



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS

"Año de la Recuperación y Consolidación de la Economía Peruana"

VICERRECTORADO DE INVESTIGACIÓN

HOJA DE TRÁMITE



EXPEDIENTE:

0086

FECHA:

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Carta N° 003-2026-UNAMAD/ITHC

PASE A:

REGISTRADO	VRI	VRI	VRI
S.G.	DUA	INI	OURH
DUAL	DCAA	DITRAF	OUT
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DUI	CIDIO	BIBLIOTECA	OUT
DEFI	CINFOR	REPOSITORIO	OUT
FED	D.A.C.B.	C. IDIOMAS	OUT
FEC-D	D.D.A.P.	C. INFORMATICA	OUT
	D.E.A.P.	OTROS:	OUT

OTROS:

Fecha: 15 ENE 2026

Reg: 0053

Folios: 29

Mora: 15-05-2026

Firma: [Firma]

ACCIONES:

1.	Acciones Necesarias
2.	Consejo Universitario
3.	Conocimiento
4.	Coordinar
5.	Informar
6.	Opinión
7.	Proyectar Resolución
8.	Atención Según lo Solicitado
9.	Difusión
10.	Archivo
11.	Publicación
12.	Otros

OBSERVACIONES:

INI

Revisión e Informe



UNIVERSIDAD NACIONAL AMAZÓNICA DE MADRE DE DIOS

Dra. Luz Marina Almanza Huamán

VICERECTORA DE INVESTIGACIÓN

Dra. Luz Marina Almanza Huamán
Vicerrectora de Investigación
UNAMAD

IMPORTANTE: La presente hoja no debe desglosarse del expediente, bajo responsabilidad.





Puerto Maldonado, 15 de enero del 2026

CARTA N° 003-2026-UNAMAD/IHC

Señor (a):

Dra. Luz Marina Almanza Huamán
Vicerrectora de Investigación-UNAMAD

Asunto. Entrega de informe anual 2025, docente investigador.

Tengo el agrado de dirigirme a usted, para saludarla e informarle que mediante la presente hago entrega del informe Anual de actividades de Docente Investigador, correspondiente al año 2025. Adjunto documento de 53 páginas donde se describen las actividades y documentos correspondientes al mencionado año.

OK

Sin otro en particular, me despido de usted y aprovecho la oportunidad para hacerle llegar mis altas consideraciones.

Dr. Isau Huamantupa Chuquimaco
Docente Investigador UNAMAD/ Investigador CONCYTEC
Código de Registro: P0016356/Nivel: Investigador Distinguido



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

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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 2025

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 2025											
			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 otros productos de investigación						X						
5	Incrementar producción científica per cápita de calidad	Generación de otros productos de investigación							X					
6	Incrementar el número de proyectos de I+D ejecutados por grupos de investigación	Contribuir a la formación de recursos humanos								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 otros productos de investigación											X	
10	Incrementar producción científica per cápita de calidad	Generación de nuevas publicaciones en revistas indizadas												X
11	Incrementar producción científica per cápita de calidad	Contribuir a la formación de recursos humanos												X
12	Incrementar el número de proyectos de I+D ejecutados por grupos de investigación	Contribuir a la formación de recursos humanos												X
...	...	...												

III. Medios de verificación

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)
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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)			
N°	ACTIVIDAD VINCULADA	Título (investigación / producto / ponencia / otro)	Medio de divulgación (revista / conferencia / repositorio / otro)	DOI / URL / otro
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	Phylogenetic conservatism in the relationship between functional and demographic characteristics in Amazon tree taxa	Artículo publicado en revista Functional Ecology (Anexo 2)	https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2435.14700
3	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	Functional composition of the Amazonian tree flora and forests	Artículo publicado en revista Communications biology (Anexo 3).	https://www.nature.com/articles/s42003-025-07768-8
4	CONTRIBUIR A LA FORMACIÓN DE RECURSOS HUMANOS	Tropical forests in the Americas are changing too slowly to track climate change	Artículo publicado en revista SCIENCE (Anexo 4).	https://www.science.org/doi/10.1126/science.adl5414
5	GENERACIÓN DE OTROS PRODUCTOS DE INVESTIGACIÓN	Proyecto de investigación seleccionado para financiamiento: Monitoreo y análisis de la diversidad, biomasa y dinámica arbórea en la cordillera Amazónica Pantiacolla y áreas adyacentes en la reserva de Biosfera del Manú	Acta de resultados finales (Anexo 5)	https://vri.unamad.edu.pe/sigvri
6	CONTRIBUIR A LA FORMACIÓN DE RECURSOS HUMANOS	Proyecto de Tesis asesorado, seleccionado para financiamiento: Caracterización de la regeneración natural de <i>Bertholletia excelsa</i> Bonpl., en dos tipos de bosque Amazónico, distrito Las Piedras, Madre de Dios.	Acta de resultados finales (Anexo 6)	https://vri.unamad.edu.pe/sigvri
7	GENERACIÓN DE OTROS PRODUCTOS DE INVESTIGACIÓN	Poster de investigación seleccionado como primer puesto en V CONFERICIS. «Flora y vegetación de las Pampas del Heath, única Sabana del Perú»	Poster y Resolución de Vicerrectorado de Investigación	Resolución N°241-2025-UNAMAD-VRI (Anexo 7)
8	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	Leaf morphometry of six Podocarpaceae species from Peru: A contribution to their taxonomic identification	Revista científica (Anexo 8)	https://repositorio.inia.gob.pe/items/21b94558-cfef-4d7e-96cd-73305d4ebf07
9	OTRAS ACTIVIDADES VINCULADAS	Participación como ponente y organizador en el XIX CONABOT	- Libro de Resúmenes - Certificados de Participación (Anexo 9, Anexo 10)	https://sites.google.com/unamad.edu.pe/xix-conabot/libro-de-res%C3%BAmenes?authuser=0 https://sgd.unamad.edu.pe/consultas/constancias
10	GENERACIÓN DE NUEVAS PUBLICACIONES EN REVISTAS INDIZADAS	Centuries of compounding human influence on Amazonian forests	Journal: The Proceedings of the National Academy of Sciences (PNAS) (Anexo 11)	https://www.pnas.org/doi/10.1073/pnas.2514040122
12	GENERACIÓN DE NUEVAS TESIS ASESORADAS Y SUSTENTADAS	Tesis sustentada con acta: Regeneración natural de <i>Bertholletia excelsa</i> Bonpl. (Lecythidaceae), en un bosque de tierra firme en la Zona de Amortiguamiento de la Reserva Tambopata - Madre de Dios	Acta de Sustentación (Anexo 12)	N° 712-2025-UNAMAD-DFI
UNAMAD: "Investigación, Innovación y Emprendimiento Global" 2				

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)
2	Elija una actividad.		
3	Elija una actividad.		
4	Elija una actividad.		
5	Elija una actividad.		
...			

Puerto Maldonado, 15 de enero de 2026



Firma (Remitente)

Jsw Humantupa Churimaco

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 Scientific reports.

www.nature.com/scientificreports

scientific reports

Check for updates

OPEN Large range sizes link fast life histories with high species richness across wet tropical tree floras

Timothy R. Baker¹, Stephen Adu-Bredu², Kofi Affum-Baffoe³, Shin-ichiro Aiba⁴, Perpetra Akite⁵, Miguel Alexiades⁶, Everton Almeida⁷, Edmar Almeida de Oliveira⁸, Esteban Alvarez Davila⁹, Christian Amani^{10,11}, Ana Andrade¹², Luiz Aragao^{13,14}, Alejandro Araujo-Murakami¹⁵, Eric Arets¹⁶, Luzmila Arroyo¹⁵, Peter Ashton¹⁷, Suspense A. Averti Ifo¹⁸, Gerardo A. C. Aymard¹⁹, Michel Baisie²⁰, William Balee²¹, Michael Balinga²², Lindsay F. Banin²³, Olaf Banki^{24,25}, Christopher Baraloto^{26,27}, Jorcely Barroso²⁸, Jean-Francois Bastin²⁹, Hans Beeckman³⁰, Serge Begne³¹, Natacha Nssi Bengone³², Nicholas Berry³³, Wemo Betian³⁴, Vincent Bezar³⁵, Lilian Blanc³⁶, Pascal Boeckx³⁷, Damien Bonal³⁸, Frans Bongers³⁹, Francis Q. Brearley⁴⁰, Roel Brienien¹, Foster Brown⁴¹, Musalmah Bt. Nasaradin⁴², Benoit Burban⁴³, David F. R. P. Burslem⁴⁴, Plinio Camargo⁴⁵, Jose Luis Camargo⁴², Wendeson Castro⁴⁶, Carlos Ceron⁴⁷, Victor Chama Moscoso⁴⁸, Colin Chapman⁴⁹, Jerome Chave⁵⁰, Eric Chezeaux⁵¹, Murray Collins^{52,53}, James Comiskey^{54,55}, David Coomes⁵⁶, Fernando Cornejo Valverde⁵⁷, Flavia R. C. Costa⁵⁸, Aida Cuni-Sanchez^{59,60}, Lola da Costa⁶¹, Douglas C. Daly⁶, Martin Dančák⁶², Armandu Daniels⁶³, Greta Dargie¹, Stuart Davies⁶⁴, Charles De Canniere⁶⁵, Thales de Haulleville³⁰, Jhon del Aguila Pasquel^{66,67}, Geraldine Derroire⁶⁸, Kyle G. Dexter^{52,69,70}, Anthony Di Fiore^{71,72}, Marie-Noel K. Djuikouo⁷³, Jean-Louis Doucet⁷⁴, Vincent Droissart⁷⁵, Gerald Eilu⁷⁶, Thaise Emilio⁷⁷, Julien Engel⁷⁵, Bocko Yannick Enock¹⁸, Fidele Evouna Ondo⁷⁸, Corneille Ewango⁷⁹, Sophie Fauset⁸⁰, Ted R. Feldpausch¹³, Muhammad Fitriadi⁸¹, Gerardo Flores Llampazo⁶⁶, Ernest G. Foli², Gabriella Fredriksson^{82,83}, David R. Galbraith¹, Martin Gilpin¹, Emanuel Gloor¹, Christelle Gonmadje⁸⁴, Rene Guillen Villaroel¹⁵, Jefferson Hall⁸⁵, Keith C. Hamer⁸⁶, Alan Hamilton⁸⁷, Olivier Hardy⁸⁸, Terese Hart^{89,90}, Radim Hédí^{91,92}, Rafael Herrera⁹³, Niro Higuchi⁹⁴, Claude Marcel Hladik⁹⁵, Euridice Honorio Coronado⁹⁶, Isau Huamantupa-Chuquimaco⁹⁷, Walter Huaraca Huasco⁴⁸, Wannes Hubau^{20,98}, Muhammad Idhamsyah⁹⁹, Sascha A. Ismail¹⁰⁰, Kath Jeffery¹⁰¹, Eliana Jimenez¹⁰², Tommaso Jucker¹⁰³, Elizabeth Kearsley¹⁰⁴, Lip Khoon Kho¹⁰⁵, Timothy Killeen¹⁰⁶, Kanehiro Kitayama¹⁰⁷, William Laurance¹⁰⁸, Susan Laurance¹⁰⁸, Miguel Leal¹⁰⁹, Simon L. Lewis^{1,110}, Stanislav Lhota¹¹¹, Jeremy Lindsell^{112,113}, Gabriela Lopez-Gonzalez¹, Jon Lovett^{1,114}, Richard Lowe¹, William E. Magnusson⁵⁸, Jean-Remy Makana⁷⁹, Yadvinder Malhi¹¹⁵, Beatriz Marimon⁸, Ben Hur Marimon Junior⁸, Andrew Marshall⁶⁰, Colin Maycock¹¹⁶, Faustin Mbayu¹¹⁷, Casimiro Mendoza¹¹⁸, Irina Mendoza Polo¹¹⁹, Faizah Metali¹²⁰, Vianet Mihindou^{32,78}, Abel Monteagudo-Mendoza⁴⁸, Sam Moore¹¹⁵, Patrick Mucunguzi⁵, Jacques Mukinzi^{121,122}, Pantaleo Munishi¹²³, Laszlo Nagy¹²⁴, Petrus Naisso³⁶, David Neill¹²⁵, Adriano Nogueira Lima⁵⁸, Percy Nunez Vargas⁴⁸, Lucas Ojo¹²⁶, Walter Palacios¹²⁷, Nadir Pallqui Camacho⁴⁸, Alexander Parada Gutierrez¹⁵, Julie Peacock¹, Kelvin S.-H. Peh¹²⁸, Antonio Pena Cruz¹²⁹, Colin Pendry⁶⁹, Toby Pennington^{13,69}, Maria Cristina Penuela-Mora¹³⁰, Pascal Petronelli¹³¹, Oliver L. Phillips¹, Georgia Pickavance¹, G. John Pipoly^{132,133}, Nigel Pitman¹³⁴, Axel Dalberg Poulsen⁶⁹, Ghilleen T. Prance¹, Adriana Prieto¹³⁵, Richard B. Primack¹³⁶, Lan Qie¹³⁷, Simon A. Queenborough¹³⁸, Terry Sunderland¹³⁹, Carlos Quesada⁵⁸, Freddy Ramirez Arevalo⁶⁷, Hirma Ramirez-Angulo¹⁴⁰, Jan Reitsma¹⁴¹, Maxime Réjou-Méchain⁷⁵, Anand Roopsind¹⁴²,



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Francesco Rovero^{143,144}, Ervan Rutishauser¹⁴⁵, Kamariah Abu Salim¹²⁰, Rafael Salomao¹⁴⁶, Ismayadi Samsoedin¹⁴⁷, Muhd Shahrune Saparudin¹²⁰, Juliana Schietti⁵⁸, Ricardo A. Segovia¹⁴⁸, Julio Serrano¹⁴⁰, Rafizah Serudia¹²⁰, Douglas Sheil³⁹, Natalino Silva¹⁴⁹, Javier Silva Espejo¹⁵⁰, Marcos Silveira^{151,152}, Murielle Simo-Droissart¹⁵³, James Singh¹⁵⁴, Bonaventure Sonké¹⁵⁵, Thaise Emilio Lopes De Sousa⁷⁷, Juliana Stropp¹⁵⁵, Rahayu Sukri¹²⁰, Terry Sunderland¹³⁹, Martin Svátek¹⁵⁶, Michael Swaine⁴⁴, Hermann Taedoumg^{157,158}, Joey Talbot¹, Sylvester Tan^{159,160}, James Taplin^{161,162}, David Taylor¹⁶³, Hans ter Steege^{24,25}, John Terborgh¹⁶⁴, Armando Torres-Lezama¹⁴⁰, John Tshibamba Mukendi¹¹⁷, Darlington Tuagben¹⁶⁵, Peter van de Meer¹⁶⁶, Geertje van der Heijden¹⁶⁷, Peter van der Hout¹⁶⁸, Mark van Nieuwstadt²⁵, Bert van Uft¹⁶⁹, Rodolfo Vasquez Martinez¹²⁹, Ronald Vernimmen¹⁷⁰, Barbara Vinceti¹⁷¹, Simone Vieira¹⁷², Ima Celia Guimarães Vieira¹⁴⁶, Emilio Vilanova Torre^{72,140}, Jason Vleminckx^{173,174}, Lee White^{32,175}, Simon Willcock^{176,177}, Mathew Williams⁵², John T. Woods¹⁷⁸, Tze Leong Yao⁴², Ishak Yassir³⁹, Roderick Zagt¹⁷⁹ & Lise Zemagho¹⁵³

Understanding how the traits of lineages are related to diversification is key for elucidating the origin of variation in species richness. Here, we test whether traits are related to species richness among lineages of trees from all major biogeographical settings of the lowland wet tropics. We explore whether variation in mortality rate, breeding system and maximum diameter are related to species richness, either directly or via associations with range size, among 463 genera that contain wet tropical forest trees. For Amazonian genera, we also explore whether traits are related to species richness via variation among genera in mean species-level range size. Lineages with higher mortality rates—faster life-history strategies—have larger ranges in all biogeographic settings and have higher mean species-level range sizes in Amazonia. These lineages also have smaller maximum diameters and, in the Americas, contain dioecious species. In turn, lineages with greater overall range size have higher species richness. Our results show that fast life-history strategies influence species richness in all biogeographic settings because lineages with these ecological strategies have greater range sizes. These links suggest that dispersal has been a key process in the evolution of the tropical forest flora.

Keywords Tropical forest, Diversification, Biodiversity, Trees, Evolution, Biogeography

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equation models (pSEM)³³ to assess whether traits influence species richness directly, or indirectly via variation in range size.

We performed an additional analysis for genera from the Americas, which also incorporated variation in genus population size³⁴, dispersal mode³⁵ and mean species range size within genera³⁶, based on published datasets that are only available for this continent. We expected genus population size to be positively correlated with species richness, given sampling considerations, and dispersal by wind to be associated with lower species richness, as higher dispersal distances may preclude effective reproductive isolation. Finally, we predicted that smaller species-level range sizes would be associated with greater species richness within a genus, as small ranges and high diversification rates are a feature of lineages in endemic hotspots associated with for example, mountain building and island formation, in the tropics³⁷.

In all analyses, we accounted for the phylogenetic relationships among genera in these analyses using a pantropical, DNA-based, genus-level phylogeny, developed from a published genus-level phylogeny for American trees^{38,39}.

Results

Variation in mortality rates was positively correlated with lineage range size using GLS analysis and in every biogeographic setting using pSEM (Figs. 1 and 2; Table S1). This relationship was also significant for a subset of genera that solely comprise lowland, tropical wet forest trees (Fig. S1) and, among Amazonian genera, mortality rates were positively correlated with mean species range size (Fig. 3). These relationships were driven by lineages from across the phylogeny that share high mortality rates and large range sizes (Fig. 4; e.g. Americas, *Inga*, mortality rate 2.8% a⁻¹, range size 15.5 million km²; Africa, *Uapaca*, 1.6% a⁻¹, range size 13.6 million km²; Asia, *Elaeocarpus*, 2.5% a⁻¹, range size 7.2 million km²). The only major clades that do not contain genera with these linked characteristics are the Dialioideae and Detarioideae subfamilies of legumes (Fig. 4). Overall, these results indicate that fast demography is associated with greater range sizes across the phylogeny and biogeographical settings of the wet tropical tree flora (Fig. 2).

In turn, lineage range size was strongly associated with variation in species richness: genera with large range sizes have greater species richness (Figs. 1 and 2, Table S1). The link between large range size and high species richness was found in all biogeographical settings and across the phylogeny (e.g. Americas, *Inga* (15.5 million km²; 281 species), *Protium* (18.8 million km²; 152 species); Africa, *Uapaca* (13.6 million km²; 25 species), *Cola* (12.9 million km², 134 species); Asia, *Aglaia* (6.6 million km²; 119 species), *Elaeocarpus* (7.2 million km², 488 species). In contrast to these linear relationships between genus range size and species richness, mean species-level range size within genera had a unimodal relationship with species richness in Amazonia: richness peaked at intermediate values and declined in lineages with the greatest mean species-level range size (Fig. 3A). This quadratic relationship between mean species range size and species richness in Amazonia was independent of a significant positive correlation between population size and species richness (Table S2, Fig. 3B).

Variation in a range of other traits were linked to variation in mortality rates among genera (Fig. 1). There was a consistent negative relationship in all biogeographic settings between mortality rate and maximum size: across the phylogeny, genera with smaller maximum size have high mortality rates (Fig. 2 and Fig. S2). For Amazonian trees, low seed mass was also associated with high mortality rates (Fig. 3). Finally, the presence of dioecy was also associated with high mortality rates for genera that occur on multiple continents and those in Amazonian forests (Figs. S3 and S4). Overall, these relationships indicate that there are linked suites of traits related to stature, dispersal and breeding system that are all associated with fast life-history strategies, larger range sizes of lineages and ultimately, greater species richness (Fig. 1).

In some biogeographical settings, there were direct relationships between traits and species richness that were independent of variation in range size (Fig. 1). For example, species richness is higher in genera with low

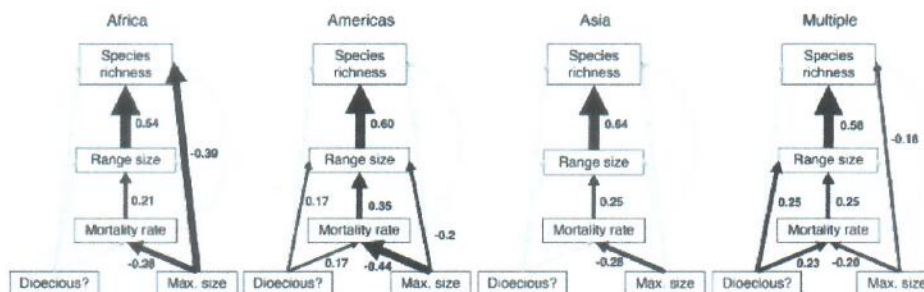


Fig. 1. Structural equation models from pSEM analysis showing the relationships between traits, range size and species richness for 463 genera of tropical trees, that occur in the Americas, Africa, Asia or on multiple continents. Standardised effect sizes shown for significant relationships; arrow width is proportional to the standardised effect size. Non-significant relationships are shown with grey dotted lines.

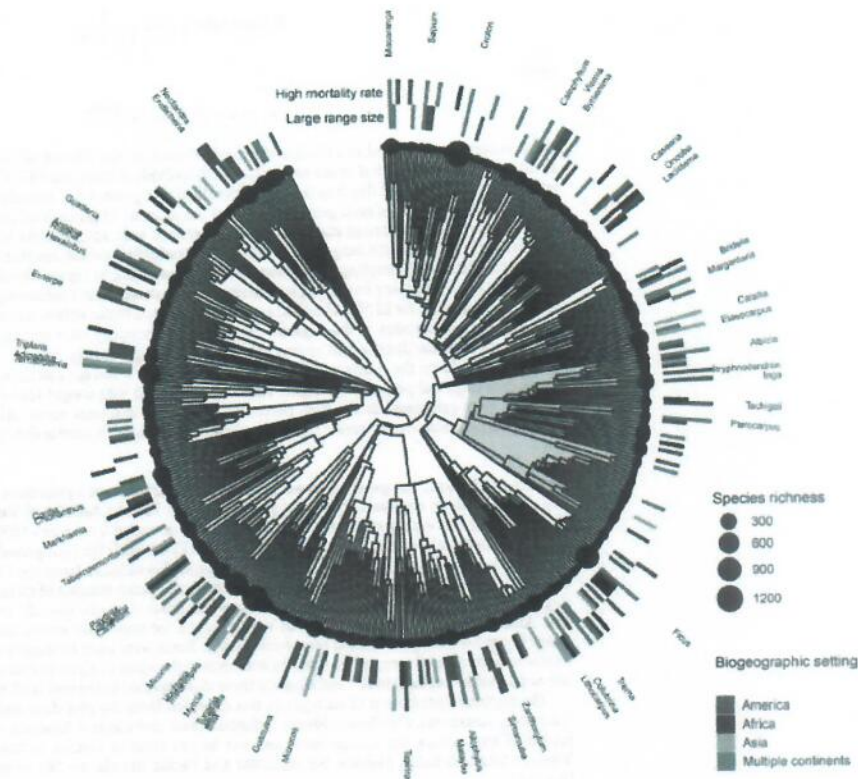


Fig. 4. Phylogenetic relationships among species richness, high mortality rates and large range size for 463 genera of tropical trees. Tip circle size is proportional to the species richness of each genus. Coloured bars indicate genera with high mortality rates and/or large range sizes. High mortality rates are classified as $> 2\% a^{-1}$; large range size classified as $> 10 M km^2$ (America), $> 8 M km^2$ (Africa), $> 5 M km^2$ (Asia) and $> 20 M km^2$ (multiple continents). Bar colour indicates the biogeographic setting of each genus. Named genera are those that share both high mortality rates and large range sizes; their distributed pattern illustrates that the association between large range size and high mortality rates is found across the phylogeny and is not restricted to certain clades. The blue segment on the phylogeny highlights the legumes, including the Dialioideae and Detarioideae subfamilies which are the only major clades on the phylogeny that do not demonstrate this association.

evolutionary 'dead-end'^{29,57}. However, these findings are consistent with a broad array of recent work showing that dioecy is common in tropical secondary forests⁵⁸ and is linked with large geographical range sizes of genera⁵⁹, species richness is higher in dioecious clades once variation in branch length between non-dioecious and dioecious clades is accounted for⁶⁰ and genetic diversity is greater and adaptation rates are faster in dioecious compared to monoecious lineages of plants⁶¹. The lack of significant associations between dioecy, mortality rates and range size in African and Asian forests may reflect the lower levels of sampling in these regions; significant relationships among these variables are only found in the two groups with the greatest number of genera (Fig. 1). Overall, our results suggest that dioecy in the tropical tree flora, at least for the Americas, may be related to a suite of traits, such as short generation times and high dispersal ability that more than compensate for the difficulty of achieving successful reproduction when sexes are on separate individuals. More generally, our findings demonstrate the need for precise estimates of species' demographic rates to understand the links between breeding systems and species richness in comparative analyses.

There are uncertainties associated with the estimates of range size, taxonomy and traits that we used in this study. First, range sizes have fluctuated over the evolutionary history of the extant diversity of tropical forests, and time-integrated estimates of range size are required to estimate the land area that has been available for each genus more precisely over geological time⁶². Second, the number of herbarium records that we used to



$$P(\text{mortality}, t) = \frac{1}{1 + e^{-k_t}}$$

where

$$k_t = a - b_1 (dbh_t) e^{b_2 dbh_t}$$

These functions were used to calculate the log-likelihood of the dataset of the status of each tree as dead or alive at the end of the period of monitoring for each individual, using Eq. (8) in⁷⁴. For each genus, the parameter estimates that minimised this function were identified using simulated annealing. Finally, the mortality rate for a median diameter tree of each genus was used as the estimate of genus-level mortality rates.

We assume that the broad extent of the plot network with sample plots widely distributed across the wet tropics (Fig. S7), covers the range of species and environmental conditions that are characteristic of each genus, and that the temporal sampling of the plots (Fig. S8) is sufficient to capture the distribution of the return time of events that cause mortality in wet tropical forests. The mean length of monitoring exceeds the typical return time of two to seven years for El Niño/La Niña events⁷⁵ which are a major driver of climatic variation and inter-annual variation in tree mortality in this region⁷⁶. Mean annual mortality rates among genera ranged from 0.1 to 10% a⁻¹ and had a similar distribution among biogeographical regions (Fig. S6).

We used data on the maximum diameter of trees within a lineage calculated from the forest plot data as a measure of dispersal potential, as higher stature is associated with longer seed dispersal distances⁴⁵. Maximum size data were calculated as the 95th percentile of the tree diameter across all individuals of each genus^{77,78}. Maximum diameter varied from 12 to 200 cm among genera, with similar distributions among continents (Fig. S6).

Species richness, range size, breeding systems, dispersal syndrome and seed mass

We used the list of accepted, species-level names in the World Checklist of Vascular Plants⁷⁹ to calculate the species richness of each genus. Species richness per genus varied from 1 to > 1000 species (Fig. S6).

We defined range size as the extent of occurrence (EOO; km²) for each genus⁸⁰. EOOs were calculated using herbarium records for all species within a given genus downloaded from the Global Biodiversity Information Facility. In total, the calculations used 336,832 records; the mean number of records per genus was 727 (Fig. S5). A greater number of genera from African forests had fewer than 100 records, compared to genera from Asian and American forests (Fig. S5). Records were checked for typos and errors, and latitudinal and longitudinal range limits for each genus based on information in floras were used to remove non-native records (Table S4). EOOs were calculated using alpha hulls, by minimising the value of alpha to encompass 99% of all records, using the *rangeBuilder* package in R⁸¹ and clipping these distributions to current land area (Fig. S10).

The regional distribution of each genus was classified from the plot data, and categorised as: the Americas (including Amazonia, the Guiana Shield, Atlantic Forest and Central America; n = 151), Africa (including the forests of west Africa, the Congo basin and wet forests areas in eastern Africa; n = 115), Asia (including the Western Ghats in India, Malesia, NE Australia and Pacific islands; n = 78), or present on multiple continents (n = 119).

We used information on the presence of dioecy in a lineage to assess the role of breeding systems in constraining species richness. Lineages with a dioecious breeding system, where male and female flowers are on different trees, are classically considered to have lower opportunities for successful establishment of new populations^{29,82} and therefore lower species richness as they require successful dispersal of both male and female plants⁵⁷. Breeding system was classified for each genus as 'at least some dioecious species' or 'no dioecious species', based on⁸³ and floras (Table S5). The proportion of genera with at least some dioecious species (approximately 27%) was similar across all biogeographical settings (Fig. S6).

Finally, for taxa from Amazonia we also compiled data on seed mass, dispersal mode, mean species-level range size and population size. Seed mass was calculated for all species within each lineage, as this trait is associated with seed dispersal distances⁴⁵. Seed mass for Amazonian taxa (n = 92) was calculated as average values for species within genera⁸⁴; there was insufficient data available to analyse this trait for genera from Africa (n = 8) or Asia (n = 17). The dispersal mode of lineages was classified as wind or non-wind dispersed³⁵. Mean species range size and total population size was calculated using estimates for all species within a lineage^{34,36}.

Statistical analysis

The phylogenetic relationships among genera were estimated using a DNA-based, genus-level phylogeny for the tropics, developed from a published genus-level phylogeny for American trees^{38,39}. Mortality rate, maximum size, range size, species richness all showed significant phylogenetic signal (mortality rate, Pagel's $\lambda = 0.56$, $p < 0.005$; range size, $\lambda = 0.24$, $p < 0.05$; maximum size, $\lambda = 0.57$, $p < 0.005$; species richness $\lambda = 0.32$, $p < 0.05$), demonstrating the importance of accounting for shared evolutionary branch lengths in our statistical analysis. Links between the phylogeny and trait values were visualised using the *ggtree* package⁸⁵.

We used species richness as the response variable in our analyses of diversification, rather than estimating diversification rates for each clade as a function of time. This approach is based on previous work for a subset of the lineages analysed here where a 'density-dependent' trajectory of diversification provided a closer fit to the observed distribution of clade ages and species richness data for 51 lineages of Amazonian trees, compared to a model where species accumulate at a constant rate¹⁶. This approach is also consistent with general findings that estimates of diversification rates based on assuming a constant rate of species accumulation perform poorly when predicting changes in species richness of lineages through the fossil record, and that variation in clade age can lead to misleading interpretations of differences in diversification rates⁸⁶. Our approach assumes that the



species richness of each lineage has reached a steady-state, and explores which traits determine variation in these steady-state values. We note that clade age is not related to species richness across our data: stem ages of each lineage estimated from the phylogeny vary extremely widely with species richness for these genera (Fig. S11) and therefore the influence of traits on species richness is not confounded by differences in clade age. Overall, our approach is a simplification of the likely wide range of trajectories of change in the number of species within each lineage over geological time. However, in the absence of a detailed fossil record or complete species-level phylogenies for each lineage, this approach represents the only means to gain a macroecological perspective on the traits that influence species richness.

Generalised least squares (GLS) models with phylogenetically correlated errors were used to identify how biogeographical distributions and traits were related to variation in range size across lineages as:

$$\log(R) = (\log(\mu) * D) + (S * D) + (B * D) + \varepsilon$$

where R is range size, μ is mortality rate, D is the biogeographic setting of each genus, S is maximum size, B is a categorical variable denoting either the presence or absence of dioecious species within a genus, and ε is distributed as $\sigma^2 C$ where C is the variance-covariance of the error term based on the shared branch lengths of the phylogeny.

Variation in species richness was analysed similarly as:

$$\log(\text{Species richness}) = (\log(R) * D) + (\log(\mu) * D) + (S * D) + (B * D) + \varepsilon$$

GLS analysis can only test for direct, independent effects of each predictor variable on the response variables. We therefore also used piece-wise structural equation modelling (pSEM) to explore the network of both direct and indirect relationships among these variables^{33,87}.

We hypothesised that the species richness of genera would be influenced by the range size of a lineage, following studies that demonstrate this link for animals and plants^{23,24} and expectations from allopatric models of speciation that assume that range expansion precedes genetic divergence²¹. We allowed traits to either influence range size and/or species richness directly, as traits may influence rates of range expansion and contraction and/or other processes that underpin speciation, such as the transition time to genetic divergence following the establishment of a lineage²¹. Initial pSEM analysis indicated that there were also significant relationships among maximum size and mortality rates within these data, consistent with findings that demographic and structural traits are linked among lineages of tropical trees^{88,89}. We therefore also allowed variation in maximum size and breeding system to be associated with variation in mortality rates in the final pSEM models. For each biogeographical setting, structural equation models based on these networks including only the statistically significant relationships showed a good fit to the data, indicating that significant relationships among the variables were not being excluded (Fig. 1; Americas, Fisher's $C=6.5$, ns; Africa, Fisher's $C=4.9$, ns; Asia, Fisher's $C=5.8$, ns; Multiple continents, Fisher's $C=5.9$, ns; core dataset, all biogeographical settings; pSEM, $C=14.7$, ns).

For the analyses focussing on Amazonia, we extended these analyses to include total population size, mean species range size, seed mass and dispersal mode, using a similar statistical approach. For Amazonian taxa, we used GLS to test how traits were related to variation in mean species range size and how traits, mean species range size and total population size were associated with species richness. We included a quadratic term to model the relationship between mean species range size and species richness, based on preliminary exploration of the relationships within the data. Similarly, we also constructed pSEMs to understand the network of direct and indirect relationships among these variables. We explored whether traits determined variation in mean species range size, and how mean species range size is related to species richness. We included total population size as an additional predictor of species richness; correlated errors were permitted between mean species range size and population size. The structural equation model based on this network including only the statistically significant relationships showed a good fit to the data (Fisher's $C=15.8$, ns).

Data availability

All metadata used in the analyses is available as supplementary information and as a Forestplots.net data package from https://doi.org/10.5521/forestplots.net/2025_1

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