Naturalis Repository

# Low phylogenetic beta diversity and geographic neo-endemism in Amazonian white-sand forests

Juan Ernesto Guevara, Gabriel Damasco, Hans ter Steege [et al.]

Downloaded from:
https://doi.org/10.1111/btp.12298

Article 25fa Dutch Copyright Act (DCA) - End User Rights

This publication is distributed under the terms of Article 25fa of the Dutch Copyright Act (Auteurswet) with consent from the author. Dutch law entitles the maker of a short scientific work funded either wholly or partially by Dutch public funds to make that work publicly available following a reasonable period after the work was first published, provided that reference is made to the source of the first publication of the work.

This publication is distributed under the Naturalis Biodiversity Center 'Taverne implementation' programme. In this programme, research output of Naturalis researchers and collection managers that complies with the legal requirements of Article 25fa of the Dutch Copyright Act is distributed online and free of barriers in the Naturalis institutional repository. Research output is distributed six months after its first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and copyrights owner(s) of this work. Any use of the publication other than authorized under this license or copyright law is prohibited.

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the department of Collection Information know, stating your reasons. In case of a legitimate complaint, Collection Information will make the material inaccessible. Please contact us through email: collectie.informatie@naturalis.nl. We will contact you as soon as possible.

BIOTROPICA
THE JOURNAL OF THE ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

BIOTROPICA 48(1): 34–46 2016 10.1111/btp.12298

# Low Phylogenetic Beta Diversity and Geographic Neo-endemism in Amazonian White-sand Forests

**Juan Ernesto Guevara**[1,2,20], **Gabriel Damasco**[1], **Christopher Baraloto**[3], **Paul V. A. Fine**[1], **María Cristina Peñuela**[4], **Carolina Castilho**[5], **Alberto Vincentini**[6], **Dairón Cárdenas**[7], **Florian Wittmann**[8], **Natalia Targhetta**[6], **Oliver Phillips**[9], **Juliana Stropp**[10], **Ieda Amaral**[11], **Paul Maas**[12], **Abel Monteagudo**[13], **Eliana M. Jimenez**[4], **Rachel Thomas**[14], **Roel Brienen**[9], **Álvaro Duque**[15], **William Magnusson**[6], **Cid Ferreira**[6], **Eurídice Honorio**[16], **Francisca de Almeida Matos**[6], **Freddy R. Arevalo**[17], **Julien Engel**[3], **Pascal Petronelli**[3], **Rodolfo Vasquez**[13], and **Hans ter Steege**[18,19]

[1] Department of Integrative Biology, University of California, Berkeley, CA, 94720-3140, U.S.A.

[2] Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador

[3] UMR Ecologie des Forêts de Guyane, Institut National de la Recherche Agronomique (INRA), Kourou, French Guiana

[4] Universidad Regional Amazonica, IKIAM, Tena, Ecuador

[5] EMBRAPA, Centro de Pesquisa Agroflorestal de Roraima, Boa Vista, Brazil

[6] Instituto Nacional de Pesquisas da Amazônia-INPA, Coordenação de Pesquisas em Ecologia, Manaos, Brazil

[7] SINCHI, Herbario Amazónico Colombiano-COAH, Calle 20 No.5-44, Bogotá, Colombia

[8] Department of Biochemistry, Max Planck Institute for Chemistry, Hahn Meitner Weg 1, 55128, Mainz, Germany

[9] School of Geography, University of Leeds, Leeds, U.K.

[10] Institute of Biological and Health Sciences, Federal University of Alagoas, Maceió, AL, Brazil

[11] Instituto Nacional de Pesquisas da Amazônia–INPA, Projeto TEAM-Manaus, Manaus, Brazil

[12] Department of Botany, Naturalis Biodiversity Center, Leiden, The Netherlands

[13] Missouri Botanical Garden, 4344 Shaw Blvd., St. Louis, MO, 63110, U.S.A.

[14] Iwokrama International Programme for Rainforest Conservation, 77 High Street Kingston, Georgetown, Guiana

[15] Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Medellín, Colombia

[16] Instituto de Investigaciones de la Amazonía Peruana, Iquitos, Peru

[17] Universidad Nacional de la Amazonía Peruana, Iquitos, Peru

[18] Naturalis Biodiversity Center, Leiden, the Netherlands

[19] Ecology and Biodiversity Group, Utrecht University, Utrecht, The Netherlands

## ABSTRACT

Over the past three decades, many small-scale floristic studies of white-sand forests across the Amazon basin have been published. Nonetheless, a basin-wide description of both taxonomic and phylogenetic alpha and beta diversity at regional scales has never been achieved. We present a complete floristic analysis of white-sand forests across the Amazon basin including both taxonomic and phylogenetic diversity. We found strong regional differences in the signal of phylogenetic community structure with both overall and regional Net Relatedness Index and Nearest Taxon Index values found to be significantly positive leading to a pattern of phylogenetic clustering. Additionally, we found high taxonomic dissimilarity but low phylogenetic dissimilarity in pairwise community comparisons. These results suggest that recent diversification has played an important role in the assembly of white-sand forests causing geographic neo-endemism patterns at the regional scale.

Abstract in Spanish is available with online material.

*Key words*: Amazon; neo-endemism; phylogenetic beta diversity; recent diversification; white sands.

Received 29 January 2015; revision accepted 2 November 2015.

[20]Corresponding author; e-mail: jeguevara@berkeley.edu

White-sand forests have been referred to as a classic case study of habitat specialization (Anderson 1981) and a source of high endemism in both animal and plant communities of

Amazonian forests (Berry *et al.* 1995, Frazier *et al.* 2008, Fine *et al.* 2010, Misiewicz & Fine 2014). We have learned much about the composition of this flora over the past three decades thanks to the many small-scale and regional floristic studies of white-sand forests across the Amazon basin that have been published (Duivenvoorden & Lips 1995, Coomes & Grubb 1998, Fine *et al.* 2010, Stropp *et al.* 2011, Damasco *et al.* 2012, Peñuela-Mora 2014). Nonetheless, there has never been a basin-wide description of both the taxonomic and phylogenetic alpha and beta diversity of Amazonian white-sand forests.

Most of the plants found in white-sand forests are rare or absent in other forest types (Vormisto *et al.* 2000, Fine *et al.* 2010, Stropp *et al.* 2011). This specialization to the white-sand habitat has evolved repeatedly, with some species belonging to lineages that are generally restricted to this habitat (*i.e.*, *Potalia, Pagamea*; Frazier *et al.* 2008, Vicentini 2016) and other species that appear to have evolved white-sand specialization relatively recently, descending from non-white-sand ancestors (*i.e.*, *Protium*, Fine *et al.* 2005, Fine *et al.* 2014, Fine & Baraloto 2016).

Strong environmental gradients, like white-sand habitats adjacent to other more nutrient-rich soil habitats, are thought to promote high levels of both phylogenetic and taxonomic beta diversity across habitats reflecting the high turnover of lineages at both shallow and deep phylogenetic scales. Such turnover of entire clades might occur if certain traits associated with white-sand specialization are conserved and phylogenetic niche conservatism is responsible for such patterns (Graham & Fine 2008, Anacker & Harrison 2012). Alternatively, *in situ* diversification may cause some groups to have many more species in certain regions according to each lineage's life history and biogeography (Ricklefs 2006). A remarkable example of this phenomenon is the diversification of the Protieae tribe which exhibits higher net diversification rates in Western Amazonia compared to Central Amazonia and the Guiana Shield with many species associated with white-sand habitats (Fine *et al.* 2014). The role of dispersal also likely plays an important role driving patterns of taxonomic and phylogenetic beta diversity of white sand forests. Species with differential seed dispersal capabilities may occupy new regions with white-sand forests promoting gene flow between populations which in turn may influence allopatric speciation and extinction probabilities. Thus, across the Amazon basin, specialization and speciation events through time in white-sand forests have been influenced by (1) the frequency of lineages to evolve white-sand specialization in different regions, and (2) the dispersal capability of already-specialized white-sand taxa from white-sands in one region to white-sand forests in other regions.

Here, we present a new and more complete depiction of the floristic relationships of white-sand forests across the Amazon basin using measures of both taxonomic and phylogenetic diversity. In addition, we test the relative role of dispersal and *in situ* radiation in the patterns of Phylogenetic beta diversity (PBD) of white-sand forests within and across regions. If little opportunity for dispersal and differential extinction rates have promoted entire lineages or clades to be absent in certain regions we would expect a significant increase in observed phylogenetic and compositional dissimilarities compared with expected phylogenetic dissimilarity as geographic distance increases. In this case we would predict a strong pattern of turnover in taxa due to the long-term disparate evolutionary histories of these taxa which in turn should lead to strong spatial replacement of lineages (Fig. 1); meaning that clusters of closely related lineages should be present in multiple distinct regions of the Amazon basin. Alternatively, if small-ranged taxa have evolved by *in situ* radiation, we expect a higher compositional dissimilarity than expected. Furthermore, if such *in situ* radiation has occurred recently in evolutionary time, we would expect a limited time to accumulate new distinct lineages leading to a pattern of geographic neo-endemism. Finally, we predict low values of both taxonomic and phylogenetic beta diversity if there have been many opportunities for dispersal among different local communities of white-sand forests maintaining gene flow and genetic cohesion across species with widespread geographic ranges (Fig. 1).

## METHODS

Study area.—White-sand forests occur across the entire Amazon basin spanning approximately 200,000 km$^2$ (Hammond 2005, Ter Steege *et al.* 2013). Our study area includes three main regions: Northwestern Amazonia (NWA), Central Amazonia (CA), and the Guiana Shield (GS) (Fig. 2). The data set includes 91 plots, ranging from 0.1 ha to 1 ha, from white-sand forests in Colombia, Ecuador, Peru, Brazil, Guyana, French Guiana, and Suriname, representing a longitudinal gradient of almost 3000 km. Because white-sand forests sometimes include vegetation types that structurally are not 'forested' we excluded plots from our analysis that had extremely low canopy cover (chamizales or caatinga scrub in Anderson 1981, Fine *et al.* 2010) and white-sand savannas (campinas; Adeney *et al.* 2016). All plots were at least 0.1 ha in size and included all trees with dbh > 5 cm per ha (most plots were 1 ha and had a dbh cut-off of 10 cm dbh). In each plot, all individual trees were tagged and identified at the species level in the field when possible. Voucher specimens for most of the species and morphospecies were collected and subsequently deposited in Herbario Nacional del Ecuador (QCNE), Missouri Botanical Garden (MO), Field Museum (F), Museo Herbario Amazonense (AMAZ), Herbário Instituto Nacional de Pesquisas da Amazonia (INPA), and ORSTOM-Cayenne Herbarium (CAY).

Analysis.—We compiled 44,579 individual trees from the 91 white-sand plot inventories. For the analysis of taxonomic beta diversity, we used a subset of 38,721 individuals from the dataset, taking into account only species with valid names (1256 named species). The omission of unnamed "morphospecies" from meta-analysis has been hypothesized to not bias the detection of ecological patterns (Lennon *et al.* 2001, 2004, Pos *et al.* 2014). In order to avoid the well-known problem resulting from the use of phylogenetic trees without fully resolved branches (Swenson *et al.* 2006), a subset of 420 species (representing 18,163 individuals) for which we have a molecular phylogeny was used for the

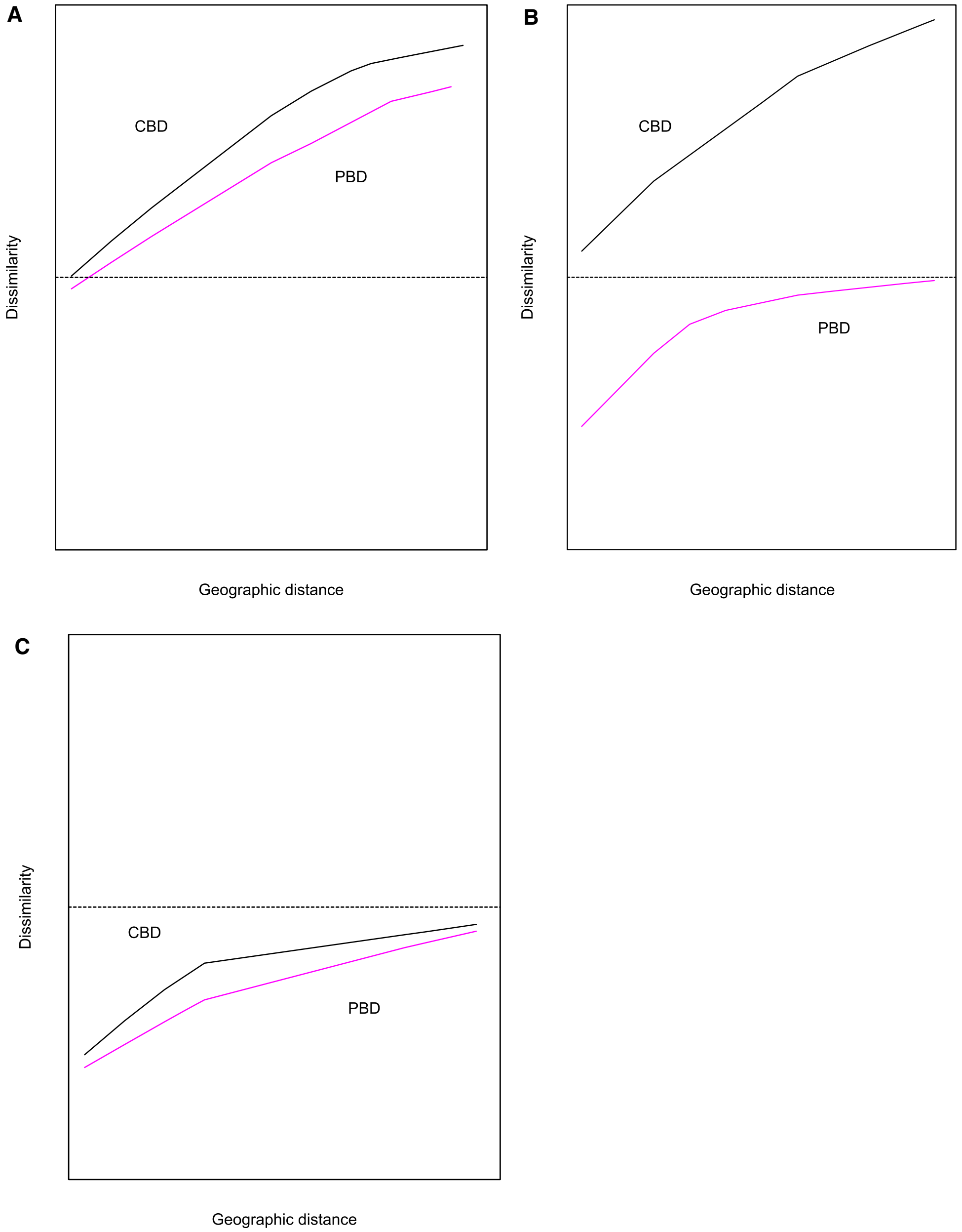

FIGURE 1. Three potential scenarios for compositional beta diversity (CBD) and phylogenetic beta diversity (PBD) in Amazonian white sand forests. The red dashed line represents the null expectation of no influence of geographic distance in the patterns of taxonomic and phylogenetic beta diversity. (A) High taxonomic and phylogenetic turnover with respect to the null expectation due to long-term disparate evolutionary histories of the taxa occupying white-sand forests across the Amazon basin. (B) Potential scenario for *in situ* radiation of small-ranged species. In this case we expect a higher compositional dissimilarity with respect to both observed and expected phylogenetic dissimilarity. (C) Long-distance dispersal capabilities over long periods of evolutionary time among different local communities of white-sand forests would cause lower values for both taxonomic and phylogenetic beta diversity.

analysis of phylogenetic beta diversity. The molecular phylogeny used in our analysis of phylogenetic beta diversity, is a pruned version of the one used by Zanne *et al.* (2014) (Fig. S1). PBD was calculated with the Phylo Sorenson index as a measure of the degree of phylogenetic relatedness between pairs of local communities. The Phylo Sorenson index measures the fraction of branch lengths (Phylogenetic distance) shared by two communities or samples (Bryant *et al.* 2008, Graham *et al.* 2009). However, in order to match the metrics used to evaluate taxonomic beta diversity, we used the complement of the Phylo Sorenson index to establish a phylogenetic dissimilarity metric (1-Phylo Sorenson).

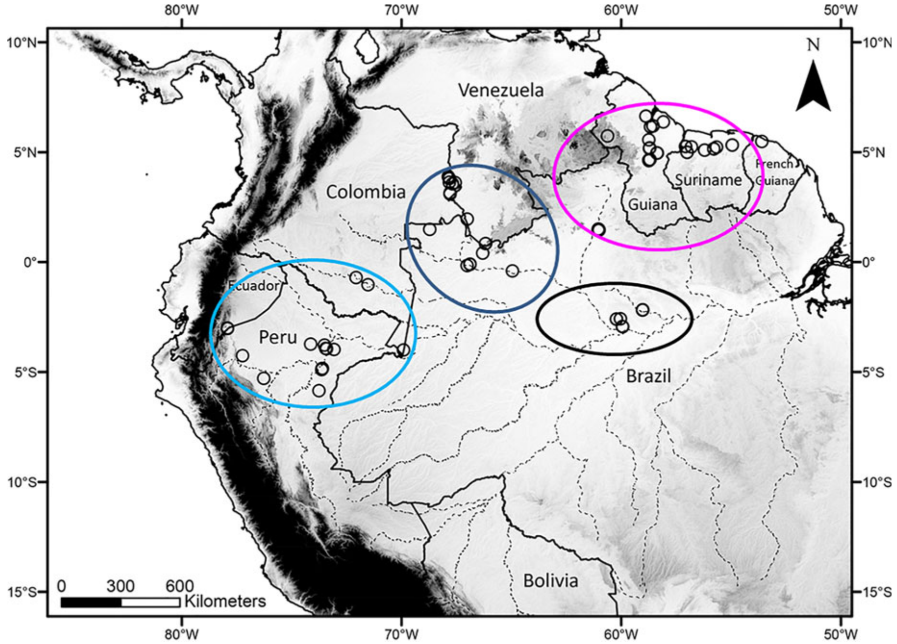

FIGURE 2. Map of the locations of the 91 ATDN plots established in white-sand forests across Amazon basin. Light blue: North Western Amazonia, Blue: Upper Rio Negro basin, Magenta: Guiana Shield, Black: Central Amazonia.

$$Phylosor_{ij} = \frac{BL_{ij}}{(BL_i + BL_j)\frac{1}{2}}$$

Where $BL_{ij}$ is the sum of branches length shared by communities $i$ and $j$, $BL_i$ is the sum of the length for branches present only in community $i$ and $BL_j$ is the sum of the length for branches present only in community $j$.

To test the influence of geographic distance as a predictor of both compositional beta diversity (CBD) and PBD, we fitted a Loess curve to our data. This non-parametric regression method fits a regression surface to the data based on multivariate smoothing and does not consider any *a priori* regression function between the descriptor and the response variable. By using a local fitting regression we can estimate a wide variety of smoothing functions such as polynomial functions based on Ordinary Least Squares regression (Cleveland & Levin 1998).

In order to test if CBD is a good predictor of PBD, we compared the observed values of PBD (1-Phylo Sorenson) with CBD. Additionally, we compared the observed PBD to the expected values of PBD based on a null model that makes random draws from the regional species pool (here defined as the total number of species in our plot network). This null model maintains species richness for each local community and the number of species shared between communities with equal probability to colonize them. The basic assumption under this model is that species in the phylogeny have equal probability of colonizing a local community in such a way that dispersal limitation or long-distance dispersal has only minor effects on the assembly of communities. Thus, when interpreting the results, if the observed values of PBD are less than the expected values based on the null model, we infer that pairs of compared communities are composed of lineages that are closely related. Conversely, if values of PBD are greater than expected based on the null model pairs of communities, then pairs of communities are composed of lineages that include distant relatives. Paired *t*-tests were performed in order to detect significant differences between observed PBD and expected PBD.

Non-Metric Multidimensional (NMDS) Analysis with both taxonomic and phylogenetic dissimilarity matrices was performed in order to have a graphical depiction of the floristic relationships of white-sand plots across different regions of the Amazon basin. We used two dimensions in the ordination and 100 random starting iterations in order to obtain the lowest stress value that determines the best solution for that ordination. The difference between 1 and Sorensen index (1-Sorenson) was used as the dissimilarity metric for the NMDS ordination based on taxonomy, while the difference between 1 and Phylosorenson (1-Phylosorenson) was used to create a phylogenetic distance matrix for the phylogenetic NMDS ordination.

To determine if species co-occurring in the same local community (plot) are more closely related than expected by chance, we calculated the Mean Phylogenetic Distance (MPD) – the pairwise comparison of phylogenetic distances between all species in the local community (Webb 2000). This value was compared with the expectation based on a null model; if $MPD_{(obs)}$ is < $MPD_{(null)}$ the communities are phylogenetically even and conversely if $MPD_{(obs)} > MPD_{(null)}$ the communities are phylogenetically clustered.

The net relatedness index, hereafter NRI, measures the phylogenetic clumpedness of taxa over the entire community phylogeny (Webb 2000). By contrast, the phylogenetic nearest taxa index, hereafter NTI, measures the extent to which taxa are 'locally clustered' within a clade irrespective of the relation among those clades (Webb 2000). In order to test the effect of ecological dominance and composition in the phylogenetic community structure of white-sand local communities we used taxon (presence/absence) and individuals (relative abundance) based analysis to calculate both NRI and NTI. Therefore:

$\mathrm{NRI}_i$ = Net Relatedness Index based on tree species abundance
$\mathrm{NTI}_i$ = Nearest Taxon Index based on tree species abundance
$\mathrm{NRI}_t$ = Net Relatedness Index based on taxon information
$\mathrm{NTI}_i$ = Nearest Taxon Index based on taxon information

To test whether there is a significant difference in the patterns of NRI and NTI at regional scale we compared observed NRI and NTI values for each region to those calculated using a null model. The null model maintains both the species richness and abundance constant for each sample while species or individuals are drawn without replacement from the list of all species in the phylogeny pool. This model assumes that null communities are structured by random draws of the 420 species present in the phylogeny.

All analyses were carried out with the functions of the packages ecodist, picante, labdsv, and custom functions in the R software platform (R Core Development Team 2011).

## RESULTS

FLORISTICS PATTERNS.—From a total of 44,579 individuals observed, we recorded 1482 morphospecies identified at the family level, 672 at genus level, 1256 at species level, and 17 remained undetermined at all levels. We found on average a lower diversity in white-sand plots compared with the *terra firme* forests, a pattern that has been reported repeatedly (Anderson 1981, Ter Steege and Hammond 2001, Fine *et al.* 2010, Stropp *et al.* 2011). However, patterns of diversity varied across regions; white-sand forests from GS have fewer species than plots from NWA and CA (Table 1).

Fabaceae was by far the most dominant family across the basin accounting for 26 percent of the total stems (11,618 individuals) followed by Chrysobalanaceae with almost 10 percent of individuals (4288 ind.), Malvaceae with 8 percent (3482 ind.), Sapotaceae with 6 percent (2596 ind.), and Euphorbiaceae (2471 ind.) with 5 percent. A different pattern arises when we consider (valid) species richness per family; the greatest number of species was concentrated in Fabaceae (234 spp.) followed by Lauraceae (86 spp.), Sapotaceae (81 spp.), Chrysobalanaceae (78 spp.), and Rubiaceae (76 spp.).

At the genus level, *Licania* with 46 (valid) species was the most species -rich genus in white-sand forests. Genera like *Pouteria* (36 spp.), *Protium* (34 spp.), *Swartzia* (30 spp.), *Inga* (30 spp.), and *Ocotea* (28 spp.) were also remarkably diverse. With the exception of *Licania* (3228 individuals), species-poor genera dominate white sand forests at both local and regional scales. *Eperua* (6101 ind.) was by far the most abundant genus in white-sand forests followed by *Catostemma* (1960 ind.), *Pachira* (1611 ind.), and *Micrandra* (1494 ind.). The most common species was *Eperua falcata,* accounting for 3343 individuals, almost 8 percent of the total number of individuals. The five most common species account for 19 percent of the number of individuals (8407 ind.), a number that was two-fold lower than patterns of dominance reported in Peru (Fine *et al.* 2010).

The NMDS ordination based on taxonomic and phylogenetic dissimilarity matrices produced contrasting patterns (Fig. 3). The ordination based on taxonomic dissimilarity matrix exhibited a clear gradient along the axis by defining four floristic regions (Fig. 3A). The first one corresponded to some of the plots defined in axis 2 of the ordination and located in the core of the Guiana Shield. These plots were characterized by the predominance of Fabaceae, especially species from genera like *Eperua*, *Dicymbe*, *Elizabetha, Dicorynia, Alexa*, or *Aldina,* as the results of the indicator species analysis demonstrates (Appendix S1). Other remarkably conspicuous elements of this region were *Catostemma* (Malvaceae s.l.)*, Cyrilla racemiflora* (Cyrillaceae)*,* the extremely rare *Cyrillopsis paraensis* (Ixonanthaceae)*,* and two species from the

TABLE 1. *Structural and ecological attributes of the 91 white-sand plots from the Amazon Tree Diversity network (ATDN). Number of species and individuals are based on the total number of trees sampled (including unidentified morphospecies).*

| | Western Amazonia | Central Amazonia | Guiana Shield | Overall |
|---|---|---|---|---|
| Number of ha sampled | 20 | 23 | 48 | 91 |
| Number of individuals | 8789 | 8121 | 27011 | 44579 |
| Number of species | 594 | 545 | 914 | 1482 |
| Number of families | 59 | 63 | 54 | 77 |
| Number of hyperdominant species *sensu* (Ter Steege *et al.* 2013, Pitman *et al.* 2001) | 10 | 11 | 17 | 34 |
| Mean species per plot | 59 | 55 | 60 | 60 |
| Mean stems per plot | 470 | 353 | 565 | 490 |
| Number of singletons | 174 | 167 | 200 | 318 |
| % stems that belongs single most common species | 12.1 | 3.7 | 12.4 | 7.6 |
| % stems that belongs to the five most common species | 29.5 | 14 | 30.3 | 19 |
| Mean taxonomic dissimilarity (1-Sorenson) | 0.84 | 0.84 | 0.86 | 0.9 |
| Mean phylogenetic dissimilarity (1-Phylosorenson) | 0.52 | 0.6 | 0.48 | 0.56 |

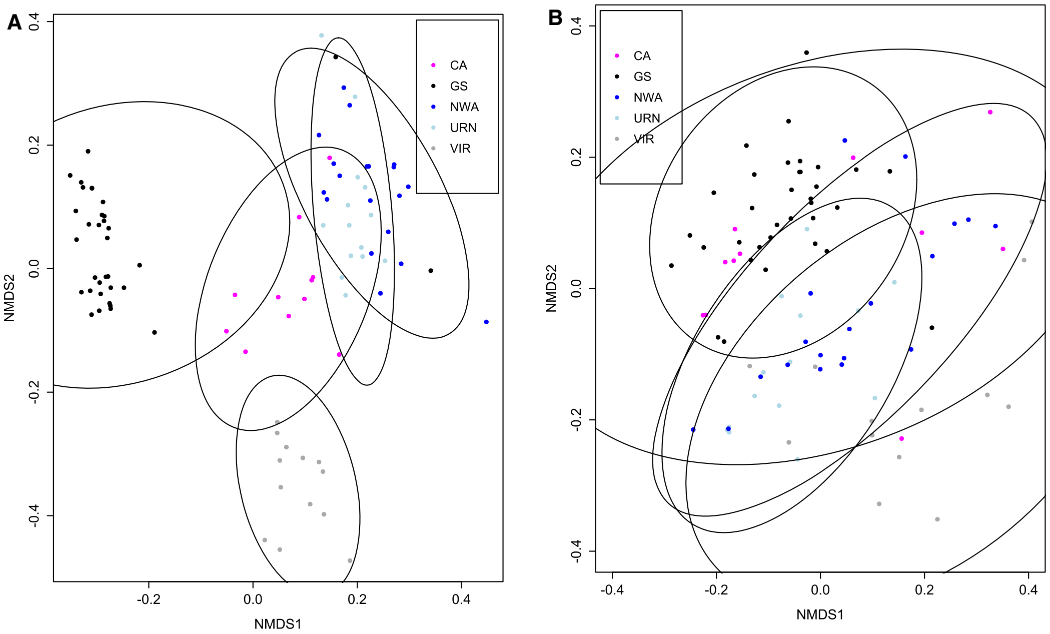

FIGURE 3. Non-Metric Multidimensional ordination for 91 white-sand plots across the Amazon basin: (A) NMDS based on compositional data dissimilarity matrix (B) NMDS based on phylogenetic distance matrix. Ellipses represent the 95% confidence interval in grouping plots as part of a particular cluster of similar floristic units. Abbreviations for regions are as follows; NWA = North Western Amazonia, CA = Central Amazonia, GS = Guiana Shield, URN = Upper Rio Negro, VIR = Virua National Park.

genus *Acioa* (Chrysobalanaceae). The second group of plots defines the northeastern portion of Central Amazonia white-sand forests; the great majority of these plots are located in Viruá National Park. This group of plots, mainly defined along axis 1 of the ordination, constitutes a region of confluence of the two regional floras of GS and CA, but was also characterized by the extremely rare and species-poor genera *Elvasia* (Ochnaceae), *Euphronia* (Euphroniaceae), *Excellodendron* (Chrysobalanaceae), and *Chaetocarpus* (Euphorbiaceae). A third floristically distinctive group in the ordination included communities spanning the Amazon, with plots from the Guiana Shield, Central and Western Amazonia. These plots are remarkably similar in floristic terms despite the large distance between them. Some of the most predominant groups in this cluster of plots include genera like *Adiscanthus* (Rutaceae), *Lorostemon* (Clusiaceae), *Ambelania* (Apocynaceae), *Pachira* (Malvaceae s.l.), and *Cinchonopsis* (Rubiaceae) (Appendix S1). Finally, plots located in the Upper Rio Negro, including areas of Colombia, Brazil and Venezuela; mostly define the fourth floristic region. Conspicuous groups in this region are *Couma* (Apocynaceae), *Parahancornia* (Apocynaceae), *Haploclathra* (Clusiaceae), *Micrandra* (Euphorbiaceae), *Dicymbe* (Fabaceae s.l.), *Eperua* (Fabaceae s.l.) *Emmotum* (Icacinaceae) as the results of the Indicator Species Analysis at genus level demonstrated.

When the phylogenetic distance matrix was used as input for the NMDS, a different pattern arises. The gradient along axis 1 of the NMDS still remained, yet the regional clusters disappeared (Fig. 3B). More than 50 percent of the local communities in CA were structured by lineages phylogenetically closely related to those lineages that contribute strongly to the local communities in GS. Furthermore, all the NWA white sand plots were composed of lineages phylogenetically closely related to lineages that dominate GS white-sand plots. Only a small fraction of CA plots including those of Upper Rio Negro and Viruá National Park were structured by distantly related lineages compared to all GS and NWA plots, meaning that the this group of CA plots were composed by evolutionary distinctive lineages.

COMPOSITIONAL AND PHYLOGENETIC DISSIMILARITY.—Overall analysis of phylogenetic beta diversity demonstrates that a weak but significant correlation of phylogenetic dissimilarity and geographic distance exists in white-sand forests across the Amazon basin (Mantel $r = 0.18$, $P = 0.003$). When we consider each regional flora independently we found on average a higher phylogenetic dissimilarity in Central Amazonian and Western Amazonian white-sand plots than in white-sand plots of the Guiana Shield (Fig. 4; Table 1). However, the white-sand forest plots in the Guiana Shield exhibited a higher correlation of phylogenetic dissimilarity with respect to geographic distance (Mantel $r = 0.54$, $P = 0.001$). White-sand plots in Central (Mantel $r = 0.35$, $P = 0.001$) and Western Amazonia (Mantel $r = 0.38$, $P = 0.002$) exhibit similar values for this relationship. Additionally, the influence of the regional pool in patterns of phylogenetic turnover is evident. White-sand forests in NWA and CA are more distinct from one another than either of them is with the plots from the Guiana Shield (Fig. 4B and C).

Overall phylogenetic dissimilarity was also significantly lower between plots than taxonomic dissimilarity (Fig. 4D and H). Thus, pairs of local communities exhibited higher compositional turnover than phylogenetic turnover with respect to geographic distance, meaning that on average plots that were spatially close were taxonomically more dissimilar than phylogenetically dissimilar (Fig. 4). The slope of both compositional and phylogenetic dissimilarity decreased considerably at geographic distances larger than 500 km as the Loess curve shows in Fig. 4. However, the compositional dissimilarity continued to increase with distance while phylogenetic dissimilarity tends to decrease. In other words, even if pairs of communities are separated by thousands of kilometers, they are generally composed of the same lineages. Similarly, the observed values of phylogenetic dissimilarity were significantly lower than those expected based on the null model ($t$ = 78.80, $P$ < 0.0001) (Fig. 4H).

PHYLOGENETIC COMMUNITY STRUCTURE.—We found non-random phylogenetic community structure for white-sand forests at regional scales which can be attributed to large-scale evolutionary processes shaping the assembly of these habitats. Overall, values

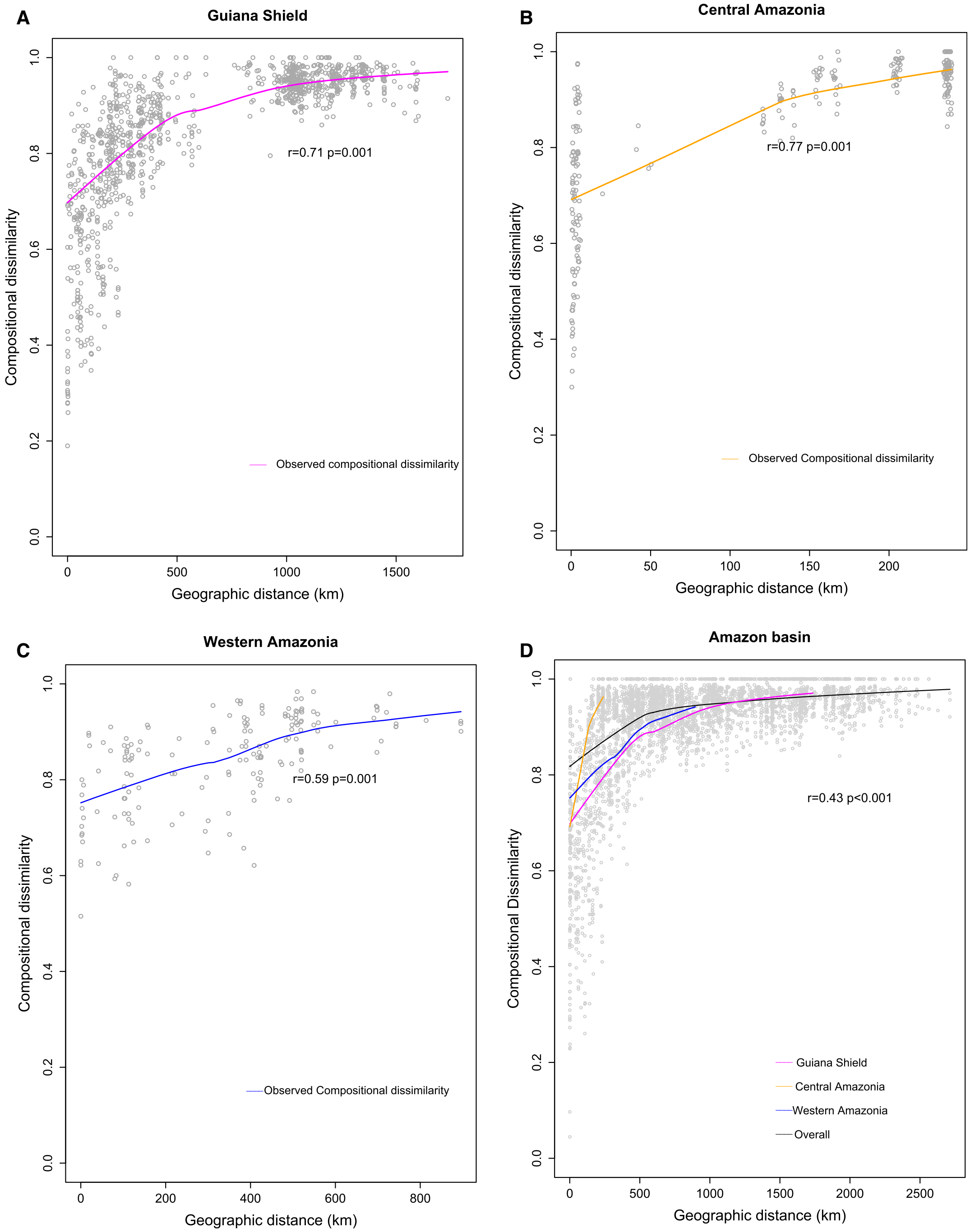

FIGURE 4. Continued

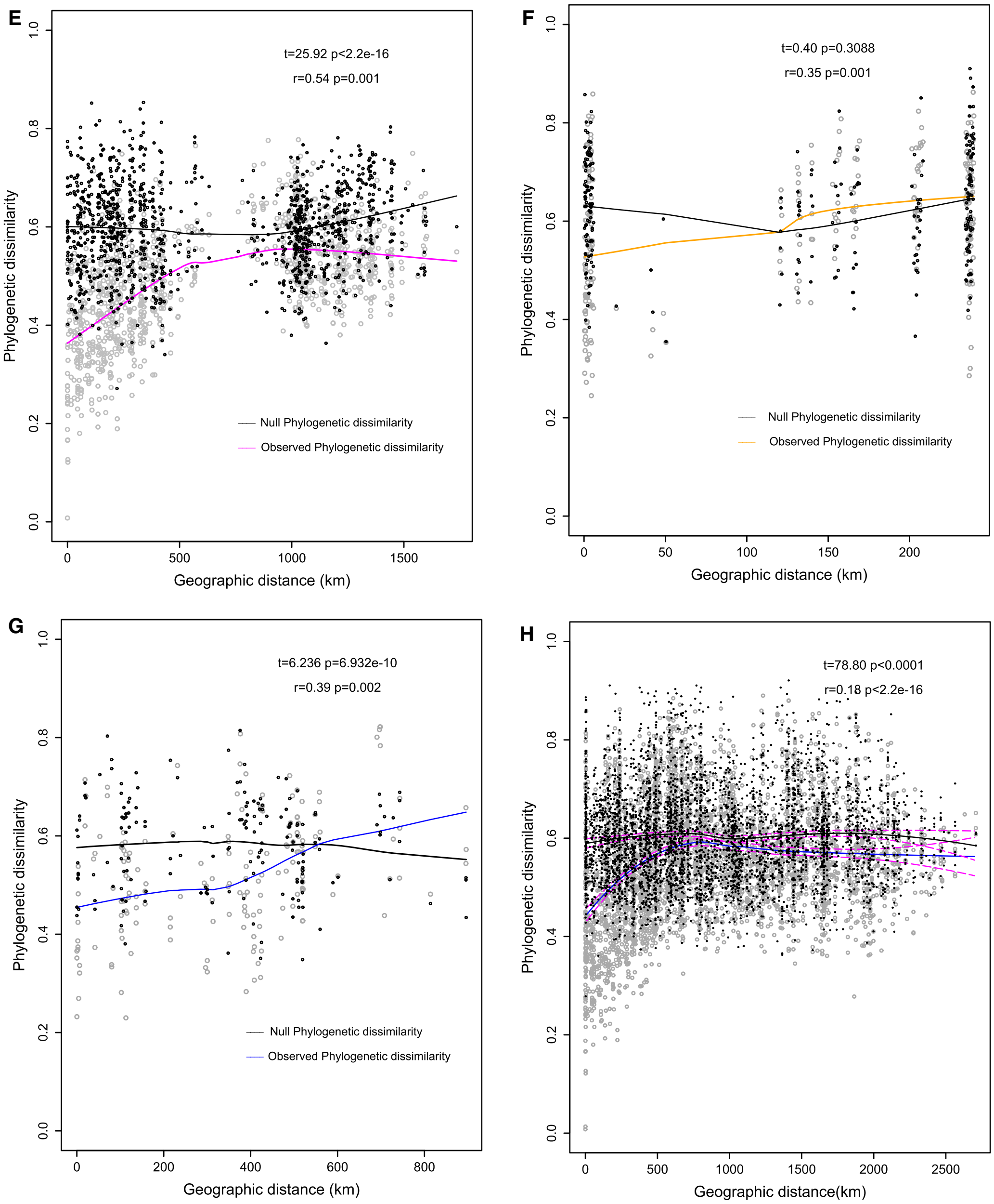

FIGURE 4. Phylogenetic dissimilarity as a function of geographic distance in white-sand forests across the Amazon basin. Phylogenetic dissimilarity is measured as the complement of Phylosorenson index (1-Phylosor). The lines represent a Loess non-parametric regression that best describes the patterns of distance decay curve in phylogenetic beta diversity. The results of *t*-tests to determine significant difference between observed average PBD and expected average PBD are shown. Confidence intervals for both observed and expected overall phylogenetic dissimilarity lowess curves are shown in Figure 4H.

of NRI and NTI were significantly positive, but some regional differences arose when considering regional pools separately (Fig. 5; Table S2). However, overall values of $NTI_i$ were not significantly different from our null expectation. The predominant pattern in white-sand forests in Western and Central Amazonia, and in the Guiana Shield, was that NRI values were significantly positive when relative abundance of species ($NRI_i$) was taken into account (Fig. 5B; Table S2).

The $NTI_i$ also indicated regional differences in how taxa within local community are distributed toward the tips of the community phylogeny. For instance, close relatives within the same clade significantly structured communities of white-sand forests in Central Amazonia and the Guiana Shield. This is in contrast to patterns found for Northwestern Amazonian white-sand forests that on average exhibited values close to zero, suggesting a random pattern of phylogenetic structure. When overall $NRI_t$ values are considered, a remarkably different pattern arises. Most of the local communities of white-sand forests across the basin exhibit negative values indicating that communities are phylogenetically overdispersed across the

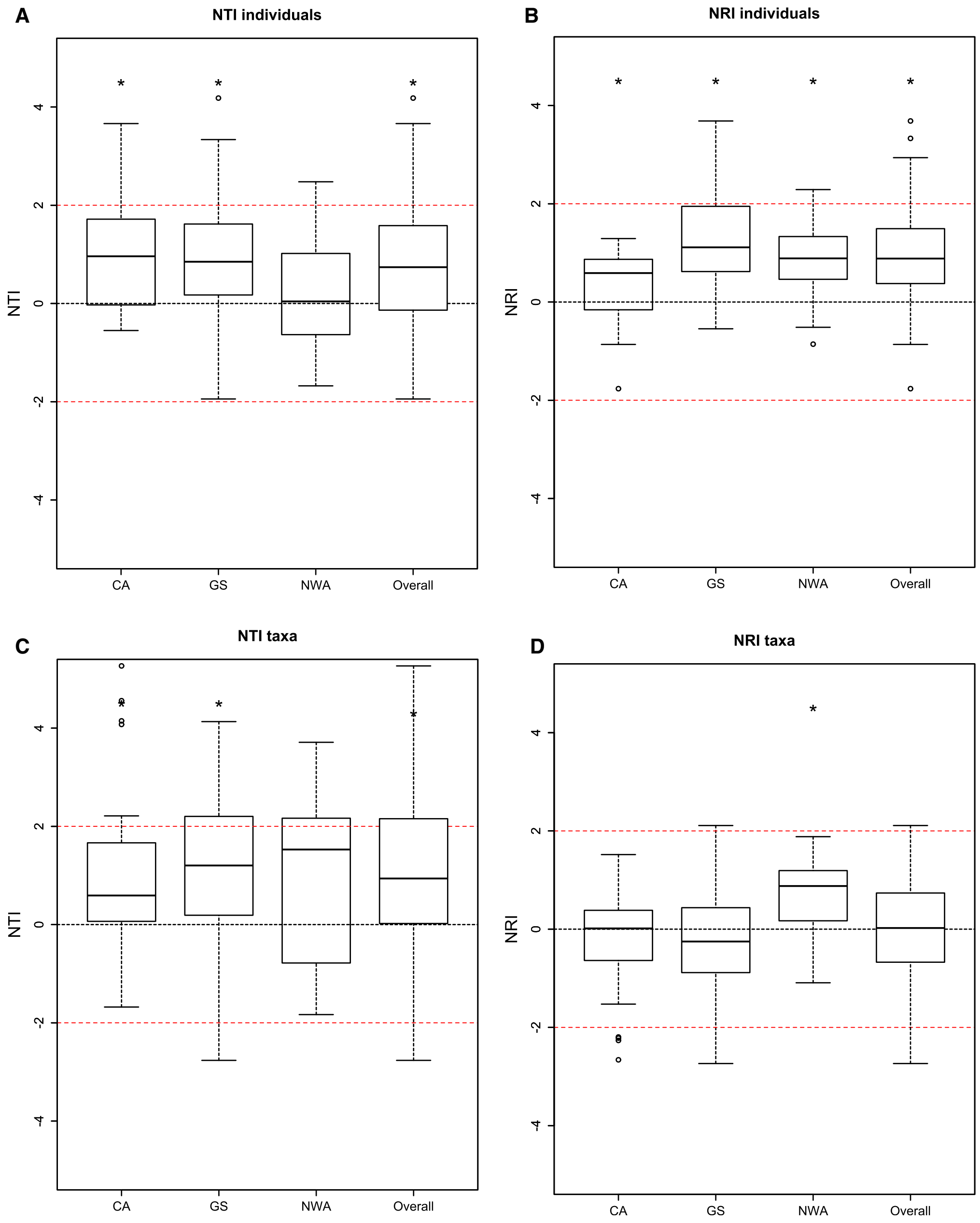

FIGURE 5. Phylogenetic local community structure in white-sand forests across the Amazon basin. The red dashed lines represent the confidence interval that is the null expectation under the 'richness' null model; asterisks represent both significantly positive and negative values of Near Relatedness Index (NRI) and Nearest Taxon Index (NTI) based on a *t*-test ($P < 0.001$).

whole community phylogeny. Interestingly, the values for NTI indicated that communities were phylogenetically clustered toward the tips of the phylogeny of the regional pool (Fig. 5; Table S2).

## DISCUSSION

Floristic patterns.—Previous attempts to characterize the species composition and structure of white-sand forests have been done only at local or within one region of Amazonia. Our results are the first attempt to describe floristic patterns of white-sand forests across the entire Amazon basin. It is important to note, however, that the plot network, while extensive and covering a large geographical extent that includes most of the major white-sand forests of the Amazon basin, certainly has overrepresented certain regions (*i.e.*, the Guiana Shield) compared to others and this spatial bias likely has influenced our results and interpretations somewhat.

The NMDS ordinations indicated two gradients in species composition. The first one defined a longitudinal gradient in species composition with plots from Guiana, Suriname and French Guiana at the left of the ordination and the CA and NWA plots in the center and right side of the ordination (Fig. S2). This pattern reflects a strong spatial component. The Loess regression comparing longitude with the first axis of the NMDS ordination explained 94 percent of variation in floristic data (Fig. S2). Furthermore, the floristic composition changed very rapidly from plots in the Guiana Shield to Central Amazonia and then more gradually from plots in Central Amazonia to plots in Western Amazonia. Terborgh and Andresen (1998) proposed that, due to different climates and geologic histories leading to edaphic gradients across the Amazon, differences in tree-species composition of forests in Northwestern Amazonia should be remarkably different than those of Central Amazonia. Based on the results of the NMDS, and compositional beta diversity, we found support for the hypothesis of strong species turnover across a longitudinal gradient (Fig. S2). Turnover in white-sand forests also showed a latitudinal gradient in the NMDS ordination, especially for white-sand plots from Central Amazonia (Fig. S3). This latitudinal gradient in floristic composition is mostly defined along axis 2 of the NMDS and suggests that there are two distinct white-sand floras of comparatively high diversity on each side of the Amazon basin. This pattern appears to be driven in large part by the high diversity, dominance and endemism of Fabaceae and Chrysobalanaceae in Guiana Shield forests (ter Steege 2000, Ter Steege *et al.* 2006).

Although species composition varies among regions, we found a geographically idiosyncratic dominance of a small number of white-sand specialist lineages. For instance, *Protium* spp., *Pachira* spp. and *Caraipa* spp. exhibited high dominance across the east–west gradient of WS patches. In some plots, this dominance may account for more than 70 percent of total tree abundance (Fine *et al.* 2010). In contrast, lineages as *Eperua* spp., *Aldi*na spp., or *Licania* spp, drive the patterns of white-sand forests composition and structure along the north–south gradient including Guiana Shield.

COMPOSITIONAL AND PHYLOGENETIC BETA DIVERSITY.—From our results, it is clear that the regional species pool has a strong influence on shaping patterns of both CBD and PBD. The distance-decay curves of CBD and PBD for central and Northwestern Amazonian white-sand plots were steeper than for Guiana Shield plots. This may be due to higher levels of dominance of a small number of lineages in Guiana Shield white-sand forests, which may be mediated by the combination of local adaptations, environmental suitability, and dispersal capability (Struwe & Albert 1997, Emerson & Gillespie 2008, Fine & Kembel 2011). White-sand specialist taxa may be able to colonize and become established more easily in the larger tracts of white-sand forest in the Guiana Shield, compared to the patchy distribution of suitable habitat in other regions. Dispersal limitation should be less severe if a contiguous suitable environment is available. Moreover, if low levels of disturbance permit environments to remain unchanged, lineages can persist over long periods of time, and therefore low phylogenetic turnover would be expected to occur in large areas with relatively stable environmental conditions (Emerson & Gillespie 2008). Satellite images from the upper Rio Negro and other areas of the Guiana Shield show that the extent of white-sand forest in this region is massive and can reach thousands of hectares (Stropp *et al.* 2011, Adeney *et al.* 2016). In contrast, the great majority of the plots established in central and Northwestern Amazonia are scattered over large tracts of adjacent *terra firme* forests making dispersal to neighboring white-sand habitats more challenging for white-sand specialists (Adeney *et al.* 2016).

Alternatively, one could explain these striking differences in PBD as the result of the different geological origins of white sand forest across the basin and the different biogeographic histories of Amazonian forests. While WS habitat in Northwestern Amazonia is interspersed in a geologically more heterogeneous landscape that varies from Cretaceous to Pliocene sediments, most of the white-sand soils in the Guiana Shield are derived from Precambrian geological formations (Wesselingh *et al.* 2006, Hoorn *et al.* 2010). Andean uplift has undoubtedly played a major role in the evolution of white-sand habitat patches becoming fragmented in waves of deposition of newer sediments which in turn would influence divergence times for different lineages that arrived to these habitat islands in Northwestern Amazonia. Nonetheless, this kind of close match between geological history and lineage formation would not be found if plants are good dispersers and easily colonize distant patches of suitable habitat.

We found evidence for regional neo-endemism in Amazonian white-sand forests. CBD was much higher than PBD meaning that local communities occurring in different regions have very different taxonomic composition even though they are derived from the same lineages. Moreover, pairwise comparisons of plots across the basin revealed significantly lower PBD values compared to the null expectation, indicating that local communities across the entire Amazon basin tend to share close relatives. In this context, our results indicate that most of the white-sand specialists appear to be geographic neo-endemics with small distributional ranges. This is also consistent with a plausible scenario of *in situ* radiation in white-sand forests by sequential allopatric speciation by white-sand specialist lineages across the basin. Therefore, pairs of compared local communities can be very different in floristic terms but at the same time exhibit low PBD if the communities compared are within *in situ* radiation centers (Graham & Fine 2008, Fine & Kembel 2011). This appears to be the case for Guiana Shield and Northwestern Amazonia white-sand forests that presumably are centers of radiation for many Fabaceae clades (*i.e.*, *Aldina*, *Eperua, Dicymbe, Dimorphandra, Clathrotropis, Swartzia*) as well as other groups like Chrysobalanaceae and *Inga,* respectively. Some of these clades have three-fold the number of species in these regions compared with other regions of the Amazon basin (Richardson *et al.* 2001, Bardon *et al.* 2013). The source-sink model of diversification assumes that a source region will exhibit higher origination rates relative to other regions and also higher levels of endemism. This model could explain the potential origination centers for these clades (Ricklefs & Schluter 1993, Rosenzweig & Sandlin 1997, Goldberg *et al.* 2005). A plausible scenario under the source-sink model, assuming that the Guiana Shield is the source and central and Northwestern Amazonia are sinks, would have allowed more time for ancient lineages to expand their ranges from the Guiana Shield toward the west, thus sink communities would be composed predominantly by early diverging lineages. However, the average age distribution and estimates of speciation, extinction, and dispersal rates of clades between regions need to be simulated in order to support a plausible source-sink scenario (Goldberg *et al.* 2005, Roy & Goldberg 2007).

Phylogenetic community structure.—Our results indicate that on average Amazon white-sand forests are phylogenetically clustered at regional scales (Fig. 5; Table S2). While our results of phylogenetic clustering at regional scales is in agreement with previous studies (Fine & Kembel 2011, Eiserhardt *et al.* 2013); we found contrasting results in the phylogenetic community structure of white-sand forests at the subregional scale. We argue that these results are not just the by-product of differences in phylogenic resolution and spatial scale, but instead are the result of the strong influence of large-scale evolutionary process underlying the nature of these communities (Cardillo 2011). For instance, the strength of environmental filtering may also be different in Western Amazon compared to the Guiana Shield, and this effect could be driving some of the differences in local phylogenetic structure. In this way, because the difference in soil fertility between white-sand and *terra firme* forests is less marked in the Guiana shield (Hammond 2005, Fine & Baraloto 2016), there may be a larger species pool able to colonize WSF in the Guianas. Therefore, we would expect more close relatives inhabiting white-sand communities in Guiana Shield forests with respect Western Amazonia white-sand forests because as the species pool able to colonize increase the probability for two species randomly chosen from this pool to be close relatives will increase as well.

Convergent adaptation to white-sand habitats could create a pattern of phylogenetic evenness if traits enhancing fitness evolved independently in distant relatives (Fine & Kembel 2011). It has been largely argued that phylogenetic clustering is the product of environmental filtering when close relatives share ecological resemblance in traits that allow them to coexist in sympatry (Webb 2000, Cavender-Bares *et al.* 2004). Alternatively, phylogenetic clustering in local communities could also be the result of many different processes including competition, pollinator facilitation, adaptive radiation and herbivore-plant interactions (Gillespie 2004, Emerson & Gillespie 2008, Cavender-Bares *et al.* 2009, Mayfield & Levine 2010). Thus, the spatial and phylogenetic scale of our analysis allows us to posit that biogeographical processes may be more important in the determination of phylogenetic structure of white-sand forests than processes operating at local scale (Hardy & Senterre 2007, Ricklefs 2007). Taken together, the results of overall phylogenetic clustering at regional scales together with low phylogenetic beta diversity support the hypothesis of regional neo-endemism mediated by recent diversification on white sand forests across the Amazon basin.

Our results contradict the main paradigm of white-sand forests as habitats structured by early divergent lineages that have colonized ‘ancient’ white-sand habitat islands that predate the Middle Miocene (Frazier *et al.* 2008, Hoorn *et al.* 2010, Pennington & Dick 2010, Fine & Kembel 2011). The arguments given for this hypothesis are that the sediments that originated in Guiana, and Brazilian Shield Precambrian geological formations were widely distributed across the basin previous to the Miocene in such a way that large portions of today’s Amazon basin were covered by extremely poor quarzitic sandstones (Hoorn 1993, Struwe & Albert 1997). In this way similar soil conditions as current white-sand habitats predate the diversification of many Amazonian tree clades promoting early divergence, colonization, and habitat specialization mediated by strong conservatism of traits that enhanced fitness in this stressful environment (Struwe & Albert 1997). On the basis of this assumption, we would expect early diverging lineages to dominate white-sand habitats. Nonetheless, Fine *et al.* (2005) demonstrated that most of the members of the tribe Protieae that inhabit white sand forest evolved from close relatives on adjacent *terra firme* forest suggesting that, at least in some lineages, recent ecological divergence from richer to poorer soils had occurred (Fine & Baraloto 2016). Similar patterns of neo-endemism have been suggested for Peruvian white-sand bird communities resulting from recent *in situ* diversification in the Western Amazon (Álvarez Alonso *et al.* 2013, Matos *et al.* 2016). While endemism could be promoted by habitat specialization, our results show that geographical endemism driven by dispersal limitation of white-sand specialist lineages may also be important in explaining floristic dissimilarity across white-sand patches. Rather than a single flora that originated in the Guianas, specialization to sandy soils appears to have evolved independently in different plant lineages over many different white-sand patches across the Amazonian landscape.

Because our analyses have some limitations, our assumptions should be considered cautiously, and our intent is that subsequent analyses will help us to identify the evolutionary processes that underlie the patterns we describe. The degree of patch isolation, asymmetries in speciation, extinction, and dispersal rates, or any specialization mediated by niche conservatism for white-sand environments could influence the divergence of plant lineages and yield patterns of geographic endemism. Therefore, to understand the floristic variation and the species turnover of white-sand forests across the Amazon basin, it is fundamental to investigate the processes responsible for local dominance, the evolutionary mechanisms for geographic endemism, and the relationship between ecological filters and species traits that allows some successful lineages from the regional species pool to establish and become common in local communities.

## ACKNOWLEDGMENTS

JEG, GD, and PVAF were supported by NSF DEB 1254214. We thank the staff at the herbaria AMAZ, INPA, GUY, MO, and QCNE for their invaluable support. Nigel C.A. Pitman, Jenna Judge and Dori Contreras provide insightful comments to earlier versions of the manuscript. We are grateful to Peru’s Instituto Nacional de Recursos Naturales, Ecuador’s Ministerio de

Ambiente (MAE), Brazil's Instituto de Pesquisas da Amazonia (INPA), French Guiana's Institute Researche Agronomique (INRA) for permission to carry out this research. Studies in Brazil were supported by the Programa de Pesquisa em Biodiversidade (PPBio) and the National Institute for Amazonian Biodiversity (INCT-CENBAM).

## SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

APPENDIX S1. Indicator Species Analysis for 91 plot network established in Amazonian white-sand forests.

TABLE S1. *Plot codes, countries, and geographic coordinates for the 91 plot network used in the study.*

TABLE S2. *Mean values of standardized phylogenetic diversity, positive values indicate phylogenetic clustering, and negative values phylogenetic evenness.*

FIGURE S1. Phylogenetic reconstruction for 420 species recorded in a 91 one-hectare plot network in Amazonian white-sand forests.

FIGURE S2. Longitudinal gradient in species composition in 91 plots established in white-sand forests across the Amazon basin.

FIGURE S3. Spatial variation of floristic dissimilarities in white-sand forests across the Amazon basin.

## LITERATURE CITED

Adeney, J. M., N. Christensen, A. Vicentini, and M. Cohn-Haft. 2016. White-sand ecosystems in Amazonia. Biotropica 48: 7–23.

Álvarez Alonso, J., M. R. Metz, and P. V. A. Fine. 2013. Habitat specialization by birds in western Amazonian white-sand forests. Biotropica 45: 365–372.

Anacker, B. L., and S. P. Harrison. 2012. Historical and ecological controls on phylogenetic diversity in Californian plant communities. Am. Nat. 180: 257–269.

Anderson, A. B. 1981. White-sand vegetation of Brazilian Amazonia. Biotropica 13: 199–210.

Bardon, L., L. J. Chamagne, K. Dexter, C. A. Sothers, G. T. Prance, and J. Chave. 2013. Origin and evolution of Chrysobalanaceae: Insights into the evolution of plants in the Neotropics. Bot. J. Linn. Soc. 171: 19–37.

Bryant, J. A., C. Lamanna, H. Morlon, A. J. Kerkhoff, B. Enquist, and J. Green. 2008. Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. Proc. Natl Acad. Sci. USA 105: 11505–11511.

Cardillo, M. 2011. Phylogenetic structure of mammal assemblages at large geographical scales: Linking phylogenetic community ecology with macroecology. Philos. Trans. R. Soc. Lond., Ser. B 366: 2545–2553.

Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. Am. Nat. 163: 823–843.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecol. Lett. 12: 1–23.

Cleveland, W. S., and S. Levin. 1998. Locally Weighted Regression: An Approach to regression analysis by local fitting. J. Am. Stat. Assoc., 83: 596–610.

Coomes, D. A., and P. J. Grubb. 1998. A Comparison of 12 Tree Species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships. Funct. Ecol. 12: 426–435.

Damasco, G., A. Vicentini, C. V. Castilho, T. Pimentel, and H. E. M. Nascimento. 2012. Disentangling the role of edaphic variability, flooding regime and topography of Amazonian white-sand vegetation. J. Veg. Sci. doi:10.1111/j.1654-1103.2012.01464.x.

Duivenvoorden, J. F., and J. Lips. 1995. A land-ecological study of soils, vegetation and plant diversity in Colombian Amazonia. Tropenbos International, Wageningen, The Netherlands.

Eiserhardt, W. L., J. C. Svenning, F. Borchsenius, T. Kristiansen, and H. Balslev. 2013. Separating environmental and geographical determinants of phylogenetic community structure in Amazonian palms (Arecaceae). Bot. J. Linn. Soc. 171: 244–259.

Emerson, B. C., and R. G. Gillespie. 2008. Phylogenetic analysis of community assembly and structure over space and time. Trends Ecol. Evol. 23: 619–630.

Fine, P. V. A., and C. Baraloto. 2016. Habitat Endemism in white-sand forests: insights into the mechanisms of lineage diversification and community assembly of the Neotropical Flora. Biotropica 48: 24–33.

Fine, P. V. A., D. C. Daly, G. Villa Muñoz, I. Mesones, and K. M. Cameron. 2005. The contribution of edaphic heterogeneity to the evolution and diversity of Burseraceae trees in the western Amazon. Evolution 59: 1464–1478.

Fine, P. V. A., R. Garcia Villacorta, N. C. A. Pitman, I. Mesones, and S. Kembel. 2010. A floristic study of the white sand forests of Peru. Ann. Mo. Bot. Gard. 97: 283–305.

Fine, P. V. A., and S. Kembel. 2011. Phylogenetic community structure and phylogenetic turnover across space and edaphic gradients in western Amazonian tree communities. Ecography 34: 552–556.

Fine, P. V. A., F. Zapata, and D. C. Daly. 2014. Investigating processes of neotropical rain forest diversification by examining the evolution and historical biogeography of the Protiae (Burseraceae). Evolution 68(7): 1988–2004.

Frazier, C. L., V. A. Albert, and L. Struwe. 2008. Amazonian lowland, white sand areas as ancestral regions for South American biodiversity: Biogeographic and phylogenetic patterns in Potalia (Angiospermae: Gentianaceae). Org. Divers. Evol. 8: 44–57.

Gillespie, R. G. 2004. Community assembly through adaptive radiation in Hawaiian spiders. Science 303: 356–359.

Goldberg, E., K. Roy, R. Lande, and D. Jablonski. 2005. Diversity, endemism, and age distributions in macroevolutionary sources and sinks. Am. Nat. 165: 623–633.

Graham, C. H., and P. V. A. Fine. 2008. Phylogenetic beta diversity: Linking ecological and evolutionary processes across space in time. Ecol. Lett. 11: 1265–1277.

Graham, C. H., J. L. Parra, C. Rahbeck, and J. A. Mcguire. 2009. Phylogenetic structure in tropical hummingbird communities. Proc. Natl Acad. Sci. USA 106: 19673–19678.

Hammond, D. S. 2005. Biophysical features of the Guiana Shield. *In* D. Hammond (Ed.). Tropical forests of the Guiana Shield: Ancient forests in a modern world, pp. 15–194. CABI Publishing, Wallingford, U.K.

Hardy, o., and B. Senterre. 2007. Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. J. Ecol. 95: 493–506.

Hoorn, C. 1993. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: Results of a palynostratigraphic study. Palaeogeogr. Palaeoclimatol. Palaeoecol. 105: 267–309.

Hoorn, C., F. P. Wesselingh, H. Ter Steege, M. A. Bermudez, A. Mora, J. Sevink, I. Sanmartin, A. Sanchez Meseguer, C. L. Anderson, J. P. Figuereido, C. Jaramillo, D. Riff, F. R. Negri, H. Hooghmiestra, J. Lundberg, T. Stadler, T. Sarkinen, and A. Antonelli. 2010. vAmazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330: 927–931.

Lennon, J. J., P. Koleff, J. J. D. Grenwood, and K. J. Gaston. 2001. The geographical structure of British bird distributions: Diversity, spatial turnover and scale. J. Anim. Ecol. 70: 966–979.

Lennon, J. J., P. Koleff, J. J. D. Grenwoow, and K. J. Gaston. 2004. Contribution of rarity and commonness to patterns of species richness. Ecol. Lett. 7: 81–87.

Matos, M. V., S. H. Borges, F. M. d''Horta, C. Cornelius, E. Latrubesse, M. Cohn-Haft, and C. C. Ribas. 2016. Comparative phylogeography of two bird species, *Tachyphonus phoenicius* (Thraupidae) and *Polytmus theresiae* (Trochilidae), specialized in Amazonian white-sand vegetation. Biotropica 48: 110–120.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecol. Lett. 13: 1085–1093.

Misiewicz, T., and P. V. A. Fine. 2014. Evidence for ecological divergence across a mosaic of soil types in an Amazonian tropical tree: *Protium subserratum* (Burseraceae). Mol. Ecol. 23: 2543–2558.

Pennington, R. T., and C. W. Dick. 2010. Diversification of the Amazonian flora and its relation to key geological and environmental events: A molecular perspective. *In* C. Hoorn, and F. P. Wesselingh (Eds.). Amazonia, landscape and species evolution, pp. 373–385. Blackwell Publishing, Oxford, U.K.

Penuela-Mora, M. C. 2014. Understanding Colombian white sand forests. PhD dissertation.

Pos, E., J. E. Guevara andino, D. Sabatier, J. F. Molino, N. C. A. Pitman, H. Mogollon, D. Neill, C. Ceron, G. Rivas, A. Di Fiore, R. Thomas, M. Tirado, K. R. Young, O. Wang, R. Sierra, R. Garcia Villacorta, R. Zagt, W. Palacios, M. Aulestia, and H. Ter Steege. 2014. Are all species necessary to reveal ecologically important patterns? Ecol. Evol. 4(24): 4626–4636. doi: 10.1002/ece3.1246.

R Development Core Team. 2011.R Foundation for Statistical Computing, Vienna, Austria.

Richardson, J., R. T. Pennington, T. D. Pennington, and P. M. Hollingsworth. 2001. Rapid diversification of a species-rich genus of neotropical rain forest. Science 293: 2242–2245.

Ricklefs, R. E. 2006. Evolutionary diversification and the origin of the diversity-environment relationship. Ecology 87: S3–S13.

Ricklefs, R. E. 2007. Estimating diversification rates from phylogenetic information. Trends Ecol. Evol. 22: 601–610.

Ricklefs, R. E., and D. Schluter. 1993. Species diversity: Regional and historical influences. *In* R. E. Ricklefs, and D. Schluter (Eds.). Species diversity in ecological communities, pp. 350–363. University of Chicago Press, Chicago.

Rosenzweig, M. L., and E. A. Sandlin. 1997. Species diversity and latitudes: Listening to area's signal. Oikos 80: 172–176.

Roy, K., and E. Goldberg. 2007. Origination, extinction, and dispersal: Integrative models for understanding present-day diversity gradients. Am. Nat. 170: S71–S85.

Stropp, J., P. Van Der Sleen, P. A. Assunção, A. L. Da Silva, and H. Ter Steege. 2011. Tree communities of white-sand and terra-firme forests of the upper Rio Negro. Acta Amazon 41: 521–544.

Struwe, L., and V. A. Albert. 1997. Floristics, cladistics, and classification: Three case studies in Gentianales. *In* J. Dransfield, M. J. E. Coode, and D. A. Simpson (Eds.). Plant diversity in Malesia III, pp. 321–352. Royal Botanic Gardens, Kew.

Swenson, N. G., B. J. Enquist, J. Pither, J. Thompson, and J. K. Zimmermann. 2006. The problem and promise of scale dependency in community phylogenetics. Ecology 87: 2418–2424.

Ter Steege, H. and D. S. Hammond. 2001. Character convergence, diversity and disturbance in tropical rain forest in Guyana. Ecology 82(11): 3197–3212.

Ter Steege, H., N. C. A. Pitman, O. L. Philips, J. Chave, D. Sabatier, A. Duque, J. F. Molino, M. F. Prevost, R. Spichiger, H. Castellanos, P. Von Hildebrand, and R. Vasquez. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443: 444–447.

Ter Steege, H., N. C. A. Pitman, D. Sabatier, C. Baraloto, R. De Paiva Salomao, J. E. Guevara, *et al.* 2013. Hyper dominance in Amazonian tree flora. Science 342: 1243092.

Terborgh, J., and E. Andresen. 1998. The composition of Amazonian forests: Patterns at local and regional scales. J. Trop. Ecol. 14: 645–664.

Vamosi, S. M., S. B. Heard, J. C. Vamosi, and C. O. Webb. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. Mol. Ecol. 18: 572–592.

Vicentini, A. 2016. The evolutionary history of Pagamea (Rubiaceae), a white-sand specialist lineage in tropical South America. Biotropica 48: 48–69.

Vormisto, J., O. L. Phillips, K. ruokolainen, H. Tuomisto, and R. Vasquez Martinez. 2000. A comparison of fine scale distribution patterns of four plant groups in an Amazonian rain forest. Ecography 23: 349–359.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. Am. Nat. 156: 145–155.

Wesselingh, F. P., M. C. Hoorn, J. Guerrero, M. Rasanen, L. Romero Pitmann, and J. Salo. 2006. The stratigraphy and regional structure of Miocene deposits in western 595 Amazonia (Peru, Colombia and Brazil), with implications for late Neogene landscape evolution. Scripta Geol. 133: 291–322.

Zanne, A., D. C. Tank, W. K. Cornwell, J. M. Eastman, S. A. Smith, R. G. Fitzjohn, D. J. M. C. Glinn, B. C. O'Meara, A. T. Moles, P. B. Reich, D. L. Royer, D. E. Soltis, P. F. Stevens, M. Westoby, I. J. Wright, L. Aarssen, R. I. Bertin, A. Calaminus, R. Govaerts, F. Hemmings, M. R. Leischman, J. Oleksyn, P. S. Soltis, N. G. Swenson, L. Warman, and J. M. Beaulieu. 2014. Three keys to the radiation of angiosperms into freezing environments. Nature 506: 89–92.