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Title: Dispersal assembly of rain forest tree communities across the Amazon basin

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Keywords: Amazonia, biogeography, community assembly, phylogenetic structure, tropical trees

ABSTRACT (250 words max)

We investigate patterns of historical assembly of tree communities across Amazonia using a newly developed phylogeny for the species-rich neotropical tree genus *Inga*. We compare our results with those for three other ecologically important, diverse and abundant Amazonian tree lineages, *Swartzia*, Protieae and *Guatteria*. Our analyses using phylogenetic diversity metrics demonstrate a clear lack of geographic phylogenetic structure and that local communities of *Inga* and regional communities of all four lineages are assembled by dispersal across Amazonia. The importance of dispersal in the biogeography of *Inga* and other tree genera in Amazonian and Guianan rain forests suggests that speciation is not driven by vicariance and that allopatric isolation, following dispersal, may be involved in the speciation process. A clear implication of these results is that over evolutionary timescales the metacommunity for any local or regional tree community in the Amazon is the entire Amazon basin.

SIGNIFICANCE STATEMENT (120 words max)

The Amazon is largely covered by contiguous rain forest. Nevertheless, previous studies have suggested that past geological and climatic events as well as limited seed dispersal may have restricted the movement of tree lineages across the Amazon. Using a phylogenetic approach, we show that dispersal into local communities and larger regions in the Amazon appears not to have been limited on evolutionary timescales. Rather, local communities have been assembled by lineages from across the Amazon. These results contrast with those from seasonally dry tropical forest, where closely related species are clustered in geographic space. Further, our results suggest a role for dispersal as an initiator for geographic isolation that may lead to speciation in Amazonian trees.

\body

INTRODUCTION

Amazonia is well known to have the most species-rich tree communities on the planet, with more than 300 species (≥10 cm diameter) found in a single hectare (1). These communities are assembled from the species pool of Amazonia, which is estimated to number 16,000 species (2). While some species are widespread across the Amazon basin (3), the majority are more restricted geographically (2), which has been the basis for schemes that divide the Amazon into floristic regions, including distinguishing the Guianan Shield flora from that of the Brazilian Shield or the western Amazon basin (4,5). The pattern of diverse local Amazonian tree communities assembled from a species pool that mostly comprises regionally restricted species begs the question of how the regional communities are assembled through time. Regional communities could result from extensive local *in situ* speciation (6-8) with little subsequent dispersal. This would predict a pattern of geographically structured phylogenies with closely related species found in the same region. However, an idea that has been little tested using phylogenies of Amazonian plant species (9) is that the assembly of regional rain forest tree communities has been heavily influenced by historical dispersal of species. This would predict a pattern for communities that lacked geographic phylogenetic structure, where species from a single genus found in a regional community would be phylogenetically scattered.

Biogeographic studies of tree families that form important components of Amazonian forest, such as legumes (10), Annonaceae (11), Burseraceae (12), Chrysobalanaceae (13) and Meliaceae (14), have demonstrated that dispersal has been important in developing their distributions across continents and oceans (15,16). The existence of long-distance, transoceanic dispersal at the intercontinental scale suggests that there should be little to hinder dispersal across the flat, continuously forested Amazon Basin because of its lack of present-day physical barriers. Whilst there is debate of the role of potential historical dispersal barriers in the Amazon, such as forest fragmentation during Pleistocene climate changes (17-19) and a large freshwater lake (Pebas) or marine incursions that occupied much of western Amazonia in the Miocene (20,21), these are far less substantial impediments to plant dispersal than major oceans. Once a species does successfully disperse to a new location, it would still need to establish a population. Establishment can be challenging given that any immigrant seed is numerically swamped by locally produced seeds (22), but large-scale resident mortality in rain forests may be sufficiently common due to drought mortality or landscape rearrangements from radical movement of river courses to allow for establishment of immigrant species (20,23). We therefore suggest that there has been ample opportunity for historical immigration to play a key role in the assembly of Amazonian tree communities, as proposed by Lavin (24) and Pennington & Dick (25), and it is this hypothesis that we test in this paper.

We use a new phylogeny of *Inga* (Leguminosae (Fabaceae): Mimosoideae) that samples local and regional communities in Amazonia, including the Guiana Shield, plus the *Inga* community on Barro Colorado Island, central Panama, to investigate patterns of historical community assembly (Fig. 1). The neotropical tree genus *Inga* is species-rich (>300 species), widely distributed, and has consistently high local abundance (2,26) and species richness, with up to 43 species recorded in 25 Ha (27). It is therefore an excellent exemplar to study community assembly in neotropical rain forests. Our phylogeny of *Inga* is novel in that it samples thoroughly across multiple, geographically dispersed, local Amazonian tree communities in the context of good phylogenetic coverage of an entire clade. We compare our *Inga* results at a regional scale with those for three other tree lineages, *Swartzia* (Leguminosae, Papilionoideae), Protieae (Burseraceae) and *Guatteria* (Annonaceae), which are also ecologically important, diverse and abundant in Amazonia, to investigate whether patterns in *Inga* are general for Amazonian tree communities. Finally, we contrast the picture of community assembly we uncover for Amazonian rain forest communities with patterns in the seasonally dry tropical forest biome, which has greater physical barriers to dispersal and different ecological barriers to establishment.

RESULTS

Our phylogeny for *Inga*, which is based on eight molecular markers and includes 210 accessions of 124 species, resolves relationships amongst major clades and shows that *Inga* communities in Peru, French Guiana and Panama comprise phylogenetically scattered species (Fig. 2, S1). These results, which show clear lack of geographic structure in the phylogeny of *Inga*, are mirrored by the other tree lineages with numerous Amazonian species that we have analysed. We evaluated geographic phylogenetic structure by calculating phylogenetic diversity metrics for local communities and regions and comparing the observed values to a null expectation generated by randomly sampling species from the phylogenies. We used three phylogenetic diversity metrics (cf. 28,29): 1) phylogenetic diversity sensu stricto (PDss), the total phylogenetic branch length present among species in a given community/region; 2) mean pairwise distance (MPD), the mean of all pairwise phylogenetic distances between species in a given community/region; and 3) mean nearest taxon distance (MNTD), the mean of the phylogenetic distance between each species and its closest relative in a given community/region. If species show significantly lower values than the null expectation, this indicates geographic phylogenetic structure or clustering, while significantly higher values than expected indicate phylogenetic overdispersion. Of the three local Amazonian communities, none show phylogenetic clustering for any of the metrics evaluated (Table S2), while Nouragues Research Station shows slight phylogenetic overdispersion. The *Inga* community on Barro Colorado Island, Panama, shows significant phylogenetic clustering, as evaluated by PDss and MPD.

For *Inga*, we obtained sufficient sampling from five Amazonian regions to test more broadly for geographic phylogenetic structure. As with local Amazonian *Inga* communities, no Amazonian region shows significant phylogenetic clustering by any metric (i.e., no points in Figs. 3, S2 or S3 below the grey area encompassing the 95% confidence interval; see also Table S2), while French Guiana shows slight phylogenetic overdispersion according to the PDss metric (Fig. 3; i.e., it is above the grey area encompassing the 95% confidence interval) and Loreto shows overdispersion using the MPD metric

(Fig. S2). Meanwhile, Central America is the only region to show significant phylogenetic clustering for all three metrics (Figs. 3, S2, S3; i.e., in every case below the grey area encompassing the 95% confidence interval).

This lack of geographic structure is duplicated in regional Amazonian communities of *Swartzia*, Protieae and *Guatteria*, as measured by all metrics (Figs. 3, S2, S3, Table S2). All species in regional Amazonian communities represent a random draw from each phylogeny, as measured by all metrics, with the sole exception of the *Swartzia* community in Guyana as measured by MNTD (Fig. S3, Table S2). The only cases where species in regional communities are consistently more closely related than would be expected by chance are in Central America (*Inga* [all metrics], *Swartzia* [all metrics], *Protieae* [PDss]) and the Atlantic coastal rain forest of Brazil (*Guatteria* and *Swartzia* [all metrics] (Figs. 3, S2, S3, Table S2). The level of sampling of different geographic regions varies widely (see x-axes in Figs. 3, S2, S3), but we note that well-sampled and poorly-sampled Amazonian regions present similar results. In general, neither depart significantly from null expectations for the phylogenetic diversity metrics.

Our results for geographic structure in Protieae differ slightly from those presented by Fine et al. (30), who calculated MTD and MNTD for major biogeographic regions in a global scale study of Protieae that included palaeotropical species. Firstly, the three Amazonian regions used by Fine et al. (30; eastern Amazonia, western Amazonia, Guianas) are larger than those used here and therefore not directly comparable. Further, we analysed only the neotropical clade of Protieae given our focus on local and regional Amazonian communities, for which the Neotropics alone may be a more appropriate wider metacommunity from which to draw random communities. Including palaeotropical species, which form two clades basal to the neotropical species of Protieae, will have the effect of inflating values of phylogenetic diversity in the random communities, which may also contribute to why Fine et al. (30) found greater evidence for phylogenetic clustering in the regional communities they considered.

DISCUSSION

The primacy of historical dispersal in the assembly of local and regional communities

Our results demonstrate that tree communities at local (for *Inga*) and regional scales (for *Inga*, *Swartzia*, Protieae and *Guatteria*) are assembled by dispersal across Amazonia. Species in all local Amazonian *Inga* communities and virtually all regional communities across all lineages are a random draw from the phylogeny in each of our exemplar taxa. This shared pattern is found despite the different fruit morphologies of these lineages, which reflects a variety of vertebrate dispersers. *Inga* is primarily dispersed by primates; Protieae's small endozoochorous fruits attract a wide variety of birds, bats, and terrestrial mammal species (31); *Guatteria* has been observed to be eaten by primates and birds (32); and *Swartzia* is dispersed by birds (33), primates (34) and in one species, water (35).

The only exception to this lack of phylogenetic geographic structuring is found outside of Amazonia in the rain forests of Atlantic coastal Brazil (in *Swartzia* and *Guatteria*) and Central America (*Swartzia, Inga*, Protieae). The phylogenetic clustering found in these areas may reflect that they are isolated from the Amazon by major physical barriers – the Andes mountains for Central America and a 'dry diagonal' of seasonally dry vegetation formations across eastern Brazil for the Brazilian Atlantic coast (36,37). In addition, the presence of physical barriers isolating these non-Amazonian areas has been suggested as an explanation for greater phylogeographic structure found there amongst populations of *Symphonia globulifera*, a widespread tree species (38).

The implication of the lack of geographic phylogenetic structure demonstrated here is that, on evolutionary timescales, the metacommunity for any regional or local tree community in the Amazon is the entire Amazon basin. This does not preclude a role for ecological filtering in the assembly of local communities. Our own and other previous work shows that *Inga* species in Madre de Dios have clear habitat preferences and that environmental filtering affects species composition of *Inga* communities (39-41). Further, our work has shown *Inga* species that defend themselves against herbivores in distinct ways are more likely to co-occur, signifying filtering based on herbivore defence traits (42). Thus, ecological processes clearly can play a role in local community assembly. However, the species that may populate any given region and provide species for local communities could have ancestry from anywhere in the Amazon and from any clade of the *Inga* phylogeny.

Interestingly, the average relatedness of co-occurring congeneric species differs markedly among the four genera we study here (Fig. S2). For example, the average phylogenetic distance between co-occurring *Inga* species is 3 myrs (divergence time of 1.5 myrs), while that among Protieae species is 36 myrs. This could have significant implications for the level of ecological interaction among co-occurring *Inga* versus Protieae species, for example competition might be considered to be more intense amongst *Inga* species because of their recent divergence (43), which could in turn influence the composition of local and regional communities. However, our analyses tend to suggest that the average phylogenetic distance among co-occurring species of a given genus may simply depend on the age of the genus, although the exact phylogenetic distance estimates will depend on how well the genus has been sampled phylogenetically. Further, the high degree of sympatric co-occurrence observed for the species-rich genera we study here suggests that there may not be strong constraints on the number of co-occurring congeneric species, especially if they differ in herbivore defence traits (42,44,45). One of the key factors influencing the number of co-occurring species of a given genus in a given Amazonian tree community may simply be the total diversity of that genus in the Amazon, because dispersal into regions, which provide species for local communities, does not seem to be limited (46).

We emphasise that the generality of our results may only apply to larger trees, and that there are indications that patterns of geographic structure in phylogenies of shrubs, understory trees and other tropical plant life forms may differ (47). For example, the phylogeny of the tropical rain forest herb genus *Pilea* is highly congruent with geography, which may reflect limited pollen dispersal and mechanical dispersal of seeds over very short distances of a few millimetres (48). Our results also contrast with studies published for large terrestrial birds (49) and primates (50), which show more geographically structured patterns in their phylogenies.

Contrasting patterns of community assembly amongst different biomes

The pattern of assembly of regional tree communities reported for the neotropical seasonally dry forest biome (24,51,52) differs markedly from that discovered here for regional Amazonian communities. Phylogenies of several genera of woody plants characteristic of seasonally dry tropical forests in the Neotropics (e.g., *Coursetia*, *Poissonia*, *Cyathostegia*, *Amicia*) demonstrate that clades of species are confined to single regions of dry forest such as the Brazilian caatingas (53) or seasonally dry Andean valleys (52). These differences are not artefacts of the age of clades because the crown clades of these dry forest genera are older than that of *Inga*; despite historical dispersal having had less time to operate in *Inga*, successful dispersal and establishment events are more prevalent.

The geographic phylogenetic structure shown in dry forest clades may reflect two factors (51). First, unlike the continuous Amazon rain forest, dry forest areas are scattered across the Neotropics, physically isolated by high mountains or areas of mesic vegetation, and this may limit dispersal amongst them (51). Second, ecological factors, operating over evolutionary timescales, are different in dry forests, and this may alter the probability of propagules establishing after dispersal (51, 54). For example, there may be more opportunities for immigration into rain forests where drought can cause widespread tree mortality (23), and landscape evolution is also known to be dynamic over evolutionary timescales in Amazonia, especially via radical movement of river courses (20,55), which may be an additional source of environmental instability creating opportunities for successful immigration.

Implications for processes of diversification in Amazonian rain forest trees

A key role for dispersal in *Inga* and other important tree genera has implications for understanding speciation histories in Amazonian rain forests. For Amazonian trees the lack of geographic phylogenetic structure that we find in local and regional communities provides little support for large-scale reconfigurations of the landscape causing common vicariance of continuous populations of multiple species, a conclusion reached recently for Amazonian birds (56). Large-scale geological events that subdivide populations would lead to congruent geographic phylogenetic patterns across lineages, but there is little evidence for common deep imprints of geological events in Amazonian tree phylogenies. For example, geographic phylogenetic structure across the Miocene Lake Pebas is not detected in the phylogenies of *Inga*, *Swartzia*, *Guatteria* or Protieae. Instead, geographic patterns are particular to lineages, reflecting a primacy for idiosyncratic historical dispersal in generating distributions (25,53). The lack of congruent patterns suggests that allopatric speciation involving population vicariance caused by common geological factors is unlikely.

Rather than geological phenomena that isolate regions, our results for multiple Amazonian tree lineages are more consistent with the founding of isolated peripheral populations by dispersal, which could then lead to speciation. This model is also consistent with patterns in some Amazonian tree lineages of phylogenetic nesting of species within paraphyletic progenitor species (57). An alternative model would be more localised speciation followed by sufficient dispersal, which could also result in the random phylogenetic composition of tree communities that we show here, and also nesting of species within paraphyletic ancestors. Such local speciation could be via hybridisation or adaptation to soil types (6,8,30,58). The documented inter-sterility of sympatric *Inga* species (59) argues against a role for hybridisation in speciation of that genus, but our biggest challenge to understanding the mechanism of speciation is that rampant dispersal may overwrite the original signature of genetic divergence. To distinguish the relative importance of ecological divergence, breeding systems and allopatric isolation in driving diversification of Amazonian trees, it would be fruitful to characterise further the variation in the functional ecology, biology and underlying genetics of species of *Inga* and other diverse tree genera across their ranges.

MATERIALS AND METHODS

Sampling

In the Amazon basin and Guianas, together comprising what we term Amazonia, we sampled 181 *Inga* individuals, representing 105 total species (including 20 unidentified morphospecies). Outside of the Amazon basin, we sampled two species in Ecuador west of the Andes, three species in the Caribbean, and 23 species in Central America. In total our phylogenetic sampling for *Inga* included four local communities and seven regional communities and comprised 210 individuals from 124 species (Tables S1, S2). This represents many more accessions and more than double the species sampling in prior *Inga* phylogenies (39,42,60; sampled from 37 to 55 species]). Because our goal was to sample as many species as possible in individual local and regional communities, we sampled 44 of the total 124 species more than once, because these species were present in more than one region. We did not sample any species more than once within any one local or regional community.

Swartzia (Leguminosae-Papilionoideae) contains approximately 200 neotropical species found from southern Mexico to southern Brazil, including the Caribbean islands (61). *Swartzia* occurs in a variety of habitats, but is especially typical of lowland rain forests, where 10 or more species can be found growing in sympatry (62). Phylogenetic data and the sampling locality for each accession of *Swartzia* come from Torke & Schaal (63), who sampled 76 species, including multiple exemplar species of each of the infrageneric groupings (see 64), covering the full geographic range of the genus.

The tribe Protieae (Burseraceae), comprising *Protium* together with *Tetragastris* and *Crepidospermum* nested within it, is an important tree lineage in terms of its diversity and abundance in neotropical and palaeotropical rain forests (2,30). The majority of Protieae species are found in the Amazon basin and the Guianas, but there are smaller numbers of species occurring in other areas, including Central America, the Caribbean, and the Brazilian Atlantic Forest. Phylogenetic data for Protieae come from Fine at al. (30), who sampled 102 species covering 75% of accepted species names and all pantropical areas of distribution.

Guatteria (Annonaceae) is an abundant and diverse component of lowland rain forests in the Neotropics and is a member of the magnoliids, a basally divergent angiosperm lineage. The genus is hypothesized to have originated in Africa and to have colonized South America via North and then Central America during the late Miocene (65). Nevertheless, *Guatteria* is most diverse in lowland Amazonia (66,67). The published phylogeny of the genus covers 97 of 265 named species from Central America to the Mata Atlantica, with 39 accessions covering 38 species sampled from Amazonia (Bolivia, Peru, Colombia, Brazil and the Guianas), representing 40% of the species found in these areas (67).

Phylogenetic reconstruction

For *Inga*, we sequenced seven chloroplast regions (*rpoCI, psbA-trnH, rps16, trnL-F, trnD-T, ndhF-rpl32, rpl32-trnL*; 5916 aligned bp) and the nuclear ribosomal internal transcribed spacer regions (*ITS 1 & 2*; 572 aligned bp) (Table S1). PCR and sequencing protocols for chloroplast regions are given by Kursar et al. (42) and for *ITS* by Richardson et al. (60) and Dexter et al. (39). Sequences were initially aligned using MAFFT (68) and then adjusted manually, which was straightforward given low sequence divergence. The phylogeny was estimated under a maximum likelihood framework using

RAxML with separate partitions and models for *ITS* and cpDNA and 1000 bootstrap replicates to estimate node support (69). The phylogeny was subsequently time-calibrated using penalised likelihood (70), where the crown age was constrained to 6 myrs (following 24,60).

The *Inga* phylogeny resolves numerous clades with reasonable bootstrap support (Fig. 2, Fig. S1) and is the best resolved *Inga* phylogeny to date, though within major clades the relationships amongst closely related species are not always well resolved, reflecting the recent evolutionary radiation of the genus (60). The topology of our phylogeny is largely congruent with that presented by Nicholls et al. (71) based upon 194 nuclear loci, which shows high support for all branches. There are only two strongly supported incongruencies between the two phylogenies, involving two species, *I. laurina* and *I. ruiziana*, and a formal statistical test (72) shows that the phylogenies are significantly congruent ($I_{cong} = 1.46$, $p = 0.0016$). Although Nicholls et al. (71) sampled only 22 *Inga* species, the topological congruence gives confidence that our less well supported phylogeny does reflect phylogenetic relationships accurately.

For *Swartzia*, aligned sequences from Torke & Schaal (63) were downloaded from TreeBase and a phylogeny estimated under a maximum likelihood optimality criterion as described for *Inga* using separate partitions and models for ITS, AAT1 and chloroplast DNA. This phylogeny was subsequently time-calibrated using penalised likelihood where the crown age was constrained to 13.6 myrs (following 73). For Protieae, the time-calibrated Bayesian phylogeny reported by Fine et al. (30) was downloaded from TreeBase. For *Guatteria*, sequences reported by Erkens et al. (66) were downloaded from Genbank and a phylogeny was estimated under a maximum likelihood optimality criterion as described above for *Inga* with a single partition and model because all loci reported are from the chloroplast genome. This phylogeny was subsequently time-calibrated using penalised likelihood where the crown age was constrained to 17.2 myrs following Erkens et al. (65).

Analyses of geographic phylogenetic structure

We analyzed geographic phylogenetic structure at two scales (Fig. 1): local communities (*Inga* only) and regions (across all groups). In the case of *Inga*, we were able to sample all or nearly all species in four local communities (see above) at Los Amigos and Madreselva Biological Stations (Peru), Nouragues Research Station (French Guiana) and Barro Colorado Island (Panama) (Fig. 1). The scale of the local communities varied from ~6 km^2 (Madreselva) to 15.6 km^2 (Barro Colorado Island).

We defined 13 geographic regions with sufficient sampling (≥5 species in nearly all cases) that could be analyzed across the different phylogenies (Fig. 1) using our knowledge for *Inga* and *Swartzia*, and information in Fine et al. (30) for Protieae and in Erkens et al. (66) for *Guatteria*. In Amazonia and the Guianas these are geographic political units of similar size, such as states in Brazil, departments in Peru, or countries such as Guyana. Beyond Amazonia and the Guianas, the defined regions were the Mata Atlântica (Atlantic coastal rain forest) of Brazil, the Chocó of Colombia and Ecuador (i.e., South American rain forests on the Pacific coast west of the Andes), Central America (Panama north to Mexico) and the Caribbean. If an accession sampled in our phylogenies came from one of these regions, as indicated by its published locality (30,63,66), it was scored as present there. An alternative approach would be to assign a given species in the phylogeny to every region in which it is known to occur (30). This approach might be problematic if accessions are misidentified or not positively identified (i.e. morphospecies) or if species distributions are imperfectly known. For *Inga*, we conducted a series of sensitivity analyses to assess if our results were robust to our approach of only assigning accessions to the regions in which they were collected, and this revealed no effect on our results (see SI).

If closely related species within a clade (in this case *Inga*, *Swartzia*, Protieae or *Guatteria*) are found near each other in geographic space because they originated by local, in-situ speciation with little subsequent dispersal then we would expect the phylogenetic diversity represented by species in regions and local communities to be less than that if the same number of species were drawn randomly from across the phylogeny. Conversely, if distant dispersal is common over one or multiple generations, causing local and regional communities to be assembled stochastically from a wide geographic pool, then we expect that the phylogenetic diversity in communities and regions would be more commensurate with a random draw from the phylogeny. We evaluated phylogenetic diversity using three metrics described above. The null expectations for each of these metrics, and the uncertainty around them, were calculated by randomly drawing the same number of species as present in communities/regions from the phylogeny and repeating this process 999 times. Significant phylogenetic clustering for a given community/region was deemed to be present when the observed phylogenetic diversity metric was less than the lower 2.5% quantile of the randomly generated distribution for that species richness, while significant overdispersion would be indicated by a value greater than the 97.5% quantile.

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AUTHORSHIP STATEMENT

KGD, PDC, TAK collected *Inga* leaf samples in the field; KGD, RTP, ML, ADT, CD, RH generated DNA sequence data; KGD and RTP performed phylogenetic analyses; KGD performed analyses of phylogenetic geographic structure; KGD and RTP wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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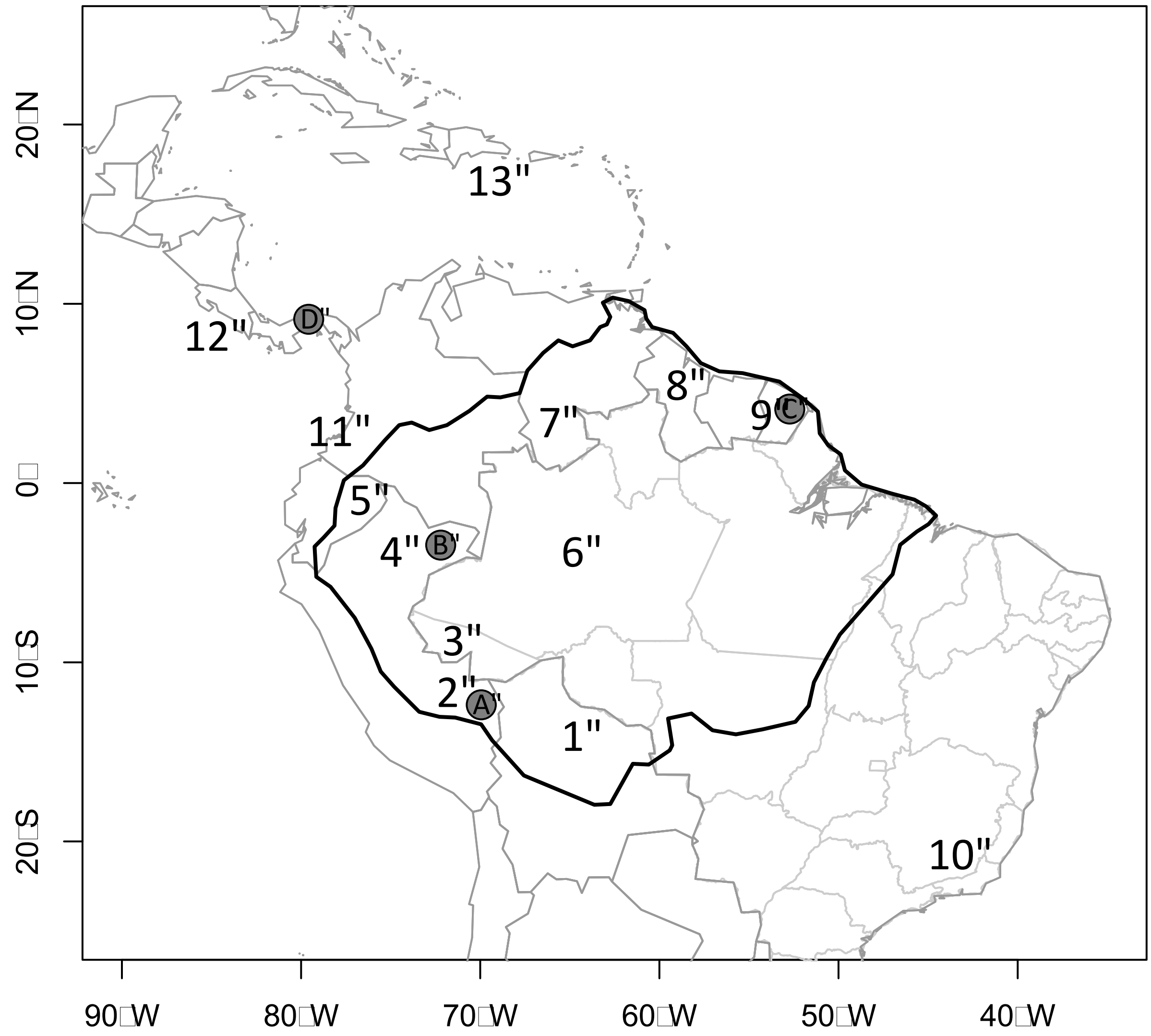
Figure 1: Map of the 13 Neotropical regions used in the analyses of phylogenetic geographic structure for the four focal genera: 1) Amazonian Bolivia, 2) Madre de Dios (southern) Peru, 3) Acre, Brazil, 4) Loreto (northern) Peru, 5) Amazonian Ecuador, 6) Amazonas, Brazil, 7) Amazonas, Venezuela, 8) Guyana, 9) French Guiana, 10) Mata Atlantica (Atlantic rain forest), 11) Choco (trans-Andean) Colombia and Ecuador, 12) Central America, and 13) the Caribbean. Letters denote location of the local communities of *Inga* (Leguminosae) that received in-depth sampling: A) Los Amigos Biological Station, B) Madreselva Biological Station, C) Nouragues Research Station, and D) Barro Colorado Island. The dark black line denotes our delimitation of 'Amazonia', which includes wet and moist forests across the Amazon Basin and the Guianan Shield.

Figure 2: Phylogeny of 210 accessions representing 124 *Inga* (Leguminosae) species with a maximum of one individual per species per region. Accessions from focal communities are colored as follows: Los Amigos Biological Station (blue), Madreselva Biological Station (purple), Nouragues Research Station (brown), and Barro Colorado Island (red). Additional accessions are colored by biogeographic region: Amazon (black), Central America (orange) and Caribbean (cyan). Circle size at nodes is proportional to bootstrap support. See Figure S1 for details of tip labels and node support values. The line drawing at the top right is *I. pitmanii*, a regionally restricted species, apparently endemic to Madre de Dios, Peru (reproduced with permission from *Novon*; 71).

Figure 3: Relationship between number of taxa sampled and phylogenetic diversity in Neotropical regions for four emblematic Amazonian tree genera. Phylogenetic diversity was evaluated as the sum of branch lengths in an ultrametric, temporally-calibrated phylogeny including the taxa from a given region. Regions are numbered following Figure 1. The solid black line gives the mean null expectation for phylogenetic diversity given the number of taxa sampled, for 1000 random draws of that number of taxa from the phylogenies. The shaded gray area denotes the 95% confidence intervals of the null expectation for the relationship. Regions that fall outside of the 95% confidence intervals are labeled.



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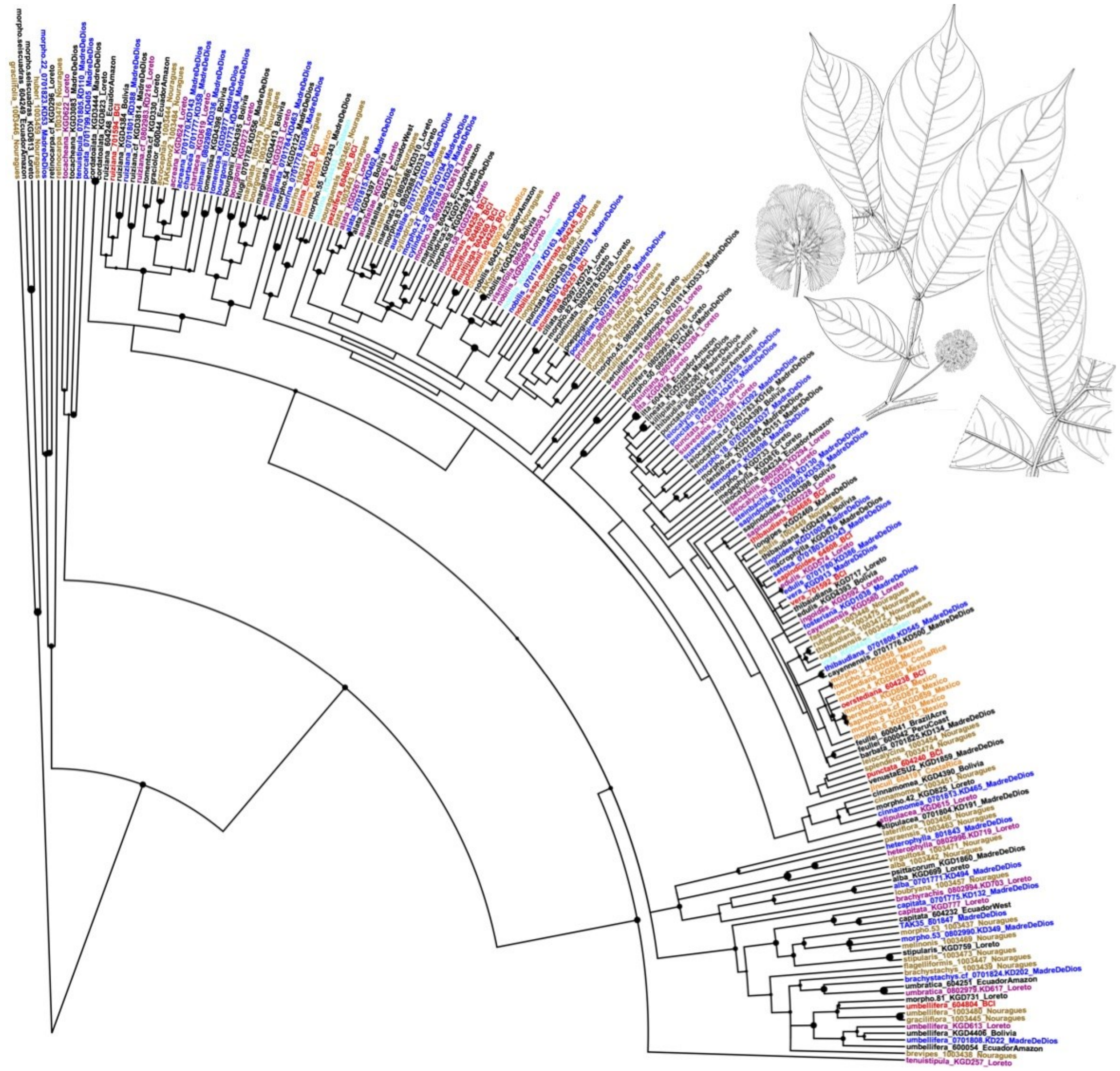

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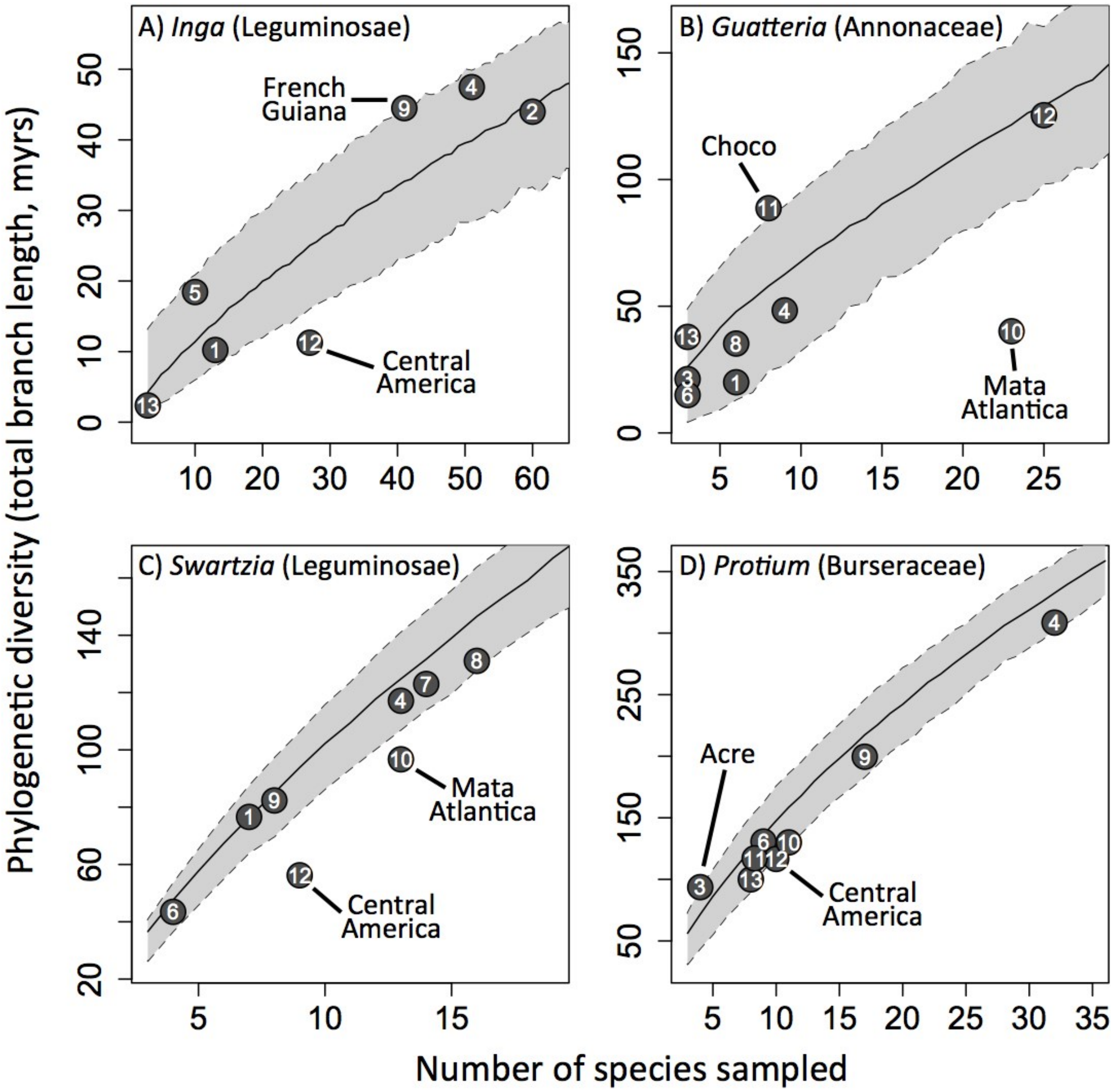

Figure 3: Relationship between number of taxa sampled and phylogenetic diversity in Neotropical regions for four emblematic Amazonian tree genera. Phylogenetic diversity was evaluated as the sum of branch lengths in an ultrametric, temporally-calibrated phylogeny including the taxa from a given region. Regions are numbered following Figure 1. The solid black line gives the mean null expectation for phylogenetic diversity given the number of taxa sampled, for 1000 random draws of that number of taxa from the phylogenies. The shaded gray area denotes the 95% confidence intervals of the null expectation for the relationship. Regions that fall outside of the 95% confidence intervals are labeled.

Supplementary Information

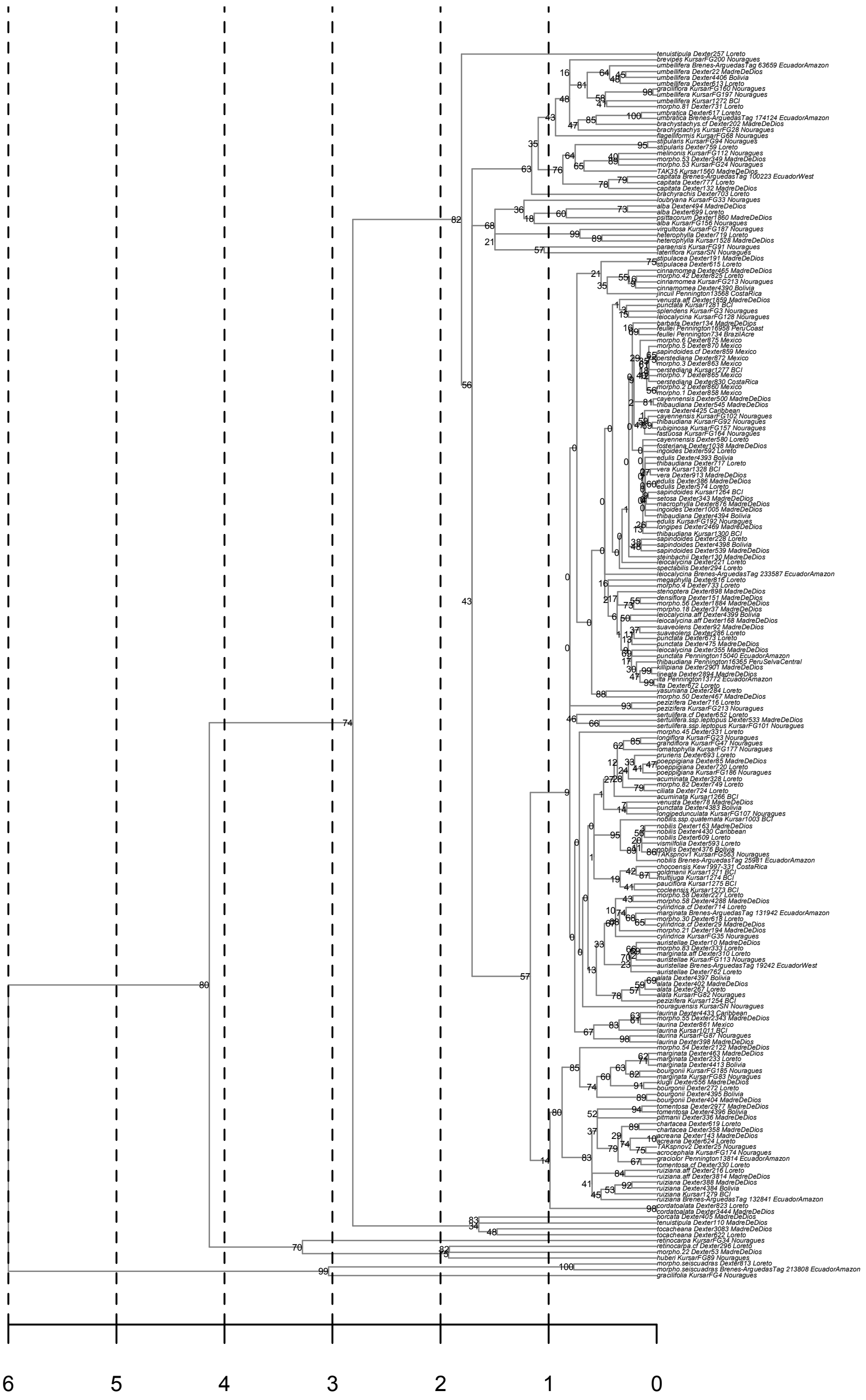

Figure S1: Maximum likelihood phylogeny for *Inga* (Leguminosae) after rate smoothing via penalised likelihood. The numbers to the left-hand side of the nodes indicate the percentage of 1000 maximum likelihood bootstrap replicates that support the relationship. Branch lengths are in terms of millions of years.

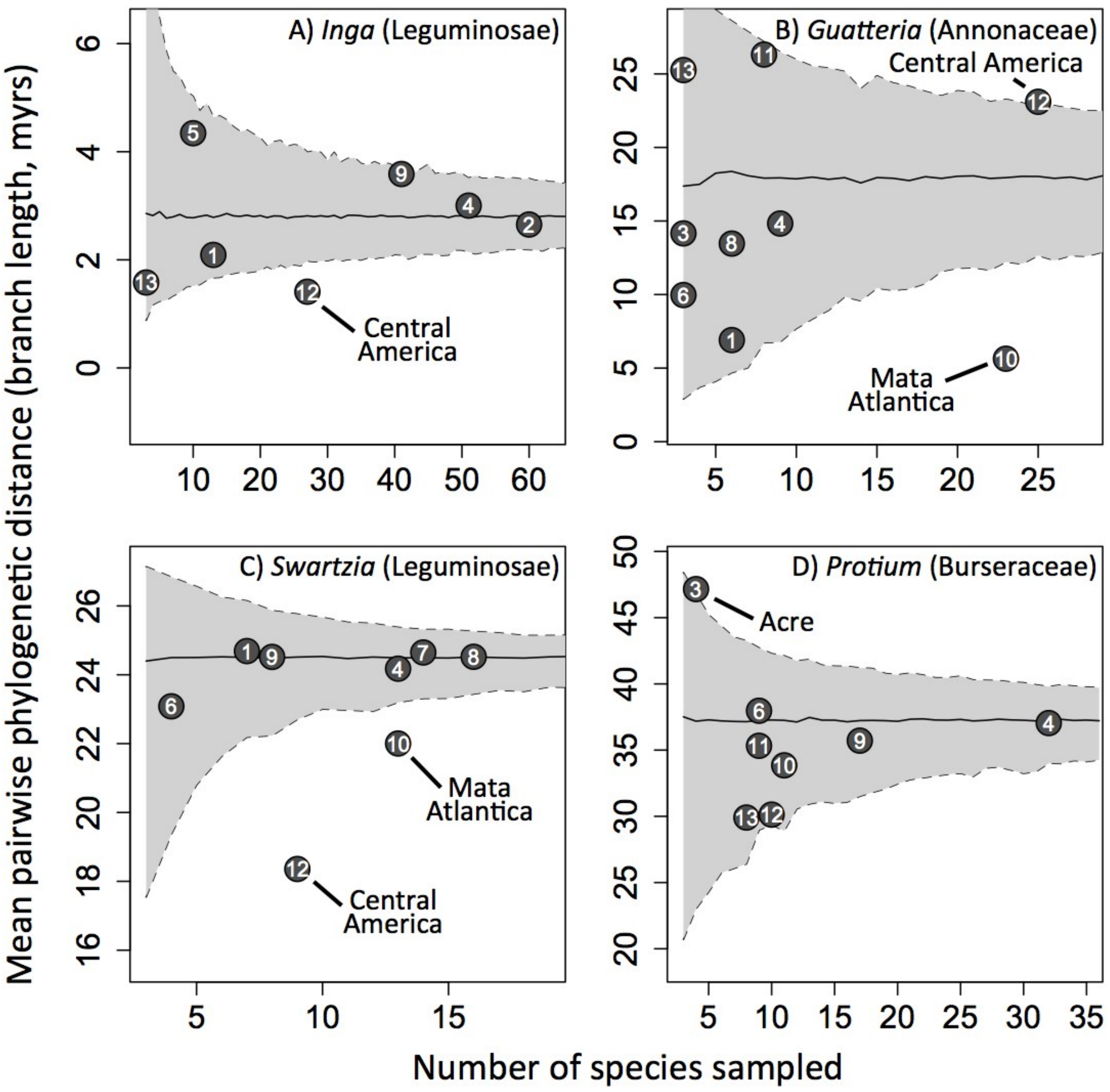

Figure S2: Relationship between number of taxa sampled and mean pairwise distance (MPD) in Neotropical regions for four emblematic Amazonian tree genera. Regions are numbered following Figure 1. The solid black line gives the mean null expectation for MPD given the number of taxa sampled for 1000 random draws of that number of taxa from the phylogenies. The shaded grey area denotes the 95% confidence intervals of the null expectation for that relationship. Regions that fall outside of the 95% confidence intervals are labelled.

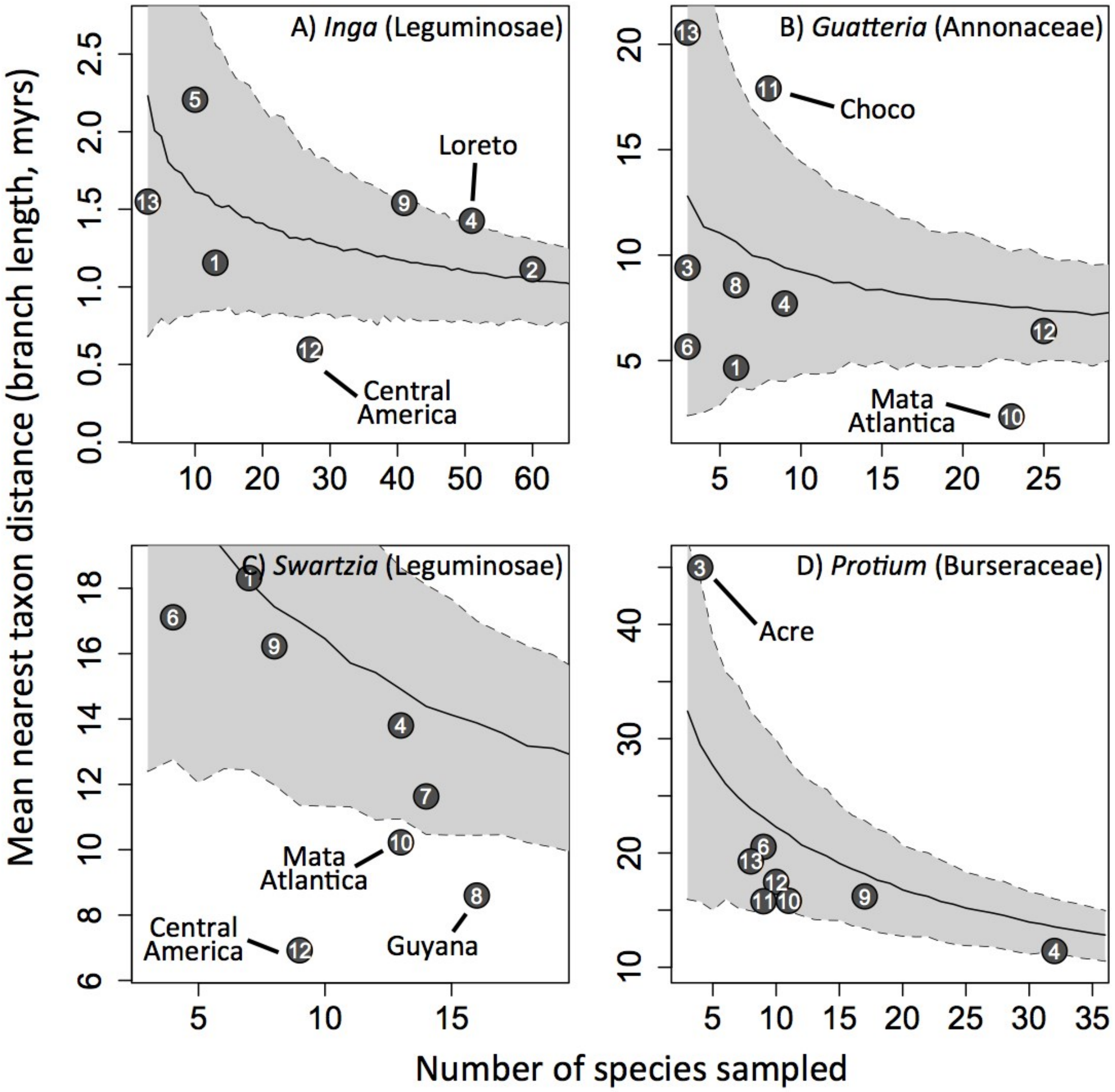

Figure S3: Relationship between number of taxa sampled and mean nearest taxon distance (MNTD) in Neotropical regions for four emblematic Amazonian tree genera. Regions are numbered following Figure 1. The solid black line gives the mean null expectation for MNTD given the number of taxa sampled for 1000 random draws of that number of taxa from the phylogenies. The shaded grey area denotes the 95% confidence intervals of the null expectation for that relationship. Regions that fall outside of the 95% confidence intervals are labelled.

Sensitivity Analyses for Phylogenetic Diversity Estimates of Amazonian Inga communities

In order to assess how robust our results were to uncertainty in the age of *Inga* clades, the topology of the *Inga* phylogeny, and in the assignment of *Inga* species to different geographic regions, we conducted sensitivity analyses. We ran a Bayesian analysis to calibrate the *Inga* phylogeny temporally while simultaneously estimating its topology, using BEAST v1.8.2 (Drummond *et al.* 2012). As there are no definitively identified fossils for *Inga*, we constrained the crown age of *Inga* in this phylogeny (using a log-normal prior with a mean of| 6 myrs and a standard deviation of 0.5) based on dates from Richardson et al. (2001) and Lavin (2006). For each iteration of the sensitivity analyses, we sampled one tree at random from the post burn-in, posterior distribution of trees from the BEAST analysis.

In our primary analyses presented in the main text, the species lists for a given geographic region are comprised of all species in a region that were sampled by accessions in the phylogeny. An alternative approach would be to include all species present in the phylogeny that are known to occur in the region based on their overall distribution (rather than just those that were sampled by accessions from the region in our phylogeny). Our primary approach has the advantages that it does not assume monophyly of species (and not all *Inga* species are monophyletic, see Fig. S1) and does not assume perfect taxonomy and knowledge of species' distributions. However, it does mean that species lists for a given region may not include many species that are found in the region. As can be seen in examining the x-axis in Figures 3, S2 and S3, our level of sampling for different regions varies greatly. Thus, we also conducted additional analyses assigning *Inga* species to each region in which they are known to occur, based on distributions in Pennington (1997) and our own field work. As many species in the phylogeny are represented by multiple accessions, we randomly selected a single accession for each species. This random selection introduces stochasticity into calculations, so we repeated this process 999 times. For each repetition, we started with a topology randomly selected from the posterior distribution of trees (see above), which serves to generate a range of results representing uncertainty in phylogenetic topology and ages.

For each iteration, we assessed whether a given Amazonian tree community showed more or less phylogenetic diversity than expected by chance by calculating the standardised effect size for each phylogenetic diversity metric (ses.pd, ses.mpd and ses.mntd). Positive values indicate phylogenetic overdispersion, while negative values indicate phylogenetic clustering. As these metrics are standardised (with an expected value of 0 and a standard deviation of 1), values that are less than -1.96 or greater than 1.96 represent communities that show significant phylogenetic overdispersion or clustering. In order to assess how are results compared to those using our primary approach, we assessed the value for each metric across the 1000 iterations and compared it to the values generated with the approach we present in the main text (Figs S4, S5 and S6). As can be seen, the median results of this alternative approach are slightly lower than those obtained in our analyses presented in the main text (on average). However, for the large majority of the iterations, none of the Amazonian communities show significant phylogenetic clustering (or overdispersion) by any metric. Thus, these sensitivity analyses demonstrate that Amazonian *Inga* communities represent a random draw from the *Inga* phylogeny, and that this result is robust to uncertainty in the age of *Inga* clades, the topology of the *Inga* phylogeny, and in the method of assignment of *Inga* species to different geographic regions.

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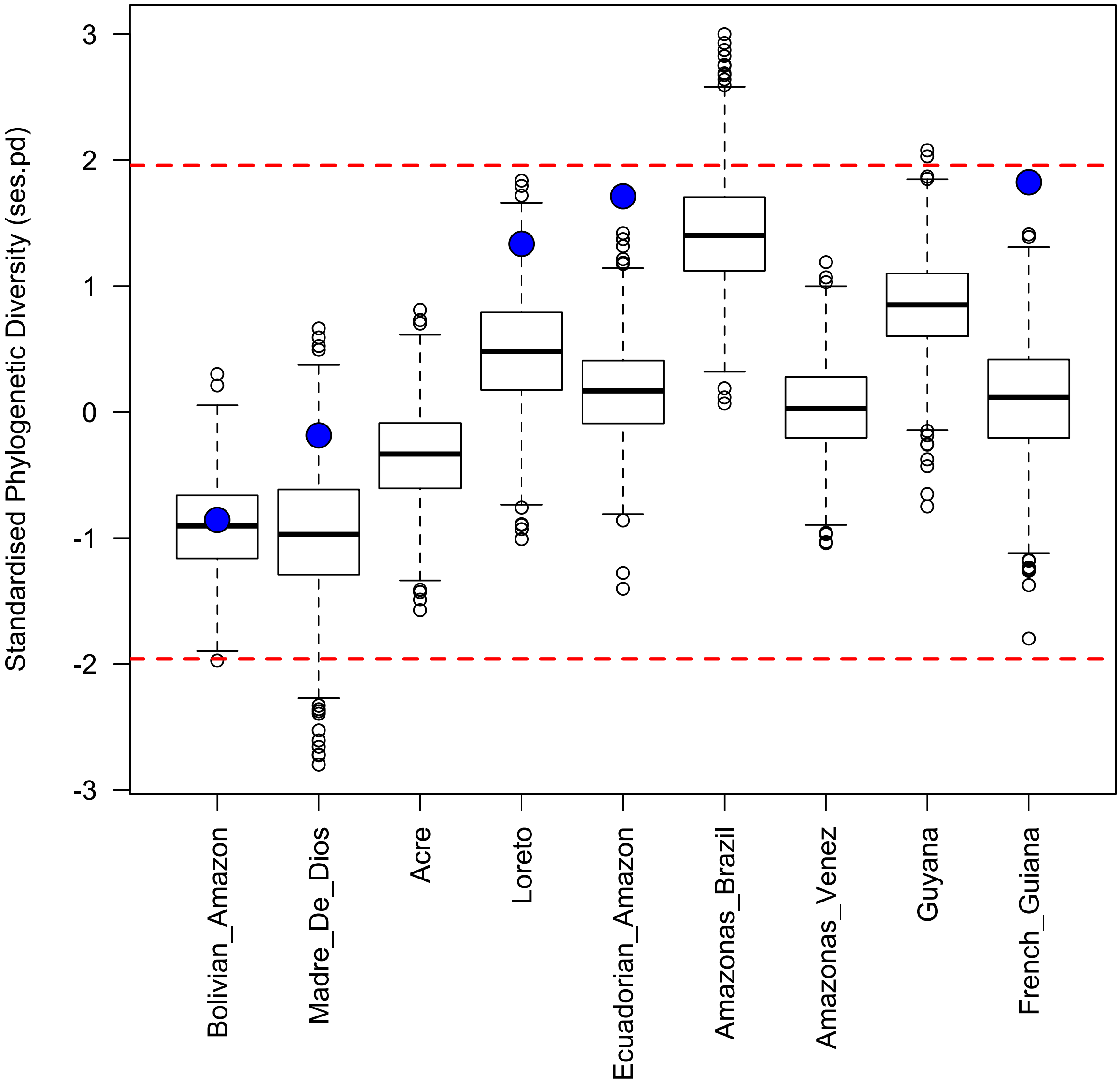

Figure S4: Distribution of ses.pd values for different Amazonian regions across 1000 iterations of the sensitivity analyses. The values from the analyses presented in the main text are shown by the large blue circles. These are only available for Amazonian regions that are actually sampled in our phylogeny. Values less than -1.96 would indicate significant phylogenetic clustering, while values greater than 1.96 would indicate significant phylogenetic overdispersion. These threshold values are indicated by dashed red lines. Overall, these results demonstrate that most iterations of the sensitivity analyses do not result in significant phylogenetic clustering or overdispersion for Amazonian regions.

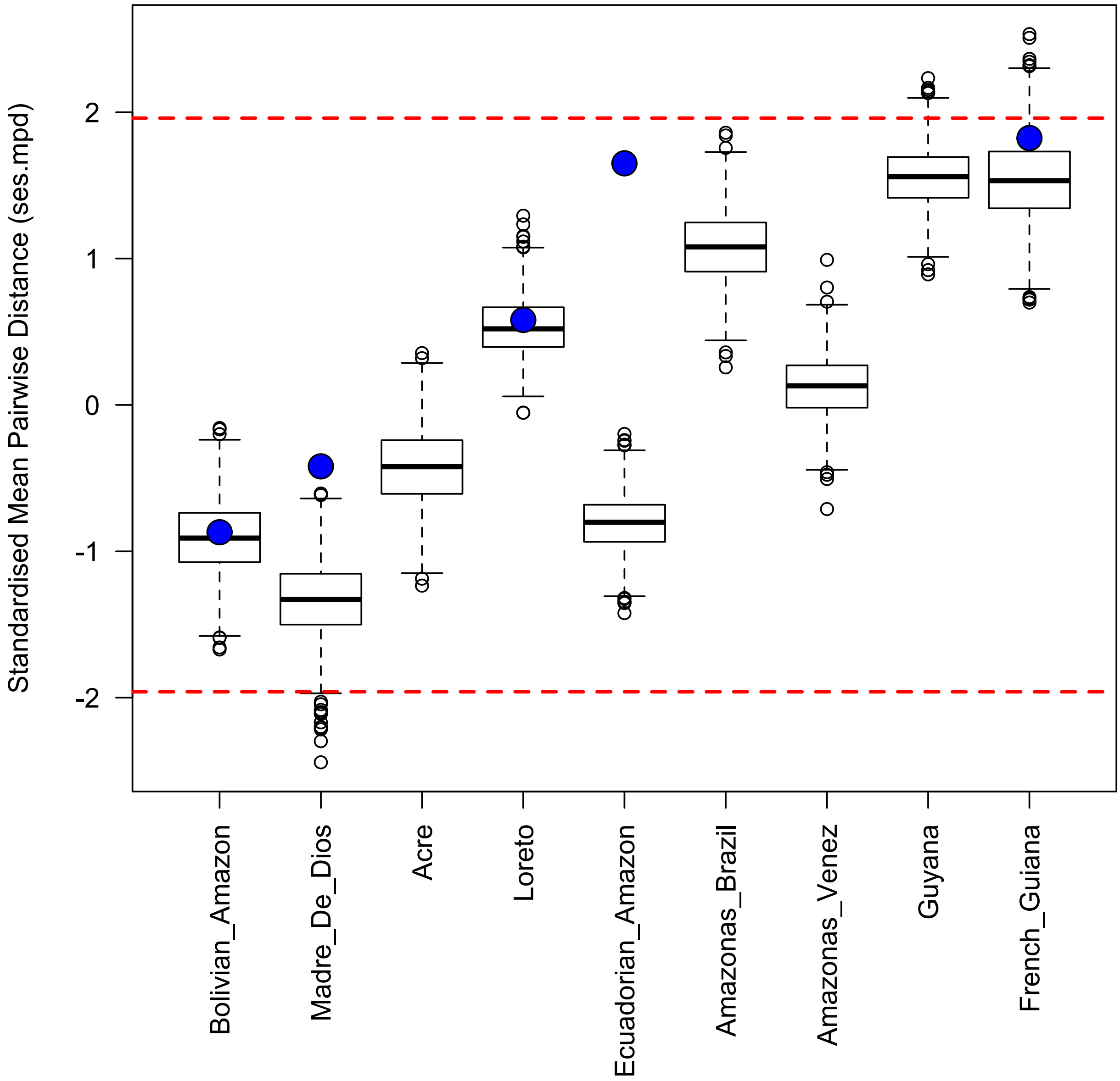

Figure S5: Distribution of ses.mpd values for different Amazonian regions across 1000 iterations of the sensitivity analyses. The values from the analyses presented in the main text are shown by the large blue circles. These are only available for Amazonian regions that are actually sampled in our phylogeny. Values less than -1.96 would indicate significant phylogenetic clustering, while values greater than 1.96 would indicate significant phylogenetic overdispersion. These threshold values are indicated by dashed red lines. Overall, these results demonstrate that most iterations of the sensitivity analyses do not result in significant phylogenetic clustering or overdispersion for Amazonian regions.

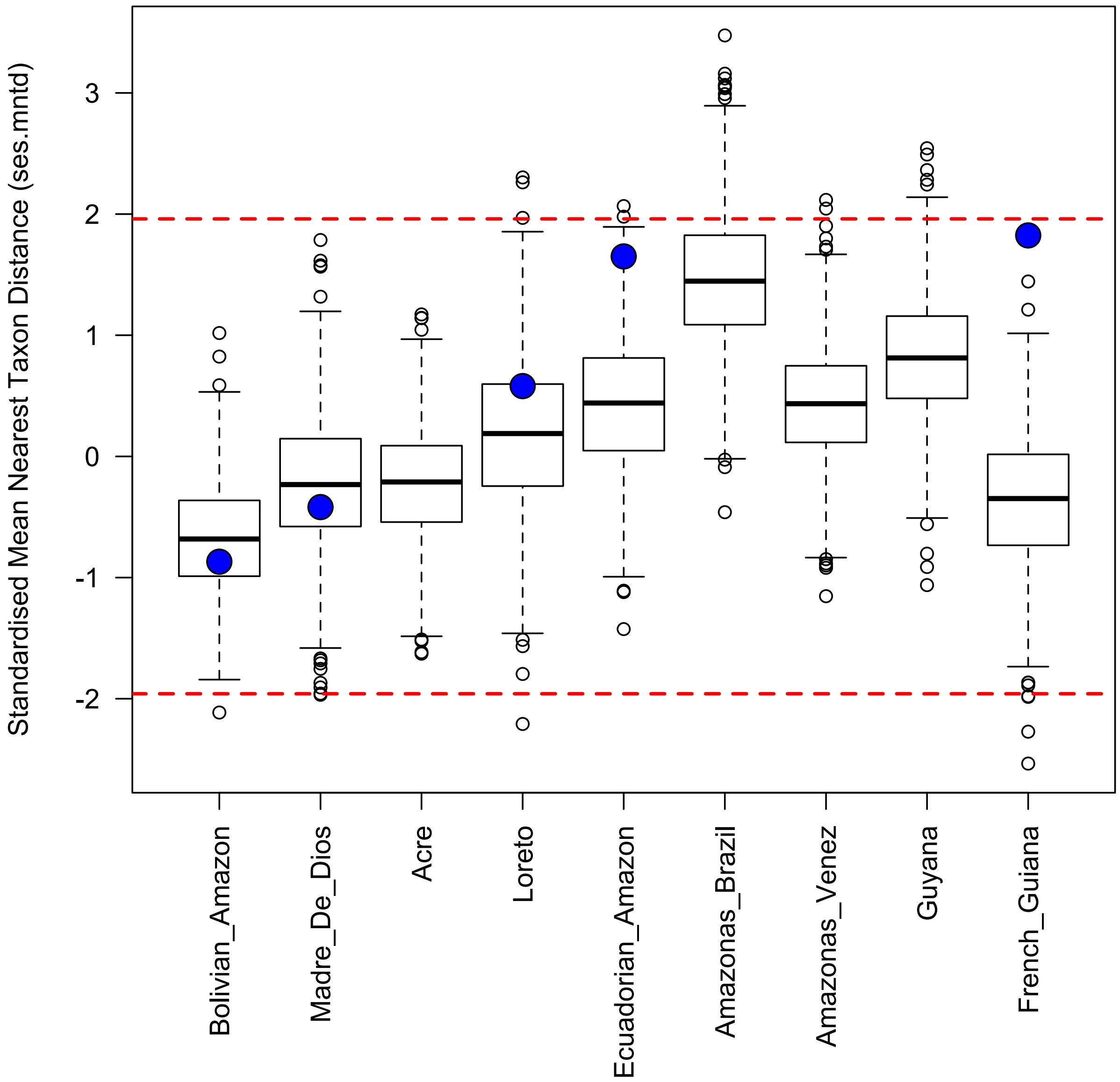

Figure S6: Distribution of ses.mntd values for different Amazonian regions across 1000 iterations of the sensitivity analyses. The values from the analyses presented in the main text are shown by the large blue circles. These are only available for Amazonian regions that are actually sampled in our phylogeny. Values less than -1.96 would indicate significant phylogenetic clustering, while values greater than 1.96 would indicate significant phylogenetic overdispersion. These threshold values are indicated by dashed red lines. Overall, these results demonstrate that most iterations of the sensitivity analyses do not result in significant phylogenetic clustering or overdispersion for Amazonian regions.