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Amazonian White-Sand Forests Show Strong Floristic Links with Surrounding Oligotrophic Habitats and the Guiana Shield

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ABSTRACT

Amazonian white-sand forests occur on quartzitic sandy soils, are distributed as an archipelago of habitat islands across the rainforests of Amazonia and contain many endemic plant species. Surprisingly, we found that only 23% of plant species in western Amazon white-sand forests are white-sand specialists, while the remaining species (77%) also occur in other habitat types. Overall, our analyses revealed (i) somewhat unexpected composition similarity of white-sand forests with nearby non-white-sand forests, (ii) phytogeographical connections among distant white-sand forests, and (iii) a large proportion of western Amazon white-sand specialists occurring in floras of the western and central Guiana Shield region (7-43%). These results suggest that dispersal from both neighbouring oligotrophic non-white-sand habitats and distant white-sand forests is fundamental in shaping western Amazonian white-sand forests' species composition and diversity. While endemism in Amazonian white-sand forests may be lower than previously estimated, conservation of this unique and fragile environment should remain a priority. Such conservation will require the maintenance of regional dispersal processes that connect these archipelagos of habitat islands and other ecologically similar oligotrophic habitats across the Amazon and the Guiana Shield.

Key words: Amazon, arenosol, biogeography, campinarana, ecoregion, floristics, Guiana Shield, habitat specialization, podzol, varillales

RESUMEN

Los bosques de arena blanca de la Amazonía ocurren en suelos arenosos quartzíticos, tienen muchas especies endémicas y están distribuidos como un archipiélago de hábitats, dispersos a lo largo de la Amazonía y la región del escudo Guyanés. Inesperadamente, encontramos una baja proporción de plantas restringidas a ellas (23%) mientras que la mayoría de las especies (77%) también ocurren en otros tipos de hábitat de la Amazonía y del Neotrópico. Estos bosques tienen (i) similitudes florísticas con bosques en otro tipo de suelos de áreas cercanas, (ii) conexiones fitogeográficas con otros bosques de arena blanca distantes, (iii) una alta proporción de su flora especialista habitando áreas del centro y oeste del escudo Guyanés (7-43%). Estos resultados sugieren que la dispersión, desde hábitats oligotróficos cercanos, distintos a arena blanca, así como desde bosques de arena blanca distantes es fundamental en estructurar su composición y diversidad. Aun cuando el nivel de endemismo en los bosques de arena blanca de la Amazonía occidental puede ser más bajo de lo que previamente se estimaba, la conservación de estos ecosistemas únicos y frágiles debería continuar siendo una prioridad. Enfatizamos la necesidad de implementar estrategias regionales de conservación que ayuden a conservar los distintos archipiélagos de arena blanca así como hábitats oligotróficos con condiciones ecológicas similares en la Amazonia y el escudo Guyanés.

Palabras clave: Amazonía, arenosol, biogeografía, campinarana, ecoregión, especialización de hábitat, florística, Guiana Shield, podzol, varillales

QUARTZ-RICH SANDY SOILS ARE FOUND ACROSS AMAZONIA, A BIOGEOGRAPHIC UNIT encompassing the Amazon basin and the Guiana Shield region. These soils support a complex of vegetation types known as white-sand forests, which occupy relatively large extensions in the Guiana Shield region and Rio Negro basin, one of the oldest geological regions in northern South America (Hammond 2005b). Across the rest of Amazonia, white-sand forest is scattered in island-like patches within a matrix of *terra firme*, upland rainforests on clay and sandy-clay soils, with patches varying in size from several to hundreds of hectares (Macedo & Prance 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 forest: a reduction in forest stature, an increase in the density of pole-like stems, and a relatively open canopy, with a large amount of sunlight reaching into the understory (Coomes & Grubb 1998, 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 as well as endemic species (Anderson 1981, Prance 1996, Gentry 1986, Fine *et al.* 2010). Given their distinctive structure, patchy distribution and floristic composition, it is not surprising that white-sand forests across the Amazon have received distinct local designations such as *varillal*, *chamizal* (in Peru, Colombia), *Amazon caatinga*, *campina*, *campinarana* (Brazil), *caatinga*, *bana* (Venezuela), *wallaba* forest, and *muri bush* (Guyana, French Guiana, Surinam) (Richards 1941, Revilla 1974, Cooper 1979, Anderson 1981).

Fundamental to the existence of these forests is the presence of nutrient-poor, sandy soils. Pedological and geological evidence about the origin of these soils (García-Villacorta 2015) suggests 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 2005a); (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, Hermoza *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).

Taxonomic revisions and local floristic studies in Amazonian white-sand forests have emphasized 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). To date, there has been no attempt to study species distribution and compositional patterns of these floras at pan-Amazonian scales. To shed light onto the phytogeography of western Amazon white-sand forests, we addressed three main questions: (1) Are western Amazonian white-sand forests comprised primarily of white-sand specialist species?; (2) What are the phytogeographic connections of western Amazon white-sand species?; and (3) Are white-sand forests of the western Amazon floristically more similar to floras on adjacent areas of non-white-sand soils or to white-sand floras of the Guiana Shield region?

METHODS

STUDY AREA AND FLORISTIC DATASETS.—The study area encompasses the Amazon and Guiana Shield region (Fig. 1). The border of the Amazon and Guiana regions was extracted from the ecoregions map of the world (Olson *et al.* 2001), following closely the limits of the Guiana Shield (Hammond 2005b) and HYBAM's Amazon basin watershed limits (Seyler *et al.* 2009). We term this entire area "Amazonia".

White-sand forests in the western Amazon occur patchily dispersed in the southwest of the Colombian Amazon, northern Peruvian Amazon, and around the area of Cruzeiro do Sul in the state of Acre, Brazil. The white-sand flora in all these three areas has been studied intensively in the last few years, making them amenable to a floristic assessment. To assess the floristic affinities of the white-sand forests from the western Amazon we compiled a list of all vascular plant species known to occur in the white-sand forests of Peru (Loreto region: loreto.wsf.PE), Colombia (Guainía region: guainía.wsf.CO, and Caquetá region: caquetá.wsf.CO), and the western Brazil (Acre region: acre.wsf.BR). The checklist of the white-sand forests of northern Peru were extracted from García-Villacorta *et al.* (2003), supplemented with a more regional study of its woody flora (Fine *et al.* 2010) as well as collections made by other botanists and projects in the same region as recorded in the Missouri Botanical Garden's Tropicos database (Tropicos-Peru 2013). The following studies were used to compile the checklists of vascular white-sand floras of Colombia (guainía.wsf.CO, and caquetá.wsf.CO), and Brazil (acre.wsf.BR): Cortés & Franco (1997), Arbeláez (2003), Silveira (2003), Cárdenas-López (2007), and Ferreira (2009).

TAXONOMIC INCLUSION AND 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's Tropicos database was the chosen source for taxonomic matching. In very few cases, especially for recently described species that are still in the process of inclusion in taxonomic databases, resolving species names was achieved by consulting The Plant List website (The Plant List 2013). 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 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 sub-specific taxa may be useful for a better understanding of floristic patterns in relation to white-sand forests.

The taxonomy at the family level for angiosperms follows the Angiosperm Phylogeny Group III system (The Angiosperm Phylogeny Group 2009). 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).

DISTRIBUTIONAL PATTERNS IN WESTERN AMAZON WHITE-SAND FORESTS.—To study the distributional patterns of species from these four floristic checklists, we searched for specimens of each taxon in the Missouri Botanical Garden herbarium online database Tropicos (http://www.tropicos.org) and determined the ecoregions in which they occur following Olson *et al.* (2001). We did not count a species as being present in an ecoregion if it was only represented by one specimen or if the identification was dubious, based on visual verification of the specimens at MO. In addition, we classified each species in the white-sand dataset into one of three categories: white-sand specialist, poor-soil specialist, or habitat generalist. 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 oligotrophic habitats (e.g. igapó forests, sandy-clay soils); and generalist species are 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 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). Species with dubious taxonomic identification were not included in the analysis.

Distributional analyses were conducted for the three groups of species separately as well as together as one group to explore which species are shared amongst ecoregions occurring within the limits of Amazonia (Fig. 1). White-sand forests from Colombia (guainía.wsf.CO, and caquetá.wsf.CO) occur at the margin of the western Guiana Shield (Fig. 1), and previous studies have shown that they have strong phytogeographic connections (i.e. they share a large number of species) with the Guiana Shield region (Cortés & Franco 1997, Cortés *et al.* 1998, Arbeláez 2003). Thus, in order to further evaluate the floristic relationship of western Amazon white-sand forests outside of the Guiana Shield, we conducted distributional analyses both including and excluding the Colombian white-sand datasets.

FLORISTIC RELATIONSHIPS OF WESTERN AMAZON WHITE-SAND FORESTS.—To carry out an analysis of the floristic relationships of western Amazon white-sand forests, province-level plant checklists were compiled for each of the countries with territories in Amazonia as defined here: Bolivia, Brazil, Colombia, Ecuador, Peru, Venezuela, Guyana, French Guiana, and Surinam (Fig. 1; Appendix 1). Political unit definitions vary depending on the country (e.g. state in Brazil, department in Peru and Colombia), and we use the name "provinces" throughout this article to refer to all such political units. Because of their relatively small extent, the four provinces located in the Ecuadorian Amazon were treated in the analysis as one unit. In total, data were collated for 26 provinces. For developing this database the following floristic 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). These checklists and floras

were used to create a presence-absence matrix of species with which we conducted analyses of floristic composition. White-sand specialists found in provinces in which the four white-sand checklists were embedded (CO.GN, CO.CQ, PE.LO, and BR.AC) were excluded from the province-level lists. Including white-sand species in these lists would not have been appropriate with the floristic dissimilarity metric that we used to conduct clustering analyses (see below), because we would have obtained a floristic dissimilarity of zero between the white-sand list and that of the floristic province in which it was embedded.

CLUSTER ANALYSIS.—In order to evaluate the floristic distance between study units we created a dissimilarity matrix by employing the one-complement of the Simpson similarity index (Simpson 1943) , which measures the proportion of the more species-poor site that is not nested within the more species-rich site (Tuomisto 2010):

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

Where *a* is the number of species present in both sites; *b* is the number of species restricted to one site; and *c* is the number of species restricted to the other site (Koleff *et al.* 2003). We then performed a hierarchical clustering of the floristic checklists based on this dissimilarity matrix using the function *hclust* in the R statistical environment (R Core Team 2015).

There are multitudes of clustering algorithms for different kinds of data and applications. Yet, evaluations of the benefits of different algorithms are seldom carried out in ecology or biogeography. 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). In order to choose which of four clustering algorithms (Ward, Average linkage (UPGMA), Single linkage, and Complete linkage) gave the best representation of floristic relationships, we calculated the correlation of distances between sites in the resulting hierarchical clusters with the dissimilarity matrix obtained with the Simpson distance index. The analysis of cophenetic correlation among the four algorithms ranged from 0.28 to 0.63 (Appendix 2), with the best performing being Average Linkage. We checked and ensured that ties in dissimilarity values among clusters were not affecting our results using algorithms in the *recluster* package (Dapporto *et al.* 2013).

We assessed the statistical support for clusters using multi-scale bootstrapping, implemented with the *pvclust* function in the *pvclust* package (Suzuki & Shimodaira 2006). We used 1000 bootstrap replicates with 10 different sampling levels and focused on approximately unbiased (AU) p-values as a measure of statistical support (Suzuki & Shimodaira 2006). The *pvclust* algorithm also facilitates the estimation of the standard error of each cluster, which provides a measure to diagnose outliers not strongly supported by the data.

ORDINATION.—As a complement to the floristic patterns revealed by the clustering analysis we performed Non-metric Multidimensional Scaling (NMDS),which extracts a reduced number of axes from the multidimensional space where the positions of the sites are defined (Minchin 1987, Borcard *et al.* 2011).

We used the R package *vegan* (Oksanen *et al.* 2015) to implement NMDS in the manner 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 only a local optimum of stress is found, we ran the analysis from different random spatial configurations up to 500 times. Convergence to the same stress value from these random spatial configurations indicated that a global optimum had been reached. The dissimilarity matrix for the NMDS analysis was constructed using the Simpson distance index.

RESULTS

PATTERNS IN HABITAT SPECIALIZATION.—Overall, a total of 1,180 vascular plant species comprising 133 families, and 491 genera were found to occur in the four western Amazon white-sand forest sites. The species distributional dataset resulted in 69,986 unique plant records representing these species' occurrences across the Neotropics. At the species level, 43% of the total vascular flora occurring on white-sand forests was found to be habitat generalist (i.e.

occurring in white-sands forests as well as diverse other habitat types), 34% poor-soil specialist (i.e. occurring in white-sand forests and other oligotrophic habitats), and 23% white-sand specialist (i.e. restricted to white-sand forests). Appendix 3 summarizes the richness of families, genera, and species found in the three designated habitat preference categories. Of the total plant records, 74% (51,790 records) corresponded to "habitat generalists," 21% to "poor-soil specialists" (14,723 records), and 5% to "white-sand specialists" (3,473 records).

DISTRIBUTION PATTERNS ACROSS ECOREGIONS.—A large proportion of the species of white-sand forests of the western Amazon occurred within ecoregions of the Guiana Shield when this region was analysed as a unit. When excluding the Colombian white-sand checklists from the analysis, we found that 65% of white-sand specialist species (56 out of 85 species) in Loreto, Peru and/or Acre, Brazil were distributed in the Guiana Shield while 35% are endemic to these white-sand areas (29 species) (Appendix 5). When considering white-sand specialists of the full dataset (i.e. including Colombian white-sand checklists), 88.8% of the total (248 white-sand specialist species out of 279 species, Appendix 4) occurred also within the limits of the Guiana Shield region, with the remaining white-sand specialists being endemic to the western Amazon. When analysing what were the proportions of white-sand specialist from Peru (loreto.wsf.PE), and western Brazil (acre.wsf.BR) found in the Guiana Shield region, the three ecoregions with the highest percentage of western Amazon white-sand species were the Caquetá Moist Forests (30%), Guayanan Highlands Moist Forests (33%), and Negro-Branco Moist Forests (43%) (Appendix 5). These proportions changed slightly when analysed using the full white-sand dataset: Caquetá Moist Forests (69%), Guayanan Highlands Moist Forests (51%), and Negro-Branco Moist Forests (49%). Similar patterns were found when looking at the Guiana Shield

ecoregions with the lowest proportion of white-sand specialists using both datasets: Rio Negro campinarana (7-8%), and Guyanan Savanna (9-17%). These ecoregions specific locations, and their shared proportions of white-sand specialists using both datasets, are shown in Figure 2.

FLORISTIC SIMILARITY ANALYSIS.—A total of 26 floristic datasets at the level of provinces were compiled and compared with four western Amazon white-sand forests. There were a total of 26,887 vascular plant species in the floristic dataset from 2865 genera and 268 APG III families. Appendix 1 gives a summary of the area and number of vascular plant species found at each province. The number of species in the white-sand forest checklists ranged from 363 (acre.wsf.BR) to 955 species (guainía.wsf.CO). The number of species in the province checklists ranged from 607 (Vichada, Colombia) to 8,355 (Amazonas, Brazil).

The hierarchical cluster analysis indicates that the four western Amazon white-sand floras cluster first with the non-white-sand flora in which they are geographically embedded, rather than with each other (Appendix 6). The four white-sand forests are then found in a large cluster, with surrounding and neighbouring provinces (Fig. 3), rather than falling with provinces of the core Guiana Shield area (VE.DA, GF, SU, GY, VE.BO, BR.RR).

Relatively high levels of unbiased bootstrap support values (AU) were found by the *pvclust* randomization procedure for all clusters containing white-sand forests sites (Fig. 3). In particular, the cluster grouping the four western Amazonian white-sand floras along with

neighbouring non-white-sand floras had an AU pv-value of 84 (Appendix 6). It is clear from the *pvclust* analysis, however, that guainía.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 = 76)) than to the other three western Amazonian white-sand sites. Overall, cluster topology support values estimated by *pvclust* (AU p-values) ranged from 59 to 100% (Appendix 6).

The standard error of the majority AU bootstrap values in *pvclust* was close to 0 for the majority of clusters (Appendix 7), which gives confidence that the existence of these phytogeographic clusters is supported by data. Only cluster 6, which does not include white-sand forests, had a relative high standard error in the bootstrap procedure (Appendix 7).

ORDINATION.—An NMDS ordination with two axes recovered similar phytogeographic patterns to cluster analysis results as interpreted by the relative distances between floras and white-sand forests portrayed in the ordination space (Fig. 3). The Shepard plot indicates that there is a good fit of the ordination distance among sites against the original dissimilarity distance (Appendix 8). Adding additional axes to the analysis did not result in any substantial reductions in the stress value. White-sand forests of Acre (acre.wsf.BR), Loreto (loreto.wsf.PE), and Caquetá (caquetá.wsf.CO) are closer to each other floristically than they are to the white-sand forests of Guainía (guainía.wsf.CO).

DISCUSSION

PATTERNS OF 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 or sandy-clay soils (Anderson 1981, Prance 1996, Coomes & Grubb 1996, Bongers *et al.* 1985, Duivenvoorden & Lips 1995, García-Villacorta *et al.* 2003, Fine *et al.* 2010, Silveira 2003, Vicentini 2004, Ferreira 2009). In terms of species composition, however, our results show that only about a quarter (23%) of the total 1183 vascular plant species inhabiting western Amazonian white-sand forests are specialized to these forests while the vast majority (77%) also occur in non-white-sand habitats (Table 2). This finding shows that a large majority of the species diversity found in white-sand forest can be attributed to plants from other habitats. Previous work on white-sand floristics and phytogeography has often examined taxonomic sub-sets of floras or taken a restricted (sub-regional) geographic approach, which despite showing the influence of plants also found in other habitats, 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%) occurring in the vegetation type were restricted to it, whereas 23.6% also occurred in non-white-sand *terra firme* forests, 20% in *igapó* forests, and 2.6% in *varzea* forests (Anderson 1978, cited in Anderson (1981)). Similarly, an analysis of tree plots in white-sand and neighbouring forests in Peru found that 52% of tree species in white sand forests were specialists, while the rest were facultative specialists (9%), or habitat generalists (39%) (Fine *et al.* 2010).

In contrast, we have used a relatively strict criterion to determine white-sand specialists, *i.e.* that they are found only in white-sand forests, and we therefore may have underestimated specialization in white-sand forests compared to a classification based on species relative abundance. For example, a previous regional study from Madre de Dios, Peru found that only 15-26% of all studied species were restricted to a single forest type or habitat (Pitman et al. 1999), while a subsequent study in the same region that used relative abundance information found that 76.5% of dominant tree species were habitat specialists, i.e. significantly more abundant in one habitat type (Phillips *et al.* 2003). In accordance with this pattern, a previous study of white-sand forests in Loreto, Peru, found that floristic differentiation between white-sand and *terra firme* forests was greater when one considered relative abundances of species rather than just presence/absence information (Fine et al. 2010). Thus, in our study, while some species may not have been classified as white-sand specialists using our strict presence/absence criterion, they may be much more abundant in white-sand forest than other forest types, thus potentially qualifying as specialists using abundance-based criteria. In other words, while there are many species present in white-sand forests that are also found in other forest types, the forest does tend to be dominated by white-sand specialists (Fine et al. 2010) or by poor-soil specialists as defined here, i.e. species with preference for waterlogged or oligotrophic soils (Freitas 1996, García-Villacorta *et al.* 2003, Vicentini 2004). Similarly, a recent study of swamp forests in the Ecuadorian Amazon found that just 8.6% of tree species in swamp forest are specialists on swamp forest, but that these specialists represent 43.6% of stems in the swamp forest (Pitman *et al.* 2014).

Another potential caveat of our results is that the number of white-sand specialist species may increase in the future via the discovery of cryptic species. For example, based upon detailed molecular and morphological studies, populations confined to white-sand habitats and previously assigned to *Protium subserratum* (Burseraceae) were found to be distinct from populations of that occurred on non-white sand soils, and it was suggested that they should be recognised at species level (Daly & Fine 2011, Fine *et al.* 2013). Similarly, a study on reproductive biology, phenotypic differences, and ecological preferences within the *Pagamea coriacea* complex (Rubiaceae) identified two sympatric species exploiting different gradient combinations of light and drainage within white-sand forests (Esteves & Vicentini 2013). Elucidating the number of cryptic undescribed species, and potentially incipient species undergoing ecological adaptation into white-sands forests, will remain uncertain without more taxonomic, field, and molecular-based studies.

In any case, our result that just 23% of species in western Amazon white-sand forest are restricted to that habitat type is much lower than previous estimates. We suggest that the ecological conditions of other oligotrophic habitats are similar enough to white sand forests such that they function like meta-ecosystems (Loreau *et al.* 2003, Gravel *et al.* 2010), harbouring species that are able to disperse into white sand habitats, and survive there, albeit at low densities. Likewise, the dispersal of propagules via mass-effect from surrounding habitats (Shmida & Wilson 1985, Holt 1993) may be an additional factor influencing the similarity values obtained when using presence/absence data rather than abundance data (cf. Vormisto, Svenning, *et al.* 2004).

DISTRIBUTIONAL PATTERNS AND PHYTOGEOGRAPHICAL CONNECTIONS.—Of the total western Amazonian white-sand specialist species, 88% of them occurred in floras within the Guiana Shield region, whereas 12% are endemic to the western Amazon (i.e. restricted to the four white-sand areas studied here). This pattern of phytogeographic connection was still high when only non-Guiana Shield white-sand forests (loreto.wsf.PE, and acre.wsf.BR) were considered (65% of the white-sand specialists were shared with floras within the Guiana Shield region). Among all ecoregions, Caquetá Moist Forests, Guayanan Highlands Moist Forests, and Negro-Branco Moist Forests shared the highest proportions of western Amazon white-sand specialists (Appendix 5). These ecoregions are located at the central and western part of the Guiana Shield region (Fig. 2b) which supports results from studies of Colombian white-sand forests showing strong phytogeographic links with the Guiana Shield flora (Cortés *et al.* 1998, Giraldo-Cañas 2001, Arbeláez & Duivenvoorden 2004). On the other hand, the ecoregions with the highest percentage of shared western Amazon white-sand specialists, when using only species from loreto.wsf.PE (Peru), and acre.wsf.BT (Brazil), are located in the western Amazon (Iquitos varzea, Napo moist forests, and Southwest Amazon moist forests) (Fig. 2a; Appendix 5). It remains unexplained to what degree the white-sand forests contained in these ecoregions is influencing the compositional similarity of the white-sand forests we studied here.

DISPERSAL AND FLORISTIC RELATIONSHIPS.—All white-sand forests clustered with the flora of the province where they belong geographically (Fig. 3). Given the overall large number of non-white-sand specialist species 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; hinting at an important influence of regional dispersal processes (Ricklefs 1987, Cornell & Lawton 1992, Holt 1993, Latham & Ricklefs 1993, Cottenie 2005, Ricklefs 2008). Collectively, our results support the hypothesis of a flora constructed via both long-distance dispersal of white-sand specialists from distant white-sand habitats and more local dispersal of poor-soil specialists and generalist species from ecologically similar oligotrophic habitats occurring in the same areas in which white-sand forests are embedded.

Certain combinations of edaphic factors that are present in white-sand habitats promote colonization by species from physiognomically distinct habitat types, such as nutrient-poor *terra firme* clayey or sandy-clay soils and waterlogged habitats (Freitas 1996, García-Villacorta *et al.* 2003, Vicentini 2004). In this regard, peat-accumulating palm swamps (Tuomisto *et al.* 1994, Lähteenoja *et al.* 2009), and old terraces of *terra firme* forests on hilly areas (García-Villacorta *et al.* 2010) may represent habitats with similar high stress and/or low resource availability (i.e. poor drainage conditions or 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.* 2010). Ancient hilly terraces on poor oligotrophic clay soils are found to be a common feature at certain drainage divides of the western Amazon (e.g. Stallard 2011). These hilly terraces can have high erosion rates (Stallard 1988), which accelerates the leaching of soil nutrients (Laurance *et al.* 2010, Vormisto, Tuomisto, *et al.* 2004), and they can be extensive and interconnected in some areas (García-Villacorta *et al.* 2010). Similarly, some non-specialist white-sand species have been found in swamp habitats of the Amazon floodplain (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 in these habitats may facilitate dispersal of white-sand species.

THE EFFECT OF GEOGRAPHICAL DISTANCE BETWEEN FLORAS—Geographical proximity may help to explain some part of the observed phytogeographical affinities of white-sand floras. The Amazonas provinces in Brazil and Venezuela (BR.AM, and VE.AM) as well as Colombian provinces are geographically adjacent and were found to have close links to western Amazonian white-sand forests. Geographical distance may also help to explain why acre.wsf.BR (Brazil) and loreto.wsf.PE (Peru) are more similar to each other and to caquetá.wsf.CO (Colombia) than to guainía.wsf.CO (Colombia), the latter being closer in geographic distance to the Guiana Shield region (Fig. 2). A correlation analysis of the geographic distance and floristic matrices (Mantel test) in the dataset found a significant association (Appendix 9), implying that spatially adjacent sites are floristically more similar, a pattern often driven by dispersal limitation (Nekola & White 1999). In this context, several studies of plant dispersal syndromes in Amazonian white-sand forests have suggested that long-distance dispersal or stepping-stone dispersal may be an important ecological process in the maintenance of Amazonian white-sand forests (Macedo & Prance 1978, Prance & Schubart 1978).

SYNTHESIS AND IMPLICATIONS FOR CONSERVATION.—Floristically, we found that western Amazon white-sand forests include a large number of plant species that are not restricted to white-sand habitats. Regardless, at the local and regional level white-sand forests possess a significant number of endemics that add to both regional and beta diversity in the Amazon and

should remain a conservation priority. It is possible that this finding may be influenced by cryptic, undescribed species –i.e., some morphologically indistinguishable populations found on white sand may actually represent different species. The high proportion of species not specialized to white-sand habitats may result from both immigration of species from other nutrient-poor/water-logged habitats and mass effect dispersal of species from neighbouring habitats with richer soils. Cluster analysis and NMDS ordination concurred that the white-sand forests of the western Amazon are floristically most similar to the non-white sand floras of the geographic regions to which they belong. More broadly, the composition of white-sand forests of the western Amazon is more similar to floras of the western and central Guiana Shield region than to other floras in Amazonia, which implies that long-distance dispersal processes may be important in shaping its species composition. 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. Dispersal processes may have more importance than local species interactions in structuring Amazonian white-sand plant communities, perhaps via stepping-stone dispersal processes across ecologically similar habitat types like Amazon peatlands, and hilly terraces on oligotrophic soils. The long term conservation of Amazonian white-sand forests will require the maintenance of regional dispersal processes, necessitating corridors connecting these archipelagos of habitat islands across the Amazon and the Guiana Shield.

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FIGURE LEGENDS

FIGURE 1. The Amazon and the Guiana Shield region (dashed area) with political division acronyms used in the floristic analysis overlaid on an elevation map (darker areas indicate higher elevations). Approximate locations of studied white-sand forests: 1 = acre.wsf.BR (Acre region, Brazil), 2 = loreto.wsf.PE (Loreto region, Peru), 3 = caquetá.wsf.CO (Caquetá region, Colombia), 4 = guainía.wsf.CO (Guainía region, Colombia). Province acronyms in Appendix 1.

FIGURE 2. Proportion of western Amazon white-sand specialists shared among different ecoregions within Amazonia constructed using (a) only loreto.wsf.PE and acre.wsf.BR, and (b) full white-sand dataset. non-GS WA ws = non-Guiana Shield western Amazon white-sand specialists. WS specialists = full list of white-sand specialists. Sites 1 and 2 = non-Guiana Shield western Amazon white-sand areas; 3 and 4 = Guiana Shield western Amazon white-sand sites. GS limit = Guiana Shield limit. Note change in the proportion and ecoregions of shared white-sand specialists according to the dataset used. Site names as in Fig. 1.

FIGURE 3. Relationships of western Amazon white-sand forests with provinces/states in the Amazon and Guiana regions as represented by non-metric Multidimensional Scaling (NMDS) ordination. Lines connecting the sites represent cluster analysis result. WSF = western Amazon white-sand forests. Province acronyms in Appendix 1.

FIGURES

Figure 1

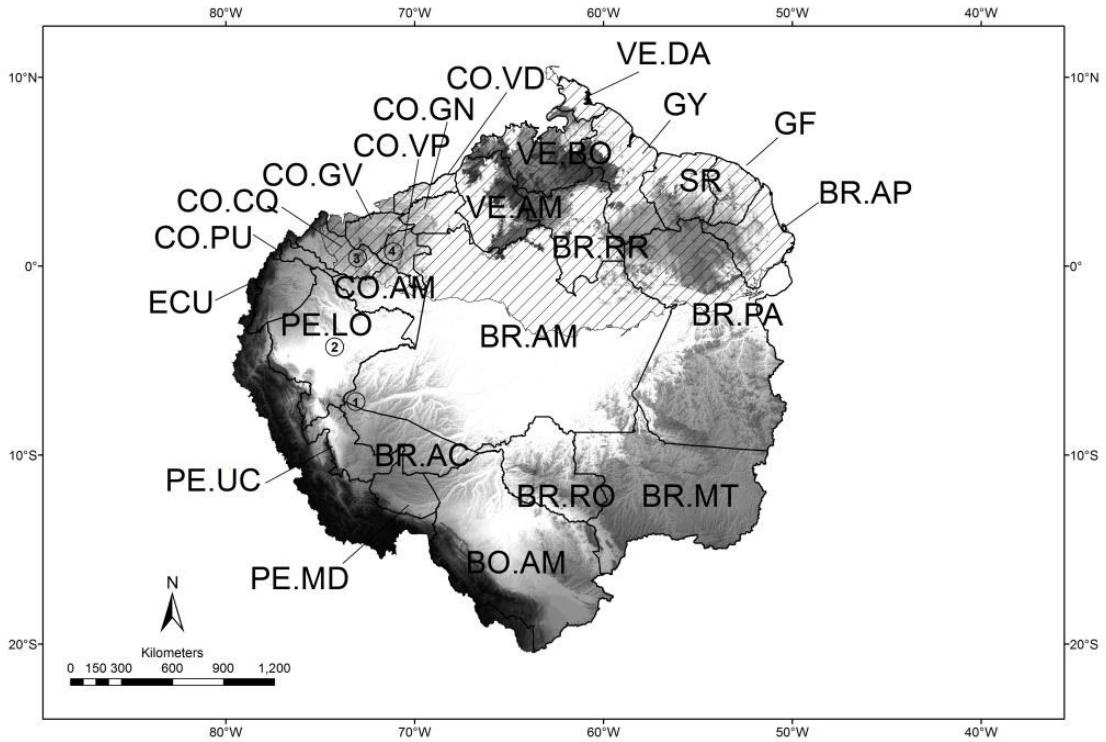
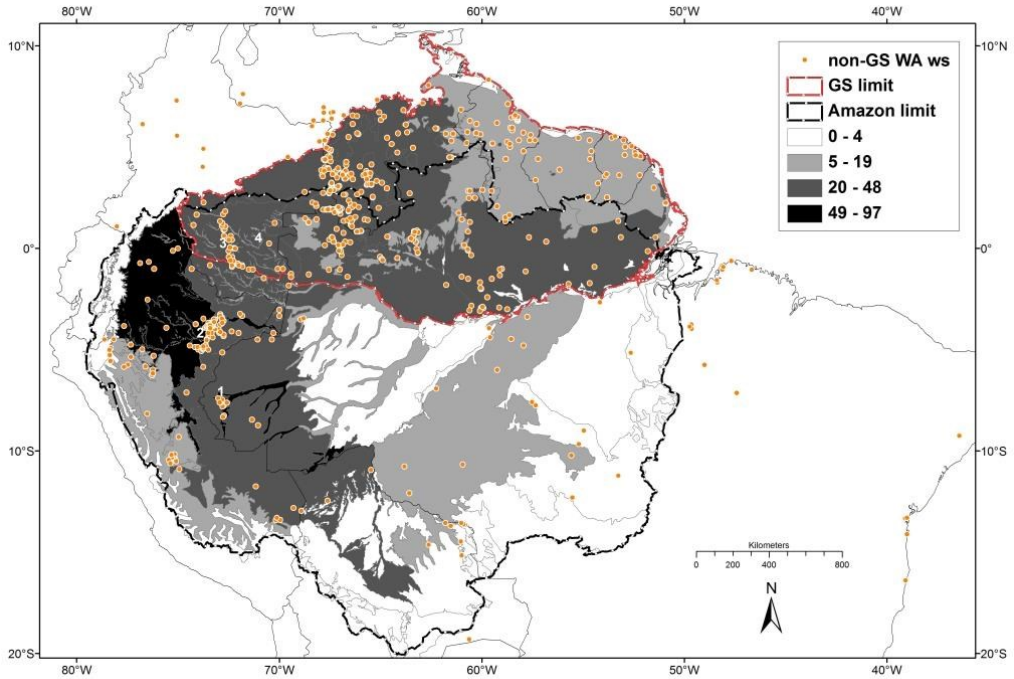


Figure. 2.

a)


non-GS WA ws
GS limit
Amazon limit
0 - 4
5 - 19
20 - 48
49 - 97
Kilometers
0 200 400 800
N
80°W
70°W
60°W
50°W
40°W
10°N
0°
10°S
20°S

b)

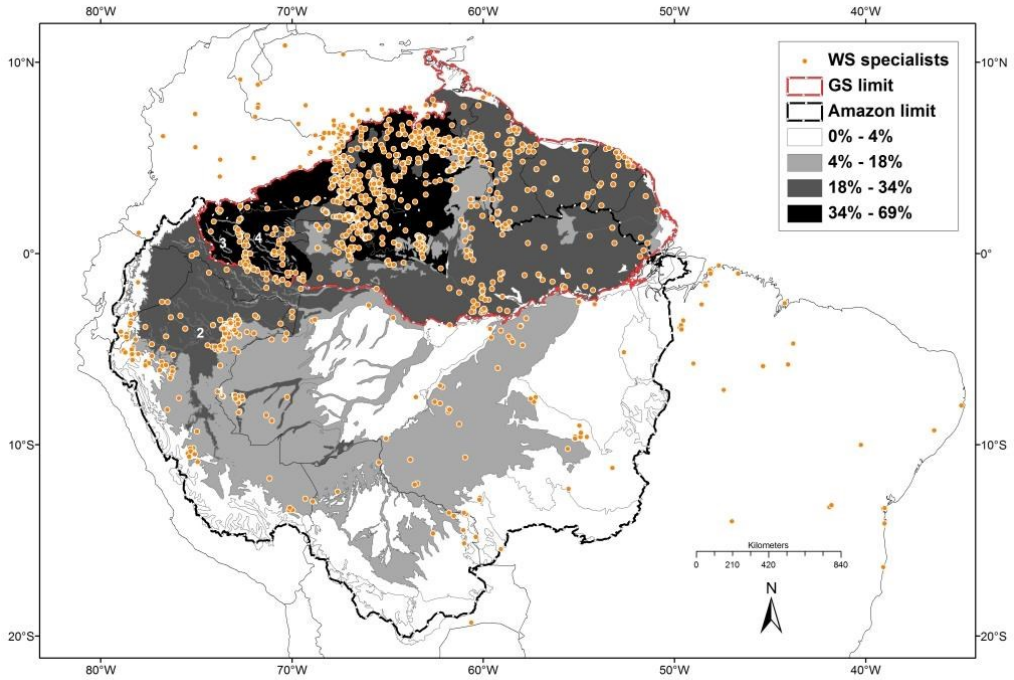
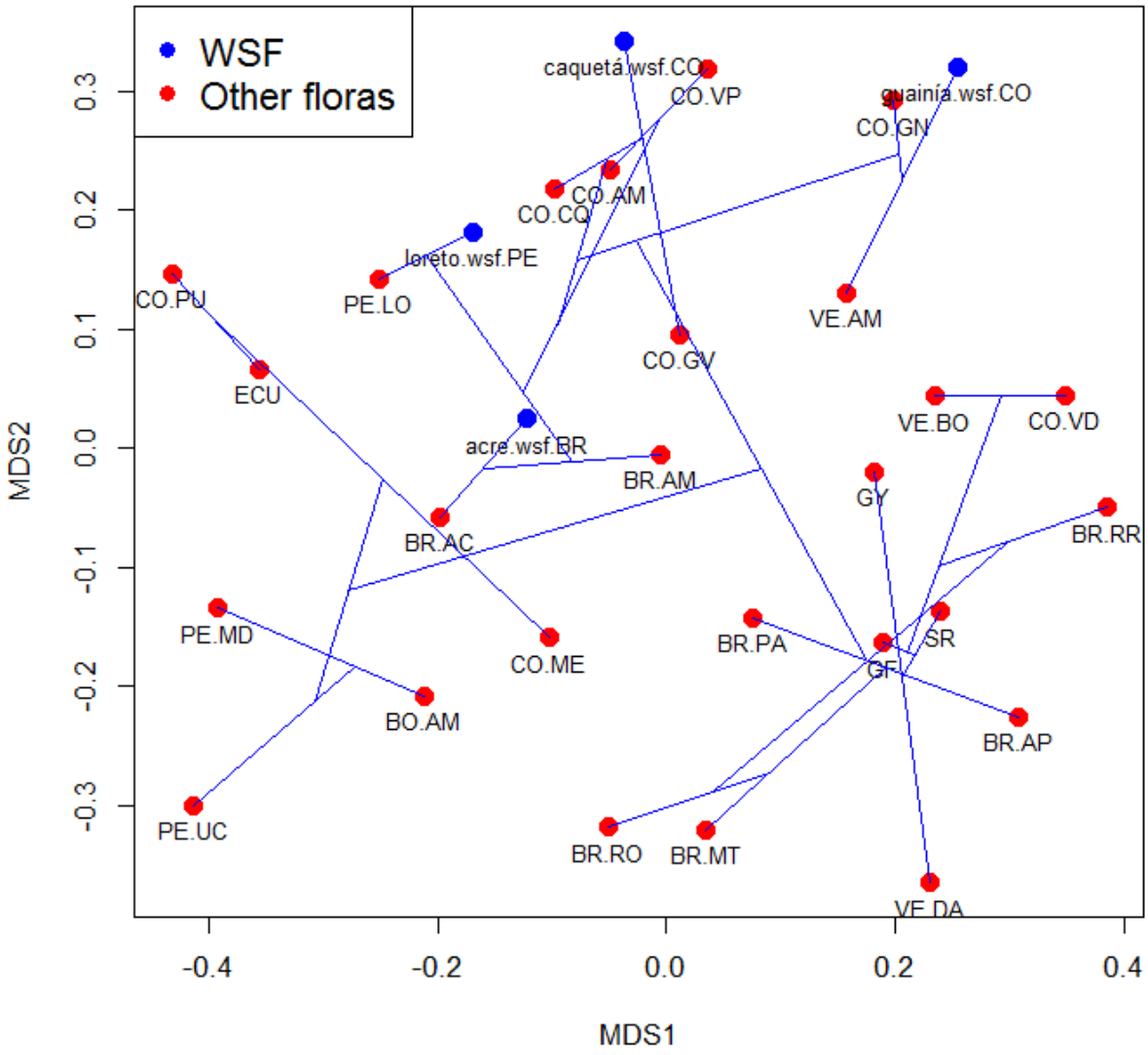

WS specialists
GS limit
Amazon limit
0% - 4%
4% - 18%
18% - 34%
34% - 69%
Kilometers
0 210 420 840
N
80°W
70°W
60°W
50°W
40°W
10°N
0°
10°S
20°S

Figure 3


WSF
Other floras
caquetá.wsf.CO
CO.VP
guainía.wsf.CO
CO.GN
CO.AM
CO.CQ
loreto.wsf.PE
PE.LO
CO.PU
VE.AM
CO.GV
ECU
VE.BO
CO.VD
acre.wsf.BR
BR.AM
GY
BR.AC
BR.RR
PE.MD
BR.PA
SR
CO.ME
GF
BO.AM
BR.AP
PE.UC
BR.RO
BR.MT
VE.DA
MDS2
MDS1
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.2
0.0
0.2
0.4

Appendix 1. Number of vascular plant species and source used to build the database ordered by ascending number of species. Studied western Amazon white-sand forests in bold.

Site code	Province	Area (km^2)	Country	No. spp.	Source
acre.wsf.BR	Acre	-	Brazil	363	(Silveira 2003, Ferreira 2009)
CO.VD	Vichada	38,734.93	Colombia	607	(SINCHI 2013)
caquetá.wsf.CO	Caquetá	-	Colombia	657	(Cortés *et al.* 1998, Arbeláez & Duivenvoorden 2004)
loreto.wsf.PE	Loreto	-	Peru	731	(García-Villacorta *et al.* 2003, Fine *et al.* 2010, Tropicos-Peru 2013)
guainía.wsf.CO	Guainía	-	Colombia	955	(Cárdenas-

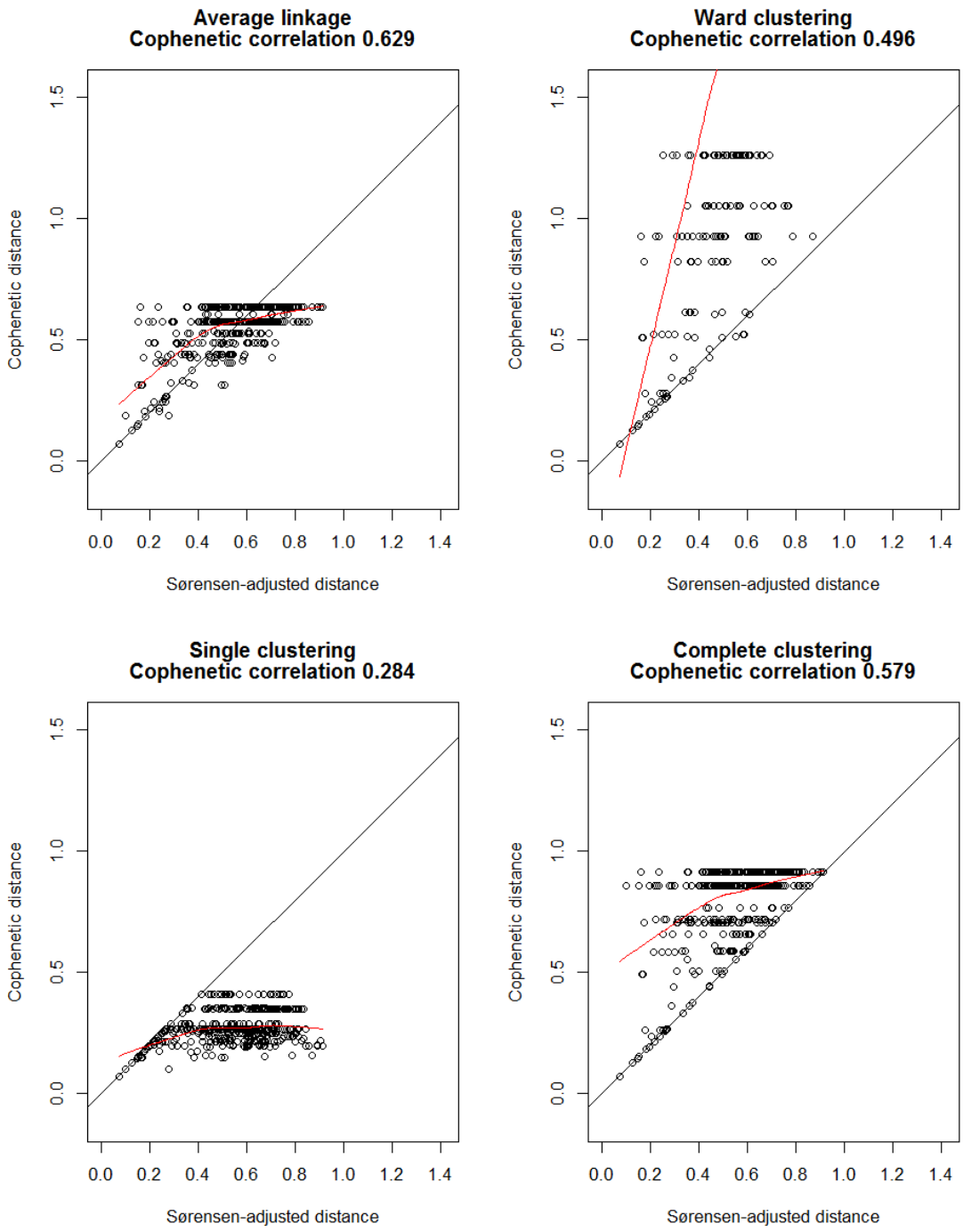
					López 2007)
PE.UC	Ucayali	105,078.38	Peru	1148	(Brako & Zarucchi 1993, Tropicos-Peru 2013)
CO.GN	Guainía	68,819.14	Colombia	1289	(SINCHI 2013)
CO.VP	Vaupés	53,242.63	Colombia	1738	(SINCHI 2013)
VE.DA	Delta Amacuro	38,230.4	Venezuela	1765	(Funk *et al.* 2007)
CO.GV	Guaviare	55,570.16	Colombia	1769	(SINCHI 2013)
PE.MD	Madre de Dios	84,420.81	Peru	2088	(Brako & Zarucchi 1993, Tropicos-Peru 2013)
BR.AP	Amapá	141,105.57	Brazil	2523	(Forzza *et al.* 2010a, b, Flora

					do Brasil 2013)
BR.RR	Roraima	224,384.08	Brazil	2688	(Forzza *et al.* 2010a, b, Flora do Brasil 2013)
BR.RO	Rondonia	236,376.67	Brazil	2882	(Forzza *et al.* 2010a, b, Flora do Brasil 2013)
CO.CQ	Caquetá	90,029.75	Colombia	3021	(SINCHI 2013)
BR.MT	Mato Grosso	599,681.47	Brazil	3247	(Forzza *et al.* 2010a, b, Flora do Brasil 2013)
CO.AM	Amazonas	107,462.42	Colombia	3431	(SINCHI 2013)
BR.AC	Acre	152,729.51	Brazil	4214	(Forzza *et al.*

					2010a, b, Flora do Brasil 2013)
SR	Surinam	146,011.49	Surinam	4886	(Funk *et al.* 2007)
GF	French Guiana	83,014.98	French Guiana	5166	(Funk *et al.* 2007)
PE.LO	Loreto	375,550.2	Perú	5271	(Brako & Zarucchi 1993, Tropicos-Peru 2013)
BO.AM	Amazon region	681,909.86	Bolivia	5378	(Tropicos-Bolivia 2013)
BR.PA	Pará	892,481.47	Brazil	6098	(Forzza *et al.* 2010a, b, Flora do Brasil 2013)
GY	Guyana	209,549.47	Guyana	6938	(Funk *et al.* 2007)

VE.BO	Bolivar	193,997.81	Venezuela	6941	(Funk *et al.* 2007)
VE.AM	Amazonas	179,579.86	Venezuela	7,146	(Funk *et al.* 2007)
ECU	Ecuadorian Amazon	105653.6	Ecuador	7,642	(Jorgensen & León-Yánez 1999, Tropicos-Ecuador 2013)
BR.AM	Amazonas	1’570,659.01	Brazil	8,355	(Forzza *et al.* 2010a, b, Flora do Brasil 2013)

Appendix 2.Cophenetic correlation results of the five assessed clustering algorithms. The highest cophenetic correlation (Average linkage, $r = 0.629$) is the one that best represent the dissimilarity matrix in its resulting dendrogram followed by Complete clustering (r = 0.579).



Appendix 3. Summary statistics and ecological preferences of 1,180 vascular plant species found in four western Amazonian white-sand forests.

Ecological preference	No. families with species in these categories	No. genera with species in these categories	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)	3473
Total	133	491	1180 (100)	69,986

Appendix 4. Species in the western Amazon white-sand specialist dataset with records found within the Guiana Shield region.

Family/Species	No. records
Acanthaceae	**1**
Aphelandra lamprantha	1
Annonaceae	**47**
Anaxagorea brachycarpa	14
Anaxagorea manausensis	1
Annona paludosa	5
Bocageopsis canescens	8
Cymbopetalum alkekengi	0
Duguetia arenicola	2
Guatteriopsis sessiliflora	0
Oxandra asbeckii	4
Oxandra leucodermis	3
Pseudoxandra revoluta	0
Tetrameranthus duckei	10
Tetrameranthus pachycarpus	0
Trigynaea lanceipetala	0
Apocynaceae	**54**
Mandevilla annulariifolia	6
Mandevilla caurensis	4
Mandevilla nerioides	8
Molongum lucidum	4
Odontadenia killipii	6
Odontadenia kochii	7
Parahancornia peruviana	2
Parahancornia surrogata	17
Aquifoliaceae	**30**
Ilex divaricata	28
Ilex spruceana	2
Araceae	**5**
Philodendron auyantepuiense	5
Araliaceae	**11**
Schefflera japurensis	11
Arecaceae	**11**
Euterpe catinga	5
Mauritia carana	6

Asteraceae	**26**
Calea abelioides	16
Chromolaena tyleri	2
Gongylolepis martiana	7
Stenopadus colombianus	1
Begoniaceae	**1**
Begonia lutea	1
Bignoniaceae	**54**
Anemopaegma oligoneuron	9
Digomphia densicoma	34
Distictella obovata	11
Bonnetiaceae	**64**
Bonnetia paniculata	11
Bonnetia sessilis	53
Bromeliaceae	**67**
Ananas parguazensis	23
Brocchinia hechtioides	23
Brocchinia paniculata	8
Pitcairnia patentiflora	1
Vriesea socialis	12
Burmanniaceae	**6**
Burmannia dasyantha	5
Burmannia vaupesana	1
Burseraceae	**44**
Protium calanense	5
Protium carolense	16
Protium heptaphyllum subsp. ulei	18
Protium leptostachyum	5
Calophyllaceae	**34**
Caraipa longipedicellata	8
Caraipa savannarum	19
Caraipa tereticaulis	6
Caraipa utilis	0
Haploclathra cordata	1
Haploclathra paniculata var. paniculata	0
Chrysobalanaceae	**92**
Couepia amaraliae	6
Couepia bracteosa	11
Couepia canomensis	7
Couepia williamsii	0
Exellodendron coriaceum	9
Hirtella punctillata	12
Hirtella revillae	0
Licania gracilipes	7

Licania hebantha	4
Licania intrapetiolaris	28
Licania stewardii	5
Parinari montana	3
Clusiaceae	**77**
Clusia cerroana	23
Clusia chiribiquetensis	15
Clusia fockeana	9
Clusia huberi	11
Clusia opaca	8
Clusia renggerioides	11
Tovomita calophyllophylla	0
Combretaceae	**7**
Terminalia yapacana	7
Connaraceae	**1**
Connarus guggenheimii	1
Droseraceae	**5**
Drosera esmeraldae	5
Ebenaceae	**6**
Diospyros myrmecocarpa	3
Diospyros tessmannii	**0**
Lissocarpa kating	3
Emmotaceae	**0**
Emmotum floribundum	0
Ericaceae	**14**
Vaccinium euryanthum	14
Eriocaulaceae	**127**
Paepalanthus fasciculatus	34
Paepalanthus formosus	4
Rondonanthus capillaceus	27
Syngonanthus allenii	1
Syngonanthus reflexus	29
Syngonanthus simplex	7
Syngonanthus tenuis var. bulbifer	7
Syngonanthus trichophyllus	11
Syngonanthus umbellatus	7
Erythroxylaceae	**13**
Erythroxylum kapplerianum	13
Euphorbiaceae	**117**
Conceveiba terminalis	23
Croton araracuarae	3
Croton chiribiquetensis	1
Croton mollis	10
Croton scutatus	8

Croton spiraeifolius	3
Hevea guianensis var. lutea	4
Hevea nitida	9
Hevea nitida var. toxicodendroides	1
Mabea subsessilis	18
Micrandra elata	3
Micrandra spruceana	18
Senefelderopsis chiribiquetensis	16
Euphroniaceae	**19**
Euphronia hirtelloides	19
Fabaceae	**145**
Abarema barbouriana var. arenaria	6
Abarema microcalyx	9
Aldina heterophylla	3
Calliandra vaupesiana	7
Dicymbe uaiparuensis	2
Dimorphandra macrostachya subsp. glabrifolia	2
Dimorphandra vernicosa	17
Heterostemon mimosoides	21
Inga gereauana	0
Inga neblinensis	8
Jacqueshuberia loretensis	0
Macrolobium arenarium	1
Macrolobium discolor var. egranulosum	3
Macrolobium limbatum var. limbatum	3
Macrolobium limbatum var. propinquum	0
Macrolobium molle	8
Macrolobium suaveolens	7
Senna kuhlmannii	0
Swartzia benthamiana var. benthamiana	13
Tachigali ptychophysca	4
Taralea oppositifolia	31
Gentianaceae	**30**
Curtia conferta	3
Irlbachia nemorosa	12
Tachia guianensis	15
Tachia loretensis	0
Humiriaceae	**43**
Humiria balsamifera	13
Humiria balsamifera var. balsamifera	9
Humiria balsamifera var. floribunda	1
Humiria crassifolia	11
Humiriastrum piraparanense	9
Vantanea spichigeri	0

Hymenophyllaceae	**17**
Trichomanes arbuscula	8
Trichomanes sprucei	1
Trichomanes superbum	2
Trichomanes vandenboschii	1
Trichomanes vittaria	5
Icacinaceae	**28**
Emmotum acuminatum	6
Emmotum floribundum	18
Pleurisanthes flava	4
Lauraceae	**13**
Aniba heterotepala	0
Endlicheria arunciflora	5
Endlicheria chrysovelutina	0
Endlicheria citriodora	1
Mezilaurus opaca	0
Mezilaurus triunca	0
Ocotea alata	0
Ocotea atrata	2
Ocotea esmeraldana	4
Ocotea immersa	1
Sextonia pubescens	0
Lindsaeaceae	**27**
Lindsaea meifolia	6
Lindsaea pendula	11
Lindsaea rigidiuscula	10
Loganiaceae	**20**
Bonyunia minor	20
Potalia coronata	0
Lythraceae	**15**
Cuphea annulata	13
Cuphea kubeorum	2
Malpighiaceae	**29**
Blepharandra heteropetala	5
Byrsonima amoena	8
Diacidia galphimioides	16
Malvaceae	**18**
Pachira amazonica	5
Pachira brevipes	5
Pachira coriacea	5
Pachira fuscolepidota	3
Melastomataceae	**97**
Acanthella sprucei	23
Clidemia epibaterium	12

Clidemia heteroneura	12
Clidemia pycnaster	3
Comolia microphylla	15
Ernestia tenella	4
Graffenrieda fantastica	3
Macairea theresiae	4
Miconia crassinervia	4
Pachyloma coriaceum	5
Siphanthera fasciculata	1
Tococa rotundifolia	11
Metaxyaceae	**0**
Metaxya lanosa	0
Myrtaceae	**40**
Myrcia clusiifolia	20
Myrcia revolutifolia	20
Nyctaginaceae	**14**
Neea obovata	14
Ochnaceae	**62**
Ouratea roraimae	12
Ouratea spruceana	21
Sauvagesia erioclada	1
Sauvagesia fruticosa	10
Sauvagesia guianensis subsp. araracuarensis	1
Wallacea insignis	17
Olacaceae	**8**
Chaunochiton angustifolium	7
Curupira tefeensis	1
Orchidaceae	**41**
Duckeella pauciflora	2
Encyclia leucantha	5
Epistephium hernandii	9
Epistephium lucidum	4
Epistephium parviflorum	16
Octomeria erosilabia	2
Octomeria taracuana	1
Stenocoryne longicornis	1
Trichosalpinx orbicularis	1
Orobanchaceae	**4**
Buchnera rubriflora	4
Pentaphylacaceae	**27**
Ternstroemia campinicola	3
Ternstroemia klugiana	**0**
Ternstroemia punctata	5
Ternstroemia pungens	19

Phyllanthaceae	**4**
Phyllanthus myrsinites	4
Piperaceae	**2**
Piper fonteboanum	1
Piper froesii	1
Piper mituense	0
Polypodiaceae	**16**
Cochlidium tepuiense	16
Primulaceae	**7**
Cybianthus reticulatus	7
Proteaceae	**1**
Euplassa saxicola	1
Rapateaceae	**42**
Duckea junciformis	7
Duckea squarrosa	9
Monotrema arthrophyllum	5
Monotrema xyridoides	15
Rapatea elongata	4
Schoenocephalium martianum	2
Rhabdodendraceae	**17**
Rhabdodendron amazonicum	17
Rubiaceae	**537**
Ferdinandusa guainiae	6
Ferdinandusa hirsuta	3
Ferdinandusa sprucei	5
Ixora intensa	9
Ladenbergia lambertiana	57
Pagamea acrensis	16
Pagamea aracaensis	5
Pagamea coriacea	49
Pagamea guianensis	54
Pagamea macrophylla	4
Pagamea montana	21
Pagamea plicata	17
Pagamea thyrsiflora	40
Palicourea nitidella	64
Platycarpum orinocense	1
Platycarpum orinocense var. orinocense	5
Remijia macrocnemia	9
Remijia roraimae	13
Retiniphyllum concolor	22
Retiniphyllum scabrum	40
Retiniphyllum schomburgkii	72
Retiniphyllum truncatum	18

Rudgea krukovii	1
Sipaneopsis huberi	4
Stachyococcus adinanthus	2
Rutaceae	**17**
Adiscanthus fusciflorus	5
Decagonocarpus cornutus	5
Decagonocarpus oppositifolius	6
Hortia vandelliana	1
Leptothyrsa sprucei	0
Ravenia biramosa var. peruviana	0
Salicaceae	**62**
Euceraea nitida	30
Laetia coriacea	20
Laetia cupulata	12
Sapindaceae	**1**
Paullinia splendida fo. chrysocarpa	1
Sapotaceae	**67**
Chrysophyllum bombycinum	0
Chrysophyllum sanguinolentum subsp. spurium	7
Elaeoluma schomburgkiana	8
Pradosia schomburgkiana	39
Pradosia schomburgkiana subsp. schomburgkiana	13
Schlegeliaceae	**0**
Schlegelia cauliflora	0
Selaginellaceae	**6**
Selaginella coarctata	6
Siparunaceae	**3**
Siparuna micrantha	3
Thymelaeaceae	**17**
Tepuianthus colombianus	2
Tepuianthus savannensis	15
Vochysiaceae	**13**
Ruizterania retusa	13
Xyridaceae	**80**
Abolboda acicularis var. granularis	2
Abolboda americana	9
Abolboda grandis	8
Abolboda grandis var. grandis	8
Abolboda macrostachya var. macrostachya	8
Abolboda pulchella	6
Xyris araracuare	2
Xyris esmeraldae	17
Xyris lomatophylla	5
Xyris spruceana	10

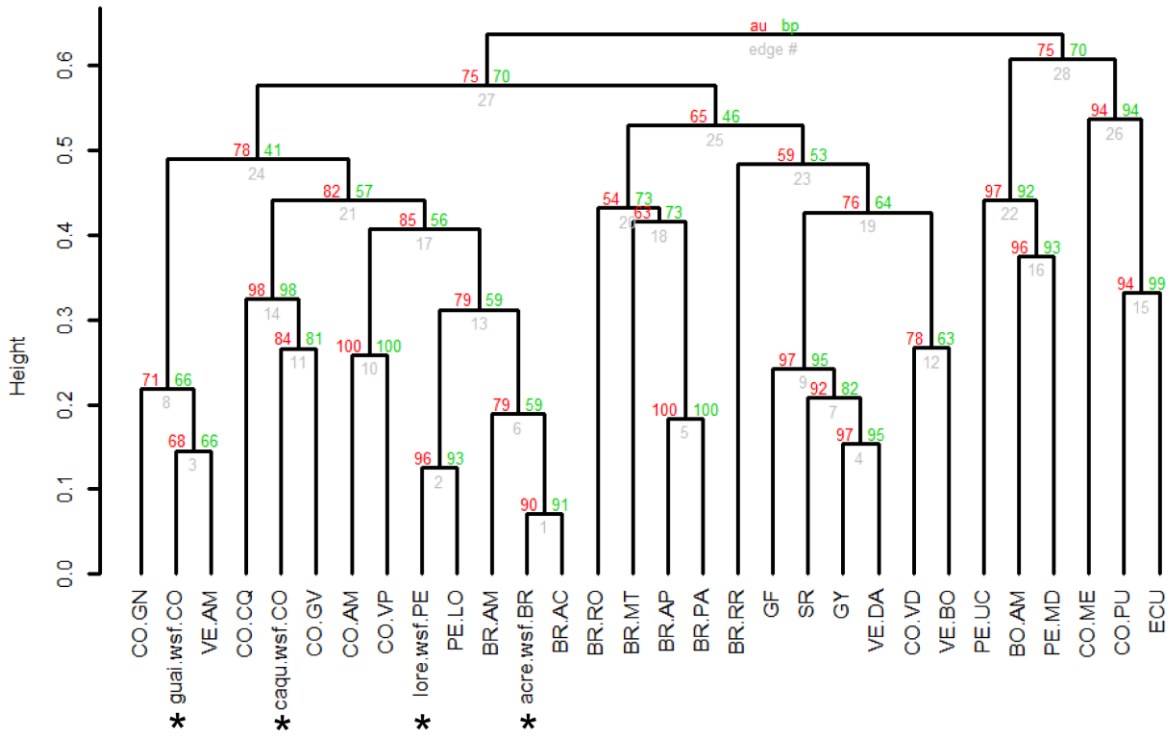
Xyris subglabrata	4
Xyris wurdackii subsp. caquetensis	1
Total No. Records	**2503**
Total No. Species	**279**

Appendix 5. 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 specialist dataset. Note changes in the proportions by ecoregions according to the dataset used.

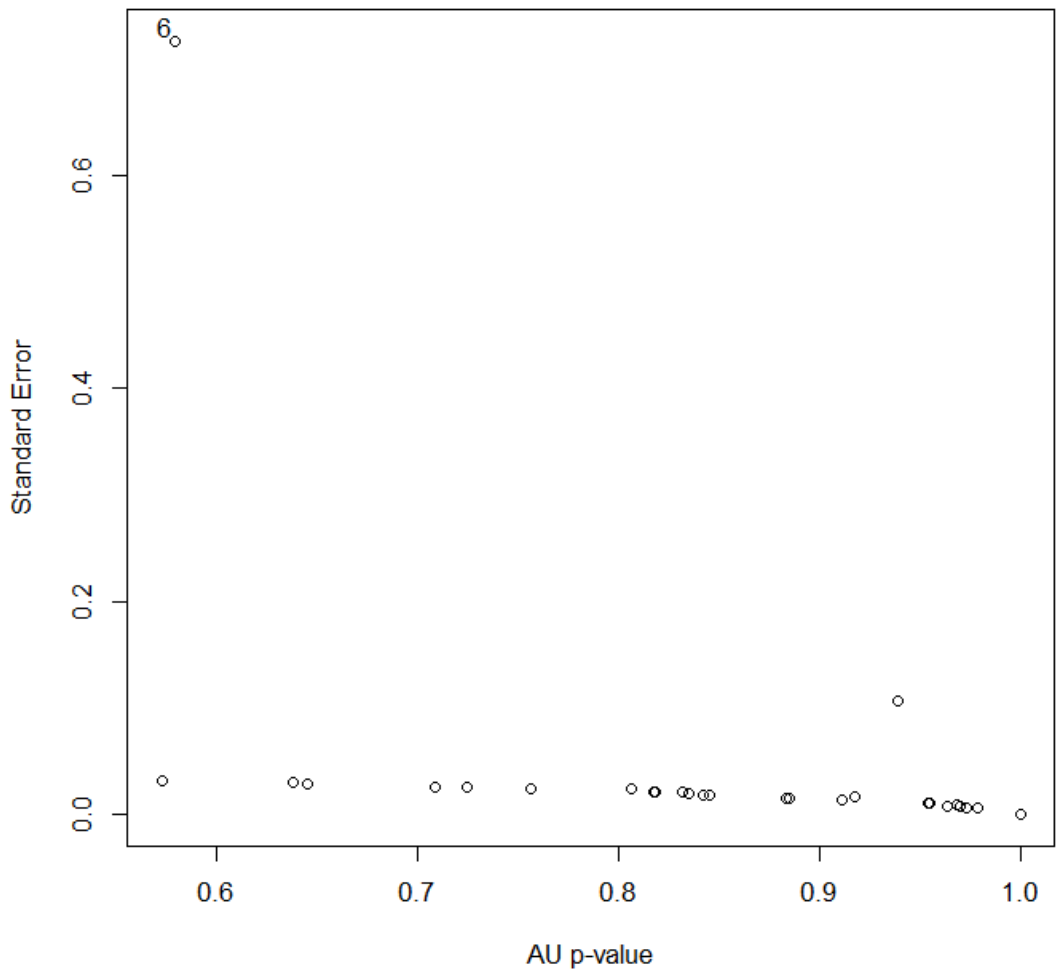
a) Full white-sand dataset: caquetá.wsf.CO (Colombia), guainía.wsf.CO (Colombia), acre.wsf.BR (Brazil), lore.wsf.PE (Peru)			b) Non-Guiana Shield white-sand dataset: acre.wsf.BR (Brazil), loreto.wsf.PE (Peru)		
Ecoregion	No. species	% species	Ecoregion	No. species	% species
Caquetá moist forests	191	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%

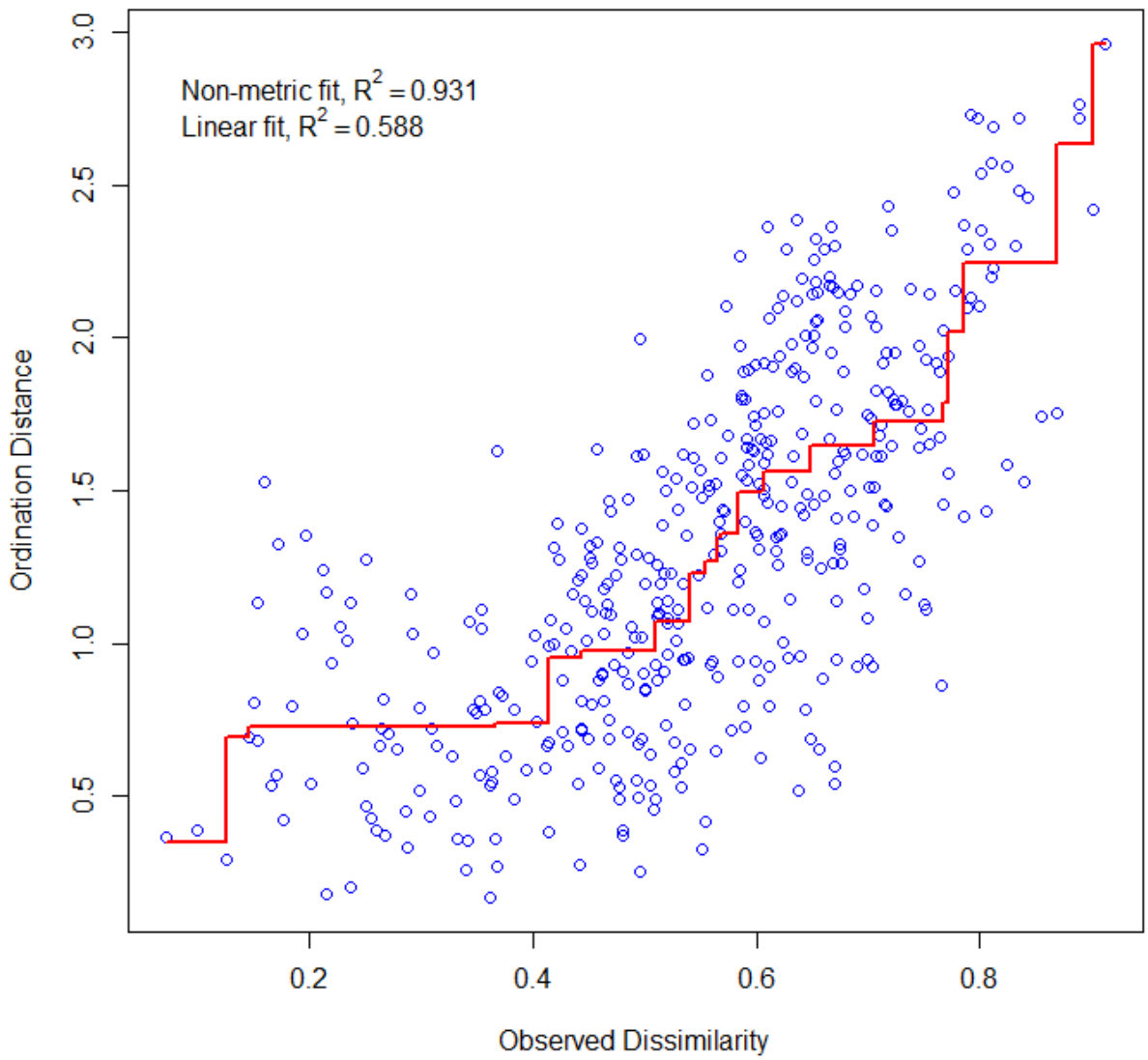
Appendix 6. Cluster analysis of Amazon and Guiana Shield sites with bootstrap support values using Average linkage as clustering algorithm and 1000 bootstrap runs. AU bootstrap p-values at each node (left), standard bootstrap values (right), and cluster number (below). Western Amazon white-sand forests are marked with asterisks: acre.wsf.BR (Brazil), caquetá.wsf.CO (Colombia), guainía.wsf.CO (Colombia), and loreto.wsf.PE (Peru).



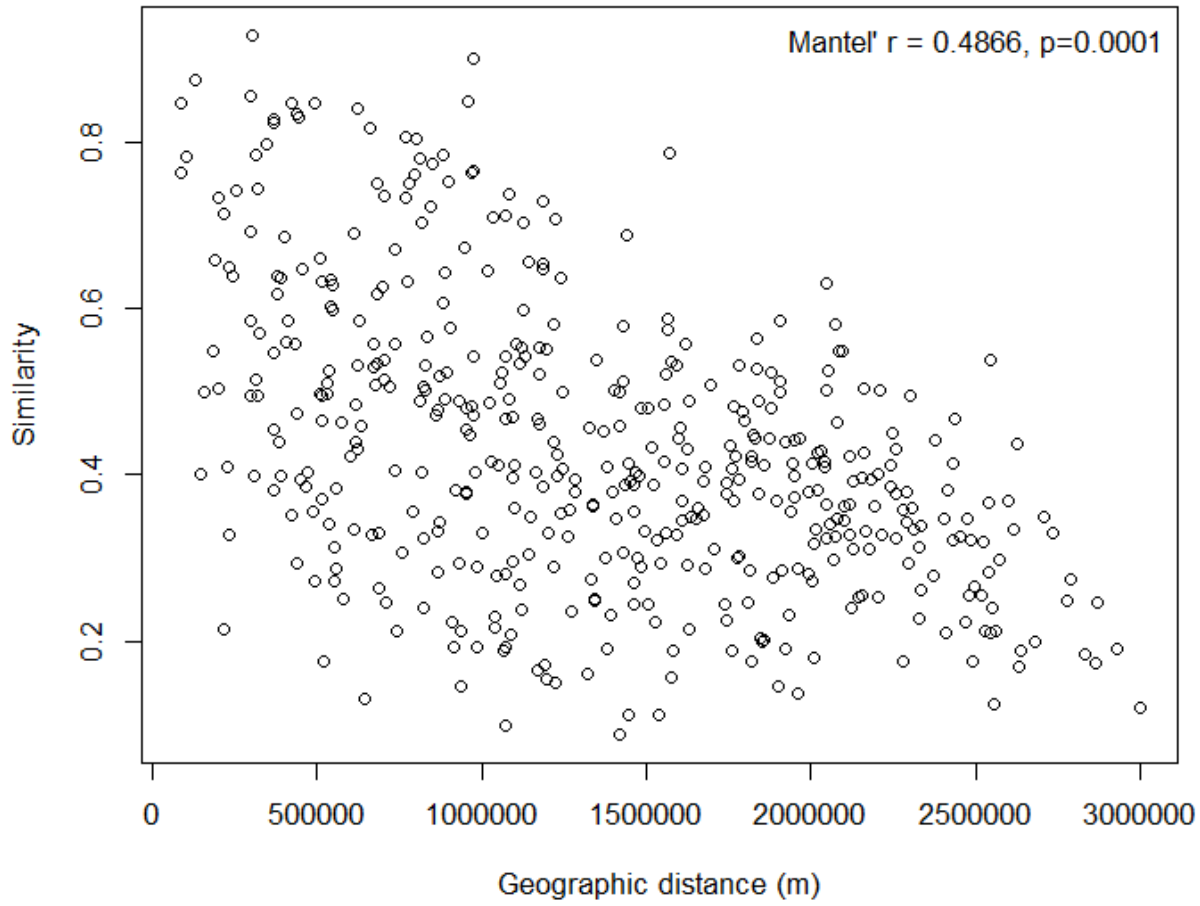
Appendix 7. Standard error of AU bootstrap p-values of each identified cluster by pvclust. Cluster 6 showed relatively high standard error (appendix 5).



Appendix 8. Shepard plot of NMDS ordination plot of Amazon-Guianan floras including four western Amazonian white-sand forests. Stress = 0.26. Iterations = 500. Dimensions = 2.



Appendix 9. Floristic similarity as a function of geographic distance between pairs of floras in the Andes-Guiana Shield region. Statistical significance from Mantel test. To test whether geographical distance between the studied floras had an influence on the floristic patterns recovered by the ordination and cluster analysis, we performed a Mantel test (Mantel 1967, Rossi 1996, Dutilleul *et al.* 2000, Legendre & Legendre 2012). To create the distance matrix we extracted the geographical coordinates of each province by using its polygon centroid in a Geographical Information System (GIS) that were then used to calculate geographical (Euclidean) distances between floras. We ran 999 permutations on the floristic dissimilarity matrix at a significance p-value of 0.05. We found a significant positive Mantel correlation between the floristic distance and geographical distance matrices (Mantel's $r = 0.4866$, $p = 0.0001$). Based on this result we 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. A Mantel test including only the four white-sand sites against their geographical distances also found a marginally significant result ($r= 0.5818$, $p=0.083$).


Mantel' r = 0.4866, p=0.0001
Similarity
0.2
0.4
0.6
0.8
0
500000
1000000
1500000
2000000
2500000
3000000
Geographic distance (m)