Received: 16 August 2023 | Revised: 18 December 2023 | Accepted: 7 January 2024

DOI: 10.1111/btp.13303

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

ORIGINAL ARTICLE

Patterns in the genetic structure of 49 lowland rain forest tree species co-distributed on opposite sides of the northern Andes

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Funding information
Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: CGSM-410253-2011; National Science Foundation, Grant/Award Number: DEB 1240869 and 1338694; University of Michigan

Associate Editor: Jennifer Powers
Handling Editor: Paul Fine

Abstract

The Andes are a major dispersal barrier for lowland rain forest plants and animals, yet hundreds of lowland tree species are distributed on both sides of the northern Andes, raising questions about how the Andes influenced their biogeographic histories and population genetic structure. To explore these questions, we generated standardized datasets of thousands of SNPs from paired populations of 49 tree species co-distributed in rain forest tree communities located in Panama and Amazonian Ecuador and calculated genetic diversity (π) and absolute genetic divergence (d_{XY}) within and between populations, respectively. We predicted (1) higher genetic diversity in the ancestral source region (east or west of the Andes) for each taxon and (2) correlation of genetic statistics with species attributes, including elevational range and life-history strategy. We found that genetic diversity was higher in putative ancestral source regions, possibly reflecting founder events during colonization. We found little support for a relationship between genetic divergence and species attributes except that species with higher elevational range limits exhibited higher d_{XY}, implying older divergence times. One possible explanation for this pattern is that dispersal through mountain passes declined in importance relative to dispersal via alternative lowland routes as the Andes experienced uplift. We found no difference in mean genetic diversity between populations in Central America and the Amazon. Overall, our results suggest that dispersal across the Andes has left enduring signatures in the genetic structure of widespread rain forest trees. We outline additional hypotheses to be tested with species-specific case studies.

KEYWORDS
Andes, comparative biogeography, dispersal barrier, genetic diversity, neotropical rain forest trees, population genomics

1 | INTRODUCTION

Widely distributed species often share broad similarities in genetic structure across their geographic ranges, reflecting similar demographic responses to climate change and landscape features (Avise, 2009; Hickerson et al., 2010). In lowland Neotropical rain forests, landscape features such as large rivers (Gascon et al., 2000; Naka & Brumfield, 2018; Nazareno et al., 2019), dry forest corridors

(Costa, 2003), and mountain ranges (Bemmels et al., 2018; Frost et al., 2022; Serrano et al., 2021) frequently structure species distributions and spatial patterns of genetic variation. Mountain ranges have long been hypothesized to represent especially strong dispersal barriers to lowland rain forest species due to the high degree of specialization to narrow, stable climatic niches exhibited by tropical taxa (Janzen, 1967). At phylogenetic scales, the Northern Andean Cordilleras are an important biogeographic barrier to rain forest trees (Frost et al., 2022; Winterton et al., 2014), birds (Cracraft & Prum, 1988), and other vertebrates (Ron, 2000), yet many lowland rain forest tree species are distributed on both sides of the Andes (Bemmels et al., 2018; Dick et al., 2005; Gentry, 1982) in both the Amazon Basin and Central America (here broadly defined to also include the Chocó or the Pacific coastal region of Colombia and Ecuador; Figure 1). Little is known about how such species dispersed across the Andes and whether dispersal has left similar patterns of population genetic structure across multiple taxa.

The strength of biogeographic barriers between the Amazon and Central America has likely varied greatly over time. The South and Central American landmasses were physically isolated by an oceanic seaway prior to the emergence of the Isthmus of Panama, which occurred in successive stages over the Late Miocene until final closure ca. 3 Ma (Bacon et al., 2015; Jaramillo, 2018; McGirr et al., 2021; Montes et al., 2015; O'Dea et al., 2016). Final closure sparked the dispersal of numerous animal lineages during the Great American Biotic Interchange (Simpson, 1980; Weir et al., 2009), yet many plant lineages dispersed between continents over water barriers before isthmus formation was complete (Bacon et al., 2015; Cody et al., 2010; Serrano et al., 2021).

While formation of the Isthmus of Panama continued to increase connectivity between South and Central America, simultaneous uplift of the Andes imposed new dispersal challenges. The northern Andes was one of the most recent regions of the Andes to experience uplift (Boschman, 2021; Hoorn et al., 2010), with rapid uplift beginning ca. 8 to 5 Ma (Pérez-Escobar et al., 2022). Today, the high elevations of the Eastern Cordillera of Colombia form a strong topographical barrier between the Amazon Basin and Central America (Figure 1), but such elevations likely did not exist in this region prior to 5 Ma (Boschman, 2021). The most rapid uplift of the Eastern Cordillera occurred ca. 6 to 2.7 Ma (Boschman, 2021; Gregory-Wodzicki, 2000). Despite large uncertainties, some estimates suggest it may have reached only 40% of its modern height by ca. 4 Ma (Gregory-Wodzicki, 2000) and increased in elevation by ≥1.4 km since the end of the Miocene (García-Delgado et al., 2021). Thus, absolute elevational barriers between opposite sides of the Andes were likely weaker throughout the Pliocene and early Pleistocene compared to today. Important gaps in the continuity of the Andean cordilleras may also have existed, including the Miocene Trans-Andean Portal (Figure 1; Montes et al., 2021). This lowland portal connected the incipient Chocó region with the Amazon Basin at ~3° N from ca. 13 Ma to at least 4 Ma, after which it was gradually filled in by increasing volcanism and tectonic uplift (Montes et al., 2021). The lack of Miocene continuity between cordilleras of the Colombian Andes also agrees with biological evidence, such as the delayed colonization of the Western and Central Cordilleras by montane *Ceroxylon* palms until the Pliocene–Pleistocene boundary (Sanín et al., 2022).

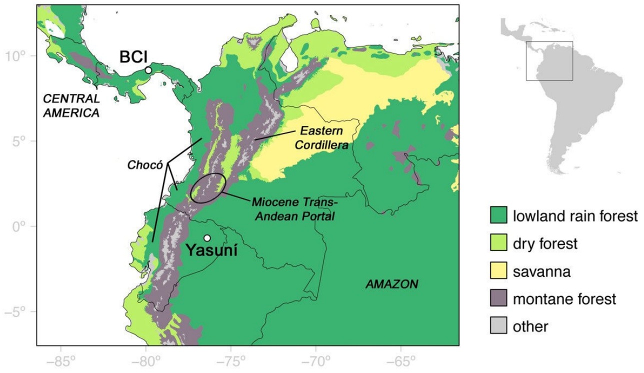

FIGURE 1 Locations of sampling sites Yasuní (Amazon) and BCI (Central America), and the distribution of lowland rain forest (dark green) and other habitat types. The montane forests (purple) and other high-elevation habitats of the Andes, as well as surrounding dry forest (light green) and savanna (yellow), form a biogeographic barrier limiting the potential for dispersal and gene flow between Yasuní and BCI. Habitat types are based on Olson et al. (2001) with reclassification of dry forest following Dick and Pennington (2019). Montane forest is defined as moist forest ≥1000 m in elevation. The approximate location of the Miocene Trans-Andean Portal follows Sanín et al. (2022).

As the Eastern Cordillera experienced uplift and the Miocene Trans-Andean Portal closed, direct dispersal across mountain passes would likely have become increasingly difficult for lowland rain forest trees. Savannahs and other lowland dry regions have abutted the cordillera to the east and north (Figure 1; Olson et al., 2001) since the onset of the Pliocene (Jaramillo et al., 2010), further restricting dispersal around the Andes for wet forest adapted taxa. However, the network of gallery forests within these savannahs shares many species in common with continuous rain forest and expanded in size during periods of cooler and wetter climates (Behling & Hooghiemstra, 1998). These gallery forests could conceivably have provided an alternative lowland biogeographic connection between regions leading around rather than across the Andes, in particular for species tolerant of seasonally dry climates (Honorio Coronado et al., 2014). The narrow band of premontane forest surrounding the Andean foothills (Figure 1) may also have provided dispersal opportunities for some taxa.

The extent to which lowland rainforest plants were capable of dispersing across these ecologically diverse biogeographic barriers—and the genetic signatures of such dispersal—may have depended on species-specific attributes (Bemmels et al., 2018). Elevational range and drought tolerance could conceivably be associated with the ability to disperse directly across the Andes and through alternative lowland dry habitats, respectively, with the relative opportunities for dispersal by each route varying over time as landscapes geologically and climatically evolved. Furthermore, attributes such as dispersal mechanism, pollination mode, mating system, successional stage, and geographic range size have previously been demonstrated to influence genetic structure of Neotropical plants (Ballesteros-Mejia et al., 2016; Hamrick et al., 1993; Hamrick & Murawski, 1990; Lowe et al., 2018). In particular, pioneer species of Neotropical trees tend to show reduced genetic diversity relative to later-successional species, likely due to increased genetic drift during the repeated colonization of new habitats following disturbance (Lowe et al., 2018). Species with smaller regional population sizes could also experience greater loss of diversity through genetic drift (Lowe et al., 2018), as could populations that have dispersed to a novel biogeographic region if population bottlenecks and founder effects occurred during dispersal (Slatkin & Excoffier, 2012).

Given the complex geological history of northwest South America, we expect that widespread rain forest tree species from this region will have experienced a diversity of biogeographic histories. Indeed, the timing of cross-Andean dispersal has likely varied greatly, with some species having dispersed as early as the Late Miocene (Dick et al., 2003, 2013). Given the potential for millions of years of separation between Amazonian and Central American populations, some widespread taxa may represent independently evolving lineages yet to be described as separate species (Damasco et al., 2021), but in other cases widespread species could still represent a single gene pool (Brito et al., 2023). As Neotropical rain forest trees have been genetically understudied relative to their temperate counterparts (Tinoco et al., 2015), it remains an open question whether dispersal between biogeographic regions has left predictable signatures in genetic structure of contemporary populations, and whether the impact of dispersal on genetic structure has been affected by species-specific traits.

To explore these questions, we generated standardized datasets of thousands of single nucleotide polymorphisms (SNPs) for 49 tree species (Table 1) co-distributed on both sides of the Andes. For each species, we sampled two to four individuals per population from two populations (one Amazonian and one Central American; Figure 1). We designed our sampling scheme in light of recent theoretical and empirical findings related to minimum sample sizes for population genomics (see Section 2: Methods) and confirmed the suitability of our sample size for the present study with sensitivity analyses. We then calculated genetic diversity (π) within populations and genetic divergence (d_{XY}) between populations for each species and tested for correlations between these genetic estimates and species attributes. We also interpreted our results in the context of the putative biogeographic origins of each species (i.e., North or South American), which we inferred based on a literature review entirely independent of our genetic data. We used these datasets to explore three different types of questions:

1. Are species-specific attributes correlated with cross-Andean genetic divergence, and if so, what do patterns suggest about cross-Andean dispersal? In particular, we propose that correlations between ecological niche traits and genetic divergence could suggest changes in the relative importance of ecologically diverse dispersal routes over time.
2. Are species attributes correlated with genetic diversity? We predict that species with pioneer life histories may exhibit low genetic diversity due to their high susceptibility to repeated loss of genetic diversity in small colonizing populations (Lowe et al., 2018).
3. How do genetic diversity levels differ between populations in the western Amazon and Central America? We predict that genetic diversity may be higher in the biogeographic region in which a species putatively originated and lower in the region to which it dispersed, due to a loss of genetic variation associated with population bottlenecks during dispersal.

2 | METHODS

2.1 | DNA collection and SNP genotyping

For each of 49 tree species (Table 1), we sampled two to four individuals per population from Forest Global Earth Observatory (ForestGEO) plots on Barro Colorado Island (BCI), Panama and in Yasuní National Park, Ecuador, representing a Central American and a Western Amazonian population, respectively (Figure 1; see also the Data S1). The 49 study species represent more than half of the 85 species that co-occur at Yasuní and BCI. We were unable to obtain sufficient tissue or high-quality DNA extractions for the remaining taxa. We extracted DNA from silica-dried leaf tissue using Machery-Nagel Nucleospin Plant II kits with SDS reagents and prepared double-digest Restriction-Associated DNA (ddRAD) libraries from a modified protocol based on that of Peterson et al. (2012), with restriction enzymes *EcoRI* and *MseI* and fragment lengths of 375–475 bp. This ddRAD protocol has previously been described in full (Bemmels & Dick, 2018) and a summary is provided in Appendix S1. In total, we prepared eight pooled libraries of 72 to 96 samples each for sequencing (50-bp, single-end reads) on an Illumina HiSeq machine at The Hospital for Sick Children (Toronto). For samples that resulted in <800,000 sequenced reads, DNA was re-extracted and re-sequenced.

We demultiplexed samples and generated SNP datasets using *Stacks* v.1.46 (Catchen et al., 2011, 2013). We demultiplexed reads using the *process_radtags* script in *Stacks* and obtained trimmed reads of 36 bp after removing barcodes and the *EcoRI* cut site. We then called SNPs using the *denovo_map.pl* pipeline in *Stacks* for each species individually, retaining only individuals sequenced at ≥70% of loci and loci sequenced in all individuals to a minimum depth of 10x. We used standardized parameter values in *Stacks* for all species to ensure that variation in the SNP-discovery procedure would not introduce bias among species. Further details are provided in the Data S1.

2.2 | Population genetic statistics

We calculated absolute genetic divergence (d_{XY}) between populations (Delmore et al., 2018; Nei, 1987) and nucleotide diversity (π) within populations (Nei, 1987; Nei & Li, 1979) using the *R* package

TABLE 1 Species included in the study, sample sizes for Yasuní (n_{Yas}) and BCI (n_{BCI}), and population genetic parameters (d_{XY}, genetic divergence between sites; π, nucleotide diversity).

Species	Family	n_{Yas}	n_{BCI}	d_{XY}	π_{Yas}	π_{BCI}
Andira inermis	Fabaceae	4	4	0.0082	0.0056	0.0048
Apeiba membranacea	Malvaceae	4	3	0.0079	0.0061	0.0057
Apeiba tibourbou	Malvaceae	3	3	0.0070	0.0035	0.0044
Astronium graveolens	Anacardiaceae	3	4	0.0143	0.0055	0.0045
Casearia aculeata	Salicaceae	3	4	0.0173	0.0025	0.0074
Casearia arborea	Salicaceae	2	3	0.0339	0.0041	0.0056
Casearia sylvestris	Salicaceae	2	2	0.0059	0.0043	0.0051
Ceiba pentandra	Malvaceae	3	4	0.0109	0.0043	0.0053
Celtis schippii	Cannabaceae	3	3	0.0062	0.0026	0.0045
Cinnamomum triplinerve	Lauraceae	3	3	0.0127	0.0043	0.0077
Cupania cinerea	Sapindaceae	4	2	0.0104	0.0051	0.0030
Dendropanax arboreus	Araliaceae	2	3	0.0184	0.0061	0.0103
Diospyros artanthifolia	Ebenaceae	3	4	0.0087	0.0056	0.0027
Erythroxylum macrophyllum	Erythroxylaceae	2	4	0.0079	0.0055	0.0031
Ficus maxima	Moraceae	2	3	0.0091	0.0035	0.0030
Guarea grandifolia	Meliaceae	4	3	0.0144	0.0059	0.0068
Hasseltia floribunda	Salicaceae	3	3	0.0061	0.0043	0.0024
Inga marginata	Fabaceae	2	3	0.0142	0.0065	0.0052
Inga nobilis	Fabaceae	3	4	0.0089	0.0069	0.0045
Inga punctata	Fabaceae	4	2	0.0105	0.0070	0.0066
Inga ruiziana	Fabaceae	2	4	0.0116	0.0062	0.0041
Inga sapindoides	Fabaceae	3	4	0.0153	0.0056	0.0053
Inga spectabilis	Fabaceae	3	2	0.0097	0.0073	0.0052
Inga thibaudiana	Fabaceae	3	3	0.0075	0.0067	0.0055
Inga umbellifera	Fabaceae	3	2	0.0134	0.0091	0.0062
Jacaranda copaia	Bignoniaceae	3	3	0.0093	0.0035	0.0031
Lacistema aggregatum	Lacistemataceae	2	3	0.0115	0.0041	0.0068
Laetia procera	Salicaceae	3	3	0.0067	0.0021	0.0014
Margaritaria nobilis	Phyllanthaceae	3	2	0.0081	0.0040	0.0047
Miconia elata	Melastomataceae	2	4	0.0069	0.0053	0.0041
Nectandra lineata	Lauraceae	3	4	0.0142	0.0069	0.0033
Ocotea oblonga	Lauraceae	2	4	0.0127	0.0057	0.0034
Palicourea guianensis	Rubiaceae	3	3	0.0098	0.0052	0.0026
Perebea xanthochyma	Moraceae	4	3	0.0205	0.0038	0.0027
Piper aequale	Piperaceae	3	2	0.0084	0.0034	0.0030
Piper arboreum	Piperaceae	3	3	0.0135	0.0087	0.0045
Piper reticulatum	Piperaceae	2	3	0.0124	0.0031	0.0028
Platymiscium pinnatum	Fabaceae	2	4	0.0181	0.0047	0.0051
Posoqueria latifolia	Rubiaceae	3	3	0.0188	0.0043	0.0053
Poulsenia armata	Moraceae	3	3	0.0133	0.0040	0.0027
Pourouma bicolor	Urticaceae	4	3	0.0093	0.0054	0.0027
Pouteria reticulata	Sapotaceae	4	3	0.0174	0.0041	0.0034
Pterocarpus rohrii	Fabaceae	3	3	0.0173	0.0076	0.0059
Sterculia apetala	Malvaceae	3	3	0.0087	0.0053	0.0018

TABLE 1 (Continued)

Species	Family	n_{Yas}	n_{BCI}	d_{XY}	π_{Yas}	π_{BCI}
Trema micrantha	Cannabaceae	3	2	0.0095	0.0010	0.0050
Trichilia pallida	Meliaceae	3	3	0.0165	0.0082	0.0018
Turpinia occidentalis	Staphyleaceae	3	3	0.0151	0.0027	0.0059
Urera baccifera	Urticaceae	3	4	0.0101	0.0061	0.0008
Vismia baccifera	Hypericaceae	3	3	0.0211	0.0021	0.0016
	Mean	2.92	3.12	0.0122	0.0050	0.0043
	Standard deviation	0.64	0.67	0.0052	0.0018	0.0019

"PopGenome" v.2.7.5 (Pfeifer et al., 2014). We calculated d_{XY} instead of the commonly employed statistic F_{ST} (relative genetic differentiation) because d_{XY} does not depend on within-population genetic diversity (Burri, 2017), and because we expect recent gene flow between Amazonian and Central American populations to be minimal, such that the populations could largely be treated as independently diverging lineages. In the absence of gene flow, d_{XY} is directly related to the time since divergence: d_{XY} equals genetic diversity in the common ancestor at the time of lineage splitting, and then increases linearly over time proportional to mutation rate (Burri, 2017; Delmore et al., 2018). Both d_{XY} and π were corrected relative to the total number of sequenced sites across all RAD loci, including invariant loci.

2.3 | Species attributes and biogeographic origins

We gathered datasets describing both inherent life-history traits and species' emergent ecological niche and distributional characteristics, which we collectively refer to hereafter as species attributes. We compiled life-history traits from datasets curated by S. Joseph Wright (Smithsonian Tropical Research Institute) for BCI species. Life-history traits included dispersal mode (animal or wind), maximum diameter at breast height (hereafter, "maximum diameter"), wood density, and leaf mass per area (LMA). The latter three traits are associated with successional stage in tropical trees: pioneer species tend to grow quickly (low wood density), invest fewer resources in their leaves (low LMA), and have long dispersal distances (large maximum diameter, which is a proxy for maximum height) (Swaine & Whitmore, 1988; Thomson et al., 2011; Wright et al., 2010). Methods for deriving these traits have previously been described (Bemmels et al., 2018).

We also calculated relative abundance, elevational range, and drought tolerance from filtered datasets of occurrence records obtained from the Global Biodiversity Information Facility (GBIF; www.gbif.org). Relative abundance was defined as the total number of filtered occurrence records. Elevational range and drought tolerance here reflect the ability to occur in areas of high elevation and low mean annual precipitation (MAP) and were calculated as the 90th percentile of elevation and 10th percentile of MAP of occurrence records, respectively, following Bemmels et al. (2018). Finally, we estimated range size (km^2) from cropped species distribution models (SDMs) constructed from the filtered occurrence-record datasets, using *Maxent* v.3.4.0 (Phillips et al., 2004, 2006, 2017). Further details are provided in Figure S1 and the Data S1. Despite our filtering of occurrence records to minimize potential biases and errors, many retained records may still be incorrect given the high rate of taxonomic misidentification inherent in Neotropical herbarium records, even for well-studied genera (Baker et al., 2017). The use of 90th percentile cutoffs in calculating elevational range and drought tolerance and 95% inclusion criteria in cropping SDMs (Appendix S1) ensures that calculated species attribute values are not driven by the most extreme data points (which may be more likely to represent misidentifications), yet would likely only partly mitigate potential biases caused by high taxonomic error overall.

We also inferred the putative biogeographic origins of each species based on a review of published literature, supplemented in some cases with our own inferences based on the geographic distributions of species within the same genus or sub-generic clade. We assigned species to lineages having putative biogeographic origins in either North America (including Central America) or South America or left biogeographic origins unassigned if evidence was inconclusive. Biogeographic origins were then used to classify each species as either being putatively native to a given region for each site (i.e., species from South American lineages at Yasuní and from North American lineages at BCI), a putative immigrant, or else with immigrant status unassigned. Further details are provided in Appendix S1, and evidence to support our classifications for each species is provided in Appendix S1.

2.4 | Data analyses

We performed principal component (PC) analysis of species attributes using the *R* package "PCAmix" v. 3.1 (Chavent et al., 2017), with varimax rotation based on the first four PC axes. We included all species attributes in calculation of PC axes except for putative biogeographic origin, because biogeographic origin is a conceptually different type of attribute reflecting deep evolutionary history, rather than describing inherent or emergent ecological characteristics. Excluding biogeographic origin from the PC analysis allowed us to evaluate its effects separately from those of ecological attributes.

We performed multivariate phylogenetic regressions that estimated the effects of species attributes on population genetic statistics (d_{XY} and π). We obtained a published phylogeny of 282 BCI tree species based on three DNA barcode regions (Kress et al., 2009; Pearse et al., 2013). We pruned this phylogeny to our 49 study species (Figure S2) and used it to control for statistical non-independence among species due to shared phylogenetic history. We modeled d_{XY} ($\log_{10}$-transformed to better approximate a normal distribution) using phylogenetic linear models implemented with the *phylolm()* function in the *R* package "phylolm" v.2.5 (Ho & Ané, 2014). Phylogenetic signal was estimated as the maximum likelihood transformation of Pagel's λ (Pagel, 1999), with statistical significance of λ assessed using a likelihood-ratio test to compare the phylogenetic model to an alternative non-phylogenetic linear regression model.

To incorporate random effects necessary to account for the two measures of π per species (one measure per site), we modeled π using phylogenetic linear mixed models with the *communityPGLMM()* function in the *R* package "pez" v. 1.2–0 (Pearse et al., 2015). Species identity was modeled as a phylogenetically controlled random effect where covariance among species was scaled relative to phylogenetic distance. We did not include site as a random effect, because preliminary tests showed that including site provided a poorer model fit (assessed using Akaike Information Criterion and R^2 values). We recoded the putative biogeographic origins of each species at each site as binary variables indicating whether the species was a putative immigrant, putatively native, or had unassigned immigrant status. The final model for π therefore included putative immigrant status and the four PCs of species attributes as fixed effects, and species as a phylogenetic random effect.

To estimate the amount of variation explained overall and by each model parameter, we calculated total R^2_{pred} and partial R^2_{pred} of each parameter using the R package "rr2" v. 0.1.2 (Ives, 2018). For our models of π, we used the calculation of R^2_{pred} for *communityPGLMM* objects that is equivalent to the calculation for *phylolm* objects, using supplemental source code distributed with the "rr2" package in the *r2_pred.R* file.

2.5 | Sensitivity to small sample size

Our sampling approach was motivated by the practical difficulty of collecting leaves from tall and sometimes locally uncommon rain forest trees and by recent theoretical and empirical work showing that very small sample sizes—even as low as two individuals per population—are adequate for accurate estimation of certain population genetic statistics from genome-scale datasets (Jeffries et al., 2016; Li et al., 2020; Nazareno et al., 2017; Qu et al., 2020; Willing et al., 2012). However, to test whether our sampling scheme could have biased our results, we conducted two sensitivity analyses. Firstly, we recalculated d_{XY} and π for each species using all possible combinations of $n = 2$ individuals (representing our lowest within-population sample size). Secondly, we recalculated our regression models 1000 times while resampling two randomly selected individuals per population across all 49 species simultaneously. These procedures were designed to test whether random sampling of a small number of individuals could have influenced our estimates of genetic statistics and the conclusions of our regression results, respectively. Details of sensitivity analyses and a rationale to justify the sampling scheme are provided in the Data S1.

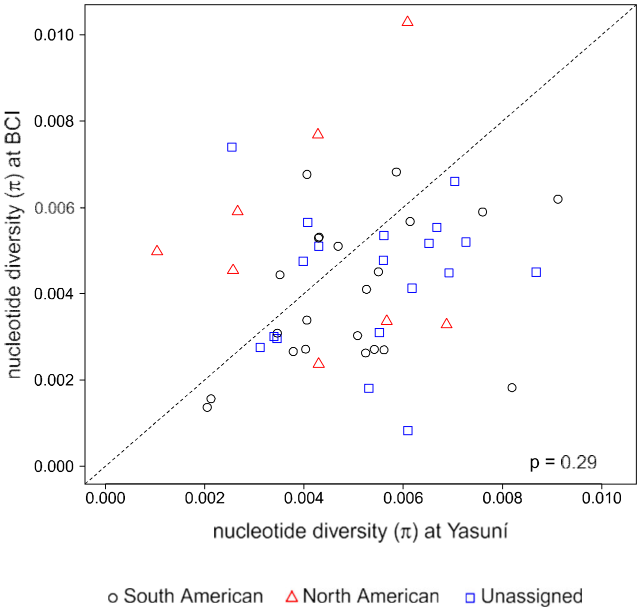

FIGURE 2 Mean nucleotide diversity (π) of each species at Yasuní and BCI, based on resampled SNP datasets of two individuals per population. Colors and symbols reflect the putative biogeographic origin of each species' lineage based on independent literature. The dashed line represents a 1:1 relationship. The *p*-value corresponds to a linear regression of π at BCI versus π at Yasuní.

3 | RESULTS

3.1 | Data processing and genetic statistics

We sequenced an average of 2.25×10^6 reads per individual (Table S1) from a mean of 6.0 individuals per species (Table 1), obtaining final datasets (Bemmels et al., 2024) with a mean of 3327 RAD loci and 2784 SNPs per species, with SNPs sequenced to a mean depth of 99.6× per individual (Table S1). Mean d_{XY} measured 0.0122 across species. Mean nucleotide diversity (π) did not differ between sites (Yasuní: 5.00×10^{-3}; BCI: 4.35×10^{-3}; two-sided *t*-test, $p = .077$) and there was no significant linear relationship between π at BCI and at Yasuní ($p = .29$; Figure 2). As expected, d_{XY} was higher than mean π in all species, but for some species d_{XY} was only slightly higher than π while for other species d_{XY} was much higher (Figure S3). The mean value of d_{XY} minus mean π was 0.0076 (range = 0.0012–0.0291), indicating that on average 0.76% novel sequence divergence has accumulated since the time of population splitting, assuming that mean

π in extant populations is approximately equal to π in the common ancestor (Burri, 2017).

3.2 | Principal coordinates of species attributes

The first four rotated principal component (PC) axes cumulatively explained 81.3% of the variance in species attributes (Figure 3). The first PC axis (PC1) primarily reflected geographic distribution and ecological amplitude. Species scoring highly on PC1 tended to have large geographic ranges (see also Figure S4), high relative abundance, and high drought tolerance. The second PC axis distinguished wind-dispersed trees with large maximum diameter (low values of PC2) from smaller, animal-dispersed species (high values of PC2). The third PC axis primarily reflected resource-investment strategies, as species with high values of PC3 had high wood density and high leaf mass per area. High values of PC4 primarily identified species with a broad elevational range.

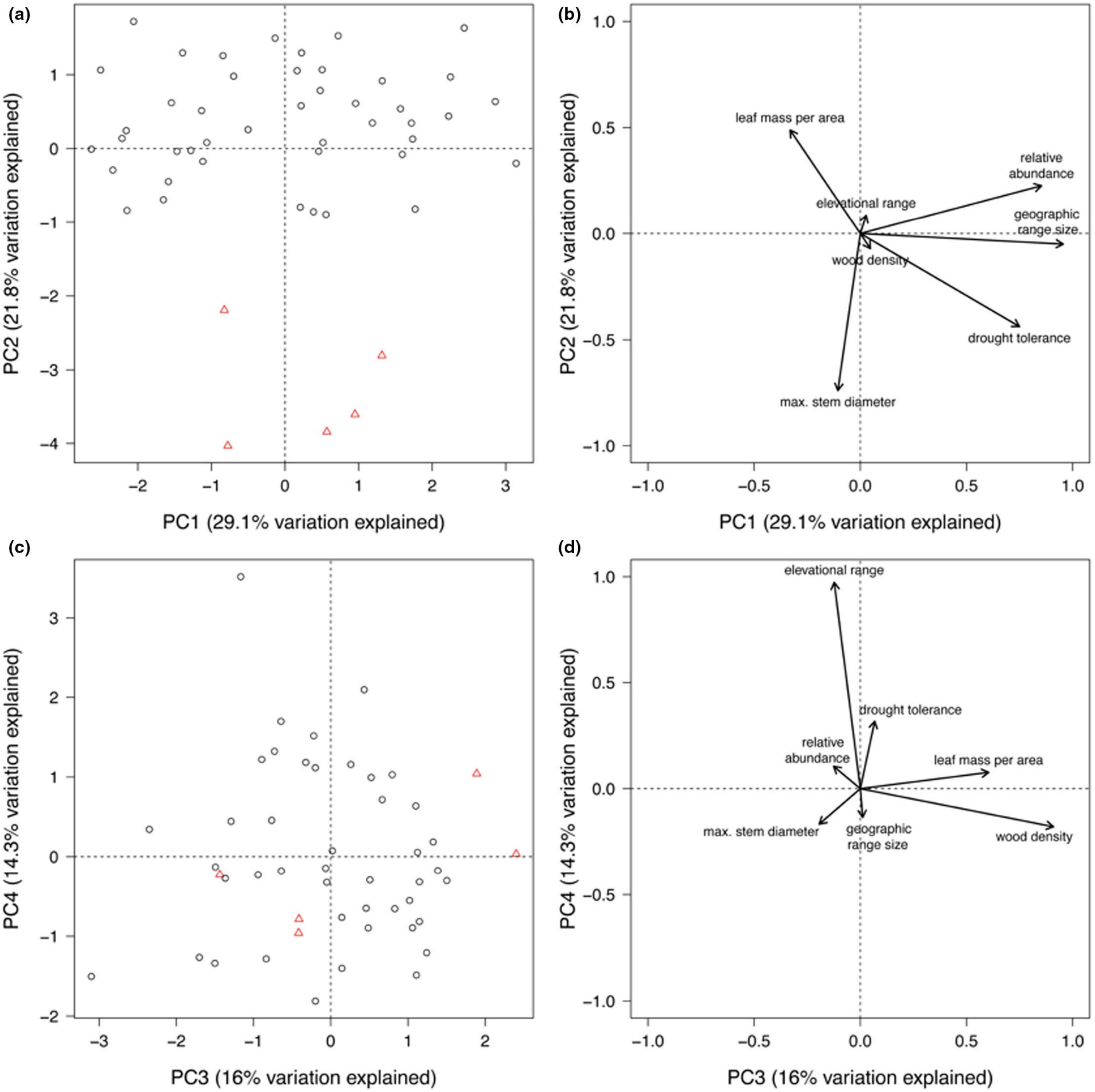

FIGURE 3 Principal component (PC) analyses of ecological traits. Panels (a) and (c) depict scores for individual species along the first four rotated PC axes separated by levels of dispersal mode (black circles: animal dispersal; red triangles: wind dispersal). Panels (b) and (d) depict the loadings of the continuous traits along each rotated PC axis.

3.3 | Predictors of genetic structure

Classifications based on our independent literature review resulted in 22 species from lineages with putative South American biogeographic origins, 8 species from North American lineages, and 19 species for which putative origins could not be assigned (Appendix S1 and Dataset S1). PC4 (elevational range) was positively associated with d_{XY} ($p=.020$, partial $R^2_{\text{pred}}=.123$) in our multivariate phylogenetic regressions (Table 2), whereas other species attributes and biogeographic origin were unrelated to d_{XY}. In contrast, all species attributes were unrelated to population genetic diversity (π; Table 3), but inferred immigrant status was a significant predictor of π, with putative immigrants having lower π than native (non-immigrant) species ($p=.015$, partial $R^2_{\text{pred}}=.064$). The phylogenetic random effect of species identity was marginally non-significant in explaining variation in π ($p=.076$; Table 3), yet had a non-negligible partial R^2_{pred} (.065; Table 3). The total variation in d_{XY} and π explained by our analyses was modest (d_{XY}: total $R^2_{\text{pred}}=.192$; π: total $R^2_{\text{pred}}=.142$; Tables 2 and 3).

3.4 | Sensitivity analyses

In agreement with theoretical predictions, our sensitivity analyses revealed little evidence that the small number of individuals sampled per population was likely to have biased our results. Estimates of d_{XY} varied negligibly due to random resampling of $n = 2$ individuals (Figure S5a), while estimates of π showed modest variation for a few particular species (Figure S5b,c), but this variation was not large enough to have altered the conclusions of our regression models. Full details are available in Appendix S1.

4 | DISCUSSION

Our results suggest several ways in which biogeographic dispersal between opposite sides of the Andes may have impacted genetic structure of widespread lowland rain forest tree species. Cross-Andean genetic divergence varied substantially among species, suggesting high interspecific variation in the timing of dispersal or rates of subsequent gene flow. Genetic divergence was higher (implying more ancient dispersal) in species with higher elevational range limits, which may suggest that the relative importance of high-elevation dispersal over mountain passes has declined toward the present as the Andes experienced uplift. Genetic diversity was higher in species putatively native to a given biogeographic region than in putative immigrants, suggesting that the process of dispersal led to population bottlenecks and a loss of genetic variation. Overall, our exploratory approach has provided a snapshot of genetic structure from only two geographic sites but nonetheless revealed statistically significant biogeographic patterns applicable across dozens of taxa. We suggest several hypotheses to be further tested with taxon-specific case studies.

4.1 | Interspecific variation in divergence

Cross-Andean genetic divergence (d_{XY}) varied substantially among taxa (range: 0.0059–0.0339) and was only slightly higher than within-population genetic diversity (π) in some species but much higher in others (Table 1; Figure S3). These results qualitatively suggest that some taxa have experienced relatively recent genetic connectivity between Central America and the western Amazon ($d_{XY} \approx \pi$), while others may have been independently evolving for a long time ($d_{XY} \gg \pi$), perhaps many millions of years (Dick et al., 2013). Future case studies should estimate timing of population divergence and rates of gene flow between opposite sides of the Andes, which may require increased sample sizes and coalescent modeling approaches (Excoffier et al., 2013; Hickerson & Meyer, 2008). High d_{XY} for some species also suggests candidate taxa that may consist of cryptic species (or subspecies) and may benefit from more detailed taxonomic study. In particular, the 3.39% divergence between *Casearia arborea* (Salicaceae) populations is much higher than observed for other species. Recent phylogenies of *Casearia* have suggested that two recognized species (*C. grandiflora* and *C. manausensis*) may be nested within *C. arborea* (de Mestier et al., 2022, 2023). This pattern could represent lack of phylogenetic resolution, but may also suggest that *C. arborea* is a paraphyletic taxon potentially consisting of multiple lineages in need of improved taxonomic delimitation (de Mestier et al., 2023). *Vismia baccifera* (Hypericaceae) and *Perebea xanthochyma* (Moraceae) also have d_{XY} values above 2% and may be strong candidates for taxonomic re-investigation.

4.2 | Species attributes and genetic divergence

We hypothesized that species with different ecological niche breadths may show differences in cross-Andean genetic divergence (d_{XY}), which could reflect changes over time in the relative importance of ecologically divergent dispersal routes across the Andes. The positive relationship between PC4 (which primarily reflects elevational range; Figure 3) and genetic divergence (d_{XY}; Table 2) suggests that species with higher upper elevational limits tend to have higher d_{XY} and thus older divergence times. This enrichment of higher-elevation species among those with older divergence timing could suggest that higher-elevation dispersal routes were more commonly utilized in the distant past and permitted ancient dispersal of a substantial number of species with high upper-elevational range limits. These routes could have included mountain passes such as the Miocene Trans-Andean Portal prior to its final closure (Montes et al., 2021) or direct dispersal across the uplifting Eastern Cordillera. Ancient dispersal across low mountains is a plausible scenario for many of our study species. Occurrence records for 27 of the 49 species extend into lower montane forest (at least 10% of records ≥1000 m, Dataset S1; see also Figure S4), and an ancient cross-Andean divergence timing is supported by previous estimates in which 7 out of 12 studied species had a divergence time dating to the Miocene (Dick et al., 2013). One alternative

TABLE 2 Phylogenetic linear regression testing the effect of principal components (PCs) of species attributes and inferred biogeographic origin on absolute genetic divergence (d_{XY}; $\log_{10}$-transformed) between Yasuní and BCI.

	$\log_{10}(d_{XY})$ (total R^2_{pred} = .192)				
Parameter	**Estimate**	**Standard error**	***t*-value**	***p***	**Partial R^2_{pred}**
λ	2.60×10^{-9}			1.000	<.001
Intercept	−1.897	0.037	−51.404	$<2\times10^{-16}$***	
PC1	0.008	0.016	0.514	.610	.006
PC2	−0.025	0.018	−1.382	.174	.043
PC3	0.006	0.021	0.307	.760	.002
PC4	0.061	0.025	2.423	.020*	.123
Inferred biogeographic origin[a]					
North American	−0.130	0.079	−1.637	.109	.020
Unassigned	−0.069	0.056	−1.238	.223	

Note: λ is a measure of phylogenetic signal in the relationship, and the *p*-value for λ is derived from a likelihood-ratio test comparing models with and without phylogenetic signal.

[a] Reference level: South American; a single partial R^2_{pred} value is reported for the effects of all inferred biogeographic origins combined.

*, $p<.05$; **, $p<.01$; ***, $p<.001$.

TABLE 3 PGLMM regression predicting nucleotide diversity (π) from principal components (PCs) of species attributes and from putative immigrant status, with species included as a phylogenetically controlled random effect.

	Nucleotide diversity (π) (total R^2 = .142)				
Random effects	**Variance**	**Standard deviation**		***p***	**Partial R^2_{pred}**
Species	1.99×10^{-7}	4.47×10^{-4}		.076	.065
Residual variance	2.63×10^{-6}	1.62×10^{-3}			
Fixed effects	**Estimate**	**Standard error**	***Z*-score**	***p***	**Partial R^2_{pred}**
Intercept	4.86×10^{-3}	5.23×10^{-4}	9.286	<2e-16***	
PC1	6.50×10^{-5}	1.38×10^{-4}	0.470	.638	.004
PC2	-4.64×10^{-5}	$1.56\times x10^{-4}$	−0.298	.765	<.001
PC3	9.86×10^{-5}	1.65×10^{-4}	0.597	.550	.001
PC4	2.92×10^{-4}	1.87×10^{-4}	1.557	.119	.034
Inferred immigrant status[a]					
Immigrant	-1.02×10^{-3}	4.19×10^{-4}	−2.438	.015*	.064
Unassigned	-5.64×10^{-4}	4.76×10^{-4}	−1.187	.235	

Note: Estimates of π from both Yasuní and BCI are included in this model. The *p*-value for the phylogenetic random effect of species is derived from a likelihood-ratio test comparing models with and without this random effect.

[a] Reference level: Non-immigrant; a single partial R^2_{pred} value is reported for the effects of all inferred immigrant statuses combined.

*, $p<.05$; **, $p<.01$; ***, $p<.001$.

explanation for the positive association between PC4 and d_{XY} is that older species may have had more time to adapt to a wider variety of habitats and expand their ecological niches, including into higher elevations. However, if increased species age tends to result in adaptation to more diverse environments per se, we would have expected an association between d_{XY} and PC1 (loading highly with range size, abundance, and drought tolerance; Figure 3), which we did not observe.

In contrast to results for elevational range, no association was found between d_{XY} and drought tolerance. Drought tolerance loaded strongly on PC1 and to a lesser extent on PC2 (Figure 3b), but neither of these PCs were associated with d_{XY} (Table 2). These results could imply that there has not been a strong trend over time in the relative importance of dispersal around the northernmost Andes through lowland dry habitats. Dry habitats have dominated landscapes to the east and north of the Colombian Andes since the end of the Miocene (Jaramillo et al., 2010) and likely presented a barrier throughout much of the timeframe relevant to dispersal of extant species. However, we consider it likely that some dispersal events could have occurred via dry habitats, as drought tolerance has previously been linked to an increased capacity for biogeographic dispersal between the Amazon and Central America (Bemmels et al., 2018).

Although we examined correlations between d_{XY} and ecological niche breadth, we caution that our data are unable to provide insights into exact dispersal timing or dispersal routes utilized by any species. Future case studies of individual taxa should expand phylogeographic sampling to include multiple populations across each biogeographic region—including along all portions of the Colombian cordilleras (Serrano et al., 2021)—in order to determine which populations from opposite sides of the Andes are most closely genetically related and to infer dispersal routes. Statistical and model-based methods of inferring expansion origins (He et al., 2017; Peter & Slatkin, 2013) could also be used to estimate the geographic coordinates where immigrant species first arrived in a biogeographic region and thus infer dispersal routes.

4.3 | Dispersal-associated founder effects

We predicted that immigrant species would show lower genetic diversity than native species at a given site, due to the increased genetic drift and loss of genetic diversity (i.e., founder effects; Slatkin & Excoffier, 2012) experienced during dispersal. This prediction was supported by our results, in which inferred immigrant status (based on independent literature) was a significant predictor of genetic diversity, with putative immigrants having lower genetic diversity than putatively native species (Table 3). It is particularly remarkable that signatures of intercontinental migration can still be detected in patterns of genetic diversity, given that previous research (Dick et al., 2013)—corroborated by the high d_{XY} values observed in this study for some species (Table 1)—suggests ancient divergence times between some populations. The substantial amount of time that immigrant populations have presumably had to recover from a loss of genetic diversity during founder events would be expected to weaken the relationship between inferred immigrant status and population genetic diversity. Instead, our results suggest that the time to recover genetic diversity following bottlenecks is quite long. Alternatively, other factors such as lower effective population size or fewer closely related species with which to hybridize in a new biogeographic region (Caron et al., 2019; Larson et al., 2021) could result in a lower equilibrium level of genetic diversity in immigrant populations.

Mean genetic diversity did not significantly differ between the two sites we sampled (Figure 2). We expected that mean genetic diversity would have been higher in the western Amazon than in Central America because the Amazon represents a larger habitat area intersected by fewer biogeographic barriers than Central America, which could facilitate greater genetic connectivity with a wider regional gene pool; because the western Amazon was more climatically stable during Pleistocene glacial cycles and could have been less susceptible to repeated population bottlenecks (Baker et al., 2020; Dick & Pennington, 2019); and because most lowland Neotropical rain forest trees are believed to have South American rather than North American origins (Antonelli et al., 2018; Gentry, 1982). Nonetheless, the difference in mean π between sites was in the expected direction and only marginally non-significant (Yasuní: 5.00×10^{-3}; BCI: 4.35×10^{-3}; $p = .077$), suggesting that future studies may benefit from further investigation of broad-scale differences in genetic diversity between biogeographic regions, preferably from a larger number of sample sites.

4.4 | Lack of influence of life-history traits

In contrast to previous studies that have detected a correlation between genetic diversity or genetic structure and traits such as dispersal mechanism, pollination mode, mating system, successional stage, and geographic range size in Neotropical plants (Ballesteros-Mejia et al., 2016; Hamrick et al., 1993; Hamrick & Murawski, 1990; Lowe et al., 2018), we found no correlation between any PCs loading heavily with life-history traits (PC1-PC3) and either genetic divergence or diversity (Tables 2 and 3). Early-successional life history has previously been associated with low genetic diversity in Neotropical trees (Lowe et al., 2018) and other plant life forms (Ballesteros-Mejia et al., 2016), likely because populations of early-successional plants are susceptible to frequent loss of genetic diversity during founder effects when repeatedly colonizing new habitats (Lowe et al., 2018). We would therefore have expected a positive relationship between genetic diversity and PC3, because low values of PC3 are associated with low resource investment in leaf and wood tissues (Figure 3d) suggesting rapid growth and an early-successional life history (Swaine & Whitmore, 1988; Wright et al., 2010), but no such correlation was detected (Table 3). Additionally, a positive relationship between geographic range size and genetic diversity has previously been reported in Neotropical trees (Lowe et al., 2018), yet we found no relationship between PC1 (highly loading with geographic range size; Figure 3b) and genetic diversity (Table 3).

The lack of a significant relationship between life-history traits and genetic structure might imply that while relevant to local-scale genetic structure, life-history traits have little influence on genetic structure at the continental scale. However, we caution against this interpretation due to the limited trait variation among the species included in the present study. Widespread Neotropical rain forest species have previously been shown to be enriched in certain ecological characteristics relative to spatially restricted species (Bemmels et al., 2018), suggesting that some ecological strategies are likely to be overrepresented among our study species. All of our study species have broad geographic ranges (Figure S4) and a demonstrated ability to disperse over great distances and colonize new habitats. Species with a broader diversity of traits could not be included in the present study because our study was by definition limited to widespread species. Future research that includes rare, endemic, and ecologically specialized species may yet uncover a strong influence of species traits on broad-scale genetic structure that was not detected here.

4.5 | Future directions

Our results suggest that cross-Andean dispersal has left a lasting legacy in the population genetic structure of widespread Neotropical rain forest trees co-distributed in the western Amazon and Central America. However, we did not investigate the precise biogeographic history of any particular species, and caution that further studies are needed to validate our interpretations, including phylogeographic studies with detailed sampling around the northern Andes and across different subregions of the Amazon. Such studies are rare but will become increasingly feasible as sequencing costs continue to drop and as ongoing resolution to decades-long civil conflict improves access to the Colombian lowlands for phylogeographic sampling (Serrano et al., 2021). The broad patterns we detect provide hypotheses that should be further tested using in-depth species-specific genomic studies that explicitly infer species' biogeographic origins, timing and routes of dispersal, geographic sources of population expansion, and range-wide patterns of genetic diversity.

AUTHOR CONTRIBUTIONS

Jordan B. Bemmels: formal analysis; investigation; visualization; writing—original draft preparation. **Álvaro Pérez:** resources. **Renato Valencia:** conceptualization; writing—review and editing. **Christopher W. Dick:** conceptualization; funding acquisition; supervision; writing—review and editing.

ACKNOWLEDGMENTS

We thank N. Wei for assistance with fieldwork in Panama and O.M. Vargas for guidance with figure preparation. Funding was provided by the National Science Foundation (DEB 1240869 and FESD Type I 1338694 to CWD), and the University of Michigan Department of Ecology and Evolutionary Biology and Rackham Graduate School. Graduate-student support was provided to JBB by the Natural Sciences and Engineering Research Council of Canada (Postgraduate Scholarship M; CGSM-410253-2011) and the National Science Foundation (Graduate Research Fellowship Program). We are grateful to fieldworkers who have assisted in characterizing the taxonomic complexity of the Yasuní Forest Plot, in particular G. Villa, P. Alvia, M. Bass, and R. Foster. Pontificia Universidad Católica del Ecuador has supported the Yasuní Forest Plot since it was established in 1995. Botanical collections and voucher specimens from Yasuní were made possible with collecting permits granted by the Ecuadorian Ministry of Environment (MAE).

CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: doi:10.5061/dryad.qv9s4mwnd (Bemmels et al., 2024).

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How to cite this article: Bemmels, J. B., Pérez, Á., Valencia, R., & Dick, C. W. (2024). Patterns in the genetic structure of 49 lowland rain forest tree species co-distributed on opposite sides of the northern Andes. *Biotropica*, *56*, e13303. https://doi.org/10.1111/btp.13303