogenetic pattern its Neotropical sister clade invaded and diversified on different edaphic conditions, mostly within its ancestral fundamental edaphic niche, to achieve almost 80% of the overall family diversity. These biogeogeographic and phylogenetic patterns strongly suggest that edaphic niche evolution, and possibly subsequent species divergence and speciation, may have been facilitated by edaphic niche lability fostering habitat switching. Habitat switching may thus have been a common ecological transition taking advantage of ecological opportunities in heterogeneous environments created ultimately by geological changes in the Neotropical landscape.

The ancestral edaphic state of Sapotaceae is more likely to have lacked the trait of nutrient-poor tolerance, whereas the ancestral state in Chrysobalanaceae is more likely to have possessed a trait for white-sand tolerance. The five studied edaphic conditions—which cover most of the habitat types from terra firme to flooded forests in the Neotropics—appear to evolve frequently over evolutionary time. White-sand specialists are not early branching members in the studied Neotropical families as proposed by Frasier *et al.* (2008) and they can arise early on or at later stages in the history of Neotropical plant clades. The results of this study support the hypothesis of habitat specialization by adaptation to different edaphic niches proposed by Gentry

(1986) and found a weak support that edaphic niche conservatism produced the diversity of species in Amazonia as proposed by Kubitzki (1990). Habitat specialization through continuous niche switching in space and time, favored by edaphic niche lability, may have been a major determinant in the evolution of tree diversity in Neotropical lowland forests.

Chapter 5: General conclusions and future prospects

5.1. Overview

This dissertation aimed to understand the origin and evolution of western Amazonian white-sand forest communities and investigate the evolution of habitat specialization to different edaphic conditions as a driver in the accumulation of plant diversity in the Neotropical lowlands. In addressing these goals, I used two different but complementary approaches. First, an analysis of the floristic composition and phytogeographical affinities of western Amazonian white-sand forests helped to put into perspective these forests in relation to various floras of the Amazon and the Guiana Shield region. Second, I used molecular phylogenies of two very diverse Neotropical plant families—Sapotaceae and Chrysobalanaceae—to investigate the historical construction of these forests in association to habitat specialization. This was done by analysing the phylogenetic patterns of habitat preferences among species—including white-sand specialists—as well as reconstructing the likely ancestral edaphic conditions in both families. In order to have a background on the edaphic and habitat conditions against which to interpret these ecological and evolutionary patterns, I reviewed the geological and soil science literature on Amazonian white-sand soils. This review put into context the different origins of these soils, the likely processes involved in their origin and the range of ages of these soils across the basin. In this final chapter I present in a summarized way the main findings of this dissertation and elaborate on several ideas that are intended as future research questions which may help us to obtain deeper insights into the origin, evolution and maintenance of Amazonian plant diversity.

5.2. On the origin of Amazonian white-sand soils

The origin of white-sand soils, one of the most stressful environments in which plants can grow in Amazonia, is related to the geo-temporal dynamics of soil formation in this region. These soils have more likely developed at different times in the different areas of the Amazon and Guiana Shield regions. The age of white-sand soils in the Amazon and Guiana Shield region can be very recent or very old, within the range of 3,000 yrs to 23 Mys. This range corresponds to white-sand soils from the Guiana Shield region (Manaus, and the Colombian Amazon respectively). This broad age range is shown to have ecological and evolutionary implications expressed in the plant community composition, phytogeographical relationships and the phylogenetic patterns of nutrient-poor edaphic tolerance and white-sand specialists (Chapter 3, and 4). The Guiana Shield region contains both the oldest and the youngest white-sand soils, whereas in the rest of Amazonia the age of these soils age ranged from 600,000 to 5 Mys. The upper age limit in both estimated ages is based on the relative position of other sediment layers (relative dating by stratigraphy) and hence it is possible that these upper limits are overestimated. For example, cosmogenic dating of a white-sand outcrop from the Peruvian Amazon puts the age range of these soils within 600,000-800,000 yrs (M. Roddaz, pers. comm.), which corresponds to the mid-Pleistocene. More geological and pedological studies with absolute dating analysis are needed to shed more light into the temporal origin of the variety of soils, and hence habitat types, in Amazonia.

The processes by which these soils developed in the Amazon and the Guiana Shield region can be classified into four mechanisms: (1) the product of deep *in situ* weathering of quartzitic sandstones (Kubitzki 1989; Hammond 2005); (2) deposition by eolian (wind) transport (Horbe *et al.* 2004); (3) as fluvial deposits after paleo-channel abandonment by fault reactivation (Klinge 1965; Hoorn 1994; Räsänen et al. 1998; Roddaz, Babby, *et al.* 2005; Rossetti *et al.* 2012); and (4) the final product of on-going Ferralsol/Acrisol to Podzol transformation (Lucas *et al.* 1984; Dubroeucq & Volkoff 1998; Lucas *et al.* 2012; Mendonça *et al.* 2014).

The relative importance of these processes across the basin varies according to the presence of different geomorphic features and past historical processes affecting the landscape. Of the four general processes suggested above for the existence of these extremely poor-soils in the Amazon and Guiana regions, fluvial deposition by paleo-channel(s) abandonment, possibly—but not necessarily— along structural highs on the terrain (the Iquitos Arch) may have been an important source in the western Amazon. I suggest an additional role of geological arches in developing contrasting topographic patterns of hills and valleys, each with differential erosive rates, which in turn create sharp edaphic gradients that affect the distribution of plants and animals. These non-white-sand habitats extend the areas on which non-white-sand specialists distribute. Erosion of *in situ* Palaeozoic or pre-Cambrian cratonic outcrops (e.g. tepuis, serranias) might be more prevalent in the areas where they are more common: the Guiana and Brazilian Shield region (e.g. Serra do Cachimbo) and some outliers at the margins of the Amazon like Serra do Moa, Sierra del Divisor, Cerro de Contamana, Cordillera del Condor. They might also have sourced extinct paleo-channels which deposited their sandy sediments later covered or recyclied by younger Andean soils.

Transformation of Ferralsol/Acrisol soils to Podzols (Podzolisation) may have also been an important process for the origin of white sands, especially in the eastern and central Amazon and the Guiana Shield where relatively older sandy-clay soils are common compared to western Amazonia. In general, eolian activity may have been of minor importance for white-sand soil formation in the Amazon but with some importance in coastal areas of the Guiana and Brazilian Shields, nearby sandstone tepuis, and at the margin of northeast Amazonia. In these marginal regions seasonal climatic regimes and paleo-winds that were stable over millennia may have provided optimal conditions for the formation of paleodunes now fixed by savanna vegetation (Teew & Rhodes 2004). The existence of white-sand soils in the Neotropics may have influenced the diversification of clades with higher tolerance to nutrient-poor soils that arrived to the Neotropical region at different geological times during the formation of the Amazon biome as may be exemplified by genera like *Potalia* (Gentianaceae), *Caraipa* (Clusiaceae), *Lissocarpa* (Ebenaceae), *Jacqueshuberia* (Leguminosae) (Barneby 1990, León 2006, Frasier *et al.* 2008), among others; all of which have western Amazon white-sand endemics.

5.3. Phytogeographical patterns of western Amazon white-sand forests

To study the phytogeographical patterns of white-sand forests of the western Amazon, 27 up-to-date vascular plant lists for each political province in the Amazon and Guiana Shield regions were compiled, as well as four western Amazon white-sand forests from Colombia, Peru, and Brazil. A combined approach of distributional analysis, hierarchical cluster analysis with support evaluation by bootstrap, and Non-metric Multidimensional Scaling (NMDS) ordination were performed on a taxonomically standardized dataset. Of a total of 1,180 vascular plant species from western Amazonian white-sand forests, the majority (77%) are found to occur on non-white-sand substrates with only 23% showing habitat specialization to white-sand soils. Of the total white-sand specialists, 87% are present in the Guiana-Shield region, whereas 13% are endemic to the western Amazon region.

A preliminary list of 166 vascular plant species (83 of which are trees) endemic to the northern Peruvian Amazonia (Pitman et al. 2013) shows that white-sand habitats there account for a substantial number of these species with ca. 24% (39 species) occurring on white-sand habitats. Thus, compared to other regions in which white-sand forests are absent, like the Madre de Dios region, south of the Peruvian Amazon, and in which the levels of endemism, at least for trees, is very low (Pitman *et al.* 2002), the existence of white-sand forests in any geographical area of Amazonia may increase local, between habitat, and regional diversity (cf. Tuomisto *et al.* 1995; Vásquez-Martinez & Phillips 2000; Vormisto et al. 2000).

Of the total white-sand specialists, 56% are found in the Caquetá moist forests, 55% in the Guayanan Highlands moist forests, and 53% in the Negro-Branco moist forests, which suggest that western Amazon white-sand forests have strong phytogeographic links with the western fringe of the Guiana-Shield lowland floras. Further supporting this result, cluster analysis and NMDS ordination concurred that the white-sand forests of the western Amazon are floristically more similar to floras of the geographic region to which they belong. In general, the composition of white-sand forests of the western Amazon is more similar to floras of the western side of the Guiana Shield than to the rest of floras in the study region. Regional dispersal processes may be one of the fundamental processes in the origin of Amazonian white-sand forests.

5.4. The evolution of habitat specialization in the Neotropics

Edaphic niche conservatism can be defined as the tendency of lineages to keep track of their ancestral edaphic preferences over evolutionary time. The evolution of ancestral edaphic preferences along a nutrient and water-conditioned gradient can be examined by studying the evolution of tolerance to these conditions under a comparative phylogenetic framework. Given that white-sand soils impose nutrient and water-related stress conditions on the plants inhabiting them it would be expected that these plants should respond with physical, chemical, physiological adaptations and trade-offs as has been documented (Fine *et al.* 2004; Fine *et al.* 2006; Lamarre *et al.* 2012). It has been suggested that white-sand soils in the Amazon may represent ancestral soil types that were in the past larger in extension, later fragmented when new Andean-derived substrates developed in the Miocene. The phylogenetically basal position of early branching *Potalia* (Gentianaceae) species from Amazonian white-sands along with Guiana Shield white-sand species gave support this hypothesis (Frasier *et al.* 2008). However, given its small size (eight species) it is hard to pinpoint whether *Potalia* represents a general pattern found in many other Neotropical plant lineages.

In this dissertation I have shown that in the western Amazon a large proportion of plant species occurring on these habitats also occur on other habitat types—from clay-rich *terra firme* forests to seasonally flooded forest to montane forests—whereas white-sand specialists can be distributed locally (local endemics) or regionally (shared with other white-sand patches). This would suggest that tolerance to nutrient-poor water-stressed soils may be a trait shared by many species of the Amazonian flora. On the other hand, if tracking ancestral edaphic preferences were important in the diversification of a clade (Kubitzki 1989; 1990) this should be reflected in the phylogenetic distribution of white-sand specialist species and in the ancestral reconstructions of their edaphic preferences. If closely related species occupy different habitat types this would suggest evolution through ecological switching related to habitat heterogeneity and environmental gradients (Gentry 1981). I used a phylogenetic comparative approach to test these hypotheses by examining phylogenetic patterns of habitat preferences, measuring phylogenetic signal and reconstructing ancestral edaphic conditions in two species-rich Neotropical families: Sapotaceae and Chrysobalanaceae.

I found that habitat preference was a highly labile trait, suggesting that habitat switching has played a major role in the evolutionary history of Neotropical tree lineages. White-sand tolerant species were not biased to any particular clade within the groups of Sapotaceae and Chrysobalanaceae; instead they were distributed randomly across the phylogenies. The same pattern of scatter was found in white-sand specialists, which were usually nested within white-sand tolerant taxa. Chrysobalanaceae showed a weak signal for convergent evolution of tolerance to extreme nutrient-poor soils (white-sand specialism). White-sand specialists are not early branching members in the studied Neotropical families as proposed by Frasier *et al.* (2008). The ancestral edaphic state of Sapotaceae is more likely to lack the trait of nutrient-poor tolerance, whereas the ancestral state in Chrysobalanaceae is more likely to have possessed a trait for white-sand tolerance.

The results of this study support the hypothesis of habitat specialization by adaptation to different edaphic niches proposed by Gentry (1986) and found weak support that edaphic niche conservatism produced the diversity of plant species in Amazonia as proposed by Kubitzki (1990), even in extremely nutrient-poor environments like white-sand forests. The existence of contrasting edaphic conditions in Amazonia (i.e. habitat heterogeneity in time and space) may facilitate ecological speciation by jointly amplifying the effect of (i) herbivory pressure in the allocation of differential growth and defence resources (Fine *et al.* 2004; Fine *et al.* 2005; Fine *et al.* 2006; Lamarre *et al.* 2012), (ii) contrasting flowering-time phenologies (Savolainen *et al.* 2006; Hall & Willis 2006; Levin 2009), pollinator shift (van der Niet *et al.* 2006; Whittall & Hodges 2007; Kay & Sargent 2009; Johnson 2010; van der Niet, T., & Johnson 2012) , and (iii) differential seed dispersal along topographic and edaphic gradients (Gomes de Freitas *et al.* 2012, Barbosa *et al.* 2013, Britton *et al.* 2014). Habitat specialization through continuous niche switching may have been a major determinant in the evolution of tree diversity in Neotropical lowland forests.

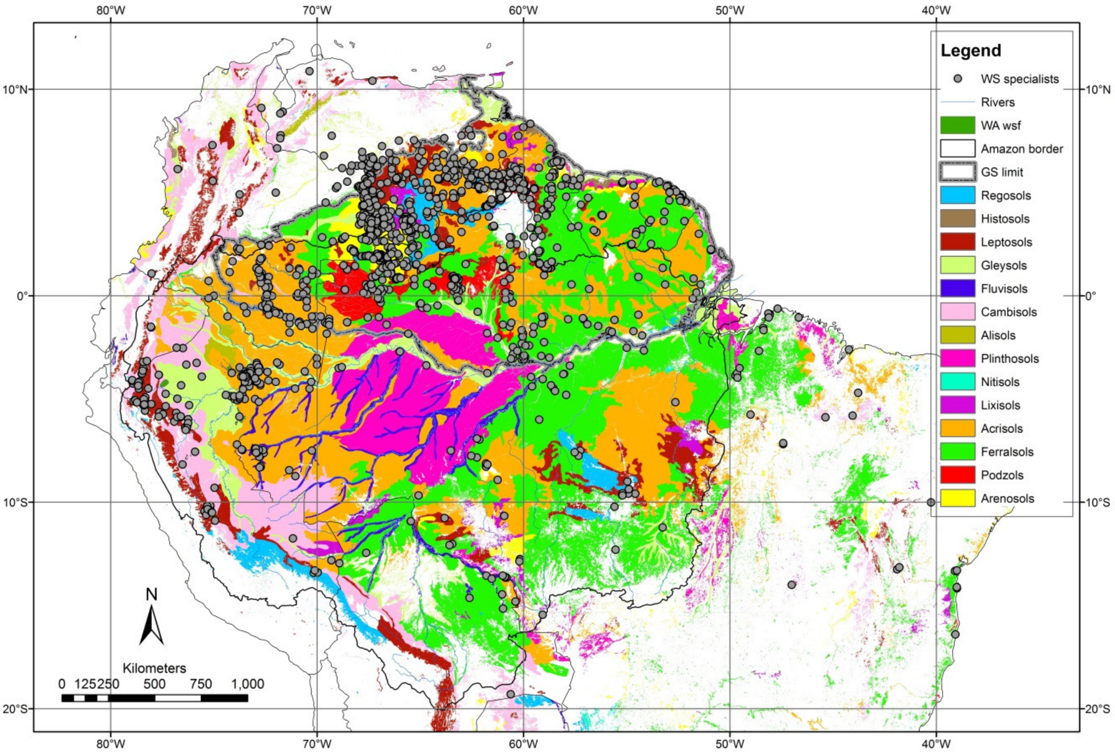
5.5. Future prospects

5.5.1. Mapping white-sand and other habitat types in the Neotropics

Our current understanding of habitat diversity in Amazonia has increased considerably in the last few years but it is still a work in progress. In order to test evolutionary questions about transitions between habitat types it is imperative to generate better vegetation and habitat maps that make sense to the plants and animals tropical biologists study in this region (Hughes *et al.* 2013). Local and regional maps of Amazonian white-sand habitats exist but have not been properly integrated (but see Adeney 2009 for a first approximation). Current vegetation maps still do not incorporate into a single map the distribution of white-sand habitats in Amazonia and this has consequences for the advance of basic research and applied conservation. There are several approaches that can be used to refine our current understanding of the distribution of these and other habitat types in the Neotropics, which include the use of freely available satellite imagery, environmental layers and canopy reflectance analysis to distinguish different vegetation types (Tuomisto *et al.* 1994, Franklin 1995, Roberts *et al.* 1998, Salovaara *et al.* 2005).

In the particular case of white-sand habitats, another approach would be to use the distribution of white-sand specialists as a proxy of this habitat type along with other environmental layers (e.g. elevation, geology, soil type) to approximate the distribution of white-sand habitats (cf. Rotenberry *et al.* 2006, Särkinen *et al.* 2011). Subsequent ground-truthing work and/or comparison with independently derived maps can then improve our knowledge of their spatial distribution in Amazonia that can be used to assess for the first time their conservation status. A preliminary glimpse of the likely distribution of these habitats within the current soil map of Amazonia, as suggested by white-sand specialist species, indicates that they are more common and patchy outside the Guiana Shield region, nested within other soil types, than is indicated on current soil maps (Figure 28).

Figure 28. Distribution of western Amazonia white-sand specialist species on a soil map of the Amazon and Guiana regions (map adapted from Quesada et al. 2012).



Given that white-sand specialists only occur on edaphic conditions classified as Podzol or Arenosol (red and yellow colours in Figure 1 respectively), the distribution of these species on other mapped soil types, especially on Leptosols (maroon) and Regosols (sky blue), indicates that all these soils have common hydro-edaphic characteristics or alternatively that Leptosols and Regosols include unmapped Arenosols and Pozdols. In either case the temporal and spatial distribution of these habitats on the Neotropical landscape may have influenced the diversity and evolution of edaphic tolerant taxa that need to be taken into account. Similar evolutionary scenarios may have influenced the plant diversity in other edaphic conditions of the *terra firme* and flooded forests in Amazonia.

5.5.2. Ancestral range reconstruction of habitat specialization in Amazonian forests

A fundamental but still largely elusive question in evolutionary biology and biogeography is to understand the specific processes involved in the evolution of diversity in different biomes of the world. This question is difficult to tackle if only because the processes involved in speciation largely surpasses biologists' lifespans. Fortunately, molecular phylogenies give us a window to the evolutionary past, which, coupled with model-based comparative approaches, can be a powerful tool to infer which specific processes may have played a major role in the accumulation of extant diversity. In this study, the phytogeographic and floristic analysis shows that western Amazon white-sand forests are more related to floras from the western Guiana-Shield region than to other floras elsewhere in Amazonia and also share a large proportion of species with extra-Amazonian biogeographic regions like Neotropical savannas and seasonally dry forests (Chapter 3). Furthermore, biogeographical studies in other families with habitat specialists (e.g. white-sand, flooded forests, clayey soils) like Lauraceae suggest that they reached the New World from the north and diversified in the lowlands and highlands of the Neotropics (Chanderbali *et al.* 2001) including on white-sand soils (Van Der Werff 1992, Rohwer & Kubitzki 1993). Thus, the contribution of other biogeographic regions and the likely routes followed to occupy the different habitat types in the Neotropics is still not well understood. To gain further insights into the evolution of habitat specialization in the Neotropics it will be useful to develop model-based ancestral range reconstructions. The most recent development of these methods assign species distributions to regions, and uses their phylogenetic relationships and probabilities of dispersal between regions under a maximum likelihood framework to infer the origin, direction, and processes thought to be responsible (e.g., various combinations of dispersal, extinction, vicariance and founder event-speciation) for extant distributional ranges across nodes of a phylogeny (Matzke 2014). A next step of this study will be to use the currently available phylogenetic datasets in Sapotaceae, Chrysobalanaceae and other taxa and attempt to answer these questions. Ancestral range reconstruction of Neotropical habitat specialists and generalists will certainly improve our understanding of the evolution and building of the plant biodiversity in this region.

5.5.3. Nutrient-poor tolerance in other Neotropical plant lineages

In Chapter 4 I have shown that two Neotropical species rich families, Sapotaceae and Chrysobalanaceae, occur specialized to different habitat types and that phylogenetically-close related species occupy different edaphic conditions. When measuring the phylogenetic signal for white-sand tolerance in both families this tended to be randomly distributed across the phylogenies. Because of the scatter in the distribution of white-sand specialists in the phylogenetic trees, the phylogenetic signal for this group of species in each family was less clear. In any case the acquisition or loss of the nutrient-poor tolerance trait in the evolutionary history of these monophyletic clades supports the finding of pervasive habitat switching in these families.

Previously, it has been found that certain clades diversified preferentially on nutrient-poor substrates with only few species occupying other habitat types. This would suggest that certain clades may show higher levels of edaphic niche conservatism than others, especially clades with Guiana-Shield-centred distributions (e.g. *Rapatea* in Givnish *et al.* 2004, *Potalia* in Frasier *et al.* 2008). In order to understand better the similarities and differences in the evolution of habitat specialization between these phylogenetic patterns it would be useful to explore this question in other lineages; especially ones with species occurring on different habitat types of the western Amazon, Guiana-Shield and other Neotropical regions.

As part of the field work during this dissertation I collected plant material for molecular work in carefully selected plant taxa. These taxa share several characteristics which make them attractive for addressing these questions which include shared species between western Amazon white-sands and Guiana-Shield white-sand forests, relatively small numbers of species (making phylogenetics feasible), and with species representatives on non-white-sand habitats (Table 9).

Molecular work carried out on some of these taxa (i.e. *Macrolobium*, *Caraipa*, *Haplochlatra*) is being undertaken in collaboration with other researchers and taxonomists. In the case of *Lissocarpa* (Ebenaceae), I have started some molecular work to attempt to complete the taxon sampling of a previously derived phylogeny. Drs. Rose Samuel and Barbara Turner (University of Vienna, Austria) shared some previously obtained sequences that were jointly analysed with sequences produced by my research. Preliminary phylogenetic results in the genus *Lissocarpa* (Ebenaceae) suggest a geographical structure in the phylogeny in which western Amazon white-sand species from Peru (*L. kating*) is sister to *L. stenocarpa* from the white-sand forests of the Amazonas state in Venezuela.

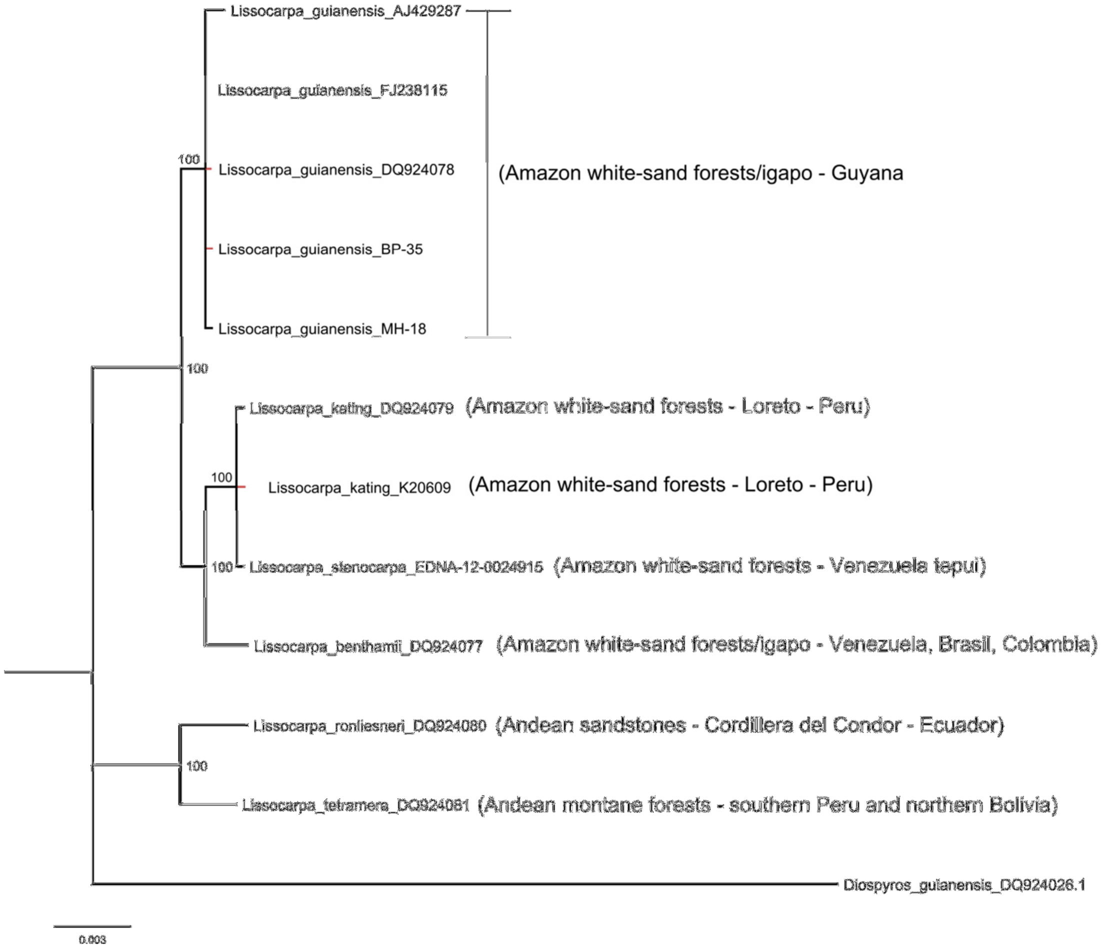
Table 9. Additional taxa for studying the origin of Amazonian white-sand forests and the evolution of habitat specialization. Y = Yes; N = No.

Taxon	**Species restricted to Amazonian white-sands**	**Species restricted to the Guiana Shield region**	**Species occurring on non-white-sand habitats**	**Total number of species**
Lissocarpa	Y	Y	Y	8
Retiniphyllum	N	Y	Y	20
Dicymbe	N	Y	N	16
Macrolobium	N	Y	Y	22
Anaxagorea	Y	Y	Y	25
Caraipa	Y	Y	Y	28
Haploclathra	Y	Y	N	6
Taralea	N	Y	N	9

Most of the species in this genus are distributed on nutrient-poor substrates in the Amazon and the Andes region suggesting edaphic niche conservatism in this clade (Figure 29). *L. benthamii* (endemic to the white-sand and *igapó* forests—seasonally flooded black-water forest) of the western Guiana-Shield region—appears early branching and sister to a clade comprised by *L. stenocarpa* (endemic to the sandstone/tepuis of the Venezuelan Amazon) and *L. kating* (endemic to the white-sand forest of the Peruvian Amazon). This phylogenetic pattern suggests that Peruvian white-sand endemics originated from western Guiana-Shield white-sand congeners supporting the finding of Frasier *et al.* (2008) in relation to the evolution of western Amazon white-sand specialists.

Along with the phytogeographical patterns analysed in Chapter 2, this preliminary result further strengthened the idea that the western fridge of the Guiana-Shield region may have acted as a source area, mirrored in the ecological and evolutionary relationships we currently observe in some members of these floras and taxa. *Lissocarpa ronliesneri* and *L. tetramera* (from Andean sandstone and montane forests of Ecuador, and Peru and Boliva respectively) form a clade apart from Amazonian lowland species. Further phylogenetic analysis to improve the molecular resolution among species, habitat and ancestral range reconstructions, molecular dating and inclusion of two missing species (*L. uyat*, and *L. jensonii*) can sketch us a better picture of the evolution in this white-sand specialist lineage as well as the biogeographic history of Amazonian and Andean white-sand vegetation.

Figure 29. Preliminary Bayesian phylogeny of *Lissocarpa* (sub-family Lissocarpoideae, Ebenaceae) based on trnK-matK plastid regions.



5.5.5. Phylogeographic patterns of specialists and generalists white-sand plant populations

The patchy spatial distribution of Amazonian white-sand forests in a sea of *terra firme* rainforest begs the question about the origin and maintenance of their populations over ecological and evolutionary time. Due to the different processes that can give rise to white-sands soils it seems clear that white-sand patches across the basin have been formed at different geological times. In the northern Peruvian Amazon these soils have originated between 5 Mya to ~700,000 yrs ago which is an order of magnitude younger than the estimates for some white-sand outcrops in the Colombian Amazon (Chapter 2). Furthermore, some patches may be closer to putative source areas, for example the white-sand forests of Manaus (Brazil) are close to the upper Rio Negro white-sands/Guiana Shield, and I found that biogeographic regions from the western margin of the Guiana-Shield shared a substantial number of species with western Amazon white-sand forests. This was also corroborated when studying the floristic composition of white-sand forests with the composition of other regions in Amazonia (Chapter 3).

In the region of Iquitos, in the Peruvian Amazon, there are white-sand patches separated by kilometres on both sides of the Amazon River. Whether these patches have different origins or have been fragmented by the incision of the modern Amazon channel in this area is not known. Are white-sand patches north of the Amazon River in this region source for south of the Amazon River white-sand populations or vice verse? Over time, however, the effect of history through dispersal may homogenize white-sand floras and a study of the genetic structure among these populations can shed light into the origin and maintenance of Amazonian white-sand plant populations. For these reasons, it would be fruitful to use a set of species, both white-sand specialists and habitat generalists, occurring in several patches of the Amazon and the Guiana Shield to investigate how gene flow between populations has been structured over recent evolutionary time and whether distance to source areas is reflected in the phylogeographic structure of populations between patches.

In a related approach, Fine *et al.* (2013) studied the phylogeography of two species of trees in the genus *Protium* (Burseraceae), a white-sand specialist (*P. alvarezianum*), and a habitat generalist (*P. subserratum*). The generalist species from the terrace and clay populations showed lower haplotype diversity than white-sand populations and were probably derived from white-sand populations (Fine *et al.* 2013). Similarly, I would expect that populations of white-sand specialists show more restricted gene flow due to separation between patches compared to population of generalist species that occur on both white-sand and non-white sand habitats.

There is congruence in several fields that during the early middle Miocene a gigantic fluvio-lacustrine system—the Pebas system—lasted from 17 to 11 Mya and covered most of the current western Amazon region (Wesselingh & Salo 2006, Hoorn, Roddaz, *et al.* 2009, Salas-Gismondi *et al.* 2015, Tejada-Lara *et al.* 2015). This aquatic system left behind marine sediments after the rise of the Andes (cf. Shephard *et al.* 2010) which covered this vast area with younger cation-rich sediments. The existence of this extensive aquatic environment in the proto-Amazon basin may have prevented the occupation of the region with floristic terrestrial elements and perhaps acting as an effective dispersal barrier (Wesselingh & Salo 2006). Antonelli *et al.* (2009) studied the biogeographic patterns in several clades of Neotropical Rubiaceae and suggested that this Pebas lake-system may have acted as a dispersal barrier between the Andes, eastern Amazonia and the Guiana Region.

The larger number of endemics in the Guiana Shield and the eastern Amazon region in two of their study taxa (*Isertieae* and *Remijia*) as well as the occurrence of putatively recently expanded species after the drying of the Pebas lake-system is suggested as supporting evidence for its role as a barrier that promoted species divergence (Antonelli *et al.* 2009). *Remijia pacimonica* Standl. is a poor-soil specialist treelet, inhabiting both white-sand substrates as well as old-cation-poor clay-terraces in the western Amazon region (García-Villacorta *et al.* 2011) and population genetic studies within this and similar white-sand tolerant taxa could help us to test more rigorously this Pebas lake-system barrier hypothesis.

Specimens of selected taxa were collected as described previously for the phylogenetic work (Chapter 4), taking special consideration to choose species that were widespread in western Amazon white-sand populations but also distributed in the Guiana Shield region. I selected four species: two white-sand specialists and two white-sand generalists. Table 10 shows the selected species as well as preliminary DNA data obtained per locality. The markers chosen to study each species were selected on the basis of variability to discern phylogenetic relationships within the selected taxa. This was facilitated by the fact that most of the selected taxa have been previously studied in a phylogenetic context which also can help to interpret phylogeographic patterns. Sampling and sequencing of more individuals and populations, especially from the Guiana-Shield region and eastern and central Amazonia (e.g. upper Rio Negro, Colombian Amazon) can help us to fill the gaps to understanding the origin and maintenance nutrient-poor tolerant taxa in Amazonia.

Table 10. Selected species characteristics and preliminary lab results for studying the phylogeographic patterns and white-sand specialists and generalists.

Species	**Family**	**Habitat preference**	**Sequenced DNA marker**	**№ of individual DNA sequenced (№ populations)**
Retiniphyllum concolor	Rubiaceae	WS specialist	trnL-trnF; rpsF-rpsR2	5(2)
Anaxagorea manausensis	Annonaceae	WS specialist	trnl-trnF	2(2)
Chrysophyllum manaosense	Sapotaceae	Edaphic generalist	ITS	9(3)
Micropholis guyanensis	Sapotaceae	Edaphic generalist	ITS	7(3)

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Appendix I

Table 11. Plant taxonomic sources used to build the Amazon and Guiana Shield floristic database and four western Amazonian white-sand forests.

Country/site	**Taxonomic Source**
caqu.wsf.CO	Cortés, R., P. Franco, Rangel-Ch. (1998); Arbeláez, M. V., & Duivenvoorden, J. F. (2004).
guai.wsf.CO	Cárdenas, D. (2007)
lore.wsf.PE	García-Villacorta et al. (2003); Fine et al. (2010)
acre.wsf.BR	Silveira 2003; Ferreira, 2009
Bolivia	Tropicos-Bolivia. (2013). Catálogo de las plantas vasculares de Bolivia. Available in: http://www.tropicos.org/Project/BC. Last access on Jan. 2013.
Brazil	Flora do Brazil (2013). List of Species of the Brazilian Flora**.** Rio de Janeiro Botanical Garden. Available in: <http://floradobrasil.jbrj.gov.br/>. Last access on: Jan. 2013.
Colombia	SINCHI (2013). Herbario Amazónico Colombiano (COAH). Available in: http://www.sinchi.org.co/coleccionesbiologicas/. Last access on Jan. 2013.
Ecuador	Tropicos-Ecuador (2013). Catalogue of the vascular plant of Ecuador. Available in: http://www.tropicos.org/Project/CE. Last access on Jan. 2013.
French Guiana	Funk et al. (Eds.) 2007. Checklist of the plants of the Guiana

	Shield (Venezuela: Amazonas, Bolivar, Delta Amacuro; Guyana, Surinam, French Guiana). Department of Botany, National Museum of Natural History.
Guyana	Funk et al. (Eds.) 2007. Checklist of the plants of the Guiana Shield (Venezuela: Amazonas, Bolivar, Delta Amacuro; Guyana, Surinam, French Guiana). Department of Botany, National Museum of Natural History.
Peru	Tropicos-Peru. (2013) Checklist. Available in: http://www.tropicos.org/Project/PEC. Last access on Jan. 2013.
Surinam	Funk et al. (Eds.) 2007. Checklist of the plants of the Guiana Shield (Venezuela: Amazonas, Bolivar, Delta Amacuro; Guyana, Surinam, French Guiana). Department of Botany, National Museum of Natural History.
Venezuela	Funk et al. (Eds.) 2007. Checklist of the plants of the Guiana Shield (Venezuela: Amazonas, Bolivar, Delta Amacuro; Guyana, Surinam, French Guiana). Department of Botany, National Museum of Natural History.

Table 12. Proportion of western Amazon white-sand specialist species occurring within ecoregions using the whole white-sand dataset: caqu.wsf.CO (Colombia), guai.wsf.CO (Colombia), acre.wsf.BR (Brazil), lore.wsf.PE (Peru).

Ecoregion	**No. families**	**% family**	**No. genera**	**% genera**	**No. species**	**% species**
Caquetá moist forests	57	88%	117	73%	191	69%
Guayanan Highlands moist forests	47	72%	92	58%	142	51%
Negro-Branco moist forests	48	74%	95	59%	137	49%
Iquitos varzea	33	51%	74	46%	95	34%
Tepuis	39	60%	69	43%	93	34%
Japurá-Solimoes-Negro moist forests	27	42%	47	29%	64	23%
Guianan moist forests	30	46%	49	31%	61	22%
Napo moist forests	24	37%	49	31%	59	21%

Uatuma-Trombetas moist forests	27	42%	45	28%	56	20%
Solimoes-Japurá moist forest	26	40%	50	31%	55	20%
Southwest Amazon moist forests	24	37%	41	26%	50	18%
Guyanan savanna	29	45%	42	26%	48	17%
Llanos	25	38%	36	23%	44	16%
Purus varzea	17	26%	30	19%	34	12%
Madeira-Tapajos moist forests	19	29%	29	18%	33	12%
Rio Negro campinarana	14	22%	17	11%	23	8%
Ucayali moist forests	12	18%	17	11%	19	7%
Tocantins/Pindare moist forests	12	18%	14	9%	14	5%
Mato Grosso seasonal forests	8	12%	10	6%	12	4%
Peruvian Yungas	10	15%	11	7%	11	4%

Cerrado	7	11%	8	5%	8	3%
Eastern Cordillera real montane forests	5	8%	6	4%	7	3%
Marañón dry forests	4	6%	5	3%	5	2%
Chiquitano dry forests	4	6%	4	3%	4	1%
Venezuelan Andes montane forests	4	6%	4	3%	4	1%
Pará mangroves	3	5%	3	2%	3	1%
Xingu-Tocantins-Araguaia moist forests	3	5%	3	2%	3	1%
Bahia coastal forests	2	3%	2	1%	2	1%
Catatumbo moist forests	2	3%	2	1%	2	1%
Guianan mangroves	2	3%	2	1%	2	1%
Magdalena Valley montane forests	2	3%	2	1%	2	1%

Maracaibo dry forests	2	3%	2	1%	2	1%
Monte Alegre varzea	2	3%	2	1%	2	1%
Orinoco Delta swamp forests	2	3%	2	1%	2	1%
Atlantic Coast restingas	1	2%	1	1%	1	0%
Beni savanna	1	2%	1	1%	1	0%
Caatinga	1	2%	1	1%	1	0%
Campos Rupestres montane savanna	1	2%	1	1%	1	0%
Chaco	1	2%	1	1%	1	0%
Chocó-Darien moist forests	1	2%	1	1%	1	0%
Cordillera La Costa montane forests	1	2%	1	1%	1	0%
Cordillera Oriental montane forests	1	2%	1	1%	1	0%
Jurua-Purus moist	1	2%	1	1%	1	0%

forests						
Maranhao Babaþu forests	1	2%	1	1%	1	0%
Maranhao mangroves	1	2%	1	1%	1	0%
Northwestern Andean montane forests	1	2%	1	1%	1	0%
Pantanal	1	2%	1	1%	1	0%
Pernambuco coastal forests	1	2%	1	1%	1	0%
Pernambuco interior forests	1	2%	1	1%	1	0%
Purus-Madeira moist forests	1	2%	1	1%	1	0%
Tapajos-Xingu moist forests	1	2%	1	1%	1	0%
Total general	65	100%	160	100%	277	100%

Table 13. Proportion of western Amazon white-sand specialist species occurring within ecoregions using non-Guiana Shield white-sand floras: acre.wsf.BR (Brazil), lore.wsf.PE (Peru).

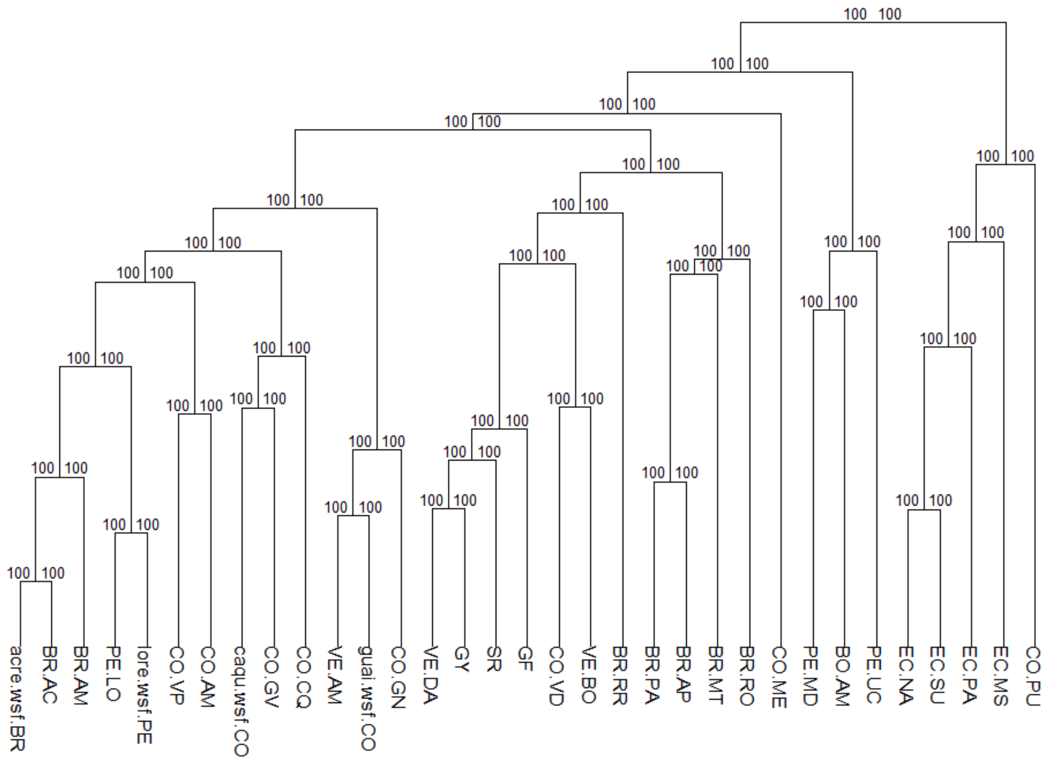
Ecoregion	**No. families**	**% families**	**No. genera**	**% genera**	**No. species**	**% species**
Iquitos varzea	30	94%	67	97%	86	97%
Napo moist forests	24	75%	48	70%	56	63%
Southwest Amazon moist forests	23	72%	38	55%	43	48%
Negro-Branco moist forests	21	66%	36	52%	38	43%
Guayanan Highlands moist forests	17	53%	26	38%	29	33%
Caquetá moist forests	14	44%	23	33%	27	30%
Japurá-Solimoes-Negro moist forests	17	53%	22	32%	25	28%
Uatuma-Trombetas moist forests	16	50%	24	35%	25	28%
Solimoes-Japurá moist forest	16	50%	22	32%	22	25%
Tepuis	15	47%	20	29%	21	24%

Guianan moist forests	10	31%	15	22%	17	19%
Ucayali moist forests	10	31%	14	20%	15	17%
Purus varzea	10	31%	14	20%	14	16%
Madeira-Tapajos moist forests	8	25%	11	16%	11	12%
Guyanan savanna	7	22%	8	12%	8	9%
Llanos	6	19%	7	10%	7	8%
Peruvian Yungas	6	19%	7	10%	7	8%
Rio Negro campinarana	4	13%	4	6%	6	7%
Mato Grosso seasonal forests	3	9%	3	4%	4	4%
Tocantins/Pindare moist forests	3	9%	3	4%	3	3%
Xingu-Tocantins-Araguaia moist forests	3	9%	3	4%	3	3%
Cerrado	2	6%	2	3%	2	2%
Eastern Cordillera real montane forests	1	3%	2	3%	2	2%
Magdalena Valley montane forests	2	6%	2	3%	2	2%

Marañón dry forests	2	6%	2	3%	2	2%
Venezuelan Andes montane forests	2	6%	2	3%	2	2%
Atlantic Coast restingas	1	3%	1	1%	1	1%
Bahia coastal forests	1	3%	1	1%	1	1%
Beni savanna	1	3%	1	1%	1	1%
Chaco	1	3%	1	1%	1	1%
Chiquitano dry forests	1	3%	1	1%	1	1%
Chocó-Darien moist forests	1	3%	1	1%	1	1%
Cordillera Oriental montane forests	1	3%	1	1%	1	1%
Guianan mangroves	1	3%	1	1%	1	1%
Northwestern Andean montane forests	1	3%	1	1%	1	1%
Orinoco Delta swamp forests	1	3%	1	1%	1	1%
Pantanal	1	3%	1	1%	1	1%
Pará mangroves	1	3%	1	1%	1	1%

Pernambuco interior forests	1	3%	1	1%	1	1%
Tapajos-Xingu moist forests	1	3%	1	1%	1	1%
Total general	32	100%	69	100%	89	100%

Figure 30. Multi-scale bootstrap results from *recluster* with Average linkage as the clustering algorithm. All cluster nodes have 100% bootstrap support values at all five re-sampling levels. Levels 1 (right) and 5 (left) presented.



Appendix 6. Cophenetic correlation results of the five assessed clustering algorithms. The highest cophenetic correlation (Neighbour Joining, $r = 0.812$) is the one that best represent the dissimilarity matrix in its resulting dendrogram followed by Avarage linkage (r = 0.674).

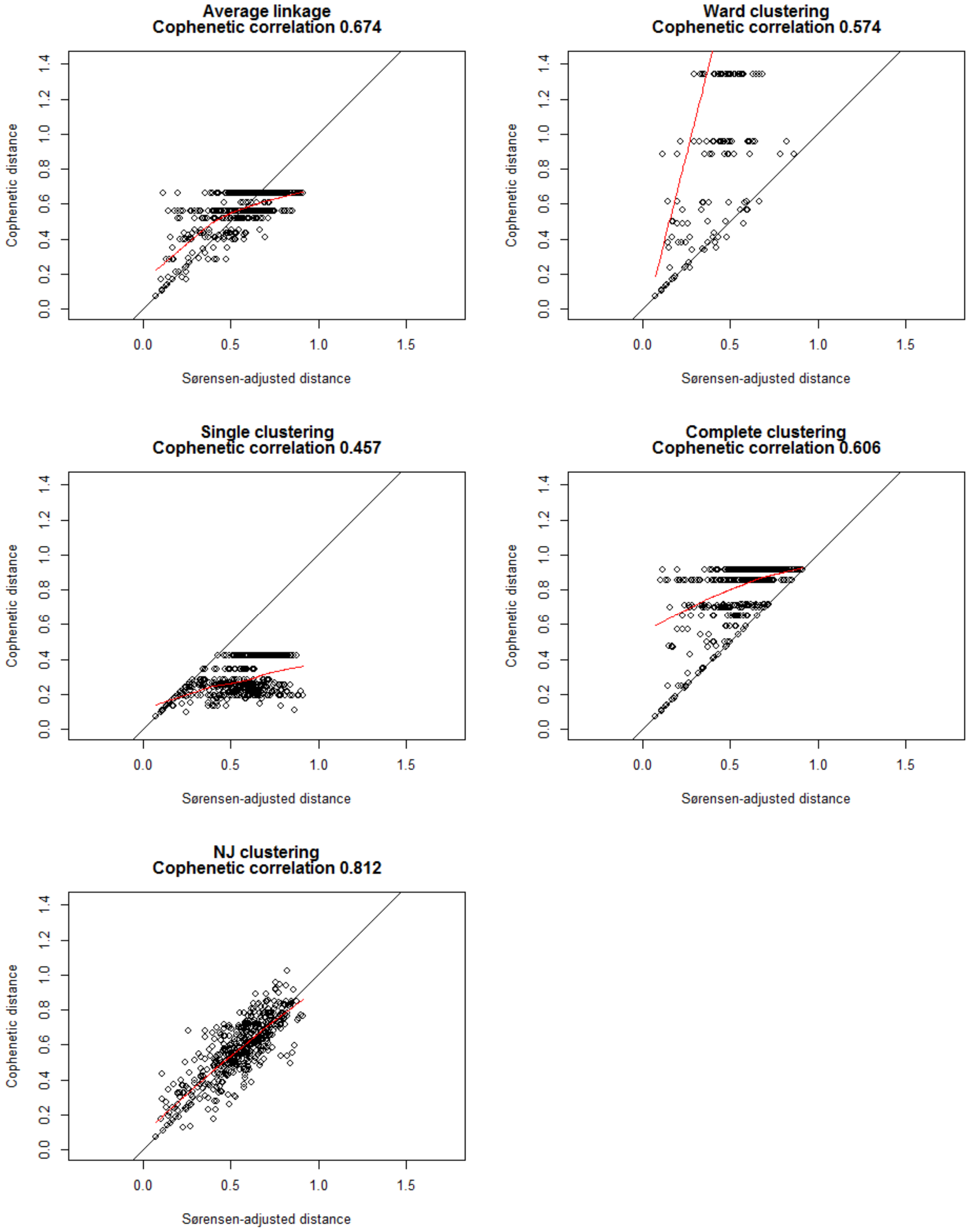


Figure 31. Floristic relationships of 31 Amazon and Guiana Shield sites created based on Neighbour Joining using an adjusted-Sørensen index. It includes 4 western Amazon white-sand forests: caqu.wsf.CO (Colombia), guai.wsf.CO (Colombia), acre.wsf.BR (Brazil), lore.wsf.PE (Peru).

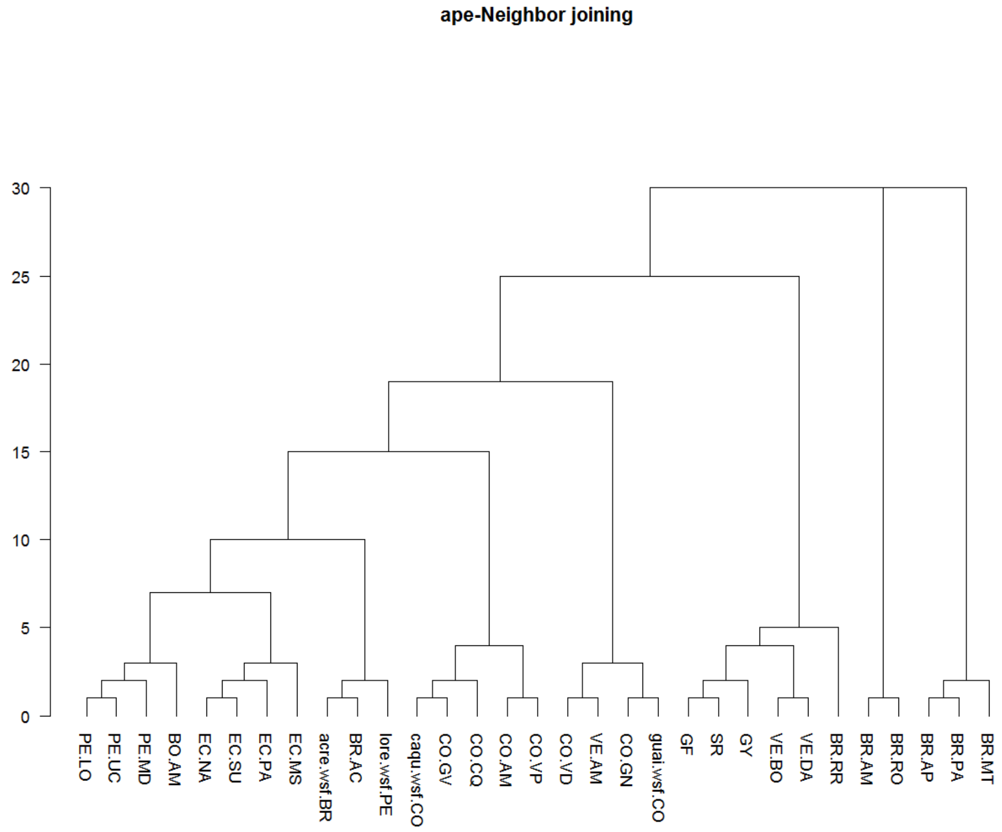


Table 14. Standard errors of AU bootstrap p-values. Note observed AU p-values for the three clusters fall within expected ranges.

cluster	**AU**	**BP**	**SE.AU**	**SE.BP**	**Expected AU p-value range (AU+SE.AU – AU-SE.AU)**
1	0.708	0.910	0.119	0.010	0.827-0.589
15	0.906	0.989	0.145	0.005	1.051-0.761

Table 15. Misclassified sites according to the Silhouette plot analysis. Neighbour value shows in which cluster these sites will be better placed.

Site	**Cluster**	**Neighbour**	**Silhouette width**
BR.AC	1	2	-0.044
BR.AM	1	3	-0.105
PE.LO	1	2	-0.256

Figure 32. Standard error of AU bootstrap p-values of each identified cluster by pvclust. Clusters 1, and 15 showed relatively higher standard errors that were within the expected ranges (Table 14).

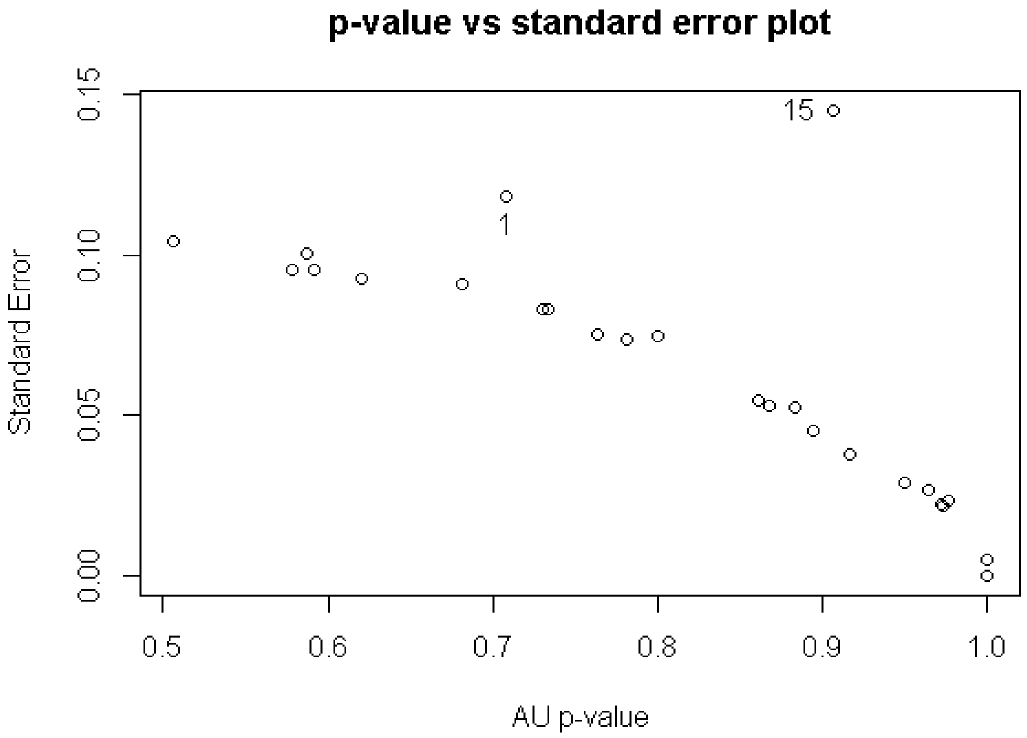
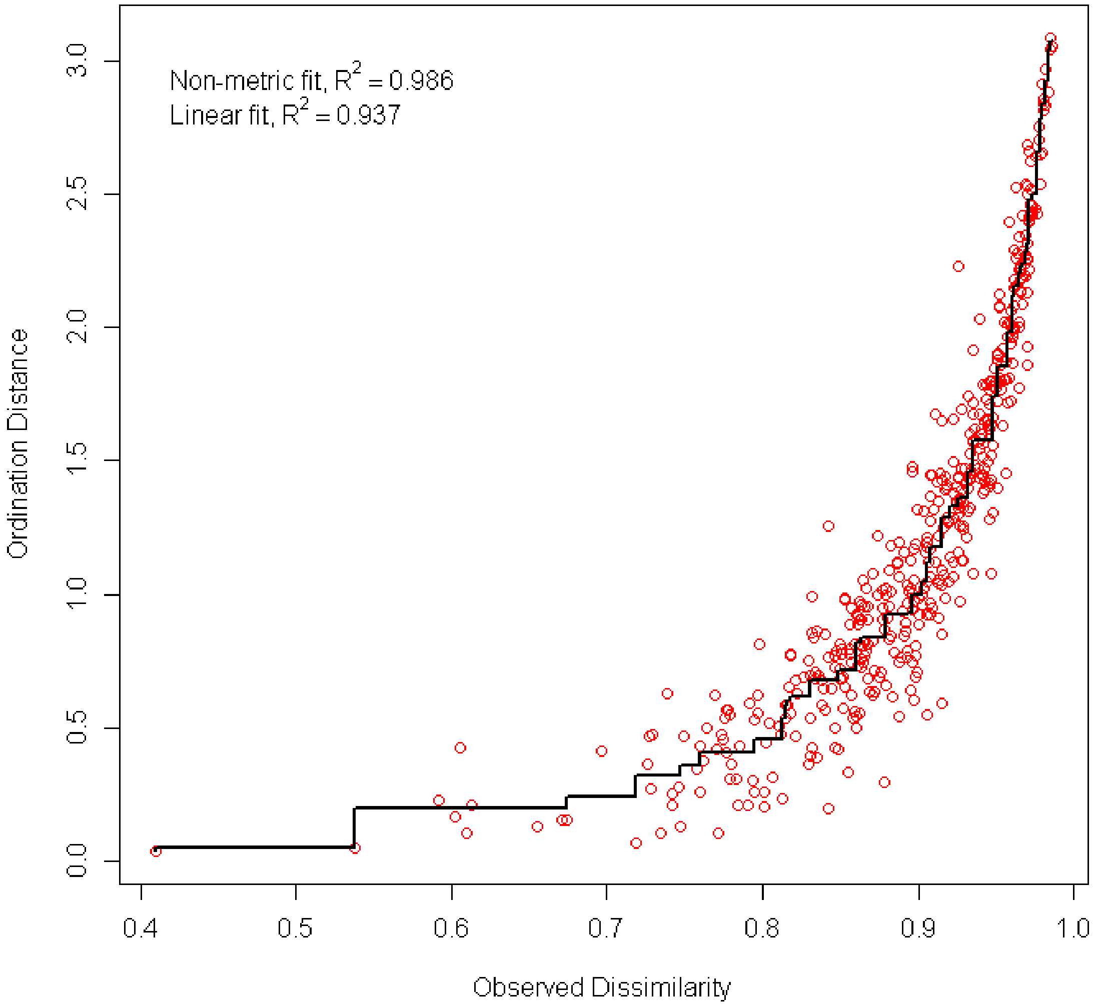


Figure 33. Sheppard plots of NMDS ordination plot of Amazon-Guianan floras including four western Amazonian white-sand forests. Stress = 0.12. Iterations = 500. Dimensions = 2.



Appendix II

The following datasets are included in the CD-ROM that accompanies this thesis:

AII: 1. Sapotaceae sequence alignment as XML file use as input for BEAST analysis. It contains the aligned sequences. File can be opened in any text editor.

AII: 2. Chrysobalanaceae sequence alignment as Nexus format used in the analysis of ancestral trait reconstruction and phylogenetic signal. . It contains the aligned sequences File can be opened by any text editor.

AII: 3. R code written for the phytogeographic and floristic analysis

AII: 4. R code written for the ancestral state reconstruction in Sapotaceae

AII: 5. R code written for the ancestral state reconstruction in Chrysobalanaceae