



ANEXO 03 – INFORME ANUAL DE EJECUCIÓN DE ACTIVIDADES DE INVESTIGACIÓN DE LA UNAMAD

SEÑOR(A) VICERRECTOR(A) DE INVESTIGACIÓN DE LA UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS

S. V.

I. Datos informativos

Nombres y apellidos:	ISAU HUAMANTUPA CHUQUIMACO
DNI N°:	42341964
Departamento académico, programa académico o dependencia de la UNAMAD:	CIENCIAS BÁSICAS
Código AIRHSP N°	000419
Registro RENACYT N°	P0016356/Nivel: Investigador Distinguido
Periodo de ejecución	Del 01 de marzo al 31 de diciembre de 2024

Universidad Nacional Amazónica de Madre de Dios
Vicerrectorado de Investigación

RECEPCION - CARGO

FECHA: 17 ENE 2025

REG: 504 FOLIO: 66

HORA: 12:08

UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS
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Huamantupa Chuquimaco

En aplicación del Artículo 9° del REGLAMENTO DEL DOCENTE INVESTIGADOR DE LA UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS (versión 4.0), remito **INFORME ANUAL DE EJECUCIÓN DE ACTIVIDADES DE INVESTIGACIÓN**, cuyos productos describo a continuación:

II. Cronograma de ejecución

N°	OBJETIVO ESTRATÉGICO	ACTIVIDAD VINCULADA + TÍTULO O DENOMINACIÓN	CRONOGRAMA DE EJECUCIÓN (MESES)											
			AÑO 2024											
			M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12
1	Incrementar producción científica per cápita de calidad	Generación de nuevas publicaciones en revistas indizadas	x											
2	Incrementar producción científica per cápita de calidad	Generación de nuevas publicaciones en revistas indizadas		x										
3	Incrementar producción científica per cápita de calidad	Generación de nuevas publicaciones en revistas indizadas			x									
4	Incrementar producción científica per cápita de calidad	Generación de nuevas publicaciones en revistas indizadas				x								
5	Incrementar producción científica per cápita de calidad	Generación de nuevas publicaciones en revistas indizadas					x							
6	Incrementar producción científica per cápita de calidad	Generación de nuevas publicaciones en revistas indizadas						x						
7	Incrementar producción científica per cápita de calidad	Generación de otros productos de investigación							x					
8	Incrementar producción científica per cápita de calidad	Generación de nuevas publicaciones en revistas indizadas								x				
9	Incrementar producción científica per cápita de calidad	Generación de nuevas publicaciones en revistas indizadas									x			
10	Incrementar producción científica per cápita de calidad	Generación de nuevas publicaciones en revistas indizadas										x		
11	Incrementar el número de proyectos de I+D ejecutados por grupos de investigación	Generación de nuevas tesis asesoradas y sustentadas												x
12	Incrementar el número de proyectos de I+D ejecutados por grupos de investigación	Generación de nuevas tesis asesoradas y sustentadas												x
...												

III. Medios de verificación



Nº	ACTIVIDAD VINCULADA	Título (investigación / producto / ponencia / otro)	Medio de divulgación (revista / conferencia / repositorio / otro)	DOI / URL / otro
11. 2	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS (Publicaciones en revista indizada en Scopus o WOS (no se incluyen revistas ESCI), con afiliación del profesor a la UNAMAD)			
11. 3	GENERACIÓN DE NUEVAS TESIS ASESORADAS Y SUSTENTADAS (asesoramiento de tesis de pre o posgrado de la UNAMAD, sustentada)			
11. 7	GENERACIÓN DE OTROS PRODUCTOS DE INVESTIGACIÓN (participación como expositor en congresos científicos, presentación de solicitud de patente o similar, publicación de libro o capítulo de libro de investigación en base científica indizada, solicitud de patente aceptada y en trámite)			
11. 8	CONTRIBUIR A LA FORMACIÓN DE RECURSOS HUMANOS (participación como ponente, asesor de trabajos de investigación para bachillerato, asesor de proyectos de investigación junior)			
1	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	Consistent patterns of common species across tropical tree communities	Artículo publicado en revista NATURE (Anexo 1).	https://www.nature.com/articles/s41586-023-06820-z
2	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	Geography and ecology shape the phylogenetic composition of Amazonian tree communities	Artículo publicado en revista JOURNAL OF BIOGEOGRAPHY (Anexo 2).	https://onlinelibrary.wiley.com/doi/full/10.1111/1/jbi.14816
3	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	One sixth of Amazonian tree diversity is dependent on river floodplains	Artículo publicado en revista Brazilian Journal of Botany (Anexo 3).	https://www.nature.com/articles/s41559-024-02364-1
4	CONTRIBUIR A LA FORMACIÓN DE RECURSOS HUMANOS	Desarrollo de curso de capacitación docente: Análisis de datos con R aplicados a las ciencias básicas	Ponencias por tres días 20,21 y 22 de marzo (Anexo 4).	Resolución de decanatura de la facultad de Ingeniería 076-2024-UNAMAD-DFI
5	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	Advances in Legume Systematics 14. Classification of Caesalpinioideae. Part 2: Higher-level classification	Artículo publicado en revista JOURNAL OF PHYTOKEYS (Anexo 5)	https://phytokeys.pensoft.net/issue/4809/
6	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	A densely sampled molecular phylogeny of <i>Tachigali</i> (Leguminosae), an evolutionarily successful lineage of neotropical ant-housing canopy trees	Artículo publicado en revista Brazilian Journal of Botany (Anexo 6).	https://link.springer.com/article/10.1007/s40415-024-01016-9
7	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	Peru's zoning amendment endangers forests	Artículo publicado en revista Science (Anexo 7)	https://www.researchgate.net/publication/378593251_Peru's_zoning_amendment_endangers_forests
8	GENERACIÓN DE OTROS PRODUCTOS DE INVESTIGACIÓN	Reconocimiento del Proyecto de investigación: Diversidad vegetal y sus procesos ecológicos en las sabanas Húmedas del Pampas del Heath, Bahuaja Sonene, Madre de Dios, Perú	RESOLUCIÓN DE VICERRECTORADO (Anexo 7).	N# 156-2024-UNAMAD-VRI

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9	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	The biogeography of the Amazonian tree flora	Revista científica: Communications Biology (Anexo 8)	https://www.nature.com/articles/s42003-024-06937-5
10	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	The pace of life for forest trees	Revista científica: SCIENCE (Anexo 9)	https://www.science.org/doi/10.1126/science.adk9616
11	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	Assembling the Brazilian flora: overview of Leguminosae diversity	Brazilian Journal of Botany (Anexo 10)	https://doi.org/10.1007/s40415-024-01034-7
12	GENERACIÓN DE NUEVAS TESIS ASESORADAS Y SUSTENTADAS	Reconocimiento como asesor del Proyecto de Tesis (ETNOBOTÁNICA CUANTITATIVA DE LA FLORA ARBÓREA DEL BOSQUE AMAZÓNICO DEL FUNDO EL BOSQUE - UNAMAD, LAS PIEDRAS, TAMBOPATA).	Resolución de decanatura (Anexo 11)	N# 624-2024-UNAMAD-DFI
13	GENERACIÓN DE NUEVAS TESIS ASESORADAS Y SUSTENTADAS	Reconocimiento como asesor del Proyecto de Tesis (Regeneración natural del "Tornillo" Cedrelinga cateniformis (Ducke) Ducke, en el bosque de tierra firme del fundo el bosque - UNAMAD, Las Piedras - Madre de Dios).	Resolución de decanatura (Anexo 12)	N# 610-2024-UNAMAD-DFI

11.4 LIDERAR, DIRIGIR O ASESORAR (grupo de investigación, semillero de investigación, centro de investigación, instituto de investigación u otra modalidad organizativa)¹

11.9 ASUMIR CARGOS VINCULADOS EN LA GESTIÓN DE LA INVESTIGACIÓN (coordinador general de proyecto de investigación, designación cargo de director de órgano de línea del VRI)²

11.10 PARTICIPACIÓN COMO EVALUADOR EN CONVOCATORIAS DE INVESTIGACIÓN (miembro de comité evaluador, miembro de comité científico de revistas institucionales, miembro de jurado de tesis)³

N°	ACTIVIDAD VINCULADA (denominación de la actividad)	Denominación (nombre / título / cargo / convocatoria / tesis / otro) del medio de verificación ^{1,2,3}	Documento sustentatorio (Acta / resolución / contrato / otro)
1	GENERACIÓN DE NUEVAS TESIS ASESORADAS Y SUSTENTADAS		
2	Elija una actividad.		
3	Elija una actividad.		
4	Elija una actividad.		
5	Elija una actividad.		
...			



Puerto Maldonado, 17 de Enero de 2025

Firma (Remitente)

Nombres y apellidos (Remitente)

OBJETIVOS ESTRATÉGICOS

- Incrementar tasa de docentes RENACYT por cada 100 docentes de la UNAMAD
- Incrementar tasa de docentes RENACYT por cada 100 investigadores en formación de la UNAMAD que participan en actividades de I+D+i+e
- Incrementar producción científica per cápita de calidad
- Incrementar el número de proyectos de I+D ejecutados por grupos de investigación

ACTIVIDADES VINCULADAS

- Generación de nuevas publicaciones en revistas indizadas
- Generación de nuevas tesis asesoradas y sustentadas
- Generación de otros productos de investigación
- Contribuir a la formación de recursos humanos



Anexo 1. Artículo publicado en revista NATURE.

Article

Consistent patterns of common species across tropical tree communities

<https://doi.org/10.1038/s41586-023-06820-z>

Received: 3 December 2022

Accepted: 1 November 2023

Published online: 10 January 2024

Open access

Check for updates

Trees structure the Earth's most biodiverse ecosystem, tropical forests. The vast number of tree species presents a formidable challenge to understanding these forests, including their response to environmental change, as very little is known about most tropical tree species. A focus on the common species may circumvent this challenge. Here we investigate abundance patterns of common tree species using inventory data on 1,003,805 trees with trunk diameters of at least 10 cm across 1,568 locations¹ in closed-canopy, structurally intact old-growth tropical forests in Africa, Amazonia and Southeast Asia. We estimate that 2.2%, 2.2% and 2.3% of species comprise 50% of the tropical trees in these regions, respectively. Extrapolating across all closed-canopy tropical forests, we estimate that just 1,053 species comprise half of Earth's 800 billion tropical trees with trunk diameters of at least 10 cm. Despite differing biogeographic, climatic and anthropogenic histories², we find notably consistent patterns of common species and species abundance distributions across the continents. This suggests that fundamental mechanisms of tree community assembly may apply to all tropical forests. Resampling analyses show that the most common species are likely to belong to a manageable list of known species, enabling targeted efforts to understand their ecology. Although they do not detract from the importance of rare species, our results open new opportunities to understand the world's most diverse forests, including modelling their response to environmental change, by focusing on the common species that constitute the majority of their trees.

Tropical forests are a crucial component of the Earth system: they cover around 10% of the Earth's land surface¹ but contribute approximately 33% of terrestrial net primary productivity². They account for around 40% of the carbon stored in live vegetation³ and are globally important carbon sinks⁴. Tropical forests are also extraordinarily biodiverse, harbouring two-thirds of all known species⁵ and the majority of the world's biodiversity hotspots⁶. Of note, as many tree species can be found in a single hectare of tropical forest as in the entire native Western European tree flora⁷. Recent estimates suggest that there are approximately 37,900 named tropical tree species in the scientific literature⁸, with potentially thousands more yet to be identified by scientists⁹. This extraordinary diversity means that little is known about the biology of the vast majority of tropical tree species. Our understanding of tropical forest ecology, productivity and carbon storage and how they may respond to environmental change is hindered by this lack of knowledge. This limited understanding also curtails scientific input into land use, biodiversity, climate and other forest-related policy and management.

Our understanding of tropical forests may improve through a focus on the most common tree species. This is a promising avenue, given that species abundance distributions (SADs) showing a modest number of common species and much larger numbers of rare species have been documented across taxa globally^{10–12}. Indeed, analyses of tropical forest inventory data from Amazonia have shown that a relatively small number of common species comprise a majority of trees in the region^{13–15}. However, whether such patterns hold in other tropical forests is unknown, as there have been no comparable analyses for African or Southeast Asian tropical forests. Perhaps, given the substantial

differences in total tree species richness¹⁶, forest structure¹⁷, contemporary climate¹⁸ and biogeographic and human-occupancy histories¹⁹ among continents, important contrasts in patterns of common species would be expected. Alternatively, if the same processes or mechanisms apply to all tropical forests²⁰, highly consistent patterns may be expected. Crucially, if a tractably modest number of common species do comprise the majority of tropical trees on Earth, this could open new ways of understanding tropical forests by investigating the ecology of the common species.

Cross-continental comparisons of common species patterns are complicated by unresolved differences in the results from published Amazon forest studies^{6,20,21}. Estimates of hyperdominance—describing the minimum number of species required to account for 50% of all trees in a sample—range from 1.4% to 8.2% of the total number of species found in each of the Amazon forest datasets analysed (corresponding to 224 and 1,312 hyperdominant species respectively, assuming 16,000 Amazon tree species). Therefore, here we: (1) investigate sample-related biases and standardize our sampling to enable meaningful comparisons among datasets; (2) test whether patterns of hyperdominance differ across Amazonia, Africa and Southeast Asia; (3) extrapolate our results to assess how many species comprise half of all Earth's tropical trees; (4) assess species abundance patterns, with differing classifications of 'common species' beyond hyperdominance; and (5) use resampling techniques to assess which sampled species are likely to be hyperdominant.

We analyse species abundance data from networks of inventory plots across three continents. We limit our analysis to closed canopy

A list of authors and their affiliations appears online. Reprints and permissions: www.nature.com/reprints. E-mail: doan.docent@unamad.edu.pe; el.louis@unamad.edu.pe



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Fig. 1 Location of the 1,568 plots, tropical forest regions, and tropical forest biome extent used in the study. Dots show the location of the plots analysed, coloured by continental region. Dark green shows the Amazonia

Africa and Southeast Asia regions that we extrapolate to. Light green shows tropical and subtropical moist broadleaf forests⁴⁰, which we extrapolate to as the closed canopy tropical forest biome.

structurally intact old-growth tropical forests. For Amazonia, defined as the lowland Amazon Basin and Guiana Shield, we use the Amazon Tree Diversity Network and RAINFOR datasets ($n = 1,097$ plots). For Africa, encompassing West, central and East Africa, we use the African Tropical Rainforest Observatory Network (African Rainforest Plot Network), and two smaller networks²² ($n = 368$ plots). For Southeast Asia, defined as extending from Myanmar in the West to Sulawesi in the East, we use a tree diversity⁴ and a carbon monitoring⁴¹ network ($n = 103$ plots). We limit our analysis to trees with trunk diameter of at least 10 cm at breast height (1.3 m along the stem or above any buttresses or deformities), the widely used minimum size for inventorying tropical trees. The combined dataset includes 1,003,805 trees, of which 93.3% are identified to species (Fig. 1 and Extended Data Table 1).

Consistent patterns of commonness

The Africa, Amazonia and Southeast Asia datasets differ in the number and size of plots sampled and the number of trees sampled (Extended Data Table 1). We therefore excluded small plots (below 0.9 ha; Extended Data Fig. 1 and Methods) and used rarefaction—that is, repeated random subsampling of plots to comparable numbers of trees—to standardize sampling across the three datasets (Fig. 2).

Rarefying to a common sample size of 77,587 stems, the size of the Asia dataset (equivalent to 150, 116 and 103 plots in Africa, Amazonia and Southeast Asia respectively), we find that 77 species (95% confidence interval: 62–92) in Africa comprise 50% of individual trees, compared with 174 species (95% confidence interval: 134–215) in Amazonia and 172 species (95% confidence interval: 125–217) in Southeast Asia (Table 1 and Fig. 2). However, the substantially lower number of hyperdominant species in Africa compared with Amazonia and Southeast Asia scales with the substantially lower number of total species. We find just 1,132 species in our standardized 77,587 tree sample in Africa, compared with 2,565 and 2,585 species in Amazonia and Southeast Asia, respectively for the same sample size. Consequently, percentage hyperdominance is statistically indistinguishable among the continents at 6.79% (95% confidence interval: 5.39%–8.20%), 6.80% (95% confidence interval: 5.24%–8.36%) and 6.65% (95% confidence interval: 4.59%–8.71%) in Africa, Amazonia and Southeast Asia, respectively (Table 1). This consistency is not affected by the aggregated spatial distribution of plots within each region (Extended Data Fig. 2) and holds true for analyses based

solely on 1-ha plots (Methods). Thus, once sampling is standardized, there is marked pan-tropical consistency in the proportion of the total number of tree species accounted for by the most common species.

The consistency of commonness is not limited to defining common species as those that account for 50% of all individual trees in a dataset. The proportions of the total number of species required to account for thresholds between 10% and 90% of individual trees are also highly consistent across the rarefied data for the three continents (Fig. 3 and Extended Data Table 3). Thus, the data from the three continents appear to result from the same underlying statistical distribution.

Our rarefaction analysis shows that the number of hyperdominants, the total number of species and the percentage hyperdominance are dependent on sample size. This is because as plots—and therefore trees—are added to the sample, increasing numbers of rare species start to appear. Meanwhile, most common species have, by definition, already appeared, but their abundances increase. Thus, with increasing sample size, the number of hyperdominants increases, but at an ever-decreasing rate that tends towards saturation (Fig. 2 and Extended Data Fig. 3). The total number of species increases at a decreasing rate with increasing sample size, without apparent saturation. Therefore, as sample sizes increase, the percentage hyperdominance decreases gradually, but does not appear to saturate (Fig. 2 and Extended Data Fig. 3). This sample size dependence is likely to explain the published differences in percentage hyperdominance in Amazonian forests, which follow expectations given the sample size in each study^{6,20,22}.

Amazonia and Southeast Asia show remarkably similar patterns of commonness and diversity. The rarefaction curves of the number of species accounting for 50% of all trees (Fig. 2a), total number of species (Fig. 2b), percentage hyperdominance (Fig. 2c) and Fisher's α —the parameter of the log series distribution shown to best describe tropical tree species abundance distributions⁴² (Fig. 2d)—are almost identical between the two datasets. Furthermore, the numbers of species required to account for any threshold between 10% and 90% of trees in the respective rarefied samples of 77,587 trees are statistically indistinguishable (Table 1 and Extended Data Tables 2 and 3). This equivalence in overall tropical forest diversity patterns between these similarly species-rich regions is particularly striking given their very different biogeographic, climatic and anthropogenic histories, and the fact that Amazonia is one large contiguous region, whereas Southeast Asia is a series of islands and island-like regions.

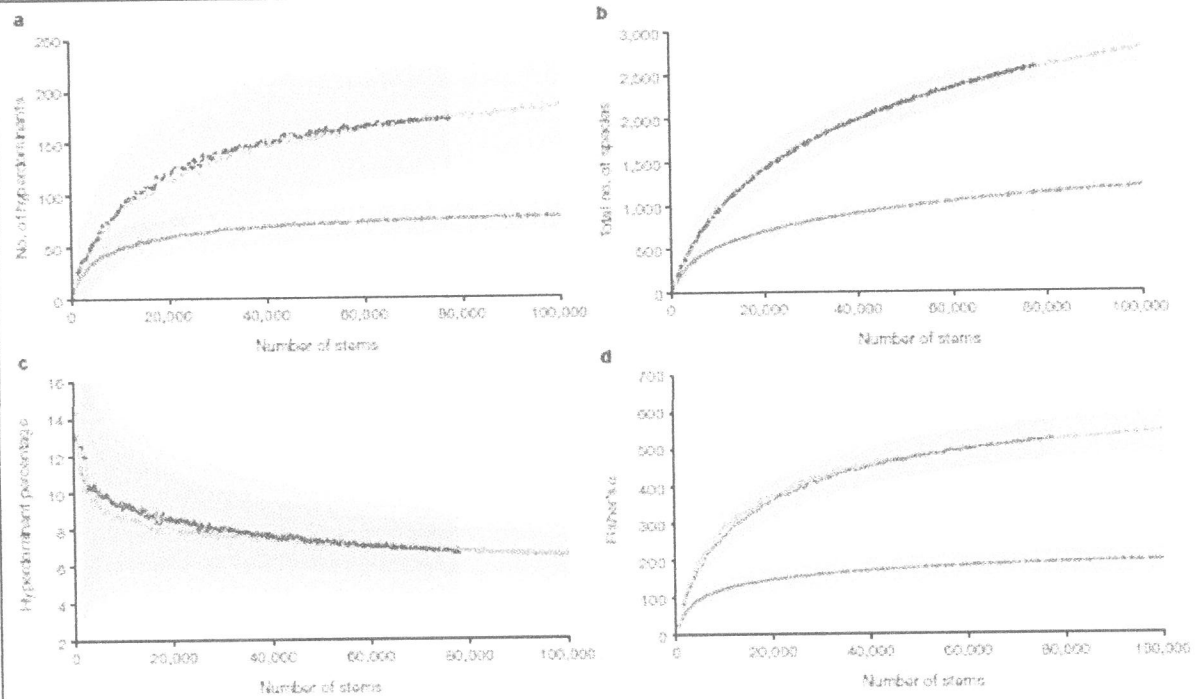


Fig. 2 Rarefaction curves showing the effect of increasing sample size on the number of hyperdominants, total species, hyperdominant percentage and fitted values of Fisher's α in tropical tree communities. **a-d**, The effect of increasing sample size on the number of hyperdominants (**a**), total species (**b**), hyperdominant percentage (**c**) and fitted values of Fisher's α (**d**) in tropical Africa (orange), Amazonia (cyan), Southeast Asia (blue). Rarefied data (mean

values across iterations of subsamples) are shown as points joined by lines for clarity, shaded areas represent 95% confidence intervals (derived via the s.d. across iterations of subsamples taken with replacement at each sampling point). Note that resampling for rarefaction was by subsampling of plots, but curves are re-plotted on an axis of number of stems.

In contrast to the similarity between Amazonia and Southeast Asia, our results provide sample size-corrected validation of the 'odd-one-out' observation^{28,29} of much lower tree species richness in Africa compared with Amazonia and Southeast Asia. Here we add a similar odd-one-out observation of a much lower number of common species in Africa than in Amazonia and Southeast Asia. However, in combination these two results lead to an almost identical percentage hyperdominance in the African, Amazonian and Southeast Asian rarefied data. This consistency extends to the proportion of species required to account for all thresholds between 10% and 90% of trees in the rarefied data (Fig. 3 and Extended Data Table 3). This pan-tropical invariance recasts the tropical forests of Africa from 'odd' in terms of

species richness to statistically indistinguishable from those in Amazonia and Southeast Asia in terms of proportional patterns of abundance. Overall, using standardization by rarefaction, we find consistent patterns of species abundance across Africa, Amazonia and Southeast Asia.

Table 1 | Tree species hyperdominance results for African, Amazonian and Southeast Asian tropical forests, resampled to the common sample size of 77,587 trees

	Number of hyperdominants	Total species	Hyperdominant percentage	Fisher's α
Africa	77 [62, 92]	1,322 [1,069, 1,584]	6.79 [5.39, 8.20]	191 [161, 220]
Amazonia	174 [134, 216]	2,565 [2,419, 2,731]	6.80 [5.24, 8.36]	525 [475, 575]
Southeast Asia	172 [125, 219]	2,585 [2,440, 2,730]	6.65 [4.59, 8.71]	526 [476, 577]

Numbers in brackets are confidence intervals derived from the s.d. across iterations of subsamples taken with replacement at the sample size of the Asia dataset. Resampling done by plot. 77,587 is the size of the Southeast Asia dataset.

Scaling to the study region

Next, we estimate commonness patterns in each of our three study regions: Africa, Amazonia and Southeast Asia. We extrapolate log series fits to the empirical Africa, Amazonia and Southeast Asia datasets (Extended Data Fig. 4), including a correction to account for the clumped spatial occurrence of species, to the total number of trees with trunk diameter of at least 10 cm in each study region. We estimate that just 104 species (95% confidence interval: 101–107) account for 50% of the 113 billion trees in Africa's closed canopy tropical forests (Table 2). We also estimate that just 299 species (95% confidence interval: 295–304) account for 50% of the 34.4 billion trees in Amazonia's closed canopy tropical forest, and 278 (95% confidence interval: 268–289) account for 50% of the 129 billion trees in Southeast Asia's closed canopy tropical forests (Table 2). Our results from Amazonia match those derived using a different extrapolation approach³⁰.

Our extrapolations again outline consistent percentage hyperdominance: just 2.2% of African, 2.2% Amazonian and 2.3% of Southeast Asian species account for 50% of all trees with trunk diameters of at least 10 cm in each region (Table 2). The dominant proportions of total species required to account for 10% to 90% of trees are also very similar across continents (Fig. 3 and Extended Data Table 5). The lower percentage dominance values from the extrapolated data compared



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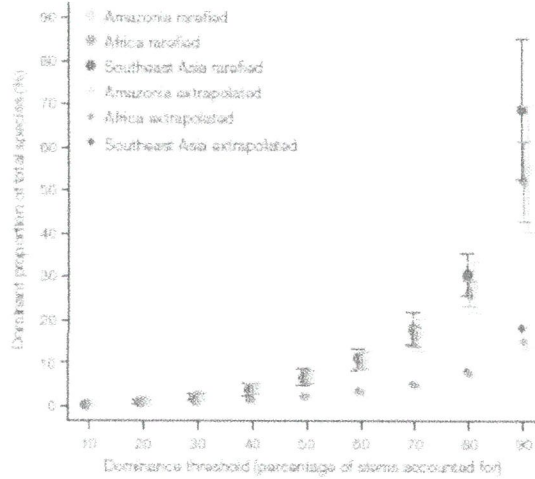


Fig. 3 | The minimum percentage of total species required to account for given dominance thresholds of the total number of stems when this varies from 10% to 90%. Circles show results as rarefied to the size of the Southeast Asia dataset (mean values across iterations of subsamples with 77,587 stems). Diamonds show the extrapolated results at the scale of the regions. Estimated rarefaction confidence intervals are derived from the s.d. across iterations of subsamples taken with replacement at 77,587 stems.

with those from the rarefied data are consistent with the pattern, described above, of many more rare species being added as the number of trees increases while many fewer common species are added (Fig. 2). Overall, the extrapolated results show that there are a tractable number of common species in tropical forests in Africa, Amazonia and Southeast Asia.

Scaling to the tropics

We next estimate the number of common tropical tree species on Earth by multiplying the pan-tropical proportion of common species by the total number of tropical tree species on Earth. Our results suggest a pan-tropical hyperdominant percentage of 2.24% (Table 2). However, our extrapolations cannot provide an estimate of the total number of tropical tree species because we do not—for this study—have data from all tropical regions, including a lack of data from Central America, New Guinea and Micronesia. Furthermore, there is no consensus estimate of the total number of tropical tree species on Earth.

A compilation of lists of species known to science suggests a total of 60,065 tree species globally³⁰. Tropical forest biomes likely comprise 63% of this list (E. Beech, personal communication, 2011), implying that there are around 37,900 known tropical tree species. This minimum estimate does not account for species that are yet to be identified and described by scientists. An alternative extrapolation method estimated that there are 46,900 species for the closed canopy tropical forest biome³¹ (range 40,500–53,300 species), implying that there are 9,000 yet-to-be-identified species. This is in agreement with a recent global study suggesting that there are around 9,200 tree species remaining yet to be formally named, almost all in the tropics³². Thus, together, these studies suggest there are likely to be approximately 47,000 tropical tree species in the world's closed canopy tropical forests.

Our best estimate is that 1,053 tree species (2.24% of 47,000 species) account for half of Earth's 800 billion trees with trunk diameters of at least 10 cm found in the closed-canopy tropical forest biome. Although the true number may be lower or higher, the conclusion that a tractable

Table 2 | Extrapolated tree species hyperdominance results for African, Amazonian, Southeast Asian tropical forests at the regional scale

	Number of hyperdominants	Total species	Hyperdominant percentage
Africa	104 [101, 107]	4,638 [4,531, 4,754]	2.23
Amazonia	299 [296, 304]	13,826 [13,615, 14,038]	2.16
Southeast Asia	278 [268, 289]	11,963 [11,431, 12,475]	2.32
Total	681 [664, 700]	30,427 [29,577, 31,275]	2.24

³⁰Calculated as the sum of the number of hyperdominants and total species across the three major tropical forest regions with hyperdominance percentage denoted therefrom. Prediction intervals (in brackets) combine uncertainty from the standard error of predicted means and the residual s.d. of the regression of the size-occupation fit.

number of species dominate tropical forests is clear. Some of these species are likely to be extraordinarily common: our best estimate is that just 61 species account for 80 billion individual trees (0.13% of 47,000 species). At the other end of the spectrum, we estimate that the rarest approximately 39,300 species account for just 80 billion trees, or 10% of individuals. Meanwhile, the other 90% of all trees are estimated to belong to just 7,487 species (15.93% of 47,000 species). Thus, these results open the possibility of focusing efforts on understanding the biology of a tractable number of species in tropical forests to approximate the whole stand.

Identifying the most common species

Our analyses showing that 104, 299 and 278 common species account for 50% of the trees in our African, Amazonian and Southeast Asian study regions, respectively, do not yield a list of named species. To assess which named species are likely to be hyperdominant, we use a subsampling procedure similar to the rarefaction methodology above. We randomly subsample from approximately 10,000 trees per subsample (drawn by plot) and increase the size of the subsample in 10,000-tree increments until the size of each regional dataset is reached, and repeat this process 100 times. For each sampled increment of 10,000 trees we then calculate the proportion of random subsamples in which each species qualifies as hyperdominant (Supplementary Table 1). We then assign the species to one of four groups:

- (1) Both hyperdominant in the full data and hyperdominant in the majority of subsamples even at very small sample sizes. These 50, 95 and 105 species in our Africa, Amazonia and Southeast Asia datasets, respectively, represent 3.5%, 2.1% and 4.1% of sampled species in each dataset. These species are likely to be geographically widespread and abundant.
- (2) Both hyperdominant in the full data and hyperdominant in the majority of subsamples, but at the smallest sample sizes only occasionally hyperdominant. These 31, 129 and 67 species in our Africa, Amazonia and Southeast Asia datasets, respectively, represent 2.3%, 2.9% and 2.6% of sampled species in each dataset. These species are likely to be geographically widespread but not always abundant.
- (3) Not quite hyperdominant in the full data, but hyperdominant in a substantial proportion of subsamples. These 101, 339 and 200 species in our Africa, Amazonia and Southeast Asia datasets, respectively, represent 7.2%, 7.5% and 7.7% of sampled species in each dataset. These species are probably locally abundant but not necessarily geographically widespread.
- (4) Not hyperdominant in the full data and almost never hyperdominant in the subsamples. These 1,232, 3,929 and 2,213 species in our Africa, Amazonia and Southeast Asia datasets, respectively, represent 87%, 87.5% and 85.6% of sampled species in each dataset. These species are probably neither geographically widespread nor abundant.



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(approximately 120,000 stems) because they did not have more than 80% of trees identified to species. Furthermore, additional taxonomic research on even the most common species is needed given that some of the most common Amazonian³¹ and African^{32,33} tree species have been found to be complexes of several distinct species that are difficult to distinguish in the field. However, the similarity of our results across the three continental regions suggests that the occurrence of such species complexes may also be similar across the continental regions, again implying the operation of fundamental processes in differing forests. Overall, our work underscores the need for investment in taxonomy, particularly given the thousands of rare species we and others¹⁶ document, but also when considering the most common species.

Our best estimate, using extrapolation, that for the tropics as a whole just 1,053 species account for half of Earth's 800 billion tropical trees has potentially profound implications. Rather than attempting to understand tens of thousands of species of tropical trees, a focus on just a few hundred of the most common species can provide a simplified characterization of these otherwise complex forests. Our analyses indicate that the most common of these species are reliably named and relatively well known. Our list of candidate hyperdominants can therefore readily serve new research, including in facilitating targeted autecological data collection to understand their role in providing ecological functions and services. Practically, this species-specific information could enhance tropical forest modelling by focusing on common species instead of relying on functional types or traits, thereby potentially improving predictions of future forest change.

In the future, analyses should be extended to investigate forest carbon stocks and hyperdominant species and their role in the provision of ecosystem services. In Amazonia, even fewer tree species were found to account for 50% of aboveground carbon stocks than the minimum number required to account for 50% of trees²². More generally, the set of common species is likely to include foundation species that define broader community assemblages, the environmental sensitivity of which will probably drive tropical forest responses to environmental change²⁷. Of course, striving to understand and protect rare and non-hyperdominant species remains crucial, particularly as they face greater extinction risk and probably also contribute to the functioning of ecosystems, particularly when more functions²⁷, longer timescales²⁸ and imposed environmental changes²⁹ are considered, and given that the hyperdominants of the future may be rarer today. Nonetheless, with a complementary grasp of the most common species, mapping, understanding and modelling of the world's tropical forests will be a much more tractable proposition.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-023-06820-z>.

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Anexo 2. Artículo publicado en revista JOURNAL OF BIOGEOGRAPHY.



Received: 8 April 2023 | Revised: 12 December 2023 | Accepted: 4 February 2024

DOI: 10.1111/jbi.14916

RESEARCH ARTICLE



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Geography and ecology shape the phylogenetic composition of Amazonian tree communities

Bruno Garcia Luize¹ | David Bauman^{2,3,4} | Hans ter Steege^{5,6} |
Clarisse Palma-Silva¹ | Iéda Leão do Amaral⁷ | Luiz de Souza Coelho⁷ |
Francisca Dionizia de Almeida Matos⁷ | Diógenes de Andrade Lima Filho⁷ |
Rafael P. Salomão^{8,9} | Florian Wittmann^{10,11} | Carolina V. Castilho¹² |
Marcelo de Jesus Veiga Carim¹³ | Juan Ernesto Guevara^{14,15} | Oliver L. Phillips¹⁶ |
William E. Magnusson¹⁷ | Daniel Sabatier² | Juan David Cardenas Revilla⁷ |
Jean-François Molino² | Mariana Victória Ireme⁷ | Maria Pires Martins⁷ |
José Renan da Silva Guimarães¹⁸ | José Ferreira Ramos⁷ | Olaf S. Bánki⁵ |
Maria Teresa Fernandez Piedade¹¹ | Dairon Cárdenas López^{19,†} | Nigel C. A. Pitman²⁰ |
Layon O. Demarchi¹¹ | Jochen Schöngart¹¹ | Evelyne Márcia Moraes de Leão Novo²¹ |
Percy Núñez Vargas²² | Thiago Sanna Freire Silva²³ | Eduardo Martins Venticinque²⁴ |
Angelo Gilberto Manzatto²⁵ | Neidiane Farias Costa Reis²⁶ | John Terborgh^{27,28} |
Katia Regina Casula²⁶ | Euridice N. Honorio Coronado^{29,30} |
Abel Monteagudo Mendoza^{22,31} | Juan Carlos Montero^{7,32} | Flávia R. C. Costa¹⁷ |
Ted R. Feldpausch^{16,33} | Adriano Costa Quaresma¹¹ | Nicolás Castaño Arboleda¹⁹ |
Charles Eugene Zartman⁷ | Timothy J. Killeen³⁴ | Beatriz S. Marimon³⁵ |
Ben Hur Marimon-Junior³⁵ | Rodolfo Vasquez³¹ | Bonifacio Mostacedo³⁶ |
Rafael L. Assis³⁷ | Chris Baraloto³⁸ | Dário Dantas do Amaral⁹ | Julien Engel^{2,38} |
Pascal Petronelli³⁹ | Hernán Castellanos⁴⁰ | Marcelo Brilhante de Medeiros⁴¹ |
Marcelo Fragomeni Simon⁴¹ | Ana Andrade⁴² | José Luis Camargo⁴² |
William F. Laurance²⁸ | Susan G. W. Laurance²⁸ | Lorena Maniguaje Rincón⁷ |
Juliana Schiatti⁷ | Thaiane R. Sousa⁴³ | Emanuelle de Sousa Farias^{44,45} |
Maria Aparecida Lopes⁴⁶ | José Leonardo Lima Magalhães^{47,48} |
Henrique Eduardo Mendonça Nascimento⁷ | Helder Lima de Queiroz⁴⁹ |
Gerardo A. Aymard C⁵⁰ | Roel Brienen¹⁶ | Pablo R. Stevenson⁵¹ |
Alejandro Araujo-Murakami⁵² | Bruno Barçante Ladvoat Cintra⁵³ | Tim R. Baker¹⁶ |
Yuri Oliveira Feitosa⁵⁴ | Hugo F. Mogollón⁵⁵ | Joost F. Duivenvoorden⁵⁶ |

†Deceased (Dairon Cárdenas López - January 5, 2022; NaKaren Davila - November 30, 2022; Cid Ferreira - September 21, 2022).

For Affiliation refer page on 16

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Journal of Biogeography, 2024, 00, 1–22.

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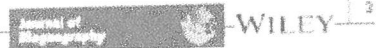



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Carlos A. Peres⁵⁷ | Miles R. Silman⁵⁸ | Leandro Valle Ferreira⁹ | José Rafael Lozada⁵⁹ |
James A. Comiskey^{60,61} | José Julio de Toledo⁶² | Gabriel Damasco⁶³ |
Nállarett Dávila^{1†} | Freddie C. Draper⁶⁴ | Roosevelt García-Villacorta^{65,66} |
Aline Lopes⁶⁷ | Alberto Vicentini¹⁷ | Fernando Cornejo Valverd⁶⁸ | Alfonso Alonso⁶¹ |
Luzmila Arroyo⁵² | Francisco Dallmeier⁶¹ | Vítor H. F. Gomes^{69,70} |
Eliana M. Jimenez⁷¹ | David Neill⁷² | Maria Cristina Peñuela Mora⁷³ |
Janaina Costa Noronha⁷⁴ | Daniel P. P. de Aguiar^{75,76} | Flávia Rodrigues Barbosa⁷⁶ |
Yennie K. Bredin⁷⁷ | Rainiellen de Sá Carpanedo⁷⁴ | Fernanda Antunes Carvalho^{17,78} |
Fernanda Coelho de Souza^{16,17} | Kenneth J. Feeley^{79,80} | Rogerio Gribel⁷ |
Torbjørn Haugaasen⁷⁷ | Joseph E. Hawes⁷⁷ | Marcelo Petratti Pansonato^{7,81} |
Marcos Ríos Paredes⁸² | Domingos de Jesus Rodrigues⁷⁴ | Jos Barlow⁸³ |
Erika Berenguer^{83,84} | Izaias Brasil da Silva⁸⁵ | Maria Julia Ferreira⁸⁶ |
Joice Ferreira⁴⁸ | Paul V. A. Fine⁸⁷ | Marcelino Carneiro Guedes⁸⁸ | Carolina Levis⁸⁸ |
Juan Carlos Licona³² | Boris Eduardo Villa Zegarra⁸⁹ | Vincent Antoine Vos⁹⁰ |
Carlos Cerón⁹¹ | Flávia Machado Durgante^{10,11} | Émile Fonty^{2,92} | Terry W. Henkel⁹³ |
John Ethan Householder¹⁰ | Isau Huamantupa-Chuquimaco⁹⁴ | Marcos Silveira⁹⁵ |
Juliana Stropp⁹⁶ | Raquel Thomas⁹⁷ | Doug Daly⁹⁸ | William Millike⁹⁹ |
Guido Pardo Molina⁹⁰ | Toby Pennington^{33,100} | Ima Célia Guimarães Vieira⁹ |
Bianca Weiss Albuquerque¹¹ | Wegliane Campelo⁶² | Alfredo Fuentes^{101,102} |
Bente Klitgaard¹⁰³ | José Luis Marcelo Pena¹⁰⁴ | J. Sebastián Tello¹⁰² |
Corine Vriesendorp²⁰ | Jerome Chave¹⁰⁵ | Anthony Di Fiore^{106,107} |
Renato Richard Hilário⁶² | Luciana de Oliveira Pereira³³ | Juan Fernando Phillips¹⁰⁸ |
Gonzalo Rivas-Torres^{107,109} | Tinde R. van Andel^{3,110} | Patricio von Hildebrand¹¹¹ |
William Balee¹¹² | Edelcilio Marques Barbosa⁷ | Luiz Carlos de Matos Bonates⁷ |
Hilda Paulette Dávila Doza⁸² | Ricardo Zárate Gómez¹¹³ | Therany Gonzales¹¹⁴ |
George Pepe Gallardo Gonzales⁸² | Bruce Hoffman¹¹⁵ | André Braga Junqueira¹¹⁶ |
Yadvinder Malhi¹¹⁷ | Ires Paula de Andrade Miranda⁷ |
Linder Felipe Mozombite Pinto⁸² | Adriana Prieto¹¹⁸ | Agustín Rudas¹¹⁸ |
Ademir R. Ruschel⁴⁸ | Natalino Silva¹¹⁹ | César I. A. Vela¹²⁰ | Stanford Zent¹²¹ |
Egleé L. Zent¹²¹ | Angela Cano^{51,122} | Yrma Andreina Carrero Márquez¹²³ |
Diego F. Correa^{51,124} | Janaina Barbosa Pedrosa Costa⁸⁸ |
Bernardo Monteiro Flores¹²⁵ | David Galbraith¹⁶ | Milena Holmgren¹²⁶ |
Michelle Kalamandeen¹²⁷ | Guilherme Lobo¹²⁸ | Luis Torres Montenegro¹²⁹ |
Marcelo Trindade Nascimento¹³⁰ | Alexandre A. Oliveira⁸¹ | Maihyra Marina Pombo⁷ |
Hirma Ramirez-Angulo¹³¹ | Maira Rocha¹¹ | Veridiana Vizoni Scudeller¹³² |
Maria Natalia Umaña¹³³ | Geertje van der Heijden¹³⁴ | Emilio Vilanova Torre^{131,135} |
Manuel Augusto Ahuite Reategui¹³⁶ | Cláudia Balder^{82,137} | Henrik Balslev¹³⁸ |
Sasha Cárdenas⁵¹ | Luisa Fernanda Casas⁵¹ | William Farfan-Rios^{22,58} |



LUIZE *et al.*



Cid Ferreira^{7†} | Reynaldo Linares-Palomino⁶¹ | Casimiro Mendoza^{139,140} |
Italo Mesones⁸⁷ | Germaine Alexander Parada⁵² | Armando Torres-Lezama¹³¹ |
Ligia Estela Urrego Giraldo¹⁴¹ | Daniel Villarroya^{52,142} | Roderick Zagt¹⁴³ |
Miguel N. Alexiades¹⁴⁴ | Edmar Almeida de Oliveira³⁵ | Karina Garcia-Cabrera⁵⁸ |
Lionel Hernandez⁴⁰ | Walter Palacios Cuenca¹⁴⁵ | Susamar Pansini²⁶ |
Daniela Pauletto¹⁴⁶ | Freddy Ramirez Arevalo¹⁴⁷ | Adeilza Felipe Sampaio²⁶ |
Elvis H. Valderrama Sandoval^{147,148} | Luis Valenzuela Gamarra³¹ | Kyle G. Dexter^{102,149} 

Correspondence

Bruno Garcia Luize, Departamento de
Biologia Vegetal, Instituto de Biologia,
Universidade Estadual de Campinas -
UNICAMP, CP 6109, Campinas, SP,
13083-970, Brazil.

Email: luize.br@gmail.com

Kyle Dexter, The University of Edinburgh,
School of Geosciences, 219 Grew
Building, King's Buildings, Edinburgh,
EH9 3FF, United Kingdom.

Email: kyle.dexter@ed.ac.uk

Funding information

Conselho Nacional de Desenvolvimento
Científico e Tecnológico; Coordenação
de Aperfeiçoamento de Pessoal de Nível
Superior; Fundação de Amparo à Pesquisa
do Estado de São Paulo; HORIZON
EUROPE Marie Skłodowska-Curie Actions

Abstract

Aim: Amazonia hosts more tree species from numerous evolutionary lineages, both young and ancient, than any other biogeographic region. Previous studies have shown that tree lineages colonized multiple edaphic environments and dispersed widely across Amazonia, leading to a hypothesis, which we test, that lineages should not be strongly associated with either geographic regions or edaphic forest types.

Location: Amazonia.

Taxon: Angiosperms (Magnoliids; Monocots; Eudicots).

Methods: Data for the abundance of 5082 tree species in 1989 plots were combined with a mega-phylogeny. We applied evolutionary ordination to assess how phylogenetic composition varies across Amazonia. We used variation partitioning and Moran's eigenvector maps (MEM) to test and quantify the separate and joint contributions of spatial and environmental variables to explain the phylogenetic composition of plots. We tested the indicator value of lineages for geographic regions and edaphic forest types and mapped associations onto the phylogeny.

Results: In the terra firme and várzea forest types, the phylogenetic composition varies by geographic region, but the igapó and white-sand forest types retain a unique evolutionary signature regardless of region. Overall, we find that soil chemistry, climate and topography explain 24% of the variation in phylogenetic composition, with 79% of that variation being spatially structured ($R^2 = 19\%$ overall for combined spatial/environmental effects). The phylogenetic composition also shows substantial spatial patterns not related to the environmental variables we quantified ($R^2 = 28\%$). A greater number of lineages were significant indicators of geographic regions than forest types.

Main Conclusion: Numerous tree lineages, including some ancient ones (>60 Ma), show strong associations with geographic regions and edaphic forest types of Amazonia. This shows that specialization in specific edaphic environments has played a long-standing role in the evolutionary assembly of Amazonian forests. Furthermore, many lineages, even those that have dispersed across Amazonia, dominate within a specific region, likely because of phylogenetically conserved niches for environmental conditions that are prevalent within regions.

KEYWORDS

community assembly, dispersal limitation, environmental selection, evolutionary principal component analysis, indicator lineage analysis, Moran's eigenvector maps, neotropics, niche conservatism, tropical rain forests

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1 | INTRODUCTION

A major goal of tropical biologists is to understand the processes involved in the origin, maintenance and coexistence of diverse species in ecological communities. Processes that play out over multiple spatial and temporal scales influence the organization of ecological communities (Ricklefs & Schlüter, 1993; Vellend, 2010), leaving an imprint on phylogenetic and functional composition. Detailed characterization of compositional patterns can help to infer the ecological and evolutionary processes at play (Carlucci *et al.*, 2017; Dray *et al.*, 2012; Graham & Fine, 2008; Kraft & Ackerly, 2010; McIntire & Fajardo, 2009). The assembly of tree communities in Amazonian tropical rain forests is structured by ecological drift (Hubbell, 2001), the local and regional dispersal of lineages (Dexter *et al.*, 2017), differential recruitment into heterogeneous forest habitats and environments (Fine & Kembel, 2011; ter Steege *et al.*, 2006; Tuomisto *et al.*, 2003), biotic interactions (Fine *et al.*, 2004; Kursar *et al.*, 2009) and historical contingency (Baker *et al.*, 2014; Dexter *et al.*, 2012; Figuerredo *et al.*, 2022).

Tree lineages that are iconic of present-day tropical rain forests have existed since the mid-Cretaceous (Davis *et al.*, 2005; Jaramillo *et al.*, 2005; Wing *et al.*, 2009), but angiosperms only came to dominate Amazonia after the Cretaceous-Paleogene (K-Pg) boundary (i.e. 66Ma) (Carvalho *et al.*, 2021). Amazonian tropical rain forests cover a huge area (approximately 39% of South America) and there is a substantial turnover of species across its extent (Baraloto *et al.*, 2021; Luize *et al.*, submitted; ter Steege *et al.*, 2006; Terborgh & Andresen, 1998). It also comprises heterogeneous geologic, edaphic and climatic conditions (Hoborn *et al.*, 2010) and hosts the highest number of tree species of any biogeographic region on Earth (Raven *et al.*, 2020; Ulloa-Ulloa *et al.*, 2017). Locally, small topographic variation is enough to cause edaphic differences (e.g. physical, chemical and hydrological soil variation) leading to major shifts in tree species composition (Bohman *et al.*, 2008; Koponen *et al.*, 2004; Marca-Zevallos *et al.*, 2022; Milton *et al.*, 2022; Phillips *et al.*, 2003; Sabatier *et al.*, 1997; ter Steege *et al.*, 1993). Such high species turnover can make it challenging to understand large-scale patterns as many tree communities share no species at all. Evolutionary approaches based on analysing the shared evolutionary heritage of communities (e.g., Pavoine, 2010; Webb, 2000), may provide a path forwards, as all tree communities in Amazonia are dominated by species derived from the same overarching clade, the angiosperms.

Tropical tree communities tend to have clustered phylogenetic structures (Baldeck *et al.*, 2016; Baraloto *et al.*, 2012; Kembel & Hubbell, 2006; Webb, 2000), which is interpreted as the signal of evolutionarily conserved preferences of tree lineages for specific environments, although other factors, such as biotic interactions and disturbances, could also result in phylogenetic clustering. Phylogenetic clustering has been found not only in local and regional studies (Baraloto *et al.*, 2012; Fine & Kembel, 2011; Guevara *et al.*, 2016; Kraft *et al.*, 2007), but also at the scale of all of Amazonia

(Carlucci *et al.*, 2017; Honório Coronado *et al.*, 2015). This broad-scale phylogenetic clustering in Amazon-wide studies (Honório Coronado *et al.*, 2015) may result from a deep phylogenetic conservatism for edaphic environments. Conversely, edaphic regime switching (i.e., the shift from one forest edaphic habitat to another), associated with restricted inter-habitat gene flow, has been suggested to be a major driver of plant speciation in Amazonia (Brousseau *et al.*, 2021; Fine *et al.*, 2005; Gentry, 1981). If edaphic regime switching is frequent, lineages should not show strong associations with forest edaphic regimes and tree communities should not show a phylogenetic composition organized within forest types.

At the spatial scale of Amazonia, the clustering of closely related species within communities and regions can also result from speciation within geographic regions, be it sympatric, parapatric or allopatric, with limited subsequent dispersal (Fine *et al.*, 2004; Mielwicz *et al.*, 2020). Phytogeographical analyses have found geographic turnover in the composition of tree species, which suggests that the dispersal of Amazonian trees can be limited (Prance, 1981; ter Steege *et al.*, 2003, 2006; Terborgh & Andresen, 1998). Nevertheless, some tree lineages have dispersed widely across Amazonia over their evolutionary history (Dexter *et al.*, 2017) and do not present any region-specific phylogenetic clustering. A recent study from a theoretical perspective also suggests widespread dispersal of lineages across Amazonia (Poo *et al.*, 2023). Finally, while the largest Amazonian rivers can provide effective geographic barriers limiting the distribution of some organisms, particularly animals, rivers do not seem to be effective barriers for most tree species (Dexter *et al.*, 2012; Luize *et al.*, submitted; Nazareno *et al.*, 2017, 2019).

Assuming that dispersal allows tree lineages to achieve widespread ranges and that migration across landscapes allows tree lineages to achieve broad niche breadths, a reasonable hypothesis might be that neither geography nor ecology are major drivers of tree-lineage distribution. If so, the phylogenetic composition of Amazonian tree communities will not align closely with geographic or environmental conditions. There is mixed evidence for the nature of the phylogenetic structure of Amazonian tree communities, including communities which do not show any clear phylogenetic structure, although most forest types tend to be phylogenetically clustered at the landscape to regional scales (Baraloto *et al.*, 2012; Fine & Kembel, 2011; Guevara *et al.*, 2016). The strongest evidence of phylogenetically clustered communities tends to be found in habitats with the most stressful ecological conditions, such as seasonally dry forests, white-sand forests and seasonally flooded forests (Baraloto *et al.*, 2021; Guevara *et al.*, 2016; Honório Coronado *et al.*, 2015). However, to date, most phylogenetic analyses of tree communities have focused on limited geographic areas (e.g., Aldana *et al.*, 2017; Cardenas *et al.*, 2017; Gonzalez-Caro *et al.*, 2021) or relied on phylogenies with relatively low phylogenetic resolution (Honório Coronado *et al.*, 2015). The growing availability of DNA sequences allows the production of phylogenetic hypotheses with a better sampling and resolution of relationships (Baraloto *et al.*, 2021; Chave *et al.*, 2020; Dexter & Chave, 2016), which in turn enables a deeper exploration of variation in the phylogenetic composition of Amazonian forests.



In this study, we characterize the phylogenetic composition of tropical rain forests across the entire Amazonian region, quantifying the roles of spatial and environmental variables in shaping the phylogenetic composition of tree communities, with the aim to discern the key evolutionary and ecological processes structuring these hyperdiverse forests. We test the null hypothesis that widespread geographic dispersal of lineages and frequent edaphic-regime switching have erased phylogenetic signal for geographic regions and forest edaphic regimes. Previous studies that have found significant phylogenetic clustering may have done so because of poorly resolved phylogenies or restricted spatial and environmental scales. In addition, we evaluated if there were significant indicator lineages for specific geographic regions or edaphic forest types, and when found, we determined their total numbers, identities and ages.

2 | MATERIALS AND METHODS

2.1 | Study region, forest-inventory dataset and environmental variables

The focus of our study is the Amazonian rain forest, including the catchment of the Amazon River, the middle-lower course of the Araguaia-Tocantins River basin, the Atlantic coastal basins surrounding the Amazon River estuary and the rain forests of the Guianas (RAISG, 2012). Our forest-inventory dataset (ATDN_20220919) results from the combined effort of thousands of botanists and field ecologists over the last 90 years. The dataset consists of 1989 forest-inventory plots with measurements for the abundance of all trees ≥ 10 cm DBH (i.e., diameter at breast height, at 1.3 m above the ground), with a few plots (26) sampling all trees ≥ 5 cm DBH; most of the plots are of standard size (1 ha) (minimum and maximum size = 0.1 and 9 ha; 533 plots < 1 ha, 1350 plots of 1 ha and 106 plots > 1 ha). The inclusion of few plots with non-standardized tree inclusion criteria or sample size did not affect the estimations of evoPCA scores (see below and Figure S2). Of the 1,099,810 measured trees, 89% were identified to a valid species name and the other 11% of individuals were excluded from further analyses. The 979,801 individual trees identified to a valid species name encompass a total of 115 families, 754 genera and 5082 species of angiosperms. Checking of valid species names followed the previous name harmonization of the ATDN database (ter Steege *et al.*, 2019).

Inventory plots were grouped into six geographic regions (Central Amazonia [CA = 506 plots], Guiana Shield [GS = 459], Northwestern Amazonia [NWA = 304], Southern Amazonia [SA = 273], Southwestern Amazonia [SWA = 224] and Eastern Amazonia [EA = 223]), for description of geographic regions (Feldpausch *et al.*, 2012; ter Steege *et al.*, 2013). These geographic regions largely follow a broad-scale classification of Amazonia based on geological, pedological and forest structural attributes (Feldpausch *et al.*, 2012; Quesada *et al.*, 2011) and which have been used in many subsequent large-scale biogeographic analyses in Amazonia (e.g., González-Caro *et al.*, 2021; Guevara *et al.*, 2016; ter Steege *et al.*, 2013). The

inventory plots were also classified by the researchers who established the plots, according to five major Amazonian forest types that develop on distinct edaphic regimes (France, 1979; ter Steege *et al.*, 2013; Terborgh & Andresen, 1998): (1) terra-firme forests on clay and/or brown sands [TF = 1326], (2) várzea forests on eutrophic seasonally flooded terrains [VA = 315], (3) igapó forests on oligotrophic seasonally flooded terrains [IG = 193], (4) terra-firme forests on white-sands (podzols) [PZ = 114] and (5) swamp forests on permanently flooded terrains [SW = 41]. An initial set of 19 environmental variables capturing climatic, topographic and edaphic aspects crucial to tree ecology were extracted for each plot location from digital databases and applied as environmental predictors of phylogenetic composition (Table 1). For details regarding characteristics of forest types on distinct edaphic regimes and the environmental variables used in the analyses, see the Supplementary material (Methods extended).

2.2 | Phylogeny of Amazonian tree species

We generated a phylogeny using the GBOTB phylogeny as the base topology (Smith & Brown, 2018), using Scenario 3 in the V.phyloMaker v.2 R package (Jin & Qian, 2022), which binds uncaptured species (those without any usable DNA sequence data available) to the phylogeny and then prunes the phylogeny to species present in the overall sample. At the time of the production of the GBOTB phylogeny (Smith & Brown, 2018), roughly 74% of the genera and 30% of the tree species found in the largest tree plot database for the Amazonian region (the ATDN dataset) had at least one usable DNA sequence in public data sources (e.g., GenBank). The 3519 species that were not found in the GTOB phylogeny were bound to the phylogeny based on their taxonomic identity (i.e., genus identity). For unsampled species where the algorithm failed to find a genus relative, we indicated the closest genus to that species according to the most recently published phylogeny for the given family. The phylogeny of Amazonian tree species, produced from Scenario 3 of the V.phyloMaker v.2, comprises 7062 lineages, of which 5082 are lower-level lineages (i.e., tips in the phylogeny and represent species) and 1980 are higher-level lineages (i.e., internal nodes in the phylogeny that may represent genera, families or other lineages above the species-level).

Previous studies of the effects of phylogenetic uncertainty on standard ecological analyses have shown that uncertainty in results is primarily due to variation in the placement of unsampled taxa, rather than uncertainty in topological relationships or node ages (Rangel *et al.*, 2015). Scenario 3 of the V.phyloMaker v.2 R package binds a given unsampled taxon on a specific branch at a determined position on that branch (e.g., halfway along the branch subtending the genus of the given species). There is an alternative scenario in the V.phyloMaker package (Scenario 2) which randomly places taxa within their given taxonomic clade. Thus, in order to explore variation in results due to uncertainty in the placement of taxa, we additionally constructed a set of 100 phylogenies using Scenario 2

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TABLE 1 Environmental variables obtained for each inventory plot were used to investigate environmental influences on the phylogenetic composition of tree communities and associated references.

Environmental predictor	Variable	References
Climate - Temperature	Mean annual temperature (°C)	Karger et al. (2017)
Climate - Temperature	Temperature range (°C)	Karger et al. (2017)
Climate - Temperature	Temperature seasonality (SD - Standard deviation of monthly mean temperatures)	Karger et al. (2017)
Climate - Precipitation	Total annual precipitation (kg m ⁻²)	Karger et al. (2017)
Climate - Precipitation	Precipitation seasonality (CV - Coefficient of Variation)	Karger et al. (2017)
Climate - Water deficit	Maximum Climatological Water Deficit (MCWD)	Funk et al. (2015); Hirota et al. (2011); Mathi et al. (2009)
Topography	Elevational position (height above sea level) - ALOS World 3D	Tadono et al. (2014); Takaku et al. (2016)
Topography	Topographic Diversity Index - TopoDiver	Theobald et al. (2015)
Topography	Multiscale Topographic Position Index - mTPI	Theobald et al. (2015)
Edaphic - Water table depth	Groundwater table depth (m below surface) - WTD	Fan et al. (2013)
Edaphic - Soil chemistry	Nitrogen (N)	This study
Edaphic - Soil chemistry	Phosphorous (P)	This study
Edaphic - Soil chemistry	Potassium (K ⁺)	This study
Edaphic - Soil chemistry	Calcium (Ca ²⁺)	This study
Edaphic - Soil chemistry	Magnesium (Mg ²⁺)	This study
Edaphic - Soil chemistry	Sodium (Na ⁺)	This study
Edaphic - Soil chemistry	Aluminium (Al ³⁺)	This study
Edaphic - Soil chemistry	Cation exchange capacity (CEC)	This study
Edaphic - Soil chemistry	Potential of hydrogen (pH _{so})	This study

of the V.phyloMaker v.2 (Jin & Qian, 2022) and conducted some of our downstream analyses on this set of phylogenies.

2.3 | Data analysis

We have opted to apply a raw data approach (i.e., ordination of community composition matrix) instead of a distance-based approach (i.e., ordination of the matrix of pairwise dissimilarities) to analyze the data. The raw data approach has been shown to be the appropriate choice for analyzing spatial and environmental patterns of community composition (Legendre et al., 2009), including the spatial and environmental influences on the phylogenetic compositional variation of tropical tree communities (e.g., Rezende et al., 2021), which is a key focus of our study. Analytical approaches based on distance metrics generally address different questions (Legendre et al., 2008), such as providing insights on the influence of more basal or recent clades to phylogenetic beta diversity patterns (e.g., Carlucci et al., 2017; Duarte et al., 2014), but these are not our focus here. We also did not focus on approaches based on null models that aim to disentangle phylogenetic beta diversity patterns from taxonomic beta diversity patterns (cf. Duarte, Debastiani, Freitas & Pillar, 2016). The phylogenetic approaches we employed here consider terminal nodes in our phylogeny (i.e., species), similar to deeper nodes in the phylogeny; they both represent evolutionary units, or lineages, of

interest. We aimed for general results that integrate across lineages at all evolutionary levels (in both deep and recent evolutionary time). Furthermore, the raw data approaches allowed the full use of advanced and versatile spatial eigenvector-based methods (such as Moran's eigenvector maps and Moran Spectral Randomization), which in turn allowed the detection and quantification of broad to fine-scaled complex spatial structures.

2.4 | Evolutionary principal component analysis (evoPCA)

We applied evolutionary principal component analysis (evoPCA, Pavoine, 2016) to summarize the key dimensions of phylogenetic compositional variation. The evoPCA performs a PCA on the abundance matrix of lineages by sites (Pavoine, 2016), ordinating, at the same time, the distributions of lineages (i.e., terminal and internal nodes) among sites and the phylogenetic composition of the sites. The phylogenetic branch lengths (i.e., evolutionary units) within communities are used to weigh and position the communities according to the structure of the phylogeny and the lineage composition of communities (Pavoine, 2016). To down-weight the influence of abundant lineages, we applied a Hellinger transformation to the abundance matrix of lineages by sites that form the basis of the analyses (Legendre & Gallagher, 2001; Pavoine, 2016). We used

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the absolute values of abundances prior to the Hellinger transformation and the ordinary weighted mean to centre the PCA matrix (arguments: `w = 'evocab'` and `option = 'centered'` in `'evopcahellinger'` function, `'adv'` R package, Pavoine, 2020). The `evopca` results in a multidimensional evolutionary space where tree communities located closer together (i.e., with similar axes scores) tend to have a more similar phylogenetic composition. To determine the number of axes to keep for further analysis, we used parallel analysis implemented with the `'fa.parallel'` function in the `'psych'` R package (Revelle, 2022), which identifies those axes explaining more variation in the ordination than expected by chance. This analysis indicated 13 axes explaining more variation than expected by chance, which together account for 51% of the total phylogenetic compositional variation described by the `evopca` (Figure S1). To visualize the multidimensional evolutionary space occupied by Amazonian forests, we produced biplots for the first three `evopca` axes. For each edaphic forest type in each geographic region, we visualized which area of the biplots contained 50% of the sampled plots, essentially representing the 'central tendency' of plots, that is, those found between the 1st and 3rd quartiles in two dimensions, for a given forest type in a region. We used a two-dimensional kernel density estimation to draw these 50% contour lines (`'geom_density_2d'` function in the `ggplot2` R package (Wickham, 2015)).

2.5 | Spatial and environmental influences on phylogenetic composition of tree communities

We used Moran's eigenvector maps (MEMs; Dray *et al.*, 2006) to test for visualize and quantify multiscale spatial patterns of variation in the phylogenetic composition of tree communities across Amazonia focusing on the 13 significant `evopca` axes. The MEM consists of the double diagonalization of a spatial weighting matrix (SWM) obtained from a connectivity and weighting matrix calculated from the spatial coordinates of the studied plots (details in SM - Methods Extended). The resulting spatial eigenvectors (or MEM variables) each consist of an orthogonal spatial pattern and together encompass broad to fine spatial-scaled patterns, whose linear combinations allow capturing multiscale patterns in the response of interest. We followed Bauman, Drouet, Fortin, and Dray (2018) to create the spatial eigenvectors, by optimizing the selection of a spatial weighting matrix (SWM) from a limited set of contrasting graph-based connectivity matrices by adjusting the initial significance threshold of 0.05 for the total number of compared spatial weighting matrices using a Sidak correction (to avoid type I error rate inflation). Graph-based MEMs were preferred given the irregular spacing of the sampling design. Significance tests were performed through permutation of the residuals of a redundancy analysis (RDA) of the `evopca` axes against the MEM variables (Anderson & Legendre, 1999). The three graph-based connectivity matrices considered were a Gabriel graph, relative neighbourhood graph and minimum spanning tree, each weighted by a function decreasing linearly with the distance between plots, hence assuming

that sites further apart will be less connected and have exchanged fewer lineages. As we aimed to capture spatial patterns in phylogenetic composition with maximum power and accuracy, we applied forward selection with a double-stopping criterion method (Blanchet *et al.*, 2008) to select a final subset of spatial eigenvectors (Bauman, Drouet, Dray, & Viennanckx, 2018; Bauman, Drouet, Fortin, & Dray, 2018) and we only retained eigenvectors capturing spatial patterns of positive autocorrelation, thereby focusing on aggregation patterns. The generation of SWMs was done with the function `'listw.candidates'` and the optimization and selection of an SWM and subset of MEM variables were performed using the function `'listw.select'`, both functions in the `'adespatial'` R package (Dray *et al.*, 2021). The fitting process of the selected spatial predictors (MEMs) to the `evopca` axes was performed through redundancy analysis (RDA) (SM - Methods Extended), such that the resulting constrained ordination axes corresponded each to a unique linear combination of the selected spatial eigenvectors and therefore to a spatial pattern present in the phylogenetic composition. We tested each of these orthogonal spatial patterns (i.e., each RDA axis) separately by permutation (999 permutations) and the scores of the forest plots over the significant RDA axes were mapped for visualization of the corresponding spatial patterns (Figure S8).

We used a variation partitioning framework (Peres-Neto *et al.*, 2006) to test and quantify the total, unique (also referred to as 'pure') and joint contributions of (a) environmental variables including attributes for climate, topography and soil chemistry and (b) the spatial predictors (MEMs) in explaining phylogenetic compositional variation. Explanatory power was quantified through the adjusted coefficient of determination (R^2_{adj}) (Legendre & Legendre, 2012). The total and unique explanatory fractions of the variation partitioning (R^2_{part}) were tested through permutation of the residuals of the corresponding RDA and partial RDA, respectively (999 permutations) (Anderson & Legendre, 1999; Peres-Neto *et al.*, 2006). The joint space-environment fraction - that is, the spatially structured effect of climate, topography and soil chemistry on phylogenetic composition - was tested with Moran Spectral Randomization (Wagner & Dray, 2015), following Bauman *et al.*'s (2019) method (SM - Methods Extended). We also visualized the 'pure' spatial patterns of phylogenetic compositional variation by mapping the constrained scores of a partial RDA (i.e., RDA constrained by MEMs for the residuals of the RDA constrained by environmental variables - Figure S9).

We conducted two main sensitivity analyses with respect to the variation partitioning analysis. Firstly, we tested the robustness of the variation partitioning fractions, by rerunning the above analyses based on the 50 `evopca` axes capturing 75% of the variation of the community phylogenetic composition (instead of the 13 axes capturing 51% of the variation). Secondly, we tested the robustness of results with respect to phylogenetic uncertainty (here, focusing on the first 13 `evopca` axes) by repeating the full workflow (including `evopca` and MEM selection) using the 100 phylogenetic trees produced from the Scenario 2 algorithm of `V.phyloMaker v.2`.

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2.6 | Indicator value of lineages for geographic regions and forest types

We tested whether lineages (lower and higher-level evolutionary lineages, that is, species and internal nodes, respectively) were indicators of certain geographic regions or edaphic forest types by performing indicator analysis (IA) based on the IndVal statistic (Dufrene & Legendre, 1997). The IndVal statistic defines the most characteristic lineages for each geographic or forest group and is calculated for each lineage independently, so the pattern observed for a given lineage does not influence the indicator value of another lineage (Cáceres & Legendre, 2009). To run the indicator analysis, we used a community matrix containing abundances of the tips (i.e., species) and the internal nodes (representing evolutionary lineages at higher taxonomic levels, e.g., orders, families and genera) within sampled communities. As the indicator analysis was based on abundances and incidence, an indicator lineage meant both that the lineage achieved markedly higher abundance in that region or forest type as compared to other regions or forest types and that the lineage would generally be found in the group in which it is an indicator. The indicator analysis was performed for geographic regions and forest types using the function 'indval' of the 'labdsv' R-package (Roberts, 2019). IndVal significance levels were tested with 999 permutations of sites among groups and all those lineages achieving p -values ≤ 0.01 were considered as indicators of their corresponding group (i.e., assuming 1 false positive over 100 indicators). To test if there was a consistent pattern of lineage association with a given geographic region or forest type over evolutionary time, we mapped the indicator lineages onto the Amazonian tree species phylogeny. We then assessed the proportion of significant indicator lineages in different time slices: time by sub-setting the phylogeny into time periods defined by the following breakpoints: 0, 2.5, 5, 10, 20, 30, 45, 65, > 65 Million years (Ma).

3 | RESULTS

3.1 | The phylogenetic composition of Amazonian forests

The first two evoPCA axes described 21.6% of the variation in the phylogenetic composition of Amazonian tree communities and no lower-order axes described more than 4.7% (Figure S1). A visual assessment of the evoPCA biplots shows some compositional overlap but mostly a gradual turnover in the phylogenetic composition of Amazonian tree communities over forest types and geographic regions (Figures 1, S3 and S4). There is a differentiation between terra-firme, white-sand and wetland forests although the level of differentiation depends on the geographic region (Figure 1). In Western Amazonia, terra-firme and várzea forests have a similar phylogenetic composition, while the phylogenetic composition of these forest types diverges in Central and Eastern Amazonia. On the Guiana Shield, the evolutionary space occupied by terra-firme forests overlaps with that occupied by

wetland and white-sand forests (Figure 1). Overall, though, the phylogenetic composition of terra-firme forests tends to differ from that of both wetland forests (várzea, igapó and swamp forests - Figure S5) and white-sand forests, even within the same geographic region (Figures 1, S5 and S6). The evolutionary space occupied by wetland forests overlaps with that occupied by white-sand forests with great overlap between white-sand forests and várzea forests in Central Amazonia (Figure 1). In addition, the evolutionary space occupied by igapó forests is remarkably close to that occupied by white-sand forests (Figure S5). Anacales and Ericales were the lineages contributing most to positive and negative scores on the first evoPCA axis, respectively (Figure S3). For the second evoPCA axis, Fabales is the lineage contributing most for communities with negative axis scores and Burseraceae the lineage contributing for communities with positive axis scores (Figure S3).

Maps of the first two evoPCA axes highlight the widespread distribution of tree communities with central values for phylogenetic composition (i.e., with values between -0.2 and 0.2), embedded among communities that occupy the extremes of the phylogenetic compositional gradient (i.e., with values less than -0.2 or greater than 0.2) (Figures 2 and S6). Values below -0.2 on the 1st evoPCA axis (Figure 2a) tended to be located east of the Negro River, whereas values above 0.2 tended to be more widespread around Amazonia. There are two geographic clusters of high values for the 1st evoPCA axis, one in western Amazonia in the Andean forelands and the other in eastern Amazonia surrounding the Amazon River mouth. For the 2nd evoPCA axis (Figure 2b), the tree communities with extreme axis values for phylogenetic composition are mixed within those tree communities attaining central axis values. However, the scores of the 2nd evoPCA axis still show a geographic trend with values below -0.2 mostly east of the Negro River and values above 0.2 mostly located close to the Andean forelands.

3.2 | Multiscale spatial patterns of phylogenetic composition across Amazonia

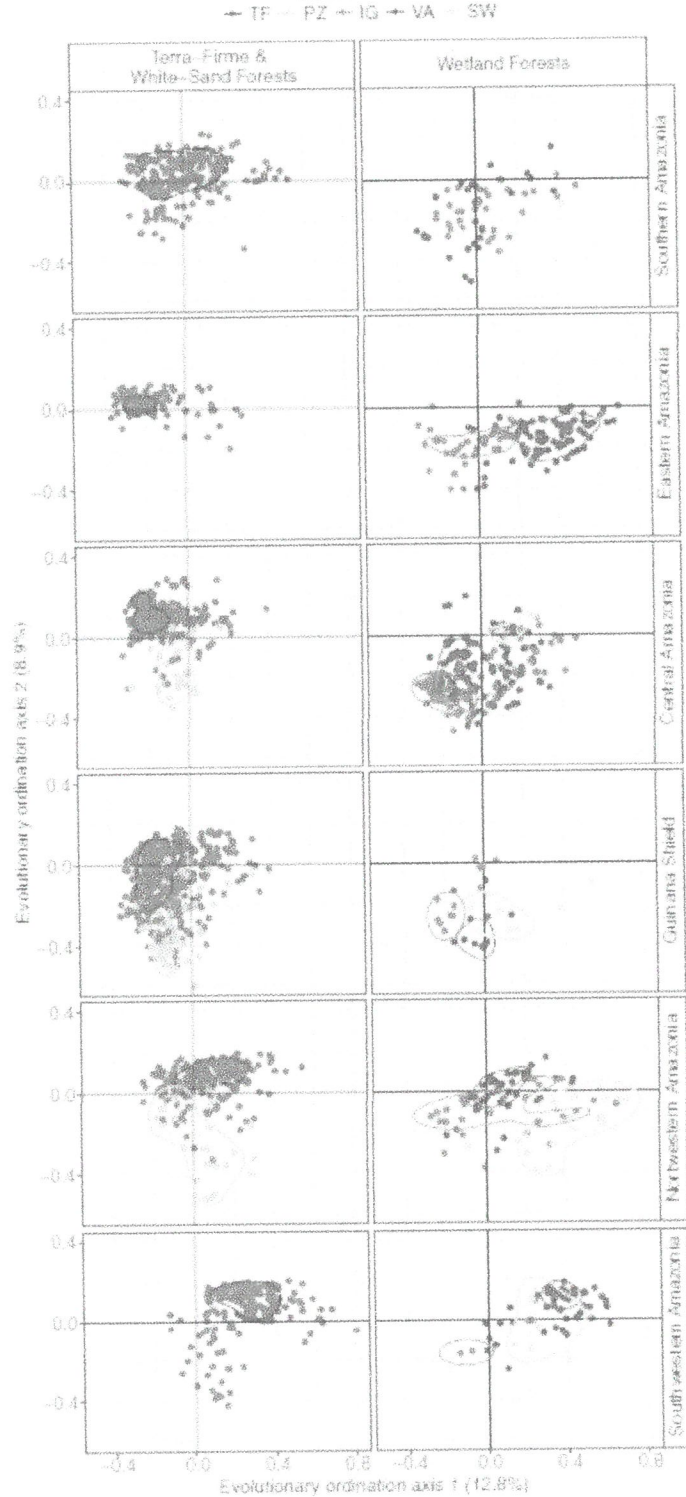
The optimized MEM analysis highlighted significant spatial structures at multiple scales ($R^2_{adj} = 0.62$) indicating a strong spatial component to the phylogenetic composition of trees across Amazonia ($R^2_{adj} = 0.47$ based on a reduced subset of 207 selected MEM variables; see Methods Extended). The first 12 dimensions of constrained RDA axes were significantly spatially structured revealing contrasting orthogonal phylogenetic spatial structures (Figure S8). The first and most significant spatial pattern captures a gradual differentiation in phylogenetic composition from communities in the central part of Amazonia towards two regions of internally similar phylogenetic composition, one located in southwestern Amazonia close to the Andean forelands and the second located in the Guiana Shield (Figure S8a; very similar map as evoPCA axis 1, Figure 2a). Subsequent phylogenetic spatial patterns tended to occur over comparatively shorter distances (finer-scaled spatial patterns; Figures S8b-j).

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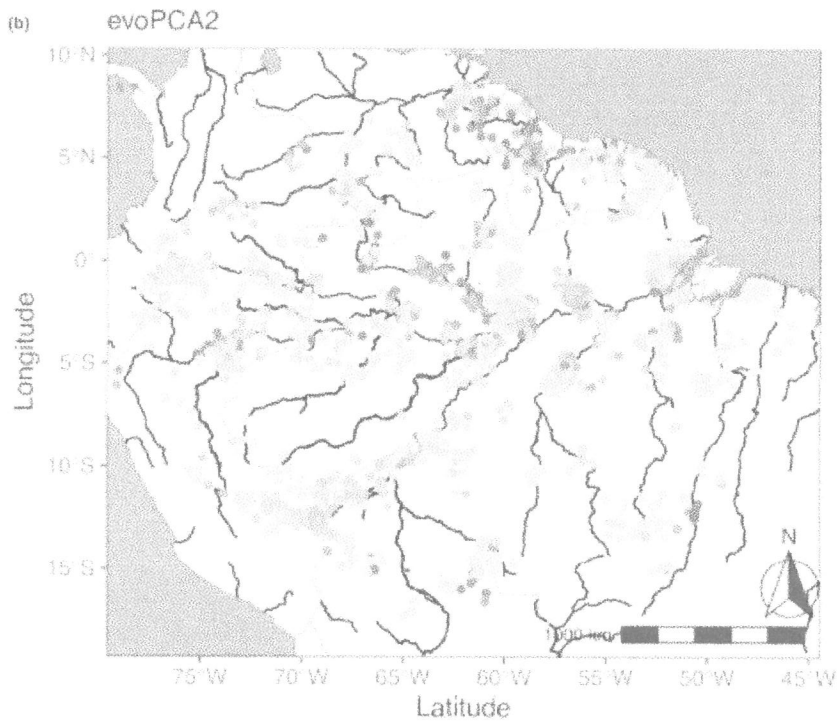
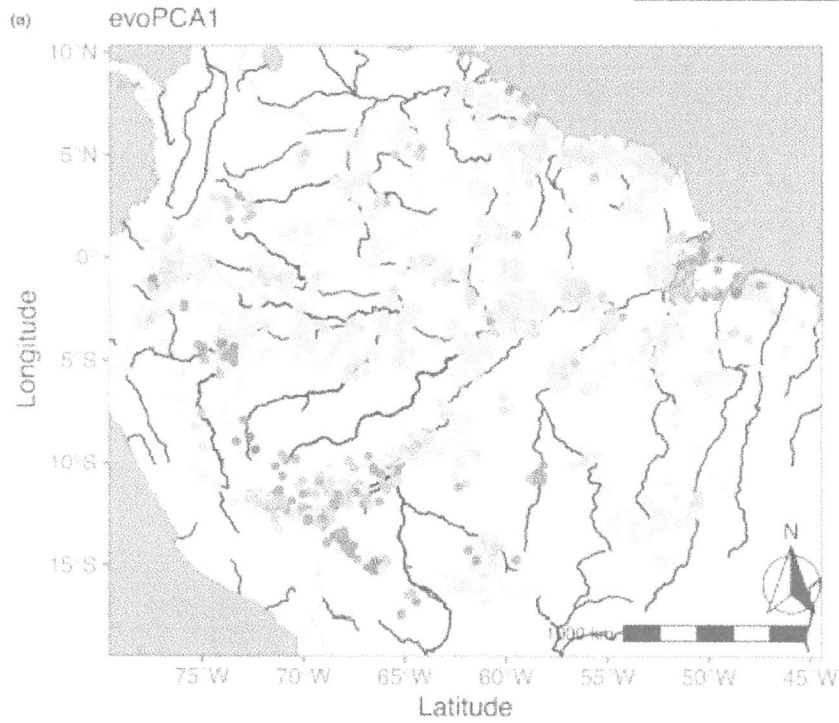
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FIGURE 1 The evolutionary space is occupied by Amazonian tree communities. Scatterplots of the first two evoPCA axes mapping the tree communities' scores according to geographic regions and forest types. The first axis of the evoPCA recovered a longitudinal gradient in the differentiation of the phylogenetic composition of Amazonian tree communities that mirrors terra-firme and the wetland forest differentiation. The second axis mainly separates terra-firme from white-sand and wetland forests. The contour lines show the central tendency (50% of plots) for each forest type in each geographic region. Contour lines could not be calculated for subsets of plots with low sample size (e.g., in wetland and white-sand forests of the southern Amazonia). Forest types: TF - Terra-Firme; PZ - White-Sand; VA - Varzea; IG - Igapó; SW - Swamp.



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K.F., Chave et al. 2020; Fine et al. 2014; Nicholls et al. 2015; ter Steege et al. 2023).

Overall, our analytical framework allowed us to explain just over half of the variation in the dominant axes that together explain half the variation in the phylogenetic composition of Amazonian tree communities. These dominant axes were those that represented more variation in phylogenetic composition than expected by chance. When we expanded our variation partitioning analyses to try and explain axes that represent 75% of the variation in phylogenetic composition, our total variation explained dropped by 1/3. Essentially, we could not explain any of the variation in these additional axes with the measured environmental variables and our decompositions of spatial structure. As a visual reflection of unexplained variation, we can see that some clusters of tree communities with heterogeneous phylogenetic composition are spatially proximate and in apparently similar environments (Figure 2). Overall, we suggest that the large amount of unexplained variation in our compositional data, while not usual, could be due to disturbance events, neutral ecological drift, non-linear relationships between the distribution of lineages and geographic and environmental gradients, and to other, poorly understood phenomena.

5 | CONCLUSION

The phylogenetic composition of Amazonian tree communities varies over multiple spatial scales, as a function of geographic, edaphic and climatic gradients. Throughout Amazonia different lineages are indicative of geographic regions and forest types on distinct edaphic regimes. Such preferences imprint a spatial structure on the phylogenetic composition of tree communities. Whereas terra-firme and wetland forests show a more variable phylogenetic composition across Amazonia, white-sand forests tend to conserve a phylogenetic composition regardless of the geographic region where they were found. Our results support a role for dispersal and selection processes in structuring the evolutionary assembly of tropical tree communities. The incorporation of an evolutionary lens contributes to improving our knowledge on variation in the composition of organisms assembling the forests of Amazonia and highlights the complex evolutionary history of trees over multiple spatial scales and environmental conditions.

AFFILIATIONS

- ¹Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas – UNICAMP, Campinas, Brazil
- ²AMAP, Université de Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France
- ³Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK
- ⁴Laboratoire d'écologie végétale et biogéochimie, Université libre de Bruxelles, Brussels, Belgium
- ⁵Naturalis Biodiversity Center, Leiden, The Netherlands
- ⁶Quantitative Biodiversity Dynamics, Utrecht University, Utrecht, The Netherlands
- ⁷Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia – INPA, Av André Araújo, Manaus, Brazil

- ⁸Programa Professor Visitante Nacional Gênera na Amazônia – CAPEL, Universidade Federal Rural da Amazônia, Belém, Brazil
- ⁹Coordenação de Botânica, Museu Paraense Emílio Goeldi, Belém, Brazil
- ¹⁰Wetland Department, Institute of Geography and Geoecology, Karlsruhe Institute of Technology – KIT, Rastatt, Germany
- ¹¹Ecology, Monitoring and Sustainable Use of Wetlands (MAUJ), Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, Brazil
- ¹²Centro de Pesquisa Agroflorestal de Roraima, Boa Vista, Brazil
- ¹³Departamento de Botânica, Instituto de Pesquisas Científicas e Tecnológicas do Amapá – IEPA, Macapá, Brazil
- ¹⁴Grupo de Investigación en Biodiversidad, Medio Ambiente y Salud-BIOMAG, Universidad de las Américas, Quito, Ecuador
- ¹⁵Keller Science Action Center, Chicago, Illinois, USA
- ¹⁶School of Geography, University of Leeds, Leeds, UK
- ¹⁷Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, Brazil
- ¹⁸Arancel Amapa Florestal e Celulose SA, Santana, Brazil
- ¹⁹Herbario Amazônico Colombiano, Instituto SINCHI, Bogotá DC, Colombia
- ²⁰Science and Education, Chicago, Illinois, USA
- ²¹Divisão de Sensoriamento Remoto – DSR, Instituto Nacional de Pesquisas Espaciais – INPE, São José dos Campos, Brazil
- ²²Herbario Vargas, Universidad Nacional de San Antonio Abad del Cuzco, Cuzco, Peru
- ²³Biological and Environmental Sciences, University of Stirling, Stirling, UK
- ²⁴Centro de Biociências, Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, Brazil
- ²⁵Departamento de Biologia, Universidade Federal de Rondônia, Porto Velho, Brazil
- ²⁶Programa de Pós-Graduação em Biodiversidade e Biotecnologia PPG-Bionorte, Universidade Federal de Rondônia, Porto Velho, Brazil
- ²⁷Department of Biology and Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA
- ²⁸Centre for Tropical Environmental and Sustainability Science and College of Science and Engineering, James Cook University, Cairns, Queensland, Australia
- ²⁹Instituto de Investigaciones de la Amazonia Peruana (IIAP), Iquitos, Peru
- ³⁰School of Geography and Sustainable Development, University of St Andrews, St Andrews, UK
- ³¹Jardín Botánico de Missouri, Oiapalpa, Peru
- ³²Instituto Boliviano de Investigación Forestal, Santa Cruz, Bolivia
- ³³Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK
- ³⁴Agropecuária-Amazônica, Santa Cruz, Bolivia
- ³⁵Programa de Pós-Graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso, Nova Xavantina, Brazil
- ³⁶Facultad de Ciencias Agrícolas, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia
- ³⁷Natural History Museum, University of Oslo, Oslo, Norway
- ³⁸International Center for Tropical Botany (ICTB) Department of Biological Sciences, Florida International University, Miami, Florida, USA
- ³⁹Cirad UMR Ecofog, AgrosParisTech, CNRS, INRAE, Univ Guyane, Kourou, Cedex, France
- ⁴⁰Centro de Investigaciones Ecológicas de Guayana, Universidad Nacional Experimental de Guayana, Ciudad Bolívar, Venezuela
- ⁴¹Empresa Recursos Genéticos e Biotecnologia, Parque Estação Biológica, Prédio da Botânica e Ecologia, Brasília, Brazil
- ⁴²Projeto Dinâmica Biológica de Fragmentos Florestais, Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, Brazil
- ⁴³Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, Brazil
- ⁴⁴Laboratório de Ecologia de Doenças Transmissíveis da Amazônia (EDTA), Instituto Leônidas e Maria Deane, Manaus, Brazil
- ⁴⁵Programa de Pós-graduação em Biodiversidade e Saúde, Instituto Oswaldo Cruz – IOC/PROCRUZ, Rio de Janeiro, Brazil
- ⁴⁶Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, Brazil
- ⁴⁷Programa de Pós-Graduação em Ecologia, Universidade Federal do Pará, Belém, Brazil
- ⁴⁸Empresa Brasileira de Pesquisa Agropecuária, Empresa Amazônia Oriental, Belém, Brazil

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Anexo 3. Artículo publicado en revista Nature ecology & evolution.

nature ecology & evolution



Article

<https://doi.org/10.1036/s41559-024-02364-1>

One sixth of Amazonian tree diversity is dependent on river floodplains

Received: 23 March 2023

Accepted: 9 February 2024

Published online: 11 March 2024

Check for updates

A list of authors and their affiliations appears at the end of the paper

Amazonia's floodplain system is the largest and most biodiverse on Earth. Although forests are crucial to the ecological integrity of floodplains, our understanding of their species composition and how this may differ from surrounding forest types is still far too limited, particularly as changing inundation regimes begin to reshape floodplain tree communities and the critical ecosystem functions they underpin. Here we address this gap by taking a spatially explicit look at Amazonia-wide patterns of tree-species turnover and ecological specialization of the region's floodplain forests. We show that the majority of Amazonian tree species can inhabit floodplains, and about a sixth of Amazonian tree diversity is ecologically specialized on floodplains. The degree of specialization in floodplain communities is driven by regional flood patterns, with the most compositionally differentiated floodplain forests located centrally within the fluvial network and contingent on the most extraordinary flood magnitudes regionally. Our results provide a spatially explicit view of ecological specialization of floodplain forest communities and expose the need for whole-basin hydrological integrity to protect the Amazon's tree diversity and its function.

Amazonia's floodplain forests border the rivers that collectively make up our planet's largest fluvial system and underpin crucial aspects of floodplain ecosystem function¹. But how and why are the Amazon's floodplain tree communities distinct from surrounding forests? These questions have long intrigued ecologists because they get to the heart of what floodplain forests mean for the maintenance of tree diversity^{2–4}, population regulation^{5,6} and speciation^{7–9}. These questions are vital for conservation planning too. Natural flood regimes are a principal driver of growth, phenology and life cycles of floodplain trees¹⁰ but are becoming increasingly altered by proliferating hydroelectric dams, changing rainfall patterns and deforestation^{11–13}. These changes threaten to reshape floodplain tree assemblages in ways that imperil both biodiversity and fundamental ecosystem functions^{14–16}. For example, compositional changes to floodplain forests are expected to affect crucial fish–tree interactions that sustain aquatic trophic webs, with unknown consequences for productive fisheries on which the livelihoods of Amazonian peoples depend¹⁷. Given the evidence that human interventions in the Amazon's hydrological system are disruptive to

floodplain tree communities and propagate over large spatial scales^{18–20}, our understanding of the species composition of floodplain forests and the extent to which they differ from surrounding forest types is still too fragmented²¹, coming mostly from studies with limited spatial extents (but see refs. 22, 23). Amid the growing pace and scope of hydrological threats, there is a pressing need for an integrated, system-wide approach that can guide floodplain conservation strategies and identify potential vulnerabilities in spatially explicit ways.

Central to this aim are two concepts that together capture essential information about linkages between species and their environment. The first is habitat specialization, which measures the restriction of a tree species' distribution to particular environments (here, to floodplains); it sheds light on species adaptation and ecological function and can be a key indicator of species vulnerability to environmental change²⁴. The second is species turnover – here as a measure of the level of compositional differentiation between floodplain and adjacent terra firme forest – which reflects the extent to which species distributions are constrained by habitat, and thus how tree diversity is spatially

✉ e-mail: john.householder@kit.edu; floren.westmann@kit.edu; hans.temstege@naturplk.nl

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Article

<https://doi.org/10.1038/s41559-024-02364-1>

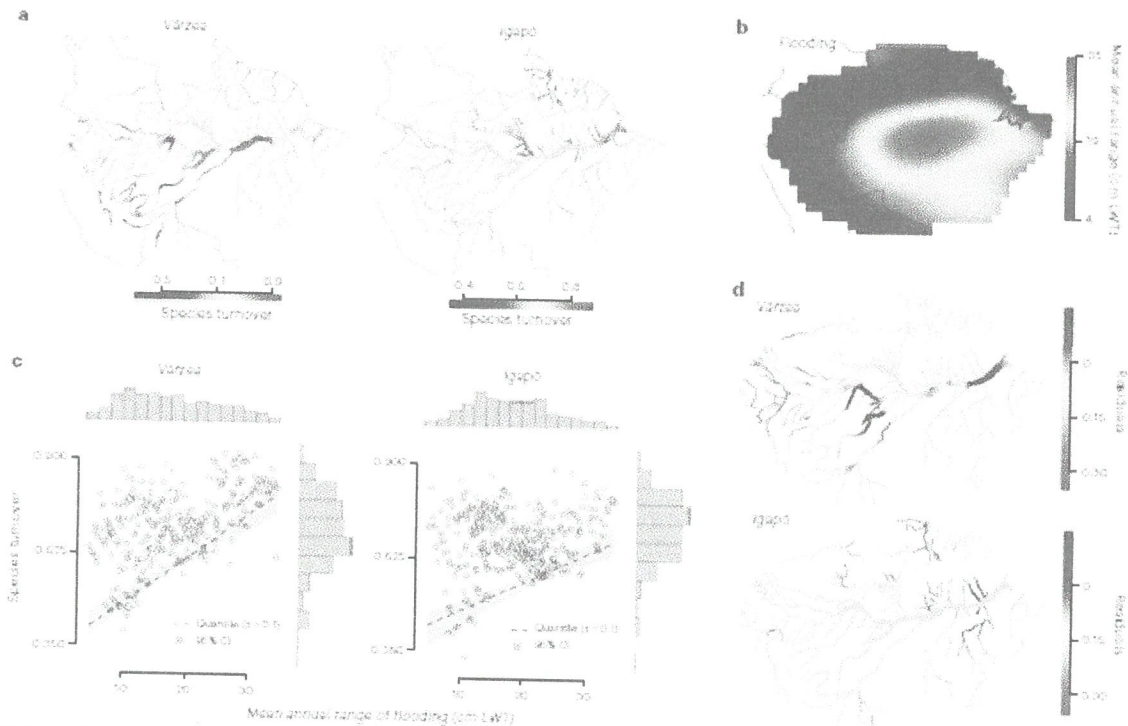


Fig. 1 Broad-scale geographic and environmental patterning of species turnover across floodplain and adjacent terra firme forest habitats, for várzea terra firme and igapo terra firme comparisons. **a**, Spatial patterns of species turnover for várzea and igapo, showing a concentration of high species turnover located centrally within the fluvial network. Grey rivers are masked out because they either correspond to a different floodplain habitat or did not meet minimum sampling criteria for analysis. **b**, Regional differences in seasonal flooding are described as an annual flood wave that originates in Andean headwaters, peaks in central Amazonia and dissipates near the Amazon mouth.

Floodplains positioned at the peak of this flood wave are seasonally inundated by the highest amplitude and longest-lasting floods. LWL, land water thickness. **c**, Patterning of species turnover of várzea and igapo with surrounding terra firme along the flood wave. The black dashed line shows the lower bound of species turnover with flooding, assessed with quantile regression at $\alpha = 0.1$. **d**, Mapped residuals from quantile regression modeling for várzea and igapo throughout much of western Amazonia; species turnover is relatively higher than expected given the lower flooding implied by its headwater position on the flood wave.

higher than expected given the region's limited flooding and peripheral position far from the peak of the flood wave (Fig. 1d). High compositional differences may be maintained by one or more unmeasured factors that interact with flooding, or, alternatively, our estimate of the broad-scale flood wave failed to capture local but nonetheless important patterns of flooding that contribute to species turnover. For example, rivers in this area drain vast catchments exposed to some of the highest annual precipitation rates in Amazonia, which may influence local flooding patterns in ways that maintain compositional differences with surrounding terra firme (we explore this further in Supplementary Discussion 1, Supplementary Fig. 1 and Supplementary Table 2).

Identifying floodplain specialist tree species

Differences in composition between floodplain and terra firme forests imply that many species may have narrow preferences for one or the other habitat. To better identify these specialized species, we employed association tests, which measure the strength of habitat preference for each species independently. We ran tests for a subset of 1,666 relatively well-sampled tree species (those with at least 20 occurrences in the plot network) using species-specific abundance information from plot inventories to test for non-random habitat selection for floodplains or terra firme. Specifically, we used a correlation index because absences outside a target habitat are also taken into account³¹, permitting us to

categorize each species as a floodplain specialist, a terra firme specialist or a habitat generalist and subsequently examine each group's relative abundance and richness in relation to species turnover.

Of the 1,666 species, a clear majority (1,450 species, 87%) occurred in floodplains at least once, and all had at least one occurrence in terra firme. Many tree species can therefore inhabit floodplains at least sporadically. Association tests revealed a smaller group of 301 species (18% of 1,666) that occurred in floodplains more often than random expectation ($P < 0.05$) and were therefore considered floodplain specialists (Supplementary Table 3). The majority of floodplain specialists had a clear preference for one type of floodplain habitat or another (várzea, 51%, 154 species; igapo, 38%, 115 species), while relatively few floodplain specialists were associated with both floodplain habitats (11%, 32 species). False positives due to multiple testing are expected for about 15 species (5% of 301 species), so we estimate the overall percentage of floodplain specialist tree species to be 17% of the 1,666 species tested. Terra firme specialists accounted for 700 species (42% of 1,666), and the remaining 665 species (40%) had no clear habitat association and were therefore considered generalists.

By cross-referencing the names of the 1,666 tested species with each floodplain composition grid, we were able to examine the cell-wise relative abundance and richness of floodplain specialists (301 species), habitat generalists and terra firme specialists (that is, spillover from

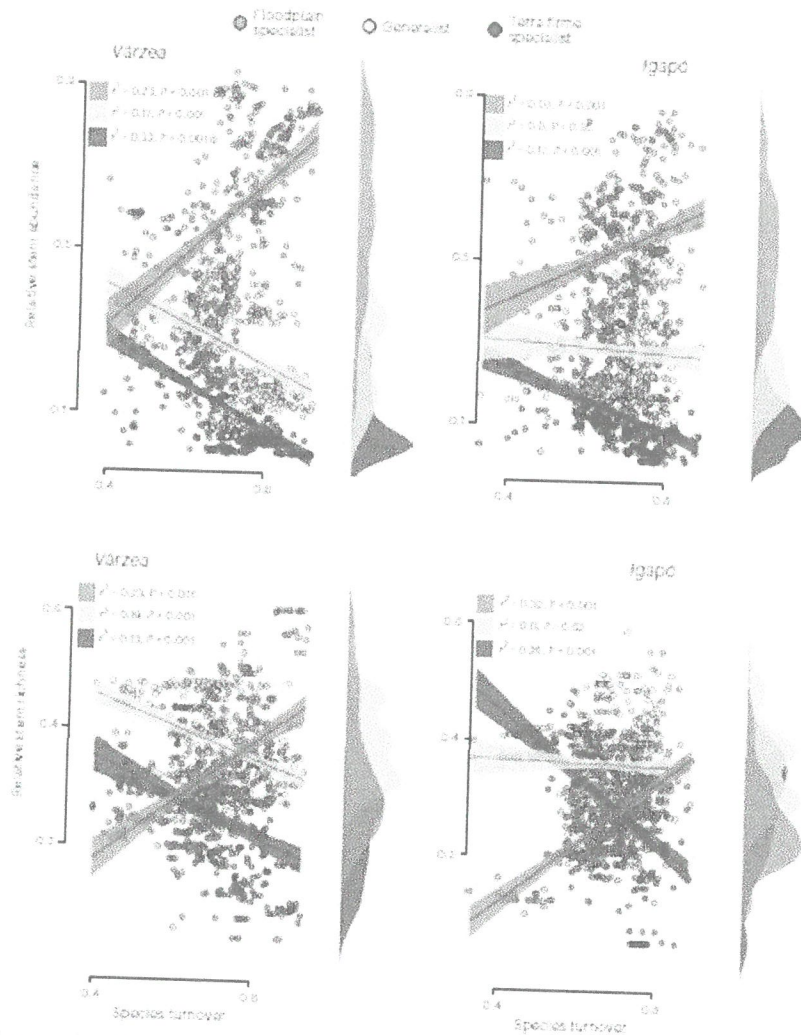


Fig. 2 | Relationships between species turnover and the relative abundance and richness of floodplain specialists, habitat generalists and spillover from terra firme (terra firme specialists) in várzea and igapó. With increasing levels of species turnover, floodplain specialists become more dominant, while spillover from terra firme species decreases. The proportions are derived from interpolated compositional grids of *várzea* and *igapó* after cross-

referencing with the names of the 1,666 species tested for habitat association. The relationships with species turnover are derived from simple least squares models. The coloured boxes indicate the proportion of explained variance (r^2) and P values. The trend lines (black) are bounded by coloured bands showing the 95% CIs. Density plots for the relative abundance and richness of each species group are shown in the right margins.

terra firme) in floodplains. As expected, the relative abundance and richness of floodplain specialists increased with species turnover. More surprising were the upper limits of floodplain specialist rates—In areas of high species turnover, floodplain forests are decidedly specialist-dominated, with nearly half of floodplain cell richness and a majority (>70%) of floodplain stems pertaining to specialist species (Fig. 2). At low levels of species turnover, generalist species and spillover species from terra firme (terra firme specialists) together accounted for the majority of species and stems in floodplains. However, even at low levels of species turnover, floodplain specialists still account for about a third of stems and 20% of tree species richness. For any floodplain anywhere, therefore, a considerable complement of its local tree diversity is strongly circumscribed to its flooded habitat. Habitat generalists, particularly in *igapó*, can remain an important

component of floodplain forests regardless of the level of species turnover. Our lower range of relative richness for habitat specialists in floodplains is remarkably similar to our previous estimate for *várzea*, but our upper range (about 60%) is nearly twice as large, undoubtedly reflecting the greater amount of quantitative abundance information available in our current database.

Optimizing conservation benefits for biodiversity

Our results suggest that although floodplains cumulatively account for only about a fifth of the regional surface area, they contain most of Amazonian tree diversity. Assuming that our sample of 1,666 species can be taken as representative of the tree flora at large, then nearly 9 of every 10 species can inhabit floodplains, albeit many of them at low densities. Importantly, a substantial fraction of Amazonian tree diversity may be



Artículo

<https://doi.org/10.1036/341559-024-0236-4-1>

bilinear interpolation. For visualization in Fig. 1b, the flooding grid was resampled to higher (0.1°) resolution using a bilinear interpolation.

Composition data

We produced three analogous compositional grids of 5671° cells covering the Amazon region for terra firme, várzea and igapó, using tree inventory data from the ATDN²². ATDN inventories falling outside of the grid were excluded. The final data subset comprises 1,705 mostly 1 ha tree inventory plots with relatively complete information on species composition and abundances (Extended Data Fig. 1 and Supplementary Table 1). Only species-level identifications were retained, accounting for 85% of species and 87% of stems. Plots were classified as terra firme ($n = 1,250$, 73%), várzea ($n = 271$, 16%) or igapó ($n = 184$, 11%), following the original habitat designations of the contributors, and species stem densities in plots were standardized to stems per ha to account for variable plot areas. We used habitat-specific plot data to populate compositional grids for each habitat separately, in two alternative manners. In the first approach, species cell abundances were interpolated from abundance information in plot inventories located within a 3° search radius, using inverse distance weighting set to a power of 2 (Extended Data Fig. 2). The search radius ensures that a species is predicted to be absent in cells where it has no nearby records of occurrence, and its maximum distance set at 3° is an optimization previously determined²³ by the match between inverse-distance-weighting maps of all species and a Fishers alpha-diversity map of Amazonian forests²⁴. In the second approach, species cell abundances were generated by pooling plots contained inside individual grid cells, without any spatial interpolation. Whereas the approach based on spatial interpolation constructs plausible cell metacommunities using all sampling localities within ~300 km, the approach of pooling samples within individual grid cells makes considerably less use of the available data but removes spatial dependencies in the response variable.

Species turnover

We assessed species turnover at analogous 1° cells of várzea-terra firme and igapó-terra firme grid pairs, using both interpolated and pooled versions of compositional data in parallel analyses. Species turnover is a function of the number of species shared between floodplain and terra firme samples (a) and the numbers of species unique to either sample (b and c). We used Simpson dissimilarity, $\beta_{sdp} = 1 - a / (a + \min(b, c))$, where $\min(b, c)$ refers to the smallest number of unique species²⁵. This species turnover metric is not influenced by differences in richness that are expected between terra firme and floodplain samples and is thus more suited to our questions regarding species replacement. Species turnover at a given cell location was assessed by repeatedly subsampling analogous terra firme and floodplain cells, each time drawing 500 stems from each habitat with replacement, setting the probability of species selection proportional to cell density of each species. Although species selection is based on predicted abundance information, our presence/absence measure of species turnover is robust to highly abundant species that alternative abundance-based indices may be overly sensitive to. Each sampled assembly is therefore of similar size to a standard hectare plot and reflects average, habitat-specific tree composition on the basis of information from the nearby plot inventories. For each cell, we report the mean Simpson's dissimilarity of 1,000 subsamples. As an additional precaution to avoid calculating species turnover at severely undersampled cells, we required cell richness for each habitat grid to be >100 species. Species tend to accumulate rapidly in tropical forests, so an accumulation of fewer than 100 species is a strong indication that sampling was either too limited or skewed towards environmentally extreme or disturbed environments. For similar reasons, for analysis based on compositional grids derived from pooling inventories, we additionally required that cells contain at least two floodplain and two terra firme inventories. In both the interpolated and pooled approaches, the total number

of cells where species turnover was calculated depended on the spatial configuration of terra firme and floodplain inventories and how these overlapped geographically. Bivariate relationships of species turnover with flooding were examined using least absolute deviation (quantile regression) models. Quantile regression was preferred over least squares because initial inspection revealed flooding to be a better predictor of minimum levels of species turnover rather than mean levels. Quantile regression models of the lower bounds of species turnover ($\tau = 0.1$) therefore provide more appropriate estimates of the relationship between flooding and minimum levels of species turnover, and residual levels of species turnover can be interpreted as the summed effect of unmeasured or unknown factors that interact with flooding to maintain species turnover^{26,27}. To test whether annual rainfall interacted with flooding to maintain species turnover, we used least squares models, comparing competing least squares models with and without a rainfall interaction using F tests. Prior to running least squares regression, we checked for multi-collinearity among environmental factors by assessing variance inflation factors. Moran's I was used to check for residual spatial autocorrelation. All analyses were performed in R v.4.1.2 (ref. 39) using custom code and the packages `vegan`²⁸, `quantreg`²⁹, `raster`³⁰, `rgdal`³¹, `gstat`³² and `ape`³³.

For visualization of the geographic patterns of species turnover, as well as residual levels of species turnover remaining from quantile regression models, we projected the original 1° grids onto higher-resolution (0.05°) floodplain maps using a bilinear interpolation method. To do this for várzea and igapó individually, we first delineated floodplains on the basis of ref. 47 and assigned floodplains to either igapó or várzea using the habitat classifications from georeferenced sampling localities in ATDN.

Habitat association

The ecological association of species to floodplain or terra firme habitat was computed as the Pearson correlation between the vector of a species' abundance among inventories and the binary vector of inventory habitat membership (that is, terra firme, igapó and várzea)³⁴. In contrast to the alternative approach using indicator values, Pearson correlation additionally takes into account absences outside the target habitat and is arguably preferable for determining the ecological preference of a given species among a set of alternative habitats^{35,36}. Because some species may associate with more than one floodplain habitat, we allowed for floodplain combinations (for example, igapó + várzea). A permutation test was used to evaluate statistical significance for the habitat or combination for which the correlation was highest, implemented with the `multipatt` function of the R package `Indicspecies`, using the `rg` option^{37,38}. Differences in sampling effort among habitats, which can influence estimated coefficients, were accounted for using a group-based stratified resampling procedure³⁹. Most species have smaller ranges than the extent of the study area, so species permutations were performed on the subset of plot inventories contained within cells predicting >0 abundance, on the basis of 3° inverse-distance-weighted interpolations of plot abundance information. Only species occurring in over 20 inventories were assessed to ensure sufficient sampling. We used a $P < 0.05$ threshold to identify habitat specialists; all others were considered as habitat generalists.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Metadata for all plots used in this study are available in Supplementary Table 1. Habitat correlation scores for 1,666 species are available in Supplementary Table 3. GRC-Tellus data on monthly land water thickness are publicly available from <https://grace.jpl.nasa.gov/data/get-data/monthly-mass-grids-land/>. WorldClim Bioclimatic data are available



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<https://doi.org/10.1038/s41559-024-02304-1>

from <https://www.worldclim.org/data/worldclim.html>. All tree inventory data can also be made available upon reasonable request to H.L.S.

Code availability

The R scripts used in the analysis are available upon reasonable request to J. E. Householder.

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Nature Ecology & Evolution



Anexo 4. Resolución de decanatura para Curso de capacitación: Análisis de datos con R aplicados a las ciencias básicas.



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS
Decanatura de la Facultad de Ingeniería

"Año del Bicentenario, de la Consolidación de Nuestra Independencia y de la Conmemoración de las
Heroicas Batallas de Junín y Ayacucho"
"Madre de Dios capital de la biodiversidad del Perú"

**RESOLUCIÓN DE DECANATURA DE LA FACULTAD DE INGENIERÍA N° 076-
2024-UNAMAD-DFI**

Puerto Maldonado, 19 de marzo de 2024

VISTO:

El Expediente N° 652, de fecha 18 de marzo de 2024, Oficio N° 066-2024-UNAMAD-R-VRA-DFI-DA/CB de fecha 18 de marzo de 2024, Carta N° 001-2024-UNAMAD-IHC/DA-CB, de fecha 14 de marzo de 2024; Ley Universitaria N° 30220; Estatuto de la Universidad Nacional Amazónica de Madre de Dios, y;

CONSIDERANDO:

Que, la Universidad Nacional Amazónica de Madre de Dios fue creada mediante Ley N° 27297, de fecha 05 de julio del año 2000 y mediante Resolución N° 626-2009-CÓNAFU, se otorga la Autorización definitiva para su funcionamiento.

Que, mediante Resolución de Consejo Directivo N° 132-2019-SUNEDU/CD, de fecha 10 de octubre de 2019, la Universidad Nacional Amazónica de Madre de Dios, obtiene su Licenciamiento Institucional, por un periodo de 06 años.

Que, el **Artículo 5° numeral 5.15 de la Ley N° 30220** – Ley Universitaria señala como uno de los principios de las universidades, "la pertinencia de la enseñanza e investigación con la realidad social". Asimismo, el Artículo 6 numeral 6.6 de la misma Ley señala que son fines de las universidades "el de difundir el conocimiento universal en beneficio de la humanidad".

Que, el **Artículo 79° de la Ley N° 30220** – Ley Universitaria, indica son funciones de los docentes universitarios: "la investigación, el mejoramiento continuo y permanente de la enseñanza, la proyección social y la gestión universitaria en los ámbitos que le corresponde".

Que, el **Artículo 20°** del Estatuto de la UNAMAD indica que, "Las Facultades de la UNAMAD son las unidades de formación académica, profesional y de gestión. Propician la investigación, la proyección social, Extensión Cultural y Universitaria. Está integrada por docentes y estudiantes. Gozan de autonomía académica y administrativa en los asuntos de su competencia dentro de la Ley y del Estatuto".

Que, mediante Resolución de Consejo Universitario N° 002-2023-UNAMAD CU, de fecha 08 de febrero de 2023, se **APRUEBA**, la **Directiva de Elaboración, Seguimiento y Evaluación de Planes de Trabajo** de la Universidad Nacional Amazónica de Madre de Dios, versión 1.0.

Que, mediante Carta N° 001-2024-UNAMAD-IHC/DA-CB, de fecha 14 de marzo de 2024, el Dr. Isau Huamantupa Chuquimaco Docente Investigador adscrito al Departamento Académico de Ciencias Básicas –UNAMAD, remite al Director del Departamento Académico de Ciencias Básicas, desarrollo del curso Taller "**ANÁLISIS DE DATOS CON R APLICADOS A LAS CIENCIAS BÁSICAS**", evento que será autofinanciado y con el apoyo del departamento de Ciencias Básicas y el Herbario Alwyn Gentry (HAG)

Que, mediante Oficio N° 066-2024-UNAMAD-R-VRA-DFI-DA/CB de fecha 18 de marzo de 2024, el Director del Departamento Académico de Ciencias Básicas, solicita a la Decanatura de la Facultad de Ingeniería de la UNAMAD, la aprobación mediante acto resolutorio del **Plan de trabajo Curso Taller "ANÁLISIS DE DATOS CON R APLICADOS A LAS CIENCIAS BÁSICAS"**, que tiene por finalidad fortalecer las capacidades y aptitudes en el uso y manejo del software estadístico R, de los docentes y estudiantes del Departamento Académico de Ciencias Básicas y la Facultad de Ingeniería UNAMAD; dicho evento se llevará a cabo los días **20, 21 y 22 de marzo del 2024**, cito Sala de Docentes del Departamento de Ciencias Básicas - UNAMAD, el mismo que será **AUTOFINANCIADO** por los docentes del área de biología y estadística del Departamento Académico de Ciencias Básicas.



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS
Decanatura de la Facultad de Ingeniería

"Año del Bicentenario, de la Consolidación de Nuestra Independencia y de la Conmemoración de las
Heroicas Batallas de Junín y Ayacucho"
Madre de Dios capital de la biodiversidad del Perú"

**RESOLUCIÓN DE DECANATURA DE LA FACULTAD DE INGENIERÍA N° 076-
2024-UNAMAD-DFI**

Puerto Maldonado, 19 de marzo de 2024

Que, mediante Expediente N° 652, de fecha 18 de marzo de 2024, el Decano de la Facultad de Ingeniería, **AUTORIZA** al Secretario Académico, proyectar la resolución de decanatura, **aprobando, el Plan de trabajo Curso Taller "ANÁLISIS DE DATOS CON R APLICADOS A LAS CIENCIAS BÁSICAS"**, evento que se desarrollará los días **20, 21 y 22 de marzo del 2024**, presentado por el Director del Departamento Académico de Ciencias Básicas de la Universidad Nacional Amazónica de Madre de Dios.

Estando dentro de las atribuciones conferidas al Decano, por la Ley Universitaria N° 30220; el Estatuto de la Universidad Nacional Amazónica de Madre de Dios y en uso de las atribuciones conferidas mediante Resolución de Comité Electoral Universitario N° 010-2023-UNAMAD-CEU, de fecha 29 de diciembre del 2023

SE RESUELVE:

ARTÍCULO PRIMERO: APROBAR, el Plan de trabajo Curso Taller "ANÁLISIS DE DATOS CON R APLICADOS A LAS CIENCIAS BÁSICAS", evento autofinanciado que se desarrollará los días **20, 21 y 22 de marzo del 2024**, organizado por el Departamento Académico de Ciencias Básicas de la Universidad Nacional Amazónica de Madre de Dios.

ARTÍCULO SEGUNDO: NOTIFICAR, la presente resolución al Departamento Académico de Ciencias Básicas de la Universidad Nacional Amazónica de Madre de Dios

ARTÍCULO TERCERO: ORDÉNESE, una vez culminado el evento mencionado en el artículo primero de la presente resolución, remitir el informe final a la Decanatura de la Facultad de Ingeniería, en un plazo no mayor a 15 días hábiles.

REGÍSTRESE, COMUNÍQUESE Y ARCHÍVESE.



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS
Dr. *Severino Quispe Flores*
Decano



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS
Dr. *Vincent Magallanes*
Secretario Académico

E.O.
D.A.C.B.
Archivo
R.D.F. Decano
VARESA



Anexo 5. Artículo publicado en revista PHYTOKEYS.



PhytoKeys 240, 1– 552 (2024)
DOI: 10.3897/phytokeys.240.101716

Monograph

**Advances in Legume Systematics 14. Classification of
Caesalpinioideae. Part 2: Higher-level classification***

Anne Bruneau¹, Luciano Paganucci de Queiroz², Jens J. Ringelberg^{3,4}, Leonardo M. Borges⁵,
Roseli Lopes da Costa Bortoluzzi⁶, Gillian K. Brown⁷, Domingos B. O. S. Cardoso^{8,9}, Ruth P. Clark¹⁰,
Adilva de Souza Conceição¹¹, Matheus Martins Teixeira Cota¹², Else Demeulenaere¹³,
Rodrigo Duno de Stefano¹⁴, John E. Ebinger¹⁵, Julia Ferm¹⁶, Andrés Fonseca-Cortés¹⁷,
Edeline Gagnon^{16,17,18}, Rosaura Grether¹⁹, Ethienne Guerra²⁰, Elspeth Haston¹⁸, Patrick S. Herendeen²¹,
Héctor M. Hernández²², Helen C. F. Hopkins¹⁰, Isau Huamantupa-Chuquimaco²³, Colin E. Hughes²⁴,
Stefanie M. Ickert-Bond²⁴, João Iganci^{25,26}, Erik J. M. Koenen²⁶, Gwilym P. Lewis¹⁰,
Haroldo Cavalcante de Lima^{8,27}, Alexandre Gibau de Lima^{8,28}, Melissa Luckow²⁹, Brigitte Marazzi³⁰,
Bruce R. Maslin^{31,32}, Matías Morales^{33,34}, Marli Pires Morim³⁵, Daniel J. Murphy³⁵,
Shawn A. O'Donnell³⁶, Filipe Gomes Oliveira³⁷, Ana Carla da Silva Oliveira³⁸, Juliana Gastaldello Rando³⁷,
Pétala Gomes Ribeiro³⁹, Carolina Lima Ribeiro³⁹, Felipe da Silva Santos³⁹, David S. Seigler³⁸,
Guilherme Sousa da Silva³⁹, Marcelo F. Simon⁴⁰, Marcos Vinicius Batista Soares²⁰, Vanessa Terra⁴¹

- 1 Institut de recherche en biologie végétale and Département de Sciences biologiques, Université de Montréal, 4101 Sherbrooke E., Montréal (QC) H1X 2B2, Canada
- 2 Universidade Estadual de Feira de Santana, Departamento de Ciências Biológicas, Av. Transpardestina s/n, Campus, Novo Horizonte, 44035-900, Feira de Santana, SA, Brazil
- 3 Department of Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland
- 4 School of Geosciences, University of Edinburgh, Old College, South Bridge, Edinburgh EH8 9YL, UK
- 5 Universidade Federal de São Carlos, Departamento de Botânica, Rodovia Washington Luís, Km 225, 13565-905, São Carlos, SP, Brazil
- 6 Programa de Pós-graduação em Produtividade Vegetal, Universidade do Estado de Santa Catarina, Centro de Ciências Aproximadas, Avenida Luiz de Camões 2090, 88520-000, Lages, Santa Catarina, Brazil
- 7 Queensland Herbarium and Biodiversity Science, Department of Environment and Science, Toowoomba, Queensland, 4066, Australia
- 8 Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, PACHECO LEÃO 915, 22460-030, Rio de Janeiro, RJ, Brazil
- 9 Programa de Pós-Graduação em Biodiversidade e Evolução (PPGBioEv), Instituto de Biologia, Universidade Federal de Bahia (UFBA), Rua Barão de Jeremoabo, s.n., Ondina, 40170-115, Salvador, BA, Brazil
- 10 Accelerated Taxonomy Department, Royal Botanic Gardens, Kew, Richmond, TW9 3AE, UK
- 11 Programa de Pós-graduação em Diversidade Vegetal, Universidade do Estado da Bahia, Herbario HUNEB, Campus VII, Rua do Gançoneiro 503, 48008-240, Paulo Afonso, Bahia, Brazil
- 12 Center for Island Sustainability and Sea Grant, University of Guam, 006 Station, Mangilao, 96920, Guam
- 13 Centro de Investigación Científica de Yucatán, A.C. (CIICY), Calle 43 No. 130 x 32 y 34, Chuburná de Méndez, CP 97205, Mérida, Yucatán, Mexico
- 14 Eastern Illinois University, Charleston, IL 61920, USA
- 15 Department of Ecology, Environment and Plant Sciences, 10691, Stockholm University, Stockholm, Sweden
- 16 Department of Integrative Biology, University of Guelph, 50 Stone Road, Guelph (ON) N1G 2W1, Canada
- 17 Chair of Phytopathology, Technical University Munich, 85054 Freising, Germany
- 18 Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, EH3 5LR, UK
- 19 Departamento de Biología, Universidad Autónoma Metropolitana-Iztapalapa, Apdo. Postal 55-535, 09340 Ciudad de México, Mexico
- 20 Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Botânica, Av. Bento Gonçalves 9500, Bloco IV - Prédio 43433, Porto Alegre, RS, 91501-970, Brazil
- 21 Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL 60022, USA
- 22 Departamento de Botânica, Instituto de Biologia, Universidad Nacional Autónoma de México, Cd. Universitaria, 04510 Ciudad de México, Mexico
- 23 Herbario Alwyn Gentry (HAG), Universidad Nacional Amazónica de Madre de Dios (UNAMAD), Av. Jorge Chávez N° 1160, Madre de Dios, Peru
- 24 Department of Biology & Wildlife & Herbarium (ALA) at the University of Alaska Museum of the North, University of Alaska Fairbanks, P.O. Box 755960, Fairbanks AK 99775-6960, USA
- 25 Programa de Pós-Graduação em Fisiologia Vegetal, Universidade Federal de Pelotas, Instituto de Biologia, Campus Universitário Capão do Leão, Passoel André Dreyfus, Departamento de Botânica, Prédio 21, Pelotas, Rio Grande do Sul, 96010-900, Brazil

* Edited by: Anne Bruneau¹, Luciano Paganucci de Queiroz² and Jens J. Ringelberg^{3,4}

PhytoKeys



Adv. in Legume Systematics 14, Part 2: Classification of Caesalpinioideae

26. Evolutionary Biology & Ecology, Université Libre de Bruxelles, Faculté des Sciences, Campus du Solbosch - CP 160/12, Avenue F.D. Roosevelt, 50, 1050 Bruxelles, Belgium
27. Instituto Nacional da Mata Atlântica / INMA-MCTI, Av. José Ruschi, 4, Centro, 29650-000, Santa Teresa, Espírito Santo, Brazil
28. Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden
29. School of Integrative Plant Science, Plant Biology Section, Cornell University, 215 Garden Avenue, Roberts Hall 260, Ithaca, NY 14853, USA
30. Natural History Museum of Canton Ticino, Viale C. Cattaneo 4, 6900 Lugano, Switzerland
31. Western Australian Herbarium, Department of Biodiversity, Conservation and Attractions, Locked Bag 104, Bentley Delivery Centre, Western Australia, 6983, Australia
32. Singapore Herbarium, 1 Cluny Road, Singapore, Singapore
33. Instituto de Recursos Biológicos, CIRN-CNIA, INTA, N. Repetto & Los Reseros s.r.l., Hurlingham, Buenos Aires, Argentina
34. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Godoy Cruz 2290 (C1423FQB), Ciudad Autónoma de Buenos Aires, Argentina
35. Royal Botanic Gardens Victoria, Melbourne, Victoria, 3004, Australia
36. Geography and Environmental Sciences, Northumbria University, Ellison Place, Newcastle upon Tyne, NE1 8ST, UK
37. Programa de Pós-graduação em Ciências Ambientais, Universidade Federal do Oeste da Bahia, Rua Professor José Seabra Lemos 316, 47800-021, Barreiras, Bahia, Brazil
38. Department of Plant Biology, University of Illinois, Urbana, IL 61801, USA
39. Instituto de Biologia, Universidade Estadual de Campinas, Campinas, 13083-876, São Paulo/SP, Brazil
40. Empresa Brasileira de Pesquisa Agropecuária (Embrapa) Recursos Genéticos e Biotecnologia, Parque Estação Biológica, Caixa Postal 02372, 70770-917, Brasília/DF, Brazil
41. Instituto de Biologia, Universidade Federal de Santa Maria, 97105-900, Santa Maria/RS, Brazil

Corresponding author: Anne Bruneau (anne.bruneau@umontreal.ca)



Abstract

Academic editor: Sandy Knapp

Received: 16 February 2023

Accepted: 19 November 2023

Published: 3 April 2024

Citation: Bruneau A, Queiroz LR, Ringelberg JJ, Borges LM, Bortoluzzi RUC, Brown GK, Cardoso DSOC, Clark RR, Conceição AG, Cota MMT, Demeulenaere E, Duno de Stefano R, Ebinger JE, Fern J, Fonseca-Cortés A, Gagnon E, Grether R, Guerra E, Haddon E, Herendeen PC, Hernández HM, Hopkins HCF, Huamantla-Chuquimaco I, Hughes CE, Ichert-Bond SM, Iganci J, Koenen EJM, Lewis GP, Lima HC, Lima AG, Luckow M, Marazzi B, MacIin BR, Moraes M, Morim MR, Murphy DJ, O'Donnell SA, Oliveira FG, Oliveira ACC, Rando JG, Ribeiro PD, Ribeiro CL, Santos PD, Seligler DG, Silva GO, Simon MF, Soares MVB, Terra V (2024) Advances in Legume Systematics 14: Classification of Caesalpinioideae. Part 2: Higher-level classification. *PhytoKeys* 240: 1–552. <https://doi.org/10.3897/phytokeys.240.101716>

Caesalpinioideae is the second largest subfamily of legumes (Leguminosae) with ca. 4680 species and 163 genera. It is an ecologically and economically important group formed of mostly woody perennials that range from large canopy emergent trees to functionally herbaceous geophytes, lianas and shrubs, and which has a global distribution, occurring on every continent except Antarctica. Following the recent re-circumscription of 15 Caesalpinioideae genera as presented in *Advances in Legume Systematics* 14, Part 1, and using as a basis a phylogenomic analysis of 997 nuclear gene sequences for 420 species and all but five of the genera currently recognised in the subfamily, we present a new higher-level classification for the subfamily. The new classification of Caesalpinioideae comprises eleven tribes, all of which are either new, reinstated or re-circumscribed at this rank. Caesalpinieae Rchb. (27 genera / ca. 223 species), Campsiandreae LPWG (2 / 5–22), Cassieae Bronn (7 / 695), Certonieae Rchb. (4 / 6), Dimorphandreae Benth. (4 / 35), Erythrophleae LPWG (2 / 13), Gleditsieae Nakai (3 / 20), Mimoseae Bronn (100 / ca. 3510), Pterogyneae LPWG (1 / 1), Schizolobieae Nakai (8 / 42–43), Sclerolobieae Benth. & Hook. f. (5 / ca. 113). Although many of these lineages have been recognised and named in the past, either as tribes or informal generic groups, their circumscriptions have varied widely and changed over the past decades, such that all the tribes described here differ in generic membership from those previously recognised. Importantly, the approximately 3500 species and 100 genera of the former subfamily Mimosoideae are now placed in the reinstated, but newly circumscribed, tribe Mimoseae. Because of the large size and ecological importance of the tribe, we also provide a clade-based classification system for Mimoseae that includes 17 named lower-level clades. Fourteen of the 100 Mimoseae genera remain unplaced in these lower-level clades: eight are resolved in two grades and six are phylogenetically isolated monogeneric lineages. In addition to the new classification, we provide a key to genera, morphological descriptions and notes for all 163 genera, all tribes, and all named clades. The diversity of growth forms, foliage, flowers and fruits are illustrated for all genera, and for each genus



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nated, specialised bat, bird, butterfly and moth pollinated flowers are also common (Arroyo 1981). In addition to having species with pollen in the more typical tricolporate monads, Caesalpinioideae is the only subfamily of legumes with taxa where pollen is arranged in polyads (Scheme 6). In Mimoseae the pollen arrangement is extremely variable across and sometimes within genera, with pollen in monads, tetrads, bi-tetrads and polyads. Fruit morphology is particularly homoplasious, and in the Mimoseae has proved misleading for generic delimitation (Borges et al. 2022; Ringelberg et al. 2022; Souza et al. 2022b). This diversity of fruit morphology (Schemes 6, 7) reflects adaptations to different seed dispersal syndromes, including passive, elastic and explosive dehiscence, as well as seed dispersal by water, wind, large herbivores, ants, and birds.

The subfamily is most diverse in lowland tropical and subtropical regions, only rarely occurring above 2500 m elevation, but a minority of genera have species in warm temperate zones that are not prone to severe frosts across the Americas, Europe, Asia, and Australia. More than half of Caesalpinioideae genera naturally occur in the Americas (104 of 163 genera), of which 84 are endemic. Africa (including Madagascar) has the second highest number of Caesalpinioideae genera, with 59 genera, 29 of which are endemic, followed by Asia (40 genera, 7 endemic), and Australia and the Pacific (27 genera, 6 endemic; See details in Tables 1, 2).

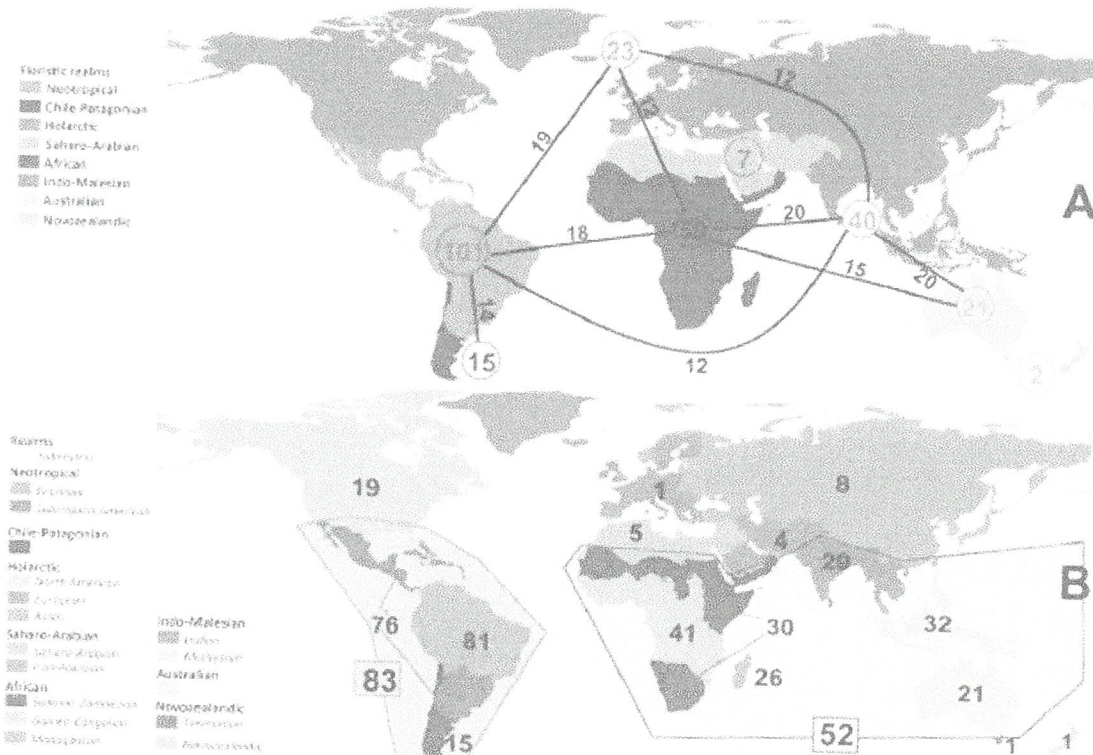


Figure 1. A Caesalpinioideae genus richness across floristic realms (according to Liu et al. 2023). The numbers within the circles represent the total number of genera in each realm. The numbers on the lines represent the number of genera shared between two realms (> 10 genera) **B** Number of Caesalpinioideae genera in the floristic subrealms (sensu Liu et al. 2023). The numbers associated with the two polygons indicate the number of genera restricted to the two major blocks of tropical and subtropical areas in the New World and the Old World (maps modified from Liu et al. 2023, CC BY 4.0).



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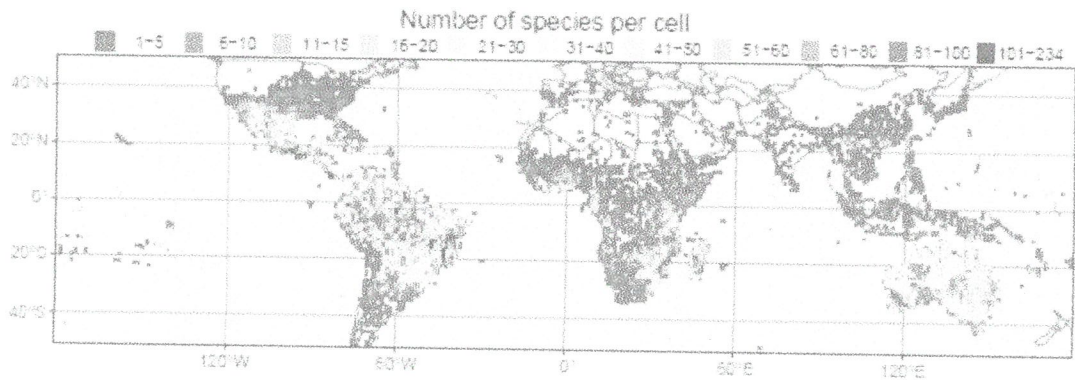


Figure 2. Map showing the global distribution of Caesalpinioideae species richness. Numbers of Caesalpinioideae species per one degree latitude / longitude grid cell. Intraspecific taxa are not counted individually but are included at the species level. All maps in this special issue are based on quality-controlled occurrence data from digitised herbarium specimens and floristic surveys (see Suppl. material 1 for details on occurrence data and methods used to generate maps).

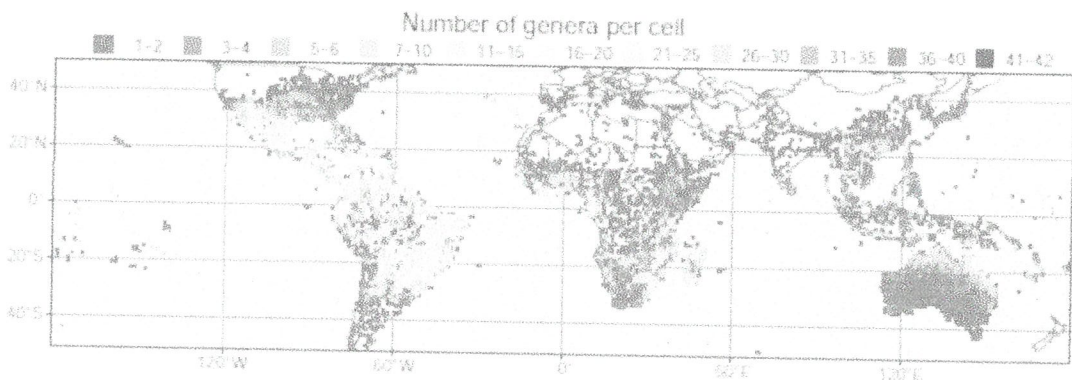


Figure 3. Map showing the global distribution of Caesalpinioideae genus richness. Numbers of Caesalpinioideae genera per one degree latitude / longitude grid cell.

and Ringelberg et al. (2022, 2023). By developing a clade-specific bait set for targeted enrichment of 964 nuclear genes, Koenen et al. (2020a) generated a DNA sequence dataset an order of magnitude larger than those used previously, thereby providing the greatly enhanced phylogenetic resolution required for classifying tribe Mimoseae. Capitalising on these foundations using a slightly modified version of the gene set covering 997 nuclear genes, and importantly extending the taxon sampling to include 300 additional species covering not only Mimoseae but also most genera of non-mimosoid Caesalpinioideae, as well as conducting transcontinental sampling of genera that occur across different continents, Ringelberg et al. (2022, 2023) established a robust phylogenomic hypothesis for subfamily Caesalpinioideae as a whole. These studies revealed or confirmed the non-monophyly of 22 genera, and this was the basis for the re-circumscription of 15 of these genera presented in *Advances in Legume Systematics 14, Part 1* (Hughes et al. 2022a).

The phylogenomic analysis presented here includes 420 Caesalpinioideae species representing all but five of the 163 genera. The five missing genera are: *Vouacoupa* Aubl., which has three species and is likely a member of tribe



Adv. in Legume Systematics 14, Part 2: Classification of Caesalpinchioideae

Description. Unarmed small or medium trees 3–5 (7) m, to canopy trees 40 (50) m; trunk buttressed or not; brachyblasts absent; usually pubescent in all parts with reddish to dark or light brown hairs. Stipules present or absent, caducous. Leaves bipinnate, rachis 5–90 cm long; pinnae 1–40 or more

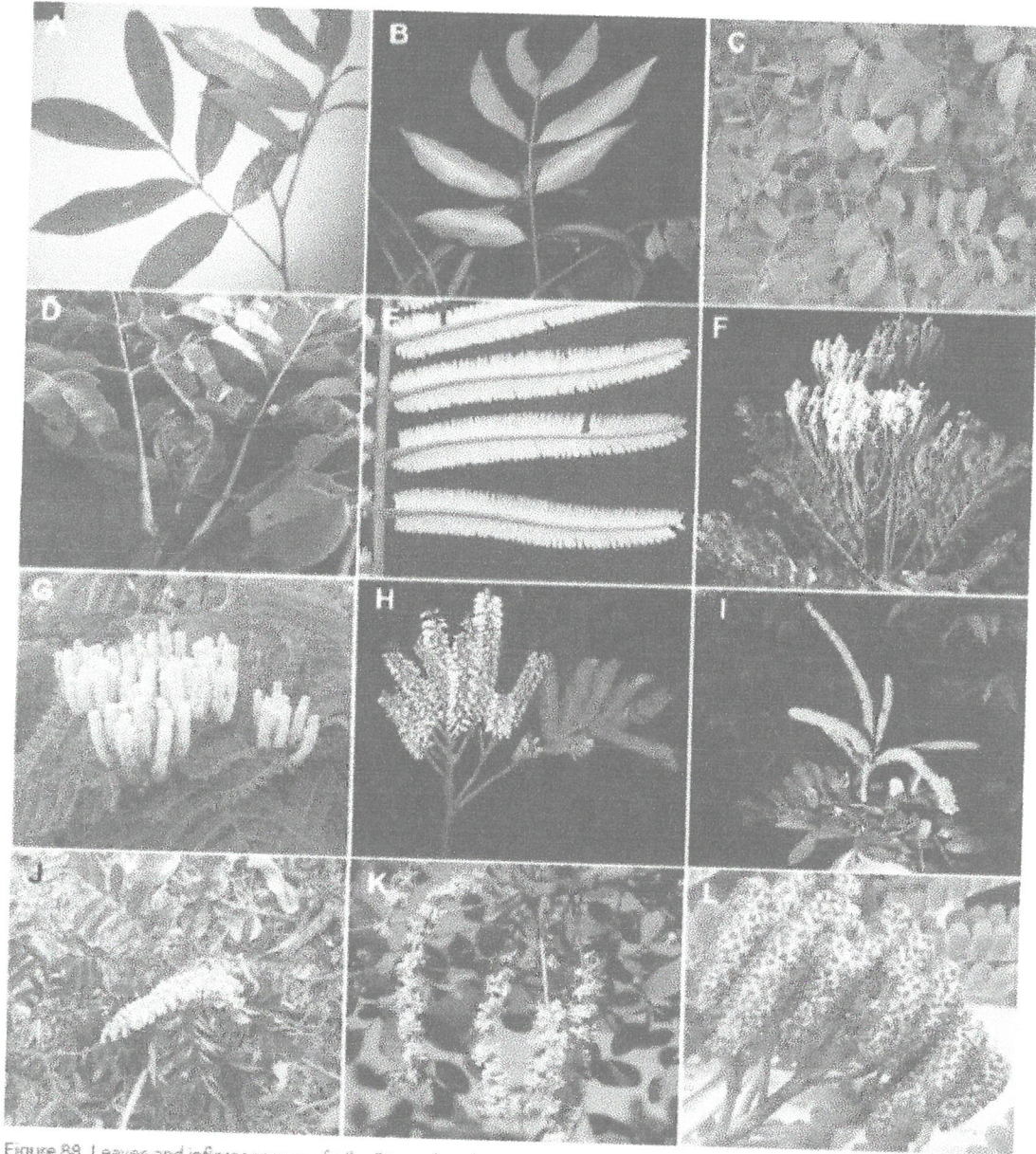


Figure 88. Leaves and inflorescences of tribe Dimorphanthereae A *Mora paraensis* (Ducke) Ducke (Simon 1663) B *Stachyothyrsus staudtii* Harms C *Burkea africana* Hook. D *Dimorphandra mediocris* Ducke (Simon 4209) E *Dimorphandra cuprea* Sprague & Sandwith (Farroñay 1804) F *Dimorphandra parviflora* Spruce ex Benth. (Simon 1176) G *Dimorphandra mollis* Benth. H *Dimorphandra pennigera* Tul. I *Dimorphandra ignea* Ducke J *Dimorphandra vermicosa* Spreng. ex Benth. (Cardoso 3279) K *Burkea africana* L *Dimorphandra garsheniensis* Tul. (Silva 21). Photo credits A, D, E, G MF Simon B Nicolas Texier (CC-BY-NC-ND-3.0) C AR Lecuona (CC-BY-NC-4.0) E, H, I F Javier Farroñay Pacaya J D Cardoso K AE van Wyk, and S Malan L G Sousa da Silva.



Adv. in Legume Systematics 14, Part 2: Classification of Caesalpinioideae

fellowships, Claraz Schenkung Foundation of Switzerland, and the University of Guam Center for Island Sustainability and Sea Grant.

Author contributions

Authors contributed different taxonomic treatments to this monograph. Contributions are noted in each treatment.

Author ORCIDs

Anne Bruneau <https://orcid.org/0000-0001-5547-0796>
 Luciano Paganucci de Queiroz <https://orcid.org/0000-0001-7436-0939>
 Jens J. Ringelberg <https://orcid.org/0000-0003-0567-5210>
 Leonardo M. Borges <https://orcid.org/0000-0001-9269-7316>
 Roseli Lopes da Costa Bortoluzzi <https://orcid.org/0000-0002-7445-7244>
 Gillian K. Brown <https://orcid.org/0000-0002-7940-5435>
 Domingos B. O. S. Cardoso <https://orcid.org/0000-0001-7072-2656>
 Ruth P. Clark <https://orcid.org/0000-0001-9974-2933>
 Adilva de Souza Conceição <https://orcid.org/0000-0002-8800-422X>
 Matheus Martins Teixeira Cota <https://orcid.org/0000-0003-0654-7501>
 Eise Demeulenaere <https://orcid.org/0000-0002-1815-3051>
 Rodrigo Duno de Stefano <https://orcid.org/0000-0003-1707-4121>
 Julia Fern <https://orcid.org/0000-0002-8762-3942>
 Andrés Fonseca-Cortés <https://orcid.org/0000-0001-7207-9940>
 Edeline Gagnon <https://orcid.org/0000-0003-3212-9688>
 Rosaura Grether <https://orcid.org/0000-0003-2673-665X>
 Ethienne Guerra <https://orcid.org/0000-0002-9495-1717>
 Elspeth Haston <https://orcid.org/0000-0001-9144-2848>
 Patrick S. Herendeen <https://orcid.org/0000-0003-2657-8671>
 Héctor M. Hernández <https://orcid.org/0000-0002-1741-5515>
 Helen C. F. Hopkins <https://orcid.org/0000-0003-4984-8224>
 Isau Huamantupa-Chuquimaco <https://orcid.org/0000-0002-4153-5875>
 Colin E. Hughes <https://orcid.org/0000-0002-9701-0699>
 Stefanie M. Ickert-Bond <https://orcid.org/0000-0001-8198-8898>
 João Iganci <https://orcid.org/0000-0002-5740-3666>
 Erik J. M. Koenen <https://orcid.org/0000-0002-4825-4339>
 Gwilym P. Lewis <https://orcid.org/0000-0003-2599-4577>
 Haroldo Cavalcante de Lima <https://orcid.org/0000-0003-2154-670X>
 Alexandre Gibau de Lima <https://orcid.org/0000-0002-9168-2507>
 Melissa Luckow <https://orcid.org/0009-0007-2543-0516>
 Brigitte Marazzi <https://orcid.org/0000-0003-3252-5816>
 Bruce R. Maslin <https://orcid.org/0000-0002-3039-0973>
 Matías Morales <https://orcid.org/0000-0001-5540-9725>
 Marli Pires Morim <https://orcid.org/0000-0003-0872-8429>
 Daniel J. Murphy <https://orcid.org/0000-0002-8358-363X>
 Shawn A. O'Donnell <https://orcid.org/0000-0003-0731-7425>
 Filipe Gomes Oliveira <https://orcid.org/0000-0003-0244-32620>
 Ana Carla da Silva Oliveira <https://orcid.org/0000-0001-7042-5360>
 Juliana Gastaldello Rando <https://orcid.org/0000-0002-3714-8231>
 Pétala Gomes Ribeiro <https://orcid.org/0000-0002-0070-9971>
 Carolina Lima Ribeiro <https://orcid.org/0000-0001-9508-2894>

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Anexo 6. Artículo publicado en revista Brazilian Journal of Botany

Brazilian Journal of Botany
<https://doi.org/10.1007/s40415-024-01016-9>

SYSTEMATICS & PHYLOGENY - ORIGINAL ARTICLE



A densely sampled molecular phylogeny of *Tachigali* (Leguminosae), an evolutionarily successful lineage of neotropical ant-housing canopy trees

Isau Huamantupa-Chuquimaco^{1,2} · Vitor Hugo Maia³ · Haroldo Cavalcante de Lima² · Maristerra Rodrigues Lemes⁴ · Cristiane Snak⁵ · Bernarda Gregório⁵ · Sérgio Ricardo S. Cardoso² · Luciano Paganucci de Queiroz⁵ · Charles E. Zartman⁴ · Gwilym P. Lewis⁶ · Euan K. James⁷ · Kyle G. Dexter^{8,9} · R. Toby Pennington^{9,10} · Marcelo F. Simon¹¹ · Domingos Cardoso^{2,12}

Received: 29 January 2024 / Revised: 2 May 2024 / Accepted: 3 May 2024
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Abstract

Despite recent advances in revealing the evolutionary history of speciose tropical plant clades, many species radiations are still poorly understood phylogenetically. One of these is the species-rich neotropical genus *Tachigali* (~90 spp.), a caesalpinioide lineage of mostly ant-housing canopy trees that has diversified in the tropical rainforest biome across the Andean foothills, Amazon basin, and Atlantic Coastal Forest of Brazil. It is also ecologically dominant across the fire-prone savanna vegetation of the Brazilian Cerrado. The taxonomic history of *Tachigali* has long been confounded with the genus *Sclerolobium*, with the two differing in floral symmetry. Here, we reconstruct the phylogeny of *Tachigali* using densely sampled Bayesian and maximum likelihood analyses of nuclear ribosomal (ITS/5.8S) and plastid (*matK* and *trnL* intron) DNA sequences for 67 species. All phylogenetic analyses support *Tachigali* as monophyletic. We recognize a broad circumscription of *Tachigali* encompassing species exhibiting both radially and bilaterally symmetrical flowers, and we suggest that the traditional generic concept of *Sclerolobium* should be abandoned. The poor resolution in the *Tachigali* phylogeny is suggestive of rapid diversification, which has been observed in other species-rich rainforest-inhabiting plant clades across the Neotropics.

Keywords Caesalpinioideae · Phylogenetics · *Sclerolobium* · Systematics

¹ Isau Huamantupa-Chuquimaco
andeanwayna@gmail.com

² Domingos Cardoso
cardosobot@gmail.com

³ Herbario Alwyn Gentry (HAG), Departamento Académico de Ciencias Básicas, Universidad Nacional Amazónica de Madre de Dios (UNAMAD), Av. Jorge Chávez N°1160, 17001 Puerto Maldonado, Madre de Dios, Peru

⁴ Programa de Pós-Graduação em Botânica, Escola Nacional de Botânica Tropical, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro (ENBT/IBRJ), Rua Pacheco Leão, 2040, Rio de Janeiro, RJ, Brazil

⁵ Departamento de Biologia, Pontifícia Universidade Católica do Rio de Janeiro, Rua Marquês de São Vicente 225, Gávea, Rio de Janeiro, RJ, Brazil

⁶ Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo, 2936, Petrópolis, Manaus, AM 69067-375, Brazil

⁷ Programa de Pós-Graduação em Botânica, Universidade Estadual de Feira de Santana (UEFS), Av. Transnordestina s/n, Novo Horizonte, Feira de Santana, BA 44036-900, Brazil

⁸ Accelerated Taxonomy Department, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK

⁹ The James Hutton Institute, Invergowrie, Dundee DD2 5DA, UK

¹⁰ School of Geosciences, The University of Edinburgh, Edinburgh EH9 3JN, UK

¹¹ Royal Botanic Garden Edinburgh, Edinburgh EH3 5LR, UK

¹² University of Exeter, Laver Building, North Park Road, Exeter EX4 4QE, UK

¹³ Embrapa Recursos Genéticos e Biotecnologia, Parque Estação Biológica (PqEB), C.P. 02372, Brasília, DF 70770-917, Brazil

¹⁴ Programa de Pós-Graduação em Biodiversidade e Evolução (PPGBioEvo), Instituto de Biologia, Universidade Federal de Bahia (UFBA), Rua Barão de Jeremoabo s/n, Ondina, Salvador, BA 40170-115, Brazil



1 Introduction

The neotropical genus *Tachigali* Aubl. (Leguminosae, Caesalpinoideae, sensu LPWG 2017) has 76 species (Silva and Lima 2007; Van der Werff 2008; Huamantupa-Chuquimaco et al. 2019), although our ongoing taxonomic revision suggests it may have more than 90 species (Huamantupa-Chuquimaco et al., unpubl. data). *Tachigali* has diversified as canopy trees in the rainforest biome across the Andean foothills, Amazon basin, and the Atlantic Forest of Brazil, as well as in the fire-prone savanna vegetation of the Cerrado (Dwyer 1957; Lewis 2005; Silva and Lima 2007; Van der Werff 2008; Pennington et al. 2009; Silva et al. 2016). The genus is particularly diverse in Amazonian terra firme forests, where about 70% of its species are found (Van der Werff 2008; Huamantupa-Chuquimaco et al., unpubl. data). The ecological prominence of *Tachigali* is exemplified by *T. paniculata*, which features among the hyper-dominant tree species of the Amazon, with an estimated population size of billions of individuals across Amazonia (ter Steege et al. 2013). The ecological dominance and evolutionary success of *Tachigali* may be rooted in its close symbiotic interactions with nitrogen-fixing bacteria in the genus *Bradyrhizobium* (Sprent et al. 2017) and/or close association with aggressive ants which provide anti-herbivore defense (Fonseca 1994; Ward 1999; Rico-Gray and Oliveira 2007). The ant-*Tachigali* mutualism, for example, has been hypothesized to be a remarkable example of co-radiation, involving waves of colonization by the same ant clade facilitated by the recurrent evolution of various strategies of ant-housing domatia in *Tachigali* (Chomicki et al. 2015). On the other hand, the high species diversity and ecological abundance of *Tachigali* could also be explained, in part, by its idiosyncratic ecology (Baker et al. 2014), particularly its fast demography (precocious attainment of reproductive age, high rates of reproductive success, and overall shorter life cycles). Some species are even monocarpic (i.e., cohorts of individuals die after first flowering; Foster 1977), which is otherwise rare in tropical trees (Poorter et al. 2005). Baker et al. (2014) have shown a trend for higher diversification rates in clades of several genera of canopy trees (e.g., *Inga*, Leguminosae; *Guatteria*, Annonaceae; *Cecropia*, Urticaceae), including *Tachigali*, which share a suite of fast life history traits.

Despite the ecological importance of *Tachigali*, obtaining a full picture of its evolutionary history has been a challenge. Previous phylogenetic analyses based on chloroplast DNA (Haston et al. 2003, 2005; Bruneau et al. 2008; LPWG 2017; Zhang et al. 2020) and low copy nuclear gene sequences (Manzanilla and Bruneau 2012) have consistently placed *Tachigali* in a clade close to the Atlantic

Forest endemic *Arapatiella* R.S. Cowan (2 spp.) and the Amazonian endemic *Jacqueshuberia* Ducke (7 spp.). The genus *Diptychandra* Tul. (2 spp.), which was closely associated with *Tachigali* based on overall morphology (Polhill and Vidal 1981) was found to be phylogenetically closer to *Moldenhawera* Schrad. (12 spp.). However, this *Diptychandra* + *Moldenhawera* clade had long remained unresolved with respect to the *Tachigali* clade (Bruneau et al. 2008; Manzanilla and Bruneau 2012; LPWG 2017; Zhang et al. 2020). In a recent phylogenomic analysis of 997 nuclear genes, all these genera were strongly supported as closely related in the same clade (Ringelberg et al. 2022), despite that clade being subtended by a short branch with notable gene tree conflict. This nuclear phylogenomic tree sampled more densely across the 158 of the 163 genera currently recognized in the subfamily and has been the basis for an entirely revised tribe-level classification of the Caesalpinoideae, where *Tachigali*, together with *Arapatiella*, *Diptychandra*, *Jacqueshuberia*, and *Moldenhawera*, are placed in the newly circumscribed tribe Sclerolobieae (Bruneau et al. 2024). Altogether, however, these phylogenetically closely related genera that comprise the Sclerolobieae are individually distinct in terms of floral architecture and leaf and fruit morphologies (Lewis et al. 2005; Ulibarri 2008; Bruneau et al. 2024), which might explain why they remained classified in different informal groups of the Caesalpinoideae for so long (Polhill and Vidal 1981; Polhill 1994). For example, the relatively small flowers of *Tachigali*, which are borne on largely paniculate inflorescences, greatly contrast with the much larger flowers of *Arapatiella*, *Jacqueshuberia*, and *Moldenhawera*. Even the apparently morphologically homogeneous flowers of *Tachigali* display considerable variation in terms of floral symmetry when examined more closely in their ontogenetic development (Fig. 1; Casanova et al. 2020). The genera *Jacqueshuberia* and *Moldenhawera* are more florally elaborate. *Jacqueshuberia* has hummingbird-pollinated flowers with exerted red stamens, while *Moldenhawera* has a Malpighiaceae-like floral architecture, where the flowers in almost all species have yellow, marginally crimped, long-clawed petals, and a cluster of small staminodes, resembling the oil glands or elaiophores typical of Malpighiaceae flowers (Queiroz et al. 2024). In addition to having unique paripinnate leaves where the leaflets are inversely symmetric and opposite (Lewis et al. 2005; Ulibarri 2008), *Tachigali* species have wind-dispersed, compressed cryptosamara fruits, unlike all other related genera of the Sclerolobieae, which have elastically dehiscent pods.

While the higher-level phylogenetic placement of *Tachigali* has been settled within the newly circumscribed tribe Sclerolobieae (Ringelberg et al. 2022; Bruneau et al. 2024), the genus has a long confounding taxonomic history with the

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Fig. 1 Representative morphology of the ant-housing genus *Tachigali*. **A–C** Examples of leaf domatia and variation of stipule shape in Amazonian *Tachigali* spp.; note in **C** the strongly revolute foliaceous stipules with impressed secondary veins (the whole structure similar to a butterfly pupa). **F** The wind-dispersed, compressed cryptosamaras of the Amazonian species *T. paraensis*. **G, H** Bilaterally symmetrical flowers of the Amazonian species *T. macrostachya* (**G**) and *T. paniculata* (**H**). **I, J** Radially symmetrical flowers of the Amazonian species *T. paraensis* (**I**) and *T. rugosa* (**J**). **K** A large, buttressed individual of *T. amplifolia*. **L, M** Candelabrum-like inflorescences *T. macrostachya* (**L**) and densely paniculate inflorescences of *T. amarumayna* (**M**). Photographs by Domingos Cardoso (**A–B, D–J, L**), and Isao Huamantupa (**C, K, M**)



genus *Sclerolobium* Vogel. Floral symmetry was previously used to differentiate *Tachigali* and *Sclerolobium* (Dwyer 1954, 1957). The radially-symmetrical-flowered *Sclerolobium* was treated as separate from the bilaterally-symmetrical-flowered *Tachigali* s.str. The bilaterally symmetrical floral architecture with curved hypanthium that is observed in the species of *Tachigali* s.str. is indeed somewhat similar morphologically to the much larger flowers of the related genera *Arapatiella* and *Jacqueshuberia*, whereas the radial flowers of the species formerly treated under *Sclerolobium* more closely resemble those of *Diptychandra*. However, evidence from wood anatomy (Gasson et al. 2003; Macedo et al. 2014), pollen morphology (Graham and Barker 1981; Banks and Lewis 2018), comparative flower development (Casanova et al. 2020), and overall floral, fruit, and

leaf morphology (Zarucchi and Herendeen 1993; Pipoly 1995; Kirkbride et al. 2000; Lewis et al. 2005; Ulibarri 2008; Van der Werff 2008) has supported merging these two genera (Lewis et al. 2005; LPWG 2017; Lima et al. 2024). Although all species of *Sclerolobium* have already been transferred nomenclaturally to *Tachigali* within the past 20 years (Oliveira-Filho 2006; Silva and Lima 2007; Van der Werff 2008) and are currently treated under the same genus-level taxonomic concept (LPWG 2023; Lima et al. 2024), the monophyly of *Sclerolobium* and *Tachigali* has not been thoroughly investigated using phylogenetic analyses of DNA sequence data.

Despite advances in morphological studies of the *Tachigali-Sclerolobium* boundary, the phylogenetic identity and monophyletic status of *Tachigali* and *Sclerolobium* still



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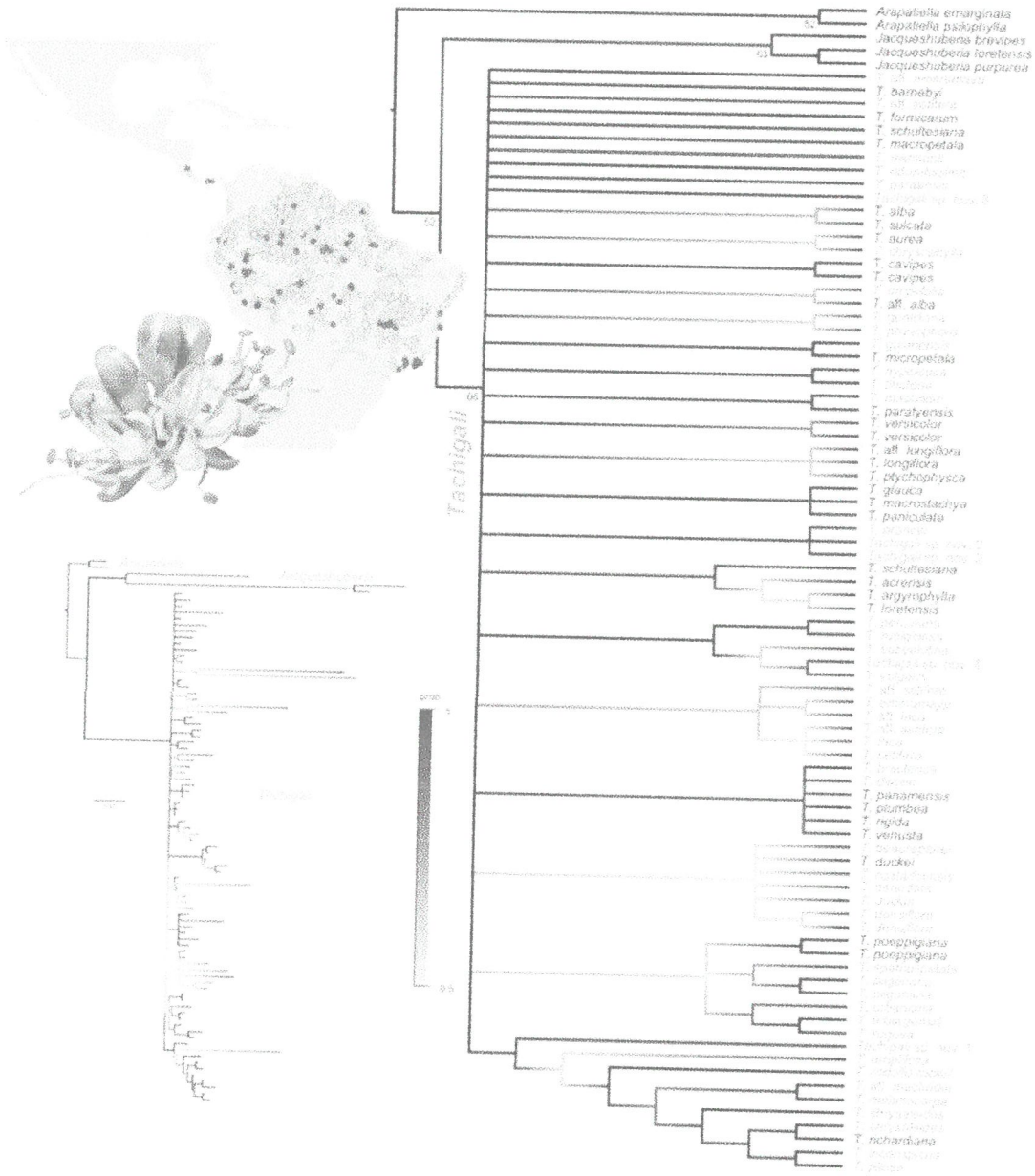


Fig. 2 Majority-rule consensus tree and respective phylogram derived from the concatenated nuclear (ITS/5.8) and plastid (*matK* and *trnL* intron) Bayesian analysis showing the relationships among the caesalpinoidean legume genera of the *Tachigali* clade, with focus on the inter-species relationships in *Tachigali*. The terminals in gray are species originally described in *Sclerolobium*. Posterior probabilities from 0.5 to 1.0 are shown as color gradient from gray to black on the branches. Numbers on branches are the maximum likelihood bootstrap support values above 50%. The full distribution of the genus is represented by all point records in the map, from which the sampled accessions in the phylogeny are highlighted in green. The general flower architecture of *Tachigali* is represented by a photograph of *Tachigali paniculata*. Photograph: Domingos Cardoso.



A densely sampled molecular phylogeny of *Tachigali* (Leguminosae), an evolutionarily...

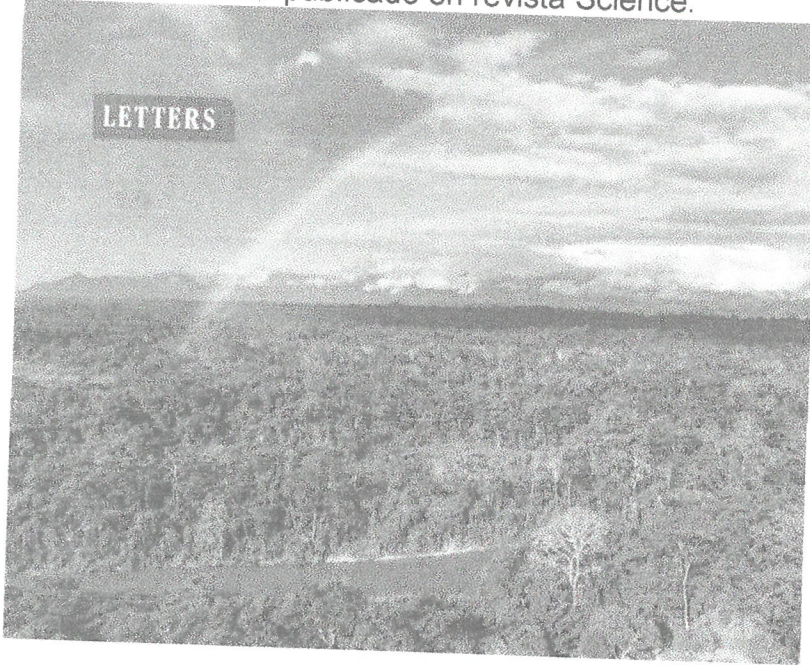
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Anexo 7. Artículo publicado en revista Science.



LETTERS

Edited by Jennifer Sills

Peru's zoning amendment endangers forests

Peru, one of the most biodiverse countries in the world (1), contains many endemic species that are at risk of extinction (2). The Peruvian Amazon biome harbors most of this diversity and provides globally important ecosystem services and benefits to all people (3, 4) as well as economic and cultural value for Indigenous communities (5). However, recent amendments to Peru's Forestry and Wildlife Law No. 29763 threaten these important forest ecosystems.

On 11 January, the Peruvian Congress amended Law No. 29763 by enacting Law No. 31973 (6), which removes obstacles to deforestation by changing zoning laws and regulatory bodies. Previously, exploitation could only take place in areas zoned as "permanent production forests." No area could be rezoned as permanent production forests without an evaluation study and approval from the Ministry of Environment, the regulatory body for land use in forested areas. Law No. 31973 removes the evaluation requirement and allows zoning changes with permission from the Ministry of Agricultural Development and Irrigation, which replaces the Ministry of Environment as Peru's forest regulatory body. Given that a priority of the Ministry of Agricultural Development and Irrigation is to increase agricultural production, it will likely facilitate zoning changes to allow forest exploitation despite

the threat they pose to diversity-rich areas. These changes allow private agricultural companies that already own forested land to freely convert it to farms, facilitating rapid land-use change.

Between 2015 and 2017, Peru lost more than 4770 km² of forest, comprising 0.7% of Peru's total forest area (7), 83% of which was transformed for agriculture and livestock (8). Such land conversions lead to biodiversity loss, alter soil properties, and reduce aboveground carbon pools (9). In addition to releasing substantial amounts of carbon into the environment, deforestation affects the hydrological cycle and other natural processes (10). The intrusion of industrial activities in the Amazon could also lead to increased crime against Indigenous communities [e.g., (11)].

Private business groups, such as the National Confederation of Private Business Institutions (CONFIEP), lobby the government in support of land-use change in the Amazon rainforest to establish large-scale intensive agriculture (12). Their demands place profits above long-term environmental and human health. Instead of capitulating to industry, the Peruvian Congress should protect the country's land and people by ensuring that its legislation serves to preserve and promote the sustainability of the Peruvian forests as well as protect the country's natural ecosystems and biodiversity. Peruvian citizens and scientists can fight the business lobby by calling on their congressional representatives to act accordingly.

Carlos Martel^{2*}, Glenda Mendieta-Leiva³,
Patricia C. Alvarez-Loayza⁴, Asunción Cano⁵,

Peru's new law removes obstacles to converting diversity rich forests to farmland.



Eric G. Cosío⁶, Cony Decock⁶, William Farfan Ríos⁷,
Kenneth Feeley^{8,9}, Euridice Honorio Coronado¹⁰,
Isau Huamantupa¹¹, Alfredo J. Ibañez², Juliane
Koeppke de Diller¹², Blanca León¹³, Reynaldo
Linares Palomino¹⁴, José L. Marcelo Peña¹⁵, Betty
Millán², Justin F. Moat¹, R. Toby Pennington^{16,17},
Nigel Pitman¹⁸, Norma Salinas², Roxana Rojas-
VeraPinto¹⁹, Philip C. Stevenson²⁰, Carolina
Tovar¹, Oliver Q. Whaley¹, Kenneth R. Young¹³
¹Royal Botanic Gardens Kew, Surrey TW9 3AB, UK, ²Pontificia Universidad Católica del Perú, 15085
Lima, Peru, ³Philipps Universität Marburg, 35032
Marburg, Germany, ⁴Duke University, Durham,
NC 27705, USA, ⁵Universidad Nacional Mayor
de San Marcos, 15081 Lima, Peru, ⁶Université
Catholique de Louvain, B-1348 Louvain-la-Neuve,
Belgium, ⁷Department of Biology and Center for
Energy, Environment, and Sustainability, Wake
Forest University, Winston Salem, NC 27106,
USA, ⁸Department of Biology, University of Miami,
Coral Gables, FL 33146, USA, ⁹Hortus Tropical
Botanic Garden, Coral Gables, FL 33156, USA,
¹⁰University of St. Andrews, St. Andrews KY16
9AL, UK, ¹¹Universidad Nacional Amazonica de
Madre de Dios, Puerto Maldonado, Peru, ¹²Area de
Conservación Privada Paiguana, Huánuco, Peru,
¹³Geography and the Environment, University of
Texas at Austin, Austin, TX 78712, USA, ¹⁴Center
for Conservation Education and Sustainability,
Smithsonian's National Zoo & Conservation
Biology Institute, Washington, DC 20008, USA,
¹⁵Universidad Nacional de Jaén, Jaén, Peru,
¹⁶Royal Botanic Garden Edinburgh, Edinburgh EH3
5LR, UK, ¹⁷Department of Geography, University
of Exeter, Exeter EX4 4RJ, UK, ¹⁸Science and
Education, The Field Museum, Chicago, IL 60606,
USA, ¹⁹University of Reading, Reading RG6 2EX,
UK, ²⁰Nature Resource Institute, University of
Greenwich, Kent ME4 4TB, UK
*Corresponding author. Email: c.martel@kew.org

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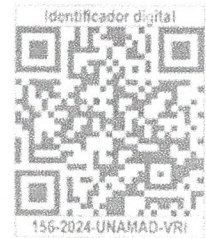
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Anexo 8. Resolución de vicerrectorado de Investigación.



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS
"AÑO DEL BICENTENARIO DEL PERÚ: 200 AÑOS DE INDEPENDENCIA"
"MADRE DE DIOS, CAPITAL DE LA BIODIVERSIDAD DEL PERÚ"
RESOLUCIÓN DE VICERRECTORADO DE INVESTIGACIÓN
N° 156-2024-UNAMAD-VRI
Puerto Maldonado, 20 de junio de 2024



VISTO:

La Resolución 189-2021-UNAMAD-VRI de fecha 07 de diciembre de 2021, correo electrónico de fecha 13 de junio de 2024, Oficio 220-2024-UNAMAD-VRI/INI de fecha 19 de junio de 2024, Expediente 1252-VRI de fecha 19 de junio de 2024, y;

CONSIDERANDO:

Que, mediante Ley 27297 de fecha 05 de julio del año 2000, se crea la Universidad Nacional Amazónica de Madre de Dios, en adelante la UNAMAD; autorizándose su funcionamiento definitivo, mediante resolución N° 626-2009-CONAFU, de fecha 27 de noviembre del año 2009;

Que, mediante Resolución 132-2019-SUNEDU/CD de fecha 10 de octubre de 2019, la Superintendencia Nacional de Educación Superior Universitaria (SUNEDU) otorga la licencia institucional a la UNAMAD con una vigencia de seis (6) años;

Que, mediante Resolución 012-2021-UNAMAD-CEU de fecha 15 de noviembre de 2021, se resuelve acreditar a la Dra. Luz Marina Almanza Huamán como Vicerrectora de Investigación de la Universidad Nacional Amazónica de Madre de Dios, a partir del 01 de diciembre del año 2021 hasta el 30 de noviembre de 2026.

Que, mediante Resolución 002-2020-UNAMAD-AU de fecha 30 de enero de 2020, se aprueba el Estatuto 2019 reformulado de la UNAMAD y entra en vigencia a partir del 03 de marzo de 2020 con su publicación en el portal web de la UNAMAD;

Que, el artículo 6° de la Ley 30220, establece que: "son fines de la universidad peruana, entre otros, formar profesionales de alta calidad de manera integral y con pleno sentido de responsabilidad social de acuerdo a las necesidades del país; realizar y promover la investigación científica, tecnológica y humanística, la creación intelectual y artística; así como proyectar a la comunidad sus acciones y servicios para promover su cambio y desarrollo";

Que, el artículo 48° de la Ley 30220, establece que: "La investigación constituye una función esencial y obligatoria de la universidad, que la fomenta y realiza, respondiendo a través de la producción de conocimiento y desarrollo de tecnologías a las necesidades de la sociedad, con especial énfasis en la realidad nacional. Los docentes, estudiantes y graduados participan en la actividad investigadora en su propia institución o en redes de investigación nacional o internacional, creadas por las instituciones universitarias públicas o privadas";

Que, el artículo 50° de la Ley 30220, Órgano universitario de investigación, establece que: "El Vicerrectorado de Investigación, según sea el caso, es el organismo de más alto nivel en la universidad en el ámbito de la investigación. Está encargado de orientar, coordinar y organizar los proyectos y actividades que se desarrollan a través de las diversas unidades académicas. Organiza la difusión del conocimiento y promueve la aplicación de los resultados de las investigaciones, así como la transferencia tecnológica y el uso de las fuentes de investigación, integrando fundamentalmente a la universidad, la empresa y los entes del Estado";

Que, de conformidad al literal "c" del artículo 210° del Estatuto de la UNAMAD, son deberes de los docentes entre otros, generar conocimiento e innovación a través de la investigación rigurosa en el ámbito que le corresponde, en el caso de los docentes orientados a la investigación; así como perfeccionar permanentemente su conocimiento y su capacidad docente y realizar labor intelectual creativa;

Que, con Resolución 189-2021-UNAMAD-VRI de fecha 07 de diciembre de 2021, el Vicerrectorado de Investigación resolvió aprobar la entrada en vigencia del «SISTEMA DE SEGUIMIENTO DE PROYECTOS DE INVESTIGACIÓN (SISPRO versión 2.0)» a partir del 07 de diciembre de 2021 en el marco de ejecución del proyecto «IMPLEMENTACIÓN DE SISTEMA INTEGRADO DE GESTIÓN DE LA INVESTIGACIÓN BAJO EL ENFOQUE PMI EN LA UNAMAD (PERIODO DIC2020-DIC2023)»;

Que, mediante correo electrónico de fecha 13 de junio de 2024, el Dr. Isau Huamantupa Chuquimaco, responsable de la investigación, solicita aprobación del proyecto de investigación de libre financiamiento por grupos de investigación titulado «DIVERSIDAD VEGETAL Y SUS PROCESOS ECOLÓGICOS EN LAS SABANAS HÚMEDAS DEL PAMPAS DEL HEATH»;

Que, con Oficio 220-2024-UNAMAD-VRI/INI de fecha 19 de junio de 2024, la directora del Instituto de Investigación (INI) de la UNAMAD remite informe favorable de evaluación del proyecto de investigación de libre financiamiento por grupos de investigación titulado «DIVERSIDAD VEGETAL Y SUS PROCESOS ECOLÓGICOS EN LAS SABANAS HÚMEDAS DEL PAMPAS DEL HEATH» para ser ejecutada durante el periodo del 19/06/2024 al 19/06/2026;





UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS

"AÑO DEL BICENTENARIO DEL PERÚ: 200 AÑOS DE INDEPENDENCIA"
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RESOLUCIÓN DE VICERRECTORADO DE INVESTIGACIÓN

N° 156-2024-UNAMAD-VRI

Puerto Maldonado, 20 de junio de 2023



Que, con Expediente 1252-VRI de fecha 19 de junio de 2024, el Vicerrectorado de Investigación de la UNAMAD, dispone proyectar resolución que aprueba la ejecución del proyecto de investigación de libre financiamiento por grupos de investigación titulado «DIVERSIDAD VEGETAL Y SUS PROCESOS ECOLÓGICOS EN LAS SABANAS HÚMEDAS DEL PAMPAS DEL HEATH» durante el periodo del 19/06/2024 al 19/06/2026;

Que, en uso de las atribuciones otorgadas como Vicerrector(a) de Investigación, de conformidad con la Ley 30220, Ley Universitaria y el Estatuto de la Universidad Nacional Amazónica de Madre de Dios;

SE RESUELVE:

ARTÍCULO 1°: APROBAR la ejecución del proyecto de investigación en la modalidad de INVESTIGACIÓN DE LIBRE FINANCIAMIENTO POR GRUPOS DE INVESTIGACIÓN titulado «DIVERSIDAD VEGETAL Y SUS PROCESOS ECOLÓGICOS EN LAS SABANAS HÚMEDAS DEL PAMPAS DEL HEATH» con código «2024-LD-004» durante el periodo del 19/06/2024 al 19/06/2026; integrado por los siguientes investigadores:

CÓDIGO DE INVESTIGACIÓN	2024-LD-004
LÍNEA DE INVESTIGACIÓN	BIODIVERSIDAD, CAMBIO CLIMÁTICO, CALIDAD AMBIENTAL Y FORESTAL.
MODALIDAD	GRUPO-L
TÍTULO DE LA INVESTIGACIÓN	DIVERSIDAD VEGETAL Y SUS PROCESOS ECOLÓGICOS EN LAS SABANAS HÚMEDAS DEL PAMPAS DEL HEATH
COORDINADOR (INVESTIGADOR PRINCIPAL)	ISAU HUAMANTUPA CHUQUIMACO
COLABORADOR (COINVESTIGADOR)	SUFER MARCIAL BAEZ QUISPE
ASISTENTE (INVESTIGADOR EN FORMACIÓN)	FARID ALAIN ROCHA SULCA
ASISTENTE (INVESTIGADOR EN FORMACIÓN)	CRISTIAN JHORDI PUMALLOCLA DE SOUZA
ASISTENTE (INVESTIGADOR EN FORMACIÓN)	NELIDA FLORES HUARCO
ASISTENTE (INVESTIGADOR EN FORMACIÓN)	ILLAMARU MACHICADO ORTIZ
ASISTENTE (INVESTIGADOR EN FORMACIÓN)	HILTON DAVID GOMEZ YUCRA
ASISTENTE (INVESTIGADOR EN FORMACIÓN)	THALIA CORAHUA ESPINOZA
ASISTENTE (INVESTIGADOR EN FORMACIÓN)	ANEL ALEXANDRA ACHULLI CHIPANA
ASISTENTE (INVESTIGADOR EN FORMACIÓN)	REYNER DAVID ACHAHUANCO LAYME
ASISTENTE (INVESTIGADOR EN FORMACIÓN)	DANTE CUEVA ALTAMIRANO
ASISTENTE (INVESTIGADOR EN FORMACIÓN)	IVAN CHAMPI COSIYUNCA
ASISTENTE (INVESTIGADOR EN FORMACIÓN)	NICOL MELANI CANAL RAMÍREZ



ARTÍCULO 2°: NOTIFICAR la presente a la dirección del Instituto de Investigación (INI) de la UNAMAD para que actualice la información en la «base de datos de proyectos de investigación, desarrollo tecnológico, innovación y emprendiendo (I+D+i+e) ejecutados a partir del año 2015» y/o SISPRO;

ARTÍCULO 3°: DISPONER que la Oficina de Tecnologías de la Información (OTI) de la UNAMAD publique la presente resolución en la página web de la UNAMAD.

REGÍSTRESE, COMUNÍQUESE Y CÚMPLASE.



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Anexo 9. Artículo de investigación.

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<https://doi.org/10.1038/s42003-024-06937-5>

The biogeography of the Amazonian tree flora

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A list of authors and their affiliations appears at the end of the paper

We describe the geographical variation in tree species composition across Amazonian forests and show how environmental conditions are associated with species turnover. Our analyses are based on 2023 forest inventory plots (1 ha) that provide abundance data for a total of 5188 tree species. Within-plot species composition reflected both local environmental conditions (especially soil nutrients and hydrology) and geographical regions. A broader-scale view of species turnover was obtained by interpolating the relative tree species abundances over Amazonia into 47,441 0.1-degree grid cells. Two main dimensions of spatial change in tree species composition were identified. The first was a gradient between western Amazonia at the Andean forelands (with young geology and relatively nutrient-rich soils) and central-eastern Amazonia associated with the Guiana and Brazilian Shields (with more ancient geology and poor soils). The second gradient was between the wet forests of the northwest and the drier forests in southern Amazonia. Isolines linking cells of similar composition crossed major Amazonian rivers, suggesting that tree species distributions are not limited by rivers. Even though some areas of relatively sharp species turnover were identified, mostly the tree species composition changed gradually over large extents, which does not support delimiting clear discrete biogeographic regions within Amazonia.

Biogeography aims to describe, explain, and ultimately predict patterns of distribution and diversity at a variety of taxonomic levels¹. It has been a century-long quest to achieve these aims for the complex distributional patterns of biodiversity in Amazonia^{2,3}, an area formed by the tropical rain forests of the Amazon basin and Guiana shield. These forests are of global interest, as they arguably support the highest biodiversity on Earth^{4,5}. The total richness of the Amazonian tree flora has been estimated at ~16,000 species^{6,7}, with most species having geographically restricted ranges and small to very small population sizes. Furthermore, even the most abundant trees in Amazonia, despite being relatively more widespread, tend to dominate under specific environments⁸.

Existing biogeographical classifications of Amazonia have often defined centres of endemism coinciding with large interfluvial areas^{9,10}. This follows early models on the distribution patterns of vertebrate species that focused on the role of large rivers in separating species and triggering speciation – the riverine barrier hypothesis¹¹. Although large rivers can act as effective barriers for land plants in some context¹², studies on plant species have provided varying results^{13–15}, depending on the taxa under analysis, often resulting in weak or no support for large rivers as effective barriers for land plants. Another hypothesis proposed that the climatic oscillations during the Pleistocene both triggered speciation and affected species range dynamics in Amazonia – the Pleistocene refuge hypothesis¹⁶. According to

this hypothesis, tropical rain forest retraction–expansion dynamics was a key driver limiting species ranges during dry glacial periods and determining range expansions from the most consistently wet regions (i.e., refuges) during wetter interglacial periods. However, the high complexity of both the Amazonian forests themselves and the potential footprint of Pleistocene climatic oscillations on habitat availability for the numerous species that form the Amazon forests make it difficult to test the original refuge hypothesis, though it has stimulated a vigorous research agenda^{17,18}. The ecoregion approach, in turn, has used a combination of biological, ecological, and geographical proxies to derive a biogeographical classification¹⁹. Other biogeographical classifications have been proposed based on the geographical distribution of soil classes²⁰, and understory floristic gradients as interpolated using remote sensing²¹. Several recent studies have acknowledged the potential importance of edaphic and climatic factors, as well as of evolutionary and ecological processes at different temporal and spatial scales, on contemporary broad-scale distributional and diversity patterns of Amazonian trees and other plants^{22,23,24}. It has also been suggested that geographical barriers and climatic oscillations have had little effect on the distribution of land plants across Amazonia, but that geographical distance among populations can limit gene flow sufficiently to trigger speciation in geographically restricted areas – the dispersal assembly hypothesis²⁵.

e-mail: hans.fersteege@matutais.ru

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It remains a daunting task to draw biogeographical inferences from a relatively poorly explored region such as Amazonia, which has enormous shortfalls in biological knowledge^{1,2,3,4,5} and collecting density, i.e., data deficiencies and sampling bias^{6,7,8,9,10}. Despite the lack of data, much progress has been made in working with scarce spatial data by employing new analytical methods to circumvent problems of data scarcity for environmental characteristics and species occurrence (e.g., soil base cation concentration^{11,12} and beta diversity^{13,14}), and joining disparate efforts to advance our understanding on the distribution of tree species diversity, composition and abundance across Amazonia^{15,16}. Especially in the last decades of the 20th century, the number of forest inventories for Amazonian tropical rain forests has risen fast, allowing a more comprehensive view on tree diversity across Amazonia (e.g. ref. 15). However, quantitative tests of the biogeographical pattern of Amazonian tree communities are scarce and based on incomplete presence/absence data^{17,18} or on genus-level identifications and very coarse spatial resolution¹⁹; but see Luize et al.²⁰, unveiling the role of dispersal and phylogenetic niche conservatism on phylogenetic compositional changes over Amazonia.

Here, making use of a set of 2,023 tree inventory plots with tree species abundance data, distributed well across Amazonia (Supplementary Fig. 1), we investigate how tree species composition varies across spatial and environmental gradients, with eyes on both ecological and biogeographical patterns. We start by ordering the tree species compositional dissimilarity between forest inventory plots, using Principal Coordinate Analysis (PCoA), to assess: (i) how the local variation on compositional turnover relates with the local variation in Amazonian forest types and among geographical regions within Amazonia; and (ii) how compositional turnover varies along spatial and environmental gradients representing edaphic and climatic features. We then use the observed abundances of tree species in each inventory plot to produce a broad-scale view of compositional turnover across Amazonia. After deriving grid layers, at the resolution of 0.1-degree grid cells (~121 km²), for the distribution of tree species' relative abundances

over the Amazon, we ordered, using Detrended Correspondence Analysis (DCA), the grid cell communities (i.e., species relative abundances over the grid cells). The resulting DCA scores are mapped over Amazonia to depict broad-scale tree species compositional turnover across the region. The maps of tree species compositional turnover were used to interpret the compositional turnover associations with geographic and broad-scale edaphic and climatic variation across the region and allowed the definition of floristic transitional zones – where changes of tree species turnover are sharper over short geographic distances. Finally, we estimated the tree species' niche position (optimum) and breadth (tolerance) for climatic, edaphic, and compositional dimensions to show how the compositional turnover patterns are determined by the ecological distribution of species over existing gradients.

Results

Plot-level patterns in tree species composition

The Principal Coordinates Analysis (PCoA) ordination shows that compositional turnover at the plot level is related to both broad ecological forest categories (Fig. 1a and Supplementary Fig. 2) and geographical location (Fig. 1b and Supplementary Fig. 3). Although there is substantial overlap among the geographical regions (Fig. 1b and Supplementary Fig. 3c), in general terms the first ordination axis (PCoA1) represents a gradient from southwestern Amazonia (with low scores) through central Amazonia to the Guiana Shield (with high scores, see also Supplementary Fig. 3). At the same time (Fig. 1a and Supplementary Fig. 2), the first ordination axis corresponds to a gradient in soil fertility (with poor soils having higher values than rich soils), and the second axis separates seasonally inundated (VA, IG) and permanently waterlogged (SW) forests (with high scores) from the non-inundated forests (TFGS, TFBS, TFPB, PZ, with lower scores). Linear regressions confirmed these observations, with the main floristic gradient (PCoA1) strongly related to sum of base cations in the soil ($R^2_{adj} = 0.27$, $P = 0.01$, Supplementary Fig. 4a), and the second floristic gradient (PCoA2)

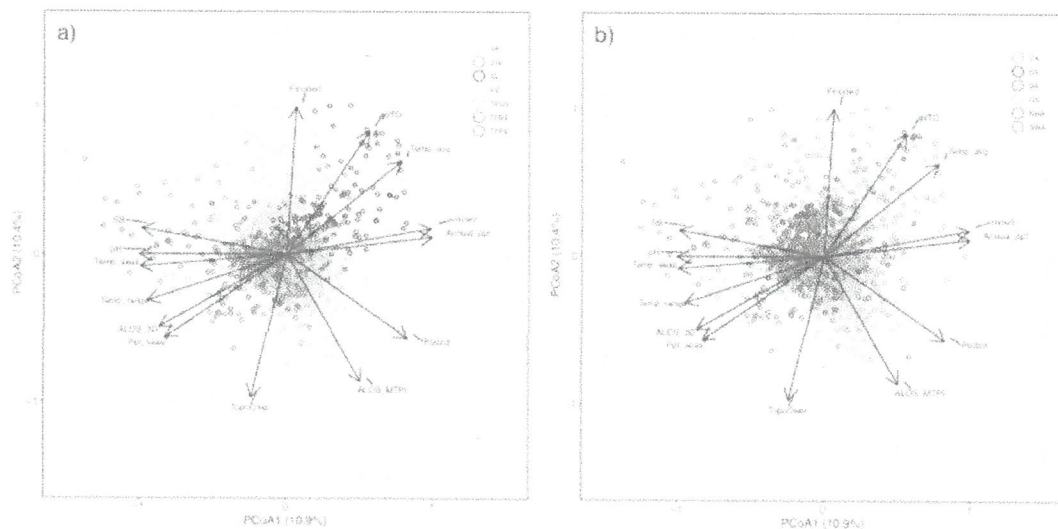


Fig. 1 | Variation in composition and relative abundance of 5188 tree species in 2023 forest inventory plots (1 ha) across Amazonian forests. Ordination biplots showing the two first principal components with inventory plots coloured by (a) ecological forest categories based on hydrology and soil characteristics and (b) geographical regions. **a** Ecological categories: VA, Várzea forests; SW, swamp forests; RG, igapó forests; PZ, white-sand [podzol] forests; TFGS, terra-firme on the Guiana Shield; TFBS, terra-firme on the Brazilian Shield; TFPB, terra-firme on the Pebas sedimentary basin. **b** Geographical regions: CA Central Amazonia; EA Eastern Amazonia; SA Southern Amazonia; GS Guiana Shield; NWA Northwestern

Amazonia; SWA Southwestern Amazonia. Arrows indicate vectors constructed with *ordifit*²¹ for 14 environmental predictors: Flooded flooding vs. non flooding terrains, WTD water table depth, Temp_avg average annual temperature, MCWD maximum climatological water deficit, Annual_ppt Annual Rainfall, Podzol White Sand vs. Clay Silt terrains, ALOS_MTP1 Multiscale Topographic Position Index, TopoDiver Topographic Diversity Index, Ppt_season precipitation seasonality, ALOS_3D elevation, Temp_range temperature range, Temp_season temperature seasonality, pH soil pH, SB soil sum of bases.



<https://doi.org/10.1038/s42003-024-06937-5>

Article

Table 1 | The association of environmental conditions and the variation in the tree species composition of Amazonian forests

Rank	Environmental predictor	R ²	AdjR ² _{curr}	F	AIC
RDA Model 1: [PCoA axis 1] - 14 environmental predictors					
1	Soil base cation concentration (SB)	0.27	0.27	764.6	-6438.3
2	Temperature seasonality	0.09	0.36	260.2	-6696.1
3	Podzol	0.04	0.4	122.7	-6816.5
4	Elevation (ALOS_3D)	0.03	0.42	86	-6896.9
5	Maximum climatological water deficit (MCWD)	0.01	0.44	47.4	-6943.8
6	Soil pH	0.01	0.45	44.1	-6985.6
7	Precipitation seasonality	0.01	0.45	26.2	-7009.7
8	Total annual rainfall	0	0.46	13.2	-7020.9
9	Mean annual temperature	0	0.46	13.3	-7032.3
10	Flooded	0	0.46	13.1	-7043.3
11	Topographic diversity (TopoDiver)	0	0.47	8.1	-7049.4
12	Groundwater table depth (WTD)	0	0.47	3.7	-7051.1
13	Multi-scale topographic index (MTPi)	0	0.47	5.8	-7054.9
14	Temperature range	Forward selection procedure stopped (not selected)			
RDA Model 2: [PCoA axis 2] - 14 environmental predictors					
1	Flooded	0.42	0.42	1450.4	-6988.9
2	Podzol	0.01	0.43	39.9	-7026.5
3	Topographic diversity (TopoDiver)	0.01	0.44	44	-7068.1
4	Precipitation seasonality	0.01	0.45	40.8	-7106.6
5	Soil base cation concentration (SB)	0.01	0.46	21.4	-7126
6	Mean annual temperature	0.01	0.46	26.9	-7150.8
7	Temperature range	0	0.47	14.9	-7163.7
8	Elevation (ALOS_3D)	0	0.47	25.9	-7187.5
9	Maximum climatological water deficit (MCWD)	0	0.48	7.3	-7192.9
10 to 14	Multi-scale topographic index (MTPi), soil pH, temperature seasonality, total annual rainfall, groundwater table depth (WTD)	Forward selection procedure stopped (not selected)			
RDA Model 3: [PCoA axis 1; PCoA axis 2] - 14 environmental predictors					
1	Flooded	0.21	0.21	470.9	-4694.5
2	Soil base cation concentration (SB)	0.18	0.39	520.2	-5149.5
3	Maximum climatological water deficit (MCWD)	0.04	0.43	132.5	-5275.6
4	Podzol	0.03	0.46	88.4	-5360.1
5	Soil pH	0.02	0.48	69.8	-5426.8
6	Precipitation seasonality	0.01	0.48	17.5	-5442.3
7	Temperature range	0.01	0.49	17.9	-5458.2
8	Mean annual temperature	0.00	0.49	14.9	-5471.1
9	Topographic diversity (TopoDiver)	0.00	0.49	10.1	-5479.3
10	Elevation (ALOS_3D)	0.00	0.50	13.4	-5490.7
11 to 14	Total annual rainfall, temperature seasonality, multi-scale topographic	Forward selection procedure stopped (not selected)			

Table 1 (continued) | The association of environmental conditions and the variation in the tree species composition of Amazonian forests

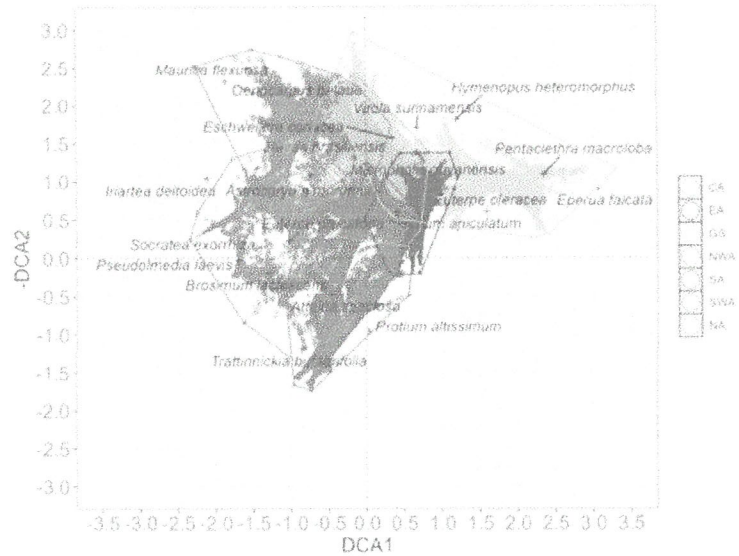
Rank	Environmental predictor	R ²	AdjR ² _{curr}	F	AIC
RDA Model 4: residuals(RDA model: [PCoA axis 1; PCoA axis 2] - 93 MEMs) - 14 environmental predictors					
1	Flooded	0.094	0.09	209.4	-6171.3
2	Soil base cation concentration (SB)	0.047	0.14	110.8	-6277.4
3	Podzol	0.016	0.16	39.3	-6314.4
4	Temperature range	0.005	0.16	13.2	-6325.6
5	Elevation (ALOS_3D)	0.002	0.16	3.1	-6326.7
6	Mean annual temperature	0.001	0.16	3.8	-6328.5
7 to 14	Temperature seasonality, total annual rainfall, precipitation seasonality, maximum climatological water deficit (MCWD), topographic diversity (TopoDiver), multi-scale topographic index (MTPi), soil pH, groundwater table depth (WTD)	Forward selection procedure stopped (not selected)			

The results of RDA models relating PCoA scores and 14 environmental predictors. The first model adjusts only the PCoA axis 1, the second model adjusts only the PCoA axis 2, the third model adjusts both PCoA axes at once, and the fourth model uses the residuals of the RDA model relating the PCoA scores and the spatial predictors (93 selected Moran's Eigenvector Maps (MEMs)) to adjust the 14 environmental predictors. PCoA axes scores were obtained from the pair-wise Bray-Curtis dissimilarities among 2,023 forest-inventory plots. Predictors are ordered from lowest to highest AIC. The R² and F statistics were estimated using permutation tests under a forward selection procedure.

strongly related to whether the plot was inundated or not ($R^2_{adj} = 0.42$, $P = 0.01$). Forward selection identified 13 environmental predictors significantly related to PCoA1, and together these explained 47% of the variation in tree species abundances along PCoA1 (Table 1). In addition to the importance of soil sum of bases, temperature seasonality ($R^2_{adj} = 0.09$, $P = 0.01$) and white sand soils ($R^2_{adj} = 0.04$, $P = 0.01$) were significant environmental predictors for the first ordination axis (Table 1). For the second floristic gradient (PCoA2), nine environmental predictors were selected, which together explained 43% of the variation in tree species abundances along PCoA2 (Table 1). In this case, flooding was clearly the most important and the other eight predictors added little explanatory power (Table 1). Although there is a lot of overlap, the ordination at plot level supports a general pattern of turnover in tree species composition between forests in ecological regimes (Fig. 1), traditionally recognised as distinct forest types, such as terra-firme, white-sand, and seasonally flooded forests, which can be geographically proximate over a landscape.

Besides the significant influence of environmental gradients to the variation in each PCoA axis separately (Table 1), and in both axes together (RDA model: [PCoA axis 1; PCoA axis 2] - 14 Environmental predictors, $R^2_{adj} = 0.47$; $P = 0.001$), we also found spatially structured variation on the compositional turnover measured at plot-level (RDA model: [PCoA axis 1; PCoA axis 2] - 93 MEMs, $R^2_{adj} = 0.51$, $P = 0.001$). After partitioning out the relative effect of environmental and spatial predictors on tree species composition, there is a significant spatial structure in the environmental predictors, shown as the shared influence of environmental and spatial predictors on tree species composition (joint Environmental + Spatial fraction of variation partition, $R^2_{adj} = 0.33$, $P = 0.001$). Ruling out this joint environmental + spatial effect, the environmental predictors alone add a little less variation on tree species composition (unique environmental fraction of variation partition, $R^2_{adj} = 0.14$; $P = 0.001$) than the spatial predictors (MEMs) alone (unique spatial fraction of variation partition,

Fig. 2 | Variation in interpolated composition and relative abundance of 5,188 tree species in 47,441 grid cells (0.1-degree squares) across Amazonian forests. Ordination biplots showing the two first DCA axes with grid cells coloured by geographic region: CA Central Amazonia, EA Eastern Amazonia, GS Guiana Shield, NWA Northwestern Amazonia, SWA Southwestern Amazonia, SA Southern Amazonia. Black marks show the average position for the abundance distribution of the 20 tree species with the highest interpolated total abundance. The distributions of these species in geographical and ordination space are shown in Supplementary Figs. 5–24.



$R^2_{adj} = 0.18$; $P = 0.0001$). The first two environmental predictors, explaining most of the variation in both PCoA axes (Flooded and Soil base cation concentration (SB) Table 1, RDA Model 3), are the same predictors responsible for most of the non-spatially structured compositional variation (i.e., the residuals of the spatial RDA model (PCoA [1:2] – 93 MEMs), Table 1 RDA Model 4). Although, some of the environmental predictors, explaining most of PCoA axes variation (maximum climatological water deficit (MCWD), Soil pH, Table 1 RDA Model 3), actually explain a small and non-significant amount of the non-spatially structured compositional variation ($R^2 \leq 0.001$, $P > 0.05$, Table 1 RDA Model 4).

Patterns in grid-level tree species composition and turnover

When the effect of local environmental variation was averaged out by interpolating relative species abundances at the resolution of 0.1° grid cells (Fig. 2), the main axis of variation in tree species composition (DCA1) clearly showed a longitudinal gradient from western Amazonian forests (SWA and NWA) through central and southern Amazonia (CA and SA) towards Eastern Amazonia (EA) and the Guiana shield (GS). Along the second axis (DCA2), the strongest contrast was between the southern regions (SA and SWA, with low scores) and northern and central regions (NWA, CA, and parts of GS, with high scores), with EA being intermediate and showing much less variation than the other regions. In fact, the biplot in Fig. 2 clearly reflects the geographical outlay of the Amazonian forest.

The general impression from the grid-level DCA ordination is that floristic transitions across Amazonia are rather gradual among the geographical regions, as adjacent regions have relatively similar floristic composition. This was confirmed when the DCA scores were plotted on the actual map of Amazonia (Fig. 3): tree species composition changed gradually over large geographical distances. The gradual change in composition recovered by DCA1 ran from the Andean forelands to the Guiana Shield (Fig. 3a). Over most of Amazonia, isolines of the DCA1 scores were far apart, indicating gradual species turnover across space, but some zones showed sharper turnover. These zones of intense compositional turnover over short geographical distances were concordant with the confluence of tree species' geographical and environmental range limits, even for very common tree species (e.g., *Eperua falcata*, *E. coriacea* and *Trattinnickia hirsutifolia*, Supplementary Figs. 5–24). These areas of sharper tree species turnover were also in agreement with abrupt changes in climatological and edaphic attributes (Fig. 3a). In particular, DCA1 showed two zones of sharp turnover. The first zone ran in the east–west direction largely coincident with the

headwaters of the rivers draining from the Guiana highlands and Acarari mountains (see the isoline of DCA1 value 1 in Fig. 3a), separating the Guianas from the rest of Amazonia. The second zone of relatively sharp turnover ran across Amazonian lowlands in the west in a north–south orientation coinciding with changes in average soil acidity (pH) and soil base cation concentration (SB), which are higher on the western than the eastern side of the transition zone (Fig. 3a). The gradual changes in tree species composition indicated by DCA2 ran from north–western Amazonia to south–eastern Amazonia (Fig. 3b). In DCA2, the zone of sharpest turnover ran in the east–west direction, being even more steep in the southern part of the Amazon basin (Fig. 3b, isoline of MCWD value -275). A slightly more gradual turnover zone can be seen further north running right across several major tributaries of the Amazon River (e.g., Juruá, Purus, Madeira), and also crossing the Amazon River itself. The zones of sharp turnover shown by DCA2 largely follow a divide between wetter and dryer climates. The wetter areas encompass the upper Negro River, the Japurá/Caquetá, the Iça/ Putumayo, and the Napo River basins, and the dryer areas the headwaters of the Tapajós and Xingu Rivers (Fig. 3b).

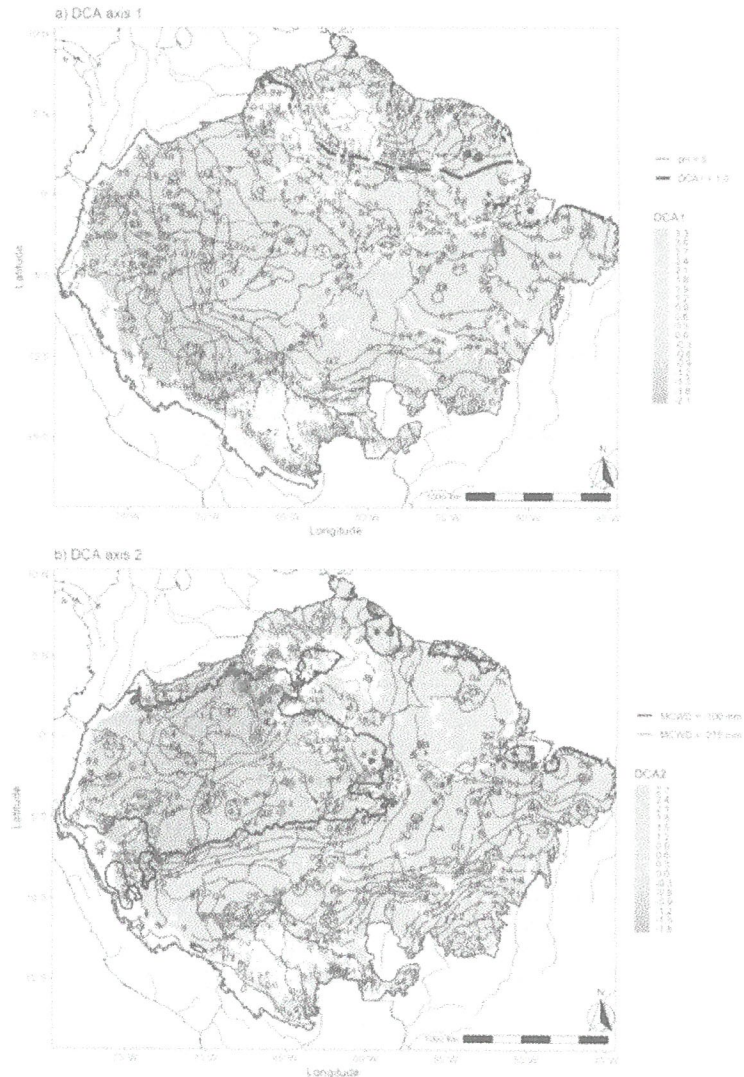
Species distributions along environmental and compositional gradients

The most common Amazonian tree species are widespread across Amazonia but show diverging centres of distribution along the compositional gradient recovered by the grid-level DCA ordination (Supplementary Figs. 5–24), suggesting they occupy different niche positions. Indeed, the niche positions of individual species are well distributed along both the climatic gradients (annual rainfall, maximum climatological water deficit), and the edaphic gradients (soil sum of bases, pH) (Fig. 4a–d), and also along the compositional gradients (based on DCA scores of the grid cells) (Fig. 4e, f). Furthermore, as suggested by the species niche breadths, most species tend to occupy only a relatively small part of the observed gradient, while a few species show broad niche breadths (Fig. 4). Among the 20 most common tree species in our plot dataset (based on the sum of plot-level abundances), those with the strongest preference for very wet climates (highest niche positions (WA) for annual rainfall, Fig. 4a) were *Rinorea riana*, *Oenocarpus bacaba*, and *Rinorea racemosa*. Fifty-three species exclusively occurred in plots with maximum climatological water deficit equal to zero (Fig. 4b); *Eperua falcata*, *Oenocarpus bacaba*, and *Mauritia flexuosa* were the three species among the most common ones with niche position for MCWD close to zero (i.e., wettest places in Fig. 4b), in contrast

<https://doi.org/10.1038/s42003-024-06937-5>

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Fig. 3 | Maps of the broad-scale spatial variation of tree species composition across Amazonia. Scores of (a) DCA Axis 1, (b) DCA Axis 2 (both from Fig. 2). In both maps, grey lines are the isolines linking equal levels of DCA scores, with the spatial distance between consecutive isolines being inversely related to the rate of compositional change across space and used to mark sharp compositional turnover zones (if closer together) or smoother compositional turnover (consecutive isolines further apart). In (a), the blue isoline corresponds to DCA score of 1.0 and the red isoline to soil pH = 5 (west of that line having a soil pH > 5). In (b), the red isoline corresponds to maximum climatological water deficit (MCWD) = -275 mm (south of that line having MCWD < -275), and the blue isoline to MCWD = -100 (west of that line having MCWD > -100). The dark green line delimits the Amazonian tropical forests³⁰, with white areas within these limits corresponding to montane areas (above 500 m elevation) and non-forested habitats such as savannas. Major river courses are shown in blue. Base map source for countries: <https://www.naturalearthdata.com/>; rivers³¹. Maps created with custom R³² script.



to *Protium altissimum* that is among the most common species with low niche position values for MCWD (i.e., dryer end of the gradient in Fig. 3b). All 20 most common species were distributed in the middle of the gradient in soil fertility (i.e. show niche position for the logarithm of soil sum of bases within -0.5 and 0.5, Fig. 3c), and in the acidic part of the soil pH gradient (i.e. have niche position for soil pH between 4.2 and 5.5). Two of the 20 most common species (*Eperua falcata*, and *Pentaclethra maculobea*) had a niche position value for DCA1 > 1 (Fig. 3d), corresponding to main occurrence area in the Guiana Shield (Fig. 2). Very common species occurring mainly in western Amazonia (DCA1 < -0.8) were *Pseudobombia laevis* and *Lirartea deltoidea*, and these were largely the same species as the ones with sum of bases optimum > -0.06. Common species from the drier areas in southern Amazonia (DCA2 > 0.4) included *Theobroma speciosum*, *Amaizoa guianensis*, *Amphiodon effusus*, *Metrodorea flavida*, and *Protium heptaphyllum*. The niche positions (niche optima) and niche breadths (tolerances) for all 5,188 tree species are given in Supplementary table 1.

The associations of species niche positions on compositional and environmental gradients show that species placed at both ends of the

compositional gradient are also placed at the ends of the environmental gradients (Fig. 5), supporting that species niche segregation does influence compositional turnover. Edaphic gradients (pH, SB) segregate the species along the first compositional dimension (DCA1; Fig. 5a, b), while the species composition along the second compositional dimension (DCA2) is segregated along the water availability gradient (Annual rainfall, MCWD; Fig. 5c, d). Species occupying the upper ends of the main compositional gradient tend to occupy a smaller fraction of the existing gradient.

Discussion

In Amazonia, tree-inventory plots generally do not share a large number of tree species³³. The high compositional differentiation between forest plots (even in the same area) reflects sampling by 1-ha plots: all species that actually exist at a site cannot be sampled with the limited number of stems that fit within 1-ha plot³⁴. Nevertheless, our analyses recovered compositional gradients that are related to environmental factors, even after removing spatially structured environmental variation. The first PCoA axis (corresponding to the strongest gradient in tree species composition at the



<https://doi.org/10.1038/s42003-024-06937-6>

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relatively narrow niches, as well as those with narrow geographical ranges, will be the ones with distribution restricted to one part of the existing environmental gradient within the large geographical extent, covered by tropical rain forests of Amazonia.

Based on the spatial distribution of the DCA scores, we identified four zones of relatively sharp spatial turnover in tree species composition (i.e., floristic transitional zones) within Amazonia. Importantly, each of those floristic transitional zones was associated with major changes along distinct environmental gradients. For example, the floristic transitional zone in the Northeastern part of Amazonia is coincident with the interfluvial divide between the Amazon basin and the river basins draining from the highlands of the Guiana Shield and Acarai Mountains. The forests along this floristic transitional zone were more dynamic in terms of vegetational changes induced by climatic variations over the last 30,000 years^{10,11}, and are still characterised by a dry transverse belt from the Rio Branco, Rupununi and Sipaliwini savannas to the Trombetas-Tapajós confluence with the Amazon River. This may be the most important biogeographical divide in Amazonia, that is less marked, however, in the lowlands of the northern coastal river basins¹² (i.e., French Guiana and the Amapá State in Brazil). The other three floristic transitional areas, however, do not show clear biogeographical barriers controlling the compositional changes over short distances. Rather, continuous changes in environment along the lowlands are likely influencing compositional turnover here. The floristic transitional zone of western part of Amazonia can be associated with changes in soil fertility (SB) and acidity (pH) and perhaps species with Andean affinity. Forests found west of that transitional area (i.e., closer to the Andean foothills) grow on relatively younger sediments that form fertile and more basic soils¹³. This compositional transition zone is largely coincident with a previously reported compositional turnover zone of biogeographical importance^{14,15} that crosses both the middle-upper Juruá river and the main Amazon River. A third floristic transitional zone forms a belt traversing the major white-water tributaries of the Amazon River (i.e., Juruá, Purus and Madeira rivers) and the Amazon River itself (Fig. 3b – blue isoline). This floristic transitional zone delimitates the region with lower elevation across Amazonia; it separates the forests at the southern and northern borders of the Amazon basin from the forests close to the Amazon River main stem. The region that this fourth floristic transitional zone crosses the Amazon river provide support for earlier biogeographic delimitations of várzea forests in the Amazon river floodplains¹⁶. The southern floristic transitional zone is largely coincident with changes from a wetter to relatively drier climate, relatively close to transition zone between the tropical rain forest and savanna biomes.

Further studies could consider the temporal dynamics of these environmental gradients to shed light on the dynamic nature of those floristic transitional zones. Historical floristic dynamics among surrounding biomes and even within the open to dense lowland rain forests may have influenced the formation of zones of sharp floristic turnover. For example, floristic legacies from Andean-centred tree species, whose distribution is skewed to mild temperatures of higher montane forests in the tropical Andes¹⁷ were reported in earlier studies in the Amazon lowland rain forests^{18,19} and are included in the western floristic zone we identified (e.g., *Ilex*, *Panopsis*). Similar reasoning may apply to the area of floristic transition in the southern part of Amazonia, which is relatively close to the confluence between the tree species in seasonally deciduous forests within the Cerrado biome and the tree species occurring in the wetter forests of the Amazonian lowlands and has been rather dynamic over historical times²⁰. The sharp compositional changes between the tropical rain forests of the Guiana Shield and the Amazon basin were perhaps earlier based on geographic and ecologic barriers (e.g., mountains, dry areas), which were more pronounced in the past, but nowadays they are likely to be maintained by ecological sorting along relatively sharp environmental gradients and limited dispersal.

The pattern of floristic compositional changes across Amazonian forests, at both resolutions we evaluated, is consistent with the description of a longitudinal gradient in floristic composition across Amazonia, with the forests in the Western Amazonia gradually differing from the forests on the Guiana Shield²⁰. Despite the overriding effect of local environmental

conditions at the plot level, the east-west compositional changes across Amazonia were apparent even in the plot data (Fig. 1). This is most likely controlled by the general east-west gradient in local environmental conditions, and perhaps by species dispersal across Amazonia.

Changes in tree species composition among local assemblages are primarily related to differences in soil fertility and to flooding conditions. Changes in tree species composition across Amazonian forests are mostly gradual over large geographical extents, but more sharply over relatively short geographical distances in certain areas. Zones of pronounced tree species turnover over short geographical distances tend to show abrupt changes in broad-scale gradients of soil fertility, temperature seasonality, and the seasonal availability or deficit of water. The Amazonian tree flora is assembled by several thousand tree species partitioned over the environmental gradients, the floristic transitional zones in Amazonia are not concordant with putative biogeographical barriers hampering the definition of strictly defined biogeographical units based on the Amazonian tree flora.

Methods

Forest inventory database and environmental correlates

Our tree-inventory data (March 2024 - ATDN20240303) are part of the Amazon Tree Diversity Network^{21,22}, which contained 2023 tree-inventory plots (Supplementary Fig. 1) with information on species composition and abundance. Most of tree-inventories were for 1-ha size and sampled trees with a diameter at breast height (DBH, at 1.30 m) or above tabular roots ≥ 10 cm (for plot metadata, see Supplementary table 2). Species synonymy was updated following ref. 23, but harmonizing names with the World Flora Online²⁴. Species with a *confer* (*cf.*) identification were accepted as belonging to the named species, while those with *affinis* (*aff.*) were accepted only at the genus level and therefore removed from this analysis. The final community matrix comprised 2,023 plots and 5,188 accepted tree species.

The plot coordinates were used to classify each plot into one of six geographic regions (Supplementary Fig. 1): (i) Northwestern Amazonia (NWA), (ii) Southwestern Amazonia (SWA), (iii) Central Amazonia (CA), (iv) Southern Amazonia (SA), (v) Eastern Amazonia (EA) and (vi) Guiana Shield (GS). Plot metadata were used to classify the forests into seven ecological categories (Supplementary Fig. 1). Four of these refer to non-inundated areas (terra-firme): (i) Terra-firme over the sedimentary basin (TFPB), (ii) Terra-Firme over the Brazilian Shield formation (TFBS), (iii) Terra-Firme over the Guiana Shield formation (TFGS), and (iv) Terra-Firme over podzols (i.e., White-Sand Forests (PZ)). The other three refer to wetland forests: (i) Várzea (VA; seasonally inundated by a white-water rivers), (ii) Igapó (IG; seasonally inundated by a black or clear water rivers), and (iii) Swamp (SW; permanently poorly drained).

To evaluate the association of tree species composition with environmental conditions, a total of 12 continuous environmental attributes were extracted from gridded data. A soil acidity (pH) surface for entire Amazonia was created with a loess model (with a span of 0.2, a degree of 2, using Gaussian fitting) based on measurements of soil pH from soil profiles available from several sources^{16,25,26} (Supplementary Fig. 25). As a measure of nutrient availability, we used the logarithm of soil base cation concentration (SB: Ca+Mg+K), as provided by Zauquim et al.²⁷. Climatic data was obtained from CHELSA²⁸. We used three variables for temperature (mean annual temperature, temperature range, and temperature seasonality) and two for precipitation (total annual rainfall, precipitation seasonality). We also estimated the maximum climatological water deficit (MCWD), which can be considered a measure of seasonal drought. This was calculated as the cumulative rainfall deficit of consecutive months with ≤ 100 mm of precipitation from 1981–2020 as measured by CHIRPS^{29,30}. The water-table depth was extracted from a gridded layer produced by Fan et al.³¹. Three topographic variables (elevation, multi-scale topographic index, topographic diversity index) were obtained from the digital surface models of the ALOS World 3D^{32,33}. In addition to the 12 continuous environmental predictors, we included two categorical environmental predictors that discriminate the major forest types of Amazonia. For that we classified the sites into Flooded vs. Non-flooded (i.e., Seasonally flooded



<https://doi.org/10.1038/s42003-024-06937-5>

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forests vs. Upland non-flooded forests), and Podzol vs. Non-Podzol (i.e., White sand forests vs. Forests on silt and clay soils). Environmental attributes were selected beforehand to represent edaphic and climatic features with recognised importance for tree species distribution. Also, before proceeding with the analysis, we tested the variance inflation factor (VIF)⁵⁵ of the 14 environmental predictors to assure that there are not multicollinearity issues between predictors. Highest VIF was obtained for elevation (VIF = 7.4), but still lower than the threshold of VIF = 10 indicating a strong collinearity between predictors⁵⁶. We then followed the analysis using all the 14 environmental predictors.

Analysis of plot-level data

We first explored gradients in tree species composition at the plot level, i.e., using the original tree inventory data. We calculated floristic dissimilarities between the plots using the Bray-Curtis index based on relative abundance data. As some pairs of plots were completely dissimilar to each other, we used the extended dissimilarities to replace the dissimilarity values saturated to the maximum value of unity (c.a. 9% of the total pairwise dissimilarities) with a path across single stepping-stone points⁵⁷, providing ecologically-realistic dissimilarities between plots that share no species⁵⁸. The resulting dissimilarity matrix was analysed using Principal Coordinates Analysis (PCoA), and scatterplots for the scores of the first two axes were used to visually interpret the variation in tree species composition in relation to geographical location and ecological classes of Amazonian forests. We focused our interpretation on the first two PCoA axes, together capturing 21.3% of variation in the dissimilarity matrix, as subsequent axes do not capture more than 6% of total variation. To aid on the interpretation of the variation in tree species composition in relation with the environmental gradients, we added, to the PCoA scatterplot, vectors showing the direction towards greatest environmental changes and increase of association with the ordination configuration. We, then, quantified the strengths (adjusted R^2) of the linear relationships between PCoA scores and the 14 available environmental predictors using Redundancy Analysis (RDA) with forward selection to evaluate which are the environmental gradients explaining most of variation in tree species composition. The forward selection fits a linear model of each predictor at a time and tests their adjusted R^2 against randomly permuted fitting.

Given the geographic extent covered by the inventory plots included in the ATDN database, and the inherent spatially irregular sampling design of the inventory plots, it is expected that the spatial structure of plots (e.g., geographic clusters) exerts an influence both on the measured environmental gradients and on the tree species compositional turnover^{59,60}. To evaluate the relative influence of unique spatial fraction, unique environmental fraction, and their shared effect (environmental + spatial) on tree species composition, we applied a variation partitioning approach, using the set of 14 environmental predictors plus a selected set of Moran's eigenvector maps (MEMs) as spatial predictors. To select the spatial weighting matrix (SWM) used to derive the MEMs, we used three graph-based criteria of connectivity (Gabriel's graph, Relative neighbourhood graph, Minimum spanning tree) and weighting following a linear decreasing function of plot coordinates distances, as recommended in ref. 85. The double diagonalization of the of the SWM results in a large set of MEMs, which were further selected based on the optimisation of adjusted R^2 using forward selection with a double-stopping criterion, following⁶¹. To test the significance of the unique spatial fraction and the shared environmental + spatial fraction of the variation partition model, we used Moran spectral randomisations, which are spatially constrained permutations that provide robust estimates of the significance of model adjustments^{62,63}. Finally, we quantified, using RDA with forward selection, the adjusted R^2 of each environmental predictor fitting only the unique environmental fraction (i.e., the residuals of the model relating both PCoA axes and the MEMs spatial predictors) to access the influence of non-spatially structured environmental gradients on tree species compositional turnover.

All analyses were done in the R environment⁶⁴. Extended dissimilarities were computed with the 'stepacross' function, environmental vectors were

fitted with the 'envfit' function, and variation partitioning were performed with the 'varpart' function of "Vegan" library⁶⁵. PCoA were computed with the 'pco' function of the "labdsv" library⁶⁶. The optimisation of selected SWM and the selection of subset of MEMs were performed with the 'listw.select' function, the spatially constrained permutation tests of the unique and the shared fractions of variation partitioning were performed with the 'msr' and 'envspace.test' functions, and the RDA with forward selection with the 'forward.sel' function of the "adespatial" library⁶⁷.

Analysis of grid-level data

Plot-level analyses are strongly affected by local ecological effects, which can vary considerably over short geographical distances (e.g., plots representing inundated vs. non-inundated forests can be in close proximity to each other). To remove this effect and focus on more broad-scale biogeographical patterns, we divided Amazonia into 47,441 grid cells at the resolution of 0.1 arc degrees ($\approx 121 \text{ km}^2$) and estimated the relative abundance of each tree species for each grid cell using the spatial interpolation method of ter Steege et al.⁶⁸. As a relative abundance measure, we used $RA_i = n_i / N_j$, where n_i equals the number of stems of species i and N_j the total number of stems in the plot (including unidentified trees). For all 5188 species with a valid name in the plots, we constructed an inverse distance weighting (IDW) model for RA_i , with a distance-decay power of 2, a maximum number of plots used for each local estimation of 150, and a maximum distance parameter of 4 degrees.

We performed a Detrended Correspondence Analysis (DCA) on the grid-level community matrix to map the broad-scale variation of tree species composition across Amazonia. This is for two reasons, we assumed that there are no strict biogeographical boundaries in Amazonia, and DCA is a perfect way of describing gradients (see below); PCoA is based on similarities among plots (in this case cells) and would average out the gradients too much. DCA is based on weighted averaging and to balance the influence of common species in the ordination pattern, we used DCA without down-weighting rare species, which are most of the species in Amazonia⁶⁹. The response curve of species is assumed to be unimodal, with the average being the mean niche position and the standard deviation being a measure of niche breadth⁷⁰. The results were visualised both with traditional ordination scatterplots and by plotting the DCA axis scores on a map of Amazonia. In the DCA ordination plot, we also visualised the distributions of the 20 most abundant tree species (those with the largest sum of relative abundances over all grid cells). On the map of Amazonia, we added isolines that link similar levels of DCA scores to assess species turnover rates: when consecutive DCA isolines are relatively close to each other, species turnover across space is sharper than when consecutive DCA isolines are relatively far from each other. To highlight the association between areas of sharper species turnover and existing environmental gradients, we overlaid the isolines for soil pH over the map of the first DCA axis and the isolines for maximum climatological water deficit with the map of the second DCA axis. To define the level for the environmental gradient isolines to be overlaid over the DCA maps, we evaluated the point of inflection in the curve associating the species distributional ranges along the environmental scales. DCA was performed using the function 'decorana' of the "Vegan" R library⁶⁵, with standard settings and without down-weighting rare species.

Gradients and species niche breadth

To aid in the interpretation of the broad-scale variation of tree species composition across Amazonia, we computed the species' mean niche positions and breadths along environmental and compositional gradients. The mean niche position was computed by calculating weighted averages (WA)⁷¹ of the plot-wise species relative abundances for four environmental variables (annual rainfall, maximum cumulative water deficit, sum of bases, pH) and for the compositional gradients obtained from the grid-level DCA analyses (DCA axes 1 and 2 scores). The values of each independent variable were extracted from the corresponding raster data using the coordinates of the forest inventory plots. Weighted Averaging scores (mean niche position or optimum) for those variables were calculated for each species using the



<https://doi.org/10.1038/s42003-024-06937-6>

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Sciences (NMBU), Faculty of Environmental Sciences and Natural Resource Management, Aas, Norway. ⁷⁷Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, Departamento de Genética, Ecologia e Evolução, Belo Horizonte, MG, Brazil. ⁷⁸Department of Biology, University of Miami, Coral Gables, FL, USA. ⁷⁹Fairchild Tropical Botanic Garden, Coral Gables, FL, USA. ⁸⁰Instituto de Biociências - Dept. Ecologia, Universidade de São Paulo - USP, Rua do Matão, Trav. 14, no. 321, Cidade Universitária, São Paulo, SP, Brazil. ⁸¹Dept. Biological Sciences, Broward County Parks and Recreation, Boca Raton, Oakland Park, FL, USA. ⁸²Servicios de Biodiversidad EIRL, Iquitos, Loreto, Peru. ⁸³Lancaster Environment Centre, Lancaster University, Lancaster, Lancashire, UK. ⁸⁴Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK. ⁸⁵Postgraduate program in Biodiversity and Biotechnology - Bionorte, Federal University of Acre, Rio Branco, AC, Brazil. ⁸⁶Scientific research program, Juruá Institute, ALEXO, Manaus, AM, Brazil. ⁸⁷Department of Integrative Biology, University of California, Berkeley, CA, USA. ⁸⁸Empresa Brasileira de Pesquisa Agropecuária, Embrapa Amapá, Macapá, AP, Brazil. ⁸⁹Graduate Program in Ecology, Federal University of Santa Catarina (UFSC), Campus Universitário - Corrego Grande, Florianópolis, SC, Brazil. ⁹⁰Dirección de Evaluación Forestal y de Fauna Silvestre, Magdalena del Mar, Peru. ⁹¹Instituto de Investigaciones Forestales de la Amazonía, Universidad Autónoma del Beni José Ballivián, Campus Universitario Final, Riberaita, Beni, Bolivia. ⁹²Escuela de Biología Herbario Alfredo Paredes, Universidad Central, Quito, Pichincha, Ecuador. ⁹³Direction régionale de la Guyane, Office national des forêts, Cayenne, French Guiana. ⁹⁴Department of Biological Sciences, California State Polytechnic University, Arcata, CA, USA. ⁹⁵Herbario HAG, Universidad Nacional Amazónica de Madre de Dios (UNAMAD), Puerto Maldonado, Madre de Dios, Peru. ⁹⁶Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco, AC, Brazil. ⁹⁷Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain. ⁹⁸Iwokrama International Centre for Rain Forest Conservation and Development, Georgetown, Guyana. ⁹⁹New York Botanical Garden, Bronx, New York, NY, USA. ¹⁰⁰Department for Ecosystem Stewardship, Royal Botanic Gardens, Kew, Richmond, Surrey, UK. ¹⁰¹Latin America Department, Missouri Botanical Garden, St. Louis, MO, USA. ¹⁰²Herbario Nacional de Bolivia, Instituto de Ecología, Universidad Mayor de San Andrés, Carrera de Biología, La Paz, Bolivia. ¹⁰³Department for Accelerated Taxonomy, Royal Botanic Gardens, Kew, Richmond, Surrey, UK. ¹⁰⁴Laboratorio de Plantas Vasculares y Herbario ISV, Universidad Nacional de Jaén, Carretera Jaén San Ignacio Km 23, Jaén, Cajamarca, Peru. ¹⁰⁵Laboratoire Evolution et Diversité Biologique, CNRS and Université Paul Sabatier, Toulouse, France. ¹⁰⁶Department of Anthropology, University of Texas at Austin, Austin, TX, USA. ¹⁰⁷Estación de Biodiversidad Tiputini, Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito-USFQ, Quito, Pichincha, Ecuador. ¹⁰⁸Fundación Puerto Rastrero, Bogotá, DC, Colombia. ¹⁰⁹Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA. ¹¹⁰Biosystematics group, Wageningen University, Wageningen, The Netherlands. ¹¹¹Fundación Estación de Biología, Bogotá, DC, Colombia. ¹¹²Department of Anthropology, Tulane University, New Orleans, LA, USA. ¹¹³PROTERRA, Instituto de Investigaciones de la Amazonía Peruana (IIAP), Iquitos, Loreto, Peru. ¹¹⁴ACEER Foundation, Puerto Maldonado, Madre de Dios, Peru. ¹¹⁵Amazon Conservation Team, Arlington, VA, USA. ¹¹⁶Instituto de Ciencia y Tecnología Ambientales, Universitat Autònoma de Barcelona, Barcelona, Spain. ¹¹⁷Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, DC, Colombia. ¹¹⁸Instituto de Ciência Agrárias, Universidade Federal Rural da Amazônia, Belém, PA, Brazil. ¹¹⁹Escuela Profesional de Ingeniería Forestal, Universidad Nacional de San Antonio Abad del Cusco, Puerto Maldonado, Madre de Dios, Peru. ¹²⁰Laboratory of Human Ecology, Instituto Venezolano de Investigaciones Científicas - IVIC, Caracas, DC, Venezuela. ¹²¹Cambridge University Botanic Garden, Cambridge University, 1 Brookside, Cambridge, UK. ¹²²Programa de Maestría de Manejo de Bosques, Universidad de los Andes, Mérida, Mérida, Venezuela. ¹²³Centre for Biodiversity and Conservation Science CBCS, The University of Queensland, Brisbane, QLD, Australia. ¹²⁴Resource Ecology Group, Wageningen University & Research, Lumen, Wageningen, Gelderland, The Netherlands. ¹²⁵Unique land use GmbH, Freiburg im Breisgau, Germany. ¹²⁶Núcleo de Estudos e Pesquisas Ambientais, Universidade Estadual de Campinas - UNICAMP, Campinas, SP, Brazil. ¹²⁷Herbarium Amazonense (AMAZ), Universidad Nacional de la Amazonia Peruana, Iquitos, Loreto, Peru. ¹²⁸Laboratorio de Ciências Ambientais, Universidade Estadual do Norte Fluminense, Campos dos Goytacazes, RJ, Brazil. ¹²⁹Instituto de Investigaciones para el Desarrollo Forestal (INDEFOR), Universidad de los Andes, Conjunto Forestal, Mérida, Mérida, Venezuela. ¹³⁰Departamento de Biología, Universidade Federal do Amazonas - UFAM - Instituto de Ciências Biológicas - ICB1, Manaus, AM, Brazil. ¹³¹Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA. ¹³²Faculty of Social Sciences, University of Nottingham, University Park, Nottingham, UK. ¹³³Wildlife Conservation Society (WCS), 2300 Southern Boulevard, Bronx, New York, NY, USA. ¹³⁴Facultad de Biología, Universidad Nacional de la Amazonia Peruana, Iquitos, Loreto, Peru. ¹³⁵Medio Ambiente, PLUSPRETOL, Iquitos, Loreto, Peru. ¹³⁶The Mauritius Herbarium, Agricultural Services, Ministry of Agro-Industry and Food Security, Reduit, Mauritius. ¹³⁷Department of Biology, Aarhus University, Aarhus C, Aarhus, Denmark. ¹³⁸Escuela de Ciencias Forestales (ESFOR), Universidad Mayor de San Simón (UMSS), Sacta, Cochabamba, Bolivia. ¹³⁹FOMABO, Manejo Forestal en las Tierras Tropicales de Bolivia, Sacta, Cochabamba, Bolivia. ¹⁴⁰Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Medellín, Antioquia, Colombia. ¹⁴¹Fundación Amigos de la Naturaleza (FAN), Santa Cruz, Bolivia. ¹⁴²Tropenbos International, Ede, The Netherlands. ¹⁴³School of Anthropology and Conservation, University of Kent, Marlowe Building, Canterbury, Kent, UK. ¹⁴⁴Herbario Nacional del Ecuador, Universidad Técnica del Norte, Quito, Pichincha, Ecuador. ¹⁴⁵Instituto de Biodiversidade e Florestas, Universidade Federal do Oeste do Pará, Rua Vera Paz, Campus Tapaçós, Santarém, PA, Brazil. ¹⁴⁶Department of Biology, University of Missouri, St. Louis, MO, USA. ¹⁴⁷Department of Physics, Federal University of Santa Catarina, Florianópolis, SC, Brazil. ¹⁴⁸Quantitative Biodiversity Dynamics, Utrecht University, Padualaan 8, Utrecht, The Netherlands. ¹⁴⁹Deceased: Dairon Cárdenas López. ¹⁵⁰Deceased: Nallarett Dávila. ¹⁵¹Deceased: Cid Ferreira. ¹⁵²e-mail: hans.tersteeg@natuurfio.nl



Anexo 10. Artículo de investigación.

RESEARCH

TREE TRAITS

The pace of life for forest trees

Lafasia Blatic-Murphy^{1*}, Robert M. McElderry^{1,2}, Adriane Esquivel-Mueibert³, Johan van den Hoogen⁴, Pieter A. Zuidema⁴, Oliver L. Phillips⁵, Edmar Almeida de Oliveira⁶, Patricia Alvarez Loayza⁷, Esteban Alvarez-Davila⁸, Luciana F. Alves⁹, Vinicius Andrade Maia¹⁰, Simone Aparecida Vieira¹¹, Lidiany Carolina Arantes da Silva¹⁰, Alejandro Araujo-Murakami¹², Eric Arets¹³, Julien Astigarraga¹⁴, Fabrício Baccaro¹⁵, Timothy Baker⁵, Olaf Banki¹⁶, Jorcely Barroso¹⁷, Lillian Blanc¹⁸, Damien Bonal¹⁹, Frans Bongers²⁰, Kauane Maiara Bordin²¹, Roel Brienen⁵, Marcelo Brilhante de Medeiros²², José Luís Camargo²³, Felipe Carvalho Araújo¹⁰, Carolina V. Castilho²⁴, Wendeson Castro²⁵, Victor Chama Moscoso²⁶, James Comiskey^{27,28}, Flávia Costa²⁹, Sandra Cristina Müller²¹, Everton Cristo de Almeida³⁰, Antonio Carlos Lóla da Costa³¹, Vitor de Andrade Kamimura³², Fernanda de Oliveira¹⁰, Jhon del Aguila Pasquel^{33,34}, Géraldine Derroire³⁵, Kyle Dexter³⁶, Anthony Di Fiore^{37,38}, Louis Duchesne³⁹, Thaise Emílio⁴⁰, Camila Laís Farrapo⁹, Sophie Fausset⁴¹, Federick C. Drake⁴², Ted R. Feldpausch⁴³, Rafael Flora Ramos⁴⁴, Valeria Forni Martins^{21,45}, Marcelo Fragomeni Simon²², Miguel Gama Reis¹⁰, Angelo Gilberto Manzatto⁴⁶, Bruno Herault¹⁸, Rafael Herrera⁴⁷, Euridice Honorio Coronado⁴⁸, Robert Howe⁴⁹, Isau Huamantupa-Chuquimaco⁵⁰, Walter Huaraca Huasco⁵¹, Katia Janaina Zanini²¹, Carlos Joly⁵², Timothy Killeen⁵³, Joice Klipel²¹, Susan G. Laurance⁵⁴, William F. Laurance⁵⁴, Marco Aurélio Leite Fontes¹⁰, Wilmar Lopez Oviedo⁵⁵, William E. Magnuson⁵⁶, Rubens Manoel dos Santos¹⁰, Jose Luis Marcelo Peña⁵⁷, Karla Maria Pedra de Abreu⁵⁸, Beatriz Marimon⁶, Ben Hur Marimon Junior⁶, Karina Melgazo⁵⁹, Omar Aurelio Melo Cruz⁵⁹, Casimiro Mendoza⁶⁰, Abel Monteagudo-Mendoza⁶¹, Paulo S. Morandi⁶, Fernanda Moreira Gílanas¹⁰, Henrique Nascimento⁶², Marcelo Nascimento⁶³, David Neill⁶⁴, Walter Palacios⁶⁵, Nadir C. Paikqui Carracho⁵, Guido Pardo⁶⁶, R. Toby Pennington^{67,68}, Maria Cristina Peñuela-Mora⁶⁹, Nigel C. A. Pitman⁷⁰, Laurens Poorter⁴, Adriana Prieto Cruz⁷¹, Hirma Ramirez-Angulo⁷², Simone Matias Reis^{73,6}, Zorayda Restrepo Correa⁷⁴, Carlos Reynel Rodríguez⁷⁵, Agustín Ruelas Lleras⁷⁶, Flavio A. M. Santos⁵², Rodrigo Scarton Bergamin⁷⁷, Juliana Schietti¹⁵, Gustavo Schwartz⁷⁸, Julio Serrano⁷⁹, André Maciel Silva-Sene¹⁰, Marcos Silveira⁸⁰, Juliana Stropp⁸¹, Hans ter Steege^{16,82}, John Terborgh^{83,84}, Matthias W. Tobler⁸⁴, Luis Valenzuela Gamarra⁸⁵, Peter J. van de Meer⁸⁵, Geertje van der Heijden⁸⁶, Rodolfo Vasquez⁸⁷, Emilio Vilanova⁸⁸, Vincent Antoine Vos⁸⁹, Amy Wolf⁹⁰, Christopher W. Woodall⁹¹, Virginia Wortel⁹², Joeri A. Zwarts⁹³, Thomas A. M. Pugh^{94,3}, Thomas W. Crowther³

Tree growth and longevity trade-offs fundamentally shape the terrestrial carbon balance. Yet, we lack a unified understanding of how such trade-offs vary across the world's forests. By mapping life history traits for a wide range of species across the Americas, we reveal considerable variation in life expectancies from 10 centimeters in diameter (ranging from 1.3 to 3195 years) and show that the pace of life for trees can be accurately classified into four demographic functional types. We found emergent patterns in the strength of trade-offs between growth and longevity across a temperature gradient. Furthermore, we show that the diversity of life history traits varies predictably across forest biomes, giving rise to a positive relationship between trait diversity and productivity. Our pan-latitudinal assessment provides new insights into the demographic mechanisms that govern the carbon turnover rate across forest biomes.

The cumulative energetic investment in survival and growth from one year to the next ultimately determines an organism's overarching pace of life, including the time it takes to grow to its maximal size and its life expectancy (1, 2). This fundamental relationship between energetic investments, developmental schedules, and longevity has been extensively studied for animals, showing that high resource allocation toward growth is inversely related to life expectancy and maximal body mass (3, 4). Trees are also assumed to retain tightly coupled relationships between growth strategies, life expectancies, and maximal sizes (Fig. 1A) (5), which determine the dynamics and structure of global forests. Yet, although these life history differences fundamentally regulate how fast carbon is sequestered in different regions of the vegetation carbon pool (6–8), we still lack a unified understand-

ing of the range of tree life history strategies that exist across global forests.

It is widely accepted that tree life history strategies should align along a primary axis of variation in their pace of life, ranging from fast-growing, short-lived species to slow-growing, long-lived species (i.e., fast-slow continuum and r/K selection theory) (Fig. 1A) (5). In this context, high energetic investment of finite resources toward fast growth is expected to come at the cost of reduced survival, which ultimately determines a species' life expectancy and maximal size (Fig. 1A) (9–11). Thus, it is expected that abiotic constraints (e.g., soil nutrients, water, and temperature) should strongly shape the pace of life for trees, giving rise to predictable variation in the strength of life history trade-offs across biogeographic gradients (Fig. 1B) (12). So far, however, the only empirical tests of these trade-offs come from

tree ring data and local-scale studies of tropical ecosystems and have produced mixed results (2, 12–14).

One potential challenge that can obscure predictable patterns in the pace of life for forest trees is that it is not only the traits that are expected to vary across environmental gradients but also the diversity of those traits. For example, strong biotic competition across tropical forests is thought to have led to high demographic niche differentiation (i.e., high demographic diversity; Fig. 1C, upper right). By contrast, resource limitations in harsh cold and dry regions are assumed to have restricted the species pool to predominantly slow-growing, long-lived species (Fig. 1C, lower left). Yet, these suppositions lack empirical evidence to support them because the extreme longevity of trees (which can live for thousands of years) has precluded our capacity to quantify the strength of tree life history trade-offs across a wide range of species. Let alone characterize the diversity of life history traits across biogeographic gradients.

In this study, we used the largest dataset of dynamic tree information to date and used age-from-stage methods to calculate the mean life expectancy and maximal life span for a wide range of trees across the Americas (15–17), spanning a latitudinal gradient from Northern Canada to Southern Brazil. This includes long-term records from an international network of researchers, including members of the Global Forest Dynamics, ForestPlots.net (18, 19), and ForestGeo (20–22) networks and the United States and Canadian forest inventory programs (23–25). To balance this dataset across our biogeographic gradient, we randomly subsampled the North American plots to equal the number of point observations in Central and South America [see supplementary materials (SM), materials and methods], resulting in 3.2 million distinct tree measurements for 1127 species (i.e., tree size and status). Our big-data approach allowed us to test for the expectation that trees align along the fast-slow continuum (Fig. 1A, H1) and to quantify whether tree growth-longevity-stature relationships covary across soil, water, and temperature gradients (Fig. 1B, H2). Apart from species with low occurrences (<100 observations; see SM, materials and methods), our systematic sampling allowed us to test for the expectation that the range of life history strategies occupied by species (i.e., demographic trait diversity) varies predictably across broadscale biogeographic gradients, with harsh cold regions in the Northern Hemisphere restricting trees to a smaller pool of predominantly slow-growing, long-lived species (Fig. 1C, H3). On the basis of the well-established diversity-productivity relationship, we also expected demographic trait diversity to be positively associated with ecosystem productivity (Fig. 1C, H3).



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To quantify tree growth, longevity, and stature for a wide range of species across biogeographic gradients and test our three core hypotheses, we first grouped the stem-level tree data into equally sized hexagon grids (size ~250,000 km²) and developed species-specific survival- and growth-generalized linear mixed-effects models that included tree diameter at breast height (dbh) at the first census interval as a predictor variable

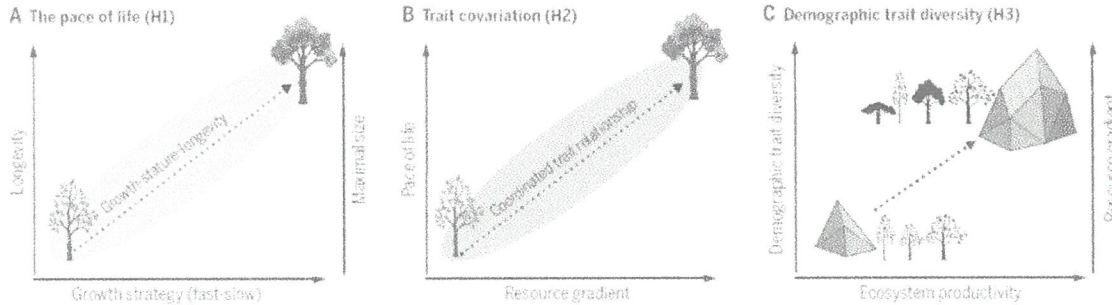


Fig. 1. Conceptual diagram of our core aims and associated hypotheses.

(A) The expectation is that trees should align along the fast-slow continuum, with fast-growing, short-lived species on one end of the spectrum and slow-growing, long-lived species on the other end (H1). (B) Life history trait relationships should be phylogenetically conserved and should covary across biogeographic gradients, leading to

more conservative life history strategies in low-resource environments (low soil and nutrient environments and colder temperatures) (H2). (C) Lastly, we expect the range of tree life history strategies (i.e. convex hull volume in life history trait space that is occupied by species) to vary predictably across biogeographic gradients, with demographic trait diversity being positively associated with ecosystem productivity (H3).

¹Institute of Integrative Biology, ETH Zurich (Swiss Federal Institute of Technology), 8092 Zurich, Switzerland; ²Forest Health and Bark Interactions, Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland; ³Birmingham Institute of Forest Research (BIFoR), University of Birmingham, Birmingham, UK; ⁴Forest Ecology and Forest Management Group, Wageningen University & Research, Wageningen, Netherlands; ⁵School of Geography, University of Leeds, Leeds, UK; ⁶Universidade do Estado de Mato Grosso (Unemat) - Pós-Graduação em Ecologia e Conservação, Nova Xavantina MT, Brazil; ⁷Nicolaus, School of the Environment, Duke University, Durham, NC 27710, USA; ⁸Escola de Ciências Agrárias, Universidade Nacional Alberta e a Distância de Colombia, Colombia; ⁹Center for Tropical Research, Institute of the Environment and Sustainability, University of California, Los Angeles, Los Angeles, CA 90095, USA; ¹⁰Universidade Federal de Lavras, Lavras, Brazil; ¹¹Universidade Estadual de Campinas, Campinas, Brazil; ¹²Museo de Historia Natural Noel Kempth Mercado, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia; ¹³Wageningen Environmental Research, Wageningen University & Research, Wageningen, Netherlands; ¹⁴Universidade de Alcalá, Department of Life Sciences, Forest Ecology and Restoration Group (FOREO), Alcalá de Henares, Spain; ¹⁵Universidade Federal do Amazonas, Manaus, Brazil; ¹⁶Naturals Biodiversity Center, Leiden, Netherlands; ¹⁷Laboratoire de Sciences Forestières, Université de la Nouvelle République de la Haute-Volta, Ouagadougou, Burkina Faso; ¹⁸Faculté de Sciences, Université Montpellier, CIRAD, Montpellier, France; ¹⁹Université de Lorraine, AgroParis Tech, INRAE, UMR SIVA, 54000 Nancy, France; ²⁰Department of Environmental Sciences, Wageningen University & Research, Wageningen, Netherlands; ²¹Plant Ecology Lab, Ecology Department, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; ²²Embrapa Gestão Recursos e Biotecnologia, Brasília, Brazil; ²³Biological Dynamics of Forest Plot - National Institute for Amazonian Research (DIFP-INPA), Manaus, Brazil; ²⁴Empresa Roraima, Boa Vista, Roraima, Brazil; ²⁵Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco, Acre, Brazil; ²⁶Universidade Nacional de San Antonio Abad del Cuzco, Cuzco, Peru; ²⁷Inventory and Monitoring Program, National Park Service, Fort Collins, CO 80525, USA; ²⁸Smithsonian Institution, Washington, DC 20004, USA; ²⁹Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, CEP 66097-375, Manaus, Brazil; ³⁰Universidade Federal do Oeste de Pará (UFOPA), Instituto de Biodiversidade e Florestas (IBEF), Santarém, Pará, Brazil; ³¹Universidade Federal do Pará - Instituto de Geomorfologia, Belém, Pará, Brazil; ³²Instituto Tecnológico Vale (ITV), Belém, Pará, Brazil; ³³Instituto de Investigaciones de la Amazonia Peruana, Iquitos, Peru; ³⁴Universidad Nacional de la Amazonia Peruana, Iquitos, Peru; ³⁵CIRAD, UMR EcoFog (AgroParisTech, CNRS, INRAE, Université des Antilles, Université de la Guyane), Campus Agronomique, Kourou, French Guiana; ³⁶School of GeoSciences, University of Edinburgh, Royal Botanic Garden Edinburgh, Edinburgh, UK; ³⁷Private Molecular Ecology and Evolution Laboratory and Department of Anthropology, The University of Texas at Austin, Austin, TX 78712, USA; ³⁸Tigipate Biodiversity Station, College of Biological and Environmental Sciences, Universidad San Francisco de Quito, Guimbal, Ecuador; ³⁹Direction de la Recherche Forestière, Ministère des Ressources Naturelles et des Forêts du Québec, Québec, QC G1P 0W5, Canada; ⁴⁰Programa Nacional de Pós-Doutorado (PNPD), Programa de Pós-Graduação em Ecologia, Instituto de Biologia, University of Campinas (UNICAMP), Campinas, Brazil; ⁴¹School of Geography, Earth and Environmental Sciences, University of Plymouth, Plymouth, UK; ⁴²School of Environmental Sciences, University of Liverpool, Liverpool, UK; ⁴³Geography, Faculty of Science, Environment and Economy, University of Exeter, Exeter, UK; ⁴⁴Biology Institute, University of Campinas, 13083-862, Campinas, SP, Brazil; ⁴⁵Department of Natural Sciences, Mathematics, and Education, Centre for Agrarian Sciences, Universidade Federal de São Carlos (UFSCar), Araras, SP, Brazil; ⁴⁶Federal University of Roraima (Una-Roraima), RR, Brazil; ⁴⁷Instituto Venezolano de Investigaciones Científicas (IVIC), Miranda, Venezuela; ⁴⁸School of Geography and Sustainable Development, University of St Andrews, St Andrews, UK; ⁴⁹Center for Biodiversity, University of Wisconsin-Green Bay, Green Bay, WI 54311, USA; ⁵⁰Herbario "Alvaro Godoy" (HAG), Universidad Nacional Amazónica de Madre de Dios (UNAMAD), Puerto Maldonado, Madre de Dios, Peru; ⁵¹Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK; ⁵²Plant Biology Department, Biology Institute, University of Campinas, Campinas, SP, Brazil; ⁵³Missouri Botanical Garden, St. Louis, MO 63110, USA; ⁵⁴Centre for Tropical Environmental and Sustainability Science, College of Science and Engineering, James Cook University, Cairns, Australia; ⁵⁵Senafril Kappa Colombia, Yumbo, Valle del Cauca, Colombia; ⁵⁶Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; ⁵⁷Universidad Nacional de Jaén, Laboratory of Vascular Plants and ISV, Hebrón, San Ignacio, Peru; ⁵⁸Federal Institute of Espírito Santo, Campos de Alegre, Alegre, ES, Brazil; ⁵⁹Universidad del Táchira, Táchira, Colombia; ⁶⁰Universidad Mayor de San Simón, Cochabamba, Bolivia; ⁶¹Universidade Nacional de San Antonio Abad del Cuzco, Jardin Botánico de Mooson, Cuzco, Peru; ⁶²Biodiversity Department, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; ⁶³Laboratório de Ciências Ambientais, CBR, Universidade Estadual de Norte Fluminense Darcy Ribeiro, Campos dos Goytacases, RJ, Brazil; ⁶⁴Universidade Estadual Amazônica, Puyo, Acre, Brazil; ⁶⁵Instituto Nacional de Biodiversidad, INABIO, Quito, Ecuador; ⁶⁶Facultad de Ciencias Forestales, Universidad Autónoma del Beni José Ballivián, Riberiatta, Beni, Bolivia; ⁶⁷Department of Geography, University of Exeter, UK; ⁶⁸Royal Botanic Garden Edinburgh, UK; ⁶⁹Universidade Regional Amazônica Itaipá, Itaipá, Tera, Ecuador; ⁷⁰Collectors, Conservation & Research, Field Museum of Natural History, Chicago, IL 60605, USA; ⁷¹UNF Amazon, Bogotá, Colombia; ⁷²Universidad de Los Andes, Facultad de Ciencias Forestales y Ambientales, INGEFOR, Mérida, Venezuela; ⁷³Ciencias Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco, Acre, Brazil; ⁷⁴Servicio Fitosanitario y Cambio Climático, Corporación COA-TREE, Medellín, Colombia; ⁷⁵Universidade Nacional Agraria La Molina, Lima, Facultad de Ciencias Forestales, Lima, Peru; ⁷⁶Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; ⁷⁷School of Geography, Earth and Environmental Science, University of Birmingham, UK; ⁷⁸Embrapa Floresta Amazônia 66095-903, Belém, PA, Brazil; ⁷⁹Universidad de los Andes, Mérida, Venezuela; ⁸⁰Laboratório de Botânica e Ecologia Vegetal, Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Acre, Brazil; ⁸¹Biogeography Department, Freer University, 54280 Trier, Germany; ⁸²Quantitative Biodiversity Dynamics, Department of Biology, Utrecht University, Utrecht, The Netherlands; ⁸³Florida Museum of Natural History, University of Florida-Gainesville, Gainesville, FL 32611, USA; ⁸⁴San Diego Zoo Wildlife Alliance, Escondido, CA 92027, USA; ⁸⁵Van Hall-Laanstein University of Applied Sciences, Velp, Netherlands; ⁸⁶School of Geography, University of Nottingham, Nottingham NG7 2RD, UK; ⁸⁷Jardin Botánico de Mooson (JBM), Oropampa, Pisco, Peru; ⁸⁸Wildlife Conservation Society (WCS), Bronx, NY 10460, USA; ⁸⁹Instituto de Investigaciones Forestales de la Amazonia, Universidad Autónoma del Beni José Ballivián, Riberiatta, Beni, Bolivia; ⁹⁰University of Wisconsin-Green Bay, Department of Natural and Applied Sciences, Green Bay, WI 54311, USA; ⁹¹US Department of Agriculture, Forest Service, Research and Development, Durham, NH 03824, USA; ⁹²Department of Forest Management, Centre for Agricultural Research in Suriname, CELOS, Suriname; ⁹³Utrecht University, Utrecht, Netherlands; ⁹⁴Department of Physical Geography and Ecosystem Science, Lund University, Sweden

*Corresponding author. Email: lafusa.bi@ecampus.utu.se
 Present address: Centre for Research on Biodiversity Dynamics and Climate Change (EvoDyna), Institute of Biosciences, São Paulo State University (UNESP), Campus Rio Claro, SP, Brazil
 Present address: Institute of Energy, Espoo, University of Lüneburg, Lüneburg, Germany
 Present address: Belém, Brazil, Unama, Un

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and grid cell as a random effect (SM, materials and methods). We then used the survival and growth coefficients to fit size-dependent integral projection models (IPMs) and derive age-related traits from size-dependent probabilities for each species within each grid cell (SM, materials and methods) (15–17, 26–28). IPMs dynamically integrate size-dependent variability in survival and growth as a continuous process, which allowed us to use cross-sectional data over discrete time steps to make interspecific comparisons of how many years it takes trees to attain key milestones in their life cycle. We parameterized our IPMs using methods specifically developed for trees (27–29). Validations of IPM model outputs, relative to tree ring data, showed that this parameterization method can provide realistic estimates of tree age demographics (27).

We used our species-specific IPMs and age-from-stage methods to calculate several quantitative measures of growth, longevity, and stature. Specifically, we calculated the number of years it takes for trees to grow from 10 to 20 cm in diameter (fig. S2, path a2) and to grow

from 10 cm to the 70th quantile of their size distribution (fig. S2, path a1) (hereafter referred to as “growth strategies”). The 10-cm-diameter lower-bound threshold was chosen because it was the size at which point trees were consistently monitored across the forest networks, and the 70th quantile threshold was chosen because it reflects a mature size at which point trees have approached their ultimate position in the forest. We also calculated two quantitative measures of tree longevity, including their average remaining life expectancy from 10 cm in diameter and their maximal life-span age (95% cohort mortality from 10 cm) and a measure of maximal tree stature (size at maximal life-span age) (fig. S2, path b) (15–17). These mean estimates capture the pace of life for trees (growth, longevity, and stature) on the basis of observed climate conditions over the last century (derived from dynamical data collected between 1926 and 2014; see SM, materials and methods).

Our estimates of remaining life expectancy from 10 cm dbh range from 1.2 to 3195 years, with a mean value of 60 years in the tropics

and 95 years in the extratropics (Fig. 2A). This trend matches our theoretical expectation of broadscale tree life history diversification patterns (Fig. 1B) and concurs with known tree longevity hotspots, in which the oldest recorded species occur in temperate conifer and boreal forests (22, 30). However, there was also considerable overlap in the range of tree life expectancies across biomes (figs. S3 and S4, and table S2) and wide variability in how longevity relates to tree growth strategies and maximal statures (Fig. 2B, figs. S3 and S4, and table S2). It is important to note that remaining life expectancy from 10 cm dbh is a species-level mean estimate (i.e., is conditional on surviving to 10 cm dbh). A low life expectancy, relative to the mean number of years it takes a species to grow from 10 to 20 cm dbh, does not imply that no individuals will reach 20 cm dbh. Instead, it implies that less than half of the individuals will survive to that size threshold.

Tree life history strategies do not strictly follow the fast-slow continuum (H1)

To test the expectation that trees align along the fast-slow continuum (Fig. 1A, H1), we first examined univariate trait correlations and found moderate support for trade-offs between tree growth, longevity, and stature (fig. S5). For example, the number of years it takes trees to grow from 10 to 20 cm in diameter was positively correlated to life expectancy [Pearson correlation coefficient (r) = 0.22] and maximal life-span age (Pearson's r = 0.21). Similarly, maximal tree size was positively related to life expectancy (Pearson's r = 0.44). The strength of these pairwise correlations also suggests that tree age demographics do not strictly follow a single axis of variation along the fast-slow continuum (i.e., the assumption that growth is tightly coupled and inversely related to longevity and maximal stature).

To examine the multidimensionality of tree age demographics (Fig. 1A, H1), we analyzed the variance-covariance matrix of tree growth, longevity, and stature using a principal components analysis (PCA). Highly correlated traits that captured redundant trait information were excluded from the PCA (fig. S5), resulting in the inclusion of tree growth strategies (i.e., growth from 10 to 20 cm dbh and the 70th quantile of their size distribution), life expectancy from 10 cm dbh, and maximal tree size (fig. S5). The first PC axis captured 46% of the life history trait variation and was heavily weighted by tree growth dynamics (i.e., years to 20 cm dbh and the 70th quantile size) (Fig. 2C). The PC loadings also showed that slow growth was correlated with high life expectancy and large maximal size (table S3). The second axis captured 28% of the trait variation. The directionality between the trait correlations flipped, whereby slow growth was negatively correlated to life expectancy and maximal size (table

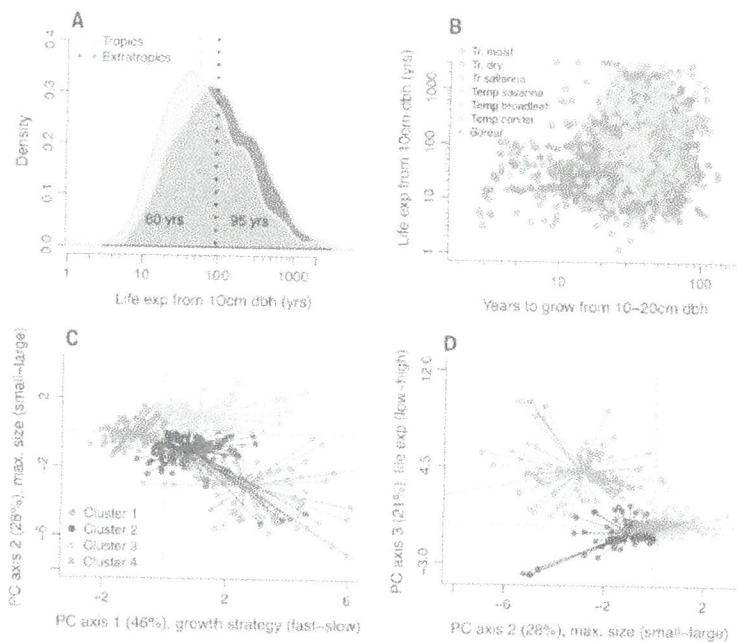


Fig. 2. Visual illustration of tree growth-longevity-stature relationships and core demographic functional types. The mean life expectancy is higher in the extratropics than in the tropics (A), with substantial variation between tree growth strategies and life expectancies (B) ($N = 6847$, i.e., species \times grid ID). The other trait relationships are represented in fig. S8. The core growth-longevity-stature functional types are presented in (C and D), which are determined using the k -means clustering algorithm of the life history trait principal components analysis (PCA) scores. PC weights and trait correlations are reported in table S3. The frequency density (A) and the life history traits (B) are scaled by the natural log. Data points are species-specific and are calculated using individual tree observations, and size-dependent integral projection models (SM, materials and methods).

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growth and biomass retention in tree longevity, with important implications for modeling the global carbon balance in a changing world (46).

Demographic diversity varies predictably across biogeographic gradients (H3)

To characterize the range of life history strategies that are expressed by trees across broad-scale biogeographic gradients, we first calculated the convex-hull volume in demographic trait space within each grid cell (SM, materials and methods) (47) and compared the relationship between the demographic trait diversity of forests and well-established patterns in species richness. The convex-hull volume was calculated by using the life history trait PC scores for axes 1 to 3, which together captured 95% of the life history trait variation. We then tested whether the demographic trait diversity of forests varied predictably across biogeographic gradients and explored potential links between demographic trait diversity and remotely sensed estimates of potential aboveground net primary productivity (NPP) (Fig. 1C, H3, and SM, materials and methods) (48). The expectation is that the diversity of life history trait strategies that are expressed by trees should vary predictably across biogeographic gradients, with higher demographic diversity being positively associated with aboveground productivity.

Our results illustrate that the demographic trait diversity of forests follows well-established patterns in species richness (Fig. 4A, adjusted coefficient of determination (adj R^2) = 0.65, $P < 0.001$). We also found that the demographic diversity of forests varied predictably across biogeographic gradients, with high demographic trait diversity across warm tropical forests and low diversity of predominantly slow-growing, long-lived species in the cold temperate and boreal forests (adj R^2 = 0.40, $P < 0.001$; Fig. 4B and table S7). Lastly, we found a positive correlation between the demographic diversity of forests and remotely sensed estimates of ecosystem productivity (Pearson's r = 0.71).

The emergence of a positive association between the demographic trait diversity and ecosystem productivity is in line with two non-mutually exclusive hypotheses. From an evolutionary perspective, ecosystem productivity is thought to drive species diversification and niche differentiation (49). Conversely, following widely established relationships between biodiversity and ecosystem function, more demographically diverse forests are commonly assumed to have access to a larger resource pool and should thus be more productive (50, 51). In this study, we found moderate support for both hypotheses. Specifically, we found that ecosystem productivity was predictive of demographic trait diversity across broadscale biogeographic gradients (adj R^2 = 0.49, $P <$

0.001; Fig. 4C and table S7). At the same time, ecosystem productivity was jointly influenced by temperature (average marginal effect = 0.83, P = 0.04; Fig. 4D) and demographic trait diversity (average marginal effect = 1.43, $P < 0.001$; Fig. 4D). This positive association was consistent across the tropics (adj R^2 = 0.26, $P < 0.01$; table S7) and extra-tropics (adj R^2 = 0.84, $P < 0.01$; Fig. 4D and table S7). It should be noted that NPP was strongly correlated with mean annual temperature (Pearson's r = 0.94), which did not allow us to explicitly test for the individual and combined effect of these variables on demographic trait diversity. Although our broadscale analysis does not establish causality in the direction of these relationships, it does highlight the inextricable link between demographic trait diversity and ecosystem productivity across forest biomes.

The established association between demographic trait diversity and ecosystem productivity is in line with emergent patterns derived from tropical forest plots, which found that the demographic composition of forests was predictive of empirically derived measures of aboveground carbon dynamics (52). Similarly, our findings match theoretical expectations that the pace of life of organisms within a community (e.g., life expectancy and generation time) should strongly regulate the relationship between carbon turnover (ecosystem fluxes) and carbon retention (ecosystem pools) (52). It is important to note that the association between demographic trait diversity and ecosystem productivity was derived from multiyear averages in remotely sensed NPP from 1997 to 2013 and from mean estimates of tree growth-longevity-stature relationships that were based on the current distribution of species (i.e., derived from dynamical data collected from the 1900s to 2000s). This approach did not allow us to account for potential biogeographic biases in the effects of human disturbance on species diversity (i.e., between boreal and tropical forests). Yet, by quantifying the current distribution of demographic functional types across broadscale resource gradients, our results provide a powerful backdrop for parameterizing next-generation vegetation models to simulate forest carbon turnover rates across a range of current and future conditions.

More generally, our analysis offers strong empirical support for the expectation of high demographic trait diversity in tropical forests as compared with temperate and boreal forests. This multi-biome finding supports the community assembly theory of strong abiotic filtering in boreal regions, which results in a restricted species pool of predominantly slow-growing, long-lived species (Fig. 1C, H3). This emergent pattern is congruent with known variability in physiological leaf trait characteristics across biogeographic gradients (43–45), with decreasing variation in leaf economic traits from lower

to higher latitudes (53). Similarly, our results match well-established species richness-productivity relationships across global forests (51, 54) and community structure-productivity relationships (55). Yet, although it makes intuitive sense that the demographic diversity of forest communities follows well-established patterns in species richness (49, 50), our findings establish a more direct link to the demographic mechanisms that generate global variation in ecosystem carbon turnover.

Conclusions

Our broadscale analysis reveals the remarkable diversity of life history strategies that exist for tree species across the Americas. Weak trade-offs between tree growth, longevity, and stature across biogeographic gradients demonstrate the modular and flexible nature of trees, highlighting the diversity of evolutionary trajectories that have arisen to address the ecological puzzle of survival. In addition, from a functional perspective, we found that although acquisitive trees sequester carbon at faster rates, they also generally appear constrained to smaller maximum sizes and shorter life spans that translate to lower carbon storage and faster carbon turnover. More importantly, we found that more demographically diverse forests tend to be more productive at the ecosystem scale across the tropics and extratropics. These findings have important implications for informing global restoration and conservation efforts and for understanding the fundamental feedback between biodiversity and climate change mitigation.

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ACKNOWLEDGMENTS

We thank the international team of network collaborators, including those who are not coauthors on this paper, for sharing their valuable plot datasets and providing their insights and support for this project. This study was enabled by the Global Forest Dynamics database, initiated by the TreeAct project, on which this study is based. The tropical tree analysis was enabled by the ForestPlots.net research project on 169 ("Placing life history trait variation of forest trees in an evolutionary and environmental context"). ForestPlots.net is a global collaboration and meta-network supported from the University of Leeds (UK, UK). **Funding:** T.A.M.P., A.E.M., and G.L.P. acknowledge support from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant agreement 758873, TreeMati), A.E.M. was further funded by the Royal Society Grants (grant RS/R011621/1 "Angiosperms: the ORR/7860 treeShapes, NE/V001946/1 "MEMBRA: the NERC/NSF Giants NE/V003942/1 and the FRB/CESAB "Synthesis", O.L.P. and ForestPlots.net data management have been supported by several grants, including from the UK Natural Environment Research Council (AMN/IN/18/015434/1 "DECID", NE/V011720/1 "TRIO-RED", NE/V010243/1 "LEAF", AMN/15/01551/1), as well as from the European Research Council, the European Space Agency, the European Union, and the Royal Society. ForestPlots.net partners acknowledge many additional sources of funding: Instituto Nacional de Desenvolvimento Tecnológico (INCT) grant 465613/2014-5, FAPESP grant 2018/057000/03, the Brazilian National Council for Scientific and Technological Development (CNPq) (PRD/CNPq grant 40370/2012-0 and CNPq/Universal grant 459941/2014-0), the British Natural Environment Research Council/NERC (G17/K016431/1) and FAPESP (BR/FA grants 2003/02985-7, 2012/0509-E and 2013/0370-5), doctoral and postdoctoral fellowships from FAPESP (FAPESP 11/11904-0 and 22/09041-0) (Pre-doctoral), landscapes (US) Forest Service, USAID, EMBRAPA, and NACA-Godard; CNPq (PRD-TRAN 441244/2016-5 and 44572/2019-0), Mato Grosso State Research Support Foundation (FAPEMAT) (grant 034633/2020), the NERC Knowledge Exchange Partnership grant NE/V018760/2), NERC Amazon Past Fire Project (NE/V01197/0-1), CAPES Project (PVE177/2017), CNPq grants 442627/2016-4, 403764/2016-2, and 518024-2/2012 for the 46 A LTER plots, FAPESP grants 16/09208, 465/2010 and PPT/08 547/2015, and CNPq grant: 4/0306/2009-6 and 408320/2019-0, which funded the monitoring of Pampa-Medera initiative. The BCI forest dynamics research project was made possible by NERC grants to S. P. Hubbell (DEB-0640386, DEB-0442663), DEB-0746498, DEB-0109474, DEB-0075301, DEB-9909347, DEB-0545226, DEB-0615276, DEB-9405933, DEB-4211031, DEB-9901058, DEB-8496659, DEB-8605042, DEB-8204992, and DEB-7822891, through support from the Forest Global Earth Observatory (ForestGEO), the Smithsonian Tropical Research Institute, the John D. and Catherine T. MacArthur Foundation, the Moore Foundation, the Small World Institute Fund, and numerous

private individuals, and through the hard work of over 100 people from 10 countries over the past three decades. Research at the Waikona Forest Dynamics Plot was supported by the 1923 Fund, the Giffen Center for Biodiversity at the University of Wisconsin-Green Bay, and the US Forest Service. The Lugulo ForestGEO dataset was supported by grants BSR-8203902, DEB-9411673, DEB-0030538, DEB-0219034, DEB-0620930, DEB-0963047, and DEB-102966 from NSF, to the Department of Environmental Science, University of Puerto Rico, and to the Interdepartmental Institute of Tropical Forestry, USDA Forest Service, as part of the Lugulo Long-Term Ecological Research Program. The US Forest Service (Department of Agriculture) and the University of Puerto Rico gave additional support. The BCI, Lugulo, and Waikona plots were part of the Smithsonian Institution Forest Global Earth Observatory, a worldwide network of large, long-term forest dynamics plots. T.A.M.P. and P.A. acknowledge funding from the CLM4 FOREST Horizon Europe Project (no. 101051835) that was funded by the European Union. G.D. acknowledges support from an "Investissement d'Avenir" grant managed by Agence Nationale de la Recherche (ANR-18-LABX-0011). **Author contributions:** L.E.M. led the writing of the manuscript, with substantial input from T.W.C., R.M.M., A.E.M., J.L.P., P.A.Z., and T.A.M.P. L.E.M. led the analyses, with input from R.M.M. and P.A.Z. A.E.M., T.A.M.P., G.L.P., J.A., K.M.B. and L.E.M. assembled and integrated the tree dynamics database with contributions from other ForestPlots.net and TreeMati network partners. All authors collected and curated data from inventory plots, provided feedback on the results, and contributed to the writing of the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** The published plot data and R code that we needed to replicate our analyses are available at <https://github.com/LuisZuidema/forest> and Zenodo (56). The tree-by-tree observations used to generate the plot-level input data are also published with this paper. However, this file does not include data from networks with sensitive species or a need for indigenous data sovereignty. These data are available upon request for the research purposes by emailing the following networks: Alberta Agriculture and Forestry Division <https://www.alberta.ca/permanent-sample-plots-program.cfm>; at-fm-limpicetrees@agv.gov.br; Saskatchewan Minister of Environment Forest Service Division <https://www.saskatchewan.ca/contributors/forestry>; <https://forestplots.usda.gov/explorer-data> (20-22); and ForestPlots.net <https://forestplots.net/en/using-forestplots/in-the-field>; admin@forestplots.net (26-39). **License information:** Copyright © 2024 the authors, some rights reserved, exclusive license Amazon Association for the Advancement of Science. No claim to original US government work. <https://www.science.org/about/science-licenses-publisher-services>

SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S19
Tables S1 to S7
References (57-68)
Submitted 28 October 2023; accepted 28 August 2024
10.1126/science.adp6166

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Anexo 11. Artículo de investigación.

Brazilian Journal of Botany
<https://doi.org/10.1007/s40415-024-01034-7>

SYSTEMATICS & PHYLOGENY - ORIGINAL ARTICLE



Assembling the Brazilian flora: overview of Leguminosae diversity

The Brazil Flora Group – Leguminosae (Recommended citation: BFG - Leguminosae)

Marli Pires Morim¹ · Fabiana Luiza Ranzato Filardi¹ · Ângela Lúcia Bagnatori Sartori² ·
Marcelo Fragomeni Simon² · João Ricardo Vieira Iganci⁴ · Gwilym P. Lewis⁵ · Haroldo Cavalcante de Lima¹ ·
Eimear Nic Lughadha⁵ · Moabe Ferreira Fernandes^{5,6} · Luciano Paganucci de Queiroz⁷ · Domingos Cardoso¹

Received: 3 February 2024 / Revised: 11 July 2024 / Accepted: 12 July 2024
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For the complete list of authors and institutions, see Appendix S1

With contributions by: Lorena Lana Camelo Antunes, Ariane Raquel Barbosa, Kamilla Lopes Barreto, Thamires Layra Alves de Barros, Luisa Maria de Paula Alves Bezerra, Leonardo Maurici Borges, Roseli Lopes da Costa Bortoluzzi, Elisa Silva Cândido, Leandro Jorge Telles Cardoso, Catarina Silva de Carvalho, Dariane do Amaral Sobreiro de Carvalho, Isabella Cristina de Castro-e-Silva, Aline Pitof Chagas, Adilva de Souza Conceição, Jorge Antonio Silva Costa, Matheus Martins Teixeira Cota, Alfonso Delgado-Salinas, Valquíria Ferreira Dutra, Marcus Jose de Azevedo Falcão Junior, Eduardo Pinheiro Fernandez, Emanuel Messias Pereira Fernando, Gláucia Crispim Ferreira, Andréia Silva Flores, Ana Paula Fortuna-Perez, Paulo Henrique Gaem, Idelme Gagnon, Flávia Cristina Pinto Garcia, Danilo Soares Gissi, Bernarda de Souza Gregorio, Ethiene Guerra, Ely Simone Cajueiro Gurgel, Paulina Hechenbäumer, Mike Hopkins, Isau Huamantupa-Chuquimaco, Lucas Sa Barreto Jordão, Valner Matheus Milanezi Jordão, Bentie B. Klitgaard, Juliana Rodrigues Kuntz, Alexandre Gribau de Lima, Laura Cristina Pires Lima, Talita Antunes Maia, Vidal de Freitas Mansano, Mikena Ventruchi Martins, Cibene Mara Jordão de Mattos, Jose Eduardo Meireles, Rosa Briggithte Melchor-Castro, Caio Vinicius Vivas Damasceno Melo, Antonio de Lima Mesquita, Silvia Teresinha Sloggia Miotto, Thiago Cobra e Monteiro, Paloma G.P. Moore, Matias Moraes, Tania Maria de Moura, Janaina Gelma Alves do Nascimento, Filipe Gomes Oliveira, Ana Carla da Silva Oliveira, Gustavo Ramos de Oliveira, Lorena Conceição Oliveira, Letícia das Graças Rosignoli de Oliveira, Marcia Carla Ribeiro de Oliveira, Juliana de Paula-Souza, Richard Toby Pennington, Rafael Barbosa Pinto, Rubens Teixeira de Queiroz, Juliana Gastaldello Rando, Osmar dos Santos Ribes, Carolina de Lima Ribeiro, Petala Gomes Ribeiro, Rodrigo Schütz Rodrigues, Marcos Vinicius Varjão Romão, Daniela Sampaio, Jessica Cauana de Oliveira Santana, Felipe da Silva Santos, Wallace Messias Barbosa São-Mateus, Viviane Renata Scalon, Najla Mara Bastos Scherzberger, Ethiene Priscila Seleme, Marcos Jose da Silva, Francismeire Bonadeu da Silva, Guilherme Sousa da Silva, Juliana Santos Silva, Tatiane Santana Silva, Wanderson Luis da Silva-e-Silva, Fernanda Schmidt Silveira, Cristiane Snak, Marcos Vinicius Batista Soares, Elvia Rodrigues de Souza, Vinicius Castro Souza, Rodrigo Duno de Stefano, Vanessa Terra, Lorena Ruiz Tierno, Benjamin M. Torke, Ana Maria Goulart de Azevedo Tozzi, Angela Maria Studart da Fonseca Vaz, Michael A. Vincent, Debora Christina Zuanny.

Extended author information available on the last page of the article

Published online: 14 November 2024

Springer



Abstract

Over the last two centuries, since the treatment of Leguminosae in *Flora Brasiliensis*, many new legume species and genera have been described, adding to the accumulated body of knowledge on species' circumscriptions and distribution, published in monographs, taxonomic revisions and regional floristic treatments of specific Brazilian phytogeographic domains. The *Flora do Brasil 2020* project was a collaborative effort conducted between 2008 and 2020 to meet the targets set by the Global Strategy for Plant Conservation, an initiative of the Convention on Biological Diversity. The project aimed to inventory and revise the taxonomy of all plant species in Brazil, including Leguminosae. The monograph of the legume family was carried out by a team of 102 taxonomists (10% of the project's total), who worked towards updating and verifying the taxonomy of these plants in an online platform. Information on the life forms, substrate, endemism level, and geographical distribution for all accepted taxa were provided, alongside morphological descriptions, identification keys, images of herbarium specimens and field photographs. In this work, we have extracted from the *Flora do Brasil 2020* project the legume data consolidated on December 31st, 2020 to provide an overview of the species diversity of Leguminosae in Brazil and its distribution across phytogeographic domains. The results revealed that the family is represented by 220 genera, of which 19 are endemic, and a total of 2901 species (1576 endemic). After fully monographing 210 genera (95%), we showcased Leguminosae as the most diverse family in the country, representing 6% of the total vascular plant species documented in the *Flora do Brasil 2020*. The species are found in all phytogeographic domains, exhibiting a wide range of life forms. The *Mata Atlântica* and *Caatinga* domains together contain the largest number of endemic legume genera in Brazil, most of them monospecific. A discussion on the conservation status of the Brazilian legume species is also provided. Knowledge of the Brazilian flora is continuously advancing, particularly with regards to Leguminosae, demanding regular taxonomic and nomenclatural updates. Current collaborations have greatly improved our understanding of legume diversity and distribution, providing evidence to inform conservation prioritization and action for the Leguminosae in Brazil's megadiverse flora.

Keywords Biodiversity · Conservation · Fabaceae · Historical background · Taxonomy

1 Introduction

The Leguminosae (or Fabaceae), encompassing 22,450 accepted species and nearly 800 genera (Legume Data Portal 2023), is among the most species-rich and ecologically and economically important families of flowering plants. Within the Americas, it ranks as the third most diverse family, with almost 7500 species (Ulloa Ulloa et al. 2017), being the most diverse in Brazil (Ulloa Ulloa et al. 2017; BFG 2022), and the second richest in Mexico, the Guianas, North America, and Venezuela (Ulloa Ulloa et al. 2017). Beyond its sheer species diversity, the family has significant economic importance, with numerous species serving crucial roles in areas such as food production, forage, timber, medicine and as ornamentals. Legume species are found throughout the World, with the exception of Antarctica, and are often dominant taxa in many different environments and major biomes, spanning the succulent, grass, rainforest, and temperate biomes (Schrire et al. 2005; LPWG 2017). The symbiosis of legumes with nodule-forming nitrogen-fixing bacteria plays an important role in sustaining essential ecosystem functions (Sprent 2009). These remarkable characteristics led Leguminosae to be the first target group for global evaluation of plant diversity and conservation (Yahara et al. 2013).

Leguminosae is acknowledged to be among the most morphologically and evolutionarily distinctive plant families (Magallón et al. 2019). Following its original description in 1789 by Jussieu (1789: 345), Leguminosae was for almost two

centuries treated as comprising three subfamilies: Caesalpinioideae, Mimosoideae, and Papilionoideae, although with many modifications in the circumscription of the constituent tribes and genera (Polhill and Raven 1981; Lewis et al. 2005). Over the past three decades, a series of phylogenetic analyses, notably one based on plastid *matK* gene sequences (LPWG 2017), have reshaped our understanding of Leguminosae classification (LPWG 2017). The Leguminosae has long been robustly supported as a monophyletic family and is presently recognized as encompassing six subfamilies: Cercidoideae, Detarioideae, Duparquetioideae, Dialioideae, Caesalpinioideae, and Papilionoideae (LPWG 2017). The traditional subfamily Mimosoideae has been redefined as the tribe Mimosae within a recircumscribed subfamily Caesalpinioideae (LPWG 2017; Bruneau et al. 2024). This revised phylogeny-based classification reflects a refined understanding of the evolutionary relationships within the Leguminosae, which has been largely confirmed by subsequent densely-sampled taxonomically broad phylogenomic analyses of nuclear and plastid genomes (Koenen et al. 2020; Zhang et al. 2020; Zhao et al. 2021; Ringelberg et al. 2022).

Historical background on the systematics of Brazilian legumes – Numerous taxonomic treatments and Flora accounts of the Leguminosae have been continuously published at all taxonomic levels within the family. Those studies are essential for understanding the diversity and distribution of species and, consequently, are essential baseline data for conservation strategies, sustainable use, and ecological restoration (BFG 2022).



to the workflow adopted for the management of this process are available in Martins et al. (2018).

The occurrence data of species for extinction risk assessment were compiled from herbarium collections available on online platforms (Virtual Herbarium REFLORA, <https://reflora.jbrj.gov.br/reflora/herbarioVirtual>; JABOT, <http://jabot.jbrj.gov.br/v3>; speciesLink, <https://specieslink.net>; GBIF, <https://www.gbif.org>). The occurrence data were georeferenced utilizing information from the specimen's herbarium labels at the georeferencing stage of record compilation. Subsequently, the data underwent validation by a legume taxonomist, followed by the preparation of species sheets, supplementary analyses, and extinction risk assessments conducted by trained Red List evaluators. All these stages constitute the process of assessing the conservation status of any plant species carried out by CNCFIora/JBRJ.

To better understand the conservation status of the family, data on native Leguminosae species were obtained for each of the phytogeographic domains according to *Flora do Brasil 2020* and compared with data from the Official List of Threatened Species of the Brazilian Flora 2022. The quantity and percentage of species assessed for each domain were determined, considering that some species occur in one or more domains. The sum of all species per domain does not represent the total number of legume species assessed, as species may repeat across domains.

Using spatial vector point data of threatened species occurrences (CR, EN, and VU) and Data Deficient (DD), a Kernel Density Estimation analysis (Parzen 1962) was conducted. Kernel maps are useful in spatial analysis, allowing visualization of areas with higher density of a specific point phenomenon based on its distribution in space. The analysis considers a circular neighborhood around each sample point, corresponding to the radius of influence, applying a mathematical function to find neighboring and overlapping points (Silverman 1986). Thus, with the density maps classified into eight quantile classes, it was possible to determine regions of higher concentration or absence of legume species occurrence reports by extinction risk category distributed across the Brazilian territory.

3 Results

The treatment of the Leguminosae in the *Flora do Brasil 2020* revealed that the family is represented in the country by 220 genera, of which 19 are endemic to Brazil, and 2901 species (1576 endemic to Brazil). Except for the monospecific West African subfamily Duparquetioideae, all the other five subfamilies under the most recent phylogeny-based Leguminosae classification (LPWG 2017) are represented in the Brazilian Flora (Fig. 1):

Caesalpinioideae, including the tribe Mimoseae (1354 species), Papilionoideae (1267), Detarioideae (172), Ceridoideae (96), and Dialioideae (12).

The majority of Brazilian legume species are terrestrial, with only a few species in the genera *Aeschynomene*, *Arachis*, *Mimosa*, *Neptunia*, and *Sesbania* growing in freshwater aquatic habitats, or in both terrestrial and aquatic environments. They exhibit a wide range of life forms, ranging from giant emergent forest trees (e.g., *Dinizia excelsa* Ducke in *Amazônia*), and robust canopy lianas, to shrubs, subshrubs, annual or perennial (erect, prostrate or decumbent) herbs, and herbaceous or semi-woody vines, with or without tendrils. Many legume species display plasticity in their life form, changing from vines or lianas to shrubs or small trees, especially in the early stages of their life cycle, as occurs in some species of *Dalbergia*, *Machaerium*, *Schnella*, and *Senegalia*.

The ten most speciose legume genera in Brazil are *Mimosa* (374 species; 73% endemic), *Chamaecrista* (268; 83%), *Inga* (134; 39%), *Swartzia* (112; 56%), *Senna* (80; 38%), *Calliandra* (74; 80%), *Machaerium* (74; 60%), *Arachis* (65; 74%), *Bauhinia* (62; 65%), and *Tachigali* (60; 43%), which together comprise 45% of the total species diversity of Brazilian legumes (Table 1; Fig. 1). Among the 220 legume genera that occur in the Brazilian flora, it is noteworthy that 19 are endemic and together comprise only 36 species (Table 2). The Brazilian endemic genus *Moldenhawera* has the greatest number of species (12), and also inhabits several phytogeographic domains (Table 2). Among the Brazilian endemic legume genera, the *Mata Atlântica* and *Caatinga* phytogeographic domains together contain the largest number of endemic genera, most of them monospecific and with a geographically restricted distribution. In contrast, *Melanoxylum*, despite being a monospecific genus, comprising only *M. brauna* Schott, commonly known as "brauna" and other derivative vernacular names, has a broad distribution across phytogeographic domains in several Brazilian states of the Northeast and Southeast regions.

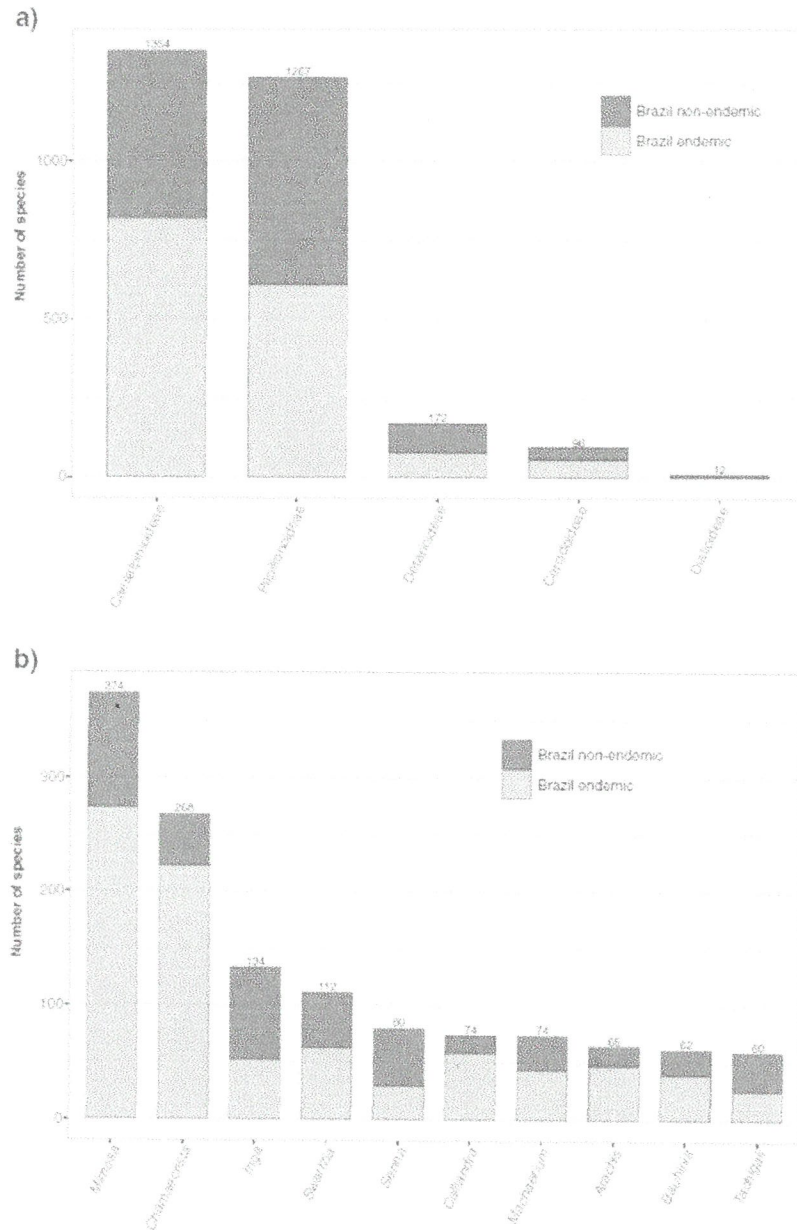
Leguminosae species are present in virtually all vegetation types across the major phytogeographic domains in Brazil, where many are endemic or narrowly restricted (Tables 2, 3, 4; Figs. 2, 3, 4, 5, 6, 7, 8; Appendix S2). The *Cerrado* phytogeographic domain is home to the largest number of legume species (1297 species; 524 [40%] endemic, in 134 genera), followed by *Amazônia* (1165 species; 219 [19%] endemic, in 152 genera), *Mata Atlântica* (1006 species; 348 [35%] endemic, in 149 genera), *Caatinga* (639 species; 158 [25%] endemic, in 129 genera), *Pampa* (245 species; 12 [5%] endemic, in 67 genera), and *Pantanal* (192 species; 10 [5%] endemic, in 73 genera).

Leguminosae species are found in all Brazilian geopolitical regions and the family has the greatest number of



Assembling the Brazilian flora: overview of Leguminosae diversity

Fig. 1 Species richness and endemism of Brazilian Leguminosae across subfamilies (a) and the ten most speciose genera (b)



species concentrated in the North (1246 species, of which 353 endemic), followed by the Southeast (1169/685), Northeast (1098/605), Central-Western (1094/472), and South (583/183).

Since the greatest peak of species description of Leguminosae in Brazil during the period of publication of *Flora Brasiliensis*, new species accumulation has continued (Fig. 9a). Indeed, our search for IPNI records of new species published 2010–2020 inclusive and based on type



Assembling the Brazilian flora: overview of Leguminosae diversity



Fig. 3 Representatives of native genera of Brazilian Leguminosae in the *Amazonia* phylogeographic domain: *Aldina latifolia* (a), *Monoptera uauacu* (b), *Androcallyma glabrifolium* (c), *Heterostemon mimosoides* (d), *Petaladenium urecoliferum* (e), and *Uleanthus erythrinoides* (f). Photos by Domingos Cardoso (a, b, d-f) and Marcus Falcão (c)

genera, such as *Adesmia* (Fig. 7a), *Lupinus* (Fig. 7f), and *Mimosa* (Fig. 7e), have many species in the *Pampa*, which are mostly shared with the high-altitude grasslands of the *Mata Atlántica*, some of them even reaching the open vegetation of the *Cerrado*. *Arachis burkartii* Handro (Fig. 7b), *Pomaria rubicunda* (Vogel) B.B.Simpson & G.P.Lewis (Fig. 7c), and *Indigofera asperifolia* Bong. ex Benth. (Fig. 7d) are other examples of species that, in addition to the *Pampa*, also occur in other domains, predominantly in the *Cerrado* and *Mata Atlántica*. Given the continuity and the subtropical climate of the *Pampa*, species of legumes, such as *Senna nama* (Benth.) H.S.Irwin & Barneby (Fig. 7h), grow in vegetation more like that encountered in Uruguay and Argentina than in other Brazilian phytogeographic domains.

Pantanal. More recent checklists assembled from newly collected specimens and taxonomic accounts of local floras (Pott and Pott 2021a; Sartori et al. 2021) have reported more than 300 species and 105 genera of legumes to the entire *Pantanal* region across Brazil, Bolivia, and Paraguay. The numbers presented here for just the Brazilian *Pantanal* phytogeographic domain (192 species) provides evidence that

Brazil is home to more than 60% of the total legume species reported from this domain.

The most speciose genera in the Brazilian *Pantanal* are *Mimosa*, *Arachis*, *Senna*, *Desmodium*, and *Bauhinia*, together representing around 32% of the legume species in the region. Arboreal and shrubby legumes are common in the domain, c. 50%, and generally occur in association with riparian forests; these include *Albizia inundata* (Mart.) Barneby & J.W.Grimes, *Inga vera* Willd., *Inga disticha* Benth., *Libidibia paraguariensis* (D.Parodi) G.P.Lewis (Fig. 8F), and *Zygia pithecolobioides* (Kuntze) Barneby & J.W.Grimes. Species such as *Peltogyne confertiflora* (Mart. ex Hayne) Benth., *Guibourtia chodatiana* Hassl., and *Cenostigma marginatum* (Tul.) Gagnon & G.P.Lewis occur in seasonal forests, the latter being restricted to the *Pantanal*. Herbaceous and subshrubby species account for almost 35% of the legume species richness in the *Pantanal*. Some of the herbaceous species are endemic, such as *Arachis appressipila* Krapov. & W.C.Greg., *A. hoehnei* Krapov. & W.C.Greg., *A. linearifolia* Valls. Krapov. & C.E.Simpson, *A. valida* Krapov. & W.C.Greg., *A. vallsii* Krapov. & W.C.Greg., *Galactia benthamiana* Micheli, and *Dolichopsis paraguariensis* (Benth.) Hassl. Subshrubby

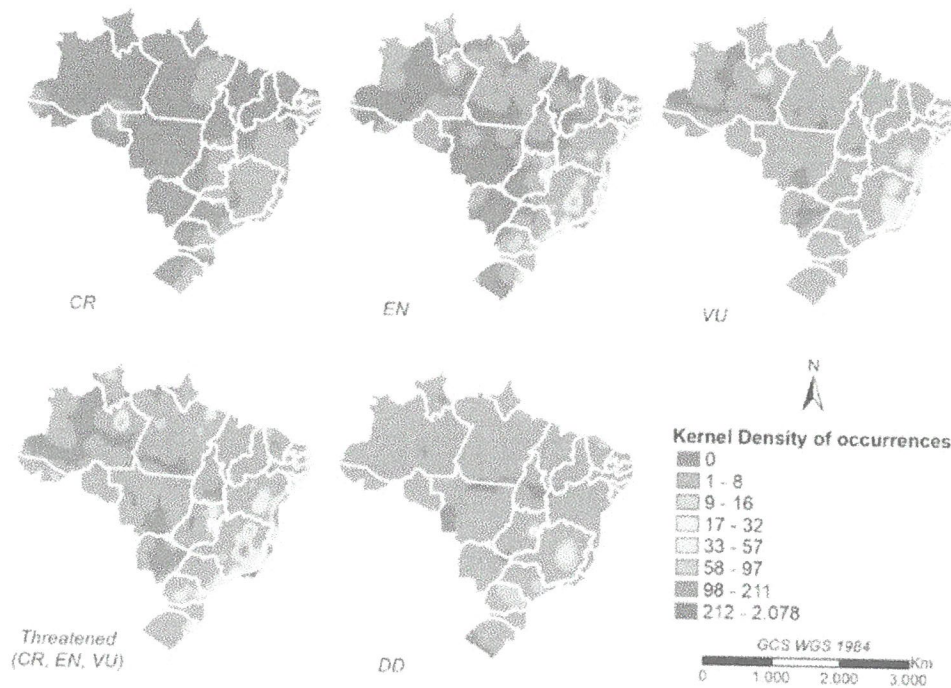


Fig. 10 Kernel density map showing the spatial distribution of the conservation status of Brazilian legume species which were assessed as threatened (233 species) or Data Deficient (125) applying the categories and criteria of the IUCN Red List of Threatened species (CR, critically endangered; EN, endangered; VU, vulnerable; and DD, data deficient)



Assembling the Brazilian flora: overview of Leguminosae diversity

2020) and Brazil, as a megadiverse country, needs to combat this crisis. The greatest challenge ahead is to halt the accelerated degradation of Brazil's biomes. We can present many reasons, and much scientific evidence, in favor of conserving Brazil's biodiversity, but one fact alone should be enough to motivate everyone to take up this cause: "Without plants, there is no life" (Global Strategy for Plant Conservation, GSPC).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s40415-024-01034-7>.

Acknowledgements We express our gratitude to the Rio de Janeiro Botanical Garden and Dra. Rafaela Forzza for coordinating the "Flora do Brasil" project since 2008 so successfully; to the herbarium curators for ensuring the maintenance of collections; to botanists for their collections deposited in herbaria; to parataxonomists who guide botanists on scientific expeditions; and two anonymous reviewers for the detailed corrections and suggestions on the manuscript. We also thanks to Jonathan Krieger for assistance with International Plant Name Index (IPNI) data. The project has been sustained with resources invested by the National Council for Scientific and Technological Development (CNPq), the Carlos Chagas Foundation for Research Support of the State of Rio de Janeiro (FAPERJ), and the Ministry of Science and Technology, responsible for the Brazilian Biodiversity Information System (SiBBri). DC's research in legume systematics is also supported by grants from CNPq (Research Productivity Fellowship, Grant No. 314187/2021-9; and Edital Universal Grant No. 422325/2018-0), and Carlos Chagas Foundation for Research Support of the State of Rio de Janeiro (FAPERJ; Programa Jovem Cientista do Nosso Estado—2022, Grant No. 200.153/2023). JRVF's research is supported by CNPq Research Productivity Fellowship (Grant No. 311847/2021-8).

Author contributions MPM, FLRF, ALBS, MFS, JRVF, GPL, HCL, ENL, MFF, LPO, EPF, LSBJ, and DC contributed to the study conception, compiled, organized, analyzed data and the writing of the article. DC, EPF, and FLRF produced tables and figures. All 94 national and international collaborators generated and reviewed Leguminosae data from original research on the *Flora do Brasil* 2020 project.

Data availability All data used in this study is available in the Supplementary Information. Weekly updated version of the Brazilian legumes can be publicly accessed at Flora e Funga do Brasil platform at <https://www.floradobrasil.jbrj.gov.br/consulta/> and also in Darwin Core Archive format through the Rio de Janeiro Botanical Garden (JBRJ) biodiversity repository at https://www.ipt.jbrj.gov.br/jbrj/resource?lista_especies_flora_brasil

Declarations

Conflict of Interest Luciano Paganucci Queiroz is Guest Editor of the Brazilian Journal of Botany, and we assure this article was entirely handled by an Associate Editor. The authors declare that there are no other competing interests.

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Anexo 12. Tesis sustentada de la bachiller Nicole Vasquez.



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS

Decanatura de la Facultad de Ingeniería

"Año del Bicentenario, de la Consolidación de Nuestra Independencia y de la Conmemoración de las Heroicas Batallas de Junín y Ayacucho"

"Madre de Dios capital de la biodiversidad del Perú"

RESOLUCIÓN DE DECANATURA DE LA FACULTAD DE INGENIERÍA N° 623-2024-UNAMAD-DFI

Puerto Maldonado, 19 de diciembre de 2024.

VISTO:

El Expediente N° 4429, de fecha 19 de diciembre de 2024; Carta N° 052-2024-UNAMAD-IFMA-PAZP, de fecha 19 de diciembre de 2024; Informe N° 028-2024-DIFMA-IF-PAZP, de fecha 17 de diciembre de 2024; Estatuto y Reglamento General de Grados y Títulos V 3.0 de la Universidad Nacional Amazónica de Madre de Dios, y:

CONSIDERANDO:

Que, mediante Ley N° 27297, de fecha 05 de julio de 2000, se crea la Universidad Nacional Amazónica de Madre de Dios, autorizándose su funcionamiento definitivo, mediante Resolución N° 626-2009-CONAFU, de fecha 27 de noviembre del año 2009.

Que, mediante Resolución de Consejo Directivo N° 132-2019-SUNEDU/CD, de fecha 10 de octubre de 2019, la Universidad Nacional Amazónica de Madre de Dios, obtiene su Licenciamiento Institucional, por un periodo de 06 años.

Que, el Reglamento General de Grados y Títulos de la UNAMAD versión 3.0, aprobado por Resolución de Consejo Universitario N° 288-2022-UNAMAD-CU, de 31 de mayo de 2022, regula el procedimiento de conferir grados académicos y títulos profesionales.

Que, el Artículo 8° de la Ley N° 30220 – Ley Universitaria señala que "El Estado reconoce la autonomía universitaria. La autonomía inherente a las universidades se ejerce de conformidad con lo establecido en la Constitución, la presente Ley y demás normas aplicable. Esta autonomía se manifiesta en los siguientes regímenes: normativo, de gobierno, académico, administrativo y económico.

Que, el Reglamento General de Grados y Títulos de la UNAMAD aprobado por Resolución de Consejo Universitario N° 288-2022-UNAMAD-CU de fecha 31 de mayo del 2022, regula el procedimiento de conferir grados académicos y títulos profesionales, y en su Artículo 95° establece la sustentación de la tesis no podrá exceder los cuarenta (40) minutos. En caso de ser dos los postulantes, el tiempo de sustentación no excederá de sesenta (60) minutos y se sorteará cual de los bachilleres inicia la sustentación.

Que, el Artículo 96° del mismo reglamento, establece el Jurado Revisor de la sustentación de tesis es el mismo que revisó el proyecto de tesis y estará integrado por un presidente (el docente de mayor prelación), un vocal y un secretario (el de menor prelación). Los miembros del Jurado Revisor deberán estar presentes a la hora fijada de la sustentación, vestidos con traje formal que el caso requiere.

Que, mediante Resolución de Decanatura N° 302-2023-UNAMAD-DFI, de fecha 13 de setiembre de 2023, se **CONFIRMA**, la Comisión Revisora Ad Hoc del Proyecto de Tesis titulado "ETNOBOTANICA CUANTITATIVA DE LA FLORA ARBÓREA DEL BOSQUE AMAZONICO DEL FUNDO EL BOSQUE – UNAMAD, LAS PIEDRAS, TAMBOPATA", presentado por la Bachiller Srta. Nicole Eliane Vásquez Bravo de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente de la Universidad Nacional Amazónica de Madre de Dios, la misma que estará integrada por los docentes: M.Sc. Telesforo Vasquez Zavaleta **Presidente**, M.Sc. Jorge Santiago Garate Quispe **Secretario**, Dr. Victor Pareja Auquipata **Vocal**, Dr. Roger Oswaldo Poccohuanca Aguilar **Accesorio**.

Que, mediante Resolución de Decanatura N° 438-2024-UNAMAD-DFI, de fecha 16 de octubre de 2024, se **APRUEBA**, el Proyecto de Tesis titulado "ETNOBOTANICA CUANTITATIVA DE LA FLORA ARBÓREA DEL BOSQUE AMAZONICO DEL FUNDO EL BOSQUE – UNAMAD, LAS PIEDRAS, TAMBOPATA", presentado por la Bachiller Srta. Nicole Eliane Vásquez Bravo de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente de la Universidad Nacional Amazónica de Madre de Dios.

Que, mediante Resolución de Decanatura de la Facultad de Ingeniería N° 647-2024-UNAMAD-DFI, de fecha 27 de noviembre de 2024, se **CONFIRMA**, el Jurado Evaluador para la emisión del dictamen del Informe Final de Tesis titulado "Etnobotánica cuantitativa de la flora arbórea del bosque Amazónico del fundo El bosque – UNAMAD, Las Piedras, Tambopata", presentado por la Bachiller Srta. Nicole Eliane Vásquez Bravo de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente de la Universidad Nacional Amazónica de Madre de Dios, la misma que estará integrada por los siguientes docentes: Dr. Percy Amílcar Zevallos Polliffo **Presidente**, M.Sc. Jorge Santiago Garate Quispe **Secretario**, Dr. Victor Pareja Auquipata **Vocal**, Dr. Roger Oswaldo Poccohuanca Aguilar **Accesorio**.

Que, mediante Informe N° 028-2024-DIFMA-IF-PAZP, de fecha 17 de diciembre de 2024 el Jurado Revisor remite al Decano de la Facultad de Ingeniería, la aprobación por unanimidad del Informe Final de Tesis titulado "Etnobotánica cuantitativa de la flora arbórea del bosque Amazónico del fundo El bosque – UNAMAD, Las Piedras,

UNAMAD: "Parque Científico Sostenible con Investigación e Innovación"



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS

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**RESOLUCIÓN DE DECANATURA DE LA FACULTAD DE INGENIERÍA N° 623-2024-
UNAMAD-DFI**

Puerto Maldonado, 19 de diciembre de 2024.

Tambopata", presentado por la Bachiller Srta. Nicole Eliane Vásquez Bravo, de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente, para su sustentación, asimismo, informa la fecha, hora y lugar de sustentación de tesis, para el día **lunes 23 de diciembre de 2024**, a las 08:00 horas, en la sala de grados de la Facultad de Ingeniería.

Que, mediante Expediente N° 4429, de fecha 19 de diciembre de 2024, el Decano de la Facultad de Ingeniería de la UNAMAD, autoriza al Secretario Académico de la Facultad de Ingeniería, proyectar la resolución de aprobación del informe final de tesis y establecer fecha, hora y lugar del acto académico de sustentación de Tesis del informe final de tesis titulado "Etnobotánica cuantitativa de la flora arborea del bosque Amazónico del fundo El bosque – UNAMAD, Las Piedras, Tambopata", presentado por la Bachiller Srta. Nicole Eliane Vásquez Bravo, de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente.

Estando dentro de las atribuciones conferidas al Decano, por la Ley Universitaria N° 30220; el Estatuto de la Universidad Nacional Amazónica de Madre de Dios y en uso de las atribuciones conferidas mediante Resolución de Comité Electoral Universitario N° 010-2023-UNAMAD-CEU, de fecha 29 de diciembre del 2023.

SE RESUELVE:

ARTÍCULO PRIMERO: APROBAR, el Informe Final de Tesis titulado "Etnobotánica cuantitativa de la flora arborea del bosque Amazónico del fundo El bosque – UNAMAD, Las Piedras, Tambopata", presentado por la Bachiller Srta. Nicole Eliane Vásquez Bravo, de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente de la Universidad Nacional Amazónica de Madre de Dios.

ARTÍCULO SEGUNDO: CONVOCAR, a los miembros del Jurado Revisor para el Acto Académico de Sustentación de la Tesis titulado "Etnobotánica cuantitativa de la flora arborea del bosque Amazónico del fundo El bosque – UNAMAD, Las Piedras, Tambopata", presentado por la Bachiller Srta. Nicole Eliane Vásquez Bravo, de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente, integrado por los docentes:

- | | |
|---|-------------|
| • Dr. Percy Amílcar Zevallos Poilto | Presidente |
| • M.Sc. Jorge Santiago Garate Quispe | Secretario |
| • Dr. Victor Pareja Auquipata | Vocal |
| • Dr. Roger Oswaldo Pocconuanca Aguilar | Accesitario |

ARTÍCULO TERCERO: ESTABLECER, fecha, hora y lugar para el Acto Académico de Sustentación de Tesis, mencionada en el artículo primero de la parte resolutive, para el día **lunes 23 de diciembre del 2024** a las 08:00 horas, en la sala de grados de la Facultad de Ingeniería.

ARTÍCULO CUARTO: NOTIFICAR, la presente resolución a los miembros del Jurado Evaluador, para que se dé viabilidad a la presente sustentación de tesis de conformidad con lo regulado en el Reglamento de Grados y Títulos de la Universidad Nacional Amazónica de Madre de Dios y a su vez remita el Acta de Sustentación a la Decanatura de la Facultad de Ingeniería, para los tramites y fines pertinentes.

ARTÍCULO QUINTO: DISPONER, se notifique la presente resolución al Asesor del informe final de tesis Dr. Isau Huamantupa Chuquimaco, para conocimiento.

REGÍSTRESE, COMUNÍQUESE Y ARCHÍVESE.



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS
FACULTAD DE INGENIERÍA
Dr. Harold Quispe Flores
DECANO



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS
FACULTAD DE INGENIERÍA
Ing. Nelson Vique Meza Meza
SECRETARIO ACADÉMICO

CC:
Vicerrectoría
Presidencia
Rectorado
Vicerrectoría

UNAMAD: "Parque Científico Sostenible con Investigación e Innovación"



Anexo 13. Tesis sustentada de la bachiller María Cristina Noriega



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS

Decanatura de la Facultad de Ingeniería

"Año del Bicentenario, de la Consolidación de Nuestra Independencia y de la Conmemoración de las
Heroicas Batallas de Junín y Ayacucho"

"Madre de Dios capital de la biodiversidad del Perú"

**RESOLUCIÓN DE DECANATURA DE LA FACULTAD DE INGENIERÍA N° 610-2024-
UNAMAD-DFI**

Puerto Maldonado, 13 de diciembre de 2024.

VISTO:

El Expediente N° 4384, de fecha 13 de diciembre de 2024. Informe N° 045-2024-JPV, de fecha 13 de diciembre de 2024; Estatuto y Reglamento General de Grados y Títulos V 3.0 de la Universidad Nacional Amazónica de Madre de Dios, y;

CONSIDERANDO:

Que, mediante Ley N° 27297, de fecha 05 de julio de 2000, se crea la Universidad Nacional Amazónica de Madre de Dios; autorizándose su funcionamiento definitivo, mediante Resolución N° 626-2009-CONAFU, de fecha 27 de noviembre del año 2009.

Que, mediante Resolución de Consejo Directivo N° 132-2019-SUNEDU/CD, de fecha 10 de octubre de 2019, la Universidad Nacional Amazónica de Madre de Dios, obtiene su Licenciamiento Institucional, por un periodo de 06 años.

Que, el Reglamento General de Grados y Títulos de la UNAMAD versión 3.0, aprobado por Resolución de Consejo Universitario N° 288-2022-UNAMAD-CU, de 31 de mayo de 2022, regula el procedimiento de conferir grados académicos y títulos profesionales.

Que, el Artículo 8° de la Ley N° 30220 – Ley Universitaria señala que "El Estado reconoce la autonomía universitaria. La autonomía inherente a las universidades se ejerce de conformidad con lo establecido en la Constitución, la presente Ley y demás normas aplicable. Esta autonomía se manifiesta en los siguientes regímenes: normativo, de gobierno, académico, administrativo y económico.

Que, el Reglamento General de Grados y Títulos de la UNAMAD aprobado por Resolución de Consejo Universitario N° 288-2022-UNAMAD-CU de fecha 31 de mayo del 2022, regula el procedimiento de conferir grados académicos y títulos profesionales, y en su Artículo 95° establece la sustentación de la tesis no podrá exceder los cuarenta (40) minutos. En caso de ser dos los postulantes, el tiempo de sustentación no excederá de sesenta (60) minutos y se sorteará cual de los bachilleres inicia la sustentación.

Que, el Artículo 96° del mismo reglamento, establece el Jurado Revisor de la sustentación de tesis es el mismo que revisó el proyecto de tesis y estará integrado por un presidente (el docente de mayor prelación), un vocal y un secretario (el de menor prelación). Los miembros del Jurado Revisor deberán estar presentes a la hora fijada de la sustentación, vestidos con traje formal que el caso requiere.

Que, mediante Resolución de Decanatura N° 545-2023-UNAMAD-DFI, de fecha 06 de diciembre de 2023, se **CONFORMA**, la Comisión Revisora Ad Hoc del Proyecto de Tesis titulado "REGENERACION NATURAL DEL "TORNILLO" *Cedrelinga cateniformis* (Ducke) Ducke, EN EL BOSQUE DE TIERRA FIRME DEL FUNDO EL BOSQUE – UNAMAD, LAS PIEDRAS – MADRE DE DIOS", presentado por la bachiller Srta. María Crisithina Noriega Mamani de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente de la Universidad Nacional Amazónica de Madre de Dios, la misma que estará integrada por los docentes: Dr. Joel Peña Valdeiglesias-**Presidente**, M.Sc. Jorge Santiago Garate Quispe-**Secretario**, M.Sc. Mauro Vela Da Fonseca-**Vocal**, M.Sc. Jimmy Jeanine Miró Agurto-**Accesitario**.

Que, mediante Resolución de Decanatura de la Facultad de Ingeniería N° 176-2024-UNAMAD-DFI, de fecha 20 de mayo de 2024, se **APRUEBA**, el Proyecto de Tesis titulado "REGENERACION NATURAL DEL "TORNILLO" *Cedrelinga cateniformis* (Ducke) Ducke, EN EL BOSQUE DE TIERRA FIRME DEL FUNDO EL BOSQUE – UNAMAD, LAS PIEDRAS – MADRE DE DIOS", presentado por la bachiller Srta. María Crisithina Noriega Mamani de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente de la Universidad Nacional Amazónica de Madre de Dios.

Que, mediante Resolución de Decanatura de la Facultad de Ingeniería N° 560-2024-UNAMAD-DFI, de fecha 02 de diciembre de 2024, se **CONFORMA**, el Jurado Evaluador para la emisión del dictamen del Informe Final de Tesis titulado "Regeneración natural del "Tornillo" *Cedrelinga cateniformis* (Ducke) Ducke, en el bosque de tierra firme del Fondo el Bosque – UNAMAD, Las Piedras – Madre de Dios", presentado por la bachiller Srta. María Crisithina Noriega Mamani de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente de la Universidad Nacional Amazónica de Madre de Dios, la misma que estará integrada por los siguientes docentes: Dr. Joel Peña Valdeiglesias-**Presidente**, M.Sc. Jorge Santiago Garate Quispe-**Secretario**, M.Sc. Mauro Vela Da Fonseca-**Vocal**, M.Sc. Jimmy Jeanine Miró Agurto-**Accesitario**.

Que, mediante Resolución de Decanatura de la Facultad de Ingeniería N° 590-2024-UNAMAD-DFI, de fecha 06 de diciembre de 2024, se **MODIFICA**, el artículo primero de las Resoluciones de Decanatura del Proyecto de Tesis titulado

UNAMAD: "Parque Científico Sostenible con investigación e innovación"



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UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS

Decanatura de la Facultad de Ingeniería

"Año del Bicentenario de la Consolidación de Nuestra Independencia y de la Conmemoración de las Heroicas Batallas de Junín y Ayacucho"
"Madre de Dios capital de la biodiversidad del Perú"

RESOLUCIÓN DE DECANATURA DE LA FACULTAD DE INGENIERÍA N° 610-2024-UNAMAD-DFI

Puerto Maldonado, 13 de diciembre de 2024

"Regeneración natural del "Tornillo" *Cedrelinga cateniformis* (Ducke) Ducke, en el bosque de tierra firme del Fundo el Bosque – UNAMAD, Las Piedras – Madre de Dios", presentado por la Bachiller Srta. María Crishtina Mamani Noriega de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente de la Universidad Nacional Amazónica de Madre de Dios.

Que, mediante informe N° 045-2024-JPV, de fecha 13 de diciembre de 2024, el Jurado Revisor remite al Decano de la Facultad de Ingeniería, la aprobación por unanimidad del Informe Final de Tesis titulado "Regeneración natural del "Tornillo" *Cedrelinga cateniformis* (Ducke) Ducke, en el bosque de tierra firme del Fundo el Bosque – UNAMAD, Las Piedras – Madre de Dios", presentado por la Bachiller Srta. María Crishtina Mamani Noriega, de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente, para su sustentación, asimismo, informa la fecha, hora y lugar de sustentación de tesis, para el día **jueves 19 de diciembre de 2024**, a las 17:00 horas, en la sala de grados de la Facultad de Ingeniería.

Que, mediante Expediente N° 4364, de fecha 13 de diciembre de 2024, el Decano de la Facultad de Ingeniería de la UNAMAD, autoriza al Secretario Académico de la Facultad de Ingeniería, proyectar la resolución de aprobación del informe final de tesis y establecer fecha, hora y lugar del acto académico de sustentación de Tesis del informe final de tesis titulado "Regeneración natural del "Tornillo" *Cedrelinga cateniformis* (Ducke) Ducke, en el bosque de tierra firme del Fundo el Bosque – UNAMAD, Las Piedras – Madre de Dios", presentado por la Bachiller Srta. María Crishtina Mamani Noriega, de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente.

Estando dentro de las atribuciones conferidas al Decano, por la Ley Universitaria N° 30220, el Estatuto de la Universidad Nacional Amazónica de Madre de Dios y en uso de las atribuciones conferidas mediante Resolución de Comité Electoral Universitario N° 010-2023-UNAMAD-CEU, de fecha 29 de diciembre del 2023.

SE RESUELVE:

ARTÍCULO PRIMERO: APROBAR el Informe Final de Tesis titulado "Regeneración natural del "Tornillo" *Cedrelinga cateniformis* (Ducke) Ducke, en el bosque de tierra firme del Fundo el Bosque – UNAMAD, Las Piedras – Madre de Dios", presentado por la Bachiller Srta. María Crishtina Mamani Noriega, de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente de la Universidad Nacional Amazónica de Madre de Dios.

ARTÍCULO SEGUNDO: CONVOCAR, a los miembros del Jurado Revisor para el Acto Académico de Sustentación de la Tesis titulado "Regeneración natural del "Tornillo" *Cedrelinga cateniformis* (Ducke) Ducke, en el bosque de tierra firme del Fundo el Bosque – UNAMAD, Las Piedras – Madre de Dios", presentado por la Bachiller Srta. María Crishtina Mamani Noriega, de la Carrera Profesional de Ingeniería Forestal y Medio Ambiente, integrado por los docentes:

- | | |
|--------------------------------------|-------------|
| • Dr. Joel Peña Valdeiglesias | Presidente |
| • M.Sc. Jorge Santiago Garate Quijpe | Secretario |
| • M.Sc. Mauro Vela Da Fonseca | Vocal |
| • M.Sc. Jimmy Jeanine Miró Agurto | Accesitario |

ARTÍCULO TERCERO: ESTABLECER, fecha, hora y lugar para el Acto Académico de Sustentación de Tesis, mencionada en el artículo primero de la parte resolutive, para el día **jueves 19 de diciembre del 2024** a las 17:00 horas, en la sala de grados de la Facultad de Ingeniería.

ARTÍCULO CUARTO: NOTIFICAR, la presente resolución a los miembros del Jurado Evaluador, para que se dé viabilidad a la presente sustentación de tesis de conformidad con lo regulado en el Reglamento de Grados y Títulos de la Universidad Nacional Amazónica de Madre de Dios y a su vez remita el Acta de Sustentación a la Decanatura de la Facultad de Ingeniería, para los trámites y fines pertinentes.

ARTÍCULO QUINTO: DISPONER, se notifique la presente resolución al Asesor del informe final de tesis Dr. Isau Huamantupa Chuquimaco, para conocimiento.

REGISTRESE, COMUNIQUESE Y ARCHIVESE.

DFI
SECRETARÍA
ACADÉMICA
UNAMAD



Dr. Renald Quijpe Flores
DECANO

UNAMAD: "Parque Científico Sostenible con Investigación e Innovación"