

Dispersal assembly of rain forest tree communities across the Amazon basin

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Edited by Charles C. Davis, Harvard University Herbaria, Cambridge, MA, and accepted by Editorial Board Member David Jablonski January 17, 2017 (received for review August 16, 2016)

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 *Gutteria*. Our analyses using phylogenetic diversity metrics demonstrate a clear lack of geographic phylogenetic structure, and show 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.

Amazonia | biogeography | community assembly | phylogenetic structure | tropical trees

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). Although some species are widespread across the Amazon basin (3), the majority are more restricted geographically (2), which provides the basis for schemes dividing the Amazon into floristic regions, including distinguishing the flora of the Guianan Shield 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 composed mostly of regionally restricted species raises 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 in which 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 the distributions of such components across continents and oceans (15, 16). The existence of long-distance, transoceanic dispersal at an intercontinental scale suggests that there should be little to hinder dispersal across the flat, continuously forested Amazon basin given its lack of present-day physical barriers. Although there is some debate about the role of potential historical

dispersal barriers in the Amazon, such as forest fragmentation during Pleistocene climate changes (17–19) and a large wetland complex (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 still needs to establish a population. Establishment can be challenging, given that any immigrant seed is numerically swamped by locally produced seeds (22), but nonetheless large-scale resident mortality in rain forests may be sufficiently common, owing to drought mortality or landscape rearrangements from radical movement of river courses, to allow for establishment of immigrant species (20, 23). Thus, we suggest that there has been ample opportunity for historical immigration to play a key role in the assembly of Amazonian tree communities, as has been proposed by Lavin (24) and Pennington and Dick (25), and we tested this hypothesis in the present work.

To do so, we used 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 in central Panama, to investigate patterns of historical community assembly (Fig. 1). The

Significance

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 to not have been limited on evolutionary timescales, but instead, local communities have been assembled by lineages from across the Amazon. These results contrast with those from seasonally dry tropical forests, where closely related species are clustered in geographic space. Furthermore, our results suggest a role for dispersal as an initiator for geographic isolation that might lead to speciation in Amazonian trees.

Author contributions: K.G.D., M.L., B.M.T., and R.T.P. designed research; K.G.D., A.D.T., T.A.K., P.D.C., C.D., R.H., and R.T.P. performed research; K.G.D. contributed new reagents/analytic tools; K.G.D. and R.T.P. analyzed data; and K.G.D., M.L., B.M.T., A.D.T., T.A.K., P.D.C., and R.T.P. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. C.C.D. is a Guest Editor invited by the Editorial Board.

Data deposition: The novel DNA sequences generated for this publication have been deposited in GenBank (accession nos. KY592383–KY593119). Dataset S1 details the sequences associated with each sequenced accession.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1613655114/-DCSupplemental.

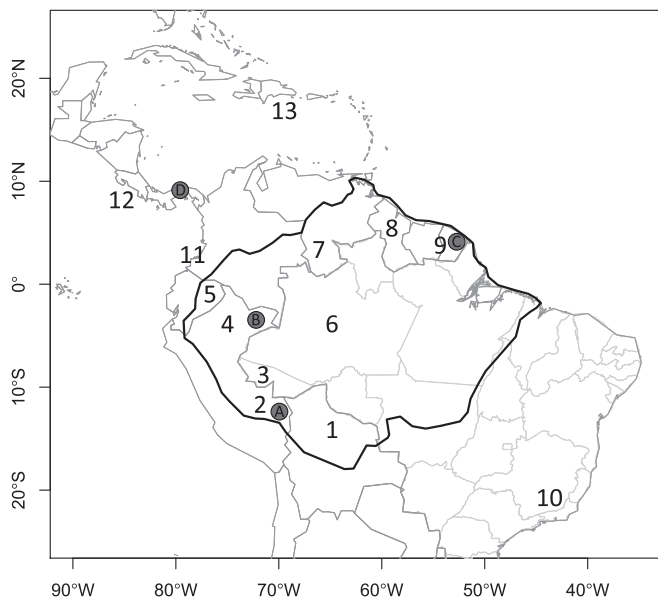


Fig. 1. Map of the 13 neotropical regions used in the analyses of phylogenetic geographic structure for the focal genera: 1, Amazonian Bolivia; 2, Madre de Dios, southern Peru; 3, Acre, Brazil; 4, Loreto, northern Peru; 5, Amazonian Ecuador; 6, Amazonas, Brazil; 7, Amazonas, Venezuela; 8, Guyana; 9, French Guiana; 10, Mata Atlántica (Atlantic rain forest); 11, Choco (trans-Andean) Colombia and Ecuador; 12, Central America, and 13, the Caribbean. Letters denote the 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.

neotropical tree genus *Inga* is species-rich (>300 species), is widely distributed, and has consistently high local abundance (2, 26) and species richness, with up to 43 species recorded in 25 Ha (27). Thus, it is an excellent exemplar for use in the study of community assembly in neotropical rain forests. Our phylogeny of *Inga* is notable 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 results for *Inga* 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 that we uncovered 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 (Dataset S1), resolves relationships among major clades and shows that *Inga* communities in Peru, French Guiana, and Panama are composed of phylogenetically scattered species (Fig. 2 and Fig. S1). These findings, which show a clear lack of geographic structure in the phylogeny of *Inga*, are mirrored by the other tree lineages with numerous Amazonian species that we analyzed. We evaluated geographic phylogenetic structure by calculating phylogenetic diversity metrics for local communities and regions and comparing the observed values with a null expectation generated by randomly sampling species from the phylogenies. We used three phylogenetic diversity

metrics (28, 29): (i) phylogenetic diversity sensu stricto (PD_{ss}), the total phylogenetic branch length present among species in a given community/region; (ii) mean pairwise distance (MPD), the mean of all pairwise phylogenetic distances among species in a given community/region; and (iii) mean nearest taxon distance (MNTD), the mean of the phylogenetic distance between each species and its closest relative in a given community/region. Communities showing significantly lower values than the null expectation indicate geographic phylogenetic structure or clustering, whereas significantly higher values than expected indicate phylogenetic overdispersion. None of the three local Amazonian communities showed phylogenetic clustering for any of the metrics evaluated (Dataset S2), whereas the Nouragues Research Station showed slight phylogenetic overdispersion. The *Inga* community on Barro Colorado Island, Panama, showed significant phylogenetic clustering, as evaluated by PD_{ss} and MPD.

For *Inga*, we obtained sufficient samples from five Amazonian regions to test more broadly for geographic phylogenetic structure. As with local Amazonian *Inga* communities, no Amazonian region showed significant phylogenetic clustering by any metric (i.e., no points in Fig. 3 or in Figs. S2 and S3 below the gray area encompassing the 95% confidence interval; see also Dataset S2), whereas French Guiana showed slight phylogenetic overdispersion according to the PD_{ss} metric (Fig. 3; i.e., above the gray area encompassing the 95% confidence interval) and Loreto showed overdispersion using the MPD metric (Fig. S2). Meanwhile, Central America was the only region showing significant phylogenetic clustering for all three metrics (Fig. 3 and Figs. S2 and S3; i.e., in every case below the gray area encompassing the 95% confidence interval).

This lack of geographic structure was duplicated in regional Amazonian communities of *Swartzia*, *Protieae*, and *Guatteria*, as measured by all metrics (Fig. 3, Figs. S2 and S3, and Dataset S2). All species in regional Amazonian communities represented 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 and Dataset S2). The only cases in which species in regional communities were consistently more closely related than would be expected by chance were in Central America [*Inga* (all metrics), *Swartzia* (all metrics), *Protieae* (PD_{ss})] and the Atlantic coastal rain forest of Brazil [*Guatteria* and *Swartzia* (all metrics)] (Fig. 3, Figs. S2 and S3, and Dataset S2). The level of sampling of different geographic regions varied widely (see the x-axes in Fig. 3 and Figs. S2 and S3), but well-sampled and poorly sampled Amazonian regions showed similar results. In general, neither departed 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 paleotropical species. First, the three Amazonian regions studied by Fine et al. (30)—eastern Amazonia, western Amazonia, and Guianas—are larger than those used here and thus not directly comparable. Furthermore, we analyzed 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 paleotropical species, which form two clades basal to the neotropical species of *Protieae*, would have the effect of inflating values of phylogenetic diversity in the random communities, which also may have contributed to the greater evidence of phylogenetic clustering reported by Fine et al. (30) in the regional communities that they studied.

Discussion

Primacy of Historical Dispersal in the Assembly of Local and Regional Communities. Our results demonstrate that tree communities at a local scale (for *Inga*) and a regional scale (for *Inga*, *Swartzia*, *Protieae*, and *Guatteria*) are assembled by dispersal across Amazonia.

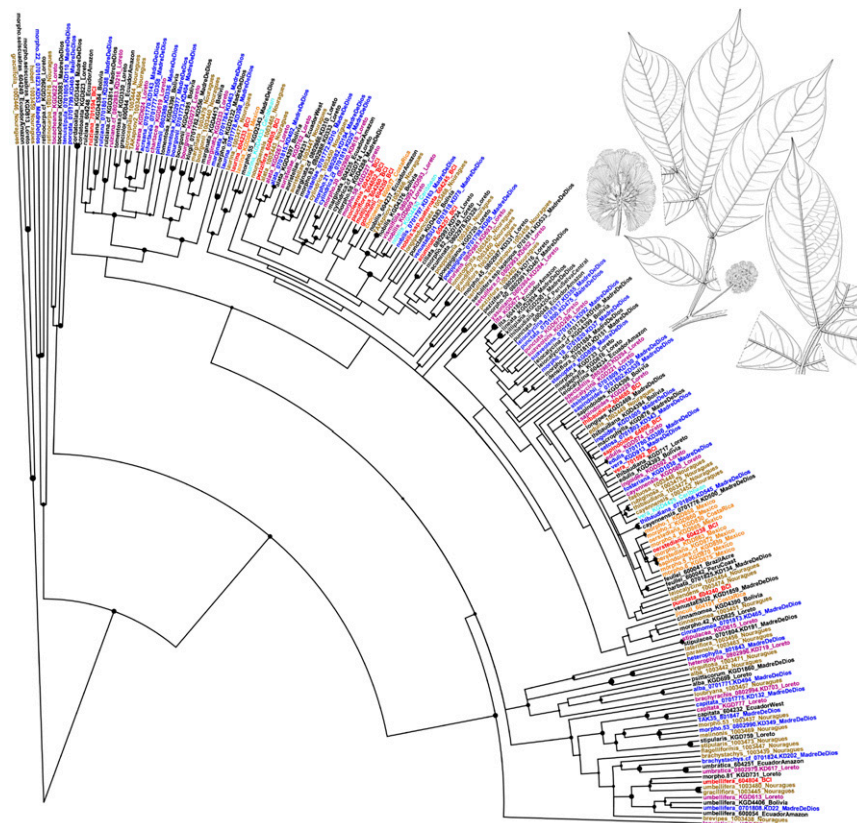


Fig. 2. Phylogeny of 210 accessions representing 124 *Inga* (Leguminosae) species, with a maximum of one individual per species per region. Accessions from focal communities are color-coded as follows: blue, Los Amigos Biological Station; purple, Madreselva Biological Station; brown, Nouragues Research Station; red, Barro Colorado Island. Additional accessions are color-coded by biogeographic region: black, Amazon; orange, Central America; cyan, Caribbean. The size of the circles at nodes is proportional to bootstrap support. Details of tip labels are shown in Fig. S1. The line drawing at the top right is of *I. pitmanii*, a regionally restricted species, endemic to Madre de Dios, Peru. Reproduced with permission from ref. 74.

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 seen despite the different fruit morphologies of these lineages, reflecting a variety of vertebrate dispersers. *Inga* is dispersed primarily by primates; Proteaceae'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 sole 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*, Proteaceae). The phylogenetic clustering found in these areas may reflect their isolation 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 the greater phylogeographic structure found there among populations of *Symphonia globulifera*, a widespread tree species (38).

The lack of geographic phylogenetic structure demonstrated here implies 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. Previous work by us and others has demonstrated that *Inga* species in Madre de Dios have clear habitat preferences, and that environmental filtering affects species composition of *Inga* communities (39–41). Furthermore, our

work has shown that *Inga* species that defend themselves against herbivores in distinct ways are more likely to co-occur, signifying filtering based on herbivore defense traits (42). Thus, ecological processes clearly can play a role in local community assembly. Nonetheless, 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 that we have studied in this work (Fig. S2). For example, the average phylogenetic distance between co-occurring *Inga* species is 3 My (divergence time of 1.5 My), whereas that among Proteaceae species is 36 My. This difference could have significant implications for the level of ecological interaction among co-occurring *Inga* and Proteaceae species; for example, competition might be considered more intense among *Inga* species because of their recent divergence (43), which in turn could 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 depend simply on the age of the genus, although the exact phylogenetic distance estimates will depend on how well the genus has been sampled phylogenetically. Furthermore, the high degree of sympatric co-occurrence observed for the species-rich genera studied here suggests that there might not be strong constraints on the number of co-occurring congeneric species, especially if they differ in terms of herbivore defense 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,

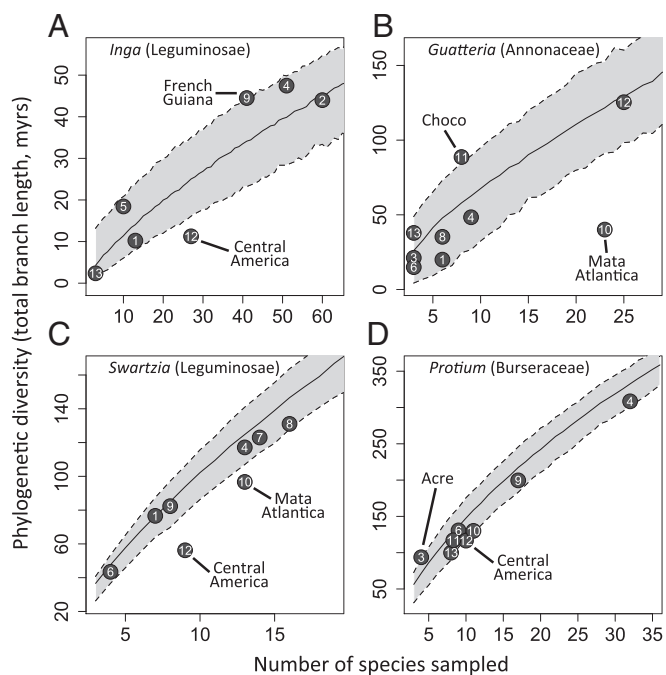


Fig. 3. Relationship between number of taxa sampled and phylogenetic diversity in neotropical regions for four emblematic Amazonian tree genera. Phylogenetic diversity was evaluated as the sum of branch lengths in an ultrametric, temporally calibrated phylogeny including the taxa from a given region. Regions are numbered as in Fig. 1. The solid black line represents the mean null expectation for phylogenetic diversity given the number of taxa sampled, for 1,000 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.

because dispersal into regions, which provide species for local communities, does not seem to be limited (46).

We emphasize that the generality of our results may apply only 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 millimeters (48). Our results also contrast with studies published for large terrestrial birds (49) and primates (50), which show more geographically structured phylogenetic patterns.

Contrasting Patterns of Community Assembly in 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 artifacts 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 seen in dry forest clades may reflect two factors (51). First, unlike the continuous Amazon rain forest, dry forest areas are scattered across the neotropics and are physically isolated by high mountains or areas of mesic vegetation, which may limit dispersal among them (51). Second, ecological

factors operating over evolutionary timescales are different in dry forests, which may affect the likelihood 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 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 suggesting common deep imprints of geological events in Amazonian tree phylogenies. For example, a geographic phylogenetic structure across the Miocene Pebas wetlands 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 of phylogenetic nesting of species within paraphyletic progenitor species seen in some Amazonian tree lineages (57). An alternative model would be more localized speciation followed by extensive dispersal, which also could result in the random phylogenetic composition of tree communities that we report here, as well as nesting of species within paraphyletic ancestors. Such local speciation could result from hybridization or adaptation to soil types (6, 8, 30, 58). The documented intersterility of sympatric *Inga* species (59) argues against a role for hybridization in speciation of that genus; however, our greatest challenge to understanding the mechanism of speciation is the possibility 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 further characterize the variations 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 composing 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 (Datasets S1 and S2). This represents many more accessions and more than double the species sampling in previously reported *Inga* phylogenies (sampled from 37–55 species) (39, 42, 60). 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 ~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 and Schaal (63), who sampled 76 species, including multiple exemplar species of each of the infrageneric groupings (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 paleotropical rain forests (2, 30). The majority of Protieae species are found in the Amazon basin and the Guianas, but smaller numbers of species occur in other areas, including Central America, the Caribbean, and the Brazilian Atlantic forest. Phylogenetic data for Protieae come from Fine et al. (30), who sampled 102 species covering 75% of accepted species names and all pantropical areas of distribution.

Gutteria (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, *Gutteria* 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 (*rpoCl*, *psbA-trnH*, *rps16*, *trnL-F*, *trnD-T*, *ndhF-rpl32*, and *rpl32-trnL*; 5,916 aligned bp) and the nuclear ribosomal internal transcribed spacer regions (*ITS 1* and *2*; 572 aligned bp) (Dataset S1). PCR and sequencing protocols for chloroplast regions have been reported by Kursar et al. (42), and those for *ITS* have been published 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 the low sequence divergence. The phylogeny was estimated under a maximum likelihood framework using RAXML with separate partitions and models for *ITS* and cpDNA and 1,000 bootstrap replicates to estimate node support (69). The phylogeny was subsequently time-calibrated using penalized likelihood (70), with the crown age constrained to 6 My, following previous work (24, 60). The phylogeny is available as Dataset S3.

The *Inga* phylogeny resolves numerous clades with reasonable bootstrap support (Fig. 2 and Fig. S1) and is the best-resolved *Inga* phylogeny to date, although within major clades the relationships among 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 on 194 nuclear loci, which shows high support for all branches. There are only two strongly supported incongruities between the two phylogenies, involving two species, *Inga laurina* and *Inga ruiziana*, and a formal statistical test (72) showed that the phylogenies are significantly congruent ($U_{\text{cong}} = 1.46$; $P = 0.0016$). Although Nicholls et al. (71) sampled only 22 *Inga* species, the topological congruence gives confidence that our less well-supported phylogeny accurately reflects phylogenetic relationships.

For *Swartzia*, aligned sequences from Torke and Schaal (63) were downloaded from TreeBase and a phylogeny was 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 penalized likelihood, with the crown age constrained to 13.6 My, following previous authors (73). For Protieae, the time-calibrated Bayesian phylogeny reported by Fine et al. (30) was downloaded from TreeBase. For *Gutteria*, 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 penalized likelihood, with the crown age constrained to 17.2 My 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 km² (Madreselva) to 15.6 km² (Barro Colorado Island).

We defined 13 geographic regions with sufficient sampling (five or more species in nearly all cases) that could be analyzed across the different phylogenies (Fig. 1) using our knowledge of *Inga* and *Swartzia* and information provided by Fine et al. (30) for Protieae and by Erkens et al. (66) for *Gutteria*. In Amazonia and the Guianas, these are geographic political units of similar size, such as states in Brazil, departments in Peru, and countries such as Guyana. Beyond Amazonia and the Guianas, the defined regions were the Mata Atlantica (Atlantic coastal rain forest) of Brazil, the Choco 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 whether results were robust to our approach of assigning accessions only to the regions in which they were collected, and this revealed no effect on our results (SI Materials and Methods and Figs. S4–S6).

If closely related species within a clade (in this case *Inga*, *Swartzia*, Protieae, or *Gutteria*) 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 would expect the phylogenetic diversity in communities and regions to 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 considered present when the observed phylogenetic diversity metric was less than the lower 2.5% quantile of the randomly generated distribution for that species richness, whereas significant overdispersion was indicated by a value exceeding the 97.5% quantile.

ACKNOWLEDGMENTS. We thank Terry Pennington for help with *Inga* species identification, and Paul Fine and Hans ter Steege for helpful comments and discussions. R.T.P. thanks the Leverhulme Trust for Study Abroad Fellowship RF/2/2006/0142, which supported DNA sequencing and the development of ideas in this paper in the M.L. laboratory. K.G.D., P.D.C., and T.A.K. thank the Peruvian Ministry of Agriculture for permission to conduct research in Peru, and the Nouragues Research Station for grants to fund fieldwork in French Guiana (2009 Call for Research at Nouragues). K.G.D. and R.T.P. acknowledge the Natural Environment Research Council for Support via NE/I028122/1. Field research by P.D.C. and T.A.K. was supported by National Science Foundation Grants DEB-0640630 and Dimensions 1125733. A.D.T. is supported by Natural Environment Research Council Fellowship NE/L011336/1.

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