

Historical effects on beta diversity and community assembly in Amazonian trees

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We present a unique perspective on the role of historical processes in community assembly by synthesizing analyses of species turnover among communities with environmental data and independent, population genetic-derived estimates of among-community dispersal. We sampled floodplain and terra firme communities of the diverse tree genus *Inga* (Fabaceae) across a 250-km transect in Amazonian Peru and found patterns of distance-decay in compositional similarity in both habitat types. However, conventional analyses of distance-decay masked a zone of increased species turnover present in the middle of the transect. We estimated past seed dispersal among the same communities by examining geographic plastid DNA variation for eight widespread *Inga* species and uncovered a population genetic break in the majority of species that is geographically coincident with the zone of increased species turnover. Analyses of these and 12 additional *Inga* species shared between two communities located on opposite sides of the zone showed that the populations experienced divergence 42,000–612,000 y ago. Our results suggest that the observed distance decay is the result not of environmental gradients or dispersal limitation coupled with ecological drift—as conventionally interpreted under neutral ecological theory—but rather of secondary contact between historically separated communities. Thus, even at this small spatial scale, historical processes seem to significantly impact species' distributions and community assembly. Other documented zones of increased species turnover found in the western Amazon basin or elsewhere may be related to similar historical processes.

historical biogeography | phylogeography | tropical trees

Studies of beta diversity, the turnover in species composition among communities, have provided major insights into the processes governing community assembly (1–3). Recent studies have principally focused on two explanations for beta diversity: species responding to environmental gradients (4, 5) and dispersal limitation coupled with demographic stochasticity within the context of neutral ecological theory (often termed ecological drift) (3, 6). Many authors have recognized the potential importance of historical and biogeographic processes in generating beta diversity (1–10), but to date no empirical study has detailed the historical biogeographies of individual species and their potential role in driving community-level patterns of beta diversity. Here we use population genetics to elucidate the historical biogeographies of the species that compose the communities in which we analyze beta diversity. This approach enables us to demonstrate that historical processes have limited the distribution of species and can directly influence present-day patterns of community assembly and species turnover among communities.

Our focal system is communities of the tropical tree genus *Inga* (Fabaceae) (11) in the lowland Amazon region of Madre de Dios, Peru. Tropical tree communities have become a model system for exploring patterns of beta diversity (3–5, 10, 12). In a landmark study, Condit et al. (3) used neutral ecological theory to analyze distance-decay in neotropical tree communities, the decline in compositional similarity of communities with geographic distance (2). They interpreted the observed distance-

decay in terms of a balance between ecological drift and spatially limited dispersal. Other studies of tropical tree communities have emphasized environmental differences when examining species turnover among habitat types (4, 5). Nevertheless, when distance-decay has been found within habitat types, many investigators have attributed it to neutral ecological processes (4, 5, 13). None of these studies assessed the potential role of historical processes in driving distance-decay (although see ref. 14).

The relative importance of neutral ecological processes and historical biogeographic processes in generating distance-decay may depend on spatial scale. At small spatial scales within range boundaries, spatial autocorrelation in the presence/absence of species driven by neutral processes may be responsible for distance-decay. At large spatial scales, species' range boundaries may be more significant. Here we focus on patterns within Madre de Dios, Peru, which for Amazonian trees is of a smaller spatial scale than the scale at which historical biogeographic processes have been considered significant.

Population genetic data can provide a means of inferring the dispersal and historical biogeography of species. For example, Dick and colleagues (14–16) found low genetic differentiation among populations of two tree species in the Amazon basin, which they interpreted to signify low dispersal limitation in the Amazon for the two species. If such population genetic studies were extended across more species and explicitly combined with analyses of species composition and turnover between communities, this could provide a powerful means of assessing the role of historical processes in shaping tropical tree communities.

In this study, we simultaneously examined spatial turnover in species composition among Amazonian tree communities, pertinent environmental data, and genetically estimated rates of seed dispersal among communities. We surveyed *Inga* communities at 13 sites arrayed along a roughly linear 250-km transect. We sampled communities in upland terra firme and bottomland floodplain separately at each site, because 76% of *Inga* species in Madre de Dios are specialists of either habitat (17). (Note: In the upper Amazon, floodplain forest is inundated only several days per year or less.) Previous work based on extensive morphological analyses and phylogenetic analysis of nuclear and plastid markers has confirmed the species identity of all sampled individuals, which is important to studies of community similarity given the difficulty of identifying tropical trees in the field (17). For 20 *Inga* species representing both terra firme and floodplain environments, we estimated plastid and nuclear gene flow between the two most thoroughly sampled communities on the

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Data deposition: Genbank accession numbers for sequences used in this paper are available in ref. 17 and Table S3.

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transect, which lie 140 km apart. For further population sampling, we selected eight *Inga* species that were abundant along the transect and that demonstrated plastid genetic variation in our initial survey. Finally, we sampled these species in northern Peru and central Bolivia, >600 km from our transect, to place our local phylogeographic results within a broader geographic framework.

Remarkably, both terra firme and floodplain *Inga* communities showed significant distance-decay despite the small spatial scale and the fact that many of the *Inga* species in these communities have ranges extending far beyond our transect (11). Furthermore, the pattern of distance decay was the same in each habitat. Using a sliding-window approach, we found that the apparently smooth distance-decay masks a zone of increased species turnover in the middle of our transect. This zone corresponds to the region of a phylogeographic break that is geographically coincident across many *Inga* species. Our results suggest that historical processes can exert a profound influence on the modern distribution of tree species, species turnover, and community assembly in the lowland Amazon basin, even at the small scale of a 250-km transect.

Results

Community Similarity Analyses. When considering all communities lying along the transect together, we found a weak, although significant, relationship between geographic distance and compositional similarity (Mantel $r = -0.30$, $P = 0.003$, $y = 0.52e^{-0.0016x}$) (Fig. S1). Floodplain and terra firme habitats have strongly contrasting soils (Fig. S2), which affects *Inga* species distribution (17), and stronger patterns of distance-decay may be evident within habitat types (4, 5). Indeed, we found greater distance-decay when restricting our analyses to terra firme or floodplain communities (terra firme: Mantel $r = -0.60$, $P = 0.007$, $y = 0.70e^{-0.0020x}$; floodplain: Mantel $r = -0.55$, $P = 0.001$; $y = 0.68e^{-0.0019x}$) (Fig. 1). The intercepts of the distance-decay relationships were notably <1, as would be expected at a distance of 0 km. This is likely due to sampling effects; that is, our community surveys likely failed to capture all rare species present in a given community.

Remarkably, even though floodplain and terra firme share few species, both habitats showed nearly the same slope and intercept for the distance-decay relationship. The smooth distance-decay observed would seem to indicate regular species turnover across space, but this apparent regularity disappeared when we applied a geographically explicit approach (Fig. 2B). We used a spatially sliding window, which revealed significant variation in

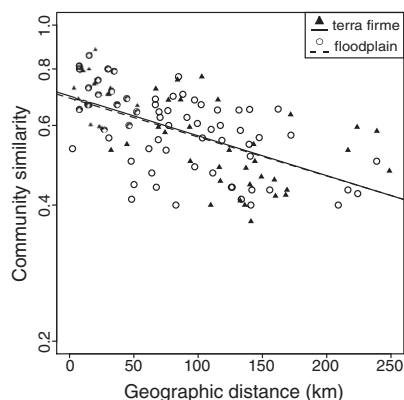


Fig. 1. Distance-decay in the compositional similarity (measured as log of Sorensen index) of *Inga* communities in Madre de Dios for terra firme and floodplain. Best-fit exponential relationships are shown (linear on the log-linear plot). The Mantel test was used to test the strength and significance of correlations (Results).

turnover along the transect. Furthermore, turnover was strikingly correlated between floodplain and terra firme ($r = 0.44$, $P < 0.001$) (Fig. 2B). In both habitats, there was notably high turnover (i.e., low compositional similarity) between the geographically proximate communities of MC and LA, as well as an extended zone of high turnover between the Manu and Los Amigos basins (Fig. 2B).

Estimates of Gene Flow Between Communities. Using a sliding-window approach as above, we found that plastid gene flow between communities, averaged across eight *Inga* species, varied substantially along the transect (Fig. 2B) and was significantly correlated with species turnover in both habitats (terra firme: $r = 0.36$, $P = 0.002$; floodplain: $r = 0.26$, $P = 0.004$).

We selected 12 additional species for population genetic sampling at two sites, Cocha Cashu (CC) and Los Amigos (LA; one site within the Los Amigos basin), which are found on either side of the zone of increased species turnover. For the plastid genetic marker, 7 of the 20 total sampled species showed no genetic variation between CC and LA, 9 showed significant genetic differentiation (including all 8 species sampled along the entire transect), and an additional 3 showed high (although statistically nonsignificant, likely due to low sample size) differentiation (Table S1). For a nuclear marker, the internal transcribed spacer (ITS), two species showed no genetic variation, whereas 11 showed significant genetic differentiation between CC and LA (Table S1). Genetic differentiation values (as measured by the fixation index F_{st}) were, on average, much higher for the plastid marker (mean F_{st} , 0.45 ± 0.10) than for the nuclear marker (mean F_{st} , 0.16 ± 0.04).

We also performed coalescent analyses of isolation with migration (18) to assess whether migration, or dispersal, occurred since the divergence between CC and LA populations, considering the two markers separately. When sample size was low (fewer than eight individuals per population) or when a species lacked genetic variation for a given marker, convergence could not be obtained for parameter estimates, presumably due to insufficient information in the data. Of the nine species for which convergence was obtained for the plastid marker, four showed significant migration since divergence between CC and LA (Table S1). Of the 14 species for which convergence was obtained for the nuclear marker, 13 showed significant migration since divergence (Table S1).

We used a community-level approach (19) to estimate the divergence time between CC and LA populations. The mean divergence time across all 20 species was at least 42 kya [lower 95% confidence interval using the upper substitution rate estimated for noncoding plastid DNA (20)] and perhaps as long as 433 kya [upper 95% confidence interval using a rate estimated for the genus *Inga* (21)]. The initial analysis of all species did not provide unambiguous support for one divergence event, although this was the most probable scenario. When we excluded species exhibiting no plastid genetic variation ($n = 7$), we found strong support for a single divergence event across the remaining species ($n = 13$). This divergence was estimated to have occurred at least 68 kya and perhaps as long as 612 kya (Table S2).

Analyses of Individual Species' Distributions. We found that soil conditions exert a strong influence on the distribution of *Inga* species and their relative abundance in communities. For example, *I. bourgonii* appears to be a floodplain specialist (Fig. 3A); its abundance was positively correlated with soil fertility, and it was most abundant on the most fertile floodplain soils. It was often absent from terra firme community surveys, which could be due either to genuine absence or to very low abundance that resulted in nondetection. In contrast, *I. auristellae* was most abundant on infertile soils and was nearly always absent from

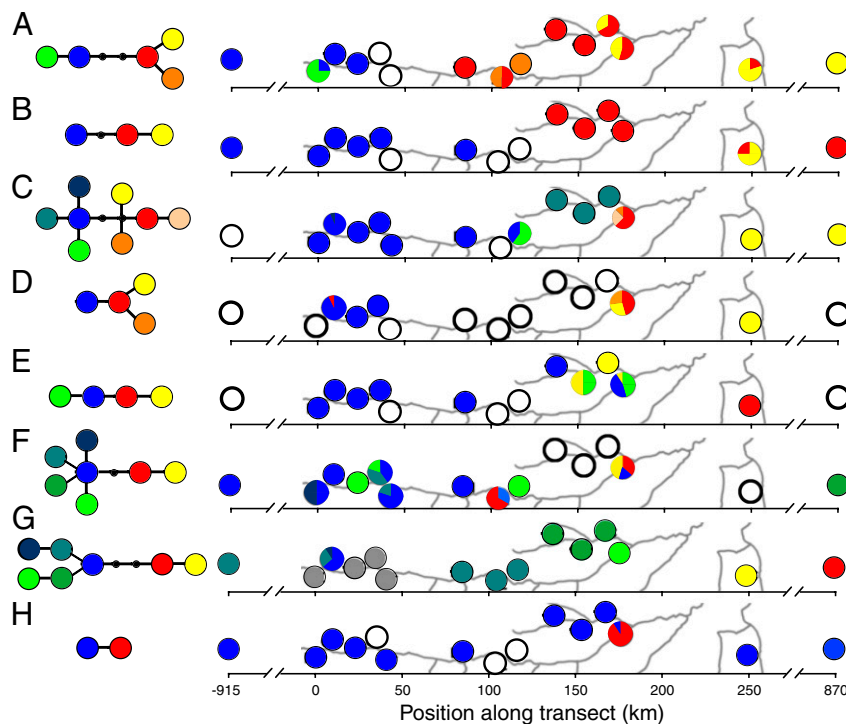


Fig. 4. Plastid haplotype networks and distribution of those haplotypes along the transect for *I. bourgonii* (A), *I. alata* (B), *I. ruiziana* (C), *I. alba* (D), *I. umbellifera* (E), *I. marginata* (F), *I. sapindoides* (G), and *I. edulis* (H). In the networks, each circle represents a unique haplotype, and each line represents a single mutation (insertion-deletion or substitution). Black circles represent unsampled haplotypes. Haplotypes are not shared between species and are color-coded separately for each species. On the maps, a hollow circle indicates that the species was not found at a given site, and a gray circle indicates the species was present at that site, but DNA sequences were not obtained.

two-dimensional terra firme habitats. At first glance, this decline in compositional similarity resembles the equilibrium between dispersal and ecological drift described by previous investigators who discovered similar patterns of distance decay (2, 4–6, 13).

Closer inspection of the compositional data—and inclusion of population genetic data—reveals a very different story, however, one of secondary contact between historically isolated floras that experienced vicariance 42–612 kya. Our geographically explicit sliding-window analysis of compositional similarity revealed not uniform turnover, but rather sharp and simultaneous dips in compositional similarity in both floodplain and terra firme habitats, particularly within a zone of increased turnover between the Manu and Los Amigos basins (Fig. 2). This pattern is driven by the absence of individual species within or on either side of the zone of increased species turnover (Figs. 3 and 4). These enigmatic absences cannot be explained by soil conditions, but are entirely consistent with a hypothesis of secondary contact between floras. Moreover, the population genetic data show a sharp genetic discontinuity in plastid genes for eight species across the zone of increased species turnover, with relative homogeneity over larger distances toward northern Peru and central Bolivia (Figs. 2 and 4). The observed geographic correspondence of genetic divergences provides strong support for a zone of secondary contact between isolated floras.

Mechanisms Underlying Distance-Decay. Distance-decay in the compositional similarity of communities may be related to underlying spatial environmental gradients to which species respond. Although habitat type (i.e., environment) clearly acts as a filter on *Inga* species distributions in Madre de Dios (17), environmental conditions do not appear to be responsible for the observed distance-decay within habitat types, because soil variation shows little evidence of spatial gradients (Fig. S2). In addition, the close

correspondence of the distance-decay relationships in floodplain and terra firme habitats, which are unlikely to have identically spatially structured environmental variation, suggests that some other process may be responsible.

An alternative explanation for distance-decay is ecological drift coupled with dispersal limitation (*sensu* neutral ecological theory). Indeed, several authors have suggested that although habitat may determine where species are found, neutral processes predominate in structuring communities within single habitat types (4, 5, 13). However, this argument depends on ecological drift being the principal determinant of the relative abundances of species in communities, and our examination of the relative abundances of *Inga* species in Madre de Dios argues against this. Most species are either floodplain or terra firme specialists (17), achieving high abundance in their preferred habitat type and being relegated to low abundance or absence in their nonpreferred habitat type. For example, *I. bourgonii* (Fig. 3A), *I. marginata*, and *I. nobilis* (Fig. S3) are floodplain specialists in Madre de Dios (17), and their low abundance when present in terra firme suggests that terra firme soils are unsuitable, not that the species have consistently drifted to low abundance in that habitat. Likewise, even within habitat types, the relative abundances of species appear to be related to soil fertility (Fig. 3 and Fig. S2), although our sample size was insufficient to allow us to adequately test this. In general, it seems illogical to conclude that environmental conditions can determine where species are found, yet have no effect on relative abundances within a single habitat type.

We suggest that rather than environment or equilibrium-neutral processes, historical processes of population subdivision and colonization are driving distance-decay patterns in both habitats. Compositional similarity between communities and its inverse, species turnover, closely track the level of plastid gene flow (Fig. 2),

suggesting that historical seed dispersal patterns impact species composition.

Further evidence for the processes of subdivision and colonization can be found when we consider the distributions of individual species. The two sites where *I. bourgonii* was enigmatically absent (SV and OT) fall precisely between the two geographically segregated, divergent plastid clades found in the species (Fig. 4A). *I. auristellae* is found across the Amazon basin, including in the eastern part of our transect, where it is the most abundant *Inga* species in terra firme (composing 30% of *Inga* stems in diverse communities of 25–30 *Inga* species), yet it was not found in the western part of the transect, where terra firme soils appear to be perfectly suitable. It seems likely that *I. bourgonii* and *I. auristellae* would do just fine in the sites where they are absent, but that historical population subdivision and subsequent, incomplete colonization have resulted in their patchy distributions. The distribution patterns of other *Inga* species reflect those of *I. bourgonii* and *I. auristellae*, suggesting that historical processes underlie the patterns of distance-decay that we have observed for *Inga* communities.

Interpretation of Population Genetic Results. Introgression can be problematic for phylogeographic analyses (22), and several of the species in this study share alleles with other *Inga* species (17). However, *Inga* species are not known to hybridize (11, 23). Rather, shared alleles among *Inga* species are likely related to incomplete lineage sorting, which should not affect phylogeographic analyses and is expected given *Inga*'s rapid rate of speciation (21).

We found strongly contrasting results for plastid and nuclear markers. Seven of 20 species showed no genetic variation across the two populations (CC and LA) for the plastid marker, and only 2 species lacked variation for the nuclear marker. This could indicate that species without plastid variability experienced recent migration of the plastid marker between the two populations (i.e., recent seed dispersal). Alternatively, these populations might have been isolated for a substantial period of time with no plastid substitutions. Plastid intergenic spacers, such as the trnD-T spacer used here, appear to have a slower rate of substitution than the nuclear ITS marker in *Inga* (21). Indeed, the finding of significant genetic differentiation for ITS in five of seven species with no plastid genetic variation (Table S1) suggests that these species might have experienced historical subdivision, as have the species showing plastid genetic divergence.

Fst values are difficult to interpret, being affected by both time since isolation and the level of migration between populations; thus, we also performed coalescent analyses that simultaneously examined isolation and migration. The majority of species that could be analyzed for the plastid marker showed no significant plastid migration since isolation between CC and LA, whereas all but one species showed significant migration for the nuclear marker. Given that plastid markers generally disperse only in seeds and nuclear markers disperse in seeds and pollen (24), this implies that seed dispersal between CC and LA has been limited, whereas pollen dispersal has been prevalent.

Our assessment of plastid gene flow between additional *Inga* populations shows that seed dispersal has been far from constant through time and space across our study region (Figs. 2 and 4). There are no evident extant barriers to seed dispersal in Madre de Dios except perhaps rivers, but the observed phylogeographic breaks are not associated with rivers (Fig. 4). Thus, extant spatial variation in seed dispersal does not seem to underlie the phylogeographic patterns. Instead, our results imply that some unknown historical barrier or process restricted seed dispersal among populations. Indeed, our finding of an abrupt genetic break between large, genetically homogeneous areas (shared alleles between either end of the transect and distant locations in northern Peru and Bolivia; Fig. 4) suggests that *Inga* species are

colonizing this landscape from two or more source communities that were historically subdivided.

Our finding of highly limited seed dispersal across short spatial scales (10–250 km) is in contrast to the results of several recent studies suggesting that Amazonian trees have extensive dispersal ability (14–16, 25, 26). Those results are not necessarily in conflict with ours, however. Many of the *Inga* species in the present study have widespread distributions, extending across the Amazon basin and even as far north as Mexico. Likewise, we find common alleles at distances of 900 km. Clearly, *Inga* species can disperse far and wide; however, in at least one corner of the Amazon basin, historical events seem to have greatly impacted the distribution of *Inga* species and their haplotypes.

Potential Historical Scenarios. The concordance of phylogeographic patterns of *Inga* species in Madre de Dios indicates that some climatic or geological process affected them in similar ways. The common divergence event that most species experienced seems to have occurred 42–612 kya, a time period extending from the middle to late Pleistocene. Thus, Pleistocene climate cycles, perhaps even the most recent glacial cycle, may be responsible for the observed divergence event. Rainforest was absent in areas of northern Bolivia during the last glacial maximum and has been expanding through the Holocene (27); a similar history may be underway in Madre de Dios.

An alternative explanation for the observed divergence is the Fitzcarrald Arch (28), which underlies the western half of our transect and began uplifting less than 4 mya. Other geologic arches in the Amazon are associated with zones of increased species turnover and/or phylogeographic breaks (29–32), although the mechanism by which geologic arches may generate these patterns is not clear (33). Although we are uncertain of the exact historical scenario underlying the observed phylogeographic and distribution patterns, it does seem clear that historical processes have impacted species turnover and community composition of *Inga* in southern Peru. Other biogeographic transition zones in the Amazon (29–32) or elsewhere may be due to similar processes.

Conclusions

Our comprehensive analysis of spatial variation in the species composition of communities in combination with a thorough, population genetic-based assessment of among-community dispersal provides insight into the processes structuring present-day ecological communities. Our results indicate that historical processes can exert a profound influence on species turnover and community assembly, even at the spatial scale of 250 km. This finding has significant implications for interpreting studies of Amazonian biodiversity and for determining the types of investigations needed to understand and preserve this biodiversity. Distance-decay in the compositional similarity of communities does not necessarily support neutral ecological theory, and the apparent determinism of relative abundances by the environment argues against it (34, 35). Future studies should use sliding-window approaches, as used in the present study and in the study of Pitman et al. (31), to determine whether species turnover is in fact uniform across seemingly homogeneous landscapes. Then, if biogeographic transition zones are documented, population genetic and environmental studies are needed to determine the underlying causes. Regarding conservation, if our aim is to preserve the maximal possible number of species, then protecting large areas and multiple habitat types might not be enough; we may also need to identify cryptic biogeographic transition zones to design protected areas that cover a multiplicity of communities with unique species compositions.

Materials and Methods

We performed *Inga* community surveys in both floodplain and terra firme habitats at all sites along the transect, except for OT, BL, and CA, where

surveys in terra firme are lacking, and MZ, where a comprehensive survey in floodplain is lacking. Soil samples were collected at all survey sites and analyzed for 21 soil variables generally considered relevant to plant survival and growth (e.g., nutrient concentrations, soil texture). We conducted a standard principal component analysis on all soil variables across all sites (Fig. S2). Details of community surveys and soil analyses have been reported previously (17). We evaluated the compositional similarity of communities using the Sorensen index, and assessed the correlation of the natural logarithm of the Sorensen index with geographic distance using Mantel tests. We used a sliding-window approach to assess the variation of compositional similarity along the transect, controlling for the effect of geographic distance between communities (*SI Materials and Methods*). We used the first principal component from the soil data analysis as an index of soil fertility, and examined how the relative abundance of individual species varied with this index.

For eight *Inga* species, we obtained sequences of the plastid trnD-T intergenic spacer from 2–20 individuals (mean, 5.5) per population from each community along the transect in which the species were present. These 8 species were selected from the 20 species sampled at CC and LA (see below) because they demonstrated genetic variation and were found in high abundance along the length of the transect. Details on laboratory and sequence editing protocols and voucher and GenBank accession numbers for Madre de Dios samples are available elsewhere (17); corresponding information for northern Peru and Bolivia specimens is provided in Table S3. We calculated intraspecific *Fst* between populations and consider 1 – *Fst* to be representative of gene flow. We then used a sliding-window approach,

analogous to that described above, to assess the variation in average plastid gene flow along the transect (*SI Materials and Methods*).

For 20 *Inga* species, we obtained plastid trnD-T and nuclear ITS sequences from 2–20 (mean, 7.6) individuals per population from CC and LA. ITS sequences often had multiple ambiguous sites, so we used PHASE v2.1.1 (36) to reconstruct ITS haplotypes for individuals. We excluded individuals for which we could not reconstruct haplotypes with high confidence (>0.8 probability) from the ITS population genetic analyses. We calculated *Fst* between the two populations for the trnD-T and ITS markers. We explicitly estimated migration after divergence between the two populations using a coalescent approach with the IMA program (18). Details of priors and preliminary runs are provided in *SI Materials and Methods*. We estimated divergence time, in number of substitutions, between CC and LA using the msBayes program, which takes a community-level approach, integrating data from multiple species (19). Details of priors and preliminary runs are available in *SI Materials and Methods*.

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Supporting Information

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SI Materials and Methods

Sliding Window Approach. To control for the effect of geographic distance on compositional similarity in analyzing how species turnover varies along the transect, we first obtained the residuals from the relationship between geographic distance and the Sørensen index. We assigned these residual values to a location on the transect at the midpoint between the two populations from which the estimate derives. We averaged all similarity estimates that fell between 0 and 26 km on the transect, and then shifted this 26-km window eastward along the transect in 1-km steps. We chose a 26-km window because this was the smallest window size that allowed us to obtain a similarity estimate at every step along the transect.

To account for the effect of geographic distance on gene flow when assessing how gene flow varied along the transect, we first obtained the residuals from the linear relationship between geographic distance and $1 - F_{st}$ separately for each species. We assigned these residual values to a location on the transect at the midpoint between the two populations from which the estimate derives. We averaged all gene flow estimates (across the eight species) that fell between 0 and 26 km on the transect and then shifted this 26-km window eastward along the transect in 1-km steps. We chose a 26-km interval to allow comparisons with the data on turnover in compositional similarity.

We compared changes in average gene flow with changes in compositional similarity by first obtaining the difference between each gene flow or composition similarity measurement and the preceding one on the transect. We then calculated the correlation between changes in gene flow and changes in compositional similarity. We used a permutation approach, controlling for the spatial autocorrelation in sampling locations, to determine whether the correlation was greater than expected at random. We performed permutations by shuffling species among communities while constraining the diversity of communities and the percentage of communities occupied by each species to that observed in the real data. The haplotype composition of species populations were maintained as the locations of the populations were randomized.

Estimating Migration between the Cocha Cashu and Los Amigos Sites.

The IMA program assumes no recombination among the sequences analyzed. We checked for recombination using the four-gamete test (1) and linkage disequilibrium tests (2). The trnD-T locus showed no evidence of recombination for any species, as might be expected given that it is in the plastid genome. For the internal transcribed spacer (ITS) marker, some species failed the four-gamete test, but these same species showed no evidence of significant recombination in linkage disequilibrium tests. This indicates either that there are multiple substitutions at some sites (thus violating assumptions of the four-gamete test and not actually demonstrating recombination) or that there is too little information in the data (too few segregating sites) to allow detection of recombination via linkage disequilibrium-based methods. For species with ITS sequences that failed the four-gamete test, we used two approaches to conduct IMA analyses: (i) implementing the HKY model of sequence evolution (allowing for multiple substitutions per site) and (ii) implementing the infinite sites model while treating recombination blocks as separate loci. Potential recombination blocks were identified using the SITES program (3). Preliminary analyses indicated that both approaches gave equivalent results, and here we report only the results from using the first approach (the HKY model). For ITS analyses that showed no evidence of

recombination and for all trnD-T analyses, we used the infinite-sites model of sequence evolution.

For all IMA analyses, we set the upper limit for the uniform prior on divergence time (t) to a value corresponding to 10 million y. This has been estimated as the maximum age of the genus *Inga* (4,5) and provides a conservative upper bound. For analysis of the trnD-T plastid marker, this corresponded to an average value of 15.96 for the parameter t , given a mutation rate of 1.3×10^{-9} substitutions per site per year (s/s/y) for plastid intergenic spacers in *Inga* (4) and an average sequence length of 1,225 bp. For analyses of the ITS marker, this corresponded to an average value of 15.32 for t , given a mutation rate of 2.34×10^{-9} s/s/y for ITS in *Inga* (4) and an average sequence length of 655 bp. We adjusted the upper limits for uniform priors on θ parameters (q_1 , q_2 , and q_4) based on results from preliminary runs of IMA. We generally left the upper bound on θ parameters at the default value of 10, although in some cases we adjusted it upward to as high as 100.

Based on preliminary runs in IMA, we set the prior upper limit for the m_1 and m_2 parameters at 1,000. Nearly all estimates of m_1 and m_2 reached zero probability well before this value. For the trnD-T marker, this upper limit is equivalent to a per generation migration rate of 0.048 (i.e., 4.8% of new individuals in a generation carry an immigrant genotype) assuming a generation time of 30 y. *Inga* species can reproduce in as little as 3 y in ideal conditions (6), but the generation time is likely much longer in closed-canopy situations. Nevertheless, *Inga* species tend to grow rapidly compared with other tropical tree species, and we believe that an estimated generation time of 30 y is conservative (lower values would result in a lower calculated per generation migration rate). For ITS, an m_1 or m_2 value of 1,000 corresponds to a per generation migration rate of 0.045.

We ran each analysis for a sufficient number of generations to ensure that effective sample size values were >50 for all parameters sampled over the course of the run (e.g., t , mutation rate scalars). For most analyses, a run of 100 million generations was sufficient to pass this effective sample size threshold. For all analyses, we used a burn-in of 10% of the total generation time. We also examined trend lines to ensure that the program was sufficiently mixing across parameter values over the course of the run. For some ITS analyses, sufficient mixing did not occur with a single chain, and we used multiple chains with a geometric heating scheme. Sufficient mixing was obtained once the heating schemes were properly calibrated to ensure adequate swapping among chains. To evaluate the stability of convergence, we ran each analysis at least twice once the final values for priors on parameters, number of generations, and heating schemes (if necessary) were established.

For each analysis, we selected genealogies from one of the final runs to obtain joint posterior estimates for migration between communities (m_1 and m_2). We also conducted nested likelihood ratio tests to assess whether models with migration in both directions were significantly better than models with migration in one direction or with zero migration. Both of these steps were implemented in the L mode of the IMA program. Table S1 reports the joint posterior estimates of migration into each community, showing which migration estimates were significantly different from zero.

Estimating Divergence Time Between the Cocha Cashu and Los Amigos Sites. We used msBayes version 20081106 (7) to estimate the divergence time, τ , at the trnD-T plastid marker among populations of all 20 sequenced species shared across the Manu and

Los Amigos basins. In conducting msBayes analyses, we set the following limits on the uniform priors: lower $\theta = 0.001$, upper $\theta = 1$ (based on the upper π_w among observed summary statistics), upper ancestral θ multiplier = 1 (meaning that ancestral population θ is expected to be $1 \times$ descendent population θ), upper migration rate = 0.01 (most of the posterior probability distribution of m for most species from IMA analyses fell below 0.01), upper recombination rate = 0 (the plastid marker showed no evidence for recombination), and upper $\tau = 10$ (most probable posterior τ values were always much lower than this). We used a default value of 500,000 simulations. We used the default summary statistics (π , $wattTheta$, $\pi_i.net$, and $tajD.denom$) and 0.002 of the simulation runs in postprocessing of the simulated data to obtain posterior distributions of parameters.

In this initial analysis, the mode for Ψ , the number of possible divergence times, was at the lower boundary of the prior (one di-

vergence event), but the 95% confidence intervals (CIs) extended from 1 to 3.2. The mode of the posterior for Ω , a parameter representing the variance in τ divided by the posterior mean of τ , was 0.03, and the 95% CIs extended from 0 to 1.58. Taken together, these results indicate that although the most likely value is one divergence event, there is substantial probability of more than one divergence event. We reran analyses excluding the 7 of 20 species that showed no nucleotide polymorphism. With just the 13 genetically variable species, we found strong support for one divergence event (95% CI for Ψ , 1–1.25; 95% CI for Ω , 0–0.02). To calculate divergence time in years, we used two estimates for the rate of substitution of non-coding plastid DNA: the rate calculated specifically for the genus *Inga* (1.30×10^9 s/s/y) (4) and the maximum observed rate across angiosperms (3.00×10^9 s/s/y) (8). The mode estimates as well as upper and lower credible intervals for the analysis of all 20 species and the 13 variable species are given in Table S2.

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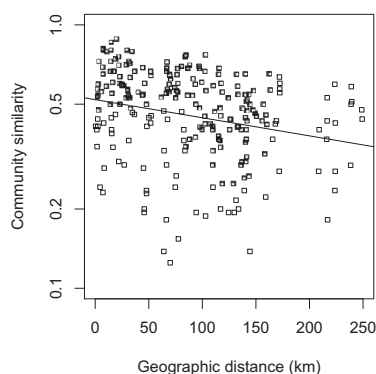


Fig. S1. Distance-decay in the compositional similarity of *Inga* communities in Madre de Dios (Jaccard index) for all communities. The best-fit linear relationship is shown; the Mantel test was used to test the strength and significance of the correlation (Results).

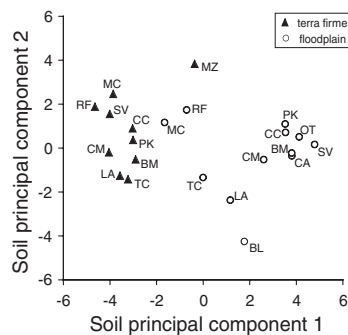


Fig. S2. The first two axes from a principal component analyses of 21 soil variables measured at community survey sites, which explain 50% and 15% of the variation in soil data, respectively. Site locations are given in Fig. 2A.

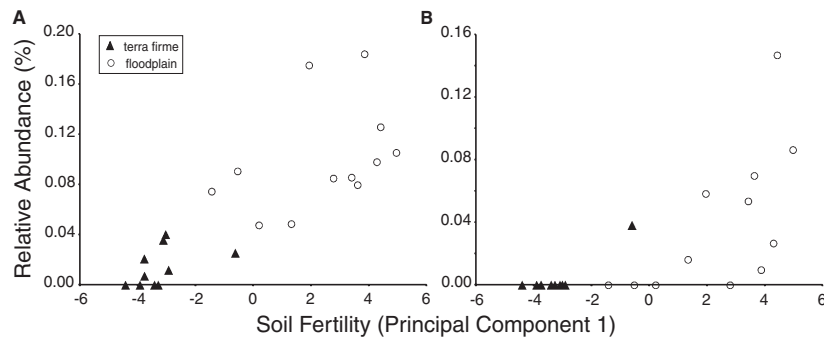


Fig. S3. Relationship between relative abundance and the first principal component axis of measured soil variables for *I. nobilis* (A) and *I. marginata* (B).

Table S1. Fst estimates between Cocha Cashu and Los Amigos and per generation migration rate estimates (from coalescent analyses) from Cocha Cashu into Los Amigos and vice versa

Species	Plastid (trnD-T spacer)			Nuclear (ITS)		
	Fst	CC→LA	LA→CC	Fst	CC→LA	LA→CC
<i>I. acreana</i>	0	NA; no genetic variation		0.09*	$1.77 \times 10^{-4†}$	$5.07 \times 10^{-4†}$
<i>I. alata</i>	1.00*	2.84×10^{-8}	$2.86 \times 10^{-4†}$	0	$6.05 \times 10^{-4†}$	$2.39 \times 10^{-5†}$
<i>I. alba</i>	0.64*	1.72×10^{-7}	$8.03 \times 10^{-5†}$	0.08*	$1.73 \times 10^{-5†}$	4.63×10^{-9}
<i>I. bourgonii</i>	0.92*	6.02×10^{-9}	2.80×10^{-5}	0.09*	$1.44 \times 10^{-4†}$	$1.85 \times 10^{-4†}$
<i>I. capitata</i>	0	NA; no genetic variation		0.44*	$1.56 \times 10^{-3†}$	4.57×10^{-5}
<i>I. chartacea</i>	0	NA; low sample size		0.45*	NA; low sample size	
<i>I. edulis</i>	0.91*	1.07×10^{-8}	1.31×10^{-3}	0	$4.42 \times 10^{-4†}$	3.64×10^{-6}
<i>I. heterophylla</i>	0.56	NA; low sample size		0	NA; low sample size	
<i>I. leiocalycina</i>	0.41*	9.54×10^{-5}	4.44×10^{-4}	0.31*	2.10×10^{-5}	4.30×10^{-5}
<i>I. marginata</i>	0.71*	$4.30 \times 10^{-5†}$	$1.09 \times 10^{-4†}$	0.21*	$5.03 \times 10^{-4†}$	2.65×10^{-5}
<i>I. morphosp_75</i>	0	NA; low sample size		0.38*	NA; low sample size	
<i>I. nobilis</i>	0.05	NA; low sample size		0.06	NA; low sample size	
<i>I. porcata</i>	0.86	NA; low sample size		0	NA; low sample size	
<i>I. punctata</i>	0	NA; no genetic variation		0	$1.02 \times 10^{-2†}$	5.93×10^{-4}
<i>I. ruiziana</i>	0.81*	5.59×10^{-9}	4.83×10^{-9}	0.01	$9.57 \times 10^{-3†}$	$1.17 \times 10^{-2†}$
<i>I. sapindoides</i>	0.82*	2.58×10^{-4}	1.85×10^{-5}	0.48*	$3.63 \times 10^{-5†}$	$3.00 \times 10^{-5†}$
<i>I. steinbachii</i>	1.00	NA; low sample size		0	NA; low sample size	
<i>I. suaveolans</i>	0	NA; no genetic variation		0	$2.47 \times 10^{-2†}$	3.49×10^{-4}
<i>I. thibaudiana</i>	0	NA; no genetic variation		0.08*	$1.12 \times 10^{-3†}$	$2.38 \times 10^{-4†}$
<i>I. umbellifera</i>	0.29*	4.83×10^{-9}	$6.93 \times 10^{-4†}$	0.56*	$1.46 \times 10^{-3†}$	6.57×10^{-5}

NA, not applicable.

*Indicates significant genetic differentiation (at $P < 0.05$) between Los Amigos and Cocha Cashu.

†Indicates migration is significantly greater than 0 (at $P < 0.05$) according to nested likelihood ratio tests.

Table S2. Community-level divergence time estimates for the chloroplast trnD-T intergenic spacer between the Cocha Cashu and Los Amigos basins for all 20 *Inga* species and for 13 genetically variable species

Species included	Mutation rate	Mode	Lower 95% CI	Upper 95% CI
All species	Upper cpDNA limit	113,892	41,682	185,735
All species	Estimated for <i>Inga</i>	262,827	96,189	428,618
Variable species	Upper cpDNA limit	145,096	67,713	265,339
Variable species	Estimated for <i>Inga</i>	334,837	156,261	612,322

The mode and 95% CIs are given for two different mutation rates: the upper rate at which noncoding plastid DNA is thought to evolve (1) and the rate at which noncoding plastid DNA was estimated to evolve in the genus *Inga* (2).

1. Wolfe KH, Li WH, Sharp PM (1987) Rates of nucleotide substitution vary greatly among plant mitochondrial, chloroplast, and nuclear DNAs. *Proc Natl Acad Sci USA* 84:9054–9058.
2. Richardson JE, Pennington RT, Pennington TD, Hollingsworth PM (2001) Rapid diversification of a species-rich genus of neotropical rain forest trees. *Science* 293:2242–2245.

Table S3. Voucher number, GenBank accession number, and locality information for all individuals from northern Peru and Bolivia

Accession no.	Species	Voucher no.	Location
JQ417354	<i>I. alata</i> Benoist	K.G. Dexter & F. Para 267	Madreselva Biological Station, Peru
JQ417355	<i>I. alata</i> Benoist	K.G. Dexter & F. Para 282	Madreselva Biological Station, Peru
JQ417356	<i>I. alata</i> Benoist	K.G. Dexter & F. Para 681	Madreselva Biological Station, Peru
JQ417357	<i>I. alata</i> Benoist	K.G. Dexter & F. Para 684	Madreselva Biological Station, Peru
JQ417358	<i>I. alata</i> Benoist	T.D. Pennington 13271	Dpto. de Cochabamba, Bolivia
JQ417359	<i>I. alata</i> Benoist	T.D. Pennington 13276	Dpto. de Cochabamba, Bolivia
JQ417360	<i>I. alata</i> Benoist	T.D. Pennington 13274	Dpto. de Cochabamba, Bolivia
JQ417361	<i>I. bourgonii</i> (Aubl.) DC	T.D. Pennington 242	Dpto. de Cochabamba, Bolivia
JQ417362	<i>I. bourgonii</i> (Aubl.) DC	K.G. Dexter & F. Para 243	Madreselva Biological Station, Peru
JQ417363	<i>I. bourgonii</i> (Aubl.) DC	K.G. Dexter & F. Para 265	Madreselva Biological Station, Peru
JQ417364	<i>I. bourgonii</i> (Aubl.) DC	K.G. Dexter & F. Para 272	Madreselva Biological Station, Peru
JQ417365	<i>I. bourgonii</i> (Aubl.) DC	K.G. Dexter & F. Para 569	Madreselva Biological Station, Peru
JQ417366	<i>I. bourgonii</i> (Aubl.) DC	K.G. Dexter & F. Para 573	Madreselva Biological Station, Peru
JQ417367	<i>I. bourgonii</i> (Aubl.) DC	K.G. Dexter & F. Para 578	Madreselva Biological Station, Peru
JQ417368	<i>I. bourgonii</i> (Aubl.) DC	K.G. Dexter & F. Para 589	Madreselva Biological Station, Peru
JQ417369	<i>I. bourgonii</i> (Aubl.) DC	K.G. Dexter & F. Para 594	Madreselva Biological Station, Peru
JQ417370	<i>I. bourgonii</i> (Aubl.) DC	K.G. Dexter & F. Para 656	Madreselva Biological Station, Peru
JQ417371	<i>I. bourgonii</i> (Aubl.) DC	K.G. Dexter & F. Para 667	Madreselva Biological Station, Peru
JQ417372	<i>I. bourgonii</i> (Aubl.) DC	K.G. Dexter & F. Para 685	Madreselva Biological Station, Peru
JQ417373	<i>I. bourgonii</i> (Aubl.) DC	T.D. Pennington 13275	Dpto. de Cochabamba, Bolivia
JQ417374	<i>I. edulis</i> Mart.	K.G. Dexter & F. Para 574	Madreselva Biological Station, Peru
JQ417375	<i>I. edulis</i> Mart.	K.G. Dexter & F. Para 585	Madreselva Biological Station, Peru
JQ417376	<i>I. edulis</i> Mart.	K.G. Dexter & F. Para 590	Madreselva Biological Station, Peru
JQ417377	<i>I. edulis</i> Mart.	K.G. Dexter & F. Para 597	Madreselva Biological Station, Peru
JQ417378	<i>I. edulis</i> Mart.	K.G. Dexter & F. Para 639	Madreselva Biological Station, Peru
JQ417379	<i>I. edulis</i> Mart.	K.G. Dexter & F. Para 640	Madreselva Biological Station, Peru
JQ417380	<i>I. edulis</i> Mart.	K.G. Dexter & F. Para 664	Madreselva Biological Station, Peru
JQ417381	<i>I. edulis</i> Mart.	K.G. Dexter & F. Para 666	Madreselva Biological Station, Peru
JQ417382	<i>I. edulis</i> Mart.	T.D. Pennington 13277	Dpto. de Cochabamba, Bolivia
JQ417383	<i>I. edulis</i> Mart.	T.D. Pennington 13282	Dpto. de Cochabamba, Bolivia
JQ417384	<i>I. ruiziana</i> G. Don	T.D. Pennington 13281	Dpto. de Cochabamba, Bolivia
JQ417385	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 228	Madreselva Biological Station, Peru
JQ417386	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 237	Madreselva Biological Station, Peru
JQ417387	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 240	Madreselva Biological Station, Peru
JQ417388	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 245	Madreselva Biological Station, Peru
JQ417389	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 568	Madreselva Biological Station, Peru
JQ417390	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 572	Madreselva Biological Station, Peru
JQ417391	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 586	Madreselva Biological Station, Peru
JQ417392	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 587	Madreselva Biological Station, Peru
JQ417393	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 604	Madreselva Biological Station, Peru
JQ417394	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 605	Madreselva Biological Station, Peru
JQ417395	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 623	Madreselva Biological Station, Peru
JQ417396	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 626	Madreselva Biological Station, Peru
JQ417397	<i>I. sapindoides</i> Willd.	K.G. Dexter & F. Para 648	Madreselva Biological Station, Peru
JQ417398	<i>I. sapindoides</i> Willd.	T.D. Pennington 13272	Dpto. de Cochabamba, Bolivia
JQ417399	<i>I. sapindoides</i> Willd.	T.D. Pennington 13284	Dpto. de Cochabamba, Bolivia
JQ417400	<i>I. sapindoides</i> Willd.	T.D. Pennington 13289	Dpto. de Cochabamba, Bolivia
JQ417401	<i>I. umbellifera</i> (Vahl) Steud.	T.D. Pennington 13285	Dpto. de Cochabamba, Bolivia
JQ417402	<i>I. umbellifera</i> (Vahl) Steud.	T.D. Pennington 13280	Dpto. de Cochabamba, Bolivia

Herbarium vouchers are deposited at the following herbaria: K, MOL, and DUKE. The corresponding herbarium voucher and Genbank accession number information for individuals from Madre de Dios is available elsewhere (1).

1. Dexter KG, Pennington TD, Cunningham CW (2010) Using DNA to assess errors in tropical tree identifications: How often are ecologists wrong, and when does it matter? *Ecol Monogr* 80:267–286.