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Fine-scale niche structure of Neotropical forests reflects a legacy of the Great American Biotic Interchange

Brian E. Sedio¹, John R. Paul², Charlotte M. Taylor³ & Christopher W. Dick^{1,4}

The tendency of species to retain their ancestral niches may link processes that determine community assembly with biogeographic histories that span geological time scales. Biogeographic history is likely to have had a particularly strong impact on Neotropical forests because of the influence of the Great American Biotic Interchange, which followed emergence of a land connection between North and South America ~3 Ma. Here we examine the community structure, ancestral niches and ancestral distributions of the related, hyperdiverse woody plant genera *Psychotria* and *Palicourea* (Rubiaceae) in Panama. We find that 49% of the variation in hydraulic traits, a strong determinant of community structure, is explained by species' origins in climatically distinct biogeographic regions. Niche evolution models for a regional sample of 152 species indicate that ancestral climatic niches are associated with species' habitat distributions, and hence local community structure and composition, even millions of years after dispersal into new geographic regions.

¹Department of Ecology and Evolutionary Biology, University of Michigan, 830 N. University, Ann Arbor, Michigan 49109, USA. ²Department of Biology, Colorado State University, Fort Collins, Colorado 80523, USA. ³Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, USA. ⁴Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama. Correspondence and requests for materials should be addressed to B.E.S. (email: bsedio@umich.edu).

Recent advances in systematic biology have revealed a closer relationship between ecological and biogeographic processes than previously assumed^{1–4}. The ancestral geographic distributions of organisms might exert lasting influences as they assemble into communities because of a phenomenon known as phylogenetic niche conservatism (PNC)³, in which related taxa retain important aspects of the niche of their common ancestors. Exceptions to this general rule are not uncommon but major evolutionary departures from ancestral niches typically involve instances of geographic or environmental isolation, in which alternative niches are uncontested^{5,6}. In the absence of such isolation or, conversely, in the presence of suitable migration corridors, Donoghue⁶ and colleagues^{1,7} have suggested that ‘it is easier to move than to evolve.’ That is, it is more likely for organisms to migrate to habitats for which they are already adapted than to adapt to marginal or novel conditions *in situ*. This hypothesis has proved useful in explaining broad-scale patterns of biodiversity, such as the latitudinal gradient in diversity (a.k.a. the tropical conservatism hypothesis)¹ and the recent radiation of cold-adapted Laurasian, even Himalayan, plant lineages in the Andean cordilleras⁸. Niche conservatism might also allow geographic history to influence the assembly of ecological communities over shorter time periods and at finer spatial scales^{9–11} if the habitat affinities of species comprising contemporary ecological communities are similar to ancestral ecological niches that evolved in response to environments experienced elsewhere.

The biogeographic history of Neotropical forests has been dominated by two geologically recent events^{12,13}. The uplift of the northern Andean cordilleras (25–3 Ma)¹⁴ increased the climatic diversity of northwestern South America¹², whereas the subsequent emergence of the Isthmus of Panama at ~3 Ma¹⁵ made possible the Great American Biotic Interchange (GABI), which brought species with a history of selection in climatically distinct geographic regions into contact with novel environments and into competition with natives as well as co-immigrants.

If functional traits have tended to evolve *in situ* in response to selection pressure exerted by the local environment and community, taxa are likely to have departed from ancestral niches and show little evidence of PNC. Alternatively, if species tend to track preferred microenvironments after dispersal to new regions, then local species composition may reflect the geographic history of species or lineages before the interchange. These alternative assembly mechanisms have important implications for our understanding of species coexistence in tropical forests, which have proved an enduring challenge to ecological theory. Neutral theory posits that niche differences are unimportant relative to stochastic drift and immigration¹⁶. Counter examples point to subtle but pervasive niche differences as evidence that communities are structured by competition, character displacement and limiting similarity¹⁷. If such niche differences are contingent upon historical geographic mixing rather than *in situ* character evolution, it may suggest that the stabilizing effect of those niche differences has a smaller role in community assembly than commonly assumed.

Here we address three questions concerning the influence of biogeographic history on the assembly of communities. Do species distributions in an environmentally heterogeneous locality reflect the geographic origins of member taxa? Was niche evolution significantly influenced by the geographic history of phylogenetic lineages? And finally, has the GABI enhanced phylogenetic and functional trait diversity in Neotropical tree communities?

To address these questions, we examine the biogeographic history, trait evolution and community structure of members of two closely related and hyperdiverse genera *Psychotria* L.

and *Palicourea* Aubl. (Rubiaceae), which comprise ~2,300 tropical woody plant species, including ~1,000 species in the Neotropics¹⁸. We find that ~50% of the variation in hydraulic traits, a strong determinant of community structure, is explained by species’ origins in climatically distinct biogeographic regions. Niche evolution models for a regional sample of 152 species indicate that ancestral climatic niches are associated with species’ habitat distributions, and hence local community structure and species composition, even millions of years after dispersal into new geographic regions.

Results

Microhabitat patterns reflect biogeographic history. We have shown previously that assemblages of *Psychotria* and *Palicourea* found co-occurring within 134 small, 3-m-radius plots on Barro Colorado Island (BCI), Panama, are more closely related than expected by chance (that is, are phylogenetically clustered)¹⁹. This pattern appears to be driven by habitat-filtering mediated by phylogenetically conserved hydraulic traits that influence a species’ tolerance of seasonal drought¹⁹.

To determine whether local microhabitat patterns reflect biogeographic history, we first determined the ancestral geographic distributions²⁰ of all nodes in a 203-taxon phylogeny of the tribe Psychotrieae (Fig. 1, see Methods). Nearly all Neotropical *Psychotria* found in Central and northern South America descend from a single lineage that diversified in Central America. *Palicourea* originated in northern South America and shows evidence of several mid-Miocene (12–15 Ma) dispersal events into the Northern Andes and into the trans-Andean biogeographic region comprising the Chocó of western Colombia and the Panamanian Darién (Fig. 1a). In addition, some Andean *Palicourea* appear to have dispersed into Central America as long ago as 8 Ma. Many of the extant taxa we analysed are widespread (Supplementary Fig. S1); their geographic origins were inferred from the distributions of less widespread relatives²⁰.

By comparing geographic origins with local microhabitats, we find that nearly 50% of the variation in species soil moisture distribution on BCI is explained by differences in the biogeographic area of origin of the study taxa (Fig. 1b,c). Likewise, biogeographic origin explains 51% of the variation in leaf water potential at turgor loss (ψ_t) among the BCI species (Fig. 1c). These associations suggest that by filtering species with similar hydraulic traits, fine-scale soil moisture environments on BCI effectively segregate species of *Psychotria* and *Palicourea* with shared biogeographic histories.

To further examine the association between geographic history and microhabitat preferences, we investigated broad climatic niche differences among species that may, in turn, reflect climatic differences between Neotropical geographic regions. We conducted a principal component analysis of species distributions with respect to 20 climatic variables (see Methods). Four principal components (PCs) explain 94% of the variation in climatic niche (Table 1). PC1, defining 46% of the variance, is largely defined by elevation and associated temperature variables, whereas PC2, comprising 27% of climatic niche variance, largely reflects a latitudinal gradient in temperature seasonality (Table 1).

The PC3 axis is largely explained by precipitation and precipitation seasonality, comprising a gradient between dry, seasonal climates and wetter, less seasonal ones (Table 1). Although PC3 defines only 12% of the variance in species regional distributions, it provides the most insight regarding microhabitat distributions on BCI. Species that tolerate very negative leaf water potentials (ψ_t) and occur in dry microsites on BCI have significantly more positive scores along PC3 (Fig. 1c). This result suggests that species distributions with respect to

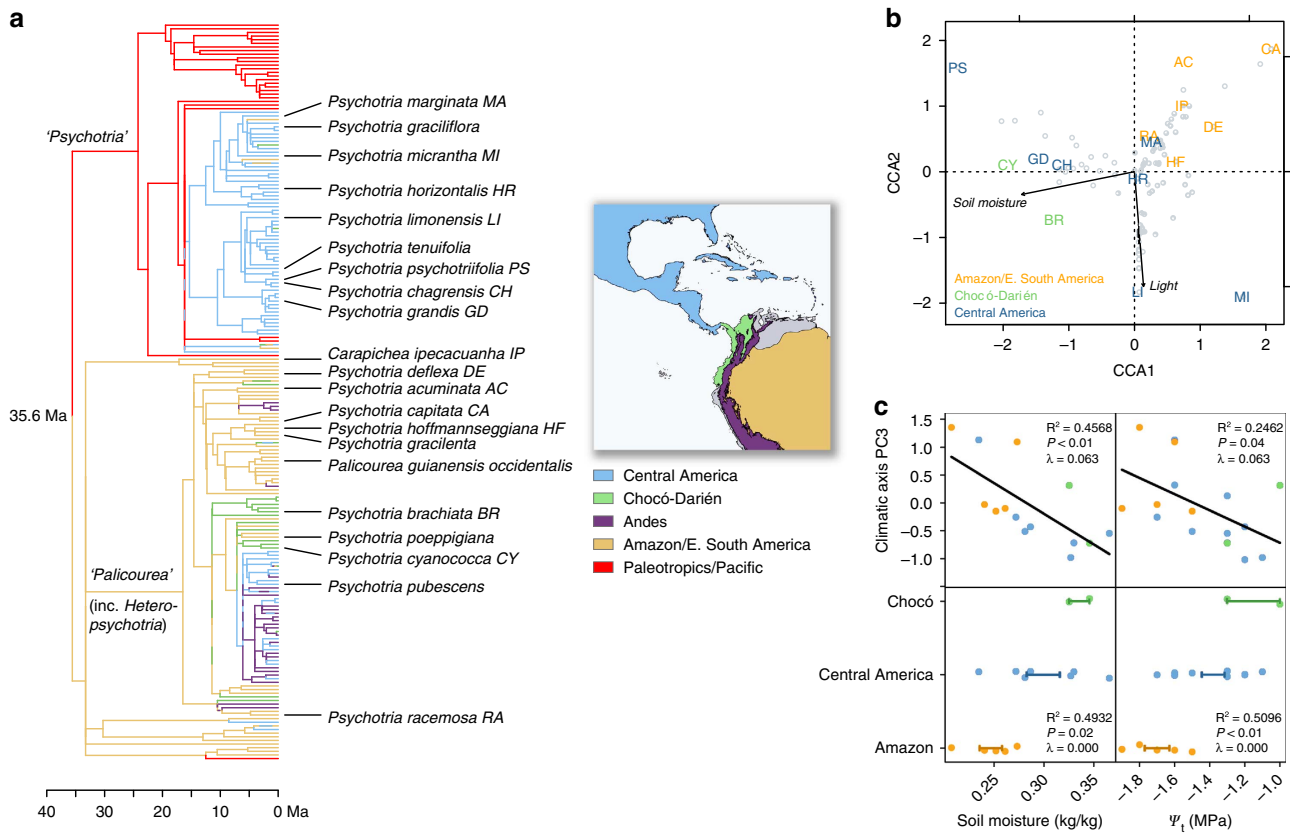


Figure 1 | Biogeographic history and community structure of *Psychotria* and *Palicourea*. The relationship of habitat distribution and hydraulic traits is indicated with respect to climatic niche and biogeographic region of origin among 20 *Psychotria* and *Palicourea* of BCI. (see Methods for discrepancy between clades and taxonomic nomenclature) **(a)** Ancestral area reconstruction. Branch colour indicates the geographic region in which the branch originated. **(b)** Canonical correspondence analysis of the habitat distributions of the 15 most abundant species censused in 134 3-m-radius plots on BCI¹⁹ showing soil moisture and light as important correlates of species composition. Abbreviations for species following complete names are provided in **a** and their colour indicates the species' geographic region of origin **(c)** PGLS linear regression of species climatic niche with respect to PC3 and PGLS analysis of variance of geographic origin versus species-weighted mean distribution with respect to soil moisture on BCI and leaf water potential at turgor loss (ψ_t); λ indicates phylogenetic signal.

regional climatic gradients, such as those defined by precipitation, are representative of their distributions with respect to local environmental variation, such as soil moisture heterogeneity²¹, providing a potential causative link between geographic history and local community composition.

Geographic history influences hydraulic niche evolution. To test whether geographic history has constrained niche evolution of *Psychotria* and *Palicourea*, we compared the relative fit of eight alternative models of climatic niche evolution²². Three models represent scenarios in which geographic regions have had no influence on species' climatic niches (Fig. 2a–c). Alternatively, if geographic history has left a signature, it may be reflected in the parameter θ , the 'optimum' niche towards which species are selected in a model of random walk with stabilizing selection²². If climatic niches are strongly conserved, broad clades may be fit by a single value of θ that reflects the climate of the region in which lineage diversification took place ('clade history' models Fig. 2d–f). Finally, if climatic niche evolution has occurred on a timescale commensurate with that of the changing geographic history of the taxa, climatic niches may have evolved with respect to a θ defined by the region in which each species originated (the 'taxon history' model, Fig. 2g). We also examined a variant of the 'taxon history' model in which the only meaningful regional

differences were between Andean and non-Andean regions (the 'Andes history' model, Fig. 2f).

Niche evolution with respect to PC3 is best characterized by the 'taxon history' model (Fig. 2g) in which the selection optimum reflects the region of origin of each taxon in the phylogeny. Broad climatic differences between major regions of the Neotropics appear to influence the niche evolution of *Psychotria* and *Palicourea*, and to continue their association with the habitat distributions of widespread species after dispersal to new regions.

Community assembly and the GABI. To assess the generality of the patterns observed on BCI, we examined the geographic origins of the *Psychotria* and *Palicourea* assemblages documented at 13 sites across the Neotropics (Fig. 3). The seven South American sites are dominated by lineages with South American origins, whereas the four Central American moist forests are inhabited by lineages with a long history in Central America and by relatively recent immigrants from South America (Fig. 3a). Central American dry forests appear species poor and largely devoid of *Palicourea*.

The contribution of immigration within the last 3 Ma to the phylogenetic diversity of each site differs significantly by region (Fig. 3b). The diversity of the four Central American moist forests

Table 1 | PCs of climatic niche variation.

Variable	PC1	PC2	PC3	PC4
Elevation	-0.30	0.18	-0.06	0.04
Bio1	0.30	-0.16	0.08	-0.06
Bio2	-0.17	-0.07	0.40	0.22
Bio3	0.02	0.36	0.14	-0.27
Bio4	-0.06	-0.33	0.10	0.37
Bio5	0.26	-0.24	0.15	0.04
Bio6	0.32	-0.05	-0.03	-0.17
Bio7	-0.15	-0.25	0.26	0.34
Bio8	0.28	-0.21	0.12	0.00
Bio9	0.31	-0.12	0.03	-0.10
Bio10	0.29	-0.20	0.08	-0.01
Bio11	0.31	-0.10	0.06	-0.13
Bio12	0.21	0.26	-0.15	0.27
Bio13	0.19	0.11	-0.38	0.33
Bio14	0.14	0.29	0.35	0.15
Bio15	-0.09	-0.29	-0.37	0.16
Bio16	0.20	0.14	-0.32	0.35
Bio17	0.16	0.30	0.33	0.13
Bio18	0.18	0.21	0.17	0.45
Bio19	0.23	0.25	-0.12	0.01
Eigenvalue	9.10	5.41	2.50	1.81
% Variance	45.48	27.03	12.49	9.06
Pagel's ⁴³ λ	0.00	0.67	0.06	0.10

Factor loadings and squared s.d. (Eigenvalues) are shown for the four PCs of climatic niche variation among 152 Neotropical *Psychotria* and *Palicourea*. Bioclimatic variables: Bio1 = annual mean temperature; Bio2 = mean diurnal temperature range; Bio3 = temperature isothermality; Bio4 = temperature seasonality; Bio5 = maximum temperature of warmest month; Bio6 = minimum temperature of coldest month; Bio7 = temperature annual range; Bio8 = mean temperature of wettest quarter; Bio9 = mean temperature of driest quarter; Bio10 = mean temperature of warmest quarter; Bio11 = mean temperature of coldest quarter; Bio12 = annual precipitation; Bio13 = precipitation of wettest month; Bio14 = precipitation of driest month; Bio15 = precipitation seasonality; Bio16 = precipitation of wettest quarter; Bio17 = precipitation of driest quarter; Bio18 = precipitation of warmest quarter; Bio19 = precipitation of coldest quarter. Pagel's⁴³ λ can be interpreted as the degree of phylogenetic signal, with $\lambda = 0$ indicating no phylogenetic signal and $\lambda = 1$ indicating a Brownian motion model. PC2 and PC4 exhibit weak phylogenetic signal (95% confidence interval (CI), PC2 $\lambda = 0.242$ -0.877; PC4 $\lambda = 0.002$ -0.614). PC1 and PC3 do not depart significantly from $\lambda = 0$ (95% CI, PC1 λ ranges to 0.556; PC3 λ ranges to 0.133).

is substantially more affected than that of sites east of the Andes ($P < 0.0001$; t -test) or in South America in its entirety ($P < 0.0001$). The effect on functional diversity as reflected in species climatic niches relative to PC3 is less substantial (Fig. 3c). Recent immigrants to sites east of the Andes appear to be functionally redundant with natives, whereas the effect varies widely among the four Central American moist forests, perhaps because of the influence of South American immigration before the closure of the land bridge (Figs 1a and 3a).

Discussion

Our results indicate that the hydraulic traits and microhabitat niches of the *Psychotria* and *Palicourea* of BCI are associated with the region of origin of species before dispersing to central Panama during the GABI. This result suggests that the filtering of species with similar hydraulic traits over fine-scale soil moisture gradients on BCI not only results in phylogenetically clustered assemblages¹⁹ but also effectively selects species of *Psychotria* and *Palicourea* with a shared biogeographic and climatic history.

An examination of the geographic origins of the *Psychotria* and *Palicourea* recorded in 13 Neotropical forests suggests that the contribution of the GABI to local community composition has been widespread in humid Central America, but much less pervasive in South American forests, even those west of the Andes (Fig. 3), a pattern noted by botanists for the broader Neotropical flora²³. What has not been recognized previously is that recent

biogeographic admixture has probably increased the phylogenetic and functional diversity of Central American forests relative to areas less influenced by the GABI. These results suggest that, because of the prevalence of ecologically conservative dispersal in community assembly, the phylogenetic and functional structure of local communities depend on the phylogenetic and climatic diversity of the source pool from which the communities were assembled, making community structure and function a product of biogeographic exchange^{11,13,15}.

The spatial scale at which community structure reflects the geographic history of species of *Psychotria* and *Palicourea* on BCI is striking. Associations between biogeographic history and large-scale climatic or macrohabitat preferences have been observed in plants in the Valerianaceae⁸ and in Emydid turtles⁹. In contrast, the hydraulic niches that characterize *Psychotria* and *Palicourea* with a common centre of origin differentiate species on a scale of only a few metres in the forest understory¹⁹, and therefore bring biogeographic assembly into a spatiotemporal scale that is commensurate with competition and ecological coexistence.

Understanding the coexistence of hundreds, even a thousand, of species of woody plants in some tropical forests has proved an enduring challenge and has stimulated some of the most influential, and controversial, theories of coexistence and community assembly^{24,25}. Hubbell's¹⁶ Neutral theory posits that the stabilizing effect of species niche differences is less important than demographic stochasticity and immigration in the assembly of communities. Meanwhile, evidence of pervasive, although subtle, trait dispersion in communities may support a role for resource- and regeneration-based niche differences in stabilizing species coexistence¹⁷. If the hydraulic niches considered here were strongly governed by interactions that limit the similarity of co-occurring species or otherwise favoured the exploitation of unoccupied niche space, *in situ* character evolution would be expected to erase the signature of a biogeographic interchange that took place 3 Ma. In contrast, our results suggest that hydraulic niche differences and their prevalence in tropical forest communities may be strongly influenced by historical contingency, making community structure and the niche differences of co-occurring species a product of biogeographic processes such as changes in dispersal barriers and corridors that connect regions with unique climates. If the patterns exhibited by two hyperdiverse genera of Rubiaceae pertain to other species-rich plant genera²³, it would suggest that hydraulic niches, and possibly other easily measured trait dimensions, contribute relatively little to the stabilization of coexistence in tropical forest communities²⁴. On the other hand, other niche dimensions may strongly stabilize coexistence, including those pertaining to interactions with natural enemies²⁶. It remains unclear to what extent the major resource- and enemy-defined niche dimensions of tropical trees are characterized by *in situ* evolution or PNC.

Our results indicate that the comparatively slow rate of niche evolution relative to changes in geographic distribution has left a notable historical signature on the community structure of one of the most diverse plant clades on the planet, particularly where biogeographic interchange has been recent and pervasive as a result of the GABI. The importance of geographic mixing for the niche structure of Neotropical communities further suggests that widespread niche differences among co-occurring tropical trees may owe as much to the history of dispersal as to selection for niche segregation imposed by competitive interactions.

Methods

Taxonomy versus Clades. The taxonomy of the Psychotriaceae does not yet reflect recent findings in molecular phylogenetics, which indicate that the generic name *Psychotria* comprises a polyphyletic group of species^{18,27}. Here we employ '*Psychotria*' to refer to the *Psychotria* subgroup *Psychotria* clade and '*Palicourea*' to

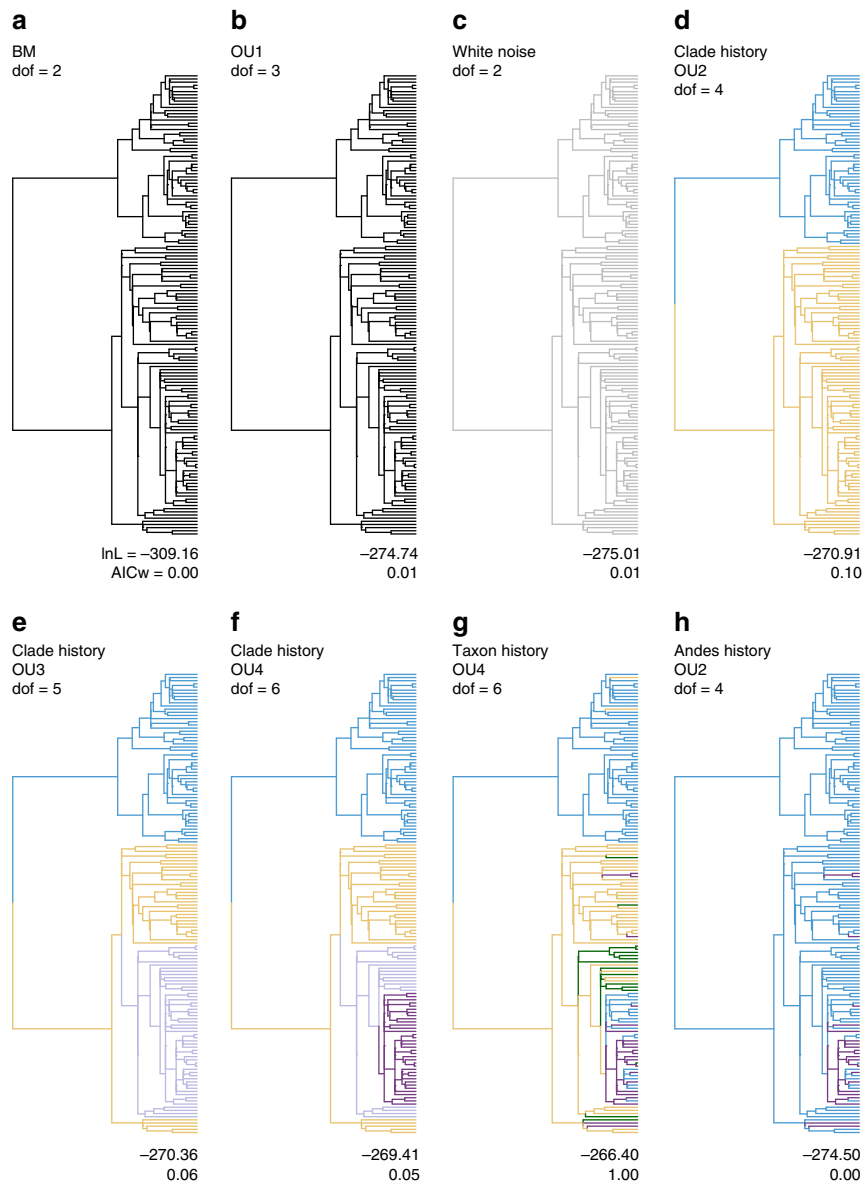


Figure 2 | Comparison of eight alternative models of climatic niche evolution. Log-likelihoods and size-corrected Akaike information criterion (AIC) weights are shown for models pertaining to climatic niche axis PC3. Complete results for all four PCs are shown in Table 2. **(a)** The Brownian motion model in which species randomly drift from the niche of their ancestors³⁹, **(b)** the Ornstein-Uhlenbeck model of random drift with stabilizing selection in which selection increases as species drift further from a single optimal climatic niche²², **(c)** a ‘white noise’ model of evolution, in which species’ climatic niches are drawn from a normal distribution without regard to their phylogenetic relationships or geographic history⁴⁰, **(d-f)** random drift with stabilizing selection towards one of several optimal niches that differ between clades with distinct geographic histories, **(g)** model in which species climatic niches evolve with respect to an optimum niche defined by the geographic region in which each taxon originated and **(h)** a variant of G in which the only meaningful differences are between Andean and non-Andean regions. Model G is the best-fit model.

refer to the clade comprising *Palicourea* plus *Psychotria* subgroup *Heteropsychotria* (that is, *Palicourea s. lat.*). These two groups represent 208 and 803 species, respectively, in the Neotropics (<http://www.tropicos.org>).

Molecular methods and phylogenetic reconstruction. We compiled 247 internal transcribed spacer (ITS) sequences from Psychotriaceae and outgroup species for analysis. These ITS sequences included all Psychotriaceae species represented in GenBank as of 30 October 2011, as well as close relatives used for outgroups, species studied by Paul *et al.*²⁸ and 26 new Psychotriaceae ITS sequences. New sequences were generated following protocols described in the Supplementary Methods and sequenced in both directions at the University of Chicago Cancer Research Center. We discarded a subset of GenBank sequences that could not be reliably attributed to a verified species.

We aligned the 273 sequences using the MUSCLE algorithm²⁹ executed in Geneious 5.1.7 (ref. 30). The resulting 856 bp alignment was then used to

reconstruct the phylogeny in a Bayesian framework based on a general time reversible model of molecular evolution, with gamma-distributed rate variation and a proportion of invariable sites. We ran two concurrent runs of four chains on MrBayes v3.1.2 (ref. 31), via the CIPRES web portal³², for 5×10^6 generations, sampling parameters every 100 generations and a burn-in of 5×10^4 . A chronogram was generated using a PATHd8 (ref. 33) age-estimation of the 50% majority rule Bayesian consensus tree, with the most recent common ancestor of the Psychotriaceae alliance fixed at 48.7 Ma and the crown node of the Psychotriaceae fixed at 35.6 Ma³⁴.

Ancestral area reconstruction. We reconstructed the evolution of geographic ranges in the Neotropical Psychotriaceae using the maximum likelihood dispersal-extinction-cladogenesis model of Ree and Smith²⁰, as implemented in ‘Lagrange’. We employed an unconstrained but temporally stratified model in which the Andes region was not available for dispersal until the oldest estimate of their origination around 25 Ma¹⁴. Dispersal probabilities between regions were assumed to be symmetric.

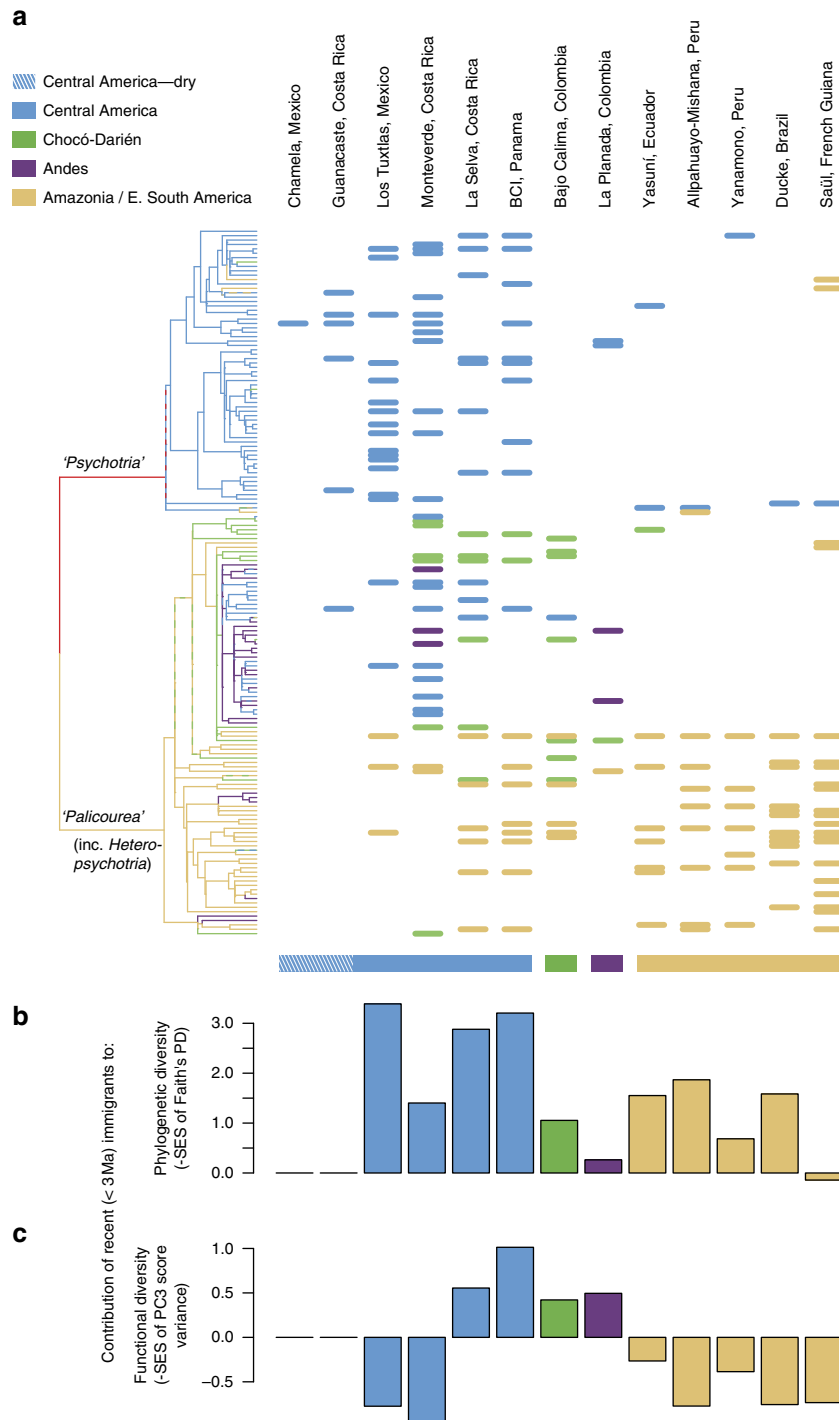


Figure 3 | Biogeographic history of *Psychotria* and *Palicourea* at 13 Neotropical sites. Geographic history and species composition are shown in **a** where the colours indicate ancestral areas of origin. The upper clade is 'Psychotria'. The contribution of immigrants within the last 3 Ma to the phylogenetic (**b**) and functional (**c**) diversity of each site reveals phylogenetic and functional asymmetry in the GABI²³. Floristic inventories of each site can be found in Supplementary Table S1. The region in which each site is located is indicated at the bottom of **a**.

The following five biogeographic regions were used in the analysis: (a) Central America and the Caribbean, (b) the Trans-Andes lowland forest comprising the Chocó region of western Colombia and Ecuador, the Darién region of eastern Panama and Magdalena Valley in Colombia; (c) the Andes at elevations > 1,500 m; (d) the Amazon Basin, Guyana Highlands and eastern Brazil; and (e) Paleotropics, encompassing Asia, Africa and Pacific islands (Fig. 1, inset). Alternative analyses in which distinct northern and central Andes regions were separated at the Huancabamba gap following Gentry²³ differed little from results shown here because only a single species in our sample is restricted to the central Andes. The Andean region is separated here from the Amazonian and Chocó-Darién regions at ~1,500 m based on recent, extensive floristic study of Rubiaceae in this

region^{18,35,36}. As the lower limits of montane forest vary locally, species are characterized as Andean or lowland based on the predominant area of their occurrence. Lastly, lowland savanna regions of northern Colombia and Venezuela and lowland xeric environments of coastal Peru and Chile (grey areas in Fig. 1, inset) were ignored in our analyses.

Climatic data. A total of 21,115 georeferenced herbarium specimens pertaining to 152 species catalogued at the Missouri Botanical Garden (<http://www.tropicos.org>) were mapped using ArcCatalog 10.0 (ESRI, Redlands, CA, USA; mean = 140 records per species, range = 3–1263). For each record, we extracted values for

Table 2 | Alternative models of niche evolution with respect to four climatic axes.

Climatic niche axis	BM	OUI	White noise	Clade history OU2	Clade history OU3	Clade history OU4	Taxon history OU4	Andes history OU2
dof	2	3	2	4	5	6	6	4
PC1								
InL	-417.22	-372.34	-372.34	-372.34	-372.15	-370.53	-369.00	-370.61
AICc	838.51	750.85	748.76	752.95	754.73	753.66	750.59	749.49
AICw	0.0000	0.3529	1.0000	0.1231	0.0508	0.0863	0.4010	0.6946
PC2								
InL	-346.54	-327.07	-330.64	-324.09	-322.59	-322.41	-323.44	-327.04
AICc	697.17	660.30	665.37	656.46	655.60	657.41	659.47	662.37
AICw	0.0000	0.0951	0.0076	0.6509	1.0000	0.4043	0.1444	0.0339
PC3								
InL	-309.16	-274.74	-275.01	-270.91	-270.36	-269.41	-266.40	-274.50
AICc	622.40	555.65	554.10	550.09	551.13	551.42	545.40	557.29
AICw	0.0000	0.0059	0.0129	0.0957	0.0569	0.0494	1.0000	0.0026
PC4								
InL	-306.32	-265.30	-265.30	-260.38	-259.12	-257.96	-253.91	-264.80
AICc	616.72	536.77	534.69	529.04	528.67	528.51	520.42	537.88
AICw	0.0000	0.0003	0.0006	0.0134	0.0161	0.0175	1.0000	0.0002

AIC, Akaike information criterion; BM, Brownian motion; OU, Ornstein-Uhlenbeck.

Log-likelihoods, size-corrected AIC scores (AICc) and relative Akaike weights (AICw) for eight alternative models of climatic niche evolution. Best-fit models that are significantly better than the second-best model by a likelihood ratio test are shown in boldface.

elevation and 19 climatic variables from the WorldClim database at 30-s resolution³⁷. The species mean for each of the 20 variables was calculated and a principal component analysis performed on 152 species pertaining to the Neotropical *Psychotria* and *Palicourea*, or ~15% of the combined hemispheric diversity of the two genera¹⁸. PC1–PC4 explained more variation than expected, based on a broken-stick distribution³⁸ for a total of 94%, and so were used in subsequent analyses. The first three PCs appear to describe geographic gradients in elevation, latitude and precipitation, respectively, based on the loadings of climatic variables (Table 1).

Phylogenetic comparative analysis and climatic niche evolution. We compared a series of eight alternative models that reflect alternative hypotheses concerning the influence of geographic history on niche evolution: a Brownian motion model³⁹, an Ornstein-Uhlenbeck model with a single selection optimum θ , a 'white noise' model in which species niches are independent of phylogeny⁴⁰ and five additional Ornstein-Uhlenbeck models in which θ was allowed to undergo a shift at phylogenetic nodes associated with historic dispersal events²² (Fig. 2). The nodes subtending each of four clades with broadly distinct biogeographic histories were identified as candidates for optimum shifts, so that the most complex model included a distinct θ parameter for each of the four geographic regions plus the parameters σ^2 (strength of drift) and α (strength of selection) for a total of six parameters. Evolution models were fit independently for each of the four PC axes using the R package 'ouch'²² and compared using size-corrected Akaike information criterion weights. Evolution models for PC1–PC4 can be found in Table 2.

Statistical analysis. We employed phylogenetic generalized least squares (PGLS) linear regression to examine the relationship between species PC factor scores and hydraulic traits and soil moisture distributions among the 20 species occurring on BCI using the 'caper' package in R^{41,42}. Pagel's⁴³ λ was estimated for PC3 with respect to the regional phylogeny of 147 taxa, and the maximum likelihood value 0.063 was used for subsequent PGLS linear regression of PC3 on local soil moisture distribution among the BCI species. PGLS analysis of variance with simultaneous maximum likelihood estimation of Pagel's λ was used to analyse the proportion of variation in local soil moisture preferences and hydraulic traits explained by geographic centre of origin for the *Psychotria* and *Palicourea* found on BCI.

Community structure and the GABI. To assess the generality of the patterns observed on BCI, we examined the geographic origins of the *Psychotria* and *Palicourea* assemblages documented at 13 sites across the Neotropics (Fig. 3, Supplementary Table S1). We measured the contribution of immigration within the last 3 Ma to phylogenetic diversity at each site by comparing Faith's⁴⁴ phylogenetic diversity metric (PD) with respect to the native flora to a distribution of expected PD pertaining to samples of equal species richness of the extant flora of each site using the R package 'picante'⁴⁵. In addition, we estimated the contribution of recent South American immigrants to the functional diversity of each site by measuring the variance of native species factor scores relative to PC3 with the variance expected from samples of equal species richness of the extant flora of each

forest site. We more directly measured the influence of the GABI on the functional diversity of BCI by conducting the same procedure with respect to species soil moisture habitat distributions and hydraulic traits. In both types of analysis, we interpreted the negative of the standardized effect size as a measure of phylogenetic or functional diversity.

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Author contributions

B.E.S. conducted the ancestral area reconstruction, climatic niche reconstruction, niche evolution modelling and diversity analyses, and led the writing of the manuscript. J.R.P. conducted the molecular lab work and phylogenetic analyses. C.M.T. conducted the taxonomic classification and specimen verification. B.E.S., J.R.P., C.M.T. and C.W.D. discussed the experimental design and results and contributed to the writing of the manuscript.

Additional information

Accession Codes: The new Psychotriaceae gene sequence data have been deposited in the GenBank nucleotide database under accession numbers KC480521–KC480546.

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