UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE ECOLOGÍA

Ecología de especies simpátricas de *Damburneya* de la selva alta perennifolia de Los Tuxtlas

TESIS
QUE PARA OPTAR POR EL GRADO DE:
DOCTORA EN CIENCIAS
Campo de conocimiento: Biología evolutiva

PRESENTA:
LAURA JUDITH GIRALDO KALIL

TUTOR PRINCIPAL DE TESIS:
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Ciudad Universitaria, CD. MX. Mayo 2023.

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UNAM POSGRADO

POSGRADO CIENCIAS BIOLÓGICAS

COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS

ENTIDAD INSTITUTO DE ECOLOGÍA

OFICIO CPCB/235/2023

ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que, en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada del día 28 de noviembre de 2022 se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **GIRALDO KALIL LAURA JUDITH** con número de cuenta: **514351045** con la tesis titulada **"ECOLOGÍA DE ESPECIES SIMPÁTRICAS DE *Damburneya* DE LA SELVA ALTA PERENNIFOLIA DE LOS TUXTLAS".** Bajo la dirección del **DR. JUAN SERVANDO NÚÑEZ FARFÁN**, Tutor Principal, quedando integrado de la siguiente manera:

Presidente: DR. GUILLERMO IBARRA MANRÍQUEZ
Vocal: DRA. JULIETA ALEJANDRA ROSELL GARCÍA
Vocal: DR. LUIS ALFREDO OSORIO OLVERA
Vocal: DR. FRANCISCO JAVIER LABORDE DOVALÍ
Secretario: DR. HORACIO ARMANDO PAZ HERNÁNDEZ

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 07 de marzo de 2023

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

Agradecimientos institucionales

Al Posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México (UNAM), por permitirme realizar mis estudios de doctorado en el Instituto de Ecología y por el apoyo recibido durante mi formación académica.

Al Consejo Nacional de Ciencia y Tecnología (CONACyT) por la beca No. 463686, otorgada para mi manutención durante la realización de mis estudios de doctorado.

A la Secretaría de Educación Pública y al Consejo Nacional de Ciencia y Tecnología (SEP-CONACyT) por la financiación del proyecto de Ciencia Básica "Ecología evolutiva de especies simpátricas de *Nectandra* (Lauraceae) en una selva húmeda tropical", del cual se deriva esta investigación (Fondo I0017, No. 284692).

Agradezco también por el apoyo económico derivado de la financiación de dicho proyecto para asistir a tres congresos nacionales para la presentación de los resultados de esta investigación.

A la International Biogeography Society y la Red Latinoamericana para el Estudio de la Biogeografía Neotropical por la beca de viaje brindada para la asistencia a un congreso internacional.

Al Programa de Apoyo para Estudios de Posgrado (PAEP, UNAM) por el apoyo económico brindado para la realización de un curso de campo.

A mi tutor principal, el Dr. Juan Núñez Farfán y a los miembros de mi comité tutor, Dr. Horacio Paz Hernández y Dr. Miguel Martínez Ramos por su apoyo constante, su asesoría y enseñanzas durante el desarrollo de esta investigación. Por creer en mis ideas e impulsar mi desarrollo profesional. Por su apertura para la discusión de ideas. ¡Mi más sincero agradecimiento!

Agradecimientos a título personal

Agradezco en primer lugar a mi asesor, Dr. Juan Núñez Farfán, por el apoyo que me brindó durante más de cuatro años para la realización de este proyecto. Juntos escribimos una propuesta de investigación original y logramos obtener financiación para desarrollarla. Esto no habría sido posible sin la confianza que tuvo en mí, y el impulso que me dio para plantear mis propias ideas y explorar nuevos caminos que poco a poco se abrieron durante el desarrollo de esta investigación. Gracias a Juan pude expandir mis horizontes, ser independiente, formarme como joven investigadora y emprender una nueva vida en México.

A mis tutores, Dr. Miguel Martínez y Dr. Horacio Paz, quién fue además miembro de mi jurado de candidatura y ahora de mi examen de titulación, porque siempre estuvieron dispuestos a discutir ideas y aportaron mucho a mejorar mi proyecto. A los demás jurados de esta tesis, Dra. Julieta Alejandra Rosell García, Dr. Francisco Javier Laborde Dovalí, Dr. Luis Alfredo Osorio Olvera, y Dr. Guillermo Ibarra Manríquez, por la revisión cuidadosa y proactiva del manuscrito. Al instituto de Ecología que se convirtió en mi segundo hogar y me permitió realizar mis estudios de posgrado aprendiendo de excelentes alumnos y maestros, e incursionar en la investigación científica.

A todas las personas que me ayudaron para la realización de mi trabajo de campo. A Rosamond Coates Lutes, directora de la Estación de Biología Tropical Los Tuxtlas (Instituto de Biología, UNAM), y a las y los trabajadores de la estación por su apoyo logístico durante todo mi proyecto. A Santiago Sinaca Colín, gran naturalista de la región de Los Tuxtlas y a Erli Velasco Sinaca, por su apoyo en todas las etapas de mi trabajo de campo, por guiarme y ayudarme durante los muestreos y censos, por mostrarme los rincones más hermosos de la región, por todas sus enseñanzas. A sus familias e hijos, especialmente a Eladio Velasco Sinaca, Santiago Sinaca y Erli Velasco, por su ayuda durante algunas salidas de campo.

Agradezco muy especialmente a mis amigos y compañeros que son o han sido parte del Laboratorio de Genética Ecológica y Evolución del Instituto de Ecología (UNAM), o han pasado temporadas cortas allí. Todos estos biólogos han contribuido de una u otra forma han contribuido a este proyecto, me han enseñado muchísimo y me han ayudado en los momentos más difíciles. A la Mtra. Edna Rodríguez Sánchez, que me apoyó durante gran parte de esta investigación, en el trabajo de campo, invernadero, laboratorio y análisis de datos. Por su amistad, por creer en mí y apoyar mi trabajo desde sus primeras etapas, por su entusiasmo y dedicación que nos permitieron expandir los resultados de esta investigación y descubrir un maravilloso universo de insectos dentro de las semillas de las lauráceas. A mi gran amiga, la Dra. Rosalinda Tapia López por su apoyo desde mi llegada a México, por impulsarme y acompañarme con tanto cariño, y por su ayuda con varios aspectos logísticos durante gran parte del proyecto, en especial durante la planeación de las salidas de campo. A Fernando López Ordaz, Javier Daniel Matías Martínez, Ana Lucia Castrejón Herrera, Andrea Alfaro, la Mtra. Brenda Hernández Hernández, la Mtra. Valeria Stephany Flores Almaraz, la Mtra. Carol Estefanía Villanueva Hernández, la Mtra. Macarena Marín Rodulfo, la Dra. Pilar Suárez Montes, el Dr. Iván De la Cruz Argüello, el Dr. Iván Darío Camargo Rodríguez, y la Dra. Lourdes Martínez, quienes me apoyaron durante el trabajo de campo, por las caminatas en la selva, la toma de datos, el procesamiento de muestras, las enseñanzas, las trasnochadas y las risas. Al Mtro. Franco Liñán, Paola Sierra, y Sandra Garrido Mijangos, por su apoyo y los buenos ratos en el laboratorio. A la Mtra. Diana Elizabeth López Cobos, por su apoyo incondicional, su escucha atenta y sus palabras sabias. A Minerva Gabriela Soto Alonso y Aura Ollin Escamilla Valentín por su ayuda durante el establecimiento de experimentos en campo.

A Enrique Solís Villalpando, técnico del Laboratorio de Biogeoquímica terrestre y Clima del Instituto de Ecología (UNAM) por enseñarme a muestrear y analizar suelos en el laboratorio, y Adriana Pérez, laboratorista del Laboratorio de Genética Ecológica y Evolución del Instituto de Ecología (UNAM), por su ayuda con el procesamiento de muestras foliares, y particularmente, durante la crianza de insectos.

A todos los colegas con los que he tenido el gusto de colaborar tanto en la escritura de los resultados de mi tesis como en la de nuestra propuesta de investigación por su proactividad y apoyo. Al Dr. Julio Campo por su paciencia, su trato siempre amable, por la discusión de ideas y por introducirme al mundo de la ecología funcional. Al Dr. Francisco Lorea Hernández, por su ayuda en la identificación de ejemplares, la revisión de localidades, mapas y bases de datos, y su amable bienvenida al herbario XAL, Instituto de Ecología A. C. (INECOL). A mi gran amigo, el Mtro. Gonzalo Pinilla Buitrago, por su ayuda durante el desarrollo de mis modelos de nicho. Al Dr. Andrés Lira Noriega por guiarme durante mis primeros pasos en el modelado de nicho en el INECOL. Al Dr. Juan Pablo Jaramillo, por su ayuda en campo, por su apertura a la discusión e impulsarme a presentar mis resultados frente a un público internacional. Ambos aportaron además a la mejora de mi trabajo con sus observaciones en mi examen de candidatura. Al Dr. Alejandro Zaldívar Riverón, por apoyar e incentivar las investigaciones sobre los insectos asociados a los frutos de Lauraceae derivados de este proyecto.

A los demás miembros del jurado de mi examen de candidatura, Dr. Daniel Ignacio Pilero Dalmau, y Dr. Luis Enrique Eguiarte Fruns, quién me permitió apoyar sus clases de genética de poblaciones como asistente docente, por sus observaciones críticas y constructivas que me ayudaron a enfocar y mejorar esta investigación.

A Yadira María Duque, que me dio herramientas para cuestionar y entender mis propias acciones y cumplir mis objetivos, y me ayudó a salir adelante en momentos muy difíciles. A Miriam Camacho, Saraí Villegas, y Guadalupe Cervantes de la Defensoría de Derechos Universitarios de la UNAM, que velaron por mi bienestar y mis derechos durante la última etapa de mi doctorado.

A mis amigas y amigos en Colombia y México, por su apoyo constante, su compañía, y su empatía. Por todos estos años en los que cerca o lejos han cambiado mi vida y me han enseñado con generosidad sus perspectivas.

A mi familia, a quienes dedico este trabajo, por su apoyo constante a la distancia a pesar de los años lejos, por impulsarme a dar grandes pasos lejos de casa y a perseguir mi carrera científica, por la alegría de nuestros reencuentros. A mi madre, que me acompañó y dio ánimos a diario por entenderme y apoyarme desde el primer día. A mi padre, por impulsarme a hacer mi doctorado y sus palabras constantes de cariño. A mi hermana, por enseñarme el valor de la constancia y la tenacidad. A Ernesto, por tanto apoyo y tanto cariño cada día, por los largos viajes a la selva, por cada paso que hemos dado juntos en Colombia y México. ¡Todo mi amor y mi admiración!¡Vamos por más!

Epígrafe

<u>*Entre laureles*</u>

Nudos de plantas enmarañan sus ramas y sus enormes cuerpos de madera. Los simios se pasean sobre estos recovecos después de devorar las carnes de sus frutos. Al banquete se unen aves, ardillas, ratones y hasta las más minúsculas alimañas, tirando a su paso miles de semillas. Estudio a estos gigantes desde el suelo, tomo muestras de sus hojas usando una larga vara metálica coronada por una cuchilla, incluso me ayudo de una escalera. Otras veces uso boomerangs improvisados, o me resigno a husmear entre lo que cae a la tierra.

He dedicado los últimos años de mi vida a investigar las condiciones en que viven varias especies vegetales de la familia Lauraceae*, grupo misterioso que lleva mi nombre a modo de predestinación. He sorteado la lluvia, las alturas, el sol, y el calor, siguiendo la pista de sus travesías a través de continentes. Después de incontables viajes hallé junto al mar una isla en tierra, el corazón de un volcán. Allí, en medio de un pedregal, se establecieron entre las sombras caprichosas de la selva.*

A falta de gallos, despertaba con los gritos guturales de los aulladores, los chasquidos de los tucanes, y el escándalo de las oropéndolas. Protegía mis brazos con una camisa larga, y mis piernas con botas anticulebras, ataba un pañuelo en mi cabeza para domar la melena. Armada de formatos, etiquetas, prensas, periódicos, lápices, marcadores, reglas, sándwiches, dulces y mucha agua, emprendía la jornada. Salía al ansiado encuentro botánico como si fuera un ritual, que iniciaba antes del calor de la mañana y terminaba entre zancudos. Volvía en las noches a meditar lo aprendido y organizar las muestras del día luego de un té canela. Tomaba una ducha para quitar los pinolillos que infestaban mi piel, y dormía arrullada por la lluvia.

Además de ser merienda de algunos roedores, descubrí que las semillas son en sí mismas un universo de vida y muerte del tamaño de una aceituna. ¡Una vida, la de embrión vegetal, por muchas otras vidas! Decenas de insectos crecen al interior consumiendo todos los tejidos que alimentarían a la planta por nacer. Otros, en cambio, matan a los anteriores para alimentar a sus propios hijos. Estas pequeñas cajas de Pandora están llenas de escarabajos, polillas, avispas, moscas y hormigas. Seguramente se ven obligados a emprender viajes inciertos en busca de un hogar en los años en que las semillas escasean. ¿Qué será de ellos cuando falte el bosque?

Las plántulas que logran emerger pasan penurias para sobrevivir a la oscuridad, una penumbra que generan sus madres al extender sus ramas para alcanzar los rayos de sol en las alturas del bosque. En compensación, cargan como mochilas los vestigios de las semillas que les dieron vida; allí almacenan reservas de alimento, la única ayuda que la nueva generación recibe para sobrevivir al ataque de hongos y herbívoros. He confirmado que, entre más pesado su itacate, mejor.

Soy testigo de cómo todas las especies de laureles sufren estos y muchos otros males. Las poblaciones se envejecen, y son pocas las plantas jóvenes que se hacen adultas de entre millones. ¿Por qué sus hijos mueren tanto? Largos meses les observé, registrando el paso del tiempo en kilos de fotos y datos. Les hice crecer en nuevas topografías, probar otros suelos, pero la oscuridad es implacable.

Entender a los adultos ha sido más difícil. Son esquivos, pero viven en grupos, así que encontrar a uno usualmente asegura encontrar más. Lograrlo requirió la ayuda de todo un ejército de biólogos *y amigos entusiastas, un sabio naturalista y varios campesinos de las lagunas, que conocen la selva como la palma de su mano y saben desde niños todos sus enigmas.*

Después de su paso por un improvisado estudio fotográfico, guardé los cientos de hojas colectadas entre periódicos, como quien construye un libro de secretos vegetales. Algunas reposan en herbarios, dónde otros curiosos podrán ver durante siglos una muestra de su existencia. Otras, reducidas a polvo, terminaron entre vasos de cristal, tubos humeantes, ácidos corrosivos, y reacciones azules y amarillas, rebelándome las huellas que los nutrientes del suelo dejaron en ellas.

Análisis químicos y modelos matemáticos me han servido para reconocer que, a pesar de parecerse, los árboles de estas especies se enfrentan a los mismos retos de diferente forma, y por ello, no deben ser asumidas cómo iguales. No administran igual sus recursos, ni toleran la misma variación ambiental. ¿Cómo influirá esto en su futuro? ¿Tendrán las mismas oportunidades de prevalecer cuando su entorno cambie? Eso aún está por verse.

Entre tanto, con más preguntas que respuestas, he escrito sobre ellas, he hablado con mis colegas sobre su complejidad. He guardado con cuidado las muestras que generosamente me ofrecieron en colecciones, refrigeradores y estantes de mi laboratorio. Ahora comparto un poco de sus secretos con el mundo, las dibujo, las admiro. Ellas, cómo lo han hecho siempre, comparten sus bondades con quienes habitan los bosques, dándoles refugio, leña y la belleza de la selva.

Laura J. Giraldo Kalil

Índice

Resumen

Al compartir su historia evolutiva, las especies cercanamente emparentadas suelen tener nichos ecológicos y fenotipos similares. La diferenciación de nicho ecológico se ha propuesto como uno de los principales mecanismos para explicar la evolución, coexistencia y distribución de dichas especies cuando habitan en una misma región geográfica, ya que permitiría distintas formas de aprovechamiento de los recursos o de respuesta a las presiones ambientales compartidas. Tal es el caso de las especies arbóreas del género *Damburneya* (Lauraceae) que abundan en el sotobosque y el dosel superior de las selvas húmedas de México y Centroamérica, donde son apreciadas y empleadas localmente por la calidad de su madera. Sus frutos carnosos son bayas de una sola semilla y constituyen una fuente importante de alimento para aves, mamíferos como monos, y roedores, además de varias especies de insectos que consumen y desarrollan su ciclo de vida dentro de las semillas. Dado que las especies de este género son principalmente dispersadas por aves frugívoras grandes y mamíferos como roedores, y comparten además el mismo síndrome de dispersión, las diferencias en su distribución y abundancia dentro de una misma región geográfica se han atribuido a otros factores como la especialización a ciertas elevaciones o tipos de suelo, o bien, a diferencias en su fenología reproductiva. Sin embargo, aún no se ha explorado a fondo la forma en que la variación ambiental afecta a las especies de *Damburneya*, ni cómo su variación fenotípica puede influir en ello. Así mismo, aún se desconoce mucho de la historia natural de las especies de este género, incluso si el reclutamiento y las condiciones que lo limitan son similares entre especies.

Esta tesis evaluó, la diferenciación de nicho ecológico, tanto desde la perspectiva abiótica a (nicho Grinnelliano, a gran escala espacial), como desde la perspectiva biótica (nicho Eltoniano, a escala local), abarcando diferentes escalas espaciales y temporales. Se investigó la importancia relativa de factores ambientales bióticos y abióticos potencialmente involucrados en la distribución, la variación fenotípica, y la diferenciación ecológica y entre especies cercanamente emparentadas de *Damburneya*. Para ello, se analizaron las diferencias ecológicas entre las cuatro especies arbóreas del género presentes a lo largo de un gradiente ambiental en la selva alta perennifolia de la Reserva de la Biosfera de Los Tuxtlas (*Damburneya ambigens, D. colorata, D. gentlei* y *D. salicifolia*), en el estado de Veracruz, en el sureste de México, integrando tres enfoques para el estudio del nicho ecológico, que se abordan en los diferentes capítulos de esta tesis.

El primer capítulo se centra en la caracterización del nicho abiótico (Grinelliano) de las especies a partir de su distribución geográfica y su relación con la variación ambiental mediante modelos de nicho ecológico a escala continental. Con este fin, se emplearon datos climáticos y

edáficos, así como las localidades en dónde se han colectado muestras de las cuatro especies arbóreas estudiadas, incluyendo colectas de campo de este proyecto y localidades de ejemplares depositados en herbarios. Además, se hicieron comparaciones entre los nichos modelados para determinar si ocurre solapamiento de nicho entre las especies.

El segundo capítulo se enfocó en el nicho funcional, y aborda el análisis de las diferencias interespecíficas en rasgos foliares asociados a las estrategias funcionales de las especies estudiadas a escala local, y su relación con la variación edáfica y la elevación en la región de Los Tuxtlas. Dichas estrategias caracterizan los compromisos entre procesos involucrados en la adquisición, el uso y retorno de recursos como la captura de luz, las tasas de ganancia de carbono y la longevidad foliar. Con este fin, se midieron las propiedades físicas y químicas del suelo en seis parcelas a baja y alta elevación (0-300 m y 650-1100m, respectivamente), y se colectaron muestras de hojas para cuantificar cinco rasgos funcionales foliares involucrados en el espectro de economía foliar (área foliar específica, contenido foliar de masa seca, contenido de nitrógeno y fósforo, y proporción nitrógeno: fosforo foliar).

En el tercer capítulo se caracterizaron y compararon los nichos de regeneración de *D. ambigens* y *D. salicifolia,* las dos especies de *Damburneya* más abundantes en la región de Los Tuxtlas, particularmente, se evaluó si el establecimiento de plántulas podría diferir entre dichas especies dependiendo de la altitud, el suelo, el ataque de enemigos naturales y el tamaño de la semilla. Se establecieron experimentos de trasplantes recíprocos en sitios con suelo y elevación contrastante (alta: 1100 m, baja: 150 m), empleando en cada sitio varias plántulas hermanas provenientes de diferentes poblaciones y árboles maternos (i.e., familias genéticas). Se midió el ataque de enemigos naturales y la masa de las semillas, y se analizaron sus efectos sobre el crecimiento de las plántulas, la supervivencia, y varios rasgos relacionados con el vigor (altura, número de hojas y área foliar). Asimismo, se hicieron análisis de genética cuantitativa para evaluar los efectos potenciales de la variación genética sobre el vigor y la supervivencia de las plántulas mediante la comparación de la variación fenotípica de plántulas provenientes de diferentes árboles parentales. Por otra parte, los efectos de la plasticidad fenotípica se evaluaron analizando la variación fenotípica de plántulas hermanas (del mismo árbol parental) creciendo en diferentes ambientes.

Además, gracias al trabajo de campo y la revisión de literatura fue posible profundizar en aspectos básicos de la historia natural de tres de las cuatro especies de *Damburneya* en las que se enfocó esta investigación (*D. ambigens, D. gentlei, D. salicifolia*), tales como la asociación de insectos a los frutos y semillas. Si bien esto no fue un objetivo de esta tesis, posibilitó generar información inédita sobre las comunidades de insectos asociadas a los frutos de las especies de

Damburneya, así como la depredación de semillas previa a la dispersión y sus efectos potenciales en la germinación. Además de mostrar nuevas vías interesantes de investigación en la ecología de estas especies, esta información dio lugar a varias publicaciones desarrolladas durante el curso de este proyecto que se resumen brevemente en la sección de anexos de esta tesis.

A grandes rasgos, el nicho climático es similar entre especies a escala continental, siendo los climas húmedos y cálidos los más idóneos para la ocurrencia de las especies de *Damburneya*. En contraste, el nicho edáfico tiende a diferir entre especies, lo que en *D. salicifolia* puede explicarse por los amplios rangos de pH que esta especie tolera en su rango de distribución. Estos resultados sugieren que las especies pueden tolerar mayor variación edáfica que climática, y apoyan la hipótesis del suelo como potencial promotor de diferenciación ecológica dentro del género *Damburneya*. Asimismo, hubo diferencias en las estrategias funcionales foliares entre las especies estudiadas, en respuesta a la variación ambiental local a lo largo de un gradiente de elevación. Las hojas de *D. ambigens* se tuvieron una estrategia conservativa (respecto a las demás especies estudiadas), con altas concentraciones de nutrientes en hojas con alta inversión en biomasa, rasgos usualmente relacionados con un alto costo y un retorno lento del carbono invertido para la construcción de hojas. En contraste, las hojas de *D. gentlei* presentaron una estrategia adquisitiva, con altas concentraciones de nutrientes en hojas de baja inversión en biomasa, mientras que las hojas de *D. salicifolia* y *D. colorata* mostraron una amplia variación abarcando ambas estrategias.

En cuanto al nicho de regeneración, tanto para *D. ambigens* como para *D. salicifolia*, la elevación, el tamaño de las semillas y la variación genética explicaron la variación de los rasgos relacionados con el vigor de las plántulas. El valor adaptativo del tamaño de la semilla difirió entre especies, pero en general las semillas grandes favorecieron la supervivencia de las plántulas en la zona baja, en donde la mortalidad fue marcadamente mayor que en las áreas con elevaciones mayores. Los experimentos de campo sugieren que el reclutamiento de semilla a plántula para las cuatro especies es bajo en las localidades con menor elevación; a esto se suma la baja abundancia de estadios juveniles (particularmente latizales y fustales) en zonas bajas en las parcelas de muestreo de árboles establecidas para la medición de rasgos funcionales. La elevación y el suelo no parecieron influir de forma distinta en el reclutamiento de las plántulas de ambas especies

Las especies estudiadas difieren en su respuesta a las presiones ambientales y en sus fenotipos, lo que podría contribuir a explicar diferencias en su abundancia y distribución a diferentes escalas espaciales, y potencialmente reducir la competencia interespecífica y favorecer su coexistencia. Si bien encontramos que los rasgos de las plántulas y árboles varían con la elevación, y que algunas diferencias ecológicas entre especies podrían estar relacionadas con la variación edáfica, los resultados sugieren un escenario más complejo. La variación entre las especies responde, probablemente, a la acción simultánea de múltiples factores ambientales bióticos y abióticos, con efectos cambiantes a lo largo de las diferentes etapas del ciclo de vida. Por lo anterior, podría esperarse que estas especies se vean afectadas de diferente manera por variaciones ambientales como el cambio climático, la deforestación o el cambio en el uso del suelo, o requerir distintas estrategias de manejo. Por último, es poco lo que se sabe del estado actual de las poblaciones de las especies estudiadas, incluso en el caso de *D. ambigens,* que ha sido investigada desde hace varias décadas en la región de Los Tuxtlas. Esto es particularmente evidente en el caso de *D. colorata,* para la cual se conocen escasos registros. Por lo tanto, se recomienda el monitoreo a largo plazo de las poblaciones naturales de *D. ambigens*, *D. colorata, D. gentlei* y *D. salicifolia* en futuros estudios.

Abstract

By sharing their evolutionary history, closely related species often have similar ecological niches and phenotypes. Ecological differentiation has been proposed as one of the main mechanisms to explain the evolution, coexistence, and distribution of these species when they inhabit the same geographic region since niche divergence would allow different forms of resource utilization or response to shared environmental pressures.

Such is the case of the genus *Damburneya* (Lauraceae). These tree species are abundant in the understory and canopy of the rainforests of Mexico and Central America, where they are used locally for timber. The fleshy fruits are one-seeded berries that are an important food source for birds, mammals such as monkeys and rodents, as well as several species of insects that consume the seeds and develop their life cycle within them. All the species of this genus are dispersed by large frugivorous birds and mammals such as rodents, and share the same dispersal syndrome; therefore, the differences in their distribution and abundance within the same geographic region have been attributed to other factors like edaphic and elevational specialization, or interspecific differences in reproductive phenology. However, it remains unexplored how environmental variation affects Damburneya species and the extent to which this relies on the species' phenotypic variation. Likewise, much remains unknown about the natural history of species in this genus, even if recruitment and the conditions constraining it are similar among species.

This thesis evaluated ecological niche differentiation from both abiotic (Grinnellian niche, large spatial scale) and biotic (Eltonian niche, local scale) perspectives, spanning different spatial and temporal scales. The relative importance of biotic and abiotic environmental factors potentially involved in the distribution, phenotypic variation, and ecological differentiation among sympatric closely related species of *Damburneya* with different spatial scales was investigated. To this end, the ecological differences among the four tree species of the genus occurring along an environmental gradient in the tropical rainforest of the Los Tuxtlas Biosphere Reserve (*Damburneya ambigens, D. colorata, D. gentlei, and D. salicifolia*) in the state of Veracruz, in southeastern Mexico, were assessed by integrating three approaches. Each approach was addressed in separate chapters of this thesis, as described below.

The first chapter focuses on the characterization of the abiotic niche (Grinellian) of the species based on their geographic distribution and its relationship with environmental variation through ecological niche models at a continental scale. For this purpose, climatic and edaphic data were used, as well as the localities where samples of the four tree species studied have been collected, including field

collections of this project and localities of specimens deposited in herbariums. In addition, modeled niches were compared to determine if niche overlap occurs among species.

The second chapter focused on the functional niche and addressed the analysis of interspecific differences in foliar traits associated with functional strategies of the species studied at the local scale, and their relationship with edaphic variation and elevation in the Los Tuxtlas region. Leaf functional strategies characterize the tradeoffs between processes involved in resource use, uptake, and return, such as light capture, carbon gain rates, and leaf longevity. Soil physical and chemical properties were measured in six plots at high and low elevations (0-300 m, and 650-1100 m, respectively), and leaf samples were collected to quantify five leaf functional traits arranged across a leaf economy spectrum (leaf dry matter content, specific leaf area, leaf nitrogen and phosphorus concentration, and nitrogen: phosphorus ratio).

The third chapter characterized and compared the regeneration niches of *D. ambigens and D. salicifolia*, the two most abundant *Damburneya* species in the Los Tuxtlas region. It was assessed whether seedling establishment could differ between these species depending on altitude, soil, natural enemy attack, and seed size. Reciprocal transplant experiments in contrasting soils and elevations (high: 1100 m, low: 150 m) were performed using several sibling seedlings from different maternal trees (i.e., genetic families) and populations. The attack of natural enemies, seed mass, and their effects on seedling growth, survival, and vigor traits (height, number of leaves, leaf area) were measured. Quantitative genetics analyses were performed to assess the potential effects of genetic variation on survival and vigor by comparing the phenotypic variation of siblings from different maternal trees. Moreover, the effects of phenotypic plasticity were evaluated by analyzing the phenotypic variation of sister seedlings (from the same parental tree) growing in different environments. In addition, as a result of fieldwork and literature review, it was possible to delve into basic aspects of the natural history of three of the four *Damburneya* species studied here (*D. ambigens, D. gentlei, D. salicifolia*), such as the association of insects to fruits and seeds. Although this was not an objective of this thesis, it allowed for generating novel information on the insect communities inhabiting the fruits of *Damburneya* and the potential effects of pre-dispersal seed predation on germination. Besides showing interesting new avenues of research in the ecology of these species, this information led to several publications developed during this project that are briefly shown in the appendices section of this Ph.D. thesis.

Overall, the climatic niche is similar among species on a continental scale, with humid and warm climates being the most suitable for the occurrence of *Damburneya* species. In contrast, edaphic niches tend to differ among species; for *D. salicifolia*, this could be explained by the wide pH ranges that it experiences across its distribution range. These results suggest that the species can tolerate wider edaphic than climatic variation and support the hypothesis of soil as a driver of ecological differentiation within *Damburneya*. In addition, there were differences in leaf functional strategies among trees of the species studied in response to local environmental variation along an elevation gradient. The leaves of *D. ambigens* had a conservative strategy (compared to the other studied species) with high nutrient concentrations in leaves with high biomass investment, a common syndrome when there are high costs and slow return of the carbon invested for leaf construction. In contrast, the leaves of *D. gentlei* had an acquisitive strategy, with high nutrient concentrations in leaves with low biomass investment. The leaves of *D. salicifolia* and *D. colorata* had a wide variation encompassing both strategies. Regarding the regeneration niche, elevation, seed size, and genetic variation explained variation in traits related to seedling vigor. Moreover, seed adaptive value differed among species, but in general, large seeds favored seedling survival at low elevations, where mortality was markedly higher than at high elevations. Field experiments suggest that seed-to-seedling recruitment for all four species is low at lower elevation locations; in addition, the abundance of juvenile stages (particularly saplings) is reduced at low elevations in the tree sampling plots established for measuring functional traits. Elevation and soil did not appear to differentially influence seedling recruitment of the two species.

The species studied differed in their phenotypes and response to environmental stresses, likely explaining differences in abundance and distribution at different spatial scales and potentially reducing interspecific competition and favoring their coexistence. The studied species differ in their phenotypes and responses to environmental stresses, likely explaining differences in abundance and distribution at different spatial scales. Although we found that seedling and tree traits vary altitudinally and that some ecological differences among species could be related to edaphic variation, our results suggest a more complex scenario. The observed variation among species is probably caused by the simultaneous action of multiple biotic and abiotic environmental factors with changing effects throughout the different stages of the life cycle. Therefore, these species could be expected to be differentially affected by environmental changes in climate, land use, or deforestation rates; hence, they likely require different management strategies. Finally, little is known about the current condition of natural populations of the studied species, even in the case of *D. ambigens*, which has been studied since several decades ago in the Los Tuxtlas region. This is particularly evident for *D. colorata*, which is known only by scarce records. Hence, long-term monitoring of natural populations of *D. ambigens*, *D. colorata*, *D. gentlei*, and *D. salicifolia* is highly recommended for future studies.

Introducción general

La forma en que cada especie responde a la heterogeneidad ambiental depende de su variación fenotípica, y genética, así como de su historia evolutiva; dichos factores interactúan de formas complejas a escala local y regional y pueden ser determinantes en el nicho de las especies (Violle & Jiang, 2009; Chase & Myers, 2011; Hart et al., 2016). El nicho es el conjunto de condiciones ambientales bióticas y abióticas que permiten a las especies satisfacer sus requerimientos para mantener poblaciones viables, además del impacto que las especies mismas tienen sobre su ambiente (Hutchinson, 1957; Hutchinson, 1959; Chase & Leibold, 2003); esta definición, que fue descrita matemáticamente como un hipervolumen de n dimensiones, surgió con el fin de entender las limitaciones a la coexistencia de especies y el mantenimiento de la diversidad en las comunidades biológicas (Hutchinson, 1957 y 1978). El nicho está estrechamente relacionado con las áreas de distribución de las especies, que dependen de la capacidad de dispersion de las mismas, así como de la accesibilidad a regiones geográficas con condiciones bioticas y abióticas favorables para sostener el creciemiento poblacional (Soberón and Nakamura, 2009; Peterson et al., 2011).

Al compartir gran parte de su historia evolutiva, las especies cercanamente emparentadas presentan similitudes ecológicas, genéticas, fenotípicas y ambientales, que hacen muy probable que ocurran en simpatría dentro de una comunidad (Peterson et al., 1999; Wiens & Graham, 2005). Sin embargo, tales similitudes entre las especies podrían llevar a que sus nichos se solapen y por lo tanto compartan parcialmente sus requerimientos de recursos, restricciones fisiológicas, interacciones bióticas, u otros factores ecológicos al encontrarse en una misma región geográfica; esto podría generar exclusión por competencia, limitando la coexistencia de especies (Hutchinson, 1959; Macarthur & Levins, 1967; Chesson, 2000) y daría lugar al desplazamiento de caracteres, es decir, a la selección de rasgos divergentes (Cavender-Bares et al., 2009; Stuart & Losos, 2013). En este contexto, un mecanismo que permitiría explicar la coexistencia estable de especies a largo plazo es la diferenciación de nicho. Esto es, el aprovechamiento diferencial de los recursos por parte de cada especie o su respuesta diferencial al ambiente, lo que afecta directamente las tasas de crecimiento poblacional de las especies y puede ocurrir a diferentes escalas temporales y espaciales (Pacala & Roughgarden, 1985; Chesson, 2000; Silvertown, 2004).

De acuerdo con la teoría moderna de la coexistencia, la diferenciación de nicho puede ocurrir por mecanismos independientes de las fluctuaciones ambientales a escala local (p. ej., la depredación dependiente la frecuencia o la diferenciación de recursos o enemigos naturales como herbívoros o patógenos), o por mecanismos dependientes de dichas fluctuaciones por los cuales las especies responderían diferencialmente a la variación espacial y temporal del ambiente (Chesson, 2000). Entre estos últimos mecanismos se encuentran el efecto de almacenamiento, según el cual las especies pueden acumular los beneficios de las temporadas favorables para compensar las temporadas desfavorables (p. ej., los nuevos individuos de la población que nacen en una época altamente productiva pueden prosperar en épocas de baja reproducción favoreciendo el crecimiento poblacional; Chesson, 2000). Otros mecanismos que contribuyen a la diferenciación de nicho son la no linealidad relativa, según la cual las especies de una comunidad son diferencialmente afectadas por la competencia, o la covarianza entre la adecuación y la densidad, que ocurriría si las especies están irregularmente distribuidas en el paisaje (Chesson, 2000). Por otra parte, la coexistencia también podría ser inestable a largo plazo si las especies y sus tasas vitales son similares entre sí, y depender de procesos aleatorios al interior de las comunidades (Chesson, 2000; Hubbell, 2001; Chase & Leibold, 2003; HilleRisLambers et al., 2012).

El estudio de la coexistencia y la diferenciación de nicho es particularmente interesante en ecosistemas altamente diversos como las selvas húmedas tropicales. Se ha sugerido que las especies de plantas cercanamente emparentadas coexistiendo en simpatría en dichos ecosistemas pueden estar divergir por compromisos ("tradeoffs") entre el crecimiento y la supervivencia si estos procesos implican diferentes patrones de asignación de recursos (Kitajima & Poorter, 2008). Esto ha dado lugar a muchas investigaciones que han integrado el análisis de la variación fenotípica y genética, y la plasticidad fenotípica con el efecto de factores ambientales como la luz (Valladares et al., 2000; Yamada et al., 2006), el suelo (Endara & Jaramillo 2011; Dent & Burslem, 2016; Bartholomew et al., 2022), la topografía (Itoh et al., 2003; Baltzer et al., 2005; Baldeck et al., 2013; Allié et al., 2015; Schmitt et al., 2021), la disponibilidad de agua y las interacciones bióticas (Eichhorn et al., 2010) para entender cómo dicha variación ambiental puede afectar a las plantas a lo largo de la ontogenia, cómo se relaciona con su distribución, las dinámicas poblacionales de las especies, su historia evolutiva, y el ensamblaje de las comunidades (Paz et al., 1999; Paz & Martínez-Ramos, 2003; Paz et al., 2005; Baraloto et al., 2007; Baraloto et al., 2012; Sedio et al., 2012; Lan et al., 2016; Dexter et al., 2017). No obstante, hacen falta estudios que aborden la diferenciación de nicho en múltiples escalas espaciales y temporales, considerando simultáneamente varios mecanismos de coexistencia para entender de forma más integral los limitantes y requerimientos de las especies dentro de sus comunidades.

El estudio del nicho se ha enfocado en dos principales aproximaciones complementarias: el nicho Grinnelliano, que es aquel descrito a partir de las variables abióticas que, siendo independientes de las especies focales, restringen la distribución de las mismas (variables scenopoeticas; Grinell, 1917; Soberón, 2007; Peterson et al., 2011); y el nicho Eltoniano, que es aquel descrito a partir de variables bionómicas que dependen de la especie (p. ej. Interacciones bióticas) y abarca tanto el consumo de recursos como el impacto de las especies sobre su entorno a una escala local (Elton, C. 1927; MacArthur & Levins 1967; Chase & Leibold, 2003; Soberón, 2007; Peterson et al., 2011). Esta investigación aborda el nicho Grinnelliano y Eltoniano, además de la variación fenotípica para entender las diferencias ecológicas entre varias especies arbóreas cercanamente emparentadas que se encuentran en simpatría en algunas partes de sus áreas de distribución y habitan las selvas húmedas tropicales de México y Centroamérica.

Un enfoque ampliamente utilizado para estudiar la diferenciación de nicho es el modelado de nichos ecológicos con base en la distribución geográfica de las especies y la variación ambiental abiótica. Este método caracteriza el nicho Grinelliano de las especies con base en la variación ambiental abiótica a gran escala y en las localidades donde se han reportado las especies (Soberón & Peterson, 2005; Peterson et al., 2011). Desde esta aproximación, la diferenciación de nicho puede evaluarse mediante la cuantificación del solapamiento o similitud de los nichos de pares de especies, comparando para ello las condiciones ambientales que experimenta cada especie respecto a aquellas que experimentan ambas (Peterson et al., 1999; Warren et al., 2008; Broennimann et al., 2012).

Con respecto al nicho Eltoniano, la diferenciación de nicho también se puede investigar mediante el estudio de la expresión fenotípica de rasgos funcionales de los individuos (Reich et al., 1999; McGill et al., 2006; Violle & Jiang, 2009; Adler et al., 2013; Carmona et al., 2016), que son aquellos rasgos fenológicos y morfo-fisiológicos que repercuten en la adecuación (*fitness*) de los individuos por su efecto sobre su supervivencia, crecimiento y reproducción (Reich et al., 2003; Violle et al., 2007; Carscadden et al., 2017). Los rasgos funcionales están involucrados en las respuestas de los organismos a su ambiente biótico y abiótico, y se espera que su variación intraespecífica refleje la amplitud del nicho de las especies, es decir, el rango de recursos, interacciones, hábitats y ambientes usados por cada especie (Adler et al., 2013; Sexton et al., 2017). La variación de los rasgos funcionales puede promover la diferenciación ecológica, en la medida en que favorezca el desempeño diferencial de las especies a lo largo de gradientes ambientales. Tal proceso de diferenciación puede ser promovido por mecanismos que afecten la abundancia, distribución y capacidad competitiva de las especies, como la heterogeneidad espacial y temporal, la explotación diferencial de recursos, y el ataque de enemigos naturales (Adler et al., 2013).

Por otra parte, la diferenciación de nicho y la coexistencia de especies de plantas también pueden analizarse mediante el estudio del nicho de regeneración, que se refiere a los requerimientos de las especies para la incorporación de nuevos individuos a las poblaciones (Grubb, 1977). El nicho de regeneración abarca varias etapas que pueden diferir entre especies e involucran varios rasgos de historia de vida como la producción de semillas viables, la dispersión de semillas y su variación espacial y temporal, la germinación, el establecimiento de las plántulas y el desarrollo de estas a briznales y estadios posteriores (Grubb, 1977; Foster, 1986; Westoby et al., 1992, 1996). Así mismo, es crucial analizar las fuentes intrínsecas y extrínsecas de variación del reclutamiento entre especies, tales como la variación genética, la plasticidad fenotípica, la depredación de semillas, el ataque de herbívoros y patógenos, o la disponibilidad de agua, luz y nutrientes (Janzen, 1971; Grubb, 1977; Foster, 1986; Chapin, 1991; Baraloto et al., 2005; Chávez-Pesqueira & Núñez-Farfán, 2016).

Esta tesis abordó la diferenciación de nicho Grinelliano (abiótico) y Eltoniano (funcional y de regeneración) entre especies arbóreas de la familia Lauraceae Juss., una familia ampliamente distribuida en los trópicos que abarca alrededor de 2500 especies y 50 géneros, y es uno de los grupos más importantes en los bosques tropicales de América (Rohwer, 1993a; van der Werff & Richter, 1996; Lorea-Hernández, 2002). Las especies de Lauraceae se distribuyen en climas cálido-húmedos, aunque algunas especies son capaces de tolerar ambientes semiáridos (Rohwer, 1993a); muchas especies son apreciadas localmente por su madera (Rohwer, 1993a, Ibarra-Manríquez et al., 1997). Los frutos son bayas de una sola semilla, de pulpa rica en lípidos y color negro al madurar (Rohwer 1993a; Kostermans, 1957). Las semillas son principalmente dispersadas por aves frugívoras, y en menor medida por mamíferos como monos, puercoespines, zarigüeyas, roedores y en algunas especies incluso por peces (Kostermans, 1957; Snow, 1981; Weber, 1981; Wheelwright et al., 1984; Gómez-Pompa & del Amo, 1985; Bustamante et al., 1993; Rohwer 1993a; Rohwer 1993b, Wenny 2000; Ganesh & Davidar, 2001). Además, las semillas son consumidas por roedores y varios tipos de insectos depredadores de semillas, entre otros grupos de animales (Gómez-Pompa & del Amo, 1985; Rohwer 1993a; Rohwer 1993b; Beltrán, 2015; Rodríguez-Sánchez et al. 2022 —Apéndice 1—). Las semillas son usualmente recalcitrantes, es decir, no tienen latencia prolongada y germinan una vez maduras (Hong et al., 1996); por lo tanto, no se incorporan al banco de semillas, sino que germinar poco tiempo después de caer al suelo contribuyendo a la formación de un banco de plántulas, especialmente alrededor del árbol parental (Cordova Casillas, 1985; Bustamante et al, 1993; Dirzo et al., 1997; De Carvalho et al., 2008). Las plántulas son criptocotilares, es decir, cuentan con cotiledones de reserva que les proveen recursos maternos durante las primeras etapas del desarrollo (Flores et a1, 1985; Gardner, 1996; Clifford, 1999; Ibarra-Manríquez et al., 2001; Barajas-Guzmán & Álvarez-Sánchez, 2004). A pesar de su importancia, la familia Lauraceae ha sido poco estudiada en comparación con otros grupos de angiospermas, debido en parte a la gran similitud morfológica entre especies, a que su compleja taxonomía depende en gran medida de los rasgos reproductivos (i. e. morfología de flores y frutos), y al hecho de que los árboles de muchas especies son bastante altos, lo que limita la colecta de estructuras vegetativas y reproductivas (Rohwer, 1993a; van der Werff & Richter, 1996; Lorea-Hernández, 2002).

Esta investigación se centró en cuatro especies del género *Damburneya* Raf., que anteriormente se incluía dentro del género *Nectandra* Rol. Ex Rottb. En el grupo *Nectandra coriacea*, y fue recientemente reinstaurado como un género distinto por Trofimov et al. (2016), con base en marcadores moleculares y particularidades morfológicas que se habían observado previamente (Rohwer, 1993b; Rohwer & Kubitzki, 1993; Chanderbali et al., 2001; Trofimov et al., 2016). La distribución de *Damburneya* se extiende desde México hasta Centro y Sudamérica, y Las Antillas (Trofimov et al., 2016). Las especies de este género son arbóreas y algunas de ellas de gran porte, llegando incluso a ser elementos emergentes en el dosel de los bosques; tienen flores hermafroditas, pequeñas, y durante su fructificación, que ocurre generalmente en periodos supra anuales, se generan miles de bayas de una sola semilla. (Rohwer, 1993b; Dirzo et al. 1997). Los principales dispersores son aves frugívoras como tucanes y tiránidos, además de mamíferos como roedores (Rohwer, 1993).

Aunque las especies de *Damburneya* comparten el mismo síndrome de dispersión y por ende probablemente también los mismos dispersores, las especies simpátricas suelen diferir en sus patrones de abundancia y distribución espacial (Rohwer & Kubitzki, 1993; Giraldo-Kalil et al., 2022). Se ha propuesto que la diferenciación ecológica podría ser frecuente en el género y actuaría como un mecanismo para su diversificación. Este mecanismo explicaría los patrones de distribución local de las especies y reflejaría su especialización y rangos de tolerancia a condiciones ambientales críticas, como la elevación y el tipo de suelo (Rohwer & Kubitzki, 1993). Según esta hipótesis, la diversificación de *Damburneya* ocurrió durante su migración hacia el sur del continente, desde Norteamérica. En el proceso, especies con amplia distribución y tolerancia ecológica generaron ecotipos especializados a determinados rangos de elevación o tipos de suelo, o con diferente fenología reproductiva, que eventualmente formaron nuevas especies, con rangos de distribución restringidos (Rohwer & Kubitzki, 1993). Lo anterior es congruente con la variación en las temporadas de fructificación y floración observada entre especies simpátricas (Rohwer, 1993b; Rohwer & Kubitzki, 1993; Ibarra-Manríquez & Sinaca-Colín, 1995), y con estudios que sugieren que el suelo y la topografía determinan la distribución en estas y otras especies de lauráceas (van der Werff, 1992; Sri-Ngernyuang et al., 2003; Srinivas & Krishnamurthy, 2019; Giraldo-Kalil et al., 2022).

La hipótesis de la diferenciación ecológica promovida por la elevación y el suelo (Rohwer & Kubitzki, 1993) fue propuesta con base en la comparación de ejemplares de herbario, las localidades de colecta, y observaciones de campo. Sin embargo, las posibles causas de las respuestas diferenciales de las especies de *Damburneya* a la variación ambiental se desconocen. Si dichas variables afectan la distribución de las especies, se podría esperar que afecten la variación fenotípica y funcional de los árboles o que repercutan sobre el establecimiento, supervivencia y crecimiento de las plántulas. Por otra parte, la variación de la elevación es difícil de evaluar de forma independiente a la variación de otros factores ambientales como la variación edáfica, topográfica, lumínica y climática (Körner, 2007). Esto es importante considerando, por ejemplo, que en las zonas tropicales la variación de la precipitación y la temperatura está fuertemente determinada por la elevación. Por lo tanto, hace falta considerar también el efecto de dichas variables como potenciales causales de la diferenciación ecológica entre las especies del género, y limitantes de sus áreas de distribución.

Este trabajo buscó hacer un análisis integral de las causas potenciales de la diferenciación ecológica entre especies de *Damburneya* a partir de la caracterización del nicho Grinelliano, y Eltoniano (i.e., la variación funcional foliar y el nicho de regeneración). Esto con el fin de entender si las variables ambientales que, en teoría, promueven la diferenciación de nicho, afectan de forma similar a las especies en diferentes escalas espaciales y etapas de su ciclo de vida. Cabe resaltar que esto requiere la consideración de múltiples escalas espaciales y temporales, pues se espera que el nicho Grinnelliano este en general conservado a lo largo de periodos extensos y cambie relativamente poco incluso ante eventos como la especiación (Pearson & Dawson 2003; Peterson, 2011; Peterson et al., 2011; Contreras et al. 2022); mientras que, las aproximaciones del nicho Eltoniano son muy variables en escalas espaciotemporales más cortas (Peterson et al, 2011; Contreras et al. 2022).

Objetivos y estructura de la tesis

Este proyecto tuvo como objetivo analizar y caracterizar de forma integral la diferenciación ecológica entre las cuatro especies del género *Damburneya* Raf presentes en la selva alta perennifolia de la Reserva de la Biosfera Los Tuxtlas, en el estado de Veracruz, México, en respuesta a la variación del suelo, la elevación y el clima. Se evaluó el efecto de estas y otras variables ambientales relevantes en diferentes escalas espaciales, temporales, y etapas del ciclo de vida de las plantas, así como otras fuentes intrínsecas de variación que podrían repercutir en la respuesta de las plantas a su entorno. Así mismo, esta investigación busca aportar información ecológica básica para el desarrollo de futuras investigaciones sobre este importante grupo de plantas.

En el primer capítulo, se evaluó la diferenciación del nicho ecológico Grinnelliano para entender la medida en que el clima y la variación edáfica pueden explicar diferencias y similitudes en la distribución de las especies, empleando para ello modelos de nicho ecológico a escala continental. Los siguientes dos capítulos se enfocaron en el nicho Eltoniano y en medidas y procesos a escala local. En el segundo capítulo, analizamos si la variación foliar de las especies responde a la variación del suelo a lo largo del gradiente de elevación, y si podría indicar diferencias en las estrategias funcionales foliares entre especies a escala local. En el tercer capítulo, se analizó cómo el suelo, la elevación, y factores determinantes para la supervivencia de las plántulas como el ataque de herbívoros y patógenos, y el tamaño de las semillas, pueden afectar el reclutamiento de *D. ambigens* y *D. salicifolia*. Por último, en la sección de anexos, se presenta información complementaria generada durante el trascurso de esta investigación sobre la importancia de los insectos asociados a los frutos y semillas de las especies estudiadas y sus efectos potenciales sobre el reclutamiento de plántulas. Un resumen de las hipótesis planteadas se presenta a continuación en la Tabla 1.

Zona de estudio y especies estudiadas

A continuación, se resume la información más relevante sobre la zona de estudio y las especies estudiadas; la información más detallada se presenta en cada capítulo. Los muestreos para los capítulos 2 y 3, y los anexos fueron realizados en la selva alta perennifolia, en la vertiente nororiental del macizo del volcán San Martín, en La Reserva de la Biosfera Los Tuxtlas. Allí, el gradiente de elevación varía desde el nivel del mar hasta alrededor de 1600 m, el clima es húmedo y cálido; los valores medios anuales de precipitación y temperatura varían altitudinalmente: mientras la precipitación aumenta en las zonas más altas, la temperatura disminuye (4000-6000 mm, 20-24 °C, respectivamente; Gutiérrez-García & Ricker, 2011). Las propiedades fisicoquímicas del suelo también varían, ya que a mayor elevación se incrementa el drenaje y el contenido de arenas, pero es menor la disponibilidad de nutrientes respecto a las zonas bajas (Siebe et al., 1996; Flores-Delgadillo et al., 1999; Sommer-Cervantes et al., 2003; Giraldo-Kalil et al., 2022). En general, los suelos de la zona de estudio presentan un suministro limitado de fósforo disponible para las plantas (Tobón Niedfeldt et al., 2011; Giraldo-Kalil et al., 2022).

La Reserva de la Biosfera Los Tuxtlas es el área protegida del país con mayor número de especies de lauráceas (Lorea-Hernández, 2002), y alberga una alta diversidad florística y faunística de la selva alta perennifolia en México (González-Soriano et al., 1997; Villaseñor et al., 2018). Sin embargo, el área está seriamente amenazada por la drástica fragmentación del hábitat, desde hace más de 50 años, como consecuencia de la agricultura de roza-tumba-quema y el posterior auge de la ganadería bovina (Dirzo & García, 1992; González-Soriano et al., 1997; Mendoza et al., 2005), lo que ha reducido drásticamente la cobertura vegetal (von Thaden et al., 2020) y ha llevado a la degradación de suelos (Figueroa et al., 2020).

Tabla 1. Resumen de las hipótesis planteadas en cada capítulo y los potenciales mecanismos que podrían explicar la diferenciación de nicho entre especies

Título del capitulo	Hipótesis	Mecanismos y procesos implicados
1. Comparación del nicho ecológico Grinnelliano de cuatro especies de *Damburneya* (Lauraceae), a partir de datos climáticos y edáficos a escala continental	Las especies difieren en sus nichos edáficos y climáticos y sus distribuciones se encuentran restringidas de forma distinta por la variación del suelo y el clima.	• Diferencias en dispersión y accesibilidad a áreas con ambientes propicios para las poblaciones de las especies, procesos aleatorios • Selección natural (diferencias en tolerancias fisiológicas entre especies) • Mecanismos de coexistencia dependientes de fluctuaciones ambientales abióticas
2. Diferenciación funcional de especies simpátricas de *Damburneya* en la selva alta perennifolia de Los Tuxtlas	Las especies difieren en patrones de correlación de rasgos funcionales foliares (estrategias funcionales), y en la variación foliar en respuesta a la variación edáfica en el gradiente de elevación	• Mecanismos de coexistencia dependientes de fluctuaciones ambientales bióticas y abióticas ○ Variación local de enemigos naturales o condiciones ambientales • Selección natural, plasticidad fenotípica.
3. Efectos del tamaño de la semilla, el ataque de enemigos naturales, la elevación y el suelo en el reclutamiento de dos especies simpátricas de *Damburneya* de la selva alta perennifolia de Los Tuxtlas	La elevación, el suelo y el ataque de enemigos naturales promueven diferenciación del nicho de regeneración (establecimiento de plántulas) entre *D. ambigens* y *D. salicifolia.* El valor adaptativo de la semilla difiere entre altitudes (es menor en zonas bajas)	• Mecanismos de coexistencia dependientes e independientes de fluctuaciones ambientales bióticas y abióticas ○ Variación local de enemigos naturales o condiciones ambientales • Selección natural • Plasticidad fenotípica.

Damburneya ambigens, conocida como “laurel chilpatillo”, y *D. gentlei* (anteriormente conocida como *Nectandra lundellii* C.K. Allen, ver Figura 3) se distribuyen desde el sur de México hasta Honduras y son árboles de gran tamaño, llegando a superar los 30 m de altura (Rohwer, 1993b). *Damburneya gentlei* suele estar restringida a zonas por debajo de los 300 m de elevación (Rohwer, 1993b). *Damburneya ambigens* es una especie abundante en el dosel de la selva alta perennifolia en la región de Los Tuxtlas (Bongers et al., 1988; Popma et al., 1988; Dirzo et al., 1997; Navarrete-Segueda et al., 2021). Esta especie alcanza su talla máxima en periodos de entre 100 y 200 años (Ricker et al., 2017) y su madera es empleada localmente para la construcción de viviendas. Por otra parte, los árboles más grandes pueden producir más de dos millones de frutos durante las épocas de fructificación, que son principalmente consumidos por aves, monos roedores, y escarabajos (Gómez-Pompa & del Amo-Rodríguez, 1985; Dirzo et al., 1997). Alrededor de los árboles adultos se forman bancos densos de plántulas, cuya tasa de crecimiento aumenta con el incremento de luz cuando se abren claros; sin embargo, el reclutamiento de árboles juveniles es muy bajo en estos sitios (Cordova Casillas, 1985; Martínez-Ramos, 1991).

Por otra parte, *D. salicifolia* es una especie que se distribuye desde México hasta Nicaragua, en varios tipos de bosques, incluyendo selvas húmedas y bosques semi caducifolios (Rohwer, 1993b), abarcando incluso zonas perturbadas y vegetación secundaria (Lorea-Hernández, 2002; Arroyo-Rodríguez et al., 2009; Carreón-Santos & Valdez-Hernández, 2014; García-Licona et al., 2014). *Damburneya colorata*, es muy similar morfológicamente a *D. salicifolia*, pero su distribución es mucho más restringida (sur de México, Belice, y Guatemala). Esta especie es muy poco conocida en diversos aspectos de su biología e incluso cuenta con un bajo número de ejemplares de herbario (GBIF.org, 2022). Las características morfológicas útiles para el reconocimiento de estas especies pueden encontrarse en detalle en la monografía de Rohwer para el género *Nectandra* (1993b).

Figura 1. *Damburneya ambigens:* A) Árbol de aproximadamente 35 m de alto, en la imagen se aprecian los contrafuertes, como referencia, a un lado, el Dr. Juan Núñez Farfán. B) Bloque experimental de plántulas (ver Capitulo 3).

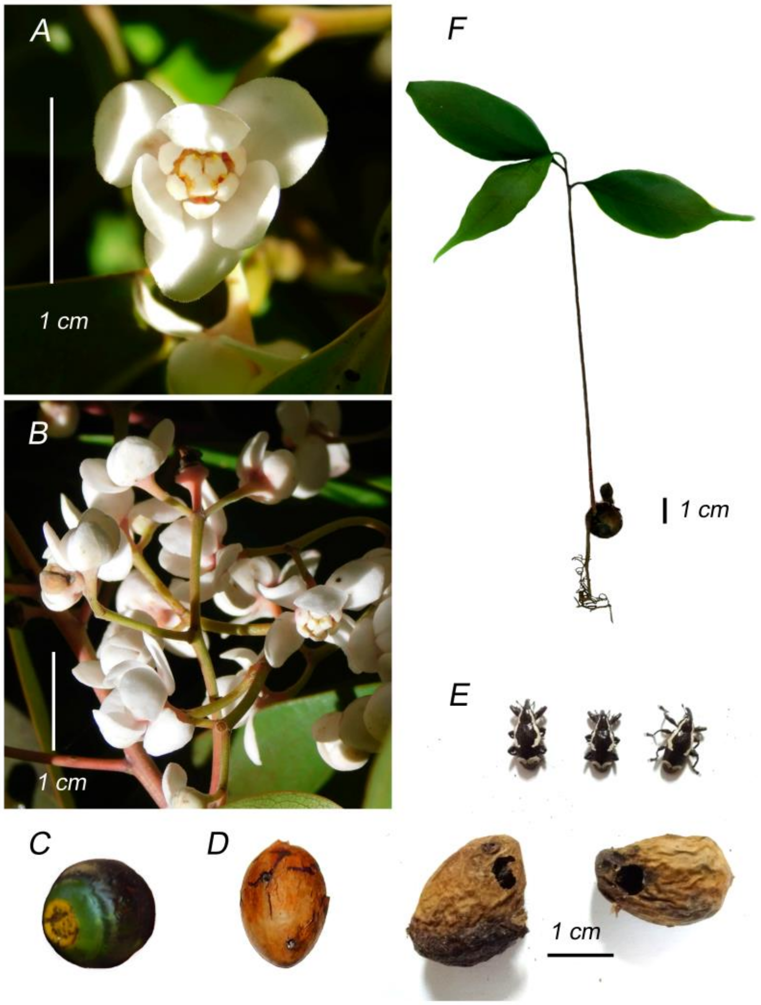

Figura 2. *Damburneya ambigens*: A) Flor, B) Detalle de inflorescencia, C) Fruto maduro, D) Semilla depredada, E) Frutos seco con semillas depredadas y adultos del escarabajo *Heilipus albomaculatus* que se desarrollaron al interior (ver Anexos). F) Plántula.

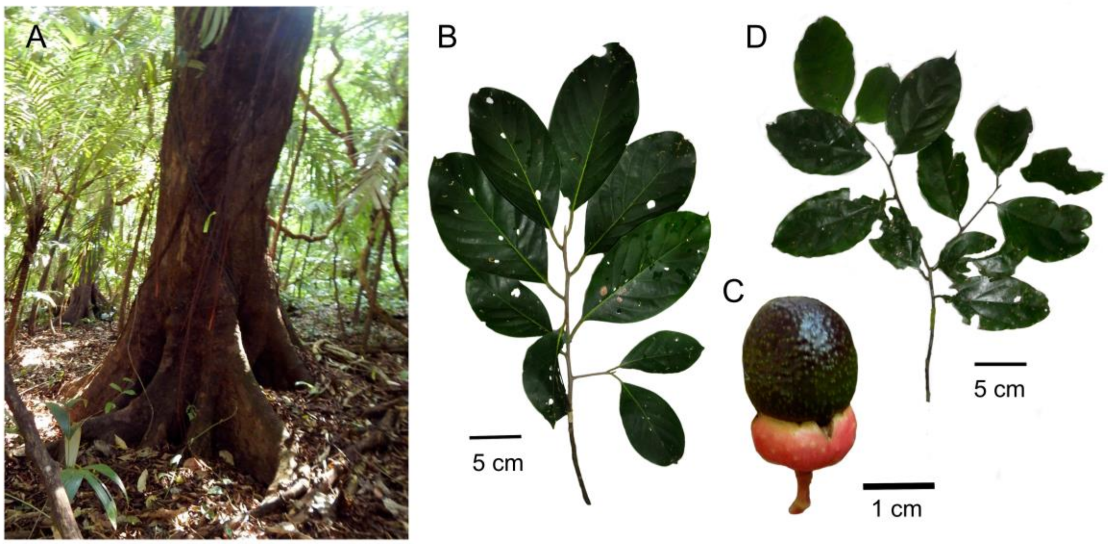

Figura 3. *Damburneya gentlei*: A) Árbol de aproximadamente 25 m, en la imagen destacan los contrafuertes. B) Hojas, C) Fruto maduro. *Damburneya colorata*: D) Hojas.

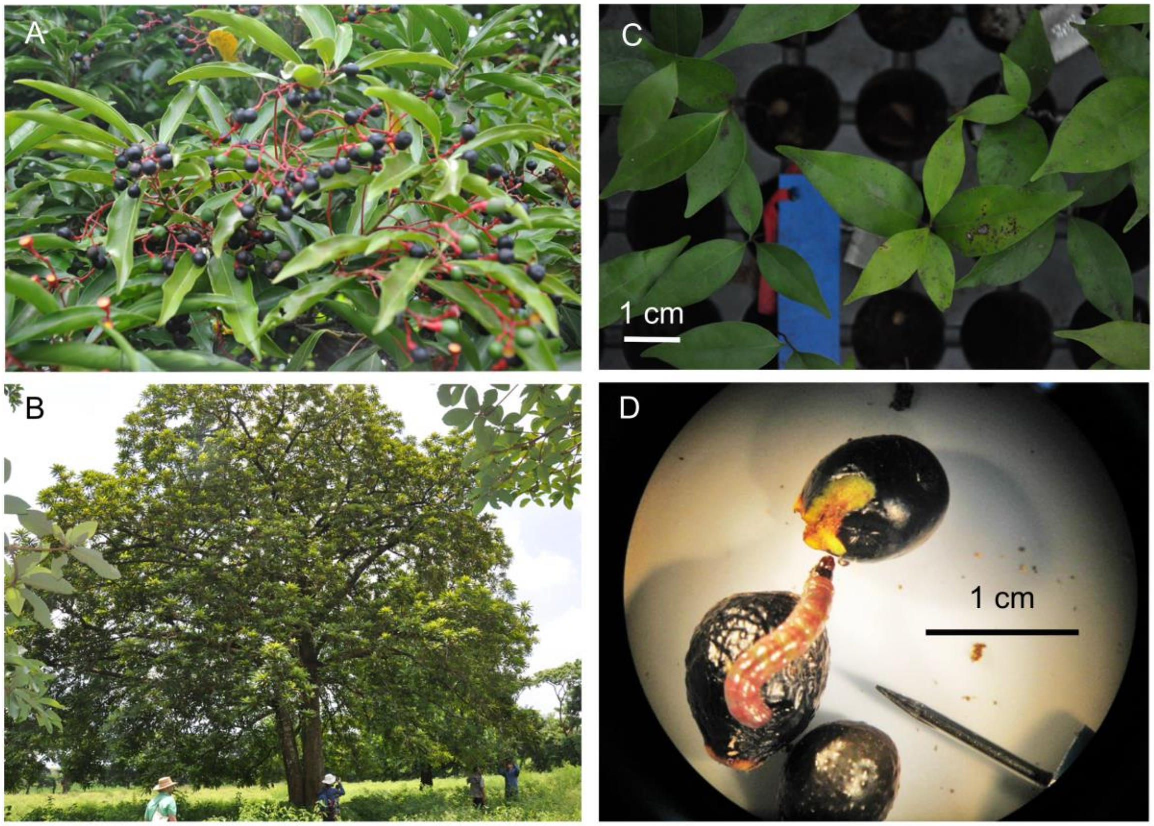

Figura 4. *Damburneya salicifolia*: A) Hojas y frutos, B) Árbol de aproximadamente 12 m de alto. C) Plántulas creciendo en almácigos antes de ser trasplantadas, algunas de ellas con manchas causadas por patógenos. D) Frutos maduros, abajo a la izquierda se ve emergiendo una larva de *Stenoma catenifer* que se alimentaba de la semilla (Ver Anexos).

Capítulo 1

Comparación del nicho ecológico Grinnelliano de cuatro especies de *Damburneya* (Lauraceae) a partir de datos climáticos y edáficos a escala continental

(Enviado para su revisión a *Frontiers of Biogeography*)

Research article

Ecological niche comparison among closely related tree species of Lauraceae using climatic and edaphic data.

Short title: Climatic and edaphic niches of *Damburneya*

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Abstract

Edaphic specialization is considered to promote ecological differentiation among sympatric, closely related, species of *Damburneya*. However, little is known about the effects of soil and other key environmental factors like climate heterogeneity on the niche and distribution of these tree species. Here, we assessed the role of climate and soil on niche divergence and potential distribution of four *Damburneya* species. We performed ecological niche modeling with MaxEnt using three sets of environmental data: climatic-only, edaphic-only, and a combination of both, to characterize species environmental niches and suitable distribution areas. Niche overlap was quantified, and niche similarity was tested to assess niche differentiation among species. Climate and soil determined species' potential distribution. While climatic niches were mostly similar, edaphic niches tended to differ. Warm and moist tropical forests with no water deficit and low seasonality in precipitation are the most suitable environments for the four species. This study supports the previous reports of wide ecological plasticity of *Damburneya salicifolia* based on its distribution and leaf trait variation, as it occurred drier environments with wider temperature and soil pH ranges than the other species. The observed patterns of niche similarity did not reflect the phylogenetic relationships between species, suggesting that the modeled environmental niches do not necessarily reflect past evolutionary processes but rather the current environmental variation along species' distribution. The results suggest that the studied species are similarly constrained by climate and tolerate wide edaphic variation, supporting a potential role for soils on ecological divergence within the genus. On the other hand, performance and predictions varied between models built with different datasets. This research supports the utility of including climate and soil data in ecological niche models to comprehensively analyze the niche and distribution of plant species.

Highlights

- Climate and water availability were more restrictive than edaphic variation to the distribution of *Damburneya* species.
- Niche divergence between the sister species *Damburneya ambigens* and *D. gentlei* was detected, suggesting differences in the environmental constraints of their distribution in agreement with previous findings of divergence in trait-based leaf functional strategies.
- Models here presented provide clues on environmental restrictions to species' distributions and are potential guides for planning future fieldwork, sampling, and data collection, particularly for poorly studied species like *D. colorata.*

Key words

Ecological niche models, Lauraceae, MaxEnt, niche differentiation, SoilGrids, species coexistence, tropical rainforest, WorldClim

Resumen en español

Se considera que la especialización edáfica promueve la diferenciación ecológica entre especies simpátricas y cercanamente emparentadas de *Damburneya*; sin embargo, se sabe poco acerca de los efectos del suelo y otros factores ambientales como la heterogeneidad del clima sobre el nicho y la distribución de estas especies arbóreas. En este trabajo evaluamos el papel del clima y el suelo en la divergencia de nicho y la distribución potencial de cuatro especies de *Damburneya*. Realizamos modelos de nicho ecológico con MaxEnt utilizando tres conjuntos de datos ambientales: sólo climáticos, sólo edáficos y una combinación de ambos para caracterizar los nichos de las especies y las áreas de distribución idóneas para ellas. Además, se cuantificó el solapamiento y se puso a prueba la similitud de nichos para evaluar la diferenciación de nichos entre las especies. El clima y el suelo determinaron la distribución potencial de las especies; mientras que la mayoría de los nichos climáticos fueron similares, los nichos edáficos tendieron a diferir. Los bosques tropicales cálidos y húmedos, sin déficit hídrico y con baja estacionalidad en las precipitaciones, son los ambientes más adecuados para las cuatro especies. Este estudio apoya reportes previos sobre la amplia plasticidad ecológica de *D. salicifolia* basados en su distribución y su variación foliar, ya que tolera entornos más secos y rangos más amplios rangos de temperatura y pH del suelo que las otras especies. Los patrones de similitud de nicho observados no reflejaron las relaciones filogenéticas entre especies, lo que sugiere que los nichos ambientales modelados no necesariamente reflejan procesos evolutivos pasados, sino la variación ambiental actual a lo largo de la distribución de las especies. Los resultados sugieren que las especies estudiadas estas restringidas de forma similar por el clima y toleran amplia variación edáfica, lo que apoya el potencial de los suelos como promotor de divergencia ecológica dentro del género. Por otra parte, el desempeño y las predicciones variaron entre los modelos construidos con diferentes conjuntos de datos. Esta investigación resalta la utilidad de incluir datos climáticos y edáficos en los modelos de nicho ecológico para analizar el nicho y la distribución de las especies de plantas.

Palabras clave:

coexistencia de especies, diferenciación de nicho, Lauraceae, MaxEnt, modelos de nicho ecológico, SoilGrids, selva húmeda tropical, WorldClim.

Introduction

Niche differentiation can promote the coexistence of closely related species by allowing a differential use of resources that can occur in different spatial and temporal scales (Macarthur and Levins, 1967; Pacala & Roughgarden, 1985; Chesson, 2000; Wright, 2002; Silvertown, 2004; Adler et al., 2013). This mechanism contributes to explaining the geographic distribution of plant species (Cavender-Bares and Pahlich, 2009; Aguirre et al., 2015; Martin et al., 2021) and can even be associated with habitat specialization (Brown et al., 2013; Edwards et al., 2013; Aguilar-Romero et al., 2017, Shivaprakash et al., 2022). However, the extent to which closely related species differ in their environmental constraints and how these affect their distribution is not yet well understood in several plant groups and particularly in highly diverse ecosystems like tropical forests.

The niche of species encompasses the ecological conditions and resources necessary to maintain populations, and the effects of species on their environment and on other co-occurring species (Hutchinson, 1957; Chase and Leibold, 2003; Peterson et al., 2011). Because of their shared evolutionary history, closely related species are expected to have conserved ecological niches (Peterson et al., 1999; Wiens and Graham, 2005; Warren et al., 2008; Peterson, 2011), and are commonly able to occupy the same environments (Wiens, 2011). This could limit coexistence if closely related species occurring in sympatry exploit environmental resources in the same way. Alternatively, niche differences could promote species coexistence by preventing interspecific competition and promoting differences in resource exploitation (Macarthur and Levins, 1967; Chesson, 2000).

Ecological niches can be described through large-scale environmental scenopoteic variables (i.e., those independent of the focal species) across the geographic areas occupied by the species. The niches assessed in this way (rather than focusing on biotic interactions and local processes of the focal species) are termed “Grinnellian niches” and inform about the environmental constraints to species distribution acting at large geographical scales (Grinnell, 1917; Hutchinson, 1957, 1978; Soberón, 2007; Peterson et al., 2011). Ecological niche models (ENMs) are useful tools to characterize Grinnellian niches through the correlative analysis between occurrence points of species’ geographic distribution and the environmental conditions in those localities (Soberón and Peterson, 2005; Peterson et al., 2011). There are numerous applications for ENMs; for instance, model predictions of species’ environmental niches can be spatialized to obtain potential distributions, which are cartographic representations of geographic areas suitable for species (Guisan and Zimmermann, 2000; Anderson and Martínez-Meyer, 2004; Peterson et al., 2011). Likewise, ENMs can be compared to quantify the divergence or similarity between species niches (Peterson et al., 1999; Warren et al., 2008; Broennimann et al., 2012). These models are performed through several algorithms (e.g., MaxEnt, GARP, BIOCLIM, GAM, etc.), which are chosen according to the available information (i.e., presence and absence data, presence-only data, presence and environmental background data) and employ different methods like maximum entropy, maximum likelihood, regression, and classification (Elith et al., 2006; Peterson et al., 2011). Since true absence data is usually scarce (i.e., data systematically collected demonstrating the absence of the species in an area), presence-background methods are commonly employed to characterize species niches (Peterson et al., 2011).

Most ENMs of plant species have been based on climatic data, particularly related to precipitation and temperature, disregarding other key drivers of plant distribution like edaphic variation (Pearson and Dawson, 2003; Austin and Van Niel, 2011; Dubuis et al., 2013; Thuiller, 2013; Diekmann et al., 2015; Mod et al., 2016; Velazco et al., 2017). Climate determines vegetation types and life forms and affects plant morphological, physiological, and functional variation (Holdridge, 1947; Harrison et al., 2010). Climatic variables such as temperature and precipitation are tightly linked to processes like evapotranspiration and water cycling (Fisher et al., 2009). On the other hand, soil properties can influence plant distribution, performance, and survival by affecting plant nutrition, rooting, access to water, and biotic interactions (Sollins, 1998; Aerts and Chapin, 2000; Weil and Brady, 2017). Soil physical and chemical properties are simple surrogates of nutrient availability for plants that depend on multiple factors difficult to measure like nutrient cycling, microorganismal activity, litter quality, soil temperature, humidity, atmospheric nutrient inputs, leaching, weathering, and parental geological substrate (Corlett and Primack, 2011).

Several studies have pointed out that the inclusion of soil data in the study of plant distributions and ecological niches can produce more robust and accurate ENMs predictions than traditional models restricted to climatic data, which are prone to overprediction (Coudun et al., 2006; Bertrand et al., 2012; Beauregard and De Blois, 2014; Diekmann et al., 2015; Velazco et al., 2017; Zuquim et al., 2020). To date, studies including soil data are scarce (Thuiller, 2013; Velazco et al., 2017; Figueiredo et al., 2018), in part because soil data covering large geographic ranges are sparse (Austin and Van Niel, 2011; Bertrand et al., 2012; Beauregard and De Blois, 2014; Figueiredo et al., 2018). Comprehensive information on soil physical and chemical properties has not been available until recently in mapping systems like SoilGrids (Hengl et al., 2017).

This research aimed to characterize the Grinnellian niches of four closely related tree species of *Damburneya* (Lauraceae) and assess whether their niches differ. The genus comprehends 24 species distributed in Central America, with some occurring in North America, Northern South America, and the Antilles (Trofimov et al., 2016; Trofimov et al., 2019). The ancestors of *Damburneya* likely diversified during a southward migration from North America at one of the two Eocene cooling periods (50 – 48 Ma and 40 –36 Ma, respectively; Trofimov et al. 2016). Diversification occurred in Mesoamerica, mostly in tropical forests of southern Mexico and Guatemala (Rohwer and Kubitzki, 1993). Despite all *Damburneya* species are mainly dispersed by birds, sympatric species (i.e., occurring in the same geographic area) differ in their local distribution along altitudinal ranges, suggesting that ecological differentiation could underlie spatial sorting. Edaphic, altitudinal, and phenological specialization have been hypothesized as the main drivers of ecological differentiation between sympatric species of *Damburneya* (Rohwer and Kubitzki, 1993), and other Lauraceae (van der Werff, 1992; Sri-Ngernyuang et al., 2003; Tsuneki et al., 2014; Srinivas and Krishnamurthy, 2019). Several studies also support climate as an important environmental restriction on the distribution and niche differentiation of Lauraceae species (Chacón De Rieger and Fournier O., 1987; Chanderbali et al., 2001; Rodríguez-Sánchez and Arroyo, 2008; Rodríguez-Sánchez et al., 2009; Ortiz-Rodríguez et al., 2018; Srinivas and Krishnamurthy, 2019). However, the role of climate and soil on species' niche differentiation and current distribution in *Damburneya* remains unexplored.

Specifically, we focused on *Damburneya ambigens* (S. F. Blake) Trofimov, *Damburneya colorata* (Lundell) Trofimov, *Damburneya gentlei* (Lundell) Trofimov, and *Damburneya salicifolia* (Kunth) Trofimov & Rohwer (formerly included within the genus *Nectandra* —*N. coriacea* group—; Trofimov et al., 2016). According to the most recent phylogenetic analyses of the genus, *D. ambigens* and *D. gentlei* are sister species of a small clade that, in turn, is sister to a second clade containing *D. colorata* and *D. salicifolia* (Trofimov et al., 2019). Widespread and variable species like *D. salicifolia* are thought to have given rise to several species of more restricted distributions like *D. colorata* via ecotypic differentiation (Rohwer, 1993; Rohwer and Kubitzki, 1993); however, both species were not retrieved as sisters in the mentioned phylogenetic analyses (Trofimov et al., 2019).

These four species were chosen because local field research suggests that they might face niche differentiation in sympatry by differing in abundance, distribution along the altitudinal gradient, and leaf functional strategies (Giraldo-Kalil et al., 2022). Leaf trait variation seems partly driven by species differential responses to local edaphic variation and potentially to other environmental factors like climate (Giraldo-Kalil et al., 2022). *Damburneya ambigens* and *D. gentlei* are tall tree species typical of the mature and well-preserved rainforest of southern Mexico and Central America and usually occur in altitudes below 1000 m and 300 m, respectively (Rohwer, 1993, Fig. 1). *Damburneya salicifolia* has a wide distribution in Mexico and Central America; it can grow in several types of tropical forests and soils from sea level up to 2300 m (Rohwer, 1993; Lorea-Hernández, 2002, Fig. 1). Contrary to most Lauraceae and *Damburneya* species, *D. salicifolia* has a wide ecological amplitude and can grow in disturbed areas and secondary vegetation (Lorea-Hernández, 2002; García-Licona et al., 2014). In contrast, there are few records of *D. colorata*, a species restricted to tropical rainforests of northern Central America and southern Mexico, between 100 and 500 m a.s.l. (Rohwer, 1993; Giraldo-Kalil et al., 2022, Fig. 1).

Based on the evolutionary history of the species, we expect greater niche similarity and overlap as species are more closely related. However, differences in local leaf trait variation and geographic distribution suggest that this expectation does not necessarily hold true. We hypothesized that the four *Damburneya* have differentiated their niches, thus are not equally affected by climatic and edaphic variation. Here, we aimed to characterize and compare the niches of the four closely related species of *Damburneya* mentioned. To this end, we built ENMs based on soil, climate data, and a combination of both sets of environmental variables to assess their importance on species' ecological niches and distributions. Furthermore, we aimed to determine whether there is niche differentiation between the four *Damburneya* species on a wide geographical scale. We assessed the effects of different sets of environmental variables on model performance and predictions to provide an integrative interpretation of environmental constraints to species distributions. Finally, we discussed potential causes of niche divergence among species and some perspectives and applications of our results.

Methods

Occurrence data and study areas

We obtained the species' occurrence data from the following repositories: Global Biodiversity Information Facility (GBIF.org[1]), Portal de Datos Abiertos UNAM[2] which contains records from Herbario Nacional de Mexico (MEXU), SEInet portal network[3], Sistema Nacional de Información

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[1] https://www.gbif.org/ last accessed: 07 February, 2023

[2] https://datosabiertos.unam.mx/biodiversidad/ last accessed: 07 March, 2018

[3] https://swbiodiversity.org/seinet/index.php last accessed: 07 March, 2018

sobre Biodiversidad de México[4], and SpeciesLink network[5]. In addition, field data from our previous studies in Los Tuxtlas Biosphere Reserve, in Veracruz, Mexico, were included (Giraldo-Kalil and Núñez-Farfán, 2022; Rodríguez-Sánchez, Giraldo-Kalil and Núñez-Farfán, 2022; Giraldo-Kalil, 2021, unpublished data). A detailed list of the data sources of occurrence data is found in Appendix S1. As correct taxonomic determination usually depends on reproductive characters and is difficult for non-experts, we only included records of preserved specimens, which are determined in herbaria by specialists, and excluded observation-only records. Occurrence data were searched with current and former species names (*Nectandra ambigens*, *N. colorata*, *N. lundellii*, and *N. salicifolia*), as the recent reinstatement of the genus *Damburneya* (Trofimov et al., 2016) is not yet reflected in several databases.

We removed data with duplicated coordinates and collector number and generated distribution maps with all occurrence data to perform a visual inspection. Data with incoherent distribution (e.g., in the desert, water bodies, very high altitudes, or other odd habitats for the studied species) were excluded. Congruence between reported localities and geographical coordinates was checked. Whenever available, detailed field locality information was employed to correct the coordinates of records with low georeferencing precision. Record taxonomic determination was crosschecked with a comprehensive database of the taxonomic determination of Lauraceae specimens of several herbaria in Mexico, using collector number, collection date, location, and collection name. The database contains collection and field information, specimen location, and specialist determination of herbaria specimens compiled during herbarium curatorial work (Lorea-Hernández, unpublished data). Occurrences from specimens incorrectly determined were corrected when possible (e.g., some specimen records of *D. salicifolia* were incorrectly named as the morphologically similar *D. coriacea* in the Yucatan peninsula), while those with unreliable or incorrigible determination were excluded. We thinned the data using a 1km filter to avoid spatial autocorrelation. The occurrence data used include: 33 records for *D. ambigens,* 20 for *D. colorata,* 53 for *D. gentlei*, and 697 for *D. salicifolia* (Fig. 1, Appendix S 2, Table S1).

The calibration areas for each species were delimited using the biotic regions where the species occur, which are assumed to represent the geographic areas historically accessible to the species (Barve et al., 2011). For that, we combined the polygons of WWF ecoregions (Olson et al.,

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[4] https://www.snib.mx/ejemplares/descarga/ data request: 13 June 2017

[5] https://specieslink.net/search/ last accessed: 04 March, 2018

2001) that intercepted species occurrence points. A 1 km buffer was added to the resulting polygons to avoid occurrence points to be very close to the edges of the study region.

Environmental data and selection of variables

Eleven environmental variables with a spatial resolution of 30 arcsec (~1 km) and WGS84 projection were employed to perform ENMs and species distribution models (SDMs) of current species distribution. All environmental variables encompass the whole study area where the studied species occur, from Mexico to Panama; units and abbreviations are shown in Table 1. We obtained 19 climatic variables derived from monthly temperature and precipitation values from WorldClim version 2.1 (Fick and Hijmans, 2017), which encompass climatic information from the year 1970 to 2000. Variables representing a combination of temperature and precipitation (Bio 8, Bio 9, Bio 18, Bio 19) were excluded, as those can cause spatial artifacts (i.e., steep discontinuities in neighbouring pixel unrelated with geographical features; Escobar et al., 2014; Campbell et al., 2015; Simões et al., 2020, Alkishe et al., 2022). Eight soil physical and chemical variables encompassing 0 – 20 cm in depth were obtained from the SoilGrids database (Hengl et al., 2017). This soil depth was chosen because nutrient and water availability are higher in the uppermost soil layers, where the roots of most tropical trees are concentrated (Jackson et al., 1996). In addition, we included a layer of total nitrogen at 5-15 cm depth built from a mosaic of more than 200 raster maps at 250 × 250 m pixel resolution (Poggio et al., 2021); this mosaic was resampled to 1 × 1 km pixel resolution using the nearest neighbor method in ArcMap 10.5. The soil variables chosen are among the most representative and commonly measured to assess soil influence on plant performance and most of them affect the variation of leaf functional traits of the species considered here (Giraldo-Kalil et al., 2022).

High correlation among predictor variables can bias niche modeling. In consequence, checking for high correlation and dimensionality reduction is advised before modeling (Dormann et al., 2013; Sillero et al., 2021). We reduced environmental variable dimensionality by testing high variable collinearity and excluding those variables with high variance inflation factor (VIF>10) with the vifcor function of the R package ‘usdm’ (Naimi et al., 2014). All variables chosen had low collinearity (VIF < 5). Several soil variables (bulk density, sand, and silt content) were excluded due to high VIF values and high correlation with clay content, which was retained over the other variables because its relationship to both soil texture and cation exchange capacity (Sollings 1998, Weil 2017). Furthermore, we prioritized those climatic variables encompassing annual periods, like mean annual temperature and precipitation (Bio 1 and Bio 12, respectively), since these are considered important drivers of plant distribution (Morecroft and Paterson, 2006) and trait variation (Wright et al., 2004). Other highly correlated variables describing extreme climatic events (i.e., Bio 5, Bio 6, Bio 10, Bio

11, Bio 16, Bio 17) were not included because those had high VIF values and describe environmental variation captured by mean annual temperature and annual precipitation.

Ecological niche modeling

We built ENMs using species occurrence data and three data sets of environmental predictors: climate, soil, and a combination of both. Accordingly, the models are named hereafter as climatic-only, edaphic-only, and combined according to the data set employed. Niche modeling was performed in R (R Core Team, 2021) using several packages through the GUI application ‘wallace’ (version 2.0; Kass et al., 2018; Kass et al, 2023). Presence-background models were performed using MaxEnt (version 3.4.4; Phillips et al., 2022) with the ‘dismo’ package (Hijmans et al., 2020). This software predicts the environmental suitability of the species using a maximum entropy algorithm (Phillips et al., 2006; Elith et al., 2011; Phillips et al., 2017). For that, it quantifies the relationship between predictor environmental variables and species observed occurrence locations and contrasts it with background random location within the study area (Muscarella et al., 2014).

The models were built using 10000 random background points. Extraction of environmental data to points and other raster operations were performed with the package ‘terra’ (Hijmans, 2021). To assess model accuracy and prevent spatial autocorrelation, we partitioned the data set into training and testing groups to perform model cross-validation using the package ‘ENMeval 2.0’ (Kass et al., 2021). The checkerboard 2 method (k = 4, aggregation factor = 2) was applied to perform structured spatial partitions for *D. ambigens*, *D. gentlei*, and *D. salicifolia*. As this method is not advisable when there are few species occurrence data, we applied the Jackknife random partition method for *D. colorata* (n = 10) (Muscarella et al., 2014). Several transformations of the predictor variables, also known as feature classes, were applied to perform flexible and complex models and regularization was implemented to control complexity by penalizing model over-fitting (Phillips et al., 2006; Elith et al., 2011; Merow et al., 2013). We set combinations of the linear (L), quadratic (Q), product (P), and hinge (H) features of classes as follows: L, LQ, LQH, LQP, LQHP. These feature classes were chosen because, besides being informative, the resulting predictors’ response curves are expected to be relatively simple and easily interpretable (Merow et al., 2013; Phillips et al., 2017). Moreover, the regularization multipliers were set from 1 to 4, with a multiplier step of 0.5. The ‘cloglog’ transformation was applied to the obtained raster predictions of species potential distributions (Phillips et al., 2017).

Besides the environmental variables included in niche models, other factors like human activities or natural disturbance can impact species modeled distributions; hence, it is advisable to post-process predicted distributional areas to account for the effects of such disturbance (Peterson et al., 2011). Deforestation due to several activities like land use change for agriculture and cattle raising, human constructions, and natural disturbances has changed tropical forest cover in the last decades (FAO , 2020; Laso Bayas et al., 2022). As the studied species occur mostly in mature well-preserved forests, the obtained rasters of species environmental suitability were post-processed to consider recent forest cover data. For that, we created a raster mosaic with the data of continuous vegetation cover at 250 m resolution (years 2000 to 2020) from MODIS/TERRA (DiMiceli et al., 2015) encompassing the whole study area. The raster was resampled to a 1 km resolution (using the nearest neighbor method), reprojected to wgs84 datum, and reclassified using a forest cover threshold of 30%. The values below the threshold were reclassified as 0, while those above the threshold were reclassified as 1. The reclassified raster was used to trim the species binary rasters of environmental suitability obtained with MaxEnt by subtracting the areas with less than 30% of forest cover.

Model evaluation

Model evaluation considered several metrics calculated with 'ENMeval 2.0' (Kass et al., 2021). These metrics include the minimum training presence omission rate (OR_{MTP}) and the 10% training presence omission rate (OR_{10}), with low values indicating a low number of testing occurrences omitted by the model predictions (Muscarella et al., 2014). In addition, the area under the receiver operating characteristic curve based on the testing data (AUC_{test}) quantifies the classification ability of the model to discriminate between background and testing data, with high values indicating a better discrimination ability (Warren and Seifert, 2011; Muscarella et al., 2014). Moreover, overfitting is accounted for with the difference between the AUC of training and testing data (AUC_{diff}), which increases with model over-parameterization (Warren and Seifert, 2011; Muscarella et al., 2014). We also obtained the delta of the Akaike Information Criterion corrected for small samples (ΔAICc), which indicates the balance between model fit and complexity based on the entire data set, independently of data partition (Muscarella et al., 2014). It is calculated as the difference between each model with the one with the lowest AICc.

Model selection per species and data set employed was performed using several criteria: we chose the top five models with lowest ΔAICc values. From this group, we selected models with the lowest omission rates (OR_{MTP} and OR_{10}), followed by those with higher AUC values (Appendix S3, Table S2). Considering that omission rates are less reliable with small sample size, we prioritized models with high AUC in the case of *D. colorata*. Model selection was complemented with the assessment of response curves of the top five models (Appendix S3, Figs. S2, S3 and S4). Curves were compared among models to detect potential signals of overparameterization that could indicate bias on model selection (i.e., abrupt changes in the curves with no intuitive biological interpretation).

Niche overlap

To analyze niche differences among species, niche overlap between pairs of species was quantified with the package ‘ecospat’ (Di Cola et al., 2017; Broennimann et al., 2021), by comparing species background environmental conditions (Warren et al., 2008). After an ordination of environmental variation by principal component analysis (PCA), both species occurrence density and the density of environmental conditions in the background extent of each species, were calculated along the first two PCA axes with a kernel density function (Broennimann et al., 2012). Niche similarity was assessed with a background similarity test that indicates the extent to which the ENM of one species is predicted by that of a second species better than expected by chance, using the calculated occurrence and background density kernels (Warren, 2008). The Schoener’s *D* metric was calculated to quantify niche overlap among species based on the ratio of occurrence density to background environmental density, this metric varies from 0, when there is no overlap, to 1, when there is complete overlap and all grid cells are equally suitable for both species (Warren et al., 2008, 2010; Broennimann et al., 2012). Niche similarity was tested by randomly shifting occurrence density in the environmental range of one species and calculating the overlap of the simulated niche in the range of the second species (Broenniman, 2012). This process was repeated over 1000 permutations to obtain a distribution of overlap values that was used to assess statistical significance of niche overlap. Species niches were considered more similar than expected by random if the observed overlap is higher than 95% of the simulated overlap ($p < 0.05$; Di Cola et al., 2017).

Results

Niche models and variable contribution

For most species, annual precipitation, precipitation of the driest month, temperature seasonality, soil pH, organic carbon content, and cation exchange capacity were among the most important variables (Table 2). Furthermore, there were interspecific differences in variable contribution to ENMs. Mean annual precipitation was one of the most important variables in combined-data and climatic-only models for all species but *D. salicifolia*. Precipitation of the driest month (particularly in combined-data models, 36%) and precipitation seasonality had a greater contribution to the ENMs of this species (Table 2). Soil pH was the most important soil variable for the edaphic-only and combined models of all species and contributed most to the models of *D. gentlei* than to those of the other species. Compared to the ENMs of the other species, those of *D. ambigens* had a lower contribution of temperature variables (Bio 1 and Bio 4) but a higher contribution of precipitation variables.

Overall, the variables contributing the most to combined-data models also had a high contribution to edaphic-only and climatic-only models. However, climatic variables contributed more than edaphic variables to combined-data models, and some edaphic variables show lower or no contribution in combined-data models compared to edaphic-only models (Table 2). For instance, although soil pH had the highest contribution in edaphic-only models of *D. colorata*, it did not contribute to combined models (Table 2). There were interspecific differences in model performance and variable contribution. *Damburneya colorata* tends to show high omission rates (OR_{10} = 10-20%, OR_{MTP}=5-10 %) in all models, while *D. salicifolia* had the lowest AUC (0.7 - 0.8) and omission rates values (OR_{10} =10-11%, OR_{MTP}< 1%; Appendix S3, Table S2). In addition, the data set employed affected model performance. Combined-data models had the highest AUC and omission rate values indicating a high discriminative ability, but with a higher proportion of localities falling outside the model prediction. In addition, climatic-only models had higher AUC and lower omission rates (OR_{10} and OR_{MTP}) than edaphic-only models (Appendix S3, Table S2).

Environmental suitability

The response curves had similar variation patterns among models for all species, especially between climatic-only and combined data models. Environmental suitability of most species increased with mean annual precipitation, temperature seasonality, soil water availability, and cation exchange capacity, but decreased with the increase in precipitation seasonality, precipitation of the driest month, annual mean temperature, soil pH, and clay content (Fig. 2). Conversely, model response curves of *D. salicifolia* differed from those of the other species. Compared to the other *Damburneya*, the environmental suitability of *D. salicifolia* increases from colder to warmer mean annual temperatures, higher soil pH (pH ≥ 7, from neutral to alkaline) and precipitation of the driest month, and with lower annual precipitation and soil organic carbon than the other species (Fig. 2). Environmental suitability of this species remains high under a wide range of temperature and precipitation seasonality values.

Suitable areas predicted from potential distribution differed between species and models. The suitable areas for *D. ambigens*, *D. colorata,* and *D. gentlei* encompass tropical rainforests of southeastern Mexico and northern Central America (but are more restricted to Mexico for *D. ambigens*); furthermore, the highly suitable areas predicted for *D. colorata* and *D. gentlei* are very similar. The humid forests of the central-southern Yucatan peninsula have portions with high climatic suitability but unsuitable soils for *D. ambigens*; conversely, large areas with suitable soils in

Nicaragua and Honduras do not have suitable climates, a pattern also observed for *D. gentlei* (Fig. 3). On the other hand, *D. salicifolia* has the largest suitable areas, comprising several types of forests. Edaphic-only models predicted wide and highly suitable areas for this species encompassing almost all of Central America, including some Mexican oak-pine forests and other forests in the Sierra Madre Occidental, the Sierra Madre del Sur, the Trans-Mexican Volcanic Belt, the Sierra Madre Oriental, and humid forests from southwestern Mexico to southern Panama. However, climatic-only and combined-data models predicted much smaller areas in the Pacific region of both Central America and Mexico (Fig. 3). Overall, predictions from combined-data models were more similar to those obtained with climatic-only models than to those from edaphic-only models (Fig. 3). Moreover, suitable areas from edaphic-only models were larger than those from the other models for all species.

Niche similarity and overlap

There were divergent patterns of niche similarity between species and models. Most species had similar climatic niches but differed in edaphic and combined niches suggesting climatic niche conservatism and differences in the edaphic environmental space of the species. There was a high niche overlap between *D. colorata* and *D. gentlei* regardless of the data set used for modeling (47 - 58%), indicating niche similarity between these species; the contrary occurred for *D. ambigens* and *D. gentlei*, which were the only species with no significant niche similarity (Table 3). The niches of *D. ambigens* and *D. salicifolia* were similar when including the combined data set for the analysis. Meanwhile, the edaphic niches of *D. gentlei* and *D. salicifolia* were similar but with a low overlap (10%). Furthermore, the explained variation of the PCAs of environmental variation also differed between models. The first two axes explain around 50% of the environmental variation of combined-data models, 70% of climatic-only models, and 62% of edaphic-only models. (Appendix S4, Figs. S1, S2, and S3).

Discussion

Climate and soil variation determine species potential distribution and environmental suitability

Response curves and variable contribution to ENMs suggest that high precipitation, warm temperatures, high soil organic carbon content, small variation of the amount of precipitation throughout the year, and acid soil pH promote environmental suitability and distribution of all species, particularly of *D. ambigens, D. gentlei,* and *D. colorata* (Fig. 2, Table 2). These species are constrained to tropical rainforests or other humid tropical forests (Rohwer, 1993; INEGI et al. 2008), where acid soils rich in organic matter are typical (Sollins, 1998; Rzedowski, 2006) and precipitation is high throughout the year, except for some short dry periods (Corlett and Primack, 2011), suggesting that they tolerate low seasonality in precipitation. For instance, mean annual precipitation in Mexican and northern Central American tropical rainforests has values above 2000 mm and even exceeds 3000 mm in some cases, but it drops below 100 mm/ month during short dry seasons (Rzedowski, 2006; Martínez-Ramos et al., 2009; Gutiérrez-García and Ricker, 2011).

On the other hand, the environmental suitability of *D. salicifolia* encompasses wider environmental ranges (Figs. 2 and 3), suggesting that this species has a broader ecological niche than the other *Damburneya* species studied here. This could reflect a divergence in physiological tolerances and likely underlies its wide distribution. In addition to humid tropical forests like rainforests and cloud forests, *D. salicifolia* can occur in dryer ecosystems with lower precipitation, more variable temperature and precipitation along the year, longer dry seasons, and different temperature ranges (i.e., colder and warmer environments), like pine-oak forests, subhumid, dry, deciduous and semideciduous forests (Rohwer, 1993; Daza-Mendizabal, 1998; Lorea-Hernández, 2002; Rzedowski, 2006; García-Licona et al., 2014). *Damburneya salicifolia* distributes in areas with a wide edaphic range and even occurs in zones with alkaline pH (Fig. 2); such tolerance likely explains the occurrence of this species in forests located in karstic areas rich in limestones like the Yucatan peninsula and Chiapas (Flores-Delgadillo et al., 1999; Rzedowski, 2006; Roa-Fuentes et al., 2015; Campo et al., 2016; Hengl et al., 2017; Navarrete-Segueda et al., 2018). Alkaline soils have lower solubility and availability of several nutrients than acid soils (Weil and Brady, 2017); thus, we do not rule out that *D. salicifolia* could have higher plasticity in nutrient and water uptake and use than the other species of *Damburneya*, but experiments assessing physiological tolerance to edaphic variation are necessary to test this assumption.

Similarities and differences between the niches of *Damburneya* species

The interspecific divergence in edaphic and climatic ranges reflects the ability of *Damburneya* species to occupy different environments. Niche similarity tests revealed complex relationships between species and environmental variation across species distribution ranges; our results suggest that environmental niche overlap is likely explained by geographic overlap, as has been previously reported in other groups (Warren et al., 2008). Combined models suggest differences in environmental constraints between most species' pairs. In contrast, the high similarity found between most pairs of species when the climatic-only data set was employed likely reflects the overlay of the distribution and accessible areas of the species (for example, those of *D. colorata* and *D. gentlei*) and suggests that they have similar climatic constraints and likely could also share some physiological restrictions (Fig.1, Fig. 2, Fig. 3 and 3). Interestingly, this divergence in the ranges of environmental variation experienced by the species could explain why the niche of *D. colorata*, which is hypothesized to diverge from *D. salicifolia* (see below), was only similar to that of *D. salicifolia* according to climatic-only models. On the other hand, *D. ambigens* and *D. gentlei* share portions of their distribution ranges and accessible areas and are the most closely related species included in this study (Trofimov et al., 2019); however, all models indicated niche differentiation between them, suggesting that they differ in their environmental restrictions.

These results are in line with previous findings of leaf functional divergence between species from a field study focused on the same *Damburneya* species studied here. Giraldo-Kalil et al. (2022) found that leaf trait variation of trees is driven by local edaphic variation along an altitudinal gradient in the Los Tuxtlas mountain range in Veracruz, Mexico, suggesting that phenotypic variation can be directly influenced by soil properties. The authors found that trait correlations underlying leaf functional strategies varied between species. Compared to the other species, *D. gentlei* had an acquisitive functional strategy characterized by a relatively fast return of biomass-invested carbon; its leaves had high nutrient concentrations but low biomass investment (Giraldo-Kalil et al., 2022), meaning that photosynthetic rates were maximized in leaves with a short lifespan (Wright et al., 2004). In contrast, *D. ambigens* had a conservative strategy characterized by a high leaf biomass investment (Giraldo-Kalil et al., 2022) that results in a long leaf lifespan but leads to slow carbon return and high construction costs (Wright et al., 2004). Such a striking divergence in leaf functional strategies is coherent with the niche divergence between *D. ambigens* and *D. gentlei* reported here for all ENMs using climatic and edaphic data. On the other hand, the leaves of *D. salicifolia* and *D. colorata* varied between acquisitive and conservative functional strategies suggesting wide plasticity. In addition, the leaves of *D. salicifolia* seemed to require a lower phosphorus investment per nitrogen biomass unit, suggesting a plastic and efficient nutrient use (Giraldo-Kalil et al., 2022). Furthermore, the higher soil nutrient availability, the higher leaf nutrient concentrations of all species (Giraldo-Kalil et al., 2022). We do not know the extent to which local phenotypic patterns could be related to niche differentiation patterns at broad geographic scales; however, both information sources can shed light on the ecological differences between sympatric *Damburneya* species.

Niche similarity tests based on subset data show contrasting results. Edaphic niches diverged among species, showing the wide edaphic heterogeneity experienced by these four species. For instance, suitable areas comprise the tropical rainforests of southern Mexico and northern Central America, characterized by a wide local variation in soil physical and chemical properties (Flores-

Delgadillo et al., 1999; Sommer-Cervantes et al., 2003; Navarrete-Segueda et al., 2018). The edaphic niche divergence could support soil as a potential driver of ecological differentiation within the genus, as species were not similarly constrained by edaphic variation (Rohwer and Kubitzki, 1993; Giraldo-Kalil et al., 2022). If this divergence allow a differential use of resources, it could favor species coexistence by avoiding interspecific competition (Chesson, 2000; Adler et al., 2013). However, we did not find clues for species specific ranges of soil variation that could support edaphic specialization. Further studies incorporating species physiological tolerances, phenotypic traits, reproductive isolation, biotic environmental variables, and population processes are needed to assess whether the edaphic niche divergence detected here can reflect relevant species' ecological innovations in an evolutionary context (Peterson, 2011).

In contrast, climatic niches were similar and overlapped between most studied species, suggesting that *Damburneya* species' distributions are similarly restricted by climate, and that species are more tolerant to edaphic than climatic variation. This result is consistent with previous studies reporting a preference for warm and humid climates, with a reliable water supply and low seasonality in precipitation in other Lauraceae species (Chacón De Rieger and Fournier O., 1987; Rodríguez-Sánchez and Arroyo, 2008). On the other hand, the high similarity between species' climatic niches could also reflect that climate is less variable than soils within ecosystems, and its effects could be more determinant at broad scales than at local scales (Pearson and Dawson, 2003). Indeed, overall suitability predictions include areas with suitable soils but unsuitable climate for species distribution (Fig. 3).

Our research supports other studies that, based on species distributions in divergent soil types, ecosystems, altitudes, and wide leaf trait variation, suggest that *D. salicifolia* has a greater ecological amplitude than the other species within the genus (Rohwer, 1993; Rohwer and Kubitzki, 1993; Lorea-Hernández, 2002; Giraldo-Kalil et al., 2022). The niche of this species differed from those of most other species according to edaphic-only and combined-data models. Our results suggest that the plasticity and divergence of this species are partly due to its tolerance to drier environments and wider temperature variation throughout the year (Fig. 2). However, further mechanistic studies linking fundamental niche, physiological variation, and environmental tolerances are needed to assess the relationship between local phenotypic variation, species distribution, and climatic and edaphic heterogeneity at a broad geographic scale.

Besides the current environmental variation, present patterns of niche similarity and divergence among species could reflect historical distribution patterns and evolutionary events. For instance, the wide edaphic and climatic niches of *D. salicifolia* likely reflect the higher adaptability that allowed this species to diversify and colonize new environments in a broad geographic range. The species of the genus *Damburneya* diversified during their migration from North America to Central America (Rohwer, 1993; Trofimov et al. 2016); widespread plastic species tolerating a broad range of ecological conditions like *D. salicifolia* lead to locally specialized ecotypes with more specific environmental requirements that evolved into narrowly distributed species like *D. colorata*, which likely remained in their differentiation sites. Eventually, closely related species, even ecologically different, became sympatric (Rohwer and Kubitzki, 1993). Future studies including information on phylogeny, phylogeography, and population genetics, are needed to assess the extent to which present climates and niches could reflect the biogeographic and evolutionary history of the group.

In addition, other ecological factors can also influence niche and distribution, promoting ecological divergence among species (Chesson, 2000; Adler et al., 2013). For instance, sympatric species within the genus exhibit phenological differentiation with asynchronous flowering and fruiting where the species ranges overlap (Rohwer and Kubitzki, 1993, Giraldo-Kalil, personal observation). Fruit production, seed predator species, and seed size also differ between *Damburneya* species (Rodríguez-Sánchez, Giraldo-Kalil and Núñez-Farfán, unpublished), likely promoting differences in seed dispersal and plant recruitment. Moreover, interspecific variation in plant performance and survival seems to occur; leaf functional trait variation of trees suggests that the species could differ in their susceptibility to herbivore attack and potentially in their light requirements (Giraldo-Kalil et al., 2022). On the other hand, spatial isolation of some highly suitable areas (e.g., Los Tuxtlas tropical rainforest in Mexico) could also limit dispersal to other areas. We do not know how far dispersers like birds and mammals could move the seeds promoting the migration of *Damburneya* species; thus, we encourage future studies on this promissory area. In line with this, disturbance and habitat loss, particularly in non-protected areas, could threaten the establishment of viable populations since most Lauraceae species do not thrive in secondary vegetation (Lorea-Hernández, 2002). In addition, it must be considered that, both climate and soil can affect species distribution, not only by their direct effects, but also because their interactions (e.g., soil water content might depend on precipitation and temperature) or indirect effects on other unmeasured biotic or abiotic factors (e.g., dispersers abundance; Wiens, 2011).

Furthermore, common methodological issues affecting ENMs must be recognized. Species occurrence records can be biased because were not systematically collected in a single study but retrieved and joined from several sources and unrelated studies. Another bias comes from accessibility since easily accessible areas like roads were overrepresented in comparison to areas with more difficult access (Peterson et al., 2011).

Insights on the use of different data sets and models

Here, we suggest that combined-data models, which have a greater discriminative ability, should be preferred over the subset-data models to avoid confounding interpretations of the effects of environmental variation on species distribution. Although the overall patterns of variable contribution and response curves observed in climatic-only and edaphic-only models were maintained also in combined-data models, other patterns were not. For example, despite soil pH and cation exchange capacity had a great contribution to edaphic-only models of *D. colorata*, no edaphic variables contributed to combined models, suggesting that some climatic factors explain the distribution of this species regardless of soil variation. Yet, edaphic-only and climatic-only models are useful for exploring the environmental variation that affects the distribution of species.

In line with previous studies, our research supports the usefulness of ecological niche models based on both climatic and edaphic correlates to assess and interpret the factors determining the niches of plant species across their distributions (Coudun et al., 2006; Bertrand et al., 2012; Dubuis et al., 2013; Beauregard and De Blois, 2014; Velazco et al., 2017; Zuquim et al., 2020; Alvarez et al., 2022, Ochoa-Zavala et al., 2022). The relative importance of soils and climate on species niche and distribution remains under debate, and some authors point out that spatial scales governing both environmental factors can be determinant (Sollins, 1998; Thuiller, 2013; Beauregard and De Blois, 2014; Diekmann et al., 2015). Several studies have found both environmental predictors affecting species distribution at local (Phillips et al., 2003; Condit et al., 2013; Diekmann et al., 2015) and broad scale (Bertrand et al., 2012; Dubuis et al., 2013; Velazco et al., 2017; Zuquim et al., 2020, Ochoa-Zavala et al., 2022), and even report higher relevance of soils (Figueiredo et al., 2018). Nevertheless, other studies have failed to determine the relationship between soil chemical properties and plant distribution in tropical forests (Aguirre-Gutiérrez et al., 2015), not because it does not occur, but because it could be difficult to detect, particularly at broad geographical scales (Sollins, 1998; Peterson et al., 2011; Thuiller, 2013; Diekmann et al., 2015). Despite such potential limitations, the inclusion of edaphic variables on plant distribution and niche models can provide valuable basic information on the ranges of soil variation that each species can tolerate, and even on the role of soils on niche divergence. Thus, we encourage the inclusion of climatic and edaphic variables in the modeling of plant niches and distributions.

On the other hand, several studies show that the ENMs of widely distributed species with large sample sizes outperformed those of narrowly distributed species with small sample sizes, likely due to statistical artifacts or a more limited representation of environmental conditions by presence localities (McPherson et al., 2004; Wisz et al., 2008; Syphard and Franklin, 2010; Velazco et al., 2017). Hence, we do not rule out the potential effect of sample size to explain the contrasting high omission rates of *D. colorata*, the species with the narrowest distribution and fewer occurrences, compared to the low omission rates of the widespread and well-represented *D. salicifolia*.

Perspectives and implications

Beyond the analysis of the factors explaining the divergence of the current distribution and ecological niche of the studied species of *Damburneya*, this research has other potential applications. The environmental ranges affecting environmental suitability can be useful in choosing planting sites for these species and provide a starting point to understand the limitations to their establishment and assess how they might cope with environmental changes. For example, the high climatic niche overlap and similarity, particularly between *D. colorata* and *D. gentlei*, suggests that they could respond similarly to climate and land-use changes. In contrast, this may not occur with *D. ambigens* and *D. gentlei*. The high environmental plasticity of *D. salicifolia* suggests that it could grow under varying environments and adapt more easily to environmental changes. Conversely, the other species could be more vulnerable to environmental changes, particularly the narrowly distributed *D. colorata*, but further studies are necessary to assess this.

Tropical rainforests have been facing accelerated deforestation for decades (Martínez-Ramos, 2006; von Thaden et al., 2018, con Thaden et al. 2020). Habitat loss is one of the main extinction threats for *D. ambigens*, *D. gentlei*, and *D. salicifolia*; thus, it is a serious concern that the current population size and trends of these species are still unknown (de Kok, 2020a, b, c). Even more worrying is the lack of information and extinction risk assessment for *D. colorata*, which has few known records. The niche analyses and models of suitable areas presented here are useful to explore other ecological factors beyond climatic and edaphic variation that could explain why the species do not occupy larger accessible areas, such as deforestation and dispersal limitation. Furthermore, they could be helpful tools for planning future fieldwork, data collection, sampling, population monitoring, and designing management strategies for *Damburneya* species at coarse spatial resolutions.

Conclusions

Our results suggest that the distribution of the four *Damburneya* species depends on climate and soil heterogeneity. Most species had climatic niche similarity and overlap but edaphic niche divergence.

These results suggest that the studied species share similar climatic restrictions while experiencing wide soil heterogeneity and could support edaphic variation as a potential promoter of ecological divergence among *Damburneya* species. Response curves and variable contribution to ENMs suggest differences in the environmental constraints to species distribution. High precipitation with low seasonality, warm temperatures, high soil organic carbon content, and acid soil pH promote environmental suitability and distribution of all species, particularly in tropical rainforests. On the other hand, compared to the other studied species, *D. salicifolia* encompasses wider environmental and geographical ranges and occurs in dryer forests under greater climatic and soil pH variation. Niche divergence occurred even between *D. ambigens* and *D. gentlei*, the most closely related species, suggesting potential differences in environmental constraints to species distributions. This research supports the use of both climatic and edaphic data to comprehensively assess the niche and distribution of plant species using ENMs.

Acknowledgements

The authors thank Rosario Landgrave for advice on environmental data management and edition, and Alfredo Esparza and Raul Badillo for the very first advice on data acquisition and cleaning. This research is part of the doctoral research of Laura J. Giraldo Kalil, who acknowledges the "Consejo Nacional de Ciencia y Tecnología" of Mexico (CONACYT) for the scholarship (No. 463686) granted for her PhD studies, and to the "Programa de Posgrado en Ciencias Biológicas" at the "Universidad Nacional Autónoma de México (UNAM)". This work was funded by SEP-CONACYT "Ciencia Básica" grant (No. 284692) to JNF

Author contributions

L.J.G.K wrote the first draft of the manuscript and conceived the research idea with J.N.F., compiled the data with A.L.N., curated the data for niche modeling with F.L.H., and performed the models and statistical analysis with the guidance of G.E.P.B. Project funding was secured by J.N.F. All authors contributed with ideas, discussed the results, commented and edited the manuscript.

Data availability statement

Data employed to perform niche models are available in the Appendix S2, Table S1 of electronic supporting information. The R scripts employed to perform niche models are available at: https://github.com/ljgiraldok/Ecological_Niche_Models_Damburneya

Tables

Table 1. Climatic and edaphic variables used for niche models of four *Damburneya* species.

Variable type	**Name**	**Description**	**Units**	**Description and effects on plants**
Climatic†	BIO1	Annual Mean Temperature	°C	Describes the temperature over the year, which is higher at tropical latitudes and can determine vegetation types and affect plant morphophysiological traits.
	BIO4	Temperature Seasonality (standard deviation ×100)	°C	Measures variation of temperature, with higher values indicating a higher departure from annual mean temperature.
	BIO12	Annual Precipitation	mm	Describes the amount of rainfall along the year, that can have widespread effects on vegetation, even determining vegetation types and affecting plant morphophysiological traits.
	BIO14	Precipitation of Driest Month	mm	Describes the amount of rainfall on the driest period of the year, which is likely stressful and affects the availability of water for plants.
	BIO15	Precipitation Seasonality (Coefficient of Variation)	mm	Measures variation of precipitation, with higher values indicating a higher departure from annual mean precipitation.
Edaphic§	AWCh1	Available soil water capacity (volumetric fraction) with FC = pF 2.0	percentage (%)	Describes the amount of water retained by soils and available for plant uptake.
	CECSOL	Cation Exchange Capacity of soil	cmolc/kg	Describes the capacity of soils to adsorb exchangeable cations, including mineral nutrients available for plants. It is promoted by the negative charges of soil organic matter and clay, and depends on soil pH, texture, and water availability
	CLYPPT	Weight percentage of the clay particles (<0.0002 mm)	percentage (%)	Determine several soil properties like texture, drainage, water availability, cation exchange capacity, porosity, and root aeration.
	ORCDRC	Soil organic carbon content	permille (‰)	Describes the amount of soil organic matter related with ecosystem processes like nutrient cycling and organic matter decomposition. It affects several soil properties and depends on texture, moisture, and temperature
	PHIHOX	pH index measured in water solution	pH	Indicates the soil acidity or alkalinity. Soil pH can limit nutrient availability for plants by affecting cation exchange capacity
	NITROGEN	Total nitrogen (N)	$g.kg^{-1}$	Describes the concentration of nitrogen in the soil, including organic and mineral forms. Nitrogen availability can limit photosynthesis, plant growth and primary productivity.

Note: All the layers have a 1km resolution. Climate layers were obtained from WorldClim version 2.1 (Fick and Hijmans, 2017). All the soil layers were retrieved from SoilGrids; most soil layers were originally published at 1km resolution (Hengl et al., 2017), the nitrogen layer was built as a 1 km mosaic from tiles at 250 m resolution (Poggio et al., 2021). Descriptions of the effects of environmental layers on plants are based on: †, Wright et al., 2004; Fick and Hijmans, 2017; §, Aerts and Chapin, 2000; Weil and Brady, 2017.

Table 2. Percentage of variable contribution to ecological niche models of four *Damburneya* species derived from the permutation importance analysis from MaxEnt. For each species, the three variables with highest contribution are highlighted in bold. The models were built with three data sets of environmental predictors: Climatic-only, edaphic-only, and a combination of both. Abbreviations and units of environmental predictors are found in Table 1.

Data set	**Environmental variables**	***D. ambigens***	***D. colorata***	***D. gentlei***	***D. salicifolia***
Combined	Bio 1	0.2	**23.4**	6.9	**17.3**
	Bio 4	11.3	18.9	**29.6**	**17.4**
	Bio 12	**45.4**	**36**	**20.2**	6
	Bio 14	**26.7**	0	0.2	**36.4**
	Bio 15	0	**21.3**	1.6	3.6
	AWCh	0	0	0	0
	CECSOL	0	0	1.4	4.6
	CLYPPT	0.9	0.3	0	0.5
	NITROGEN	0	0	0	6.4
	ORCDRC	2	**0**	0.2	0.2
	PHIHOX	**13.4**	0	**39.9**	7.6
Climatic	Bio 1	0	**14.9**	9.2	**17.9**
	Bio 4	6.7	**37.6**	**23.2**	**27**
	Bio 12	**46.6**	**22.6**	**50.3**	14.7
	Bio 14	**37.9**	12.4	3.8	12
	Bio 15	8.8	12.6	**13.5**	**28.5**
Edaphic	AWCh	1.6	0	**7.6**	0
	CECSOL	0	**29.2**	8.3	15.3
	CLYPPT	0	0	0	10.8
	NITROGEN	0.4	7.4	0	**15.9**
	ORCDRC	**24.7**	**0**	4.9	**39.8**
	PHIHOX	**73.3**	**63.3**	**79.2**	**18.2**

Table 3. Paired niche comparisons among four *Damburneya* species. The models were built with three data sets of environmental predictors: Climatic-only, edaphic-only, and a combination of both. Overlap values (Schoennner's D) are provided for the tests of niche similarity of species *a* with species *b* and vice versa. Significance is symbolized as: *(P<0.05), **(P<0.01), ***(P<0.005). Significant values are highlighted in bold.

Data set	**Species a**	**Species b**	**Niche overlap (D)**	***P* (a → b)**	***P* (b → a)**
Combined	*D. ambigens*	*D. colorata*	0.212	0.18	0.198
	D. ambigens	*D. gentlei*	0.181	0.162	0.156
	D. ambigens	*D. salicifolia*	**0.26**	**0.044***	**0.034***
	D. colorata	*D. gentlei*	**0.579**	**0.015***	**0.012***
	D. colorata	*D. salicifolia*	0.233	0.162	0.174
	D. gentlei	*D. salicifolia*	0.221	0.065	0.081
Climatic-only	*D. ambigens*	*D. colorata*	**0.508**	**0.010***	**0.016***
	D. ambigens	*D. gentlei*	0.372	0.117	0.095
	D. ambigens	*D. salicifolia*	**0.222**	**0.029***	**0.04***
	D. colorata	*D. gentlei*	**0.56**	**0.006****	**0.004*****
	D. colorata	*D. salicifolia*	**0.12**	**0.039***	**0.045***
	D. gentlei	*D. salicifolia*	**0.217**	**0.039***	**0.031***
Edaphic-only	*D. ambigens*	*D. colorata*	0.27	0.155	0.168
	D. ambigens	*D. gentlei*	0.209	0.238	0.246
	D. ambigens	*D. salicifolia*	0.196	0.196	0.356
	D. colorata	*D. gentlei*	**0.468**	**0.027***	**0.025***
	D. colorata	*D. salicifolia*	0.166	0.115	0.13
	D. gentlei	*D. salicifolia*	**0.102**	**0.04***	**0.036***

Figures

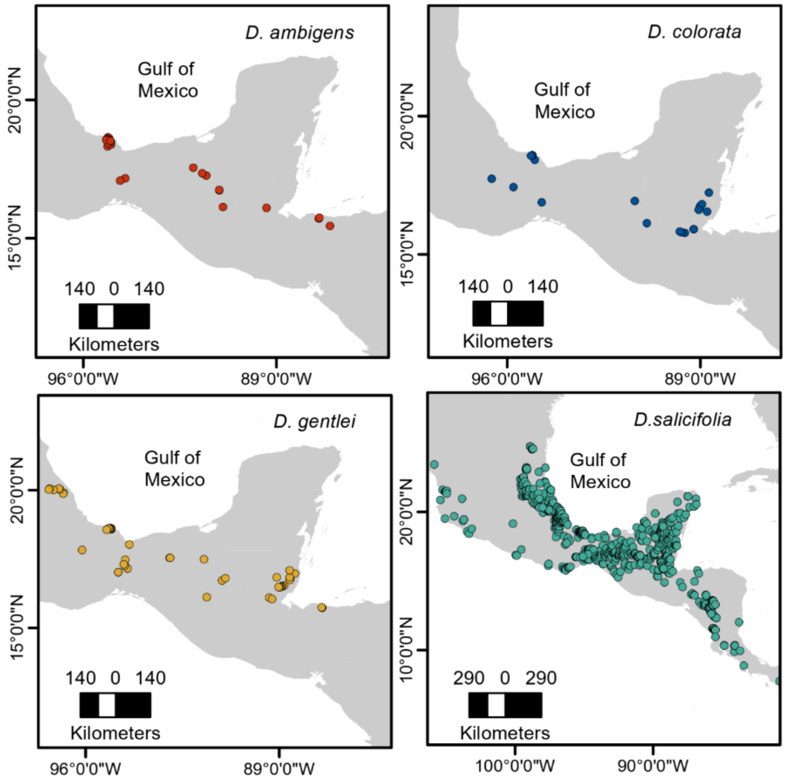

Figure 1. Maps of occurrence data of four *Damburneya* species employed to perform ecological niche models (ENMs) with MaxEnt. a) *Damburneya ambigens*:33 records, b) *D. colorata*: 20 records, c) *D. gentlei*: 53 records d) *D. salicifolia*: 697 records. The points show the location of collected samples reported in data repositories and authors' field work.

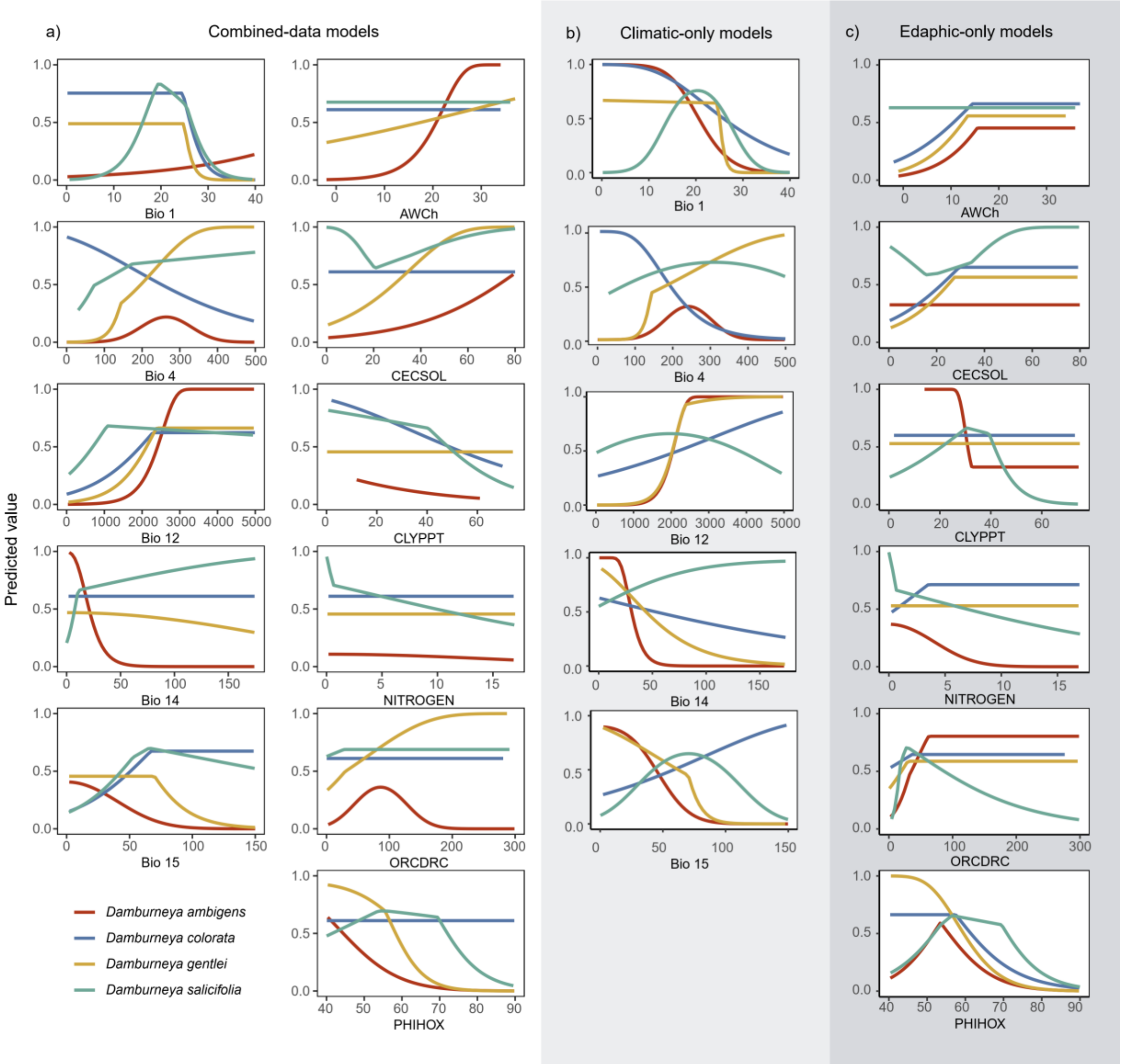

Figure 2. Response curves based on ecological niche models for four *Damburneya* species. The curves show the ranges of environmental variation favorable to species distributions and were based on models built with a combination of a) climatic and edaphic data, b) climatic-only, and c) edaphic-only datasets. Species are shown in colors. The x and y axis represent the ranges of the environmental variables and the predicted suitability values, respectively. Variable abbreviations and units can be seen in Table 1. The pH (PHIOHX) values are multiplied by 10.

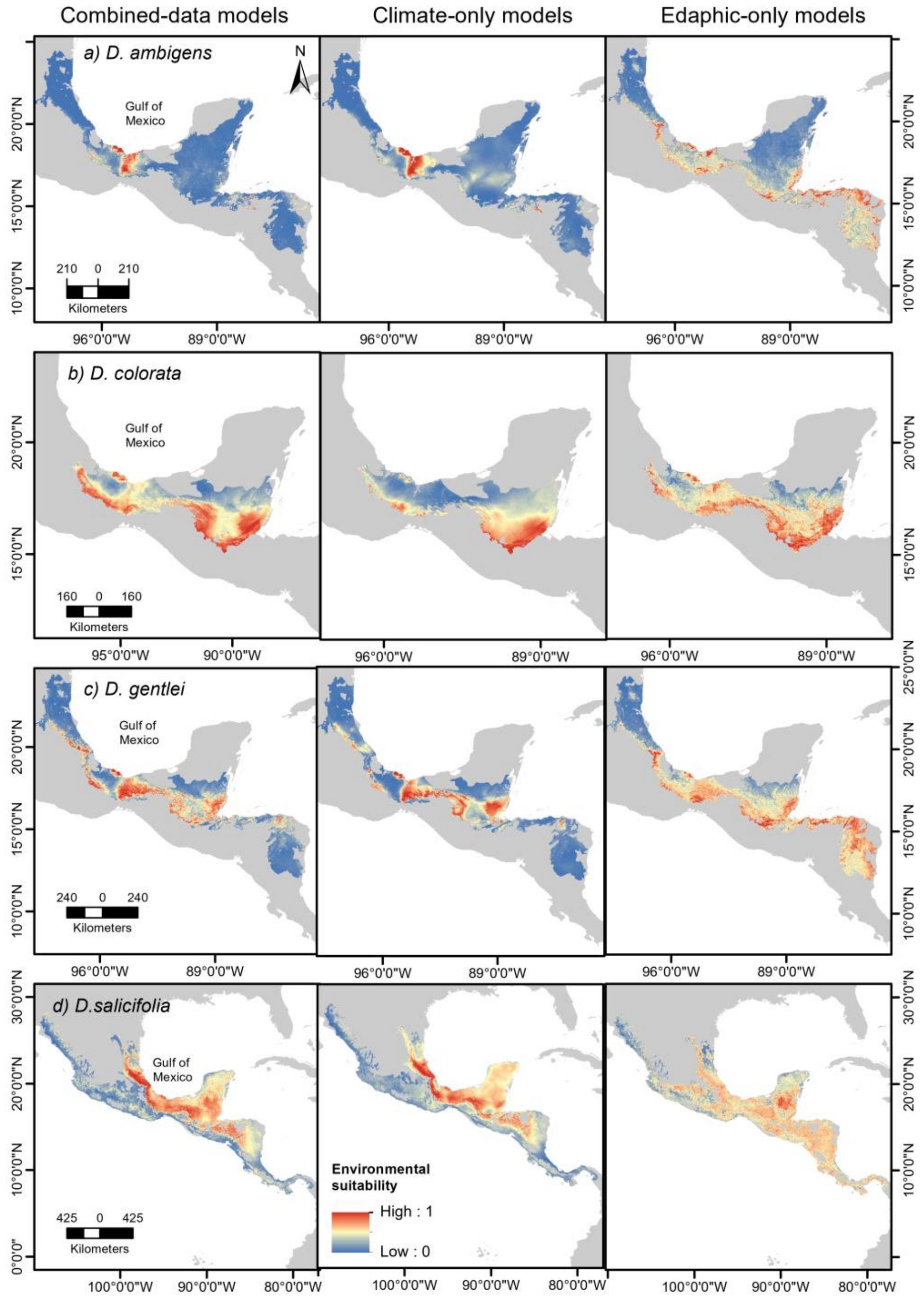

Figure 3. Geographic projection of niche models of four *Damburneya* species. Based on the environmental variables used to build the models, they were classified as combined-data models (combining climatic and edaphic variables, left column), climatic-only (center), and edaphic-only. The maps of each species models are organized in rows: a) *Damburneya ambigens*, b) *D. colorata*, c) *D. gentlei*, d) *D. salicifolia*. The coordinates and scale bar of the first map (left) are the reference for the other maps in the same row. Environmental suitability ranges from 0 to 1 (low and high, respectively) and is shown in bright colors; blue areas are the less suitable, yellow ones have intermediate suitability, and the red are the most suitable areas.

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Supplementary material

The following materials are available as part of the online article at https://escholarship.org/uc/fb

Appendix S 1. Comprehensive citation of data sources of specimen records of *Damburneya* species

Appendix S2. Occurrence data of four *Damburneya* species employed to perform ecological niche models (ENMs).

Table S1. Occurrence data retrieved from five repositories, and data set references of *Damburneya* species employed for ecological niche models

Appendix S3. Model selection and evaluation of ecological niche models (ENMs) for four *Damburneya* species.

Table S2. Ecological niche models (ENMs) chosen for four *Damburneya* species among the top five models with lower ΔAICc according to five evaluation metrics.

Figure S1. Response curves of the top five ecological niche models (ENMs) of combined-data models with the lower ΔAICc values for four *Damburneya* species.

Figure S2. Response curves of the top five ecological niche models (ENMs) of climatic-only models with the lower ΔAICc values for four *Damburneya* species.

Figure S3. Response curves of the top five ecological niche models (ENMs) of edaphic-only models with the lower ΔAICc values for four *Damburneya* species.

Appendix S4. Niche overlap and environmental variable ordination for four *Damburneya* species.

Figure S4. Niche overlap and environmental variable ordination for paired comparisons of four *Damburneya* species calculated with R package ecospat based on climatic and edaphic data.

Figure S5. Niche overlap and environmental variable ordination for paired comparisons of four *Damburneya* species calculated with R package ecospat based on climatic data.

Figure S6. Niche overlap and environmental variable ordination for paired comparisons of four *Damburneya* species calculated with R package ecospat based on edaphic data.

Supplementary material of the paper:

Laura J. Giraldo-Kalil, Gonzalo E. Pinilla-Buitrago, Andrés Lira-Noriega, Francisco Lorea-Hernández, Juan Núñez-Farfán. Ecological niche comparison among closely related tree species of Lauraceae using climatic and edaphic data. *Frontiers of Biogeography*.

Appendix S 1. Comprehensive citation of data sources of specimen records of *Damburneya ambigens*, *D. colorata*, *D. gentlei*, and *D. salicifolia*.

Species' occurrence data of *Damburneya ambigens*, *D. colorata*, *D. gentlei*, and *D. salicifolia* were retrieved searching the current and former names of those species (*Nectandra ambigens*, *N. colorata, N. lundellii,* and *N. salicifolia*, respectively) because the current name had not been updated in all consulted repositories at the date of the query. The data were obtained from the following repositories: Global Biodiversity Information Facility (GBIF), Portal de Datos Abiertos de la Universidad Nacional Autónoma de México (Instituto de Biología, —IBUNAM—, Herbario Nacional Mexicano —MEXU—), SEInet portal network, Sistema Nacional de Información sobre Biodiversidad de México (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad—CONABIO), and SpeciesLink network. In addition, field data from our previous studies were included (Giraldo-Kalil and Núñez-Farfán, 2022; Rodríguez-Sánchez, Giraldo-Kalil and Núñez-Farfán, 2022; L.J. Giraldo-Kalil, 2021, unpublished data).

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Supplementary material of the paper:

Laura J. Giraldo-Kalil, Gonzalo E. Pinilla-Buitrago, Andrés Lira-Noriega, Francisco Lorea-Hernández, Juan Núñez-Farfán. Ecological niche comparison among closely related tree species of Lauraceae using climatic and edaphic data. *Frontiers of Biogeography*

Appendix S 2. Occurrence data of four *Damburneya* species (*D. ambigens*, *D. colorata*, *D. gentlei*, *D. salicifolia*) employed to perform ecological niche models (ENMs)

Table S 1. Occurrence data and data set references of four *Damburneya* species (*D. ambigens*, *D. colorata*, *D. gentlei*, *D. salicifolia*) employed for ecological niche models. The data were retrieved from five repositories and field collections. Respositories are abbreviated as: IBUNAM (Datos abiertos, Instituto de Biología, Herbario Nacional Mexicano -MEXU-, Uiversidad Nacional Autónoma de México), GBIF (Global Biodiversity Information Facility), SNIB-CONABIO (Sistema Nacional de Información sobre Biodiversidad de México, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad), and SEINET (SEInet portal network). Field data recorded by Laura Judith Giraldo Kalil are also included. Please see the comprehensive citation of these data sources in Appendix S1

scientific_name	longitude	latitude	data_source	record_idNum
Damburneya ambigens	-95.1667	18.5444	SNIB - CONABIO	39b6887981ab7b87216cf1a5241a75fc
Damburneya ambigens	-95.13859	18.5781	Giraldo-Kalil field data	LJGK_plots_tree#256
Damburneya ambigens	-95.12342	18.57213	Giraldo-Kalil field data	LJGK_plots_tree#174
Damburneya ambigens	-95.117	18.583	IBUNAM	NA
Damburneya ambigens	-95.108	18.586	SNIB - CONABIO	a855c965dbdf32b2fd6d8acb937bd150
Damburneya ambigens	-95.1072	18.5669	SNIB - CONABIO	b6c69eaa9cd2d2abcae65d163155cceb
Damburneya ambigens	-95.107	18.585	SNIB - CONABIO	8ac582f458394e0e52467bcafb99c3fc
Damburneya ambigens	-95.106	18.583	SNIB - CONABIO	4a95042e2dfe37a971aa523618bc77d4
Damburneya ambigens	-95.1028	18.315	SNIB - CONABIO	9650d8570ea427a43f86d116428310e6
Damburneya ambigens	-95.0956	18.6428	SNIB - CONABIO	40e2fc0a61a583f2d018f74b1813ff51
Damburneya ambigens	-95.091	18.591	SNIB - CONABIO	9d0dca10eea981371826f845c622c2a2
Damburneya ambigens	-95.09094	18.4298	Giraldo-Kalil field data	Damb300
Damburneya ambigens	-95.089	18.588	SNIB - CONABIO	b18877e236cff49652c0a6f9a42d4c99
Damburneya ambigens	-95.0882	18.57975	Giraldo-Kalil field data	LJGK_plots_tree#62
Damburneya ambigens	-95.07752	18.58703	Giraldo-Kalil field data	LJGK_plots_tree#27
Damburneya ambigens	-95.062	18.497	IBUNAM	NA
Damburneya ambigens	-95.0589	18.601	SNIB - CONABIO	fa31e990f811daebe2b2948944f9fa34
Damburneya ambigens	-95.0481	18.4653	SNIB - CONABIO	f3a7d915d335cbe713153fe479f264af
Damburneya ambigens	-95.011	18.517	SNIB - CONABIO	ec3c19374905eb382ceee19eefb79567
Damburneya ambigens	-95.008	18.513	GBIF	NA
Damburneya ambigens	-95.00007	18.36996	Giraldo-Kalil field data	Damb332
Damburneya ambigens	-94.9917	18.475	SNIB - CONABIO	856423e166aadaa96a234846d12f5486

Damburneya ambigens	-94.99076	18.3681	Giraldo-Kalil field data	Damb338
Damburneya ambigens	-94.65583	17.06667	IBUNAM	NA
Damburneya ambigens	-94.4725	17.1486	SNIB - CONABIO	1a345493460e33667256407830280c43
Damburneya ambigens	-92.0106	17.5361	SNIB - CONABIO	639f9d0ba6b7b09160cc78352df7ac37
Damburneya ambigens	-91.6825	17.3308	SNIB - CONABIO	73b8b875dd25b250575d5a2aa87a692b
Damburneya ambigens	-91.5342	17.2514	SNIB - CONABIO	fbf1e42454849aca3c52b935d38c99f9
Damburneya ambigens	-91.0692	16.7308	SNIB - CONABIO	ff9563fa02ef4e16e3d507602fac90ce
Damburneya ambigens	-91.0653	16.7089	SNIB - CONABIO	0c15e553a932a4e14a3bceac409d0819
Damburneya ambigens	-90.9339	16.1158	SNIB - CONABIO	15252e7415dbc987c961befda6cfcc96
Damburneya ambigens	-89.35083	16.08111	GBIF	NA
Damburneya ambigens	-87.46666	15.69972	GBIF	NA
Damburneya ambigens	-87.44417	15.73222	GBIF	NA
Damburneya ambigens	-87.05416	15.42194	GBIF	NA
Damburneya colorata	-96.54083	17.72222	IBUNAM	NA
Damburneya colorata	-95.7583	17.425	SNIB - CONABIO	2e30f583442caeb30b3def9fd0ff3dd8
Damburneya colorata	-95.1234	18.57182	Giraldo-Kalil field data	LJGK_plots_tree#168
Damburneya colorata	-95.0882	18.57974	Giraldo-Kalil field data	LJGK_plots_tree#63
Damburneya colorata	-95.0739	18.5847	SNIB - CONABIO	67bd0972724c277382b4bb2bd4a792f4
Damburneya colorata	-94.976531	18.42012	GBIF	1260902297
Damburneya colorata	-94.733	16.867	IBUNAM	NA
Damburneya colorata	-91.3583	16.925	SNIB - CONABIO	73faf8270d268e3055e82f9f392490a1
Damburneya colorata	-90.931062	16.11998	GBIF	1419486034
Damburneya colorata	-89.734774	15.820057	GBIF	1138059028
Damburneya colorata	-89.676268	15.778398	GBIF	1138994343
Damburneya colorata	-89.550658	15.758785	IBUNAM	2958287
Damburneya colorata	-89.232811	15.894818	GBIF	1139451971
Damburneya colorata	-89.231886	15.906663	GBIF	1426059047
Damburneya colorata	-89.04722	16.61	GBIF	NA
Damburneya colorata	-89.020278	16.681111	GBIF	2268997338
Damburneya colorata	-88.996052	16.742417	GBIF	1138994345
Damburneya colorata	-88.92306	16.80972	GBIF	NA
Damburneya colorata	-88.75	16.533	IBUNAM	NA
Damburneya colorata	-88.684767	17.217668	GBIF	1056522734
Damburneya gentlei	-97.32167	20.00111	IBUNAM	NA
Damburneya gentlei	-97.29667	20.04361	IBUNAM	NA
Damburneya gentlei	-97.1528	19.9811	SNIB - CONABIO	8c080003b5d2c2f3d1e48c97e06c8da2
Damburneya gentlei	-96.9583	20.0417	SNIB - CONABIO	7eccf057e2a58a69175f65478beaae73
Damburneya gentlei	-96.9175	20.0067	SNIB - CONABIO	e2e6c95415b7204a83148332cb2ec9eb
Damburneya gentlei	-96.8083	19.8583	SNIB - CONABIO	267cd10d704a72c8e9a8fcc8bc17de73
Damburneya gentlei	-96.7944	19.8833	SNIB - CONABIO	0b1b1a4997d87501c2ae5438a1a5c14f
Damburneya gentlei	-96.125	17.8083	SNIB - CONABIO	a60f2fafe72deeae04b6e0c0d1b2f2d0

Damburneya gentlei	-95.2267	18.5563	GBIF	NA
Damburneya gentlei	-95.1583	18.5917	SNIB - CONABIO	c718cd3121d3f42471b1b7f35cb80844
Damburneya gentlei	-95.1259	18.5815	GBIF	NA
Damburneya gentlei	-95.107	18.585	SNIB - CONABIO	8ac582f458394e0e52467bcafb99c3fc
Damburneya gentlei	-95.095	18.599	IBUNAM	NA
Damburneya gentlei	-95.089	18.595	SNIB - CONABIO	c364506f1e7c2e3b21cdcd1963088a2c
Damburneya gentlei	-95.08779	18.57959	Giraldo-Kalil field data	LJGK_plots_tree#75
Damburneya gentlei	-95.086	18.592	GBIF	NA
Damburneya gentlei	-95.0842	18.5915	IBUNAM	NA
Damburneya gentlei	-95.081	18.586	IBUNAM	NA
Damburneya gentlei	-95.081	18.581	SNIB - CONABIO	f422e6aef95d9b1440fc081a74f02224
Damburneya gentlei	-95.08	18.5886	SNIB - CONABIO	a4de07102156ddba80ea3a02a69d2e93
Damburneya gentlei	-95.0769	18.5863	SNIB - CONABIO	ad08e0c7909885817ef40ffb10a806bf
Damburneya gentlei	-95.07623	18.58082	Giraldo-Kalil field data	LJGK_plots_tree#13
Damburneya gentlei	-95.076	18.583	SNIB - CONABIO	c29878be65c4fbed6d59ec2baf658b80
Damburneya gentlei	-95.061	18.562	SNIB - CONABIO	1a3f602b83eb88dd1e68593b3b42bf1d
Damburneya gentlei	-95.05889	18.5925	SNIB - CONABIO	e5f622daed7be76489287e3d4e444596
Damburneya gentlei	-94.8167	17.0167	SNIB - CONABIO	6fb7c8047561167776badcf3c8e38a32
Damburneya gentlei	-94.8083	17.0083	SNIB - CONABIO	a382da95d173908a9b5518ddda3e38de
Damburneya gentlei	-94.6083	17.2917	SNIB - CONABIO	1e6748ab66c1288af7e7cd09e9b8bae1
Damburneya gentlei	-94.575	17.2417	SNIB - CONABIO	0f134b652c50ae2970cdfee0d6ce3f14
Damburneya gentlei	-94.56	17.23	GBIF	NA
Damburneya gentlei	-94.5583	17.4583	SNIB - CONABIO	1712218c2c24b00fe14f1523b959530a
Damburneya gentlei	-94.4725	17.1486	SNIB - CONABIO	1a345493460e33667256407830280c43
Damburneya gentlei	-94.4075	18.01361	IBUNAM	NA
Damburneya gentlei	-92.95	17.5258	SNIB - CONABIO	52022e894f87c52d41f39856d736e78c
Damburneya gentlei	-92.9311	17.5267	SNIB - CONABIO	7604fcb2722ed5ea7eb178c3c69f1e1f
Damburneya gentlei	-91.7186	17.4739	SNIB - CONABIO	19dd579a208d0534d16d7bcf3bc13d5c
Damburneya gentlei	-91.6167	16.1097	SNIB - CONABIO	c4606249fb9d2b2f14d73408df13a248
Damburneya gentlei	-91.06	16.7	GBIF	NA
Damburneya gentlei	-90.9447	16.7832	SNIB - CONABIO	94562c959debe185827983303017aaa1
Damburneya gentlei	-89.35083	16.08111	GBIF	NA
Damburneya gentlei	-89.2524	16.0448	SNIB - CONABIO	9e2d239071a9a1e3f80e5cf92bc74727
Damburneya gentlei	-89.0802	16.8189	SNIB - CONABIO	f18e9876d03f5cbdacba5b80deb765a4
Damburneya gentlei	-89.0178	16.465	SNIB - CONABIO	db5bd06542fc1b55d73eeebe298e5f45
Damburneya gentlei	-88.98111	16.45972	GBIF	NA
Damburneya gentlei	-88.96639	16.47444	SNIB - CONABIO	01ad0af4fac25749ac70ad21ec20c0f1
Damburneya gentlei	-88.9242	16.4942	SNIB - CONABIO	2bae329ed4e1cfdd2970cb73f29bfe49
Damburneya gentlei	-88.91667	16.48333	SNIB - CONABIO	fd92f152012cb0ac8ba0fb2ba4da512e
Damburneya gentlei	-88.91305	16.49555	GBIF	NA
Damburneya gentlei	-88.90361	16.50277	GBIF	NA

Damburneya gentlei	-88.89306	16.49555	SNIB - CONABIO	f1ace1512cc18b842e3c4702c3dc167a
Damburneya gentlei	-88.81667	16.51667	SNIB - CONABIO	f1ace1512cc18b842e3c4702c3dc167a
Damburneya gentlei	-88.62139	16.82972	SNIB - CONABIO	93843b023642e07e488f26174afcccb9
Damburneya gentlei	-88.616667	17.083333	GBIF	NA
Damburneya gentlei	-88.61666	16.71666	GBIF	NA
Damburneya gentlei	-88.5917	16.7583	SNIB - CONABIO	93843b023642e07e488f26174afcccb9
Damburneya gentlei	-88.43528	16.95194	SNIB - CONABIO	98a9ceb91beba931ed2c4f6da4d8993e
Damburneya gentlei	-87.4575	15.7314	SNIB - CONABIO	af51ea9797d5ce2c110fe77a9561ece5
Damburneya gentlei	-87.44917	15.72722	GBIF	NA
Damburneya gentlei	-87.445	15.71917	GBIF	NA
Damburneya salicifolia	-105.82083	23.43917	IBUNAM	NA
Damburneya salicifolia	-105.38333	20.83333	IBUNAM	NA
Damburneya salicifolia	-105.217	21.583	IBUNAM	NA
Damburneya salicifolia	-105.065	21.4375	SNIB - CONABIO	975c89d37d1425ea156688cab42a505e
Damburneya salicifolia	-105.044	19.4983	SNIB - CONABIO	213f15782285c4eac1b6947710ff6652
Damburneya salicifolia	-105.005	21.4372	SNIB - CONABIO	0f466a4afece7dab0cbdea24eb16e590
Damburneya salicifolia	-104.995	21.4767	SNIB - CONABIO	47b28d14d318fb7fcf7d4911a9b130c8
Damburneya salicifolia	-104.983	21.4972	SNIB - CONABIO	eab4786000b4028a733d9667d9418a89
Damburneya salicifolia	-104.923	21.5214	SNIB - CONABIO	88bc1e0300deb621ca0a262dddd27f0c
Damburneya salicifolia	-104.913	21.3053	SNIB - CONABIO	7a87a3ed1c382ee044009dacf158507f
Damburneya salicifolia	-104.368	19.6686	SNIB - CONABIO	ba9087e6d483498fc0cbffb8fdae81ac
Damburneya salicifolia	-103.825	20.9417	SNIB - CONABIO	263929ac00cad406800cfea2211f9b4e
Damburneya salicifolia	-103.758	19.325	SNIB - CONABIO	9d4f4d71c1b5b9d6eed575615f971c39
Damburneya salicifolia	-103.69167	19.44583	SEINET	NA
Damburneya salicifolia	-103.66667	19.43333	SEINET	NA
Damburneya salicifolia	-103.447	18.5567	SNIB - CONABIO	f1ace1512cc18b842e3c4702c3dc167a
Damburneya salicifolia	-103.317	18.3931	SNIB - CONABIO	fd92f152012cb0ac8ba0fb2ba4da512e
Damburneya salicifolia	-103.118	18.7675	SNIB - CONABIO	01ad0af4fac25749ac70ad21ec20c0f1
Damburneya salicifolia	-100.11678	19.12483	IBUNAM	NA
Damburneya salicifolia	-99.9081	16.8603	SNIB - CONABIO	8e3d71494946ab4e14ff500b2d3e1ff9
Damburneya salicifolia	-99.8553	16.8206	SNIB - CONABIO	1e6aeabf9d03b84bc2c0e651b34fc921
Damburneya salicifolia	-99.5942	22.3506	SNIB - CONABIO	9b937383360acaa0dda4228a4ed04d22
Damburneya salicifolia	-99.5581	21.9664	SNIB - CONABIO	5882699c63b7d24e4a0b12cad593a7ef
Damburneya salicifolia	-99.5306	22.3867	SNIB - CONABIO	f406099f06bf999074b882690fd7c74a
Damburneya salicifolia	-99.5261	17.2475	SNIB - CONABIO	cf61215c610d915be6ceec825cb77881
Damburneya salicifolia	-99.5203	21.6572	SNIB - CONABIO	8b421888a863d7e14124f081142c33ca
Damburneya salicifolia	-99.4964	21.9106	SNIB - CONABIO	bc66cfa65e677076598af9e9446ebaad
Damburneya salicifolia	-99.4933	21.1539	SNIB - CONABIO	56d98e35b40686eb7afbd9a922322e40
Damburneya salicifolia	-99.3992	22.4953	SNIB - CONABIO	0b7e3de56497842a2c258399cd516167
Damburneya salicifolia	-99.3983	21.9186	SNIB - CONABIO	76ee11665b351b697d2a1959f6ff04b1
Damburneya salicifolia	-99.3858	22.0872	SNIB - CONABIO	c469c527a9beabf915bb1d340209c7fa

Damburneya salicifolia	-99.3836	21.1039	SNIB - CONABIO	88d31d3a4b00b5b061bc7b1a7b099079
Damburneya salicifolia	-99.3572	22.5217	SNIB - CONABIO	52bc3eb7bd72684c9021cbfe203276ab
Damburneya salicifolia	-99.3372	21.4386	SNIB - CONABIO	627d047e3c7b843d985fdf73a202b27a
Damburneya salicifolia	-99.2539	21.1842	SNIB - CONABIO	1e2df45a58e5489f55ed73b5905e2933
Damburneya salicifolia	-99.2508	22.1847	SNIB - CONABIO	867e979e9eeb0e76920df808cf322681
Damburneya salicifolia	-99.1986	23.0597	SNIB - CONABIO	98f789d2f23644401dbaa0871579a605
Damburneya salicifolia	-99.1917	21.1583	SNIB - CONABIO	7e20d756f28d809bdc0af1f9db650e5c
Damburneya salicifolia	-99.1891	21.4909	SNIB - CONABIO	55008bd41a9442ea17654a6076997849
Damburneya salicifolia	-99.175	23.0917	SNIB - CONABIO	5ef854d34346fa43bc9f73c6cec8436b
Damburneya salicifolia	-99.1704	21.1761	SNIB - CONABIO	fad00b4f0238567455ccc0f826b0dca7
Damburneya salicifolia	-99.1583	23.175	SNIB - CONABIO	476d82ad13d7668b52f3103e8a2c458a
Damburneya salicifolia	-99.1583	23.225	SNIB - CONABIO	7df9814e546d3acfcdff07dec6b0b4f8
Damburneya salicifolia	-99.1583	23.1417	SNIB - CONABIO	73fece025d94b57d704e1b549e11eeac
Damburneya salicifolia	-99.1581	21.5627	SNIB - CONABIO	42e90f2e66265d585919dd72d870225b
Damburneya salicifolia	-99.1517	21.6108	SNIB - CONABIO	228041939fffb880b43d891ba061be3e
Damburneya salicifolia	-99.1417	23.0583	SNIB - CONABIO	4e2cd6e51e315a72edefc26ffc63f48f
Damburneya salicifolia	-99.1417	23.0417	SNIB - CONABIO	65a2f30cef689e2702dfecf297159fae
Damburneya salicifolia	-99.1417	23.125	SNIB - CONABIO	2880f363c86eb5b3eb51086e9bc1e9ba
Damburneya salicifolia	-99.1265	23.0165	SNIB - CONABIO	84592e381191335ee58b91ddf9acabff
Damburneya salicifolia	-99.126	21.1459	SNIB - CONABIO	dc2d540a0955c13385977711f67183a6
Damburneya salicifolia	-99.1208	21.1822	SNIB - CONABIO	c28e7963bdba80af25168900f0fe3a41
Damburneya salicifolia	-99.1181	21.1922	SNIB - CONABIO	81ff4bcfbce3a0e65a8774e46c309e20
Damburneya salicifolia	-99.1153	23.1458	SNIB - CONABIO	4707d9bba3cde9392ffa2219ec9f5ed1
Damburneya salicifolia	-99.1142	21.9614	SNIB - CONABIO	f1a043e7608495016b3ecb688b172937
Damburneya salicifolia	-99.1081	21.1589	SNIB - CONABIO	d52d615843d226c1d74b8b7d6fed76d2
Damburneya salicifolia	-99.1061	23.1408	SNIB - CONABIO	6f3adbb6ba103a73fe17f278c4d7b7aa
Damburneya salicifolia	-99.075	21.2167	SNIB - CONABIO	4453007e1e46ccce1f13979a48617235
Damburneya salicifolia	-99.0468	21.2598	SNIB - CONABIO	e887e46bced370a165ed3c459044bc56
Damburneya salicifolia	-99.0431	21.1619	SNIB - CONABIO	0c66bb2997b656210e06b5e103a4a66c
Damburneya salicifolia	-99.033	21.1599	SNIB - CONABIO	5368a8beee93f507d71ba1e0b26c0b30
Damburneya salicifolia	-98.9789	21.2064	SNIB - CONABIO	4949f46a8f649962768ef6dcaa074526
Damburneya salicifolia	-98.9769	21.5994	SNIB - CONABIO	67b65c0fb58bc5687785558739604c5a
Damburneya salicifolia	-98.9601	21.4225	SNIB - CONABIO	d357fd493c4018b90108c92178bc5925
Damburneya salicifolia	-98.9028	21.6194	SNIB - CONABIO	1a7f745d6fe0a7c80383267e95dddece
Damburneya salicifolia	-98.8839	24.7167	SNIB - CONABIO	dc225630aa47484a6d429b97724b04ea
Damburneya salicifolia	-98.8508	24.7183	SNIB - CONABIO	83c0b4d601e030c9b7520e31f9be6112
Damburneya salicifolia	-98.7575	20.7811	SNIB - CONABIO	551b199881856f69ba40ade01733a38a
Damburneya salicifolia	-98.7356	24.5192	SNIB - CONABIO	528f23307576883893fc5d6f0e8970fc
Damburneya salicifolia	-98.7339	24.5692	SNIB - CONABIO	16ca09bbb9765671eae55fcef18bddc5
Damburneya salicifolia	-98.7253	21.2869	SNIB - CONABIO	01642b3b2203bbb17d3c835dd8f0d9f7
Damburneya salicifolia	-98.6983	24.575	SNIB - CONABIO	6d868596cae0dafdd58a224974fe3a47

Damburneya salicifolia	-98.6856	24.5503	SNIB - CONABIO	30177296ed2e86edb63da1c1c25178d5
Damburneya salicifolia	-98.6856	24.5681	SNIB - CONABIO	8758b634c0e7e227760e142b72957bce
Damburneya salicifolia	-98.6569	21.6353	SNIB - CONABIO	65448b1620b2ee7911e9248ca10718ea
Damburneya salicifolia	-98.651	21.1812	SNIB - CONABIO	2cf6eee861a126f26f82e35eab7fd472
Damburneya salicifolia	-98.6217	20.6267	SNIB - CONABIO	e779943c5418c7e8a84048dbba555d3d
Damburneya salicifolia	-98.6078	21.1703	SNIB - CONABIO	bd260fbfda1673ef359ab0d0573b80ee
Damburneya salicifolia	-98.6072	20.6217	SNIB - CONABIO	ebbe8bfc2088e6f61da16d253dafe3d3
Damburneya salicifolia	-98.4783	20.535	SNIB - CONABIO	4222e8f1860490b4f81fa41db58d84be
Damburneya salicifolia	-98.3917	21.1956	SNIB - CONABIO	9d947b650bb5ac61bbfe86c51440b3df
Damburneya salicifolia	-98.34944	20.75556	IBUNAM	NA
Damburneya salicifolia	-98.33333	20.43333	GBIF	NA
Damburneya salicifolia	-98.2694	21.3444	SNIB - CONABIO	66318ffddca258b1b658cb7dfde1be53
Damburneya salicifolia	-98.2569	20.3358	SNIB - CONABIO	31560711cc0ec9509a3fc626f9a6f122
Damburneya salicifolia	-98.2417	22.8917	SNIB - CONABIO	583b1b6e7d40bd7f9d3c6ea85e1b83ec
Damburneya salicifolia	-98.2122	20.3242	SNIB - CONABIO	c1dafbee4c4b598c2f6beb61d482ee92
Damburneya salicifolia	-98.2083	20.9417	SNIB - CONABIO	8dd4f686041d41e1a82de150b592b365
Damburneya salicifolia	-98.1917	22.0583	SNIB - CONABIO	09370d2d4a187e9542a9ebf3265967fe
Damburneya salicifolia	-97.9917	20.2917	SNIB - CONABIO	da0cf2dc48dab7346cb2004060f8b399
Damburneya salicifolia	-97.9597	19.9425	SNIB - CONABIO	f338357dfe640967c836bf1d074d2de3
Damburneya salicifolia	-97.9567	21.2611	SNIB - CONABIO	dc4978cf7d0c0a2af347576511416e0a
Damburneya salicifolia	-97.925	21.2083	SNIB - CONABIO	bccab4499723b34f69f53b6c56fe30d4
Damburneya salicifolia	-97.9133	20.225	SNIB - CONABIO	2a5db2d900f278f62d0b9caccef10bbe
Damburneya salicifolia	-97.8739	21.1844	SNIB - CONABIO	c5d9b110fce9c1c6ceb46c7a902c3749
Damburneya salicifolia	-97.82611	21.30694	IBUNAM	NA
Damburneya salicifolia	-97.825	22.1917	SNIB - CONABIO	5b8229527f20baf4a8d58ff1ac766650
Damburneya salicifolia	-97.8083	20.325	SNIB - CONABIO	cc1405a97b043bb417f9946cc2074d70
Damburneya salicifolia	-97.8033	22.1106	SNIB - CONABIO	31cf705a2540be78d2d94e4db055931e
Damburneya salicifolia	-97.775	23.175	SNIB - CONABIO	448281271e3cd62a41a351bacb6b4ad6
Damburneya salicifolia	-97.7706	22.1117	SNIB - CONABIO	0265a3a2515857346cfb2feb0ee38b7f
Damburneya salicifolia	-97.7433	20.6033	SNIB - CONABIO	59db38ee34564a27c00710615c974e2e
Damburneya salicifolia	-97.6008	21.7928	SNIB - CONABIO	4931c5d0a4ee4e8a980e387652103932
Damburneya salicifolia	-97.575	20.175	SNIB - CONABIO	c5247ec40238d73c093e0df689ed26bb
Damburneya salicifolia	-97.575	20.0283	SNIB - CONABIO	563c50850a0d7d338025f98125eba25e
Damburneya salicifolia	-97.5742	20.0658	SNIB - CONABIO	a7e9db8acb622f18297881d2d8661999
Damburneya salicifolia	-97.5583	16.075	SNIB - CONABIO	4e5789933e5401424e379468aac1dc1e
Damburneya salicifolia	-97.5583	20.075	SNIB - CONABIO	ba16264eecb90be323323b971e731767
Damburneya salicifolia	-97.5417	16.225	SNIB - CONABIO	c2b80a42003f06f4fa53db7822cc8e38
Damburneya salicifolia	-97.535	20.715	SNIB - CONABIO	5e0bb4518bdb9520ad0aed86d0ab105b
Damburneya salicifolia	-97.5319	20.705	SNIB - CONABIO	f18eb3ab5cef6322abbfaa19b4cee850
Damburneya salicifolia	-97.5206	20.0169	SNIB - CONABIO	6c7929f85d2b374ea4995465eb439252
Damburneya salicifolia	-97.5083	20.0283	SNIB - CONABIO	03a778558e7765589ac47f4122f77a62

Damburneya salicifolia	-97.49722	20.125	IBUNAM	NA
Damburneya salicifolia	-97.465	20.0561	SNIB - CONABIO	27545869d2c83196d82b3e406f92d9f3
Damburneya salicifolia	-97.4364	20.0347	SNIB - CONABIO	212171caf2d81a0233f754023e04c918
Damburneya salicifolia	-97.425	20.9583	SNIB - CONABIO	cf2b6883ae97ec8ad627d11139d86802
Damburneya salicifolia	-97.4183	21.3369	SNIB - CONABIO	a9ba5cff853c913eb381083567b42cf2
Damburneya salicifolia	-97.4125	20.0222	SNIB - CONABIO	c939bb0fa2bdc44b72e399a94f29281e
Damburneya salicifolia	-97.4032	21.5811	SNIB - CONABIO	c830595cb46dc3e164e32f6ca564e301
Damburneya salicifolia	-97.4014	21.5689	SNIB - CONABIO	75b4874ec58796bf0341cffba447a64a
Damburneya salicifolia	-97.3822	21.5703	SNIB - CONABIO	1e9d18a48ff502b6ac152e7e83c8bb04
Damburneya salicifolia	-97.3694	21.5814	SNIB - CONABIO	e8c58c5184aecd5a0eebb62114e7ec24
Damburneya salicifolia	-97.3687	20.4479	SNIB - CONABIO	e0deb23c995360c16c8bc68014a1b032
Damburneya salicifolia	-97.325	20.4417	SNIB - CONABIO	2fc510c47274f3a7bd3b02f5f60b0a28
Damburneya salicifolia	-97.3047	20.9597	SNIB - CONABIO	5476ceb3cabccd90086236161ecfba62
Damburneya salicifolia	-97.2853	20.455	SNIB - CONABIO	84de69e9139b22bbfeefd22e540a0927
Damburneya salicifolia	-97.2467	20.83667	IBUNAM	NA
Damburneya salicifolia	-97.2417	20.125	SNIB - CONABIO	6117c83e42e4efb5b3257c1ea7459a09
Damburneya salicifolia	-97.2175	20.0203	SNIB - CONABIO	3119e67c0deb0684eeb235ee5c074be3
Damburneya salicifolia	-97.2064	20.6711	SNIB - CONABIO	f50cb367a2ddac432f5ea03c93119a84
Damburneya salicifolia	-97.1681	19.9278	SNIB - CONABIO	5f06df8ff8dde6c73b6958b946e6ce74
Damburneya salicifolia	-97.125	19.3583	SNIB - CONABIO	2990fef27fae7ae93bc3d195d6686a33
Damburneya salicifolia	-97.105	20.0064	SNIB - CONABIO	64b7e7e4d9c0e79301e0271798e06125
Damburneya salicifolia	-97.1036	18.8497	SNIB - CONABIO	68784cd14ee1cd26905a11426ba1a39c
Damburneya salicifolia	-97.0967	20.0583	SNIB - CONABIO	b395a179902e8f2be1f5bd70a62cd408
Damburneya salicifolia	-97.055	20.0556	SNIB - CONABIO	50b9a9319e457d54d5dd39a5eaf53a68
Damburneya salicifolia	-97.0169	19.475	SNIB - CONABIO	9899cca566f027da78439cbcc9283737
Damburneya salicifolia	-97.01248	18.65332	GBIF	NA
Damburneya salicifolia	-96.9983	18.1656	SNIB - CONABIO	1f023749afff35ae4faf4bfaad258d11
Damburneya salicifolia	-96.9981	19.3797	SNIB - CONABIO	e15c4ce421067f7b5450e9d9fc18fc2c
Damburneya salicifolia	-96.9978	18.8969	SNIB - CONABIO	e9ad93080db7567debc8adcc82a9feba
Damburneya salicifolia	-96.9917	19.1417	SNIB - CONABIO	bdd6611255f92717a0014eb59914503c
Damburneya salicifolia	-96.9917	19.425	SNIB - CONABIO	77a6ea8f7af724b0cb42204b60dc9ea2
Damburneya salicifolia	-96.9881	19.4575	SNIB - CONABIO	f767a1129b3470e1abf86b7dcf3f2a4c
Damburneya salicifolia	-96.9778	19.5889	SNIB - CONABIO	98ddfbe15b58aefd9747894ac8914fcd
Damburneya salicifolia	-96.975	19.5583	SNIB - CONABIO	ef316f50680b5c8e316d50bf472e030e
Damburneya salicifolia	-96.9717	19.3853	SNIB - CONABIO	37fae73df311a3704cd564a27d951aa1
Damburneya salicifolia	-96.9633	19.4278	SNIB - CONABIO	fc36f50d42a071e3f26951499e9206a7
Damburneya salicifolia	-96.9603	19.1497	SNIB - CONABIO	424708d4e461c8fa0b7872911beb75f2
Damburneya salicifolia	-96.9492	19.1711	SNIB - CONABIO	962b15fe3b515b91ecc1165fc1776e6a
Damburneya salicifolia	-96.9442	19.5683	SNIB - CONABIO	288a4d3a90934560a88ad15cfdab8021
Damburneya salicifolia	-96.9442	19.6525	SNIB - CONABIO	a634963b0544725da81b950e74eeb524
Damburneya salicifolia	-96.9317	18.8911	SNIB - CONABIO	6d8a6e10a3b60f7619fb430a61f89e93

Damburneya salicifolia	-96.925	19.5083	SNIB - CONABIO	435537232e54ca17508ff6cf1a1a6c36
Damburneya salicifolia	-96.925	18.8417	SNIB - CONABIO	cb69e03dabd672250cba33300f5938cc
Damburneya salicifolia	-96.9206	19.5481	SNIB - CONABIO	af34aa98d6760a922e011b648b2428ed
Damburneya salicifolia	-96.9203	20.3736	SNIB - CONABIO	c93cd7c187a3d989ac573b955dc9181c
Damburneya salicifolia	-96.9167	19.4086	SNIB - CONABIO	3ca7b6aff243f5eeff6fc7865c53c13e
Damburneya salicifolia	-96.9083	20.3583	SNIB - CONABIO	b01e37ebaf82f7c23394686b8bd1f529
Damburneya salicifolia	-96.9083	19.375	SNIB - CONABIO	46d76f82b65c6569d5585cb3db61e42a
Damburneya salicifolia	-96.9025	19.4994	SNIB - CONABIO	9fa1bda441ab77cef24b6c5744d5f496
Damburneya salicifolia	-96.8917	20.325	SNIB - CONABIO	19c7f6466d71f1327e9b0c948e5eda33
Damburneya salicifolia	-96.8786	19.2125	SNIB - CONABIO	1693e795f421ee51817970ed0fe610ae
Damburneya salicifolia	-96.8622	19.5458	SNIB - CONABIO	5eeabb33259a737198d5f13b3797d0db
Damburneya salicifolia	-96.8583	19.4083	SNIB - CONABIO	a9df1887e0f446c42282e0f2aa90b508
Damburneya salicifolia	-96.8553	19.2181	SNIB - CONABIO	5be6c11118ef50ae36533095aede5d80
Damburneya salicifolia	-96.8517	19.6844	SNIB - CONABIO	a91d7449af161b7d5b65d67df57950db
Damburneya salicifolia	-96.8333	19.9333	SNIB - CONABIO	13474bb9a152696650a94c2ffbfb3df5
Damburneya salicifolia	-96.825	19.5417	SNIB - CONABIO	1fb5fd296ef87b37b984381a7fdadacc
Damburneya salicifolia	-96.8225	18.8994	SNIB - CONABIO	6d1a1a1fa2aa5b429d3ca9da0e427995
Damburneya salicifolia	-96.7908	18.5294	SNIB - CONABIO	d5a74f5c1f476d07fe9f523874517171
Damburneya salicifolia	-96.7883	19.3967	SNIB - CONABIO	cbbf5c9d54c8fff3d8f7427fbef19ce2
Damburneya salicifolia	-96.7858	18.7461	SNIB - CONABIO	0a707ba7ff42e58a1de7cb8b848ff191
Damburneya salicifolia	-96.775	20.2083	SNIB - CONABIO	41a4d72c2ce00617547e14bddbdcd77e
Damburneya salicifolia	-96.775	19.87083	IBUNAM	NA
Damburneya salicifolia	-96.775	19.8917	SNIB - CONABIO	eb07db1cfd8c382085eac05411523d16
Damburneya salicifolia	-96.7617	19.3319	SNIB - CONABIO	1e3a308fc1d3518b87ac9ef8255a6b68
Damburneya salicifolia	-96.7583	19.9083	SNIB - CONABIO	87d8f4389113832cd8c580ce383a1b62
Damburneya salicifolia	-96.7583	18.925	SNIB - CONABIO	46d76e84bd2147ff6f9095d471056223
Damburneya salicifolia	-96.7417	19.9083	SNIB - CONABIO	5b1a9c3ec43d7279f05a06e1c52cdcc1
Damburneya salicifolia	-96.7417	19.875	SNIB - CONABIO	d0217b489f0ca4e1e7cd58c519062a82
Damburneya salicifolia	-96.7378	19.2039	SNIB - CONABIO	3d0af43593f1488169efd65babba46d6
Damburneya salicifolia	-96.7317	19.6228	SNIB - CONABIO	6f338544e96db9e8a3039b2c2dfa93c3
Damburneya salicifolia	-96.7281	19.9233	SNIB - CONABIO	95e22f91f2c664153772209041d359c5
Damburneya salicifolia	-96.725	19.9417	SNIB - CONABIO	f0d8a2b66de4900adc5a245804e43990
Damburneya salicifolia	-96.7175	20.1564	SNIB - CONABIO	f22066629b93f94de1f234a0c7d09240
Damburneya salicifolia	-96.7153	19.325	SNIB - CONABIO	e875606b98b6f04ec5721018ff9d3947
Damburneya salicifolia	-96.7083	19.3083	SNIB - CONABIO	cbe3aa976871ebc5c1d2421a77cd6288
Damburneya salicifolia	-96.7053	19.1711	SNIB - CONABIO	a98b96bcff1c12050a345e4c080a2f84
Damburneya salicifolia	-96.6878	19.725	SNIB - CONABIO	aab925c875e003056ff89ab9728276b5
Damburneya salicifolia	-96.6731	19.7278	SNIB - CONABIO	ace042bad480157ce4b62b43166dd593
Damburneya salicifolia	-96.6694	19.2433	SNIB - CONABIO	69eac29e2ac0952d837bc1b819ecdc09
Damburneya salicifolia	-96.6494	20.0272	SNIB - CONABIO	4c2387844c34116a1ee6027df7d5f08b
Damburneya salicifolia	-96.6467	19.2131	SNIB - CONABIO	c79e12b3b780ee618e1fa512fdf79549

Damburneya salicifolia	-96.6417	19.3417	SNIB - CONABIO	67c1a9139c7bdefb766312275ea2284e
Damburneya salicifolia	-96.625	19.3417	SNIB - CONABIO	d6ad42a433f4714abefcfd570e9e51ca
Damburneya salicifolia	-96.5808	19.8458	SNIB - CONABIO	797a1a627cdbb0f179d5f6b533469e0b
Damburneya salicifolia	-96.5786	19.2528	SNIB - CONABIO	3b51fd1f4800ecea3ab5c332b0ac5521
Damburneya salicifolia	-96.5628	19.2597	SNIB - CONABIO	8dd08497dfc27fb088d6bce103a24d5e
Damburneya salicifolia	-96.5417	16.025	SNIB - CONABIO	07fcd71d3f5bf169b71cc0e56ffa3e22
Damburneya salicifolia	-96.5106	19.2903	SNIB - CONABIO	5b799f1130429814faf09f42e359fa9e
Damburneya salicifolia	-96.4917	19.5583	SNIB - CONABIO	9ac839b162070066bb4fc01cdef7e378
Damburneya salicifolia	-96.4917	19.3417	SNIB - CONABIO	3ec561d1ff1ab137c85b6ce5c9622865
Damburneya salicifolia	-96.4917	19.325	SNIB - CONABIO	17ba55e932e3fa87b7d8dd3a0fe19600
Damburneya salicifolia	-96.4808	19.3289	SNIB - CONABIO	1d5d1a97c1724b03667c3519ff32e997
Damburneya salicifolia	-96.4607	15.8601	SNIB - CONABIO	4ef9514f12c50ffa3d82f8a53ca0feb7
Damburneya salicifolia	-96.4083	18.2417	SNIB - CONABIO	9cb5ce6b1e64ac3a7a429e095d9ecfca
Damburneya salicifolia	-96.4047	19.7244	SNIB - CONABIO	e8eaf676a05109f9c8e7f0eec49e8c10
Damburneya salicifolia	-96.3875	19.5044	SNIB - CONABIO	a69ddddf64cc0e60497686c535db5346
Damburneya salicifolia	-96.3808	19.5744	SNIB - CONABIO	80b48160b9aab815d7205fa60ab2a710
Damburneya salicifolia	-96.375	19.6083	SNIB - CONABIO	edc2aac00b5793c90c14708bf821f1b6
Damburneya salicifolia	-96.375	15.8417	SNIB - CONABIO	d177cf9a7646343a00557a9b7bf9a586
Damburneya salicifolia	-96.3625	15.85722	IBUNAM	NA
Damburneya salicifolia	-96.3417	17.625	SNIB - CONABIO	881239623946c695b685ea045d3b4378
Damburneya salicifolia	-96.33333	17.61667	GBIF	NA
Damburneya salicifolia	-96.32833	15.85639	IBUNAM	NA
Damburneya salicifolia	-96.325	19.325	SNIB - CONABIO	bb8b1cbd2892071d8e3e959d05e2ff86
Damburneya salicifolia	-96.2917	15.7417	SNIB - CONABIO	720e741217b83e280d7db95207ee176b
Damburneya salicifolia	-96.2742	19.1986	SNIB - CONABIO	2d94ea97cb6192145b688a56a9c50c29
Damburneya salicifolia	-96.2434	17.7203	SNIB - CONABIO	dabfe297adb24e51554be390085a5dc2
Damburneya salicifolia	-96.1706	17.9467	SNIB - CONABIO	82e29079541098f4f0e60ea59ae5d68d
Damburneya salicifolia	-96.1547	19.0589	SNIB - CONABIO	6e7546ab6e9d5eba326a7b2da739e87f
Damburneya salicifolia	-96.1417	18.0917	SNIB - CONABIO	f56c8dfc1664574c8980c0c3304406f7
Damburneya salicifolia	-96.13547	15.96917	IBUNAM	NA
Damburneya salicifolia	-96.11083	15.93081	IBUNAM	NA
Damburneya salicifolia	-96.10147	15.97603	IBUNAM	NA
Damburneya salicifolia	-96.10016	15.988	IBUNAM	NA
Damburneya salicifolia	-96.08944	15.94806	GBIF	NA
Damburneya salicifolia	-96.07583	15.95417	IBUNAM	NA
Damburneya salicifolia	-96.0222	17.8728	SNIB - CONABIO	7a24ab7fbdcf3f826e588055a9c2399e
Damburneya salicifolia	-95.96778	16.00806	GBIF	NA
Damburneya salicifolia	-95.583	16.717	IBUNAM	NA
Damburneya salicifolia	-95.53602	18.68596	IBUNAM	NA
Damburneya salicifolia	-95.5239	18.6908	SNIB - CONABIO	29148bb1d4f7c55461b96aca4ec0488e
Damburneya salicifolia	-95.52194	16.72667	GBIF	NA

Damburneya salicifolia	-95.51706	16.70922	GBIF	NA
Damburneya salicifolia	-95.483	16.717	IBUNAM	NA
Damburneya salicifolia	-95.43	18.13333	GBIF	NA
Damburneya salicifolia	-95.4033	18.5217	SNIB - CONABIO	48e2a4b89d79e1fefee828e0c9094a84
Damburneya salicifolia	-95.3286	18.5378	SNIB - CONABIO	845513176f801752d2ea175163e1ae62
Damburneya salicifolia	-95.3083	18.5417	SNIB - CONABIO	caafeaaa2bd11e8decfe1d5732993b52
Damburneya salicifolia	-95.267	16.683	IBUNAM	NA
Damburneya salicifolia	-95.2578	18.5731	SNIB - CONABIO	758f83dca7fe545bee6e7ff57d984308
Damburneya salicifolia	-95.2122	18.4497	SNIB - CONABIO	7b1dadaa9b5a0a46d5a412e283b6be5c
Damburneya salicifolia	-95.2014	18.5586	SNIB - CONABIO	f6b0c058eea8e7184f57fd2af41ea1c6
Damburneya salicifolia	-95.2006	18.3889	SNIB - CONABIO	ca4ddbdb78d7df8a4cd49245e5b38b00
Damburneya salicifolia	-95.1911	18.4575	SNIB - CONABIO	df27371854b7c3c7ee6a8fd9c483511c
Damburneya salicifolia	-95.1825	18.3489	SNIB - CONABIO	5b56389de83cb146c39c5daa788f3631
Damburneya salicifolia	-95.17777	18.57916	GBIF	NA
Damburneya salicifolia	-95.16961	18.49347	IBUNAM	NA
Damburneya salicifolia	-95.1583	18.6083	SNIB - CONABIO	4b26f48741c8ed6261b4c3f6d71570fd
Damburneya salicifolia	-95.1418	18.54144	Giraldo-Kalil field data	LJGK_plots_tree#97
Damburneya salicifolia	-95.13857	18.57853	Giraldo-Kalil field data	LJGK_plots_tree#222
Damburneya salicifolia	-95.1246	18.57085	Giraldo-Kalil field data	LJGK_plots_tree#154
Damburneya salicifolia	-95.1081	18.5806	IBUNAM	NA
Damburneya salicifolia	-95.0967	18.3333	SNIB - CONABIO	39be6592f2d37ebe0232c1cab83762c2
Damburneya salicifolia	-95.095	18.6417	SNIB - CONABIO	3872dd9d7316bfd36cc453686a0c4a9b
Damburneya salicifolia	-95.08816	18.57941	Giraldo-Kalil field data	LJGK_plots_tree#55
Damburneya salicifolia	-95.0881	18.5892	SNIB - CONABIO	d8dc8c3d6b613574ec7b18daf12f54b8
Damburneya salicifolia	-95.0847	18.4331	SNIB - CONABIO	3e124c8bc89f084b2ecdbe000f21a38f
Damburneya salicifolia	-95.0788	18.5648	IBUNAM	NA
Damburneya salicifolia	-95.0739	18.5847	SNIB - CONABIO	67bd0972724c277382b4bb2bd4a792f4
Damburneya salicifolia	-95.0733	16.7517	SNIB - CONABIO	2964c71dc1fb2f07d6695ab12396904b
Damburneya salicifolia	-95.071	18.614	IBUNAM	NA
Damburneya salicifolia	-95.06917	18.57667	IBUNAM	NA
Damburneya salicifolia	-95.0631	18.5594	SNIB - CONABIO	8b0e1e22f6081fafe1b0c2903105305d
Damburneya salicifolia	-95.0583	18.475	SNIB - CONABIO	0bf6960e0bc173031688a56666478d9f
Damburneya salicifolia	-95.0583	16.775	SNIB - CONABIO	56bcda6c75f5eec14b80eb4d7fd340af
Damburneya salicifolia	-95.0517	18.5917	SNIB - CONABIO	dea621eb571294f34bb191127cb09e7b
Damburneya salicifolia	-95.0481	18.4653	SNIB - CONABIO	f3a7d915d335cbe713153fe479f264af
Damburneya salicifolia	-95.03972	16.69806	IBUNAM	NA
Damburneya salicifolia	-95.01389	16.67306	IBUNAM	NA
Damburneya salicifolia	-95.0092	16.9728	SNIB - CONABIO	10e6bfbd82a734a1fba05e992d9e68a0
Damburneya salicifolia	-95.0083	16.425	SNIB - CONABIO	283395f99c6798cf720fc666f9b88ea1
Damburneya salicifolia	-94.9917	18.3917	SNIB - CONABIO	34356cec50f2b46297c5a8b44cfc568f
Damburneya salicifolia	-94.9417	18.3417	SNIB - CONABIO	e39322b396d628c9d995e054cbadb9b6

Damburneya salicifolia	-94.9394	18.3875	SNIB - CONABIO	3eebeeebcf21120a9d6d317b9b4af464
Damburneya salicifolia	-94.93444	16.61153	IBUNAM	NA
Damburneya salicifolia	-94.925	18.4083	SNIB - CONABIO	cdafadde294e6ad806978aa94dae74b1
Damburneya salicifolia	-94.8939	17.2569	SNIB - CONABIO	86ee8da35917f2656f169ef26d0ab573
Damburneya salicifolia	-94.8917	18.325	SNIB - CONABIO	4cfdcb70a3d8c2df3b3cdeebea5a04ed
Damburneya salicifolia	-94.84611	16.62631	IBUNAM	NA
Damburneya salicifolia	-94.8222	17.0192	SNIB - CONABIO	b8a5f0a9b2d052112080be751665d4b7
Damburneya salicifolia	-94.7194	18.375	SNIB - CONABIO	e6a8a81faafd5af392cd681ff69bfbbf
Damburneya salicifolia	-94.7139	17.2079	SNIB - CONABIO	3274026a2b71de2d5555f537ad27ade1
Damburneya salicifolia	-94.675	16.9167	SNIB - CONABIO	1bced4250989787f6181edc1560fd33c
Damburneya salicifolia	-94.675	17.2583	SNIB - CONABIO	7e50683a2af051b074f29bfd68357935
Damburneya salicifolia	-94.675	16.9417	SNIB - CONABIO	8b5fe20d27e95e137d5b6371c9de3881
Damburneya salicifolia	-94.6676	16.5068	SNIB - CONABIO	4bd97c6913fb65483fea2b2c14a361e6
Damburneya salicifolia	-94.633	17.283	IBUNAM	NA
Damburneya salicifolia	-94.625	16.925	SNIB - CONABIO	201b56c9fa560ff089934901fe2103cb
Damburneya salicifolia	-94.625	17.2917	SNIB - CONABIO	fbc0fcb4d6c3a66f2b2b788667272589
Damburneya salicifolia	-94.6139	17.275	SNIB - CONABIO	9c26254f2501194c7ad73b81b8792972
Damburneya salicifolia	-94.6083	16.5583	SNIB - CONABIO	caa4f3d8c91ca233a913de6698d54476
Damburneya salicifolia	-94.6028	17.2403	SNIB - CONABIO	1110b10aa825ef42f9597a8637b14e2c
Damburneya salicifolia	-94.595	17.2528	SNIB - CONABIO	69d9225ffce36fa54c8ecd00b39356b6
Damburneya salicifolia	-94.5892	17.3064	SNIB - CONABIO	63aea10945465071af0bc2f50c758292
Damburneya salicifolia	-94.5167	17.3167	SNIB - CONABIO	2b39fb2c3f87bee543127247547e20cf
Damburneya salicifolia	-94.4353	18.1378	SNIB - CONABIO	3a095b5804fc83f0467100a900c649da
Damburneya salicifolia	-94.41096	18.01212	IBUNAM	NA
Damburneya salicifolia	-94.3917	17.2917	SNIB - CONABIO	c1214d595af3a091909f112da110bda6
Damburneya salicifolia	-94.3917	17.2917	SNIB - CONABIO	c1214d595af3a091909f112da110bda6
Damburneya salicifolia	-94.25833	17.225	IBUNAM	NA
Damburneya salicifolia	-94.1917	16.7417	SNIB - CONABIO	6e62c68d2bc2a50a491b53887b521fb6
Damburneya salicifolia	-94.1917	16.7583	SNIB - CONABIO	7774af0af7fd19b8025d97f4931e71e4
Damburneya salicifolia	-94.1889	16.5786	SNIB - CONABIO	ac2a54f71b34df394676d3336fba6663
Damburneya salicifolia	-94.175	16.7333	SNIB - CONABIO	f765a1236b94175a3837501c4ea8bbdb
Damburneya salicifolia	-94.1583	16.7083	SNIB - CONABIO	d7f675136b516c7279bc0ca1865cc6dd
Damburneya salicifolia	-94.1417	16.775	SNIB - CONABIO	1710441fedc1bca7bc4becd9a45c6a53
Damburneya salicifolia	-94.0917	16.475	SNIB - CONABIO	cc98dddcf81512d6034fe30a3dace509
Damburneya salicifolia	-94.0917	16.6583	SNIB - CONABIO	c224745673fbe503a82833aaa79ecb1f
Damburneya salicifolia	-93.9917	16.6417	SNIB - CONABIO	aa032074c78169fe853cce2397957721
Damburneya salicifolia	-93.9269	16.4367	SNIB - CONABIO	c7fa8b81cc01787e8952f5d0214bc40f
Damburneya salicifolia	-93.9083	18.175	SNIB - CONABIO	f8321b8e51fb2cb4e1d5f6d3c51e048e
Damburneya salicifolia	-93.8417	16.7083	SNIB - CONABIO	a24631717af272fc6562d52a77725886
Damburneya salicifolia	-93.8417	16.625	SNIB - CONABIO	e16f3e81d96226ca0632d6b86fbf60ea
Damburneya salicifolia	-93.767	16.967	IBUNAM	NA

Damburneya salicifolia	-93.7578	17.2353	SNIB - CONABIO	71f370dfd7e6dacb9d8a55233e560f3e
Damburneya salicifolia	-93.72722	16.845	GBIF	NA
Damburneya salicifolia	-93.725	16.6917	SNIB - CONABIO	6ec967a5cc881f6cbeb8a57e0022e65a
Damburneya salicifolia	-93.625	17.5583	SNIB - CONABIO	9ba3f717a0b2704b576de8361984881c
Damburneya salicifolia	-93.60222	16.20917	GBIF	NA
Damburneya salicifolia	-93.5844	16.2322	SNIB - CONABIO	0aa051046e30fdbfac41873102d7da26
Damburneya salicifolia	-93.58194	16.20417	IBUNAM	NA
Damburneya salicifolia	-93.51333	18.28944	GBIF	NA
Damburneya salicifolia	-93.5083	16.675	SNIB - CONABIO	826b6cd07de824cccdc6cc331a803345
Damburneya salicifolia	-93.5003	17.0047	SNIB - CONABIO	f014d081bb37eb8cc475c394c5035850
Damburneya salicifolia	-93.4583	16.8417	SNIB - CONABIO	26a090cc372c1d74420f328bb72a330f
Damburneya salicifolia	-93.44167	16.79694	GBIF	NA
Damburneya salicifolia	-93.43528	16.89639	GBIF	NA
Damburneya salicifolia	-93.4083	18.1083	SNIB - CONABIO	bce0b2f0b9cd9e07e01fd51872174c8a
Damburneya salicifolia	-93.38944	16.75583	IBUNAM	NA
Damburneya salicifolia	-93.375	17.0583	SNIB - CONABIO	bd8315bd5c1d6ba09cd5f25cd59bd5c9
Damburneya salicifolia	-93.375	16.7417	SNIB - CONABIO	6bff2d20f34f3aaafc6c585da90a414d
Damburneya salicifolia	-93.3583	17.3153	SNIB - CONABIO	7aebb2ed25c6e0d0bb6d63edd587e8e2
Damburneya salicifolia	-93.2769	16.9656	SNIB - CONABIO	1dfe1a6c7850ec1f1fa380b788ac9fa5
Damburneya salicifolia	-93.2583	16.8417	SNIB - CONABIO	2c22ecf1088406921ef8067740e845c2
Damburneya salicifolia	-93.2244	16.9478	SNIB - CONABIO	798735c4d3f9305cbcca915c0b6cd136
Damburneya salicifolia	-93.1583	17.1306	SNIB - CONABIO	1f068fcc7ab834e3338a109894c0a315
Damburneya salicifolia	-93.1167	16.7528	SNIB - CONABIO	9cd1c55cdfb33f7cd6387650432fa616
Damburneya salicifolia	-93.0767	16.9362	SNIB - CONABIO	5c31a81f5b32f0e62f15438347104f05
Damburneya salicifolia	-93.0611	16.6092	SNIB - CONABIO	8c4ac84dde37a3b9271ca005c299dd25
Damburneya salicifolia	-93.0417	17.1917	SNIB - CONABIO	662feb52a962b573c2c63dce1dd02428
Damburneya salicifolia	-93.025	17.6417	SNIB - CONABIO	fd1638d31ac443a9867e33baa0bd211c
Damburneya salicifolia	-93.02278	16.03278	GBIF	NA
Damburneya salicifolia	-92.975	16.0417	SNIB - CONABIO	3a28f2eeb2bc6f4cc3a53415aebf07e2
Damburneya salicifolia	-92.9731	16.7533	SNIB - CONABIO	cda6a65f2512e11bc7f1a13e8a799728
Damburneya salicifolia	-92.9675	17.21194	GBIF	NA
Damburneya salicifolia	-92.9083	17.1917	SNIB - CONABIO	26307f73120693c3f38779a43df9f0fb
Damburneya salicifolia	-92.9028	17.5172	SNIB - CONABIO	61cbce8019168bbcfaa18c957a3adc94
Damburneya salicifolia	-92.8917	16.9917	SNIB - CONABIO	5a2b01ad9f6c6ce6885d7c89fbf285b9
Damburneya salicifolia	-92.8583	17.075	SNIB - CONABIO	d751c5ee033d52f41476afa98f223b06
Damburneya salicifolia	-92.8414	15.7694	SNIB - CONABIO	0319a9a38a736bf17b904f3ee73cb4d0
Damburneya salicifolia	-92.8069	15.6569	SNIB - CONABIO	821cb3d582cbf1ea0dad60bca4cb33c6
Damburneya salicifolia	-92.8019	17.0019	SNIB - CONABIO	439f61eee7acf3de2c4185d9a1f4e3ca
Damburneya salicifolia	-92.7836	16.9731	SNIB - CONABIO	01309add10e5c457ccd01be8be7c8a90
Damburneya salicifolia	-92.7239	16.9531	SNIB - CONABIO	b9c368e625b1388387ad25868cd19aaf
Damburneya salicifolia	-92.7203	17.0617	SNIB - CONABIO	2b5def3218eaa4898ae49758be4cf2d8

Damburneya salicifolia	-92.7119	16.4144	SNIB - CONABIO	5f360d0d8c5c2ec9bc160579b7c05e2b
Damburneya salicifolia	-92.70167	17.09083	GBIF	NA
Damburneya salicifolia	-92.6583	18.4417	SNIB - CONABIO	5593433e5ad13dca8c8e44a2c2782e94
Damburneya salicifolia	-92.6417	16.625	SNIB - CONABIO	4f273e06673f05e0aa3bb18240f18482
Damburneya salicifolia	-92.6417	18.525	SNIB - CONABIO	69a2aa00664cadebfe5cb5ebcebd3fe4
Damburneya salicifolia	-92.6172	15.4153	SNIB - CONABIO	64918586785a80767aea7f92eec073c6
Damburneya salicifolia	-92.5917	17.7583	SNIB - CONABIO	cd1de805bc7841e2b976ee6185dedcb3
Damburneya salicifolia	-92.5083	16.825	SNIB - CONABIO	3780aa1549408c8ece5d49cd6a947e33
Damburneya salicifolia	-92.5006	15.2417	SNIB - CONABIO	3bd2909af6fe61c6bd9deec99f965493
Damburneya salicifolia	-92.4867	16.8811	SNIB - CONABIO	87275bd11c9b322102c6331fb52d4ce0
Damburneya salicifolia	-92.4769	16.8717	SNIB - CONABIO	9ddf74de57bfd6d2337756a17b2886a0
Damburneya salicifolia	-92.4758	16.8953	SNIB - CONABIO	d1e16a5fcdb7de7f2a8341d43a499f47
Damburneya salicifolia	-92.47028	16.825	GBIF	NA
Damburneya salicifolia	-92.4622	16.8972	SNIB - CONABIO	23d12800dc7845ca15563156889d48d1
Damburneya salicifolia	-92.4456	16.8203	SNIB - CONABIO	f078c050927e2c7a47d463ce1a708418
Damburneya salicifolia	-92.4383	16.9086	SNIB - CONABIO	b8d5889b4cb6d7aa483a205057246bd8
Damburneya salicifolia	-92.4064	17.4314	SNIB - CONABIO	d9fe21ca243f444c40eb117b99c4179d
Damburneya salicifolia	-92.375	16.8917	SNIB - CONABIO	b41c81356c63bc11a1679cce9f44764a
Damburneya salicifolia	-92.3708	17.2097	SNIB - CONABIO	34222b7f1ac6f5f415734d47f5c1da1c
Damburneya salicifolia	-92.3592	15.6508	SNIB - CONABIO	757ae62d80d84791f5edb4debafab157
Damburneya salicifolia	-92.3397	17.1678	SNIB - CONABIO	30a66a431f07826e1bed45f7646d4366
Damburneya salicifolia	-92.2667	17.935	SNIB - CONABIO	93ca5c1efc113b3d5be26d3d6735ab90
Damburneya salicifolia	-92.24111	16.82111	GBIF	NA
Damburneya salicifolia	-92.2292	17.0611	SNIB - CONABIO	dda52c2e384a72b47494bab8b8f3a454
Damburneya salicifolia	-92.2153	16.8214	SNIB - CONABIO	612114ec9cc13b6318394538240affd2
Damburneya salicifolia	-92.14389	16.81917	GBIF	NA
Damburneya salicifolia	-92.1417	17.2583	SNIB - CONABIO	aeca092c33fd5c5871ccdb5ddcd4156a
Damburneya salicifolia	-92.11556	17.26444	GBIF	NA
Damburneya salicifolia	-92.0889	17.4917	SNIB - CONABIO	cf759773e70d138fec9e10620a46eebd
Damburneya salicifolia	-92.0675	16.6081	SNIB - CONABIO	eccec1344c987b92fa0a4ed05742cab9
Damburneya salicifolia	-92.0583	16.125	SNIB - CONABIO	cad31ef960e147ab4fb93f346f7c9004
Damburneya salicifolia	-92.0417	16.7417	SNIB - CONABIO	0da899e7bd22d434abae888d38952ce0
Damburneya salicifolia	-92.0417	16.9083	SNIB - CONABIO	ff2630a4d58bfaaed2113bf779b4e419
Damburneya salicifolia	-92.025	16.2583	SNIB - CONABIO	95202e6e7412ef0cdbbc479107b451d4
Damburneya salicifolia	-92.0069	17.7333	SNIB - CONABIO	401827e48fdb82b907348f6f712fbe7b
Damburneya salicifolia	-91.9925	17.53333	GBIF	NA
Damburneya salicifolia	-91.99222	17.43417	GBIF	NA
Damburneya salicifolia	-91.8708	17.7583	SNIB - CONABIO	5a09ad3c2197ba8f6f9788821194b2c1
Damburneya salicifolia	-91.8417	16.9819	SNIB - CONABIO	970390d88e5c04c2a3bce98c5c6cca48
Damburneya salicifolia	-91.7583	16.8944	SNIB - CONABIO	4937165f3c90ef0291f0f1442a291349
Damburneya salicifolia	-91.74777	15.80416	GBIF	NA

Damburneya salicifolia	-91.7083	16.1083	SNIB - CONABIO	09072f544a37bf079119b672709e3fc0
Damburneya salicifolia	-91.63805	16.09361	GBIF	NA
Damburneya salicifolia	-91.61333	17.82056	IBUNAM	NA
Damburneya salicifolia	-91.6083	16.9917	SNIB - CONABIO	75a6d415599df67ff16563042bdd9aed
Damburneya salicifolia	-91.5792	16.9975	SNIB - CONABIO	e4b9d94fb665aa2cdcbd7a26d310dedc
Damburneya salicifolia	-91.4583	16.825	SNIB - CONABIO	b580f9ff34f348152219ec3b102938d5
Damburneya salicifolia	-91.43361	17.43417	GBIF	NA
Damburneya salicifolia	-91.37306	16.93639	IBUNAM	NA
Damburneya salicifolia	-91.3614	16.9222	SNIB - CONABIO	b8662a566a476e6fb25f4682f93fe302
Damburneya salicifolia	-91.30083	16.99333	IBUNAM	NA
Damburneya salicifolia	-91.2956	16.1389	SNIB - CONABIO	d7b16741b20d0afcaf33ea4c4d891149
Damburneya salicifolia	-91.29083	16.98806	SNIB - CONABIO	3244b1fab99145f8ebe35289294bf7bc
Damburneya salicifolia	-91.28806	16.93722	IBUNAM	NA
Damburneya salicifolia	-91.2506	16.9572	SNIB - CONABIO	f8cc295a4dd4efd3ac279f724f404846
Damburneya salicifolia	-91.175	18.875	SNIB - CONABIO	7abde85e99d9ff43ee6e8f2f0f81b3a6
Damburneya salicifolia	-91.1303	16.7606	SNIB - CONABIO	cade6806b895fcbd8442a9e30895da8d
Damburneya salicifolia	-91.1158	16.7547	SNIB - CONABIO	955033485c9ec9a72c57cf284e31265b
Damburneya salicifolia	-91.1064	16.7989	SNIB - CONABIO	ea2466fccb359ef2bc1fe75271165001
Damburneya salicifolia	-91.065	16.7083	SNIB - CONABIO	26b1a447471aae84603c26aa06c4e090
Damburneya salicifolia	-91.0625	16.7811	SNIB - CONABIO	816c8fb724cf5655e1cf3713b3849451
Damburneya salicifolia	-91.0417	16.725	SNIB - CONABIO	359c41cbd112e37df641da34bf281a20
Damburneya salicifolia	-91.025	16.7583	SNIB - CONABIO	d8d291917a5fdae77fcf812a42f556e2
Damburneya salicifolia	-91.0244	18.3953	SNIB - CONABIO	ce29d8df3e243d519ee39a94729c38a2
Damburneya salicifolia	-91.0094	18.1333	SNIB - CONABIO	26e00bb9726b625252b1a87715f26b95
Damburneya salicifolia	-90.9736	16.898	SNIB - CONABIO	3a2906f46dc31fad8314cef415ad3b05
Damburneya salicifolia	-90.9475	16.10917	IBUNAM	NA
Damburneya salicifolia	-90.925	16.125	SNIB - CONABIO	7e73a8e84a9f36b97e002ab1b554c954
Damburneya salicifolia	-90.90961	16.80586	IBUNAM	NA
Damburneya salicifolia	-90.90944	16.81839	IBUNAM	NA
Damburneya salicifolia	-90.8989	18.3131	SNIB - CONABIO	5d31a633ec053b801624638ba0ee0e3c
Damburneya salicifolia	-90.89033	16.81358	IBUNAM	NA
Damburneya salicifolia	-90.8478	16.2519	SNIB - CONABIO	e1c13482dcb4eb58df10a3f78c8d6075
Damburneya salicifolia	-90.795	17.8922	SNIB - CONABIO	b0fa203a37f6c1e8acf2e8e4ccdc00b1
Damburneya salicifolia	-90.78333	18.78333	IBUNAM	NA
Damburneya salicifolia	-90.7583	17.8917	SNIB - CONABIO	1084f6807075b90596b79447f23802d8
Damburneya salicifolia	-90.7319	18.2736	SNIB - CONABIO	4a9c033c0200bf27be265d36de531e81
Damburneya salicifolia	-90.64861	19.27083	IBUNAM	NA
Damburneya salicifolia	-90.6167	19.2814	SNIB - CONABIO	70ebf328504d1c0e553a42adbed297ca
Damburneya salicifolia	-90.5667	19.2972	SNIB - CONABIO	1f0278441a692749cc4522a21f3a7bec
Damburneya salicifolia	-90.4667	16.4667	SNIB - CONABIO	359349fe908e71bf21907fb23a995ab3
Damburneya salicifolia	-90.4403	17.8653	SNIB - CONABIO	4e3454496139ce82464829709bd53ef6

Damburneya salicifolia	-90.4361	19.1444	SNIB - CONABIO	df937770908e3ddd74acde382b581179
Damburneya salicifolia	-90.417	16.083	IBUNAM	NA
Damburneya salicifolia	-90.39222	16.63722	GBIF	NA
Damburneya salicifolia	-90.3711	16.6009	SNIB - CONABIO	d322c472f703931906574362360a9685
Damburneya salicifolia	-90.275	18.6583	SNIB - CONABIO	1f9f976ddb954bd0fb3056437efcfb44
Damburneya salicifolia	-90.23666	17.25944	GBIF	NA
Damburneya salicifolia	-90.18916	16.53166	GBIF	NA
Damburneya salicifolia	-90.16527	16.68055	GBIF	NA
Damburneya salicifolia	-90.15861	16.63888	GBIF	NA
Damburneya salicifolia	-90.11472	16.78805	GBIF	NA
Damburneya salicifolia	-90.075	18.5417	SNIB - CONABIO	8f687b21f254d8da0e3f73a6937a733a
Damburneya salicifolia	-89.9503	15.8011	SNIB - CONABIO	464bcf2cf4fc589b769246a38954e629
Damburneya salicifolia	-89.93722	16.94611	GBIF	NA
Damburneya salicifolia	-89.92916	16.80638	GBIF	NA
Damburneya salicifolia	-89.9183	16.9647	SNIB - CONABIO	c05d3e210e0d75e71ab7580a2cf77d25
Damburneya salicifolia	-89.9183	17.0358	SNIB - CONABIO	3bae966555a02c195f3a86c8607bfdb5
Damburneya salicifolia	-89.9025	16.98111	GBIF	NA
Damburneya salicifolia	-89.89666	16.99472	GBIF	NA
Damburneya salicifolia	-89.89528	18.37917	IBUNAM	NA
Damburneya salicifolia	-89.89388	16.90361	GBIF	NA
Damburneya salicifolia	-89.8917	17.075	SNIB - CONABIO	ac9bbe77866892799a44d03b9ee1cf5a
Damburneya salicifolia	-89.89083	16.92111	GBIF	NA
Damburneya salicifolia	-89.8819	18.3472	SNIB - CONABIO	481cd893e9dc731e2199603db9c68063
Damburneya salicifolia	-89.87833	16.95055	GBIF	NA
Damburneya salicifolia	-89.85722	18.31694	IBUNAM	NA
Damburneya salicifolia	-89.84722	18.30194	IBUNAM	NA
Damburneya salicifolia	-89.8275	18.2631	SNIB - CONABIO	6553c36eeb18fd3d2c8ceccccc8d9c7b
Damburneya salicifolia	-89.8244	19.8847	SNIB - CONABIO	fe1a767eefb0b77e082904f3b672012f
Damburneya salicifolia	-89.8222	18.0889	SNIB - CONABIO	f22a3844216aa08790a38c46697101df
Damburneya salicifolia	-89.81556	18.12444	IBUNAM	NA
Damburneya salicifolia	-89.8111	18.8167	SNIB - CONABIO	fe7a9c16945fcdc94ad6a160bdc79a99
Damburneya salicifolia	-89.80472	18.14194	IBUNAM	NA
Damburneya salicifolia	-89.80278	18.24556	IBUNAM	NA
Damburneya salicifolia	-89.7833	18.1464	SNIB - CONABIO	35636edb4103f20f1216487dbb134d88
Damburneya salicifolia	-89.77083	17.01388	GBIF	NA
Damburneya salicifolia	-89.733	18.083	IBUNAM	NA
Damburneya salicifolia	-89.70389	15.29972	GBIF	NA
Damburneya salicifolia	-89.6758	17.3228	SNIB - CONABIO	1cb1cbd018588d467d6e03dcb8230401
Damburneya salicifolia	-89.625	15.3083	SNIB - CONABIO	b9f375037ccb44585aa3821d25546370
Damburneya salicifolia	-89.61305	17.225	GBIF	NA
Damburneya salicifolia	-89.60111	15.79555	GBIF	NA

Damburneya salicifolia	-89.6004	15.7859	SNIB - CONABIO	4b659d70ceb726b31908f28180100bc4
Damburneya salicifolia	-89.5911	15.7525	SNIB - CONABIO	36a0d2196c0878f3969eb3d8b062683c
Damburneya salicifolia	-89.59027	15.78694	GBIF	NA
Damburneya salicifolia	-89.58611	17.92639	IBUNAM	NA
Damburneya salicifolia	-89.57888	17.38722	GBIF	NA
Damburneya salicifolia	-89.5292	17.6819	SNIB - CONABIO	1d83c5ca6e7d9359ad08de65723ada57
Damburneya salicifolia	-89.475	18.5125	SNIB - CONABIO	5322e3e3525fb3b0b0d284947522d9dc
Damburneya salicifolia	-89.4731	18.2303	SNIB - CONABIO	28a97d733b99fcf913e4335598acdcaa
Damburneya salicifolia	-89.45333	18.22778	IBUNAM	NA
Damburneya salicifolia	-89.44444	16.39472	GBIF	NA
Damburneya salicifolia	-89.435	16.4986	SNIB - CONABIO	a0f9ee0f7bc683187296c7d387be4bee
Damburneya salicifolia	-89.4258	16.3917	SNIB - CONABIO	fd3962a6278748c6233ff5fd83f3df39
Damburneya salicifolia	-89.42111	18.01972	IBUNAM	NA
Damburneya salicifolia	-89.417	18.617	IBUNAM	NA
Damburneya salicifolia	-89.417	18.583	IBUNAM	NA
Damburneya salicifolia	-89.41666	16.31666	GBIF	NA
Damburneya salicifolia	-89.41389	18.59444	IBUNAM	NA
Damburneya salicifolia	-89.4086	16.3042	SNIB - CONABIO	67dd0768f18effe9271d7cdceea20efd
Damburneya salicifolia	-89.40694	17.70444	GBIF	NA
Damburneya salicifolia	-89.40194	18.53917	IBUNAM	NA
Damburneya salicifolia	-89.39472	18.73417	IBUNAM	NA
Damburneya salicifolia	-89.38055	16.32444	GBIF	NA
Damburneya salicifolia	-89.36944	18.80722	IBUNAM	NA
Damburneya salicifolia	-89.35583	18.50028	IBUNAM	NA
Damburneya salicifolia	-89.35417	18.77639	IBUNAM	NA
Damburneya salicifolia	-89.35083	16.08111	GBIF	NA
Damburneya salicifolia	-89.3389	15.5208	SNIB - CONABIO	5465fee9930e2c430330d3895eb110e2
Damburneya salicifolia	-89.3339	16.1286	SNIB - CONABIO	0aeb71ebe1de40528860217d98c2ba0d
Damburneya salicifolia	-89.33333	16.01666	GBIF	NA
Damburneya salicifolia	-89.3211	19.2214	SNIB - CONABIO	da77c9d81cfe317459bc72c2584bd03e
Damburneya salicifolia	-89.3203	18.9319	SNIB - CONABIO	933098e260d5b340bf02ca62acd1064f
Damburneya salicifolia	-89.29389	19.02444	IBUNAM	NA
Damburneya salicifolia	-89.27111	17.78944	GBIF	NA
Damburneya salicifolia	-89.2675	18.0183	SNIB - CONABIO	1e8cbb971cb75dc319f8ab1865cb2edf
Damburneya salicifolia	-89.26638	15.89833	GBIF	NA
Damburneya salicifolia	-89.26556	18.59972	IBUNAM	NA
Damburneya salicifolia	-89.25806	18.945	IBUNAM	NA
Damburneya salicifolia	-89.25278	18.81167	IBUNAM	NA
Damburneya salicifolia	-89.2508	15.8642	SNIB - CONABIO	be3f329dfaf4b6c7a5ccc6e826e1f6c8
Damburneya salicifolia	-89.2489	19.1458	SNIB - CONABIO	5d27d05e5511089a94d552ce9ecb2185
Damburneya salicifolia	-89.24222	15.94888	GBIF	NA

Damburneya salicifolia	-89.23028	18.81417	IBUNAM	NA
Damburneya salicifolia	-89.22916	15.89833	GBIF	NA
Damburneya salicifolia	-89.2156	15.8408	SNIB - CONABIO	fe84cbed90f3baf7ce7ded4145ed6487
Damburneya salicifolia	-89.2125	15.86694	GBIF	NA
Damburneya salicifolia	-89.2083	15.7997	SNIB - CONABIO	6844ffe3d782254203b4336d1781b983
Damburneya salicifolia	-89.20777	15.85166	GBIF	NA
Damburneya salicifolia	-89.19639	17.93056	IBUNAM	NA
Damburneya salicifolia	-89.19139	15.84528	GBIF	NA
Damburneya salicifolia	-89.18806	18.47722	IBUNAM	NA
Damburneya salicifolia	-89.1667	18.0667	SNIB - CONABIO	d4618127458d2e86343c6643ccb9a7de
Damburneya salicifolia	-89.16667	14.86667	GBIF	NA
Damburneya salicifolia	-89.15972	18.445	IBUNAM	NA
Damburneya salicifolia	-89.15055	15.805	GBIF	NA
Damburneya salicifolia	-89.1477	17.2627	GBIF	NA
Damburneya salicifolia	-89.1411	15.8536	SNIB - CONABIO	f00b506747cd3ecf2d1185cd15d1f040
Damburneya salicifolia	-89.1083	16.8417	SNIB - CONABIO	4caf4dd6b6fde73c878f7e9e0923b183
Damburneya salicifolia	-89.08333	17.08333	GBIF	NA
Damburneya salicifolia	-89.075	17.1083	SNIB - CONABIO	9f0c56ccb589bd8bfbc6de524ebfaa94
Damburneya salicifolia	-89.06528	17.14722	GBIF	NA
Damburneya salicifolia	-89.0639	15.8606	SNIB - CONABIO	dc305aaa821784d540b8c8c17ec16f52
Damburneya salicifolia	-89.0633	17.0325	SNIB - CONABIO	3ebe206617b05a4289fa0570c8db904c
Damburneya salicifolia	-89.05056	16.86861	GBIF	NA
Damburneya salicifolia	-89.0417	16.8583	SNIB - CONABIO	c2abcb4a6e9c51a12cf9ad160032f186
Damburneya salicifolia	-89.03333	17.81666	GBIF	NA
Damburneya salicifolia	-89.01666	16.9	GBIF	NA
Damburneya salicifolia	-89.0083	17.1083	SNIB - CONABIO	dff2d78a1101271fbad3144de5ecd7d1
Damburneya salicifolia	-88.9934	18.1846	SNIB - CONABIO	76d4a68c687103130e414c76f77b7d0f
Damburneya salicifolia	-88.9917	16.725	SNIB - CONABIO	56266f7d09c2423b51bfd53f94f91e91
Damburneya salicifolia	-88.98333	16.71666	GBIF	NA
Damburneya salicifolia	-88.9706	18.4914	SNIB - CONABIO	0cee085a469f084f045c639f94aa1ae6
Damburneya salicifolia	-88.9583	17.975	SNIB - CONABIO	c4d1511586930d4aabae29cb1828a538
Damburneya salicifolia	-88.9417	16.875	SNIB - CONABIO	7353d99be1a969968a6b38d149a27652
Damburneya salicifolia	-88.93361	16.81222	GBIF	NA
Damburneya salicifolia	-88.93333	16.78333	GBIF	NA
Damburneya salicifolia	-88.93333	16.86666	GBIF	NA
Damburneya salicifolia	-88.9214	15.8175	SNIB - CONABIO	df6e8048b3ff85721fd8c3303b9d2078
Damburneya salicifolia	-88.89472	19.33194	IBUNAM	NA
Damburneya salicifolia	-88.885	17.9583	SNIB - CONABIO	0724c514acbfbf140d6aa990813fa300
Damburneya salicifolia	-88.87306	19.32528	IBUNAM	NA
Damburneya salicifolia	-88.867	17.933	IBUNAM	NA
Damburneya salicifolia	-88.84305	15.53972	GBIF	NA

Damburneya salicifolia	-88.8167	16.1667	SNIB - CONABIO	f7fb6776ba23b08205526a9d57d7af7c
Damburneya salicifolia	-88.81667	16.51667	GBIF	NA
Damburneya salicifolia	-88.81639	19.13778	IBUNAM	NA
Damburneya salicifolia	-88.80777	16.09333	GBIF	NA
Damburneya salicifolia	-88.805	15.51083	GBIF	NA
Damburneya salicifolia	-88.80083	17.25806	GBIF	NA
Damburneya salicifolia	-88.7931	18.4306	SNIB - CONABIO	316dae6a54e1e103175d3791bba94cad
Damburneya salicifolia	-88.78333	17.31666	GBIF	NA
Damburneya salicifolia	-88.77972	17.22361	GBIF	NA
Damburneya salicifolia	-88.7583	16.5417	SNIB - CONABIO	35278841991fb6bb0caf477ac3f07472
Damburneya salicifolia	-88.75778	19.48667	IBUNAM	NA
Damburneya salicifolia	-88.75472	16.14055	GBIF	NA
Damburneya salicifolia	-88.7503	15.8031	SNIB - CONABIO	895b57166b2ca653d8971572a1bb0043
Damburneya salicifolia	-88.73416	19.23527	GBIF	NA
Damburneya salicifolia	-88.725	16.5583	SNIB - CONABIO	24dc2c51766fcf5564015165ef18603b
Damburneya salicifolia	-88.7083	18.0083	SNIB - CONABIO	7e4ae3844b833a59d670a88209ce6d0c
Damburneya salicifolia	-88.70528	17.57917	GBIF	NA
Damburneya salicifolia	-88.67611	19.50139	IBUNAM	NA
Damburneya salicifolia	-88.6583	18.2917	SNIB - CONABIO	6676eb58df72ba806ff6c0e8a3145b9a
Damburneya salicifolia	-88.61666	17.41666	GBIF	NA
Damburneya salicifolia	-88.6042	18.0764	SNIB - CONABIO	a5e886f3933572217d9298fcb76fbea6
Damburneya salicifolia	-88.55861	17.30194	GBIF	NA
Damburneya salicifolia	-88.5583	18.375	SNIB - CONABIO	681ca1ea5cbab7c7a58e53787cabb5a7
Damburneya salicifolia	-88.5417	19.5583	SNIB - CONABIO	e682c0f2624fafd70f2f48247d9587ad
Damburneya salicifolia	-88.5417	15.675	SNIB - CONABIO	2b6cff2cb2e86e86128eb110b15d77b9
Damburneya salicifolia	-88.54083	18.23972	GBIF	NA
Damburneya salicifolia	-88.5298	17.556	SNIB - CONABIO	7360fe7ca1b854df20e1092a290c921a
Damburneya salicifolia	-88.515	18.5028	SNIB - CONABIO	1131de4abf36ec2508f79cc9f022fb7e
Damburneya salicifolia	-88.44278	17.37556	GBIF	NA
Damburneya salicifolia	-88.38556	17.56972	GBIF	NA
Damburneya salicifolia	-88.375	18.7583	SNIB - CONABIO	00364c60396ad7839f969524d704a985
Damburneya salicifolia	-88.34583	17.56611	GBIF	NA
Damburneya salicifolia	-88.34111	17.72027	GBIF	NA
Damburneya salicifolia	-88.32722	17.56361	GBIF	NA
Damburneya salicifolia	-88.31305	17.87833	GBIF	NA
Damburneya salicifolia	-88.3039	18.5217	SNIB - CONABIO	8cee90d268f7021e0faed23987eb478f
Damburneya salicifolia	-88.28833	17.54555	GBIF	NA
Damburneya salicifolia	-88.25	17.53333	GBIF	NA
Damburneya salicifolia	-88.2367	20.7	SNIB - CONABIO	dea0957c37d9b2f23b12310f9e9bc2e1
Damburneya salicifolia	-88.175	19.8569	SNIB - CONABIO	706cf25eac2c8ebd3c7bb73b60b2f65d
Damburneya salicifolia	-88.1633	18.9533	SNIB - CONABIO	d22f62845aa3753b47659d6ccf719d03

Damburneya salicifolia	-88.0275	19.89472	IBUNAM	NA
Damburneya salicifolia	-88.0194	19.4953	SNIB - CONABIO	eabded7ea9d81a44a84ba2ece5c01f0e
Damburneya salicifolia	-88.0083	14.875	SNIB - CONABIO	c092264178038affc4769f0145f12fe6
Damburneya salicifolia	-88.00417	19.89139	IBUNAM	NA
Damburneya salicifolia	-87.8617	14.5428	SNIB - CONABIO	cb8b02e72277ba6326882763c6cda4f7
Damburneya salicifolia	-87.7583	19.575	SNIB - CONABIO	3e82d56695d43e628742a2b4d8e3fd22
Damburneya salicifolia	-87.6083	19.7917	SNIB - CONABIO	70576834bc08542ba940f02c56713833
Damburneya salicifolia	-87.4917	21.1083	SNIB - CONABIO	53c38b41fe00b42fa8e6e6c5bc798392
Damburneya salicifolia	-87.4667	21.1167	SNIB - CONABIO	9a55076f811314ba31e3fbe8d912df87
Damburneya salicifolia	-87.3583	20.3417	SNIB - CONABIO	f14bd6bedd89eac165e061c6fce910a5
Damburneya salicifolia	-87.21444	13.99138	GBIF	NA
Damburneya salicifolia	-87.153	14.0811	SNIB - CONABIO	22370dc54c3e76faab053342650d6254
Damburneya salicifolia	-87.0192	13.9856	SNIB - CONABIO	457aee6cbf0efdf04d29bbb95510ec46
Damburneya salicifolia	-87.0083	20.375	SNIB - CONABIO	7b695ccaed7149822fa8b326004b53e4
Damburneya salicifolia	-86.98361	13.92833	GBIF	NA
Damburneya salicifolia	-86.96917	14.94222	GBIF	NA
Damburneya salicifolia	-86.875	20.9486	SNIB - CONABIO	cfbe63dc3320ce5b0e77c2e0e453ad75
Damburneya salicifolia	-86.8333	20.5333	SNIB - CONABIO	6d0c0ca3ca7f73adbb331ce5d5c83b39
Damburneya salicifolia	-86.76972	15.74944	GBIF	NA
Damburneya salicifolia	-86.67861	15.52333	GBIF	NA
Damburneya salicifolia	-86.63333	13.46666	GBIF	NA
Damburneya salicifolia	-86.45167	13.22972	GBIF	NA
Damburneya salicifolia	-86.325	13.2583	SNIB - CONABIO	80a524a8fe9e1804160248009011bbff
Damburneya salicifolia	-86.2583	13.2583	SNIB - CONABIO	01b5dfb18d47e7dbffc82d78957106a7
Damburneya salicifolia	-86.2583	13.2417	SNIB - CONABIO	92232d1748785a7ede12fc6ccf78bdc2
Damburneya salicifolia	-86.2417	13.2417	SNIB - CONABIO	f7cfbac0c390e12d0384fa456204e56e
Damburneya salicifolia	-86.2417	13.175	SNIB - CONABIO	6f11a1ced4321e81227f84842f1dcfe9
Damburneya salicifolia	-86.2417	13.2083	SNIB - CONABIO	c8f7dede6a28701c6326484385b85eb6
Damburneya salicifolia	-86.24028	13.43444	GBIF	NA
Damburneya salicifolia	-86.23333	13.23333	GBIF	NA
Damburneya salicifolia	-86.23333	13.21666	GBIF	NA
Damburneya salicifolia	-86.23333	13.16666	GBIF	NA
Damburneya salicifolia	-86.2083	13.175	SNIB - CONABIO	386d7f57009b088ecee3cd8aa1efe066
Damburneya salicifolia	-86.18806	13.98389	GBIF	NA
Damburneya salicifolia	-86.175	13.2583	SNIB - CONABIO	c34da64e3dcf5a128780c50bf32a0c5f
Damburneya salicifolia	-86.1583	13.875	SNIB - CONABIO	9ef3c6aeef8ddd78a4f1f729c83c5318
Damburneya salicifolia	-86.14056	13.9475	GBIF	NA
Damburneya salicifolia	-85.96611	13.09139	GBIF	NA
Damburneya salicifolia	-85.925	12.975	SNIB - CONABIO	4b15b90ab9cc9a50887da3bc13623719
Damburneya salicifolia	-85.92222	12.99167	GBIF	NA
Damburneya salicifolia	-85.9167	12.9167	SNIB - CONABIO	7e19ece3bf3d15a427b343568d128970

Damburneya salicifolia	-85.9167	13.0667	SNIB - CONABIO	b787676582685434beaaf9b61e64f595
Damburneya salicifolia	-85.91667	12.88333	GBIF	NA
Damburneya salicifolia	-85.91667	12.96667	GBIF	NA
Damburneya salicifolia	-85.91666	13.00916	GBIF	NA
Damburneya salicifolia	-85.9047	12.9835	SNIB - CONABIO	14295da221f906c1492f2844a9c5fd49
Damburneya salicifolia	-85.875	12.95833	GBIF	NA
Damburneya salicifolia	-85.875	12.975	SNIB - CONABIO	1a444376e9d99a793517618ff14bb95e
Damburneya salicifolia	-85.86667	12.96667	GBIF	NA
Damburneya salicifolia	-85.8583	12.975	SNIB - CONABIO	5b7853694b6567ea680f532a09d8de16
Damburneya salicifolia	-85.775	12.6417	SNIB - CONABIO	f6183db07192870459e3a7da368589b2
Damburneya salicifolia	-85.7667	12.8833	SNIB - CONABIO	da355522e49603e56dd0d13275544855
Damburneya salicifolia	-85.76666	12.63333	GBIF	NA
Damburneya salicifolia	-85.7583	12.6083	SNIB - CONABIO	c0031ba0c9b8fdddad4a94973e54f0ba
Damburneya salicifolia	-85.7417	12.6083	SNIB - CONABIO	71eee2c58dbab191c015fd13e214f548
Damburneya salicifolia	-85.71667	12.66667	GBIF	NA
Damburneya salicifolia	-85.7083	13.575	SNIB - CONABIO	1b19c2bc39237f1d246d7ff0cfc38021
Damburneya salicifolia	-85.6917	13.5417	SNIB - CONABIO	fda996844c76a7a034062410470d6d3f
Damburneya salicifolia	-85.6917	13.5583	SNIB - CONABIO	0a16f859ecc0a08828c41710ddde4af7
Damburneya salicifolia	-85.675	13.575	SNIB - CONABIO	972f8e0d284feec7d95b39126124a90a
Damburneya salicifolia	-85.66667	13.21667	GBIF	NA
Damburneya salicifolia	-85.666667	13.216667	GBIF	NA
Damburneya salicifolia	-85.66666	13.56666	GBIF	NA
Damburneya salicifolia	-85.65833	11.54166	GBIF	NA
Damburneya salicifolia	-85.64806	13.23194	GBIF	NA
Damburneya salicifolia	-85.63333	11.53333	GBIF	NA
Damburneya salicifolia	-85.625	11.575	SNIB - CONABIO	d9c7ffccba4d4024929cc53774bdb687
Damburneya salicifolia	-85.625	11.5583	SNIB - CONABIO	554d1391c82d12049fa0748e08ed23b9
Damburneya salicifolia	-85.625	13.525	SNIB - CONABIO	f0519e8c00d5ae189d6b1ed4b9f0c578
Damburneya salicifolia	-85.617	11.533	IBUNAM	NA
Damburneya salicifolia	-85.61667	13.51667	GBIF	NA
Damburneya salicifolia	-85.61666	11.56666	GBIF	NA
Damburneya salicifolia	-85.6083	11.5583	SNIB - CONABIO	abe42b3f2bb3f961f0548a3d92d8b212
Damburneya salicifolia	-85.5583	12.4083	SNIB - CONABIO	b00032d3e2479b1b724bbdff7ad7d19b
Damburneya salicifolia	-85.53333	12.41666	GBIF	NA
Damburneya salicifolia	-85.525	11.4375	GBIF	NA
Damburneya salicifolia	-85.525	11.4583	SNIB - CONABIO	eaf3e94814f2e751511f80416c0cffcf
Damburneya salicifolia	-85.51666	11.43333	GBIF	NA
Damburneya salicifolia	-85.5083	11.475	SNIB - CONABIO	f5353c4a198f78b996d38bf41e943581
Damburneya salicifolia	-85.48333	11.425	GBIF	NA
Damburneya salicifolia	-85.475	13.2583	SNIB - CONABIO	6676238098c50ae81bc300e1e0115d12
Damburneya salicifolia	-85.4708	10.9292	SNIB - CONABIO	89a8cf1a805d22e78b48981c3d89028b

Damburneya salicifolia	-85.4083	12.3083	SNIB - CONABIO	1baa5d9ef01e0a0454a0b033fc8ce660
Damburneya salicifolia	-85.39722	12.30222	GBIF	NA
Damburneya salicifolia	-84.83333	10.31667	IBUNAM	NA
Damburneya salicifolia	-84.825	10.275	IBUNAM	NA
Damburneya salicifolia	-84.0839	9.86472	SNIB - CONABIO	ec350f5fc8f27a08e34b8627b5cfa504
Damburneya salicifolia	-84.0825	10.2772	SNIB - CONABIO	6930bb4a1140bebd2ec42809c2fa14c7
Damburneya salicifolia	-84.0789	10.3328	SNIB - CONABIO	795ae06441c7fb0f4c1d9907cfaecc30
Damburneya salicifolia	-84.0736	10.2972	SNIB - CONABIO	b85e1660ece4b0643c99c17263d591db
Damburneya salicifolia	-83.775	12.0083	SNIB - CONABIO	4f2df3574d3a4b753c34e99dec32ea9d
Damburneya salicifolia	-83.6811	9.90861	SNIB - CONABIO	4e754b186ca8b667d5a5812c2dba0a6e
Damburneya salicifolia	-83.41638	8.85444	GBIF	NA
Damburneya salicifolia	-80.85111	7.70111	IBUNAM	NA

Supplementary material of the paper:

Laura J. Giraldo-Kalil, Gonzalo E. Pinilla-Buitrago, Andrés Lira-Noriega, Francisco Lorea-Hernández, Juan Núñez-Farfán. Ecological niche comparison among closely related tree species of Lauraceae using climatic and edaphic data. *Frontiers of Biogeography*

Appendix S 3. Model selection and evaluation of ecological niche models (ENMs) for four *Damburneya* species.

Table S 2. Ecological niche models (ENMs) chosen for four *Damburneya* species among the top five models with lower ΔACIc according to five evaluation metrics.

Notes: The data are shown according to the set of environmental variables employed for modeling. Chosen models for each species and set of environmental variables are highlighted in bold. Evaluation metrics were calculated with the R package ENMeval 2.0 (Kass et al., 2021) and are shown according to the environmental variables employed to perform ENMs. Evaluation metrics are: minimum training presence omission rate (OR$_{MTP}$), 10% training presence omission rate (OR$_{10}$), area under the receiver operating characteristic curve based on testing and training data (AUC$_{test}$ and AUC$_{train,}$ respectively), the difference between the AUC of training and testing data (AUC$_{diff}$), delta of the Akaike Information Criterion corrected for small samples (ΔAICc). Feature classes (fc) are linear (L), quadratic (Q), product (P) and hinge (H). Regularization multipliers (rm) and the number of coefficients included (ncoef) are shown for each model. Model selection was performed from the top five models with the lower ΔAICc, prioritizing those with the lower omission rates (OR$_{10}$ and OR$_{mtp}$) and higher AUC values (AUC$_{train}$ and AUC$_{test}$). Model position within the top (indicated in the Top column) was assigned according to ΔAICc decreasing order. The occurrence data used include: 33 records for *D. ambigens*, 20 for *D. colorata*, 53 for *D. gentlei*, and 697 for *D. salicifolia*.

Data set	**Species**	**Top**	**fc**	**rm**	**AUC$_{train}$**	**AUC$_{diff}$**	**AUC$_{test}$**	**OR$_{10}$**	**OR$_{mtp}$**	**AICc**	**ΔAICc**	**ncoef**
Combined	*D. ambigens*	top1	LQ	1.5	0.873	0.083	0.861	0.156	0.031	764.216	0	12
		top2	LQ	2	0.872	0.082	0.86	0.188	0.031	769.499	5.283	12
		top3	LQ	2.5	0.871	0.081	0.86	0.146	0.052	770.247	6.031	11
		top4	**LQ**	**1**	**0.877**	**0.083**	**0.862**	**0.156**	**0.031**	**770.466**	**6.25**	**14**
		top5	LQ	3	0.871	0.081	0.857	0.146	0.073	776.729	12.513	11
	D. colorata	top1	LQP	4	0.714	0.238	0.642	0.25	0.15	484.292	0	1
		top2	LQHP	3.5	0.814	0.156	0.686	0.2	0.05	485.261	0.97	5
		top3	LQP	3.5	0.721	0.221	0.639	0.25	0.2	485.315	1.023	2
		top4	**LQHP**	**3**	**0.824**	**0.141**	**0.705**	**0.2**	**0.05**	**486.286**	**1.995**	**6**

Data set	**Species**	**Top**	**fc**	**rm**	**AUC_{train}**	**AUC_{diff}**	**AUC_{test}**	**OR_{10}**	**OR_{mtp}**	**AICc**	**ΔAICc**	**ncoef**
		top5	LQ	3.5	0.766	0.195	0.608	0.3	0.15	486.448	2.156	3
	D. gentlei	top1	LQH	2.5	0.922	0.044	0.888	0.213	0.054	1260.193	0	19
		top2	LQH	3.5	0.914	0.044	0.878	0.168	0.054	1270.031	9.839	17
		top3	LQHP	4	0.913	0.04	0.882	0.168	0.025	1270.232	10.04	14
		top4	**LQH**	**4**	**0.91**	**0.042**	**0.876**	**0.139**	**0.054**	**1271.352**	**11.159**	**15**
		top5	LQHP	2.5	0.925	0.042	0.888	0.247	0.039	1272.254	12.061	21
	D. salicifolia	top1	LQHP	1.5	0.806	0.019	0.791	0.126	0.012	18793.542	0	75
		top2	LQHP	2.5	0.799	0.016	0.787	0.114	0.012	18809.569	16.026	58
		top3	**LQHP**	**3**	**0.798**	**0.015**	**0.786**	**0.113**	**0.009**	**18815.236**	**21.694**	**52**
		top4	LQHP	2	0.802	0.017	0.789	0.116	0.012	18821.589	28.047	74
		top5	LQHP	4	0.795	0.015	0.782	0.116	0.009	18827.877	34.335	41
Climatic-only	*D. ambigens*	**top1**	**LQ**	**1**	**0.866**	**0.088**	**0.85**	**0.094**	**0.031**	**759.932**	**0**	**7**
		top2	LQ	1.5	0.854	0.088	0.845	0.094	0.031	768.369	8.437	7
		top3	LQ	2	0.849	0.084	0.845	0.094	0.031	772.87	12.938	6
		top4	LQHP	3.5	0.902	0.117	0.872	0.156	0.031	773.136	13.204	14
		top5	LQ	2.5	0.847	0.076	0.848	0.073	0.031	777.177	17.245	6
	D. colorata	top1	LQP	1.5	0.728	0.165	0.706	0.1	0.05	482.383	0	2
		top2	**LQP**	**1**	**0.745**	**0.146**	**0.713**	**0.1**	**0.05**	**482.84**	**0.457**	**3**
		top3	LQP	2	0.72	0.182	0.696	0.1	0.05	483.633	1.25	2
		top4	LQP	3	0.697	0.203	0.696	0.1	0.05	483.961	1.579	1
		top5	LQP	3.5	0.697	0.201	0.697	0.1	0.05	484.973	2.59	1
	D. gentlei	**top1**	**LQHP**	**2**	**0.901**	**0.042**	**0.868**	**0.107**	**0.015**	**1271.658**	**0**	**16**
		top2	LQHP	3	0.899	0.038	0.867	0.107	0.015	1274.836	3.179	13
		top3	LQHP	3.5	0.897	0.032	0.866	0.107	0.015	1287.333	15.676	14
		top4	LQ	1	0.845	0.049	0.791	0.163	0.096	1287.809	16.152	7
		top5	LQHP	2.5	0.901	0.04	0.867	0.107	0.015	1287.815	16.158	18

Data set	Species	Top	fc	rm	AUC_{train}	AUC_{diff}	AUC_{test}	OR_{10}	OR_{mtp}	AICc	ΔAICc	ncoef
Edaphic-only	*D. salicifolia*	top1	LQHP	2	0.773	0.011	0.766	0.11	0.003	18939.78	0	42
		top2	LQHP	3	0.771	0.01	0.764	0.107	0.003	18943.552	3.772	33
		top3	LQHP	2.5	0.771	0.011	0.765	0.107	0.003	18949.506	9.725	40
		top4	**LQP**	**1**	**0.761**	**0.009**	**0.757**	**0.101**	**0.001**	**18952.875**	**13.095**	**13**
		top5	LQHP	3.5	0.77	0.011	0.763	0.113	0.003	18958.58	18.799	35
	D. ambigens	**top1**	**LQHP**	**2**	**0.842**	**0.062**	**0.807**	**0.135**	**0.094**	**819.507**	**0**	**10**
		top2	LQHP	3	0.837	0.075	0.798	0.135	0.115	820.722	1.215	7
		top3	LQHP	2.5	0.84	0.069	0.801	0.135	0.094	821.027	1.521	9
		top4	LQ	1	0.838	0.075	0.812	0.156	0.094	822.67	3.163	7
		top5	LQHP	3.5	0.832	0.075	0.797	0.135	0.115	823.426	3.92	6
	D. colorata	**top1**	**LQHP**	**2**	**0.784**	**0.217**	**0.662**	**0.2**	**0.05**	**486.314**	**0**	**5**
		top2	LQP	4	0.5	0.067	0.46	0.1	0	486.384	0.07	0
		top3	LQP	3	0.596	0.187	0.568	0.1	0.05	487.226	0.911	1
		top4	LQHP	4	0.654	0.227	0.461	0.15	0.1	487.561	1.247	1
		top5	L	4	0.596	0.169	0.584	0.1	0.05	487.643	1.329	1
	D. gentlei	top1	LQH	1	0.826	0.074	0.811	0.153	0.025	1317.219	0	13
		top2	LQHP	2.5	0.801	0.062	0.785	0.154	0.025	1319.399	2.18	6
		top3	LQHP	3	0.795	0.06	0.776	0.139	0.025	1321.655	4.435	5
		top4	**LQHP**	**3.5**	**0.792**	**0.06**	**0.767**	**0.111**	**0.025**	**1322.8**	**5.581**	**4**
		top5	LQHP	1	0.824	0.075	0.809	0.167	0.025	1322.824	5.605	14
	D. salicifolia	**top1**	**LQHP**	**1.5**	**0.694**	**0.024**	**0.677**	**0.103**	**0.003**	**19340.586**	**0**	**20**
		top2	LQHP	1	0.696	0.027	0.677	0.106	0.003	19347.753	7.167	28
		top3	LQH	1.5	0.693	0.025	0.677	0.108	0.003	19353.114	12.527	23
		top4	LQHP	2	0.693	0.023	0.677	0.107	0.003	19359.541	18.954	24
		top5	LQH	2	0.693	0.023	0.676	0.107	0.003	19360.357	19.771	23

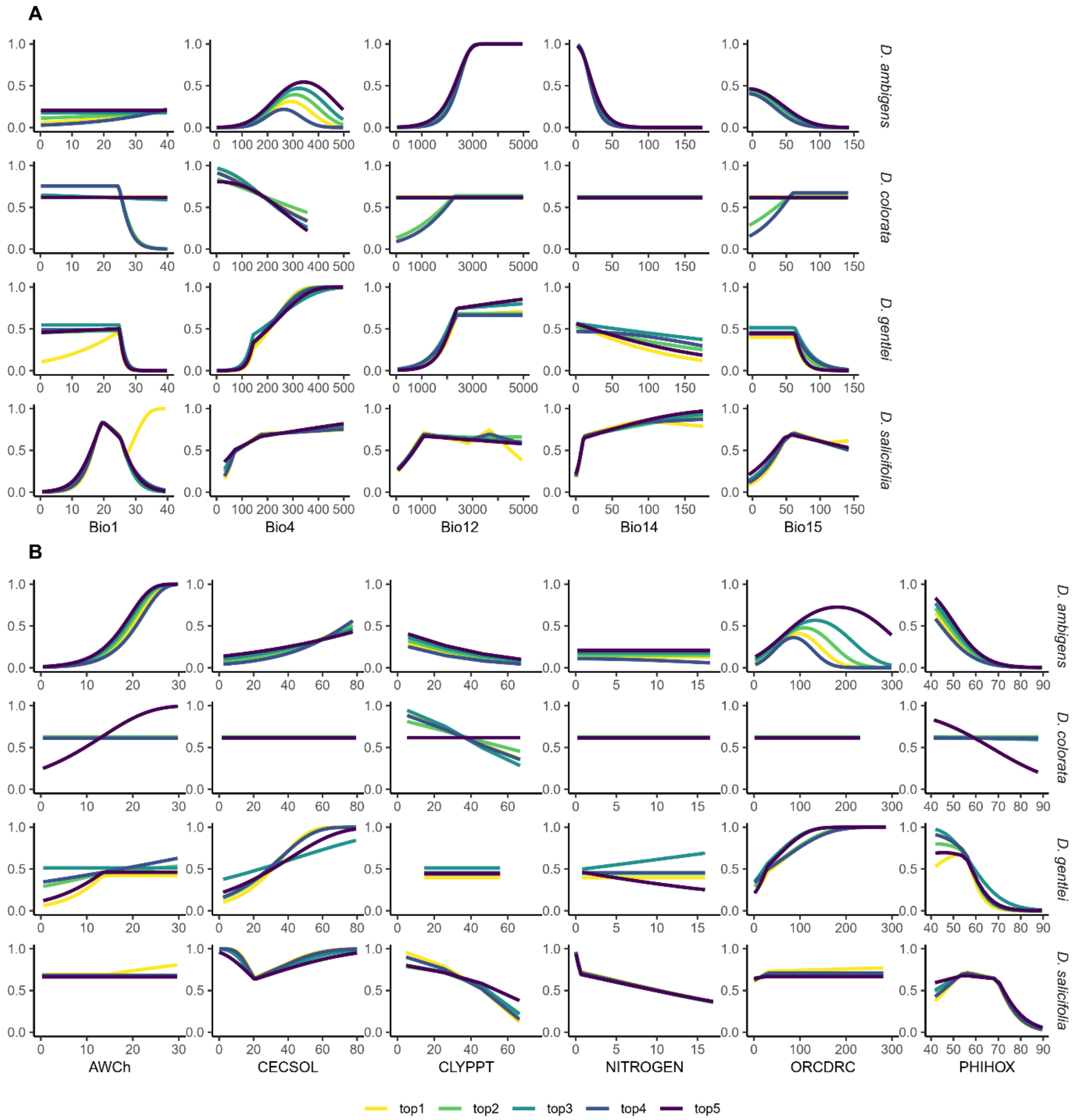

Figure S1. Response curves of the top five ecological niche models (ENMs) with the lower ΔAICc values for four *Damburneya* species. The models were built with a combination of A) climatic and B) edaphic variables. The curves show the ranges of environmental variation favorable to species distributions. The x and y axis represent the ranges of the environmental variables and the predicted suitability values, respectively. Variable abbreviations and units can be seen in Table 1. The pH (PHIOHX) values are multiplied by 10. Chosen models can be found in Table S2.

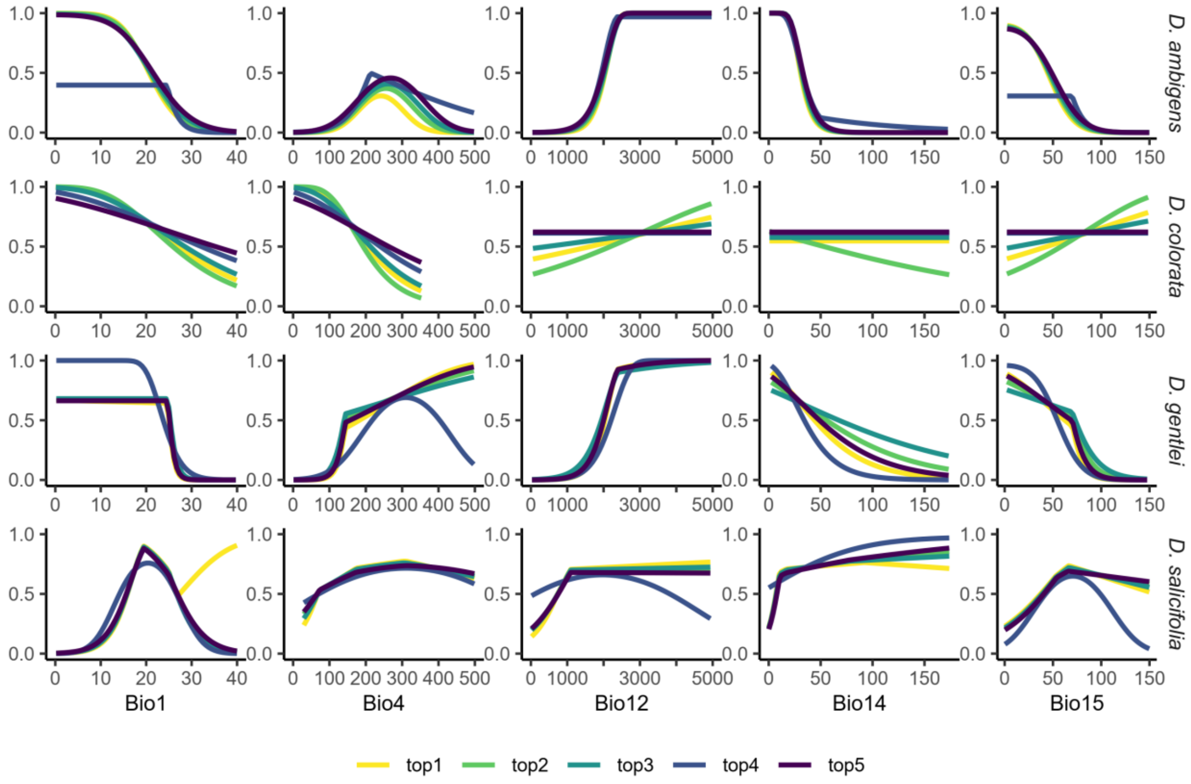

Figure S2. Response curves of the top five ecological niche models (ENMs) with the lower ΔAICc values for four *Damburneya* species. The models were built with a climatic-only data set. The curves show the ranges of environmental variation favorable to species distributions. The x and y axis represent the ranges of the environmental variables and the predicted suitability values, respectively. Variable abbreviations and units can be seen in Table 1. Chosen models can be found in Table S2.

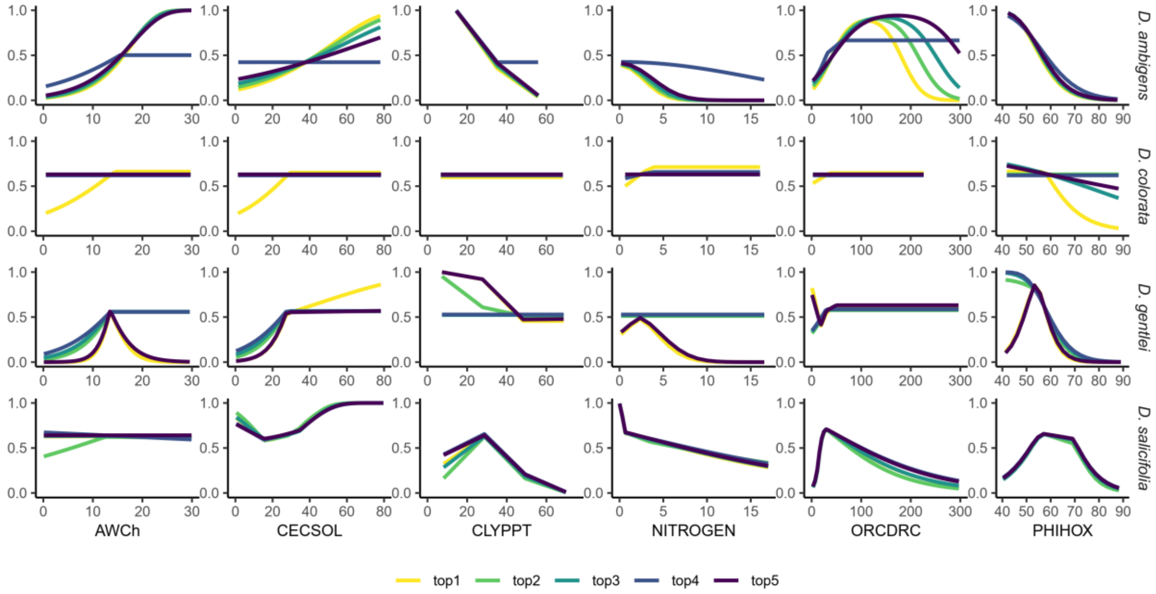

Figure S3. Response curves of the top five ecological niche models (ENMs) with the lower ΔAICc values for four *Damburneya* species. The models were built a with edaphic-only data set. The curves show the ranges of environmental variation favorable to species distributions. The x and y axis represent the ranges of the environmental variables and the predicted suitability values, respectively. Variable abbreviations and units can be seen in Table 1. The pH (PHIOHX) values are multiplied by 10. Chosen models can be found in Table S2.

Supplementary material of the paper:

Laura J. Giraldo-Kalil, Gonzalo E. Pinilla-Buitrago, Andrés Lira-Noriega, Francisco Lorea-Hernández, Juan Núñez-Farfán. Ecological niche comparison among closely related tree species of Lauraceae using climatic and edaphic data. *Frontiers of Biogeography*

Appendix S 4. Niche overlap and environmental variable ordination for four *Damburneya* species calculated with the R package ecospat.

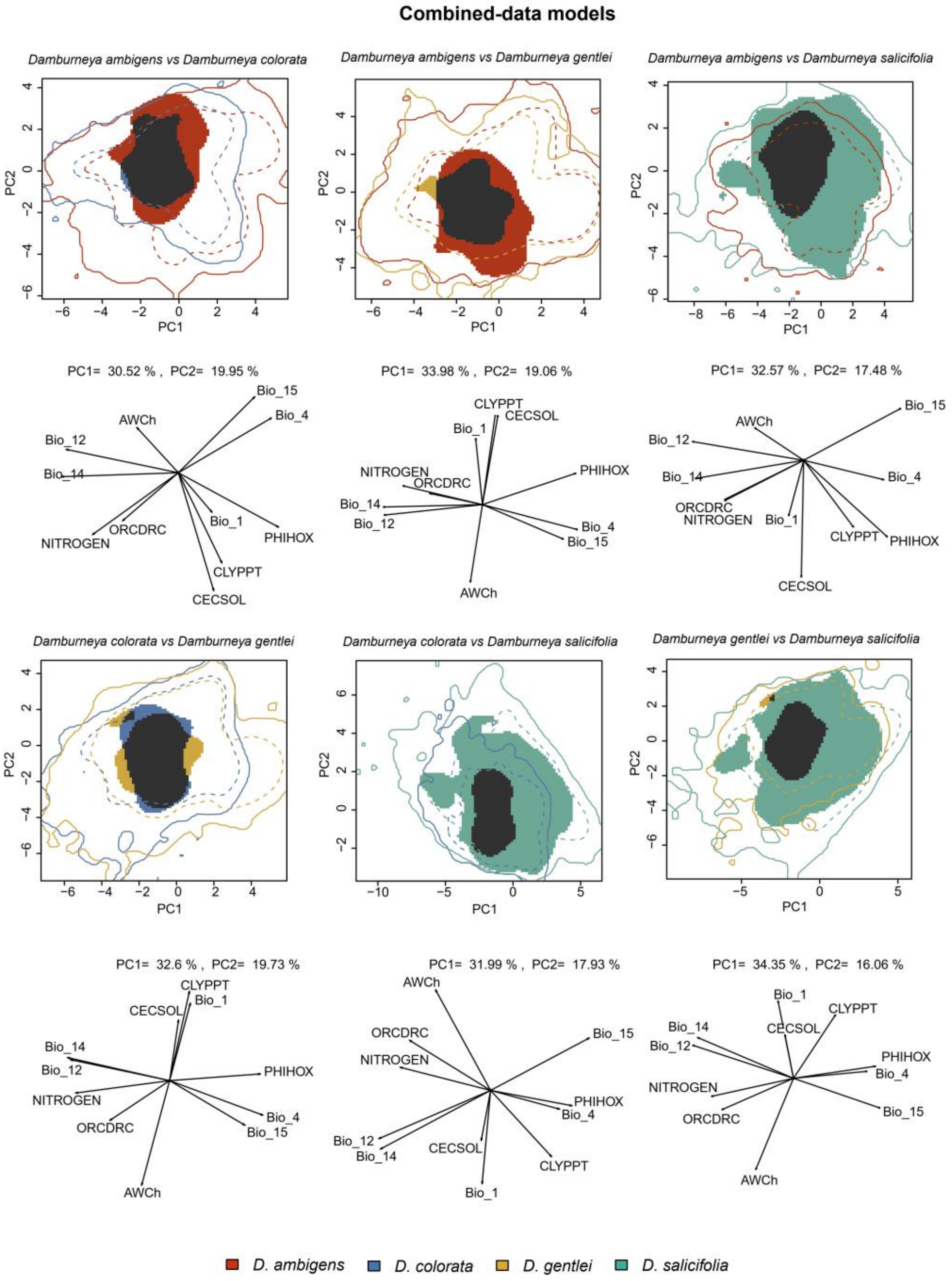

Figure S4. Niche overlap and environmental variable ordination for paired comparisons of four *Damburneya* species calculated with R package ecospat. The analyses were performed with habitat suitability based on models combining climatic and edaphic environmental variables. Species niches are shown in colors, niche overlap is shown in dark brown. Solid lines represent 100% of each species available environment, while dashed lines represent 50%.

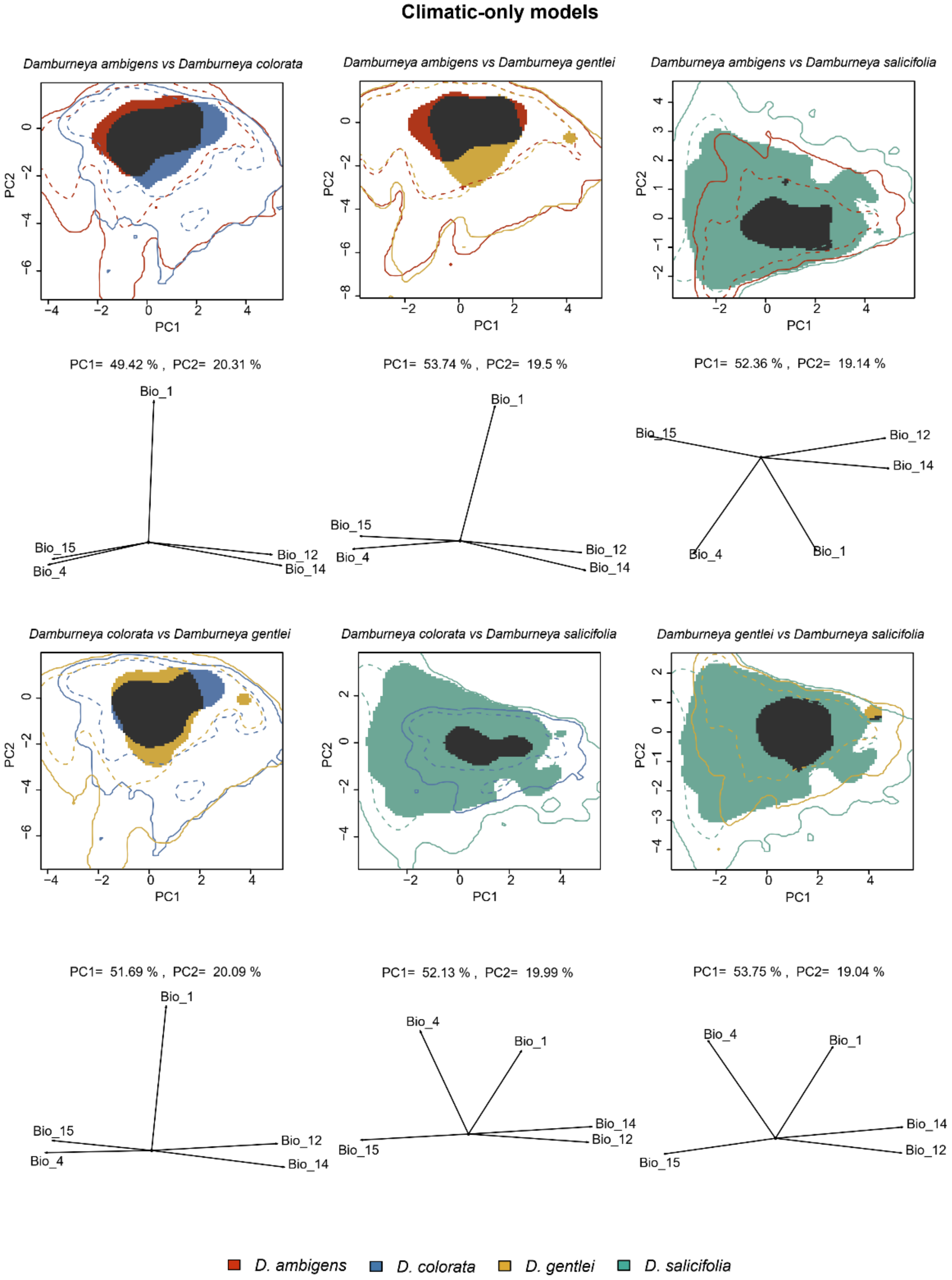

Figure S5. Niche overlap and environmental variable ordination for paired comparisons of four *Damburneya* species calculated with R package ecospat. The analyses were performed with habitat suitability based on climatic-only models. Species niches are shown in colors, niche overlap is shown in dark brown. Solid lines represent 100% of each species available environment, while dashed lines represent 50%.

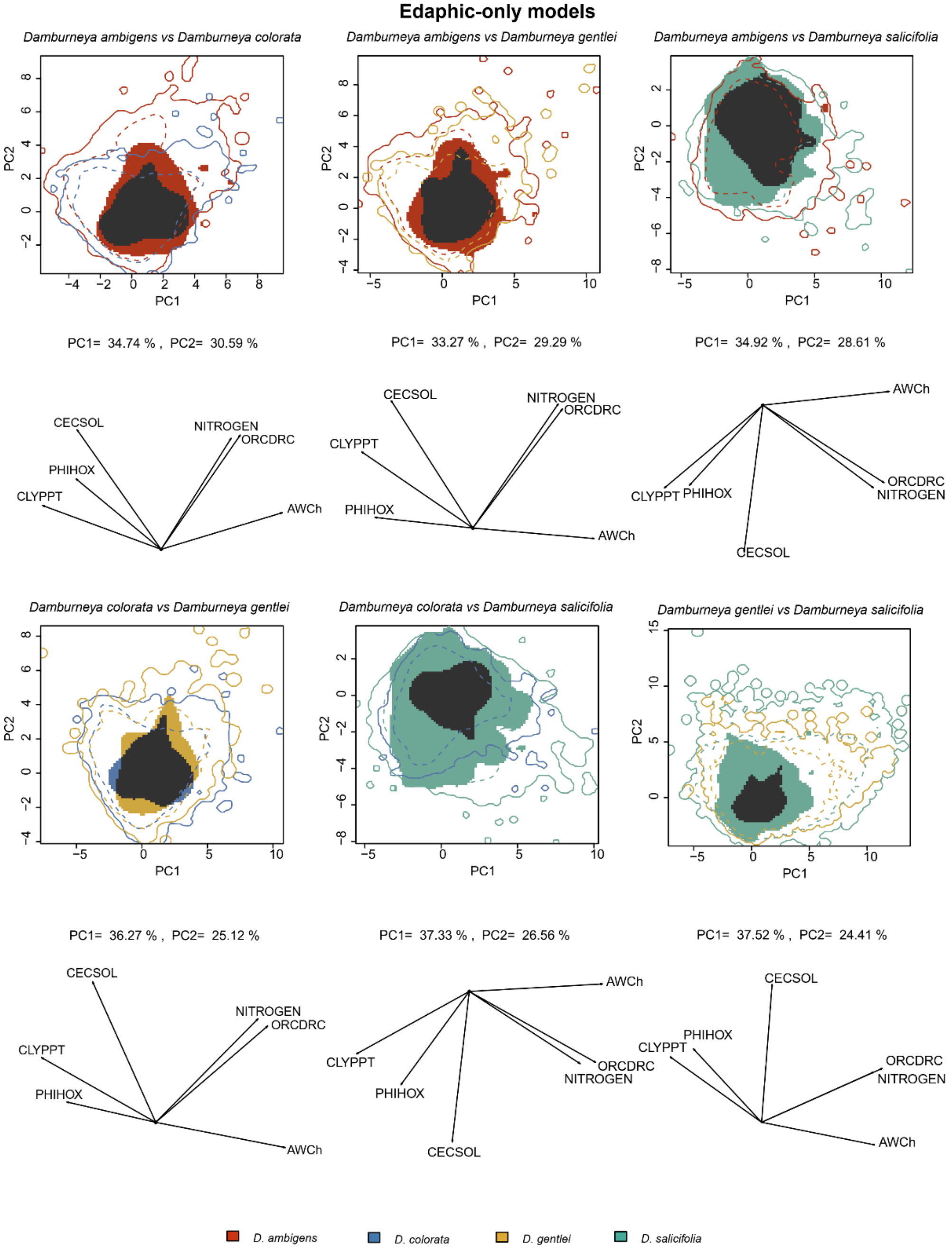

Figure S6. Niche overlap and environmental variable ordination for paired comparisons of four *Damburneya* species calculated with R package ecospat. The analyses were performed with habitat suitability based on edaphic-only models. Species niches are shown in colors, niche overlap is shown in dark brown. Solid lines represent 100% of each species available environment, while dashed lines represent 50%.

Capítulo 2 (Artículo de requisito)

Diferenciación funcional foliar de especies simpátricas de *Damburneya* en la selva alta perennifolia de Los Tuxtlas

(Publicado en *American Journal of Botany* 109 (9): 1394– 1409.https://doi.org/10.1002/ajb2.16056)

Received: 8 July 2021 | Accepted: 12 August 2022

DOI: 10.1002/ajb2.16056

RESEARCH ARTICLE

Patterns of leaf trait variation underlie ecological differences among sympatric tree species of *Damburneya* in a tropical rainforest

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Abstract

Premise: Although ecological differentiation driven by altitude and soil is hypothesized to promote coexistence of sympatric tree species of *Damburneya* (Lauraceae), the mechanistic role of leaf functional variation on ecological differentiation among co-occurring species remains unexplored. We aimed to determine whether the patterns of leaf trait variation reflect ecological differences among sympatric *Damburneya* species. We tested whether trait correlations underlying functional strategies and average species traits vary in response to local soil heterogeneity along an altitudinal gradient, potentially affecting species distributions.

Methods: At two contrasting altitudes (100, 1100 m a.s.l.) in a Mexican tropical rainforest, we characterized soil chemical and physical properties and sampled four *Damburneya* species to quantify five leaf functional traits. We used linear models to analyze paired and multivariate trait correlations, spatial and interspecific effects on trait variation, and trait response to local soil heterogeneity. Relative contributions of intra- and interspecific variation to local trait variability were quantified with an ANOVA.

Results: Soil nutrient availability was higher at low altitude, but all species had a high leaf N:P ratio across altitudes suggesting a limited P supply for plants. Species distribution differed altitudinally, with some species constrained to low or high altitude, potentially reflecting soil nutrient availability. Leaf traits responded to altitude and local soil properties, suggesting interspecific differences in functional strategies according to the leaf economics spectrum (conservative vs. acquisitive).

Conclusions: The interspecific divergence in functional strategies in response to local environmental conditions suggests that trait variation could underlie ecological differentiation among *Damburneya* sympatric species.

KEYWORDS

closely related species, ecological differentiation, environmental gradient, Lauraceae, leaf economics spectrum, Mexico, plant functional traits, soil heterogeneity, topographic effects, tropical rainforest,

Resumen en Español

Premisa: Aunque se ha propuesto que la diferenciación ecológica impulsada por la variación del suelo y la altitud ha promovido la coexistencia de especies arbóreas simpátricas de *Damburneya* (Lauraceae), el papel de la variación de funcional foliar como mecanismo para explicar las diferencias ecológicas entre especies que coocurren sigue sin explorarse. Nuestro objetivo fue determinar si los patrones de variación de los rasgos funcionales foliares reflejan diferencias ecológicas entre especies simpátricas de *Damburneya*. Hipotetizamos que, tanto las correlaciones entre los rasgos que determinan

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las estrategias funcionales, como los valores promedio de los rasgos de las especies, varían en respuesta a la heterogeneidad local del suelo a lo largo de un gradiente altitudinal, afectando potencialmente la distribución de las especies.

Método: En dos altitudes contrastantes (100, 1000 m s.n.m) en una selva húmeda tropical mexicana caracterizamos propiedades físicas y químicas del suelo y muestreamos cuatro especies de *Damburneya* para cuantificar cinco rasgos funcionales foliares. Usamos modelos lineales para analizar las correlaciones pareadas y multivariadas entre rasgos, los efectos espaciales e interespecíficos en la variación de rasgos, y la respuesta de los rasgos a la heterogeneidad local del suelo. Además, cuantificamos la contribución relativa de la variación intra- e interespecífica en la varianza local de los rasgos con un análisis de varianza.

Resultados: La disponibilidad de nutrientes en el suelo fue mayor en la zona baja, pero todas las especies tuvieron valores altos de N:P foliar en ambas altitudes, lo que sugiere un suministro limitado de P para las plantas. La distribución de las especies difirió altitudinalmente y algunas de ellas se restringieron a zonas altas o bajas, reflejando potencialmente la disponibilidad de nutrientes en el suelo. Los rasgos foliares respondieron a la altitud y a las propiedades edáficas locales, sugiriendo diferencias interespecíficas en las estrategias funcionales según el espectro de economía foliar (conservativa vs. adquisitiva).

Conclusiones: La divergencia interespecífica en las estrategias funcionales en respuesta a las condiciones ambientales locales sugiere que la variación de rasgos podría explicar algunas diferencias ecológicas entre las especies simpátricas de *Damburneya*.

PALABRAS CLAVE

diferenciación ecológica, efectos topográficos, especies cercanamente emparentadas, espectro de economía foliar, gradiente ambiental, heterogeneidad del suelo, Lauraceae, México, rasgos funcionales foliares, selva húmeda tropical

Closely related species are expected to have similar phenotypes and conserved ecological niches (Wiens and Graham, 2005); consequently, the ecological differences between them can greatly impact their performance, coexistence within communities, and evolution (MacArthur and Levins, 1967; Chesson, 2000). Several differences in species' niches, ecological strategies, and other factors promoting plant species coexistence can be robustly assessed by analyzing the environmental effects on functional trait variation across species (Reich et al., 1999; Mcgill et al., 2006; Violle and Jiang 2009; Adler et al., 2013; Carmona et al., 2016). Functional traits are physiological or morphological features that affect the individuals' survival, growth, or reproduction and determine their responses to the environment (Violle et al., 2007). Variation in leaf functional traits can drive ecological niche differentiation whenever it favors differential performance among plant species along environmental gradients. Trait-driven ecological differentiation can be promoted by mechanisms that affect species abundance, distribution and competition at a local scale such as spatial and temporal heterogeneity, resource partitioning, and natural enemy attack (Adler et al., 2013).

Functional trait correlations reflect trade-offs underlying plant strategies that vary across species depending on resource availability (Reich et al., 2003; Wright et al., 2004; Shipley et al., 2006; Reich, 2014; Maynard et al., 2022). A key example is the worldwide leaf economics spectrum (LES) that describes global patterns in leaf trait correlations and variation across species encompassing plant functional strategies from slow to fast resource uptake, use, and return along environmental gradients. The LES is based on trade-offs between light capture, photosynthetic carbon-gain rates, nutrient use, leaf longevity and turnover, and resource investment in tissue construction (Reich et al., 1999; Wright et al., 2004; Shipley et al., 2006, Díaz et al., 2016; Onoda et al., 2017).

Briefly, species with an "acquisitive" strategy have a fast return of biomass and nutrient investment. They are expected to have high leaf nutrient concentrations and photosynthetic rates, with low investments in leaf mass per area and leaf lifespan that allow high rates of leaf turnover. In contrast, "conservative" species with slow return have increased construction costs due to high mass investment and long lifespan. They usually have low nutrient concentrations and carbon-gain rates, and reduced vulnerability to physical damage and herbivory. The patterns of leaf trait correlations underlying these functional strategies can be widely affected by the simultaneous effect of several environmental factors like soil properties (Koerselman and Meuleman, 1996; Aerts and Chapin, 2000; Campo et al., 2014; Roa-Fuentes et al., 2015a), herbivory, climate, and water and light availability (Campo and Dirzo, 2003; Wright et al., 2004; Hodgson et al., 2011).

Nevertheless, several studies report that trait relationships predicted by the LES at a global scale do not necessarily hold at local scales, in part because the LES does not consider local drivers of trait variation like intraspecific variation (Violle et al., 2012; Niinemets, 2015; Messier et al., 2017; Anderegg et al., 2018; Fajardo and Siefert, 2018). Furthermore, the LES predictions can also fail to hold between closely related species owing to environmental variation, and the effects of natural selection on particular trait combinations within and between species (Donovan et al., 2011; Mason and Donovan, 2015; Muir et al., 2017; Agrawal, 2020; Ji et al., 2020). Thus, the assessment of intraspecific variation, and the contrast of local trait correlations with those expected according to the LES could be a helpful approach to disentangle the constraints to functional variation in sympatric closely related plant species.

Our research is focused on a group of species from the genus *Damburneya* Raf. (Lauraceae) that diversified in tropical rainforests of southern Mexico and northern Central America (Rohwer, 1993). Some of these species are locally abundant (Popma et al., 1988) and constitute genetic reservoirs for tropical rainforest regeneration (Arroyo-Rodríguez et al., 2009; Sánchez-Gallen et al., 2010). Their fruits are an important food source for birds, rodents, and insects, and the trees are used locally for timber (Rohwer, 1993). As with other Lauraceae in Mexico, *Damburneya* trees are threatened by deforestation (Lorea-Hernández, 2002, 2011; de Kok, 2020a, 2020b, 2020c). Despite this threat, ecological studies of most species of this genus (and even of the Lauraceae more broadly) are still scarce due to complex taxonomy and difficulty in collecting samples from tall trees. Distinguishing species in the field is challenging because identification often requires the examination of flowers or fruits, which are produced at intervals of several years and thus not always available (Rohwer, 1993; van der Werff and Richter, 1996; Lorea-Hernández, 2002).

Although all *Damburneya* species have ornithochorous seed dispersal (i.e., by birds), sympatric species usually differ in their local abundance and distribution, suggesting that ecotypic differentiation has a key role in their speciation (Rohwer and Kubitzki, 1993). This divergence process likely occurred by edaphic specialization, altitudinal sorting, and other factors such as phenological isolation (Rohwer and Kubitzki, 1993). Elevation and soil nutrient variation are local environmental drivers of plant distribution and ecological differentiation in other Lauraceae (van der Werff, 1992; Sri-Ngernyuang et al., 2003; Srinivas and Krishnamurthy, 2019). Ecological divergence between sympatric *Damburneya* in response to such environmental variation seems to be common (Rohwer and Kubitzki, 1993); however, the role of leaf functional trait variation on ecological differentiation has been unexplored.

Here we aimed to determine whether sympatric species of *Damburneya*, co-occurring in the tropical rainforest at Los Tuxtlas Biosphere Reserve, display ecological differences in leaf functional traits and to describe how traits vary in relation to soil heterogeneity along an altitudinal gradient. Specifically, we hypothesized that *Damburneya* species differ in (1) leaf trait correlation patterns and consequently, in functional strategies, and in (2) leaf trait variation in response to the soil heterogeneity at high and low altitudes. Furthermore, we aimed to analyze the effects of functional strategies and soil physical and chemical variation on local patterns of abundance and distribution along the altitudinal gradient. To this end, we characterized the distribution of four *Damburneya* species co-occurring in the studied area and analyzed the correlations between five leaf functional traits. Moreover, we assessed how leaf trait variation responds to soil heterogeneity and the extent to which it is determined locally by inter- and intraspecific variation. Finally, we discuss our findings in light of the drivers of leaf functional trait variation and its potential implications considering the current threats to *Damburneya* species.

MATERIALS AND METHODS

Study site

The study was conducted in August 2018 in well-preserved areas of mature tropical rainforest within the core zone of Los Tuxtlas Biosphere Reserve at the San Martín Volcano. The altitudinal gradient ranges from sea level to 1700 m a.s.l. and impacts the local temperature and the precipitation regimes (Gutiérrez-García and Ricker, 2011). The regional climate is perhumid (based on the Lang aridity index, the annual ratio of precipitation to temperature is greater than 100). With increasing altitude, the mean annual temperature decreases (from 23–24°C at 1100 m a.s.l. to 20–21°C at 100 m a.s.l.) and the mean annual precipitation increases (from 4000–5000 mm at 100 m a.s.l. to 6000–7000 mm at 1100 m a.s.l.). The precipitation varies through the year and is concentrated in the rainy season (June to February), while monthly precipitation can drop below 100 mm during the dry season (March to May; Gutiérrez-García and Ricker, 2011). In addition, the forest canopy is more open at higher altitudes allowing more light entrance in comparison to lower altitudes (maximum illuminance: 8331.34 lx at 1100 m a.s.l. to 5941.73 lx at 150 m a.s.l., L. Giraldo-Kalil, unpublished data).

The mountain ranges in this region originated from volcanic activity; as a result, soils are young, and their physical and biological properties are spatially variable (Flores-Delgadillo et al., 1999; Krasilnikov et al., 2013). Soils in low altitudes are entisols, including typic ustorthents and lithic ustorthents (Tobón et al., 2011), and at high altitudes are predominantly andisols (Sommer-Cervantes et al., 2003). Soil drainage is good at high altitudes and moderate at low altitudes (Siebe et al., 1996).

The Los Tuxtlas region sustains more than 40% of the floristic richness of the tropical rainforest of Mexico (Villaseñor et al., 2018). However, changes in land cover and land-use for livestock have caused soil chemical, physical and biological degradation (Figueroa et al., 2020) and the loss of approximately 60% of the original vegetation cover (von Thaden et al., 2020).

Study system

This study focused on the four *Damburneya* species reported for the state of Veracruz and for Los Tuxtlas Biosphere Reserve (Ibarra-Manríquez and Sinaca-Colín, 1995; Lorea-Hernández, 2002): *Damburneya ambigens* (S.F Blake) Trofimov, *Damburneya colorata* (Lundell) Trofimov, *Damburneya gentlei* (Lundell) Trofimov, and *Damburneya salicifolia* (Kunth) Trofimov. These four tree species were formerly included in the genus *Nectandra* Rol. ex Rottb. and were recently reinstated in the genus *Damburneya* Raf. by Trofimov et al. (2016).

The species differ in altitudinal range, distribution, and stature. *Damburneya ambigens* and *D. gentlei* are distributed in lowland tropical rainforests from southern Mexico to Honduras (Rohwer, 1993) and are locally used for timber (Ibarra-Manríquez and Sinaca-Colín, 1995). Generally, *D. ambigens* occurs from sea level up to 1100 m a.s.l. and is abundant in the upper canopy of forests in the study area (Bongers et al., 1988; Dirzo et al., 1997). In contrast, *D. gentlei* is usually restricted to altitudes below 300 m a.s.l. (Rohwer, 1993). Both species are large trees, reaching 35 m or more in height. Unlike most Lauraceae species, *D. salicifolia* can resist disturbed conditions (Lorea-Hernández, 2002); it occurs in soils with different fertility (Rohwer, 1993) at a wide altitudinal range from sea level up to 2300 m a.s.l., and is distributed from Mexico to Nicaragua (Rohwer, 1993). The distribution and variety of habitats where this species occurs suggest high ecological plasticity (Rohwer and Kubitzki, 1993). The trees of *D. salicifolia* range from 10 to 20 m in height, and the wood is used for construction (Rohwer, 1993; Ibarra-Manríquez et al., 1997). Moreover, *D. salicifolia* has been described as a species complex because its phenotypic variation has led to several local forms from which very similar *Damburneya* species originated, making them difficult to distinguish (Rohwer, 1993). Indeed, *D. colorata* is part of the *D. salicifolia* complex, but contrary to that species, it is rarely found and reports of it in the study area and through its entire distribution have been very scant. The trees of *D. colorata* can reach 25 m in height and are used as firewood (Rohwer, 1993). The species is found in forests at altitudes close to 650 m a.s.l. in southern Mexico, Belize, and Guatemala (Rohwer, 1993).

Sampling design

We established six 1-ha rectangular plots (200 × 50 m) in a mature tropical rainforest to characterize the distribution of *Damburneya* trees and soil variation in the study area. The plots were located in two zones with contrasting altitudes to encompass the variation in soil properties and species distribution and abundance. Three plots were established at low altitude below 300 m a.s.l. and three at high altitude between 675 and 1100 m a.s.l. The plots were located between 18°32′N and 18°35′N, and 95°4′W. To characterize soil properties, we collected 10 soil samples per plot at two depths (0–10 and 10–20 cm); we used a soil auger to sample along a diagonal line covering the soil variation across the plot. The soil samples were homogenized, sifted (2-mm mesh), and refrigerated in plastic bags until processed in the laboratory.

All trees of *Damburneya* in each plot with a diameter at breast height (DBH) > 1 cm were tagged, sampled, and their geographic coordinates recorded with a portable GPS (Garmin Oregon 550; Garmin, Olathe, KS, USA). We collected one to three branchlets and up to 25 mature fully expanded green leaves per tree, including shade and sun leaves, and avoided leaves damaged by pathogens and/or herbivores. Leaf samples were stored in black plastic bags with water to keep them hydrated and avoid transpiration until processing in the laboratory. Fresh leaves with petioles were photographed beside a millimeter scale, then oven-dried and individually weighed to record the dry mass. A branchlet sample per tree was preserved as a reference voucher to confirm species identity with the help of Dr. Francisco Lorea, a specialist in the Lauraceae. The vouchers of 26 representative specimens of the four species were deposited in three herbaria (Appendix S1).

Soil physicochemical, physical, and chemical properties

We quantified the following soil properties from air-dried subsamples: soil pH, soil texture, and soil organic carbon (SOC), total nitrogen (STN), ammonium (NH_4), nitrate (NO_3), total and available phosphorus (STP and SAP, respectively) concentrations, and the C:N and NO_3:NH_4 ratios.

The pH of the soil was measured in a water suspension with a pH meter. Soil texture was characterized by determining the clay, sand, and silt contents with a density analysis (Elliott et al., 1999) and classified with the texture triangle. Soil organic C was analyzed in an automated C-analyzer (SHIMADZU 5005 A) after an air-dried subsample (5 g) was ground and passed through a 100-mesh screen. The STN and STP in a soil subsample (1 g) were determined after Kjeldahl acidic digestion in concentrated H_2SO_4 (Anderson and Ingram, 1993), and the concentrations of N and P were quantified with an NP elemental analyzer (Technicon Autoanalyzer III, methods G-188-97 and G-189-97, respectively). To determine mineral N concentrations, NO_3 and NH_4, were extracted from a subsample (15 g) of each composite soil sample in 100 mL 2 M KCl (Sollins et al., 1999) by shaking for 1 h and allowing the sample to settle overnight. A 20-mL aliquot of the supernatant was then transferred into vials and frozen for later analysis. All KCl extracts were analyzed colorimetrically using the NP autoanalyzer system to determine

NO_3–N + NO_2–N (method G-109-94), which were reported as NO_3 concentration. The salicylate–hypochlorite procedure (method G-102-93) was employed to determine NH_4 concentration.

Soil available P was extracted from a soil subsample (0.5 g) in 30 mL of 0.5 N $NaHCO_3$ by shaking for 16 h. The sample was centrifuged at 10,000 rpm at 0°C for 10 min, then digested with ammonium persulfate (Anderson and Ingram, 1993), and later analyzed on a NP autoanalyzer system (method G-304-04) by the molybdate method after ascorbic acid reduction (Murphy and Riley, 1962) to determine available P concentration. The $NaHCO_3$ extract provides a measure of relative labile and plant-available P, including readily solubilized inorganic P and mineralized organic P (Lajtha et al., 1999). We calculated the NO_3:NH_4 and the C:N ratios (using SOC and STN concentrations) to assess soil N availability and quality of soil organic matter. Briefly, high NO_3:NH_4 ratios indicate high NO_3 availability in the system due to high nitrification. Additionally, low C:N ratios (close to 10) indicate a high quality of soil organic matter (Chapin et al., 2011).

Leaf functional traits

We measured five traits involved in the LES that are associated with plant productivity and competitive ability (specific leaf area, SLA; leaf nitrogen concentration, LNmass; and leaf phosphorus concentration, LPmass), with drought tolerance and resistance to physical damage (leaf dry matter content, LDMC), and with soil nutrient supply (Leaf N:P ratio).

Specific leaf area (cm^2/g), which accounts for the investment of leaf area for light capture per unit of biomass, was calculated as the leaf area divided by leaf dry mass. Leaf area was quantified from leaf photographs with ImageJ (Schneider et al., 2012). Leaf dry matter content (mg/g), which reflects biomass investment on the leaves, was calculated as leaf dry mass divided by fresh mass, including leaf petioles (Pérez-Harguindeguy et al., 2013). These morphological traits reflect the trade-off between carbon gain and leaf longevity (Wright et al., 2004).

The leaves from each tree were dried and powdered to determine leaf nutrient concentration (i.e., LNmass and LPmass; mg/g) using the Kjeldahl acidic digestion method (Anderson and Ingram, 1993). We calculated the leaf N:P (per mass), which reflects nutrient limitation to plant growth and productivity according to threshold values. Low values ($N:P < 14$) are indicative of limited soil N availability for plant demand, high values ($N:P > 16$) indicate limited availability of P, and intermediate values indicate a limited availability of both (i.e., N and P; Koerselman and Meuleman, 1996).

Data analyses

R version 3.6.1 (R Core Team, 2021) and the averaged trait values per tree were used for all statistical analyses and graphs. The packages and functions are described for each analysis.

Functional strategies

Leaf trait variations

Descriptive statistical analyses were used to characterize leaf trait variation. Additionally, multivariate patterns of variation for all leaf traits were explored using standardized values in a principal component analysis (PCA) in the FactoMineR package (Lê et al., 2008). The leaf N:P ratio was excluded from these analyses because leaf nutrient variation is already accounted for by including LNmass and LPmass.

Trait correlations

Scaled bivariate correlations between leaf metrics were calculated to analyze whether there were differences in trait variation or in trade-offs that could account for differences in the functional strategies among sympatric *Damburneya* species. For that, standardized major axis regressions were performed using the smatr package and log-transformed axes (Warton et al., 2012). We tested whether there was a common slope among species using a likelihood ratio test.

Environmental effects on leaf trait variation

Mixed models

We performed linear mixed models to analyze the effect of spatial and interspecific variation on leaf trait. The models were built for standardized trait values and included the sampling plot, which accounts for local soil variation, and the species as effects with random intercepts using the lmer function in the lme4 package (Bates et al., 2015). Altitude (i.e., low and high altitudes) was included as a fixed effect. Since the four species did not occur in all plots, we did not include the species × plot interaction. REML-likelihood ratio tests were performed to determine whether the random effects significantly affected the variance explained by the models (Luke, 2017); we used the ranova function in the lmerTest package, which indicates whether the model becomes significantly worse when each random effect is dropped. The denominator degrees of freedom of the fixed effects were approximated with the Satterthwaite method (Kuznetsova et al., 2017). Furthermore, we quantified the percentage of variance explained by random effects.

Environment–trait regressions and variance partition

We performed linear regression models to understand how soil heterogeneity affects local trait variation in sympatric *Damburneya* species. All measured soil properties were modeled as independent variables. Abundance-weighted average trait values per plot (i.e., community weighted mean trait values) were included as response variables (further calculation details are as described by Kichenin et al., 2013).

Furthermore, we quantified the relative contribution of intra- and interspecific variation to local trait variance in response to soil variables. An analysis of variance was performed for linear regression models with the flexanova function proposed by Lepš et al. (2011). According to the approach of Kichenin et al. (2013), the total sum of squares of the abundance-weighted plot average trait variance was decomposed as $SS_{specific} = SS_{fixed} + SS_{intraspecific} + SS_{covariation}$, where $SS_{specific}$ refers to the species average trait values in the plot and SS_{fixed} is the site independent trait value calculated using the mean trait values for the species in all plots and weighted by the species relative abundance. $SS_{intraspecific}$ accounts for intraspecific variation and is calculated as the difference between the last two terms. $SS_{covariation}$ is the effect of the covariation between intra- and interspecific variation in response to the soil variables calculated as $SS_{specific} - (SS_{intraspecific} + SS_{fixed})$.

RESULTS

Soil variation and species distribution

Soil properties varied with altitude, indicating a greater content of organic nutrient sources and a lower mineralization rate at high altitude, and consequently, lower nutrient availability than at low altitude (Appendix S2). The soils at low altitude had a loamy and sandy loam texture, with higher clay content and available nutrient concentrations (NH_4, NO_3, and available P), and more basic pH than the soils of higher altitude sites. In contrast, at high altitude, the predominant soil textures are loamy sand and sandy loam, and the sand content, organic C, total P, and total N concentrations, C:N and NO_3:NH_4 ratios were higher in the soils at high altitude than at low altitude.

We censused a total of 135 trees, with 62 *D. ambigens*, 45 *D. salicifolia*, 16 *D. colorata*, and 12 *D. gentlei*. The spatial distribution differed among species: *D. gentlei* occurred only at low altitude (12 trees); in contrast, *D. salicifolia* was present only at high altitude (45 trees). *Damburneya ambigens* occurred at both low and high altitudes with similar abundance (28 and 34 trees, respectively); *D. colorata* was also present at both altitudes but more abundant at low than at high altitude (12 and 4 trees, respectively).

Functional strategies

Leaf trait variation

There were differences in trait variation patterns that suggest both diverging functional strategies among species and differences on trait variation across altitudes (Figure 1, Table 1; Appendix S3). Leaf nutrient concentrations were the most variable traits across species (coefficients of variation, CV > 20%) and were higher at low than at high altitudes (Appendix S3); morphological traits were the least variable (CV < 20%). In addition, mean leaf N:P ratio of all species ranged from 21 to 42 across altitudes, suggesting a limited soil P supply for plant demand (Appendix S3). On the other hand, the PCA showed differences in multivariate trait variation among species. Most of the trait variance (72.9%) was explained by the first two principal components (50.0% and 22.9%, respectively), and all traits contributed significantly to PC1 and PC2 (Figure 1, Table 1).

The first axis reflects the LES and shows the positive correlation of leaf nutrient concentrations with SLA against a negative correlation with LDMC. Clearly, all species

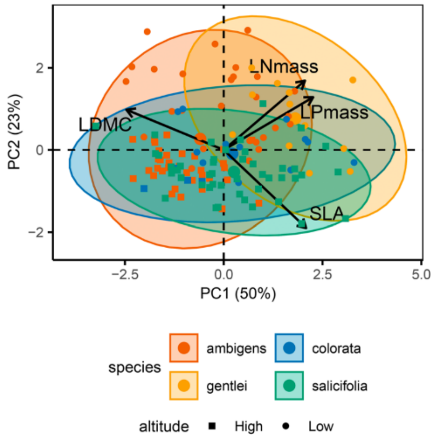

FIGURE 1 Principal component analysis of the variance of leaf functional traits of four sympatric *Damburneya* species (*D. ambigens, D. colorata, D. gentlei, D. salicifolia*) at Los Tuxtlas. SLA = specific leaf area, LDMC = leaf dry matter content, LNmass = leaf nitrogen concentration, LPmass = leaf phosphorus concentration. Squares: samples from high altitudes; circles: samples from low altitudes.

TABLE 1 Eigenvalues, cumulative percentage of variation and eigenvectors of the first three principal components analysis for four leaf traits that best predicted the functional leaf trait spectrum of four sympatric *Damburneya* species at Los Tuxtlas Biosphere Reserve.

	PC1	PC2	PC3
Eigenvalue	2.00	0.92	0.61
Cumulative % of variance	49.97	72.92	88.14
Eigenvectors			
SLA	0.66***	−0.60***	0.25**
LDMC	−0.78***	0.31***	0.21*
LNmass	0.65***	0.53***	0.52***
LPmass	0.72***	0.40***	−0.48***

Notes: The lower panel of the table shows trait correlations with the principal components. SLA = specific leaf area, LDMC = leaf dry matter content, LNmass = leaf nitrogen concentration, LPmass = leaf phosphorus concentration. Significance: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

spanned the continuum from quick to slow return on investments of biomass and nutrients, with *D. ambigens* at the resource conservative end and *D. gentlei* at the resource acquisitive end. These two species occupied different zones of the multivariate trait space, suggesting functional differences between them and the other two species. (Figure 1; see Appendix S3). *Damburneya salicifolia* and *D. colorata* showed a wide intraspecific variation across the slow–fast tradeoff (PCA 1), suggesting high trait plasticity.

The second axis shows differences in trait variation according to altitude among and within species; leaf nutrient concentrations decreased and SLA increased as altitude increased. Contrasting leaf trait variation occurred between two species segregated by altitude: *D. gentlei*, a low-altitude species with high leaf nutrient concentration, and *D. salicifolia*, a high-altitude species with high SLA (Figure 1). Similarly, the intraspecific trait variation of *D. ambigens* encompassed individuals at low altitude that had higher leaf nutrient concentrations and lower SLA than those at high altitude.

Trait scaling and correlations

Leaf morphological traits were correlated with nutrient concentration within species; however, the slope and direction (i.e., slope sign) differed among species, indicating differences in nutrient investment on leaf construction (Appendix S4). In *D. salicifolia* and *D. colorata*, LNmass was positively correlated with SLA (*D. salicifolia*: slope = 4.63, $r^2 = 0.29$, $P < 0.001$; *D. colorata*: slope = 3.40, $r^2 = 0.22$, $P = 0.064$) and negatively with LDMC (*D. salicifolia*: slope = –5.11, $r^2 = 0.29$, $P = 0.005$, slope = –6.96; *D. colorata*: $r^2 = 0.24$, $P = 0.056$), suggesting that N concentration increases in leaves with low construction costs. In contrast, these two traits were negatively correlated in *D. ambigens*, indicating a high nutrient investment on leaves with high construction costs and supporting a functional conservative strategy (slope = –3.25, $r^2 = 0.13$, $P = 0.004$), but had no significant correlation in *D. gentlei* (slope = –1.22, $r^2 = 0.10$, $P = 0.326$). Leaf N:P ratio was negatively correlated with SLA in *D. ambigens* and *D. gentlei* (*D. ambigens*: slope = –3.24, $r^2 = 0.27$, $P < 0.001$; *D. gentlei*: slope = –1.52, $r^2 = 0.43$, $P = 0.021$) but positively in *D. salicifolia* (slope = 5.32, $r^2 = 0.08$, $P = 0.058$), suggesting that *D. salicifolia* allocates less P to leaves that have higher area per unit biomass.

In contrast, some traits had the same correlation patterns in all the species. For instance, LDMC decreased as SLA increased, and LPmass was negatively correlated with LDMC, but positively with SLA (Appendix S4). In general, the slopes showed an allometric relationship among traits. The only exception was the isometric scaling between nutrients (i.e., LPmass and LNmass) in *D. ambigens* and *D. colorata* (slope ≈ 1, $P < 0.05$). Furthermore, the scaling between foliar nutrients was also isometric in *D. gentlei* and close to 2/3 for *D. salicifolia*, but these relationships were not significant (Appendix S4).

Environmental effects on leaf traits variation

The mixed models showed that spatial variation and interspecific differences explained the variation in leaf traits. Altitude only significantly affected LPmass variation (slope = 0.948, $P = 0.054$; Appendix S5). On the other hand, differences among plots significantly explained the variation of all leaf traits except in the case of LPmass ($P = 0.082$). Interspecific differences contributed significantly to the variation of SLA, LDMC, and LNmass, accounting for more than 20% of the variation of these traits, and notably explaining 43% in LDMC (Figure 2; Appendix S6). Conversely, less than 10% of variation of LPmass and leaf N:P ratio was determined by interspecific differences. The

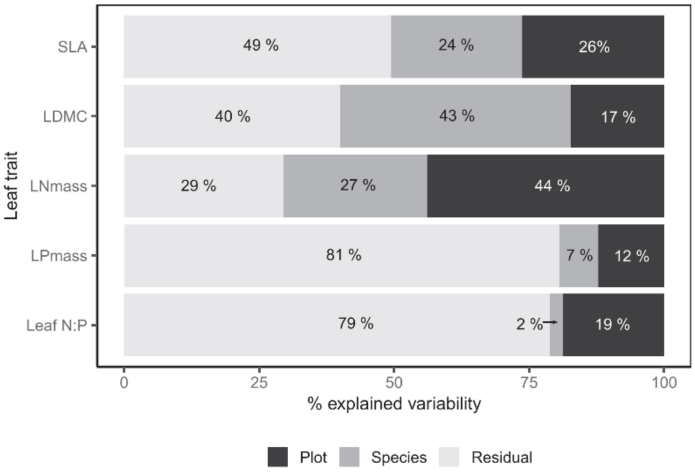

FIGURE 2 Variance structure of leaf functional traits in four sympatric *Damburneya* species at Los Tuxtlas according to mixed linear models. The models were built with REML considering altitude as fixed effect, the species and sampling plot were modeled as effects with random intercepts. SLA = specific leaf area, LDMC = leaf dry matter content, LNmass = leaf nitrogen concentration, LPmass = leaf phosphorus concentration, Leaf N:P = leaf nitrogen to phosphorus ratio.

variance of all traits, except LDMC, was mostly explained by plot variation (i.e., local environmental variation) rather than by interspecific differences. Both factors explained less than 25% of the variance of LPmass and leaf N:P ratio (Figure 2).

Soil–leaf trait relationships

Linear regressions between average plot leaf traits and soil variables indicate that the edaphic properties influence local leaf trait variation. Leaf nutrient concentrations were sensitive to several soil properties: LPmass decreased with increasing SOC and STP concentrations and C:N ratio (Appendix S7) but increased with increasing soil pH and SAP concentration (Figure 3). The same applied to LNmass, which increased with soil clay content (Figure 3), decreased with STN and NO_3 concentrations, and had no significant relationship with NH_4 concentration in soil (Figure 4). Also, Leaf N:P ratio had a negative relationship with SOC, STN, NO_3, and STP concentrations (Figure 3; Appendix S7). Leaf morphological traits were only significantly affected by soil N availability (Figure 4; Appendices S7 and S8). Specific leaf area was negatively correlated with NH_4 concentrations, and LDMC had a positive significant relationship with the concentrations of NO_3 and NH_4 (Figure 4).

The variance partitioning analysis showed that interspecific differences significantly affected the average plot trait variation in response to local soil properties. Conversely, intraspecific variation and its covariance with interspecific variation explained less than 10% of the average plot trait variance and did not affect it significantly. Intraspecific variation better explained the variance of morphological traits rather than that of leaf nutrients. Additionally, soil properties mostly affected leaf nutrients and, in contrast, explained less than 30% of morphological trait variation (Appendix S9).

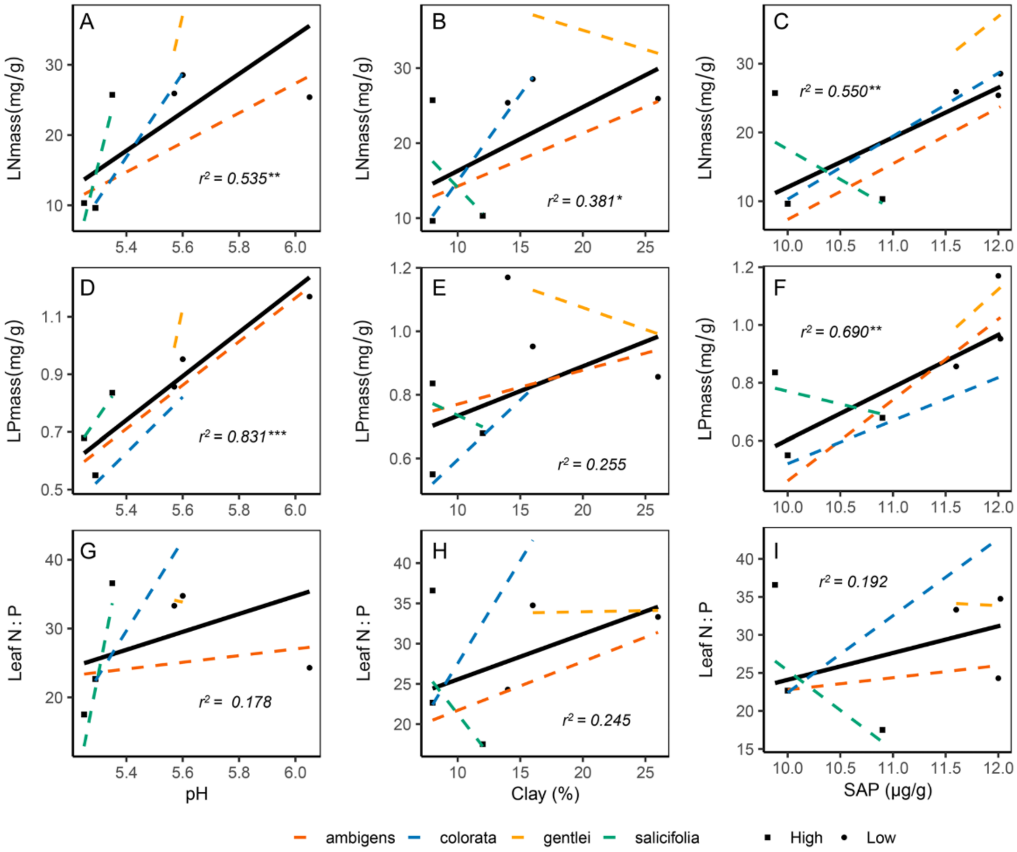

FIGURE 3 Relationships of the plot average leaf nutrient concentrations of four sympatric *Damburneya* species (*D. ambigens, D. colorata, D. gentlei, D. salicifolia*) at Los Tuxtlas with pH, clay content, and soil available phosphorus (SAP). LNmass: leaf nitrogen concentration (A–C), LPmass: leaf phosphorus concentration (D–F) and leaf N:P (G–I). Points represent the abundance-weighted average plot trait values, and the shape symbolizes the altitude. Plot trait variation in response to soil properties is represented by solid black regression lines, and the regression coefficient (r^2) and significance are provided for these values. Significance: $*P < 0.05$; $*P < 0.01$; $***P < 0.001$. Colored dashed lines represent each species trends of variation.

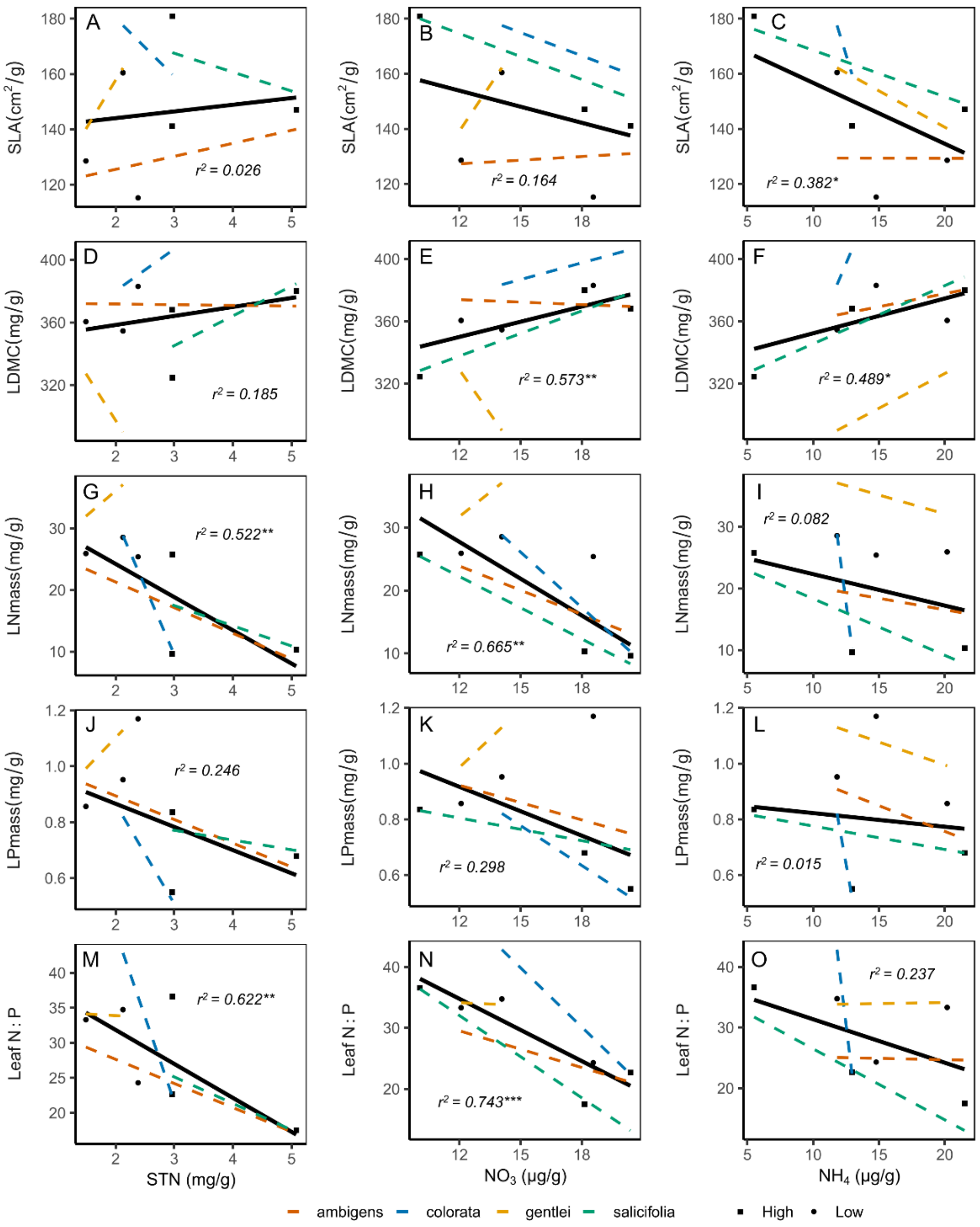

FIGURE 4 Relationships of the plot average leaf functional traits of four sympatric *Damburneya* species (*D. ambigens, D. colorata, D. gentlei, D. salicifolia*) at Los Tuxtlas with soil total nitrogen (STN), nitrate (NO_3), and ammonium (NH_4). SLA = Specific leaf area (A–C), LDMC = leaf dry matter content (D–F), LNmass = leaf nitrogen concentration (G–I), LPmass = leaf phosphorus concentration (J–L), and leaf N:P (M–O). Points represent the abundance-weighted average plot trait values, and the shape symbolizes the altitude. Plot trait variation in response to soil properties is represented by solid black regression lines, and the regression coefficient (r^2) and significance are provided for these values. Significance: $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Colored dashed lines represent each species trends of variation.

DISCUSSION

Our results suggest that the patterns of leaf trait variation along the altitudinal and edaphic gradient partially explained ecological differences among species and support the study of trait variation as a promising tool to assess the performance of *Damburneya* species in different environments.

Soil variation and species distribution

Besides their high biodiversity, tropical rainforests have a high soil biogeochemical heterogeneity at multiple scales (Townsend et al., 2008). The tropical rainforest at Los Tuxtlas is not the exception, as evidenced by the altitudinal variation of soil pH, texture, and nutrient availability, which is likely driven by the interaction of soil processes and climate. For example, high nutrient concentrations at low altitudes could be promoted by higher temperature and better soil moisture for microbial activity as expected by high water retention associated with a greater clay content (Siebe et al., 1996; Benner et al., 2011; Weil and Brady, 2017) and nutrient transport from the upper to the lower slope (Campo-Alves, 2003). In contrast, at higher altitude, the greater precipitation can promote higher rates of soil weathering and nutrient leaching (Campo et al., 2001; Santiago et al., 2004), while the lower temperature slows decomposition rates, as evidenced by the higher organic matter content (Benner et al., 2011).

The distribution and abundance of the four studied species of *Damburneya* differed between altitudes and are consistent with previous reports (Rohwer, 1993; Ibarra-Manríquez and Sinaca-Colín, 1995; Dirzo et al., 1997; Lorea-Hernández, 2002). *Damburneya ambigens* spanned the altitudinal gradient; it was the most abundant species and occurred in almost all the plots. *Damburneya colorata* was less abundant and occurred at high and low altitude plots, below 650 m a.s.l. In contrast, *D. gentlei* occurred only at low altitude and *D. salicifolia* was abundant at high altitudes and absent from low altitude plots. However, we have seen several trees of *D. salicifolia* in the study area along roadsides and forest edges and fragments, from sea level up to 1100 m a.s.l. (L. Giraldo-Kalil, unpublished data); these observations support the tolerance of this species to disturbance (Lorea-Hernández, 2002). The absence of *D. salicifolia* at low altitude in well-preserved areas of mature tropical rainforest may be due to other unmeasured biophysical factors (e.g., light availability, competition, limited seed dispersal) and decreased plant survival and recruitment in undisturbed compared to open disturbed areas. Although few trees of *D. gentlei* and *D. colorata* were recorded, our study accurately reflects the distribution of both species considering the limited reports within the study area (GBIF.org, 2021a, 2021b). We stress that our reports of *D. colorata* are among the most complete so far, as this rare species has not been well sampled throughout its distribution and is poorly represented in herbaria (GBIF.org, 2021a). It is difficult to establish whether the very few reports of this species are due to small population sizes or to a lack of records or erroneous determination in herbaria because of its notorious similarity with *D. salicifolia* (Rohwer, 1993); in any case, further studies of the natural populations of this species are necessary.

Effects of interspecific differences and environment on leaf trait variation

We hypothesized that leaf trait variations will differ among species according to soil heterogeneity at low and high altitudes. In support of this hypothesis, the variation of SLA, LDMC, and LNmass differed among *Damburneya* species and was determined by altitude and soil spatial variation among plots (Figure 2; Appendices S3, S5, and S6). It is noteworthy that the leaf morphological traits were less sensitive than leaf nutrient concentrations to soil variation and were only significantly affected by soil N availability (Figure 4; Appendices S3 and S8). For example, SLA decreased with increasing soil NH_4 concentration, while LDMC increased with NO_3 and NH_4, suggesting that soil N availability could favor the construction of thick and/or dense leaves.

Morphological traits could be influenced by herbivory and altitudinal variation of climate and light, in addition to nutrient availability. Thick and dense leaves with high LDMC increase mechanical resistance against herbivores (Westoby et al., 2002; Onoda et al., 2011) and heat tolerance in tropical forests (Slot et al., 2021); hence, they usually occur in habitats with high temperatures (Niinemets, 2001; Wright et al., 2004) like the low altitude zone. Conversely, SLA usually correlates positively with precipitation amount and temperature but negatively with light availability (Wright et al., 2004; Poorter et al., 2009; Gong and Gao, 2019). The finding of high SLA values at higher altitudes in our study (Figure 1) suggests that the signal of low light in lower altitude overrides other factors and that leaf traits are shaped by several interacting environmental factors rather than simple relationships with physical environmental variables.

Leaf nutrients vary depending on soil nutrient availability and the factors affecting it (Aerts and Chapin, 2000; Hodgson et al., 2011). Leaf P varied significantly with altitude (Appendix S5), likely because P uptake by plants increases at pH close to six (Schachtman et al., 1998; Marschner, 2012), which explains the increase in LPmass with SAP and pH at lower altitudes (Figure 3). In addition, unlike other traits, LPmass did not vary significantly among species (Appendix S6), suggesting that *Damburneya* species share similar P requirements (Dalling et al., 2016) and/or limitations. When plants experience P deficiency, they increase P absorption at the expense of N absorption, resulting in higher leaf N:P values, suggesting a pervasive P limitation at our study site (Chapin, 1991; Koerselman and

Meuleman, 1996; Güsewell, 2004; Chapin et al., 2011). This finding is consistent with the argument that the tropical rainforest of Los Tuxtlas is a P-limited ecosystem (Tobón et al., 2011), as in many lowland tropical rainforests (Vitousek, 1984; Tanner et al., 1998; Turner et al., 2018) and other tropical ecosystems (Augusto et al., 2017; Hou et al., 2021). This hypothesis could be verified with a study of primary production at the ecosystem level, analyzing how P-limited forests respond to a release of such a limitation (Harrington et al., 2001; Turner et al., 2018).

Interestingly, LNmass and Leaf N:P ratio were negatively correlated with soil NO_3 and STN concentrations and were not significantly related to NH_4 concentration in the soil, suggesting a decoupling between N supply and plant demand. This decoupling could be due to reduced N uptake by the roots under excess soil N (Chapin et al., 2011) and/or low P supply (Chapin, 1991) and is concordant with the hypothesized P limitation of *Damburneya* species at Los Tuxtlas. Moreover, besides soil N availability, LNmass could be determined by plant demand and regulatory mechanisms affecting nutrient accumulation and metabolism in plant organs (Marschner, 2012; Lambers and Oliveira, 2019).

On the other hand, the response of leaf functional traits to local soil heterogeneity was determined by interspecific variation (Appendix S9), suggesting that species vary in the way they adjust to environmental heterogeneity (Chesson, 2000; Adler et al., 2013; Schulze et al., 2019). Moreover, the intraspecific variation in *Damburneya* had a higher influence on morphological traits than on leaf nutrient concentrations, likely due to the high variability of plant nutrient contents (Cárdenas and Campo, 2007; Lepš et al., 2011; Kichenin et al., 2013; Fajardo and Siefert, 2018).

Functional strategies differ among species

As predicted, our results show diverging patterns of trait variation that suggest interspecific differences in functional strategies involved in plant productivity and light and nutrient demands among species. Why leaf strategies involved in leaf resource gain and use differ among coexisting species of *Damburneya* is unclear. However, the observed patterns of trait variation could arise in response to simultaneous environmental pressures like herbivory (Givnish, 1988; Kitajima, 1994; Valladares and Niinemets, 2008; Poorter, 2009; Westbrook et al., 2011; Onoda et al., 2017) and to contrasting gradients of resource availability, as occur in sites with richer soils and lower light availability (Baltzer and Thomas, 2007; Coomes et al., 2009; Dent and Burslem, 2016; Fajardo and Siefert, 2018).

In our study, the analysis of intraspecific variation shows that some species (*D. colorata* and *D. salicifolia*) express the patterns of trait correlations expected by the leaf economic spectrum, such as a positive association between SLA and LNmass or a negative association between LDMC and LNmass; but strikingly, other species do not. For example, *D. ambigens* has high nutrient content and LDMC in nutrient-rich soils at low altitude (Figure 1; Appendices S3 and S4). The high nutrient allocation to leaves and the high carbon investment in leaf construction (Onoda et al., 2017) likely favor CO_2 fixation when light is limited (Valladares and Niinemets, 2008; Schlesinger and Bernhardt, 2020) and/or tissue is lost due to high herbivory (Valladares and Niinemets, 2008) as expected in tropical rainforests (Kitajima, 1994; Poorter, 2009; Westbrook et al., 2011). Previous studies analyzing responses to simultaneous nutrient and light gradients in other forests have shown that the number of coexisting functional strategies to deal with shade may increase in nutrient-rich soils (Givnish, 1988; Commes and Grubb, 2000; Coomes et al., 2009; Mason et al., 2012; Dent and Burslem, 2016). Whether the relaxation of one factor of resource limitation allows for the expression of alternative functional strategies to deal with other environmental factors, and if such may drive departures from the LES expectations, are very interesting hypotheses worth to be investigated for *Damburneya* species.

Interestingly, *D. colorata* and *D. salicifolia* exhibit functional overlap, probably due to their high morphological similarity (Figure 1). The wide intraspecific trait variation of these species encompasses both conservative and acquisitive strategies, suggesting wide ecological plasticity (Figure 1). Such intraspecific trait variation could explain the adaptability of *D. salicifolia* to divergent habitats and environmental pressures (Rohwer and Kubitzki, 1993; Lorea-Hernández, 2002). Significant positive correlations between SLA and leaf N:P ratio suggest that *D. salicifolia* could require lower P investment for leaf construction compared to the other species (Appendix S4). The high SLA values of *D. salicifolia* suggest that this species can optimize carbon gain in the environment with higher light availability. These trait relationships suggest a differential efficiency in resource-use between *D. salicifolia* and *D. colorata* trees, but further research is needed to test this possibility. In addition, the functional divergence between species could also lead to divergent herbivory rates. For example, *D. salicifolia* and *D. colorata* likely face lower costs of leaf construction and a faster replacement of lost tissue than *D. ambigens*, at expenses of higher vulnerability to the attack of natural enemies (Poorter, 2009) and shorter leaf longevity (Wright et al., 2004).

Perspectives on ecological differentiation of *Damburneya* species

According to Rohwer and Kubitzki (1993), landscape elevation and soil variation play a critical role in ecological differentiation among *Damburneya* species and explain differences of local distribution and abundance in sympatric species. Here, we showed the effects of soil properties on leaf functional trait variation for four *Damburneya* species. The interspecific divergence of leaf traits relationships in our study are potentially good indicators of the differential effects of soil heterogeneity on sympatric *Damburneya* and could explain differences in distribution and abundance among species. For example, *D. gentlei* was restricted to low altitude, likely due to a high nutrient demand (i.e., an acquisitive strategy). In addition, *D. salicifolia*, which seems to use P more efficiently, was the most abundant species at high altitudes, where soil P availability is lower.

On the other hand, our data suggest that leaf traits and species distribution could vary in response to herbivory or abiotic drivers of ecological differentiation (e.g., climate and the availability of light) that vary along the altitudinal gradient. For example, differences in leaf mechanical resistance underlying divergent herbivory rates could explain the wide distribution of *D. ambigens* in contrast to the restricted distribution of *D. gentlei*, and higher light availability at higher altitudes could favor the establishment of *D. salicifolia*. Nevertheless, studies regarding the impact of leaf trait variation on plant fitness and other factors impacting species abundance and distribution like recruitment, demography, phenology, competition, and even timber extraction, are still needed.

We do not know to what extent leaf functional trait variation reflects phylogenetic signal or evolutionary processes like local adaptation, nor how much of this variation is genetically or environmentally determined. Common garden experiments could be used to test how species respond to the same ranges of environmental variation (i.e., light, soils, elevation) and whether patterns of trait correlation exhibit phenotypic plasticity or are maintained under changing environments (Reich et al., 2003).

Like most Lauraceae species in Mexico, the *Damburneya* species studied here are threatened by habitat loss and deforestation (de Kok, 2020a, 2020b, 2020c) and are vulnerable to disturbance because they usually do not thrive in secondary vegetation (Lorea-Hernández, 2002). Among the natural protected areas in Mexico, the Los Tuxtlas Biosphere Reserve harbors the greatest number of Lauraceae species (Lorea-Hernández, 2002). During the last decades, yhis reserve has suffered deforestation and fragmentation (Dirzo et al., 2007; von Thaden et al., 2018), causing soil deterioration and nutrient loss (Tobón et al., 2011; Roa-Fuentes et al., 2015b) that could be especially harmful to *Damburneya* species with small population sizes.

The variation in leaf traits and distribution among species of *Damburneya* can inform future management and ecological restoration projects of tropical rainforests in the region. We provided evidence that the *Damburneya* species are sensitive to local environmental variation and exhibit divergent functional strategies. Based on our results, we would expect these species to be differentially affected by environmental changes, including the collateral effects of deforestation (i.e., changes in light incidence, water, and soil nutrient availability) and global climate change (in precipitation, temperature, evapotranspiration, and soil moisture; IPCC, 2021). Hence, the species of *Damburneya* may require different management strategies; we encourage future research on this topic and highlight the need for monitoring natural populations.

CONCLUSIONS

Here we explored the potential role of leaf trait variation as a mechanistic basis of ecological divergence among sympatric, closely related species of *Damburneya* in a tropical rainforest. The results suggest that interspecific differences in trait correlations and variation in response to soil heterogeneity along the altitudinal gradient could explain some ecological differences among species. Our research highlights the role of soil variation as a potential driver of functional divergence within the genus. However, we acknowledge that other unmeasured factors (i.e., climate, light, and herbivory) could be key potential drivers of ecological differentiation among *Damburneya*. Species of *Damburneya* exhibited divergent functional strategies, but all appear to be limited by soil phosphorus supply. Altogether, the patterns of trait variation likely contribute to explain local differences in species abundance and distribution and are a promising tool to compare species performance across environmental gradients. Given the impact of land-use change in the tropical rainforest biome and the need for deeper knowledge of forest tree species for effective management and ecological restoration of this threatened ecosystem, the topic of the present study warrants further investigation.

AUTHOR CONTRIBUTIONS

L.J.G.K. and J.N.F. planned and designed the research, conducted the fieldwork, collected the samples, and recorded the data. J.C. gave advice on fieldwork sampling and supervised laboratory work. J.C. and H.P. gave advice on research planning and data analysis. L.J.G.K. compiled and analyzed the data and wrote the first draft of the manuscript. All authors contributed to data interpretation and helped with revising the manuscript.

ACKNOWLEDGMENTS

The authors thank Santiago Sinaca Colín for help and guidance on fieldwork and Fernando López Ordáz, Brenda Hernández, Valeria Flores, Daniel Matías, Ana Lucia Castrejón and Pilar Suárez, who helped with sample collection and processing. Also, we acknowledge Enrique Solis Villalpando for help and guidance with soil analysis, Francisco Lorea-Hernández (INECOL-Xalapa) for the taxonomic determination of collected specimens, Rosalinda Tapia-López for logistical support during planning and execution of the project, and the staff at the Estación de Biología Tropical Los Tuxtlas, especially the Director, Rosamond Coates-Lutes for ensuring several facilities for our research team in the field. We thank Miguel Martínez Ramos for his valuable comments and advice and the anonymous reviewers and Associate Editor for detailed suggestions on our previous drafts. This paper is part of the doctoral research of L.J.G.K., who acknowledges the Posgrado en Ciencias Biológicas at the Universidad Nacional Autónoma de México for its support and the Consejo Nacional de Ciencia y Tecnología (CONACYT) of Mexico for the scholarship no. 463686. This article constitutes a prerequisite for the Ph.D. in Science degree in the Programa de Posgrado en Ciencias Biológicas. The project was funded by SEP-CONACYT Ciencia Básica grant to J.N.F. (no. 284692).

CONFLICT OF INTEREST

None of the authors have any conflict of interest to declare.

OPEN DATA BADGE

This article has earned an Open Data Badge for making publicly available the digitally shareable data necessary to reproduce the reported results. The data are available at https://doi.org/10.6084/m9.figshare.20452599.v4. Learn more about the Open Practices badges from the Center for Open Science: https://github.com/ljgiraldok/ecological_differentiation_Damburneya.

DATA AVAILABILITY STATEMENT

The data are available at Figshare at https://doi.org/10.6084/m9.figshare.20452599.v4 (Giraldo-Kalil and Núñez-Farfán, 2022). Scripts employed for statistical analyses and figures are available at GitHub at https://github.com/ljgiraldok/ecological_differentiation_Damburneya.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Vouchers of representative specimens of four species of *Damburneya* collected in the tropical rainforest in Los Tuxtlas Biosphere Reserve.

Appendix S2. Soil physical, physicochemical, and chemical properties at low and high altitude in Los Tuxtlas Biosphere Reserve.

Appendix S3. Leaf functional trait variation in four sympatric *Damburneya* species (*D. ambigens, D. colorata, D.gentlei, D. salicifolia*) at Los Tuxtlas Biosphere Reserve according to altitude (high vs. low).

Appendix S4. Bivariate relationships among leaf functional traits of four sympatric species of *Damburneya* at Los Tuxtlas Biosphere Reserve calculated with standardized major axis regressions.

Appendix S5. Effects of altitude on leaf functional trait variation of four sympatric *Damburneya* species at Los Tuxtlas Biosphere Reserve according to linear mixed models.

Appendix S6. Likelihood ratio test and significance of the random effects of mixed linear models for leaf functional traits of four sympatric *Damburneya* species (*D. ambigens, D. colorata, D. gentlei, D. salicifolia*) at Los Tuxtlas Biosphere Reserve, according to species, altitude, and sampling plot.

Appendix S7. Relationships of the plot average leaf functional traits of four sympatric *Damburneya* species (*D. ambigens, D. colorata, D. gentlei, D. salicifolia*) at Los Tuxtlas with soil organic carbon (SOC), C:N ratio, and soil total phosphorus (STP).

Appendix S8. Relationships of the plot average morphological leaf traits of four sympatric *Damburneya* species (*D. ambigens, D. colorata, D. gentlei, D. salicifolia*) at Los Tuxtlas with soil available phosphorus (SAP), pH, and clay content.

Appendix S9. Decomposition of the variation of intra- and interspecific effects of abundance weighted average plot trait values of four sympatric species of *Damburneya* (*D. ambigens, D. colorata, D. gentlei, D. salicifolia*) at Los Tuxtlas tropical rainforest in response to soil nutrients.

How to cite this article: Giraldo-Kalil, L. J., J. Campo, H. Paz, and J. Núñez-Farfán. 2022. Patterns of leaf trait variation underlie ecological differences among sympatric tree species of *Damburneya* in a tropical rainforest. *American Journal of Botany* 109(9): 1394–1409. https://doi.org/10.1002/ajb2.16056

Supporting information

APPENDIX S1. Vouchers of representative specimens of four species of *Damburneya* collected in the tropical rainforest in Los Tuxtlas Biosphere Reserve

Species names are highlighted in bold type, followed by collector number and herbarium (in parentheses). All vouchers were collected by L.J. Giraldo Kalil (LJGK). Herbarium abbreviations are: MEXU – Herbario Nacional de México, Universidad Nacional Autónoma de México; EBTLT-TUX- Herbario Estación de Biología Tropical Los Tuxtlas, Universidad Nacional Autónoma de México, XAL – Herbario Instituto de Ecología A.C.

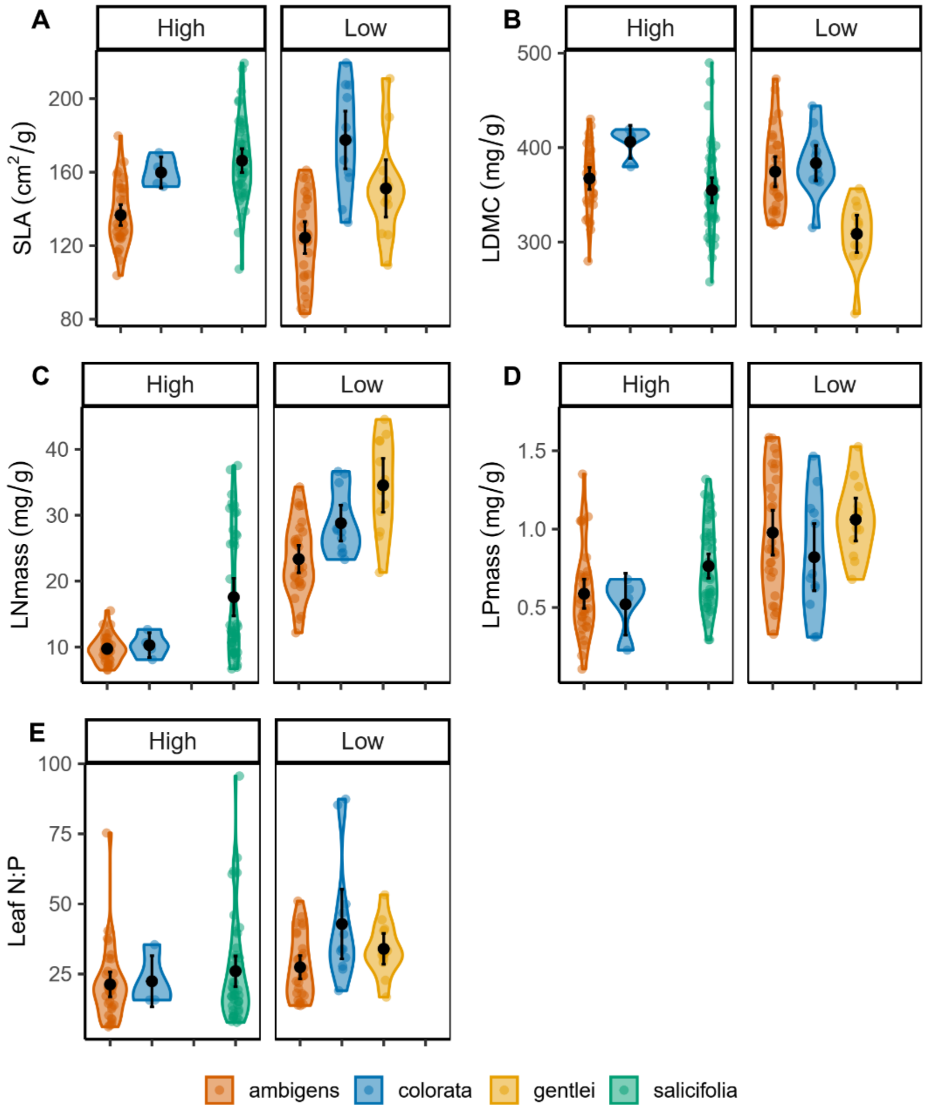
Damburneya ambigens Veracruz, San Andrés Tuxtla, Reserva de la Biosfera Los Tuxtlas. LJGK897, LJGK905, LJGK938, LJGK946 (MEXU); LJGK890, LJGK893, LJGK913, (EBTLT-TUX); LJGK894 (XAL). ***D. colorata*** Veracruz, San Andrés Tuxtla, Reserva de la Biosfera Los Tuxtlas. LJGK843, LJGK855 (MEXU); LJGK840, LJGK852 (EBTLT-TUX); LJGK845, (XAL). ***D. gentlei*** Veracruz, San Andrés Tuxtla, Reserva de la Biosfera Los Tuxtlas. LJGK886, LJGK888, (MEXU); LJGK882 (EBTLT-TUX); LJGK884 (XAL). ***D. salicifolia*** Veracruz, San Andrés Tuxtla, Reserva de la Biosfera Los Tuxtlas. LJGK797, LJGK816, LJGK837, LJGK838 (MEXU); LJGK799, LJGK834, LJGK836, (EBTLT-TUX); LJGK808, LJGK826 (XAL)

APPENDIX S2. Soil physical, physicochemical, and chemical properties at low and high altitudes in Los Tuxtlas Biosphere Reserve.

	Altitude	Low				High			
	Soil depth (cm)	0-10		10-20		0-10		10-20	
Variable	unit	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Altitude	m	197.4	7.9	197.4	7.9	829.9	124.2	829.9	124.2
pH	-	5.7	0.16	5.9	0.16	5.3	0.03	5.2	0.09
Silt	%	28.0	5.0	35.3	1.8	14.7	2.9	16.0	4.0
Sand	%	53.3	8.7	37.3	5.9	76	4.2	74.7	5.3
Clay	%	18.7	3.7	27.3	4.4	9.3	1.3	9.3	1.3
SOC	mg/g	25.4	2.4	21.5	1.8	75.1	9.0	56.2	12.9
STN	mg/g	2.00	0.26	1.71	0.35	3.67	0.7	3.79	0.5
NO_3	µg/g	14.9	1.9	19.1	6.2	16.2	3.1	10	3.6
NH_4	µg/g	15.6	2.4	19.3	4.3	13.3	4.6	6.5	3.1
NO_3:NH_4	-	1.02	0.21	1.08	0.41	1.41	0.29	1.87	0.46
C:N	-	13.1	1.7	13.1	1.4	21.2	2.8	14.5	1.6
STP	µg/g	416	35	412	42	591	80	508	87
SAP	µg/g	11.9	0.1	11.6	1.5	10.3	0.3	10.3	0.7

Notes: Values are means of n = 3 plots, with standard error (SE). Data are shown according to soil depth. Soil variables are abbreviated as: SOC = soil organic carbon, STN = soil total nitrogen, NO_3 = nitrate, NH_4 = ammonium, C:N = carbon: nitrogen ratio, STP = soil total phosphorus, SAP = soil available phosphorus.

APPENDIX S3. Leaf functional trait variation in four sympatric *Damburneya* species (*D. ambigens*, *D. colorata*, *D.gentlei*, and *D. salicifolia*) at Los Tuxtlas Biosphere Reserve according to altitude (high vs. low).



Notes: High and low altitudes are approx..1100 and 100 m a.s.l., respectively. (A) SLA= specific leaf area, (B) LDMC = leaf dry matter content, (C) LNmass = leaf nitrogen concentration, (D) LPmass = leaf phosphorus concentration, (E) Leaf N:P = leaf nitrogen: phosphorus ratio. In black the 95% confidence interval of the mean.

APPENDIX S4. Bivariate relationships among leaf functional traits of four sympatric species of *Damburneya* at Los Tuxtlas Biosphere Reserve calculated with standardized major axis regressions.

Variable		**Slopes**	***D. ambigens***			***D. colorata***			***D. gentlei***			***D. salicifolia***		
Y	**x**	**LR**	**slope**	**CI**	r^2	**slope**	**CI**	r^2	**slope**	**CI**	r^2	**slope**	**CI**	r^2
LDMC	SLA	10.96 *	-0.62	(-0.78, -0.49)	0.31 ***	-0.52	(-0.72, -0.37)	0.71 ***	-0.47	(-0.84, -0.26)	0.18	-0.89	(-1.1, -0.72)	0.56 ***
LNmass	SLA	13.73 ***	-3.25	(-4.23, -2.50)	0.13 ***	3.40	(2.16, 5.34)	0.22	-1.22	(-2.32, -0.65)	0.1	4.63	(3.53, 6.07)	0.29 ***
LNmass	LDMC	6.34	5.02	(4.04, 6.23)	0.04	-6.96	(-12.01, -4.04)	0.24 †	-2.22	(-4.55, -1.08)	0.03	-5.11	(-6.51, -4.02)	0.29 ***
LPmasss	SLA	10.26 *	3.45	(2.65, 4.49)	0.03	3.71	(2.36, 5.82)	0.36 *	1.18	(0.64, 2.16)	0.32 †	2.89	(2.11, 3.97)	0.09 *
LPmass	LDMC	14.25 **	-5.12	(-6.52, -4.02)	0.05	-7.62	(-12.35, -4.71)	0.32 *	-2.92	(-4.5, -1.89)	0.05	-3.22	(-4.31, -2.41)	0.22 **
LPmass	LNmass	8.18 *	1.05	(0.86, 1.28)	0.24 ***	1.07	(0.61, 1.86)	0.27 *	1.11	(0.53, 2.33)	0.01	0.64	(0.48, 0.85)	0.01
Leaf N:P	SLA	13.72 **	-3.24	(-4.13, -2.53)	0.27 ***	-3.45	(-5.6, -2.13)	0.03	-1.52	(-2.84, -0.81)	0.43 *	5.32	(3.91, 7.25)	0.08 †
Leaf N:P	LDMC	5.17	4.96	(3.89, 6.32)	0.18 **	7.12	(4.23, 11.98)	0.01	3.08	(1.72, 5.52)	0.09	-5.73	(-7.67, -4.29)	0.04

Notes: The analyses were performed with standardized major axis regressions between all pairs of y and x log10 transformed variables. The “Slope comparison” column show the test of a common slope for the bivariate trait relations for all the species. Likelihood ratio models (LR) were built to test the significance of slopes differences among species, with 3 degrees of freedom. The shaded columns show the slopes of the bivariate leaf traits correlations for each species with 95% confidence intervals, the coefficients of determination (r^2) and the significance of trait correlations. Significance is symbolized as: †, $P > 0.06$); *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Traits are abbreviated as: SLA= specific leaf area, LDMC = leaf dry matter content, LNmass = leaf nitrogen concentration, LPmass = leaf phosphorus concentration, Leaf N:P = leaf nitrogen:phosphorus ratio.

APPENDIX S5. Effects of altitude on leaf functional traits variation of four sympatric *Damburneya* species at Los Tuxtlas Biosphere Reserve according to linear mixed models.

Trait	**model**	**npar**	**logLik**	**AIC**	**LRT**	***P***
SLA	none	5	-155.2	320.3	0	
	species	4	-167.7	343.3	25	< 0.001
	Plot	4	-165.1	338.2	19.9	< 0.001
LDMC	none	5	-174	358.1	0	
	species	4	-186	380	23.9	< 0.001
	Plot	4	-184.3	376.5	20.4	< 0.001
LNmass	none	5	-113.8	237.6	0	
	species	4	-125.6	259.1	23.5	< 0.001
	Plot	4	-143.7	295.3	59.8	< 0.001
LPmass	none	5	-178.4	366.8	0	
	species	4	-179	366.1	1.3	0.253
	Plot	4	-179.9	367.8	3	0.082
Leaf N:P	none	5	-182.3	374.6	0	
	species	4	-182.4	372.9	0.2	0.621
	Plot	4	-187.8	383.5	10.9	< 0.001

Notes: Total observations: 135, plots: 6, species: 4. Slope estimates are shown according to altitude. The models were built with REML considering altitude (High, Low) as fixed effect, the species and sampling plot were modeled as effects with random intercepts. Traits are abbreviated as: SLA= specific leaf area, LDMC = leaf dry matter content, LNmass =leaf nitrogen concentration, LPmass = leaf phosphorus concentration, Leaf N:P = leaf nitrogen:phosphorus ratio. Significance of fixed effects was calculated using the Satterthwaite's approximation for degrees of freedom. Significance is symbolized as * ($P < 0.05$).

APPENDIX S6. Likelihood ratio test and significance of the random effects of mixed linear models for leaf functional traits of four sympatric *Damburneya* species (*D. ambigens*, *D. colorata*, *D. gentlei*, *D. salicifolia*) at Los Tuxtlas Biosphere Reserve, according to species, altitude, and sampling plot.

Trait	**model**	**npar**	**logLik**	**AIC**	**LRT**	***P***
SLA	none	5	-155.2	320.3	0	
	species	4	-167.7	343.3	25	< 0.001
	Plot	4	-165.1	338.2	19.9	< 0.001
LDMC	none	5	-174	358.1	0	
	species	4	-186	380	23.9	< 0.001
	Plot	4	-184.3	376.5	20.4	< 0.001
LNmass	none	5	-113.8	237.6	0	
	species	4	-125.6	259.1	23.5	< 0.001
	Plot	4	-143.7	295.3	59.8	< 0.001
LPmass	none	5	-178.4	366.8	0	
	species	4	-179	366.1	1.3	0.253
	Plot	4	-179.9	367.8	3	0.082
Leaf N:P	none	5	-182.3	374.6	0	
	species	4	-182.4	372.9	0.2	0.621
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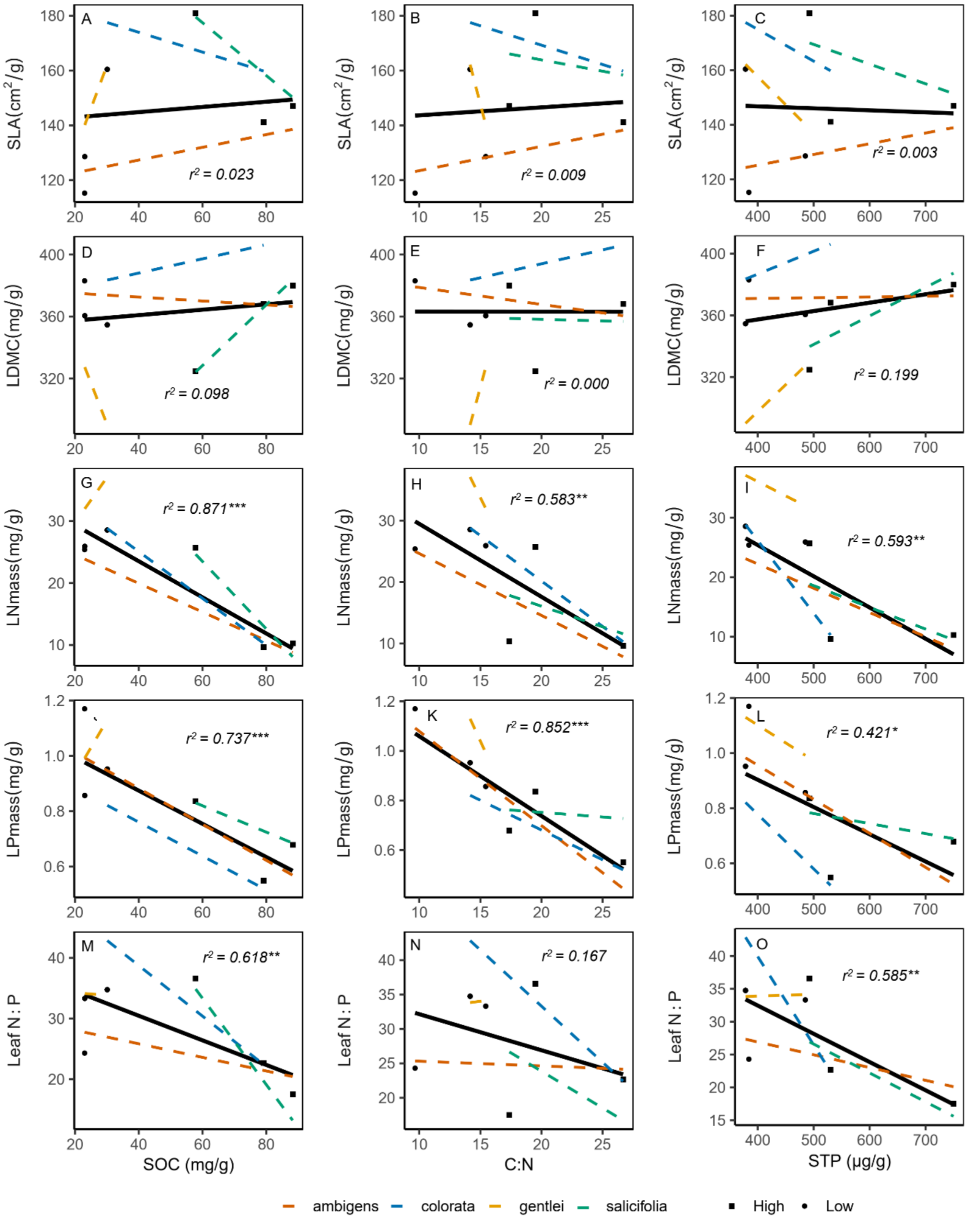
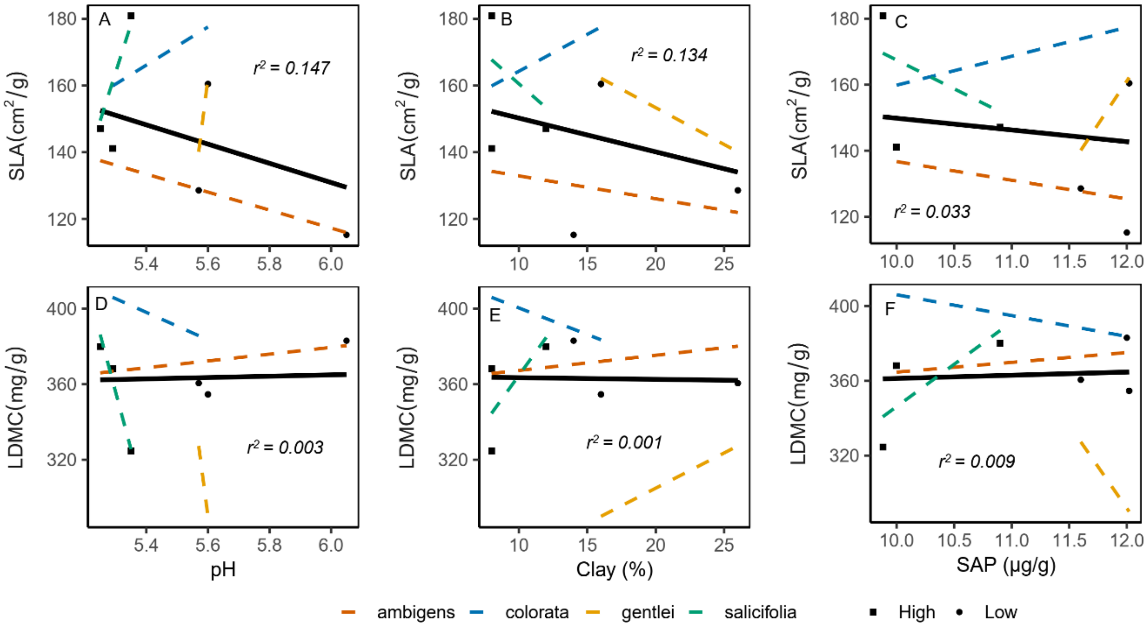
Notes: Total observations: 135, plots: 6, species: 4. The models were built with REML considering altitude (High, Low) as fixed effect, the species and sampling plot were modeled as effects with random intercepts. Traits are abbreviated as: SLA = specific leaf area, LDMC = leaf dry matter content, LNmass = leaf nitrogen concentration, LPmass = leaf phosphorus concentration, Leaf N:P = leaf nitrogen: phosphorus ratio. Table abbreviations are npar: number of model parameters. logLik: REM log likelihood, AIC: Akaike Information Criteria, LRT: Likelihood Ratio Test statistic. The column "model" refers to the terms dropped from the model. df = 1.

APPENDIX S7. Relationships of the plot average leaf functional traits of four sympatric *Damburneya* species (*D. ambigens, D. colorata, D. gentlei, D. salicifolia*) at Los Tuxtlas with soil organic carbon (SOC), C:N ratio, and soil total phosphorus (STP).



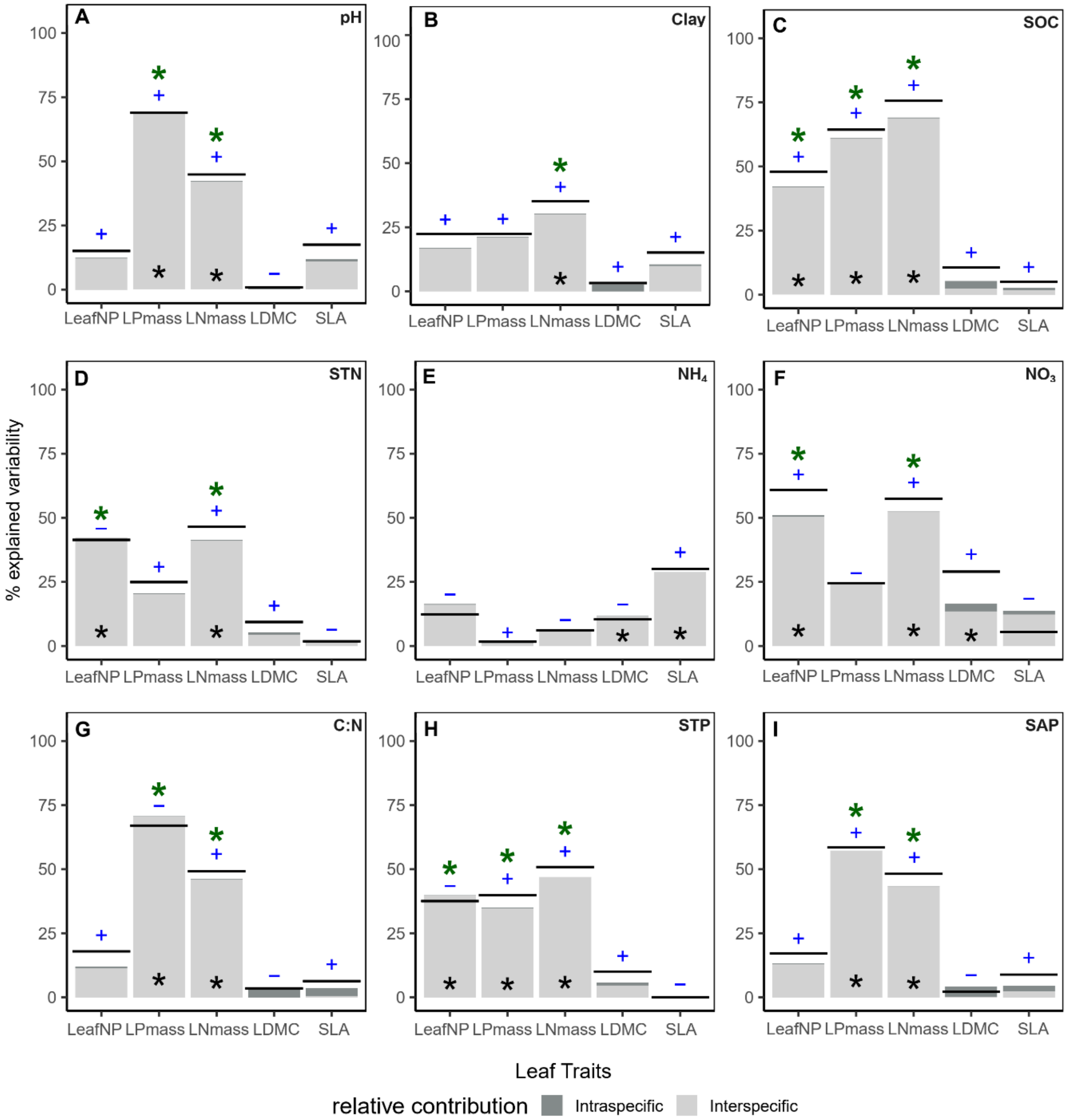
Notes: Trait abbreviations are = SLA: apecific leaf area (A-C), LDMC: leaf dry matter content (D-F), LNmass: leaf nitrogen content (G- I), LPmass: leaf phosphorus content (J-L) and leaf N:P (M-O). Points represent the abundance-weighted average plot trait values, and the shape symbolizes the altitude. Plot trait variation in response to soil properties is represented by solid black regression lines, and the regression coefficient (r^2) and significance are provided for these values. The statistical significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Colored dashed lines represent each species trends of variation.

APPENDIX S8 Relationships of the plot average leaf functional traits of four sympatric *Damburneya* species (*D. ambigens, D. colorata, D. gentlei, D. salicifolia*) at Los Tuxtlas with pH, clay content and soil available phosphorus (SAP).



Notes: Trait abbreviations are = SLA: Specific leaf area (A-C), LDMC: leaf dry matter content (D-F). Points represent the abundance-weighted average plot trait values, and the shape symbolizes the altitude. Plot trait variation in response to soil properties is represented by solid black regression lines, and the regression coefficient (r^2) and significance are provided for these values. The statistical significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Colored dashed lines represent each species trends of variation.

APPENDIX S9. Decomposition of the variation of intra and interspecific effects of abundance weighted average plot trait values of four sympatric species of *Damburneya* (*D. ambigens, D. colorata, D. gentlei, D. salicifolia*) at Los Tuxtlas tropical rainforest in response to soil nutrients.



Notes: (A) pH, (B) Clay, (C) SOC = soil organic carbon, (D) STN = soil total nitrogen, (E) NO_3 = nitrate, (F) NH_4 = ammonium, (G) C:N = carbon-nitrogen ratio, (H) STP = soil total phosphorus, (I) SAP = soil available phosphorus. Leaf functional traits are abbreviated as: SLA= specific leaf area, LDMC = leaf dry matter content, LNmass = leaf nitrogen concentration, LPmass = leaf phosphorus concentration, Leaf N:P = leaf nitrogen: phosphorus ratio. The statistical significance is represented with asterisks ($P < 0.05$). Black asterisks at the bottom of the bars refer to the significance of interspecific variation, green asterisks at the top of the bars refer to the significance of the total variance (including the effects of intra and interspecific variance and the covariance between them) which is represented as black lines. Intraspecific variation did not have a significant effect in any case. In blue are the signs of the covariation between intra and interspecific variation.

Capítulo 3

Efectos del tamaño de la semilla, el ataque de enemigos naturales, la elevación y el suelo en el reclutamiento de dos especies simpátricas de *Damburneya* de la selva alta perennifolia de Los Tuxtlas

(Artículo en preparación)

Effects of seed size, natural enemies, elevation, and soil on seedling recruitment of two tree species of *Damburneya* (Lauraceae)

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Abstract

Elevation and edaphic variation are potential drivers of ecological divergence between *Damburneya* (Lauraceae) species. However, the effect of those environmental variables on early seedling recruitment is not yet understood. We aimed to assess whether there is interspecific divergence in seedling establishment of two congeneric species of *Damburneya* cooccurring in a tropical rainforest, and characterize the impact of biotic factors like herbivory, pathogen attack and seed size on seedling vigor and survival under different elevations and soils. Also, we hypothesized that the adaptive value of seed size could differ between species depending on those environmental conditions.

We quantified seed size and established two experimental sites at contrasting elevations (150 m and 1100 m) in the rainforest of Los Tuxtlas. In each site, plots with local soil and soil from the other elevation were stablished to plant seedlings of the two species and record survivorship and vigor-related traits for over more than two years. We quantified seedling vigor by measuring seedling height, leaf area, and the number of leaves and recorded the incidence of herbivore and pathogen attack, to assess their potential effect on seedling survival. Seed size differed more than ten times between species. Seedling survival was determined by the number of leaves and seed size but not affected by the attack of natural enemies. Seedling survival and vigor of both species were higher at high than at low elevation, while the adaptive value of seed size was higher at low elevation. Elevation likely affected the adaptive value of seed size through its effect on light incidence, while soils probably determined seedling performance by affecting water availability. We did not detect interspecific differences in the effects of external and intrinsic factors affecting seedling vigor and survival suggesting that there was not divergence of regeneration niche between the two species.

Key words: herbivore, pathogen, regeneration, seed size, seedling, tropical rainforest, vigor

Introduction

Plant recruitment refers to the incorporation of new juvenile individuals to plant populations (Gaillard et al., 2008), it involves intrinsic plant traits and processes and depends on several environmental requirements and constraints shaping plant success during the early stages of life cycle, also known as regeneration niche (Grubb, 1977). Interspecific divergence in regeneration niche can promote long term species coexistence and the maintenance of diversity within plant communities by allowing each to use the available resources in a different way during the early stages of the life cycles (Grubb 1977, Chesson, 2000; Poorter 2007).

One of the most critical stages of regeneration niche differentiation in tropical rainforests plants is seedling establishment, which is largely determined by seed size, particularly in shaded environments (Grubb, 1977; Foster, 1986; Paz and Martínez-Ramos, 2003). Seed size determines seedling survival through its effect on vigor and tolerance to biotic and abiotic environmental stresses like resource limitation and negative interactions such as the attack of pathogens and herbivores (Foster, 1986; Westoby et al., 1992 and 1996; Paz y Martínez-Ramos, 2003). Natural selection can favor large-seeded seedlings in stressful environments as large seeds provide nutritional reserves that promote seedling growth and survival. On the other hand, seed size is regulated by several tradeoffs caused by conflicting selective pressures like seed dispersal, removal, and predation, as large seeds are more attractive for seed predators but less likely dispersed than small seeds (Foster, 1986; Chapin, 1991; Westoby et al., 1992, 1996; Baraloto et al., 2005). Moreover, the adaptive value of seed size can be determined by environmental stress affecting seedling performance (Foster, 1986; Paz and Martínez-Ramos, 2003; Chávez-Pesqueira and Núñez-Farfán, 2016).

Several studies have pointed that regeneration niche and seedling and sapling traits likely influences ulterior stages of plant life cycle (Grubb, 1977; Thomas and Bazzaz, 1999; Reich, 2000; Poorter, 2007). However, further studies are necessary to assess whether the differentiation of regeneration niches at early stages is encompassed with niche differentiation processes in adult and young plants and the environmental factors promoting it (Lasky et al., 2015). This would shed light the ontogenetic changes on resource use and tolerance to environmental constraints that can ultimately affect species distribution and coexistence. Here we assessed whether environmental factors involved in niche differentiation in adult plants could be also involved in regeneration niche differentiation between congeneric species of Lauraceae, and whether other local factors like variation in the attack of natural enemies or microclimatic conditions can have divergent effects on the seedlings of different species.

The divergence of local distribution patterns of closely related species of Lauraceae has been attributed to ecological differentiation driven by interspecific differences in the ranges of elevation, climate, topography and soil variation (Giraldo-Kalil et al., in review; Rohwer and Kubitzki, 1993; Sri-Ngernyuang et al., 2003; Srinivas and Krishnamurthy, 2019; Giraldo-Kalil et al., 2022). Previous research on *Damburneya* species suggest interspecific differences in the climatic and edaphic ranges constraining spatial distribution at large geographical scales (Giraldo-Kalil et al., in review), and in the–trait- based leaf functional strategies across an elevation and edaphic gradient in the study area (Giraldo-Kalil et al., 2022). However, the impact of these environmental factors on seedling recruitment and the potential interspecific divergence in plant establishment are not yet understood within the genus.

This research aims to investigate the influence of intrinsic factors and extrinsic environmental conditions that hypothetically promote niche differentiation divergence in *Damburneya* on the seedling recruitment of *Damburneya ambigens* and *D. salicifolia,* the two most abundant species of *Damburneya* (Lauraceae) in the tropical rainforest of Los Tuxtlas Biosphere Reserve. We hypothesized that both congeneric species differ in their regeneration niches, specifically, in the constraints to seedling establishment. If this were the case, we could expect that seedling establishment of both species to be differentially affected by the elevational variation of climate and soil, the main promoters of niche differentiation in adult trees, and by the attack of natural enemies. High elevations at the study area have better soil drainage, and light incidence, but lower nutrient availability than low elevations (Siebe et al. 1996; Flores-Delgadillo et al., 1999; Giraldo-Kalil et al. 2022). Furthermore, one study reported that seed size of *D. ambigens* is adaptive under low light intensities and can promote survival under high biotic stress like herbivore and pathogen attack in the study area (Chávez-Pesqueira and Núñez-Farfán, 2016). We hypothesized that the adaptive value of seed size differs between species and is higher in the stressful shaded understory at low elevation.

We performed two field experiments designed to quantify and compare survival, seed size, intensity of herbivory and pathogen attack, and vigor traits of seedlings of both species growing at contrasting elevations and soil types. Furthermore, we quantified trait genetic variance and determined the adaptive value of seed size under divergent environments. We analyzed the intra- and interspecific divergence of seedlings performance and discuss their implications in the ecological context of the species.

Methods

Study area and species

This research was carried out at the tropical rainforest of the Los Tuxtlas Biosphere Reserve, in Veracruz, Mexico, in the north-eastern slope of the San Martin Tuxtla volcano mountain range, that elevates from sea level up to 1680 m (Gutiérrez-García and Ricker, 2011). The climate is humid and warm, with high precipitation during the year except in the dry season, from March to May, when monthly mean precipitation drops below 100 mm. Precipitation and temperature vary with elevation. In the lower zones, at 100 m, annual mean temperature is 23-24°C and precipitation varies from 4000 to 5000 mm. In contrast, in higher elevations, at 1100 m, annual mean temperature is colder, ranging from 20 to 21°C and the mean annual precipitation is higher, ranging from 6000 to 7000 mm (Gutiérrez-García and Ricker, 2011). In winter, the climate is highly influenced by cold humid winds from North America locally known as "nortes" that diminish temperature and increase precipitation (Soto and Gama, 1997).

The area has a complex edaphic heterogeneity, and soil physical and chemical properties also vary with elevation (Flores-Delgadillo et al., 1999). The soils at high elevations are mostly andisols, with high phosphorus retention and higher sand content (Sommer-Cervantes et al., 2003). Soils at low elevations are commonly entisols (Tobón Niedfeldt et al., 2011), having higher clay content, nutrient availability but lower drainage than the soils (Siebe et al., 1996; Giraldo-Kalil et al., 2022). Volcanic rock outcrops increase with elevation, while the soil layer thickness decreases (Sommer-Cervantes et al., 2003). Previous analyses of soil physical and chemical properties nearby the experimental sites established here suggest that soil phosphorus supply for plants is limited in the study area (Tobón Niedfeldt et al., 2011; Giraldo-Kalil et al., 2022).

The Los Tuxtlas region encompasses a high floristic and faunistic richness of the humid tropical forests in Mexico (González-Soriano et al., 1997; Villaseñor et al., 2018). Tropical rainforest with evergreen trees reaching heights of 30 m or more dominate the landscape (Bongers et al., 1988, Ibarra-Manríquez et al., 1997a). This region has suffered a drastic change in land cover and land use that intensified since the late 1970's because of deforestation, and the expansion of agricultural and livestock areas (Dirzo and García, 1992), causing a strong reduction of the original forest cover (von Thaden et al., 2020), forest fragmentation (Dirzo and García, 1992; Mendoza et al., 2005), and soil degradation (Figueroa et al., 2020).

Study system

This study is focused on *Damburneya ambigens* (S.F. Blake) Trofimov, and *D. salicifolia* (Kunth) Trofimov & Rohwer (formerly *Nectandra ambigens*, and *N. salicifolia* Trofimov et al., 2016), two abundant species in the study area. Flower and fruit production are massive and variable with fruiting production reaching thousands of fruits per tree, and occur at supra-annual intervals, from august to November (Carabias-Lillo and Guevara Sada, 1985; Cordova Casillas, 1985; Rohwer, 1993; Ibarra-Manríquez and Sinaca-Colín, 1995). The fruits are one-seeded berries turning from green to black at maturity and are consumed and dispersed by birds and monkeys (Rohwer, 1993; Dirzo et al., 1997; Anzures-Dadda et al., 2011). Seeds are mostly predated by insects and rodents (Sánchez-Garduño, 1995; Dirzo et al., 1997; Sánchez-Cordero and Martínez-Gallardo, 1998; Rodríguez-Sánchez et al., 2022). The seeds are recalcitrant and germinate soon after falling from the mother tree (Puchet and Vázquez-Yanes, 1987; Rohwer, 1993). The seedlings are cryptocotylar (i.e., with storage cotyledons) and the seeds remain attached to the seedlings providing nutritional reserves during several months (Barajas-Guzmán and Álvarez-Sánchez, 2004; Ibarra-Manríquez et al., 2001).

Damburneya ambigens is distributed in the tropical rainforests from southern Mexico to Honduras, from sea level up to ca. 1000 m a.s.l. (Rohwer, 1993), and is a dominant species of the tropical rainforest canopy at Los Tuxtlas region, reaching up to 35 m in height (Bongers et al., 1988; Popma et al., 1988). The wood of these tall trees is locally used for logging (Ibarra-Manríquez et al., 1997b), to build houses and furniture (Dirzo et al., 1997). The fruits are spheroid, ranging from 1.2 to 1.6 mm in diameter, and have a distinctive bowl-shaped red cupule when mature (Rohwer, 1993). Despite the massive reproduction, recruitment is poor, and the predominance of tall adult trees contrasts with the few saplings (Bongers et al., 1988). Seedling mortality is high in the dense seedling carpets formed around adult trees (Gómez-Pompa and del Amo-Rodríguez, 1985; Martínez-Ramos, 1991). Litterfall, branches fallen from the canopy, herbivore and pathogen attack, harvest by ants, high aggregation, and light stress, among other factors, can cause seedling mortality (Cordova Casillas, 1979; Gómez-Pompa and del Amo-Rodríguez, 1985; Martínez-Ramos, 1991; Dirzo et al., 1997; García-Guzmán and Benítez-Malvido, 2003). The seedlings tolerate the deep shade of the understory and exhibit higher growth and establishment with the increase of light incidence in forest gaps and forest fragments (Gómez-Pompa and del Amo-Rodríguez, 1985; Dirzo et al., 1997; Chávez-Pesqueira and Núñez-Farfán, 2016).

On the other hand, *D. salicifolia* occurs in several types of forests besides tropical rainforests; the trees can reach 25 m and occur in several soil types from Mexico to Panamá, ranging from sea level to 2300 m a.s.l. (Giraldo-Kalil et al., in review; Rohwer, 1993). Contrary to most *Damburneya* and Lauraceae species, *D. salicifolia* shows high phenotypic variation and occurs in wider environmental ranges than other related species (Giraldo-Kalil et al., in review; Rohwer and Kubitzki, 1993; Giraldo-Kalil et al., 2022); it can tolerate disturbed conditions and occurs in secondary vegetation (Lorea-Hernández, 2002; Arroyo-Rodríguez et al., 2009; Carreón-Santos and Valdez-Hernández, 2014; García-Licona et al., 2014). This species is locally used for timber; the fruits are globose, from 8-12 mm in diameter, and have funnel-shaped red cupule (Rohwer, 1993). The seedlings occur in high densities, while the saplings are comparatively scarce (Carreón-Santos and Valdez-Hernández, 2014).

Experimental design

We collected mature fruits of the two species to perform two field experiments (one per species). Fruit availability determined the onset and duration of the experiments as well as fruit collection sites, which were mostly outside the experimental sites; furthermore, fruiting periods differed between species. The fruits of *D. salicifolia* were obtained in 2016 from 16 trees of one population and were collected directly from the branches, avoiding those with obvious signals of insect damage (Table S 1). The fruits of *D. ambigens* were obtained in 2018 from two populations (10 trees per population) and were collected from the ground because the height of the trees prevented a direct collection (Table S 1).

A float test of viability was performed to discard seeds severely damaged by insect seed predators. About 10% of the viable seeds of *D. salicifolia* showed insect damage; in contrast, seed predation of viable seeds varied from 10 to 50% for *D. ambigens*, depending on the population (Table S 1). The seeds were individually weighted with an electronic balance and sowed in seedling nursery trays in humid peatmoss. The trays were placed at the Estación de Biología Tropical Los Tuxtlas (here after EBT Tuxtlas) in a mesh covered greenhouse that provides shade and allows natural seedling watering. Once the seedlings developed fully expanded leaves (ca. 2-3 months) were tagged for their field transplant in the experimental sites. In total, 479 seedlings of *D. salicifolia* and 961 of *D. ambigens* were used for the experiments (Table S 1).

The field experiments were established in two sites with contrasting elevations and soils. The first is located at the EBT Tuxtlas (latitude: 18,583957, longitude: -95,074501, WGS84), at low elevation (150 m; hereafter LE site) and is characterized by loamy soils, with higher nutrient availability, clay content and less acidic pH than the soils of the second site (Table 1). The latter is located at the ejido Caleria (latitude: 18,52257, longitude: -95,143316, WGS84), at high elevation (1100 m; hereafter HE site) in the upper limit between the tropical rainforest and the cloud forest. It has loamy-sand soils with higher organic matter content (Table 1), and more open canopy than the LE site (mean morning luminance = 112.95 ± 13.81 lux and 49.67 ± 9.34 lux for HE and LE sites, respectively; see Table S 3). Soil physical and chemical properties were assessed in a previous study in two 1ha plots nearby the experimental plots and quantified from homogenized superficial soil samples (0-20 cm). Further details on soil sampling and laboratory procedures can be found in Giraldo-Kalil et al. (2022). Moreover, to characterize microclimatic conditions of each site, temperature (°C), relative humidity (%), dew point (°C), and light intensity (lux) of the experimental blocks were measured with HOBO data loggers for five months (Jan-May 2018). The HE site has lower temperature, and dew point, but higher relative humidity and light intensity than the LE site (Table S 3).

A total of 379 seedlings of *D. salicifolia* and 961 of *D. ambigens* were transplanted in the experimental sites in blocks of approximately 1 × 1.2 m (Table S1). Following Chávez-Pesqueira and Núñez-Farfán, (2016), several seedlings per maternal tree (i.e., half-sib family) were included as replicates to assess the potential effects of genetic variation on trait expression and plant performance. Both experiments had a complete randomized block design (Quinn and Keough, 2002) to represent randomly and equally all maternal trees in all sites and blocks. For the experiment of *D. salicifolia*, seedlings from 16 maternal trees were transplanted directly into the soil of the forest in three blocks per site (187 in the HE site and 192 in the LE site), and were monitored in six censuses over 853 days, approximately every two months (Table S2). On the other hand, seedlings from 20 maternal trees and two populations were used for the experiment of *D. ambigens*; soil type was included as a treatment using local-site soil and foreign soil from 0-20 cm depth, transferred from the site with contrasting elevation. We transplanted 484 seedlings in the HE site (238 in the foreign loamy soil and 247 in the local loamy-sand soil) and 476 in the LE site (241 and 235 in the local loamy soil and in the foreign loamy-sand soil, respectively). Transplants were performed directly into the soils in three blocks per site and soil type (foreign and local), and were monitored in three censuses for 761 days, approximately every six months (Table S1). During the censuses and the day of transplant, we recorded seedling survival (0=dead, 1= alive), incidence of leaf damage by herbivores and pathogens (0= absence of damage, 1=damage), and seedling height (cm) to quantify growth. Furthermore, we characterized plant vigor by counting the number of leaves and measuring leaf dimensions to quantify total leaf area (cm^2). Further details can be found in Chávez-Pesqueira and Núñez-Farfán (2016). A detailed summary of the data recorded on each census is provided in Table S 2.

Leaf area per plant was calculated with a linear regression equation. For that, several seedlings that were not included in the experiments were randomly picked and collected and all the leaves were measured and scanned to calculate leaf area using ImageJ. The equation obtained to calculate leaf area of *D. ambigens* is: $A_{amb} = 0.611212 \times W \times L$ ($R^2 = 0.993$, $P < 0.005$, 190 leaves from 70 individuals); and the equation of *D. salicifolia* is: $A_{sal} = 0.622005 \times W \times L$ ($R^2 = 0.997$, $P < 0.005$, 60 leaves from 29 individuals), where A is leaf area, W is the maximum leaf width, and L is the maximum leaf length. Total leaf area, calculated as the sum of the leaf area of all the leaves per seedling, is reported.

Data analysis

All the analyses were performed with R (R Core Team, 2021) using RStudio (RStudio Team, 2022). All the figures were performed with the packages ggplot2 (RStudio Team, 2022) and ggpubr (Kassambara, 2020). We performed Cox proportional hazard regression analyses (Cox, 1972) with the survival package (*coxph* function, Therneau and Grambsh, 2000; Therneau, 2022), to assess the association of elevation and soil type with seedling survival, including seed size as a covariate. Survival curves were plotted with the package survminer (s*urvfit* function, Kassambara, 2021).

Genetic variance of seed size and seedling traits was determined with one-way ANOVAs including the maternal tree as a random-intercept effect (Falconer and Mackay, 1996) using the package lmer4 (Bates et al., 2015). The significance (*P*-values) of this effect was obtained by likelihood ratio tests with the lmerTest package using a maximum likelihood chi-squared test (*ranova* function) to compare the model with and without the random effect (Kuznetsova et al., 2017). The Satterthwaite’s approximation for degrees of freedom was employed to calculate the significance of fixed effects. Furthermore, to quantify the amount of explained variance, we calculated the conditional R^2 (which includes fixed and random effects) using the package MuMIn (*r.squaredGLMM* function; Barton, 2022). Both phenotypic and upper limit of additive components of genetic variance were determined using individual and average familial trait values, respectively.

Natural selection acting on seed size was assessed on phenotypic (individual) values in relation to seedling survival with a binary logistic regression. We adapted the analysis of natural selection on seed size from Chávez-Pesqueira and Núñez-Farfán (2016). Seed size was standardized to measure selection intensity (Lande and Arnold, 1983; Falconer and Mackay, 1996) as $Z_i' = (Z_i - \bar{Z})/\sigma_i$, where Z_i is the seed mass of the individual i, $\bar{Z}$ and σ_i are the population mean and standard deviation of seed size, respectively. Positive selection gradients (β) indicate that larger seed size increase survival probability.

To assess the effects of seed mass, elevation, and soil on plant vigor over time, we performed MANOVA models of repeated measures of height, leaf number, and leaf area of individual plants, including with seed mass as a covariate. The models were built with the package rstatix (Kassambara, 2021a). Furthermore, to compare seedling vigor under divergent environments (i.e., contrasting elevation and soil type) we assessed the effect of elevation, soil, seed mass and family in trait variation with linear mixed models, using the same R packages and general procedures employed to assess genetic variance. We assessed seedling performance at the third census of both species (231 for *D. ambigens*, and 277 days for *D. salicifolia*) because sample sizes allowed us to perform statistical tests (see details of census in Table S2). We did not include the family × environment (i.e., soil type and elevation) interaction because the model complexity increased considerably, and seedling mortality reduced our sample size and statistical power. However, we plotted trait familial differences under contrasting soils and elevations as a proxy to assess phenotypic plasticity.

The effects of natural enemies' attack, seed size, and vigor traits (seedling height, number of leaves, total leaf area) on future survival (i.e., in the next census) were assessed with generalized linear models. We performed binary logistic regressions using a logit link function with the data of survival of the fifth census (761 days) in relation to predictors measured on the third census (231 days) for *D. ambigens*. Similarly, we assessed the survival of the seedlings of the *D. salicifolia* in the fourth and fifth censuses (473 and 639 days) in relation to predictors of the third (277 days) and fourth censuses, respectively. The significance of predictors was assessed with a Wald z-test.

Results

Seed size and seedling survival

Genetic variance was detected for breeding values of all traits of the seedlings, and for seed mass in both species (explaining 76% of seed mass in *D. ambigens* and 82% in *D. salicifolia*), suggesting a great influence of genetic background on trait variation (Table 2). Overall, seedling survival was higher at the HE site than at the LE site. Also, the loamy soil increased the mortality hazard of the seedlings of *D. ambigens* (Figure 1, Figure 2, Figure 3, Table S4). Genetic variation also affected seedling mortality. The seedlings from some maternal trees of *D. salicifolia* exhibited lower proportional risk of mortality than those from others. Similarly, seedlings from two maternal trees of *D. ambigens* had contrasting trends of mortality hazard, it increased for the seedlings from one maternal tree but decreased for those from the other (Table S 4).

Seedling survival differed between species. By the third census (231 days), less than 15% of the seedlings of *D. ambigens* at the HE site died, while more than half died at the LE site, indicating a strong altitudinal divergence in seeding mortality since the early stages of the experiment. In contrast, independently of elevation, less than 30% of *D. salicifolia* seedlings were dead by the third census in a similar period (third census, 277 days), and less than 50% had died at the end of the experiment.

Seed size varied considerably between species. It ranged from 0.1 g to 0.9 g in *D. salicifolia* (mean= 0.5 g, standard deviation ± 0.1 g). In contrast, seed size of *D. ambigens* could be 10-fold larger, ranging from 1.4 g to 8.9 g (mean= 4.4 g, sd ± 1.1 g). The adaptive value of seed size differed between sites for both species but expressed at different times for each one. Large seeds only shown a positive adaptive value for *D. ambigens* at the beginning of the experiment (65 days) in loamy-sand soil at the LE site (β=0.505, z=2.546, P=0.011, Table 3); in addition, seed mass did not differ significantly between surviving and dead seedlings (Figure 2). Overall, the increase of seed mass did not significantly reduce the mortality of the seedlings of *D. ambigens* (hazard ratio = 0.004, P=0.872, Table S4, Figure S2). In contrast, large seeds reduced 39% of mortality hazard of the seedlings of *D. salicifolia* (P<0.005, Table S4). A positive selection gradient was detected for seed mass at the end of the experiment at the LE site after 639 days (β=0.409, z=2.497, P=0.013); and at HE and LE sites (β=0.380, z=2.503, P=0.012 and β=0.374, z=2.386, P=0.017, respectively) after 853 days (Figure 2, Table 3, Figure S3).

The effect of seed size and environment on seedling vigor

Up to the third census, all mean trait values of the two species increased with seed mass (Table S5) and differed between maternal trees (Table S6). The traits of the seedlings of *D. salicifolia* were not yet significantly affected by elevation (and consequently, by local soil). In contrast, the number of leaves and the leaf area of the seedlings of *D. ambigens* decreased at the LE site, and the seedling height and leaf number decreased in the loamy soil.

After nine months, and until the end of the experiments, seedling trait variation of *D. ambigens* and *D. salicifolia* was affected by elevation and seed mass (Table 4, Table S5, Figure S1, Figure S2, Figure S3). Over the duration of the experiments, height, total leaf area, and number of leaves of *D. ambigens* seedlings were higher at HE than at the LE site in several censuses, suggesting that seedling vigor increased at high elevation for this species (Table 4, Figure S1). Furthermore, soil type only affected leaf number and seedling heigh; trait values were lower in loamy soil than in loamy-sand soil, but the soil had not an effect as strong as elevation in seedling vigor (Table 4, Figure S 1). On the other hand, although elevation and time simultaneously affected the traits of the seedlings of *D. salicifolia* (Table 4), only seedling height was consistently higher at the HE site in all censuses, while leaf traits shown less predictable patterns (Figure S 1). For instance, leaf area and number of leaves were larger in the HE site until 15 months (473 days). However, five months later (639 days), both traits decreased at the HE site, and leaf area was even larger at the LE site. In addition, seed mass largely influenced vigor traits; all mean vigor trait values of *D. ambigens* and *D. salicifolia* tended to be larger in seedlings with larger seeds (Table 4, Table S 5, Figure S 1, Figure S 2, Figure S 3). Moreover, vigor traits variation differed between elevations and maternal trees, suggesting phenotypic plasticity (Figure S 4, Figure S 5).

Temporal effects of environment, vigor, and natural enemies on seedling survival

The likelihood of seedling survival in both species increased as the number of leaves in midterm and final censuses increased (*D. ambigens:* day 761, *D. salicifolia:* day 473, Table 5, Table S7). The likelihood of survival of *D. salicifolia* significantly increased with seed size until 20 months (639 days, *P*=0.078; Fig. 2, Table 5, Table S7). Although seedling mortality was higher at the LE site (even regardless of soil type in the case of *D. ambigens*), the proportion of survivor seedlings attacked by herbivores, pathogens or both agents simultaneously was higher at the HE than at the LE site (Figure 3), suggesting that natural enemy attack was not as determinant for seedling survival as elevation. *Damburneya ambigens* had a greater proportion of dead seedlings and a lower proportion of undamaged seedlings than *D. salicifolia* at the end of the experiments (Figure 3). Moreover, natural enemy attack at third and fourth censuses (277 and 473 days, respectively) did not have a significant effect on the likelihood of survival for the subsequent censuses (Table 5, Table S 7). The proportion of seedlings of *D. salicifolia* damaged by herbivores was lower than that of seedlings damaged by pathogens; both types of damage were similar in *D. ambigens.* Simultaneous herbivore and pathogen damage was the most common type of damage in the seedlings of both species (Figure 3).

Discussion

Effects of environment on seedling survival and vigor

Seedling survival and vigor was determined by several extrinsic environmental factors. Overall, the higher seedling survival and vigor of *D. ambigens* and *D. salicifolia* at the HE site (Figure S 1, Table S 5, Table S 4) could be explained due to higher light incidence at high elevation (Table S 3). The seedlings of both species had on average fewer leaves and smaller size at the LE site (Table S 4), such limitation of photosynthetic area likely contributed to reduction of survival because of a limited ability for resource acquisition by those seedlings. In line with this, previous studies report a positive relationship between seedling survival and the number of leaves (García-Guzmán and Benítez-Malvido, 2003; Chávez-Pesqueira and Núñez-Farfán, 2016). Seedling vigor directly affects seedling survival and is very sensitive to light availability (Foster, 1986; Chapin, 1991; Paz and Martínez-Ramos, 2003; Chávez-Pesqueira and Núñez-Farfán, 2016). Several studies point out that the light demanding trees of *D. ambigens*, which eventually reach the upper canopy, can survive under low light intensities during several early stages of their life cycles. The seedlings are widely benefited by disturbances that open the canopy such as forest gaps, that increase the growth rate and survival likelihood of the seedlings aggregated in carpets under the adult trees (del Amo, 1985; Dirzo et al., 1997). Similarly, seedling growth and survival are also high in forest fragments and experimental pasture plantings, characterized by high light intensity (Martínez-Garza and Howe, 2010; Chávez-Pesqueira and Núñez-Farfán, 2016). Independent tests including different light incidences per site are needed to confirm the effect of light on seedling performance across the altitudinal gradient.

Besides altitudinal light variation, soils also vary by elevation and affected seedling vigor and survival. Seedling survival and vigor of *D. ambigens* diminished in loamy soil which, compared to the loamy-sand soil, has higher nutrient availability and a less acid pH that favors nutrient uptake by plants. Furthermore, it has higher clay content which promote nutrient adsorption and water retention, but reduce drainage and porosity (Siebe et al., 1996; Weil and Brady, 2017). Thus, the differences in vigor and survival between soil types observed for *D. ambigens* could be likely explained by soil texture rather than by nutrient availability. However, the effect of soil texture on seedling performance can be also determined by the variation on precipitation. Although precipitation decreases at low altitude, the higher clay content and finer texture in the soils at the LE site, in addition to the lower slope, makes them prone to waterlogging. Flooding can reduce seedling growth rates and affect nutrient absorption and combined with the strong light limitation and the attack of natural enemies, it can diminish seedling vigor (Chapin, 1991). Such excess of water occurred in the LE experimental plots in the winter during the rainy season and could explain the lower seedling vigor in loamy soils.

On the other hand, loamy soil could be more favorable than the well-drained loamy-sand soils under hydric stress during the dry season. Thus, despite we did not test it independently, we do not rule out that soils could explain the observed differences in vigor and survival on the seedlings of *D. salicifolia* between experimental sites, and future studies on this are encouraged. On the other hand, in line with previous studies (Foster, 1986; Baraloto et al., 2005), our results suggest that the effects of soil variation on seedling survival and vigor were not as important as those of altitudinal light availability.

We must acknowledge that other uncontrolled environmental factors could have influenced seedling vigor and survival. For instance, mechanical damage due to excessive rain is an important cause of seedling mortality of *D. ambigens* (Cordova Casillas, 1979 and 1985). There was an abrupt reduction of the number of leaves that likely explained the reduction of leaf area of the seedlings of *D. salicifolia* growing at the HE site in the latest censuses; this reduction could be caused by an unusual event at high elevation. The study area suffered intense precipitation because of the entrance of strong “nortes” winds in October 2018 that caused tree fall and the opening of a forest gap close to the HE experimental site, causing great disturbance and branch falling. We do not rule out that the observed reduction of the number of leaves at the HE site could be related to this natural disturbance that has been reported as an important cause of seedling mortality (Cordova Casillas, 1985). Moreover, we observed animal disturbance (digging nearby the experimental plots) that could also contribute to explain the differences in seedling vigor and survival between experimental sites.

Despite seedling mortality was higher in the LE site, herbivore and pathogen attack on seedlings of the two species was higher at the HE site; in addition, natural enemies attack did not reduce survival likelihood in intermediate censuses, suggesting that natural enemies attack was not the main cause of mortality. These results are in line with previous studies that have not found drastic effects of natural enemies’ attack on seedling survival and vigor (Nava and del Amo, 1985; Martínez-Ramos, 1991) and report higher incidences of combined attack of herbivores and pathogens than by each natural enemy alone (García-Guzmán and Benítez-Malvido, 2003; Chávez-Pesqueira and Núñez-Farfán, 2016). This could be explained in part if the damage caused by natural enemies is not large enough to cause immediate significant effects on seedling performance, or if it only has important effects in the long term (García-Guzmán and Benítez-Malvido, 2003). On the other hand, contrary to previous studies, we did not find more herbivory and pathogen attack on seedlings growing in the more shaded sites, nor in the most poorly drained soils (García-Guzmán and Dirzo, 2001; García-Guzmán and Benítez-Malvido, 2003; Chávez-Pesqueira and Núñez-Farfán, 2016). Probably herbivores, which seem to promote pathogen infection (Nava R. et al., 1985; García-Guzmán and Dirzo, 2001), are more abundant at high elevation, or alternatively, plant defenses could be stronger at low elevation, in the most unfavorable environment (Coley, 1983; Coley et al., 1985; Chapin, 1991). We are aware that the reduction of vertebrate herbivores in this region (i.e., defaunation), might also affect seedling herbivory and mortality (Dirzo et al., 2020). However, further research is needed to understand the effects and costs of anti-herbivore defenses on seedling vigor and survival in this context.

The adaptative value of seed size

Contrary to our expectations, although seed size directly influenced seedling vigor of *D. ambigens*, it did not significantly affect mortality hazard along the experiment and was adaptive only at the beginning of the experiment in the well-drained loamy sand soil at the LE site. In contrast, seed size affected seedling survival of *D. salicifolia* only after the latest stages of the experiment, when cotyledons were already detached from the seedlings. This apparent divergence between species was very likely consequence of a strong environmental selection acting simultaneously on the seedlings of both species, which faced it at different ontogenetic stages, as experiments of each species were not established synchronically. While the seedlings of *D. salicifolia* grew in periods with few severe and abnormal droughts, the seedlings of *D. ambigens* suffered more water stress (CONAGUA, 2022), as the drought occurred during several months until the end of the experiment of *D. ambigens*.

The sowing season of *D. ambigens* (October 2018) was carried out after a severe drought and coincided with the penultimate census of *D. salicifolia,* when the study area suffered intense flooding and tree falling because of the entrance of strong "nortes" winds. Such disturbance likely increased seedling mortality of *D. salicifolia*, especially in less vigorous seedlings originated from small seeds, and could explain the high adaptive value of large seeds during the mentioned period (Table 3). Furthermore, the first census of *D. ambigens* coincided whit the last of *D. salicifolia* (June 2019), when the study region suffered severe drought that continued and even worsened during the year (CONAGUA, 2022). Such a drastic water stress combined with the light stress at low elevation likely explains the increase of seedling mortality, and the positive selection acting on seedlings derived from large seeds in this period, and in the case of *D. ambigens*, it also explains the lower survival of small-seeded seedlings in the soils with less water retention capacity (Table 3). These results are in line with previous studies pointing the adaptive value of seed size in the seedlings of tropical rainforest tree species, and the critical role of seed nutritional reserves for seedling growth and survival under several environmental stresses. Genetic variance evidenced the evolutionary potential of seed size that was expressed under the most stressful environments (Paz and Martínez-Ramos, 2003; Chávez-Pesqueira and Núñez-Farfán, 2016), with larger seeds increasing seedling survival under simultaneous water and light stress through its effect increasing seedling vigor. Nutrient uptake under light stress can be reduced and more dependent on plant demand than on soil nutrient availability (Chapin, 1991).

The support provided by maternal nutritional reserves decreases over time and can be determined by several factors and tradeoffs acting on seed size (Foster, 1986; Westoby et al., 1992, 1996). Cotyledon reserves promote seedling growth during the first months of development until depleted, promoting increasing stem elongation followed by leaf production (Barajas-Guzmán and Álvarez-Sánchez, 2004); large seeds are thus advantageous during early recruitment. However, seed size not only impacts seedling vigor and survival, it can also determine animal interactions like seed removal and predation (Janzen, 1971; Foster, 1986; Geritz, 1998; Paz et al., 1999; Dirzo et al., 2007; Dylewski et al., 2020). Large seeds can be more attractive to predators which, when do not kill the embryo, can dramatically reduce the amount of nutritional reserves available for the seedlings to grow (Janzen, 1969; Foster, 1986). On the other hand, the likelihood of lethal seed predation (i.e., with embryo damage) is lower in large than in small seeds (Dalling et al., 1997; Mack, 1998; Sousa et al., 2003; Bonal et al., 2007), and is more likely in seeds of *D. salicifolia* than in seeds of *D. ambigens* (Rodríguez-Sánchez et al., in preparation). Interestingly, non-lethal seed damage is known to accelerate seed germination of *D. ambigens* by promoting seed imbibition (Sánchez-Garduño, 1995; Vallejo-Marín et al., 2006).

Perspectives on seedling recruitment and species ecology

We found similar patterns of seedling vigor and survival between *D. ambigens* and *D. salicifolia*; however, early recruitment might differ because of the differences in the ecology, life cycles and life history traits between species. Large-seeded seedlings typically have a slow growth rate and a conservative strategy with well defended structures and high reserve allocation to storage (Coley et al., 1985; Chapin, 1991; Paz and Martínez-Ramos, 2003). *Damburneya ambigens* is characterized by slow seedling growth rates in the dense seedling carpets beneath the crown of maternal trees, that increase with the increment of light availability after the opening of forest gaps in mature tropical rainforest (Gómez-Pompa and del Amo-Rodríguez, 1985; Martínez-Ramos, 1991). These trees can take decades or even more than 100 years to reach their taller sizes (Ricker et al., 2017); furthermore, adult trees show a conservative leaf functional syndrome (Giraldo-Kalil et al., 2022), suggesting that slow growth rates and conservative phenotypic syndromes are maintained throughout the ontogeny.

The seeds of *D. ambigens* were 10 times larger than those of *D. salicifolia*, a common understory tree species in mature well-preserved forests, but also in disturbed areas and secondary vegetation in early and advanced successional stages (Lorea-Hernández, 2002; Arroyo-Rodríguez et al., 2009; Carreón-Santos and Valdez-Hernández, 2014; García-Licona et al., 2014). These ecological and phenotypic differences suggest higher growth rates in *D. salicifolia*, and very likely, shorter life cycles. Some studies suggest that the trees of *D. salicifolia* are more plastic and tolerant to changing environments than those of other species of *Damburneya* (Rohwer and Kubitzki, 1993; Giraldo-Kalil et al., in review). Although we observed phenotypic plasticity on the seedlings of *D. ambigens* and *D. salicifolia*, further tests are needed to determine whether plasticity and its effect on seedling vigor and survival differ between species. The understanding of the environmental and intrinsic factors affecting seedling establishment and growth would contribute to future restoration and natural regeneration studies and to assess species response to environmental changes.

Concluding remarks

This research suggests that seedling vigor and survival of *D. ambigens* and *D. salicifolia* were determined by environmental variation and seedling intrinsic factors. Elevation can affect the survival and performance of the seedlings *D. ambigens* and *D. salicifolia*, mainly through its local effect on light while soils could affect seedling vigor by constraining water use and availability under varying precipitation. On the other hand, the attack of natural enemies did not have critical effects on seedling survival. Seed size determined seedling survival by affecting vigor but natural selection towards large-seeded seedlings only occurred in the most stressful environments at low elevations under simultaneous light and water stress. We have not found direct evidence of regeneration niche divergence between both species nor a differential response to the extrinsic environmental factors affecting early seedling establishment. However, differences in seed size suggest potential differences in seedling recruitment that deserve further research.

Data availability statement

The data will be available at figshare.com once the manuscript is accepted for publication. The R scripts employed for statistical analysis and figures will be available at: https://github.com/ljgiraldok/Plantulas_Damburneya once the manuscript is accepted for publication.

Acknowledgements

The authors acknowledge Rosamond Coates Lutes and the staff of the Estación de Biología tropical Los Tuxtlas (IB-UNAM) for logistic support and Santiago Sinaca-Colín, Erli Velasco Sinaca for help, guidance, and assistance during all the stages of field work. To Ernesto Samacá, Edna Rodríguez Sánchez, Ana Lucía Castrejón, Fernando López, Iván De la Cruz, Valeria Flores, Estefanía Villanueva, Macarena Marín Rodulfo, Eladio Velasco Sinaca, Minerva Soto and Aura Ollín for field assistance during seedling monitoring. To Andrea Alfaro, Iván Camargo, and Lourdes Martínez for help during fruit and seed processing. To Rosalinda Tapia, for logistic support at the Instituto de Ecología, UNAM. To Horacio Paz and Miguel Martínez Ramos for advice during project planning and data analysis. LJGK thanks to CONACYT for the grant provided for her Ph. D. studies (No. 463686), and to the Programa de Posgrado en Ciencias Biológicas, at the Universidad

Nacional Autónoma de México for its support during her postgraduate studies. This research was funded by SEP-CONACYT grant (No. 284692) to JNF.

Author contribution

L.J.G.K and J.N.F designed the research project, conducted and coordinated the fieldwork, and recorded the data. L.J.G.K. wrote the first draft, compiled, processed, and analyzed the data. Both authors contributed with ideas, data interpretation, discussion, and manuscript revision. J.N.F. secured project funding.

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Tables

Table 1. Soil physicochemical properties in experimental sites at low and high elevation in the tropical rainforest of Los Tuxtlas Biosphere Reserve.

Elevation	Low (150 m)		High (1100 m)	
Depth (cm)	0-10	10-20	0-10	10-20
Texture	sandy loam	loam	Loamy sand	Loamy sand
Clay (%)	14	24	8	8
Silt (%)	22	36	10	12
Sand (%)	64	40	82	80
pH (H2O)	6.05	6.18	5.35	5.36
Organic C (mg/g)	23.01	20.44	57.84	37.79
Total N (mg/g)	2.38	1.47	2.97	2.87
C:N ratio	9.7	13.9	19.5	13.1
NO3 µg/g	18.6	15.3	10.1	6.0
NH4 µg/g	14.8	27.6	5.5	2.2
NO3:NH4 ratio	1.3	0.6	1.8	2.8
Total P µg/g	384	331	493	483
Available-P µg/g	12.0	12.6	9.9	9.4

Table 2. Genetic variation of seed mass and traits of the seedlings of *Damburneya ambigens* and *Damburneya salicifolia* growing in contrasting soils and elevation in the Los Tutlas Biosphere Reserve.

Species	Trait	AIC	BIC	logLik	deviance	R^2	X^2	*P*
D. ambigens	Seed mass	63.926	68.228	-28.963	57.926	0.76	13.269	**0.0003**
	Height	69.602	73.904	-31.801	63.602	0.732	9.1895	**0.0024**
	Leaf number	28.350	32.652	-11.175	22.35	0.839	8.3498	**0.0039**
	Leaf area	149.21	153.51	-71.605	143.21	0.62	6.4945	**0.01082**
D. salicifolia	Seed mass	67.028	74.174	-30.514	61.028	0.824	79.477	**<0.0001**
	Height	338.51	345.65	-166.25	332.51	0.707	50.917	**<0.0001**
	Leaf number	21.636	28.782	-7.8178	15.636	0.495	22.789	**<0.0001**
	Leaf area	659.03	666.18	-326.52	653.03	0.656	42.238	**<0.0001**

Notes: The table shows the results of a likelihood test between a model including the maternal tree (half- sib family) as a random effect, and a null model without this term. The analyses are based on breeding values. Significant values ($P < 0.05$) are highlighted in bold type.

Table 3. Adaptive value of seed size of seedlings of *Damburneya ambigens* and *Dambureya salicifolia* in relation to survival in contrasting soils and elevations in the Los Tuxtlas Biosphere Reserve according to a logistic regression analysis.

	D. ambigens					*D. salicifolia*			
Days	Statistic	H – Lm	H – Ls	L – Lm	L - Ls	Days	Statistic	H (Ls)	L (Lm)
65	*β*	0.16	-0.057	0.483	0.505	20	*β*	-0.248	-0.084
	se	0.366	0.334	0.296	0.199		se	0.434	0.355
	z	0.438	-0.172	1.631	2.546		*z*	-0.571	-0.236
	P	0.662	0.864	0.103	**0.011**		P	0.568	0.814
160	*β*	-0.259	0.163	0.019	0.185	277	*β*	0.15	-0.022
	se	0.265	0.279	0.134	0.173		se	0.151	0.185
	z	-0.979	0.583	0.14	1.066		*z*	0.994	-0.119
	P	0.328	0.56	0.889	0.286		P	0.32	0.906
231	*β*	-0.227	0.004	-0.12	0.069	473	*β*	0.16	0.231
	se	0.233	0.253	0.138	0.186		se	0.145	0.169
	z	-0.974	0.017	-0.867	0.372		*z*	1.103	1.366
	P	0.33	0.987	0.386	0.71		P	0.27	0.172
296	*β*	-0.148	-0.081	-0.174	0.267	639	*β*	0.215	0.409
	se	0.218	0.247	0.148	0.205		se	0.145	0.164
	z	-0.679	-0.329	-1.17	1.305		*z*	1.477	2.497
	P	0.497	0.742	0.242	0.192		P	0.14	**0.013**
761	*β*	0.114	0.103	-0.294	-0.015	853	*β*	0.38	0.374
	se	0.167	0.194	0.225	0.634		se	0.152	0.157
	z	0.68	0.531	-1.307	-0.024		*z*	2.503	2.386
	P	0.497	0.595	0.191	0.981		P	**0.012**	**0.017**

Note: The top rows indicate the day when the census occurred. The elevations are H: high (1100 m) and L: low (150 m). Th soils are Ls: Loamy-sand and Lm: Loam. The seedlings of *D. salicifolia* only grew in local soil, indicated in parenthesis. Selection gradient is indicated with *β*, and the error with se. Significance of predictor variables was assessed with a Wald *z* test, and significant P values are highlighted in bold type.

Table 4. Repeated measures MANOVA of seedling trait of *Damburneya ambigens* and *Damburneya salicifolia* growing in contrasting elevations and soils in the Los Tuxtlas Biosphere Reserve.

		Leaf area				Number of leaves				Height			
Species	Effect	DFn	DFd	F	P	DFn	DFd	F	P	DFn	DFd	F	P
D. ambigens	Seed mass	1	537	165.752	**<0.0001**	1	436	50.627	**<0.0001**	1	436	133.745	**<0.0001**
	Elevation	1	537	0.241	0.6230	1	436	17.98	**<0.0001**	1	436	7.762	**0.0060**
	Soil	1	537	1.592	0.2080	1	436	5.072	**0.0250**	1	436	2.614	0.1070
	Days	1	537	9.491	**0.0020**	1.06	463.67	2.93	0.0850	1.15	502.22	0.25	0.6510
	Elevation: Soil	1	537	0.259	0.6110	1	436	0.029	0.8640	1	436	0.024	0.8770
	Seed mass: Days	1	537	0.052	0.8200	1.06	463.67	43.289	**<0.0001**	1.15	502.22	43.771	**<0.0001**
	Elevation: Days	1	537	33.999	**<0.0001**	1.06	463.67	26.822	**<0.0001**	1.15	502.22	18.162	**<0.0001**
	Soil: Days	1	537	0.201	0.6540	1.06	463.67	3.378	0.0640	1.15	502.22	2.311	0.1250
	Elevation: Soil: Days	1	537	2.606	0.1070	1.06	463.67	0.362	0.5610	1.15	502.22	1.145	0.2930
D. salicifolia	Seed mass	1	209	58.905	**<0.0001**	1	186	15.213	**0.0001**	1	180	28.31	**<0.0001**
	Elevation	1	209	0.122	0.7270	1	186	6.138	**0.0140**	1	180	11.265	**0.0010**
	Days	1.9	397.78	0.071	0.9240	2.47	458.68	2.293	0.0900	3.6	647.3	3.623	**0.0080**
	Seed mass: Days	1.9	397.78	6.152	**0.0030**	2.47	458.68	4.684	**0.0060**	3.6	647.3	1.73	0.1490
	Elevation: Days	1.9	397.78	19.965	**<0.0001**	2.47	458.68	8.882	**<0.0001**	3.6	647.3	17.405	**<0.0001**

Notes: DFn and DFd are the degrees of freedom in the numerator and in the denominator, respectively. Significant values (P<0.05) are highlighted in bold type.

Table 5. Temporal effects of seed size and seedling traits on survival of seedlings of *Damburneya ambigens* and *Damburneya salicifolia* growing in contrasting soils and elevations in the Los Tuxtlas Biosphere Reserve.

Species	Predictor	Estimate	se	*z*	*P*	Survival from	Model predictors from
D. ambigens	H	-0.445	0.825	-0.54	0.589	5th census (761 days)	3rd census (231 days)
	H and P	-1.562	0.868	-1.8	0.072		
	P	-0.629	0.494	-1.273	0.203		
	Undamaged	0.005	0.455	0.011	0.991		
	Seed mass	-0.067	0.112	-0.6	0.548		
	Leaf area	0.006	0.004	1.361	0.174		
	Height	-0.018	0.028	-0.637	0.524		
	Number of leaves	0.862	0.196	4.406	<**0.001**		
D. salicifolia	H	-1.408	1.573	-0.895	0.371	4th census (473 days)	3rd census (277 days)
	H and P	0.198	0.79	0.251	0.802		
	P	1.052	0.734	1.433	0.152		
	Undamaged	0.231	0.668	0.346	0.729		
	Seed mass	-0.124	2.056	-0.06	0.952		
	Leaf area	0.027	0.056	0.484	0.628		
	Height	0.073	0.135	0.543	0.587		
	Number of leaves	1.072	0.514	2.083	**0.037**		
D. salicifolia	H	1.165	1.692	0.689	0.491	5th census (639 days)	4th census (473 days)
	H and P	-0.101	0.989	-0.103	0.918		
	P	-0.575	0.928	-0.62	0.535		
	Undamaged	-0.451	0.862	-0.523	0.601		
	Seed mass	3.527	2.004	1.76	**0.078**		
	Leaf area	0.066	0.047	1.401	0.161		
	Height	-0.235	0.145	-1.622	0.105		
	Number of leaves	0.333	0.34	0.981	0.327		

Notes: Natural enemy attack is abbreviated as: H= Herbivore attack, P= Pathogen attack, H and P= herbivore and pathogen attack. Undamaged refers to the plant without natural enemy attack. Significance of predictor variables was assessed with a Wald *z* test, and significant P values are highlighted in bold type. Goodness of fit is reported in Table S7.

Figures

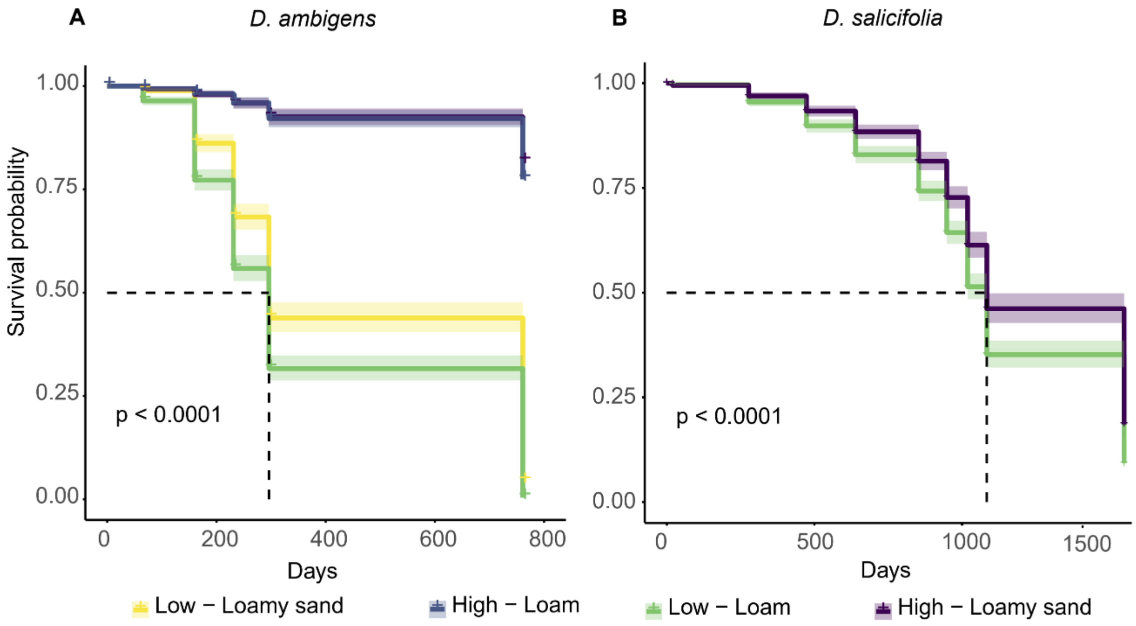

Figure 1. Seedling survival in high and low elevations in the Los Tuxtlas Biosphere Reserve. A) *Damburneya ambigens* B) *Damburneya salicifolia* (sowed only in local soils). Soil types are shown with lines of different colors according to elevation; low elevation is 150 m and high elevation is 1100 m. Standard error is shown in light colors around the lines.

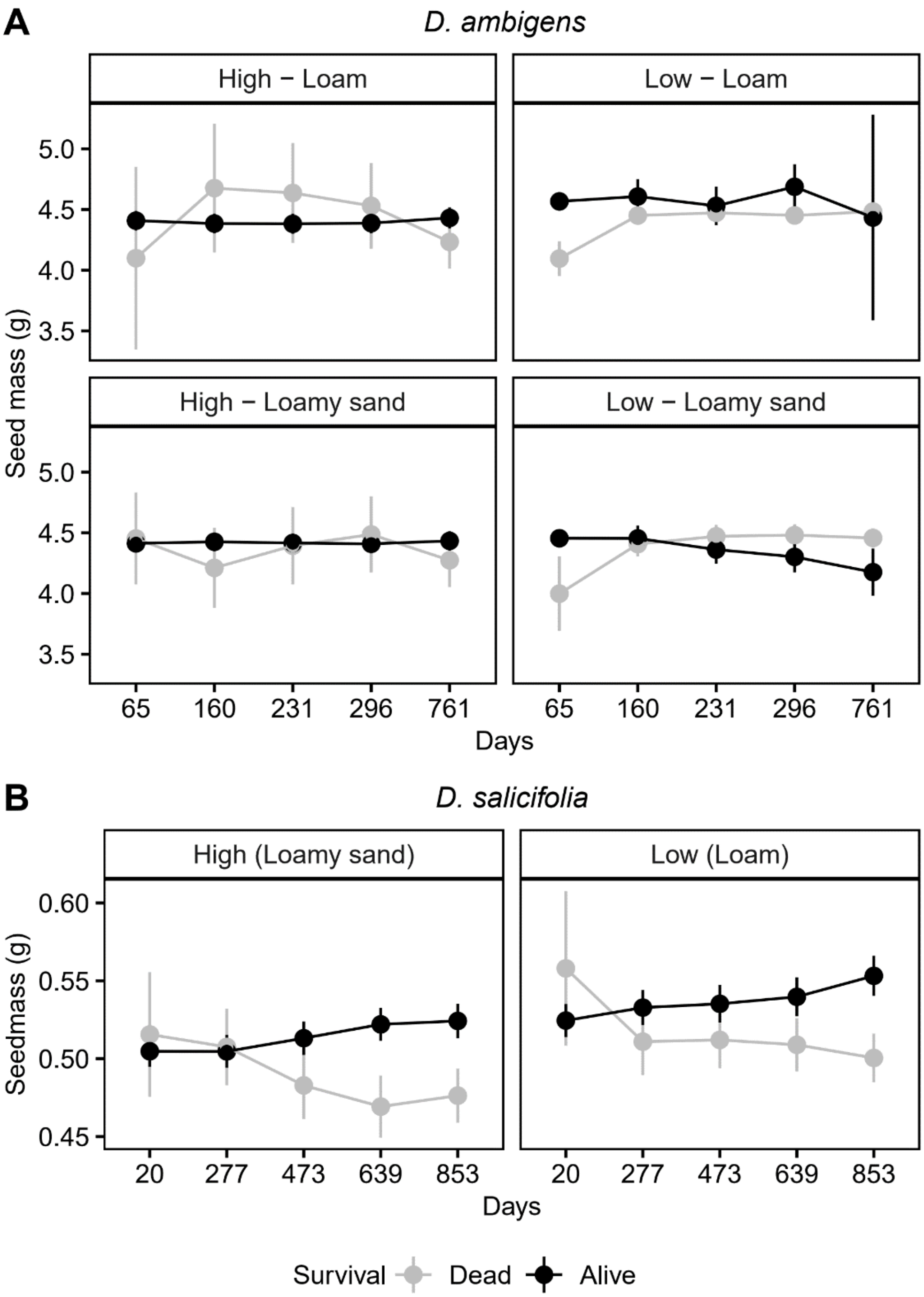

Figure 2. Seed mass (± SE) of accumulated dead vs. alive seedlings per census period for A) *Damburneya ambigens* and B) *Damburneya salicifolia* growing in local and foreign soils at high (1100 m) and low (150 m) elevations in the Los Tuxtlas Biosphere Reserve. Seedlings of *D. salicifolia* were planted only in local soils, indicated in parentheses.

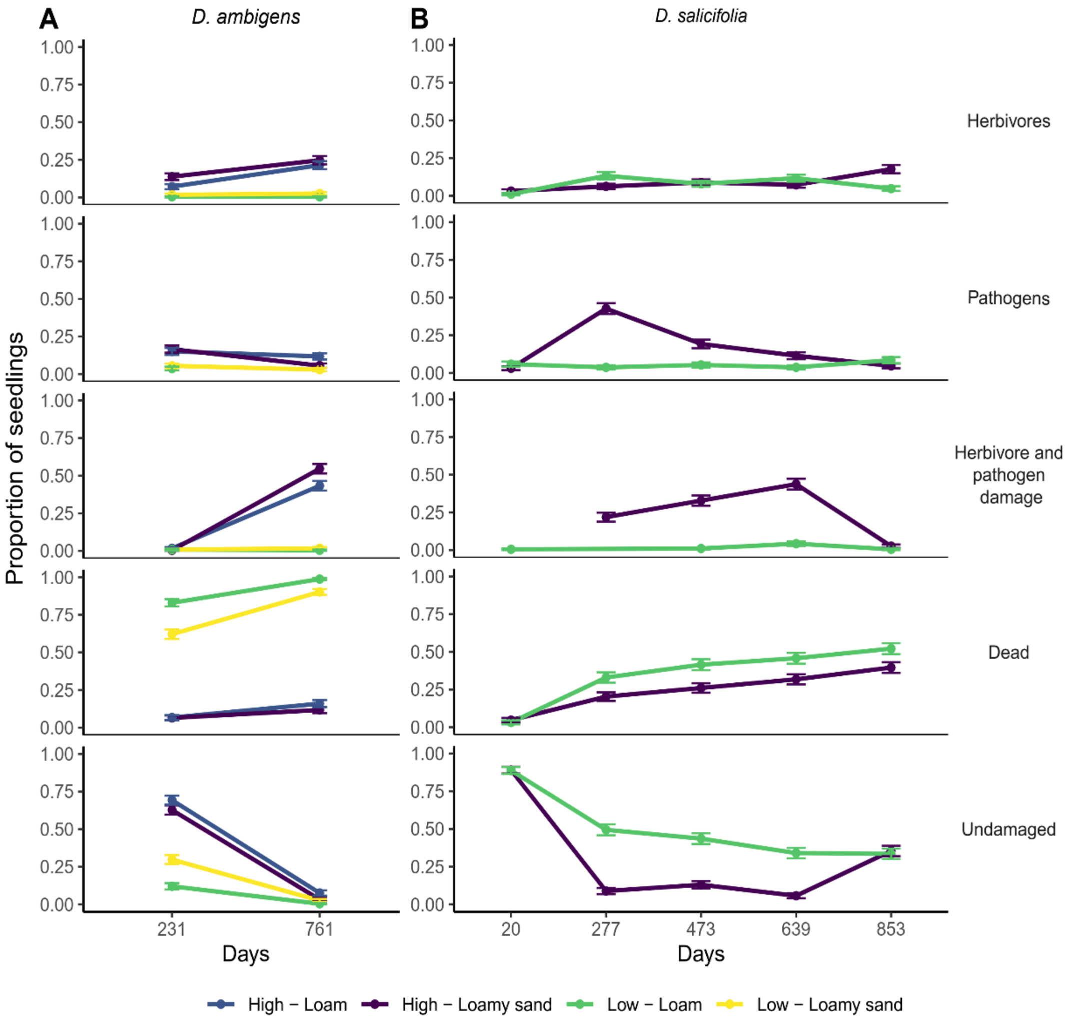

Figure 3. Proportion of dead and surviving seedlings with and without herbivore or pathogen damage, according to census day, elevation, and soil type in the Los Tuxtlas Biosphere Reserve. Colors represent different species (A). *Damburneya ambigens* in Loam and (B) Loamy-sand soils, and (C) *Damburneya salicifolia*. Elevation is presented as H: High and L: Low. Except by the non-significant comparisons indicated as "ns", all proportions differed significantly between elevations according to two proportional z-tests (α = 0.05). Standard error is indicated at the top of the bars.

Supplementary material

Table S 1. Details on seeds and maternal trees of two species of *Damburneya* from the tropical rainforest in Los Tuxtlas Biosfere Reserve.

Species	***D. ambigens***		***D. salicifolia***
Blocks / altitude/ soil	3	3	3
Blocks per site	6	6	3
Mean seedling number /family /block	4	4	8
Experiment duration (days since transplant)	761	761	853
Number of censuses	5	5	6
Maternal trees (families)	10	10	16
Total planted seeds	1907	2719	2623
Total seedlings	1162	1129	667
Germination (%)	60,9	41,5	25,4
Viable predated seeds planted (%)	55,6	10,1	7,9
Trasplanted seedlings	484	477	379
Treatments	Altitude + Soil	Altitude + Soil	Altitude
Population	EBT Tuxtlas	Ejido Benito Juarez	Ejido Zapata
Latitude	18,586712	18,404641	18,448984
Longitude	-95,077173	-94,997894	-95,049031
Altitude (m)	187	624	405
Collection date	1-Sep-2018	1-Oct-2018	1-Oct-2016
Date of transplant (day 0)	08 April-2019	08 April-2019	9-Feb-2017
Date of the last census	8-May-2021	8-May-2021	12-June-2019

Note: The decimal coordinates provided are representative of the sampling locality and are provided in WGS84 datum.

Table S 2. Summary of data recording according to census for *Damburneya ambigens* and *Damburneya salicifolia* in two field experiments in Los Tuxtlas Biosphere Reserve

Species	Census	Day	Survival	Height	Number of leaves	Leaf measurement	Incidence of herbivore and patogen attack
D. ambigens	0	0	✓	✓	✓	✓	✓
	1	65	✓		✓		
	2	160	✓	✓	✓		
	3	231	✓	✓	✓	✓	✓
	4	296	✓	✓			
	5	761	✓	✓	✓		✓
D. salicifolia	0	0	✓	✓	✓	✓	✓
	1	20	✓				✓
	2	198	✓	✓	✓		✓
	3	277	✓	✓	✓	✓	✓
	4	473	✓	✓	✓	✓	✓
	5	639	✓	✓	✓	✓	✓
	6	853	✓	✓	✓		✓

Table S 3. Microlimatic conditions in the two experimental sites with contrasting elevations in Los Tuxtlas Biosphere Reserve during the dry season.

Elevation	Part of the day	n	Environmental variable	mean	sd	median	min	max	range	se	CV
High	Morning	2446	Temperature (C°)	18.58	2.61	18.28	9.82	28.31	18.49	0.05	14.06
			Relative humidity (%)	33.73	14.27	26.9	23.4	89.2	65.8	0.29	42.32
			Dew Point (C°)	2.23	4.07	1.04	-7.26	17.97	25.23	0.08	183.06
			Absolute humidity (gm/m^3)	5.27	1.95	4.6	2.3	15.2	12.9	0.04	36.93
			Luminance (lux)	112.95	683.01	21.53	10.76	8331.34	8320.57	13.81	604.69
High	Night	2054	Temperature (C°)	16.97	2.25	16.76	9.42	30.31	20.89	0.05	13.25
			Relative humidity (%)	35.3	13.85	29.9	23.4	89.2	65.8	0.31	39.23
			Dew Point (C°)	1.65	4.25	1.27	-9.63	15.35	24.98	0.09	257.51
			Absolute humidity (gm/m^3)	5.05	1.82	4.5	2.3	13	10.7	0.04	36.1
			Luminance (lux)	66.63	465	21.53	10.76	8223.7	8212.93	10.26	697.9
Low	Morning	1784	Temperature (C°)	24.27	2.29	24.01	18.66	29.9	11.24	0.05	9.44
			Relative humidity (%)	34.51	14.31	26.8	23.4	80.7	57.3	0.34	41.48
			Dew Point (C°)	6.66	4.4	5.33	-2.65	20.32	22.97	0.1	66.06
			Absolute humidity (gm/m^3)	7.44	2.49	6.5	3.7	17.4	13.7	0.06	33.43
			Luminance (lux)	49.67	394.65	10.76	10.76	5941.73	5930.96	9.34	794.56
Low	Night	1243	Temperature (C°)	22.68	1.6	22.86	18.66	26.34	7.68	0.05	7.07
			Relative humidity (%)	37.2	14.43	32	23.4	80.7	57.3	0.41	38.79
			Dew Point (C°)	6.41	4.7	5.47	-2.65	17.49	20.14	0.13	73.22
			Absolute humidity (gm/m^3)	7.39	2.49	6.6	3.7	14.7	11	0.07	33.74
			Luminance (lux)	10.76	0	10.76	10.76	10.76	0	0	0

Note: Microclimatic data were recorded from January to May 2018 using HOBO (H08-04) data loggers. The measurements performed between 06:00:00 and 18:00:00 were categorized as “Morning”, while the measurements performed between 18:00:01 and 05:59:59 were categorized as “Night”

.Table S 4. Cox proportional hazard regressions of the effects of genetic variance, seed mass, elevation, soil and elevation on the survival of seedlings of *Damburneya ambigens* and *Damburneya salicifolia* in the Los Tuxtlas Biosphere Reserve.

Species	Effect	coef	exp (coef)	se (coef)	z	P
D. ambigens	Seed mass	0.004	1.004	0.027	0.161	0.872
	Elevation (High)	-2.514	0.081	0.117	-21.451	**<0.0001**
	Soil (Loam)	0.332	1.394	0.052	6.428	**<0.0001**
	Maternal tree 15	-0.320	0.726	0.166	-1.929	**0.054**
	Maternal tree 102	0.476	1.609	0.148	3.353	**0.001**
	Elevation (High): Soil (Loam)	-0.190	0.827	0.159	-1.189	0.234
D. salicifolia	Seed mass	-0.942	0.390	0.176	-5.43	**<0.0001**
	Elevation (high)	-0.498	0.608	0.05	-9.905	**<0.0001**
	Maternal tree 504	-0.701	0.496	0.115	-6.117	**<0.0001**
	Maternal tree 505	-0.303	0.738	0.123	-2.455	**0.014**
	Maternal tree 506	-0.645	0.525	0.250	-2.581	**0.010**
	Maternal tree 507	-0.464	0.628	0.146	-3.184	**0.001**
	Maternal tree 508	-0.255	0.775	0.131	-1.939	**0.052**

Note: Only those maternal trees (half-sib families) with significant effect on survival are shown. The sign of correlation coefficients indicates whether the effect increases (positive) or decreases (negative) the risk of death; hazard ratios indicate the proportional magnitude of the effects. Column names are abbreviated as follows. Regression coefficients: coef, standard error of regression coefficients: se(coef), hazard ratios: exp (coef), Wald statistic: z. Significant values ($P < 0.05$) are highlighted in bold type.

Table S 5. Effect of elevation, soil type, and seed mass on seedling trait variation of *Damburneya ambigens* and *Damburneya salicifolia* by the third census (231 and 277 days respectively) in the Los Tuxtlas Biosphere Reserve according to linear mixed models.

Species	Trait	Fixed effect	Estimate	se	df	*t*	*P*	R^2
D. ambigens	Leaf area	Intercept	0,011	0,091	27,778	0,126	0,9009	0,293
		Altitude (Low)	-0,22	0,092	526,524	-2,384	**0,0175**	
		Soil (Loamy)	-0,054	0,073	524,66	-0,731	0,4653	
		Seed mass	0,419	0,043	477,878	9,804	**<0.0001**	
D. ambigens	Height	Intercept	0,021	0,097	27,927	0,211	0,8342	0,29
		Altitude (Low)	-0,041	0,084	560,952	-0,485	0,6282	
		Soil (Loamy)	-0,162	0,069	559,737	-2,338	**0,0197**	
		Seed mass	0,36	0,041	546,156	8,719	**<0.0001**	
D. ambigens	Number of leaves	Intercept	0,213	0,069	51,842	3,096	**0,00316**	0,124
		Altitude (Low)	-0,689	0,097	567,33	-7,131	**<0.0001**	
		Soil (Loamy)	-0,166	0,079	562,799	-2,106	**0,03561**	
		Seed mass	0,136	0,043	226,681	3,179	**0,0017**	
D. salicifolia	Leaf area	Intercept	-0,109	0,098	19,34	-1,115	0,278	0,31
		Altitude (Low)	0,06	0,103	260,17	0,581	0,561	
		Seed mass	0,489	0,065	85,028	7,55	**<0.0001**	
D. salicifolia	Number of leaves	Intercept	-0,07	0,105	18,307	-0,67	0,51126	0,151
		Altitude (Low)	0,06	0,113	261,697	0,527	0,59841	
		Seed mass	0,288	0,071	73,111	4,089	**0,0001**	
D. salicifolia	Height	Intercept	0,032	0,115	19,723	0,275	0,787	0,201
		Altitude (Low)	-0,167	0,112	259,217	-1,487	0,138	
		Seed mass	0,327	0,073	116,33	4,482	**<0.0001**	

Notes: The models included family as an effect with random intercept, elevation and soil type as fixed effects, and seed mass as a covariate, the degrees of freedom were approximated with the Satterthwaite's method. *R^2* is the conditional coefficient of determination. Significant *P* values (*P* < 0.05) are highlighted in bold type.

Table S 6. Likelihood ratio test of the maternal tree effects of mixed linear models for seedling traits of *Damburneya ambigens* and *Damburneya salicifolia* at Los Tuxtlas Biosphere Reserve growing in contrasting soils and elevations.

Species	Trait	Model effects	npar	logLik	AIC	LRT	df	P
D. ambigens	Leaf area	none	6	-688,71	1389,4			
		Maternal tree	5	-705,93	1421,9	34,438	1	**<0.0001**
D. ambigens	Height	none	6	-719,95	1451,9			
		Maternal tree	5	-755,58	1521,2	71,251	1	**<0.0001**
D. ambigens	Number of leaves	none	6	-782,41	1576,8			
		Maternal tree	5	-784,52	1579	4,2225	1	**0,04**
D. salicifolia	Leaf area	none	5	-331,97	673,93			
		Maternal tree	4	-335	678	6,0689	1	**0,0138**
D. salicifolia	Height	none	5	-356,49	722,98			
		Maternal tree	4	-360,64	729,29	8,3065	1	**0,0039**
D. salicifolia	Number of leaves	none	5	-360,79	731,58			
		Maternal tree	4	-362,94	733,87	4,2908	1	**0,0383**

Notes: The models included maternal tree (half-sib family) as an effect with random intercept, elevation and soil type as fixed effects, and seed mass as a covariate, with 1 degree of freedom. Significant P values of X^2 tests are highlighted in bold type and indicate that models including the effect of maternal tree are significantly better than the models excluding it.

Table S 7. Goodness of fit of generalized linear models of the temporal effects of seed size and vigor traits on seedling survival of *Damburneya ambigens* and *Damburneya salicifolia* growing in contrasting elevations and soils in the Los Tuxtlas Biosphere Reserve

Species	null deviance	df.null	logLik	AIC	BIC	deviance	df residuals	Number of observations	Survival from	Model predictors from
D. ambigens	538.532	541	-238.54	493.081	527.443	477.081	534	542	5th census	3rd census
D. salicifolia	161.038	264	-71.349	158.697	187.335	142.697	257	265	4th census	3rd census
	132.665	238	-54.659	125.319	153.13	109.319	231	239	5th census	4th census

Notes: The models were obtained using predictor data from 3rd and 4th census to predict seedling survival of censuses 4th and 5th with binary logistic regressions, including seed size, seedling heigh, total leaf area and number of leaves as covariates. Model predictions are in Table 5.

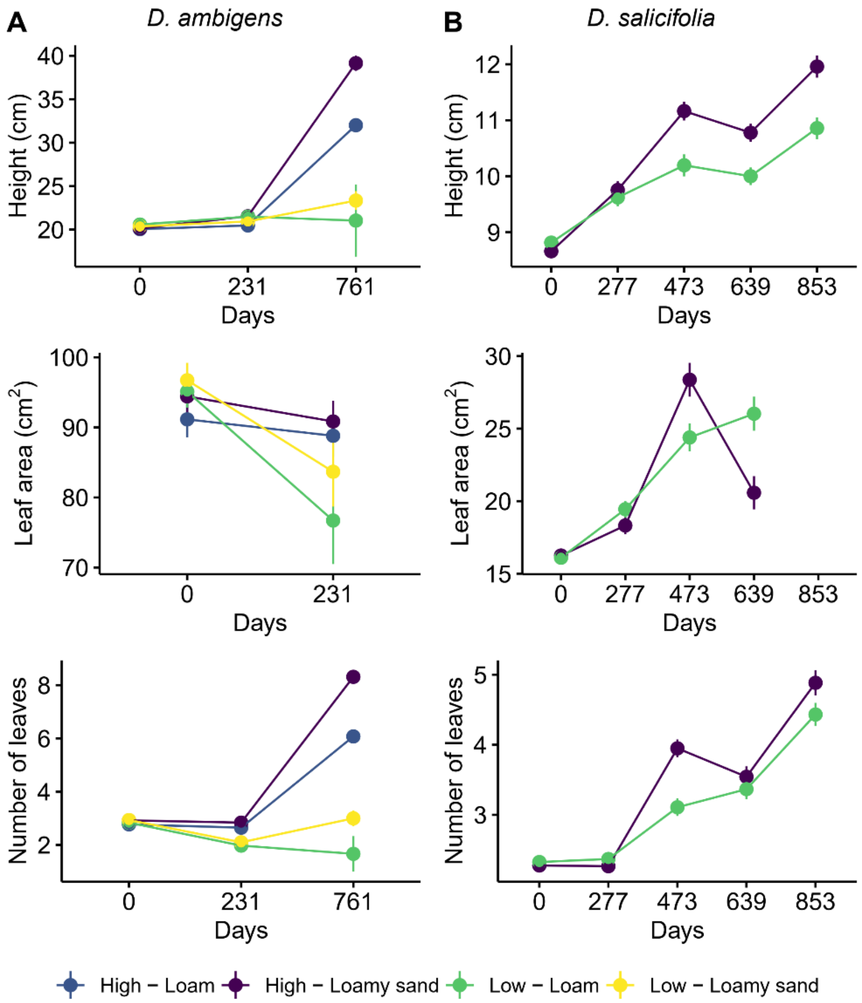

Figure S 1. Variation of leaf traits of the seedling of A) *Damburneya ambigens* (left column) and B) *Damburneya salicifolia* (right column) over time according to elevation and soil type in the Los Tuxtlas Biosphere Reserve. Elevation is noted as High (1100 m) and Low (150 m). The seedlings of D. salicifolia grew on local soil. Soil types are indicated in colors, vertical bars indicate standard error.

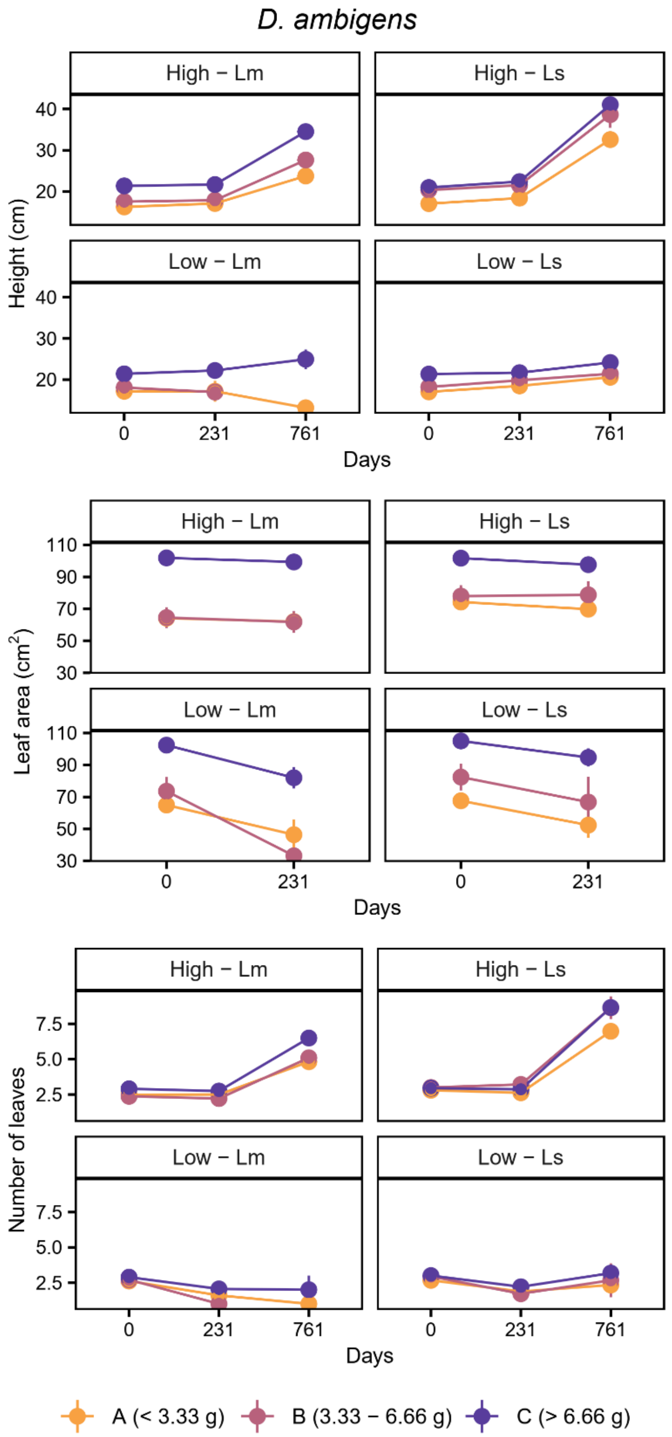

Figure S 2. Variation of leaf traits of the seedling of *Damburneya ambigens* over time according to seed mass in divergent elevations and soil types in the Los Tuxtlas Biosphere Reserve. Seed mass categories are shown in colors. Elevation is noted as High (1100 m) and Low (150 m). Soil types are Loamy sand (Ls) and Loam (Lm).

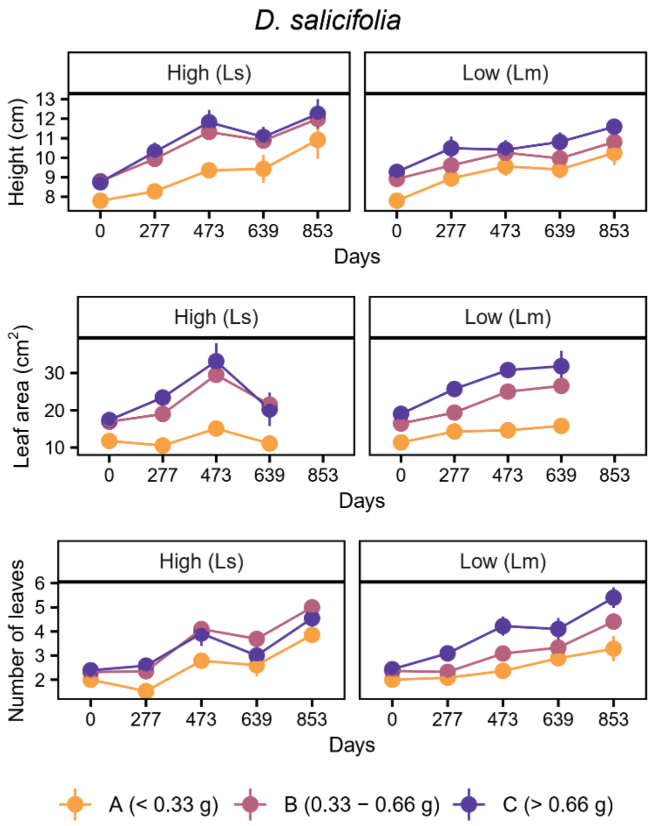

Figure S 3 Variation of leaf traits of the seedling of *Damburneya salicifolia* over the time according to seed mass in divergent elevations and soil types in the Los Tuxtlas Biosphere Reserve. Seed mass categories are shown in colors. Elevation is noted as High (1100 m) and Low (150 m). Soil types are Loamy sand (Ls) and Loam (Lm), and are local from each elevation.

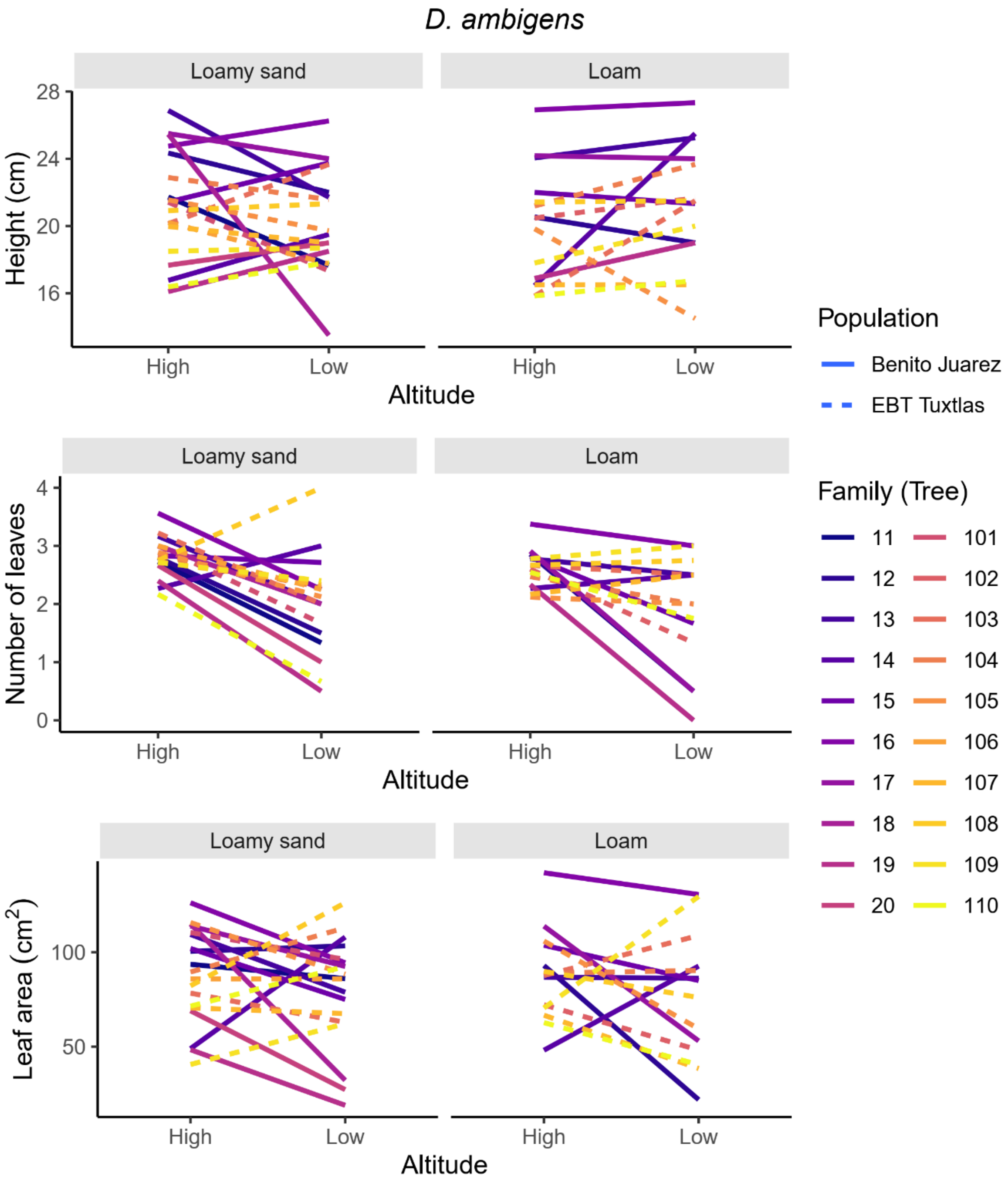

Figure S 4. Reaction norms of vigor traits of *Damburneya ambigens'* seedlings growing in contrasting soils and elevations in the Los Tuxtlas Biosphere Reserve. Color indicates family and line type indicates population.

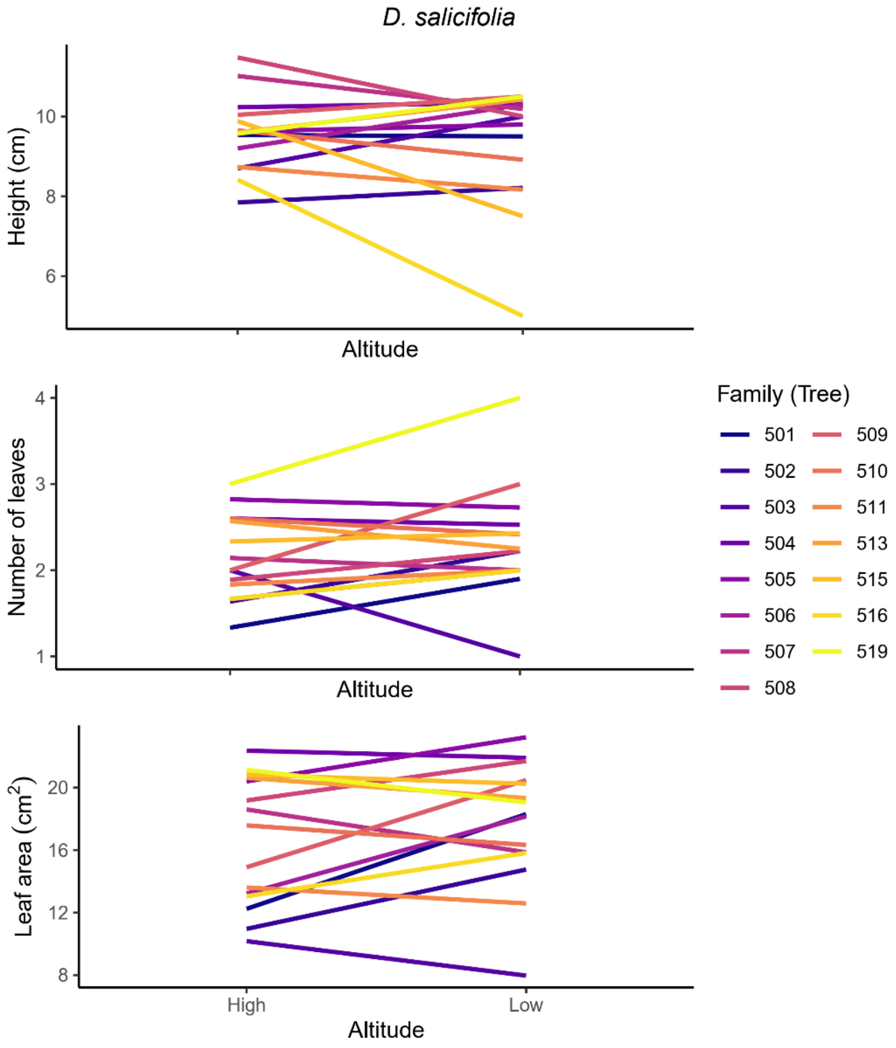

Figure S 5. Reaction norms of vigor traits of *Damburneya salicifolia's* seedlings growing in contrasting soils and elevations in the Los Tuxtlas Biosphere Reserve. Color indicates family and line type indicates population.

Discusión general y conclusiones

Panorama general

La presente investigación abordó la diferenciación ecológica entre especies cercanamente emparentadas de *Damburneya* que coocurren en simpatría en la Reserva de la Biosfera de Los Tuxtlas analizando para ello el nicho Grinnelliano, la variación funcional foliar a nivel local, y el nicho de regeneración. Los resultados sugieren que la elevación y la variación edáfica pueden afectar, diferencialmente a *D. ambigens, D. colorata, D. gentlei* y *D. salicifolia*. Sin embargo, estos efectos dependen tanto de la escala espacial y las condiciones ambientales locales, como de la etapa del ciclo de vida de las plantas.

En el capítulo 1, se evaluaron los efectos del clima y el tipo de suelo sobre la distribución y la idoneidad ambiental de las cuatro especies de *Damburneya* que coocurren en los Tuxtlas, además del solapamiento de nicho Grinelliano mediante modelos de nicho ecológico. Las especies difirieron en sus nichos edáficos, y pueden tolerar mayor variación edáfica que climática. En general, la disponibilidad de agua parece ser una de las limitantes más críticas para la distribución de estas especies. Las zonas idóneas para la distribución de las cuatro especies estudiadas de *Damburneya* son bosques húmedos y cálidos, sin déficit hídrico drástico y variación estacional moderada de la temperatura; no obstante, *D. salicifolia* difiere de sus congéneres por su capacidad de distribuirse en zonas más secas y con suelos más variables (Capítulo 1; Giraldo-Kalil et al, en revisión).

En el capítulo 2, se caracterizó la variación de rasgos funcionales foliares de árboles juveniles y adultos de las especies de *Damburneya* y su relación con la heterogeneidad del suelo a lo largo del gradiente altitudinal, para evaluar si los patrones de variación foliar reflejan diferencias ecológicas entre especies. Las propiedades edáficas difirieron con la elevación y afectaron el contenido de nutrientes foliares. Por otra parte, además de divergir en sus estrategias funcionales foliares según el espectro de economía foliar (i.e., síndromes foliares adquisitivos o adquisitivos, Wright et al., 2004), las especies difirieron localmente en su respuesta a la variación edáfica (Capítulo 2, Giraldo-Kalil et al., 2022). Estos resultados confirman la importancia del suelo y la elevación para la variación fenotípica de las especies de *Damburneya* y sugieren que el suelo puede ser localmente importante para explicar la divergencia ecológica entre especies. No obstante, las diferencias interespecíficas en las estrategias funcionales observadas muy probablemente responden a la acción de estas y otras variables ambientales que influyen simultáneamente, como la herbivoría, la disponibilidad de luz y el clima (Giraldo-Kalil et al., 2022), que varían con la elevación en la zona de estudio (Capítulo 3; Gutiérrez-García y Ricker, 2011).

En el capítulo 3 de esta tesis se investigó si la elevación y el suelo pueden promover diferenciación del nicho de regeneración de *D. ambigens* y *D. salicifolia*, y determinar el valor adaptativo del tamaño de la semilla. Así mismo, se evaluó el efecto de estas variables ambientales y otros factores bióticos como el ataque de herbívoros y patógenos sobre el vigor y la supervivencia de las plántulas. Encontramos que las plántulas de ambas especies sobrevivieron más a mayor elevación, probablemente porque allí la disponibilidad de luz a nivel del suelo en el sotobosque es más alta que en la zona baja. Aunque la incidencia de ataque de enemigos naturales fue mayor en la zona alta, esto no impactó considerablemente la supervivencia de las plántulas. Por otra parte, el tamaño de las semillas difirió drásticamente entre especies; sin embargo, el valor adaptativo de las semillas fue mayor a baja elevación para ambas especies, y en el caso de *D. ambigens*, fue más alta en suelos bien drenados, probablemente por el estrés causado por una fuerte sequía en la zona de estudio (CONAGUA, 2022). Estos resultados sugieren que en etapas tempranas del reclutamiento no hay diferencias interespecíficas en la respuesta a la variación altitudinal y edáfica, y que otras presiones como el estrés hídrico y lumínico pueden ser más críticas en el establecimiento y supervivencia de las plántulas. (Capítulo 3, Giraldo-Kalil y Núñez-Farfán, en prep.).

Diferencias ecológicas entre especies de *Damburneya*

La diferenciación ecológica puede promover la coexistencia de especies (Macarthur y Levins, 1967; Chesson, 2000), y es uno de los principales mecanismos para explicar las diferencias de distribución geográfica y la especiación en el género *Damburneya* (Rohwer y Kubitzki, 1993). Nuestra investigación sugiere que el suelo, y la elevación (y el clima en el caso de *D. salicifolia*) pueden promover respuestas diferenciales en la variación fenotípica de las especies de *Damburneya* e impactar potencialmente la distribución y desempeño de las plantas. Sin embargo, otros factores ecológicos actuando a escala local, como la disponibilidad de luz, la disponibilidad de agua, el tamaño de la semilla o la depredación de semillas (Apéndices 1 y 3) pueden ser también determinantes en las diferencias ecológicas entre especies, dependiendo de su etapa de desarrollo. Probablemente la diferenciación de nicho dentro del género ocurra gracias a varios mecanismos de coexistencia dependientes e independientes de las fluctuaciones ambientales actuando simultáneamente en diferentes escalas espaciales y temporales.

Esta investigación da soporte a varios estudios previos que sugieren que *D. salicifolia* es más plástica y tolerante a cambios ambientales que otras especies del género (Rohwer, 1993b; Rohwer y Kubitzki, 1993; Lorea-Hernández, 2002). Tal afirmación surge de la amplia distribución latitudinal y a lo largo del gradiente de elevación de esta especie (0-2300 msnm), y de su presencia en varios tipos suelos y de bosques (desde bosques de pino-encino hasta bosques perennifolios y bosques subcaducifolios), incluyendo vegetación secundaria (Rohwer, 1993b; Daza-Mendizabal, 1998; Lorea-Hernández, 2002; Arroyo-Rodríguez et al., 2009; García-Licona et al., 2014). La alta idoneidad de hábitat de *D. Salicifolia* en ambientes con amplia variación edáfica e hídrica (Capítulo 2; Giraldo-Kalil et al., en revisión), es coherente con la variación funcional foliar observada localmente (abarcando los síndromes adquisitivo y conservativo) y puede ser ventajosa para responder a múltiples fuentes de estrés ambiental actuando simultáneamente.

Esta investigación sugiere que *D. salicifolia* se distingue de sus congéneres por su alta capacidad de tolerar el estrés debido a la limitación de nutrientes y agua, y una mayor variación hídrica y térmica, lo que potencialmente se explica por una mayor plasticidad en la absorción y uso de agua y nutrientes. La construcción de sus hojas requiere, por ejemplo, una menor inversión de nutrientes (i.e., menos fósforo por unidad de nitrógeno foliar) que la de las otras especies (Capítulo 2, Giraldo-Kalil et al. 2022). La plasticidad en el uso de nutrientes podría ser ventajosa en ambientes con limitación de fósforo como ocurre en la región de Los Tuxtlas y en muchas selvas húmedas tropicales (Vitousek, 1984; Tanner et al., 1998; Tobón Niedfeldt et al., 2011; Turner et al., 2018; Giraldo-Kalil et al., 2022), y podría explicar, en parte, la alta idoneidad de hábitat de esta especie en suelos alcalinos de origen cárstico, dado que el pH afecta, en gran medida, la disponibilidad de nutrientes (Weil y Brady, 2017). Por otro lado, cabría esperar que la expresión del síndrome foliar conservativo en *D. salicifolia* (con relación a las demás especies estudiadas) favorezca su capacidad para distribuirse en bosques con mayor variación en la disponibilidad de agua que las selvas húmedas. Sin embargo, la acción simultánea del estrés hídrico y la baja incidencia de luz pueden serle limitantes durante el reclutamiento, al disminuir notablemente el vigor y la supervivencia de las plántulas (Capitulo 3, Giraldo-Kalil y Núñez-Farfán, en preparación). Aún se requiere mayor investigación respecto a la variación de los rasgos foliares, tanto a lo largo de la ontogenia como en otros tipos de bosques; así mismo, es necesario profundizar en la acción conjunta del estrés hídrico y otras limitantes ambientales.

Por otra parte, la variación foliar y edáfica no necesariamente se relacionan de forma obvia con la distribución de *D. colorata*. Esta especie presentó, a escala local, síndromes funcionales foliares plásticos y muy similares a los observados en *D. salicifolia* (Giraldo-Kalil et al., 2022) (Rohwer, 1993b; Rohwer y Kubitzki, 1993). Sin embargo, *D. colorata* experimenta una variación climática y edáfica mucho más limitada; su distribución en el gradiente latitudinal es más restringida (100-500 msnm) y su abundancia es drásticamente menor, ya que se conocen pocos ejemplares para esta especie. Además, su distribución potencial se restringe a zonas de selva alta perennifolia en el sur de México y el norte de Centroamérica y su nicho climático es similar al de las otras tres especies que también abarcan estas zonas (Giraldo-Kalil *Et al.* en revisión).

Cabe entonces preguntarse qué determina la distribución de esta especie y qué la hace distinta de *D. salicifolia*. La respuesta posiblemente es la historia evolutiva de ambas especies, ya que *D. colorata* probablemente surgió como un ecotipo especializado de *D. salicifolia*, que permaneció geográficamente restringido (Rohwer y Kubitzki, 1993). La variación funcional foliar puede afectar indirectamente la supervivencia, el vigor, o la reproducción (Violle et al., 2007), por ello es difícil saber en qué medida la variación foliar podría impactar en las dinámicas poblacionales, explicar la distribución de esta especie, o evidenciar su historia evolutiva. Probablemente las diferencias de distribución entre ambas especies podrían atribuirse más fácilmente a barreras reproductivas, dadas por diferencias en la fenología floral, que se han reportado para ambas especies en las zonas dónde se encuentran en simpatría (Rohwer y Kubitzki, 1993), o a diferencias en otros rasgos relacionados con la tolerancia fisiológica o la historia de vida.

Por el contrario, a pesar de encontrarse en simpatría en buena parte de sus rangos de distribución y estar más cercanamente emparentadas entre sí que respecto a las otras especies, *D. gentlei* y *D. ambigens* difieren en sus nichos climáticos y edáficos, sugiriendo que no están restringidas de forma similar por el ambiente (Capítulo 1, Giraldo-Kalil et al., en revisión; Trofimov et al., 2019). Lo anterior es coherente con las marcadas diferencias en la variación funcional foliar de ambas especies. Las hojas de *D. gentlei* presentaron un síndrome adquisitivo (respecto a las demás especies estudiadas) con alta inversión de nutrientes en las hojas con menor inversión en biomasa por unidad de área. Este síndrome se caracterizó, además, por una alta concentración de nutrientes respecto a lo observado en las otras especies, sugiriendo que la demanda de nutrientes de *D. gentlei* podría ser mayor (Giraldo-Kalil et al., 2022). En contraste, las hojas de *D. ambigens* presentaron localmente un síndrome conservativo, con mayor concentración de nutrientes en las hojas con mayor biomasa. Este síndrome sugiriere que hay un alto costo de construcción y reemplazo de hojas (Giraldo-Kalil et al., 2022), por ello podría ser ventajoso en el sombreado sotobosque de la selva o ante el ataque de herbívoros (Kitajima, 1994; Valladares y Niinemets, 2008; Poorter, 2009; Westbrook et al., 2011). No es del todo clara la medida en que la variación foliar puede explicar las diferencias de nicho, ni que tanto depende de la historia evolutiva de las especies. Aun así, la variación foliar muy probablemente contribuye al uso diferencial de recursos por parte de ambas especies y a diferencias en la longevidad foliar y en la susceptibilidad de las hojas a daño mecánico o por herbívoros (Capítulo 2, Giraldo-Kalil et al. 2022).

Aun es necesario investigar a fondo otros factores ecológicos que podrían explicar las diferencias ecológicas, y de abundancia y distribución entre *D. ambigens* y *D. gentlei*. Aunque la variación en las estrategias funcionales foliares sugiere que ambas especies son capaces de aprovechar diferencialmente los nutrientes, y se encuentran limitadas de forma distinta por presiones ambientales como la luz o la herbivoría, *D. ambigens* y *D. gentlei* presentan muchas similitudes en sus historias de vida. Los árboles de ambas especies son característicos del dosel superior de la selva alta en la región de Los Tuxtlas (Bongers et al., 1988; Popma et al., 1988) por lo que podrían experimentar un ambiente lumínico similar a lo largo de su ciclo de vida. La floración y fructificación de ambas especies ocurre durante los mismos periodos (Rohwer, 1993b; Ibarra-Manríquez y Sinaca-Colín, 1995), así que probablemente comparten los mismos polinizadores y dispersores. Así mismo, los frutos y semillas son casi idénticos en tamaño y forma, lo que sugiere que podrían dar un aporte similar de nutrientes a las plántulas durante sus primeros estadios, o bien, experimentar presiones selectivas como la depredación de semillas de forma similar. Además, estas especies comparten las principales especies de insectos depredadores de semillas (Apendice 1, Rodríguez-Sánchez et al., 2022). Mientras que *D. ambigens* ha sido ampliamente estudiada en la región de Los Tuxtlas, por ser una de las especies dominantes de la selva, es muy poco lo que se ha documentado sobre *D. gentlei,* que tiene menor abundancia, y está generalmente mucho más restringida a zonas bajas (aunque hay un reporte a 700 m, usualmente se encuentra entre 100 y 300 m, Rohwer, 1993b). Experimentos incluyendo plántulas de ambas especies en diferentes tipos de suelos y condiciones podrían ayudar a esclarecer las diferencias encontradas en este trabajo, y las implicaciones que podrían tener dichas variables ambientales sobre su distribución.

No descartamos que las diferencias en el nicho, la abundancia y distribución entre las especies de *Damburneya* estudiadas puedan relacionarse con diferencias ecológicas en el reclutamiento. Los resultados aquí reportados indican que el tamaño de la semilla, además de determinar el crecimiento de las plántulas (Capítulo 3, Giraldo-Kalil y Núñez-Farfán, en preparación), influye en los efectos potenciales de la depredación de semillas sobre la germinación. Por ejemplo, en semillas de *D. ambigens* y *D. salicifolia*, la probabilidad de que los insectos depredadores dañen los embriones es menor entre más grandes sean las semillas (Apéndice 3). Además, las semillas de *D. ambigens* y las de *D. gentlei,* tienen alrededor de 10 veces más biomasa que las de *D. salicifolia*, cuyo tamaño es similar a las de *D. colorata* (Rohwer 1993b; Giraldo-Kalil, observación personal; Capítulo 3, Giraldo-Kalil y Núñez-Farfán, en preparación). Dado que las especies de este grupo presentan cotiledones de reserva, es de esperar que tales diferencias en el tamaño de las semillas impacten diferencialmente la supervivencia, el desempeño, y las tasas de crecimiento de las plántulas de dichas especies.

Por otra parte, un estudio sugiere que la alta agregación de plántulas de *D. ambigens* bajo la copa de los árboles adultos podría explicarse por la disminución de la diversidad y abundancia de herbívoros grandes y medianos en la región de Los Tuxtlas (Dirzo y Miranda, 1991). Vale la pena investigar si la alta densidad de plántulas y el bajo reclutamiento de juveniles podrían relacionarse también con la disminución de la dispersión de semillas por parte de frugívoros grandes y medianos, o con una baja eficiencia en la dispersión por aves grandes (Rohwer, 1993b), monos (Estrada y Coates-Estrada, 1984) y mamíferos pequeños que también puede depredar las semillas (Rohwer, 1993b). Aún no se sabe si las diferencias en la distribución de estas especies podrían relacionarse con preferencias de los animales dispersores por el tamaño de los frutos y semillas; por ejemplo, a pesar de que el síndrome de dispersión es compartido entre especies, probablemente los frutos grandes de *D. gentlei* y *D. ambigens* sean preferidos por animales más grandes, o menos dispersados que los de *D. colorata* y *D. salicifolia*. Desconocemos mucho del reclutamiento de plántulas y fases ulteriores para *D. gentlei*, *D. colorata* y *D. salicifolia*, por lo que además de la necesidad de caracterizarlo y monitorearlo, se requieren estudios para entender la medida en que es afectado por las interacciones bióticas.

Por otro lado, las tasas de crecimiento podrían relacionarse con la demanda y el uso de nutrientes, determinar las dinámicas de reclutamiento, e incidir en las diferencias interespecíficas en distribución, o en la fenología. Los árboles inmensos de *D. ambigens*, pueden tardar entre 100 y 200 años en alcanzar su talla máxima (Ricker et al., 2017), lo que probablemente ocurre también con los árboles de *D. gentlei*; en contraste, es probable que los árboles de *D. salicifolia* y los de *D. colorata*, que usualmente miden entre 10 y máximo 20 m, tengan tasas de crecimiento más rápidas. Además, se ha reportado que los árboles de *D. ambigens* podrían tardar por lo menos 20 años en alcanzar la madurez reproductiva (Cordova Casillas, 1985), mientras que los árboles de *D. salicifolia*, que pueden llegar a reproducirse teniendo tallas pequeñas, probablemente tarden menos en iniciar su reproducción. Dada la importancia de las lauráceas en la estructura y regeneración de la selva alta perennifolia, estos temas merecen mayor atención en futuras investigaciones.

La complejidad de la variación ambiental

Aunque nuestros resultados respaldan la importancia del suelo como potencial promotor de las diferencias en la distribución y variación funcional foliar entre especies de *Damburneya*, no evidenciaron que esto también ocurra en la etapa de reclutamiento de plántulas. No obstante, los efectos de la variación ambiental sobre las especies de *Damburneya* son muy complejos, y su interpretación requiere la consideración de muchos factores actuando de manera simultánea.

La variación edáfica, por ejemplo, además de determinar la disponibilidad de nutrientes, puede determinar el estrés hídrico, y potenciar de forma indirecta los efectos de la variación climática (e. g., los suelos de textura fina podrían favorecer la retención de agua durante una sequía). Por otra parte, los efectos de la elevación requieren la consideración simultánea de muchas variables que son difíciles de separar de la variación de la elevación sobre el nivel del mar por sí misma (Körner, 2007). En la región de Los Tuxtlas, la elevación de los macizos montañosos determina la variación de las propiedades fisicoquímicas del suelo; por ejemplo, a en zonas bajas la disponibilidad de nutrientes es más alta y la textura del suelo es más fina, en parte por los procesos naturales de arrastre desde mayores zonas más altas (Siebe et al., 1996; Campo-Alves, 2003; Giraldo-Kalil y Núñez-Farfán, 2022). De forma similar el clima se hace más húmedo, lluvioso y frío a medida que incrementa la elevación; no obstante, su efecto no es el mismo en la vertiente noreste, que recibe directamente la descarga de humedad del golfo, que en la vertiente suroccidente, que tiende a ser más seca y cálida (Soto y Gama, 1997; Gutiérrez-García y Ricker, 2011). Así mismo, la disponibilidad de luz fue mayor a mayor elevación por una apertura más amplia del dosel. Lo anterior evidencia la importancia de considerar la complejidad de la variación ambiental para interpretar sus efectos sobre la diferenciación ecológica de las especies de *Damburneya,* ya que la variación observada localmente en la región de Los Tuxtlas no necesariamente ocurre de la misma forma en otras regiones.

Vale la pena entonces analizar las características ambientales en su contexto ecológico; en ese sentido, aunque ciertas variables ambientales como la precipitación pueden ser altamente limitantes para la distribución y el establecimiento de las especies de *Damburneya*, es su acción simultanea con otras variables lo que tendrá un efecto en las propiedades ecosistémicas que limitan o favorecen a las especies. Por ejemplo, más que estar limitadas independientemente por suelos ligeramente ácidos, o climas lluviosos, las especies de *Damburneya* probablemente están en general más limitadas por la regulación hídrica y los flujos de materia orgánica y nutrientes característicos de las selvas húmedas.

Perspectivas en la ecología y el estudio del género *Damburneya*

De acuerdo con Rohwer y Kubitzki (1993), la diferenciación ecológica entre especies de *Damburneya* es fundamental para explicar las diferencias en abundancia y distribución entre especies simpátricas, y es además uno de los mecanismos de diversificación del género. Por eso, la interpretación de dichas diferencias invita a la revisión de su historia evolutiva. Las especies de este género migraron desde Norteamérica hacia Centroamérica durante el Eoceno, principalmente gracias a la dispersión de semillas por aves frugívoras. En el proceso, especies plásticas y ampliamente distribuidas, capaces de tolerar amplios rangos de variación ambiental (como *D. salicifolia*), habrían dado lugar a ecotipos de distribución restringida (como *D. colorata*), gracias a la diferenciación ecológica entre especies, fomentando la especialización fenológica, edáfica y altitudinal dentro de una misma región geográfica (Rohwer y Kubitzki, 1993). Esto es congruente con las diferencias en la distribución de especies, y con la asincronía en las temporadas de floración y fructificación, que ocurren incluso a nivel local para algunas especies, en el gradiente altitudinal en la Reserva de la Biosfera Los Tuxtlas (Rohwer, 1993b; Rohwer y Kubitzki, 1993; Giraldo-Kalil y Núñez-Farfán, 2022). Es difícil saber si la variación fenotípica a nivel local podría reflejar especialización ambiental a los ambientes dónde las especies se distribuyen actualmente, o si podría responder a eventos evolutivos en el pasado. Aunque es posible que la especialización ocurra, es la acción simultánea de varios factores ambientales bióticos y abióticos, los rasgos de historia de vida, la variación genética y fenotípica, y procesos históricos (p. ej., dispersión, dinámicas poblacionales pasadas, deforestación) y evolutivos (P. ej. especiación) lo que probablemente explica las diferencias ecológicas y de distribución entre las especies de *Damburneya* documentadas en este trabajo. Por otra parte, si bien la diferenciación ecológica sugiere que ocurre desplazamiento de caracteres y que las diferencias ecológicas entre especies podrían resultar de procesos selectivos (Rohwer y Kubitzki, 1993), otros factores aleatorios como la deriva génica deben ser considerados a futuro para entender la evolución de este grupo.

Aún es necesario entender con mayor profundidad las dinámicas poblacionales de estas especies y su variación fenotípica a lo largo de toda su distribución. Algunos rasgos de historia de vida pueden dificultar la recuperación de las poblaciones naturales ante la deforestación. Por ejemplo, *D. ambigens* presenta ciclos de vida largos (Ricker et al., 2017), reproducción en periodos de pocos meses espaciados por más de un año (Rohwer, 1993b; Ibarra-Manríquez y Sinaca-Colín, 1995), y un bajo reclutamiento, en el que la gran cantidad de plántulas contrasta con los escasos árboles juveniles de tamaños intermedios (Cordova Casillas, 1985; Martínez-Ramos, 1991). Si bien cabría esperar patrones similares para las otras especies, aún desconocemos estos y otros aspectos básicos para el mantenimiento de las poblaciones, como la polinización (Rohwer, 1993b). Es más, *D. colorata* es una especie muy poco conocida y muestreada, para la cual probablemente este estudio constituye el registro más completo hasta la fecha, ya que solo se conocía por escasos ejemplares de herbario.

Al estar separada geográficamente de otras cadenas montañosas de México, la región de Los Tuxtlas podría ser vista como una isla biogeográfica (Wendt, 1993). Una visión más completa de la divergencia ecológica de estas especies debería evaluar su variación fenotípica y fenológica en varias partes de su área de distribución, ya que no es posible determinar hasta qué punto las diferencias ecológicas observadas localmente podrían explicar las que pueden ocurrir en otras regiones. Por ejemplo, aunque la variación funcional foliar observada en los Tuxtlas fue consistente con la diferenciación de nicho a gran escala espacial, no sabemos si tal variación se mantendría fuera de esta área. En una revisión de *Nectandra* y el actual género *Damburneya* (Rohwer, 1993b), resaltó que *D. gentlei* (anteriormente *N. lundellii*) presenta una variación morfológica tan particular en Los Tuxtlas, que incluso llegó a considerar su separación como una especie distinta. La variación morfológica de *D. salicifolia*, en ciertas zonas como Veracruz, Chiapas y la costa occidental de México, difiere de lo observado en otras regiones de México; además, *D. salicifolia* ha sido descrita como un complejo de especies, lo que suele dificultar su distinción de otras especies cercanas como *D. colorata* (Rohwer, 1993b). Sugerimos la realización de estudios sobre la variación genética y la plasticidad fenotípica para entender más ampliamente las causas de la variación fenotípica en estas especies a lo largo de sus áreas de distribución.

Cabe resaltar la importancia de las especies de *Damburneya* y la necesidad de realizar un seguimiento de sus poblaciones naturales para monitorear su respuesta a presiones ambientales actuales como la deforestación y el cambio en la cobertura de suelo, que sus principales amenazas (Lorea-Hernández, 2002; de Kok 2020a; 2020b; 2020c). La deforestación de las selvas húmedas tropicales en México y Centroamérica puede tener repercusiones importantes en las poblaciones ya que podría reducir considerablemente el flujo génico entre ellas. Además, el aislamiento geográfico de Los Tuxtlas sugiere que el flujo génico entre esta y otras poblaciones (p. ej. Chiapas, Chimalapas, Norte de Guatemala, etc.) podría ser bastante limitado, si es que acaso ocurre, por lo que cabría esperar alta endogamia. Por otra parte, el reclutamiento parece ser menor para todas las especies en las zonas bajas, tal como indican la alta mortalidad de plántulas, el bajo número de individuos juveniles y la mayor abundancia de individuos de tallas grandes respecto a las zonas altas (Giraldo-Kalil y Núñez-Farfán, 2022). Aunque una explicación posible a lo anterior es la menor disponibilidad de luz a menor altitud, desconocemos si hay otras causas detrás de este fenómeno, y sugerimos su estudio a mayor profundidad, ya que además de afectar la distribución, esta segregación espacial podría influir a futuro en la reproducción y dispersión.

Al diferir ecológicamente, las especies aquí estudiadas podrían tener diferentes respuestas ante cambios ambientales y, por lo tanto, requerir diferentes estrategias de manejo. Dichas especies están principalmente amenazadas por la pérdida de hábitat y la deforestación (Lorea-Hernández, 2002; de Kok, 2020b, a; c) y, probablemente, a excepción de *D. salicifolia*, son vulnerables al disturbio, dado que no suelen prosperar en vegetación secundaria (Lorea-Hernández, 2002). Tal situación es preocupante considerando que la Reserva de La Biosfera de Los Tuxtlas es una de las zonas con mayor abundancia de *D. ambigens*, *D. gentlei* y *D. colorata* (ver mapas de distribución, capítulo 1). Esta reserva, que es el área natural protegida que mayor número de especies de lauráceas alberga en México, ha sufrido una fuerte deforestación y fragmentación desde hace más de 50 años, en gran parte debido a la expansión de la frontera agrícola y el aumento de la ganadería (Dirzo y García, 1992; Dirzo et al., 2007; von Thaden et al., 2018). Si bien la reserva ha sido fundamental para la protección de los ecosistemas de la región, y ha reducido considerablemente las tazas de deforestación en la región, este problema aún persiste (PSSM y CONANP, 2011; von Thaden et al., 2018, 2020). La deforestación y el cambio del uso del suelo han traído efectos colaterales que podrían afectar diferencialmente a las especies, tales como cambios en la humedad, la temperatura, la disponibilidad de luz, agua y nutrientes en el suelo, o en la abundancia y diversidad de especies que interactúan con las plantas de *Damburneya* como herbívoros, patógenos, dispersores y depredadores de semillas, u otros organismos (Apéndices 1, 2 y 3). Por lo anterior, exhortamos la realización de estudios poblacionales para este grupo de especies y un monitoreo de los efectos que tienen sobre ellas la deforestación y el cambio de uso del suelo.

Además de discutir las diferencias ecológicas entre especies, esta investigación buscó analizar su contexto ecológico y resaltar su importancia dentro de las comunidades en dónde habitan. Se ha documentado, por ejemplo, que además de encontrarse en las áreas mejor conservadas de la zona núcleo de la Reserva de la Biosfera de Los Tuxtlas, *D. ambigens*, *D. gentlei*, y *D. salicifolia* se han reportado en fragmentos de bosque y zonas con diferentes grados de deforestación (Arroyo-Rodríguez et al., 2009; Sánchez-Gallen et al., 2010), e incluso hay árboles creciendo aislados en potreros (Guevara et al., 2005; Laborde et al., 2011), lo que podría contribuir a mantener el flujo génico en la región, y favorecer el mantenimiento de las poblaciones de animales que dependen de estas especies. Además, se ha observado un reclutamiento exitoso de *D. ambigens* en fragmentos de selva, que podría promover la regeneración natural en las áreas fragmentadas (Chávez-Pesqueira y Núñez-Farfán, 2016). Así mismo, estudios previos sugieren que esta especie podría ser empleada exitosamente en esfuerzos de restauración activa en la región (Martínez-Garza y Howe, 2010; Chávez-Pesqueira y Núñez-Farfán, 2016), y no se descarta que esto pueda ocurrir también en el caso de otras especies como *D. salicifolia* o *D. colorata* que, dada su plasticidad foliar, podrían tolerar condiciones ambientales cambiantes.

Finalmente, vale la pena destacar el valor de las colecciones biológicas en la realización de investigaciones como esta, ya que permitieron la obtención de información valiosa y confiable sobre la distribución de las especies. Así mismo, es necesario reconocer la importancia de la asesoría especializada por parte de taxónomos, particularmente en grupos taxonómicamente complejos como las Lauraceas. Por lo anterior, varias de las muestras de árboles e insectos colectadas para la realización de esta investigación (específicamente para los capítulos 2, 3 y anexos) fueron depositadas en el Herbario Nacional Mexicano (MEXU), el Herbario del Instituto de Ecología A.C., el Herbario y la Colección de Insectos de la Estación de Biología Tropical Los Tuxtlas, y la colección Nacional de Insectos tal como se detalla en las secciones correspondientes.

Conclusiones

Esta investigación sugiere que, aunque las especies de *Damburneya* pueden responder diferencialmente a la variación edáfica o verse fuertemente afectadas por ciertas variables ambientales como el clima, su distribución, su abundancia y sus poblaciones dependen a nivel local de otras variables bióticas y abióticas (p. ej., disponibilidad de luz). Probablemente la diferenciación de nicho dentro del género depende de varios mecanismos de coexistencia actuando simultáneamente en diferentes escalas espaciales y temporales. En su conjunto, estas especies se ven afectadas por las propiedades ecosistémicas de la selva alta perennifolia. Allí confluyen un rápido ciclado de nutrientes, alta humedad y precipitación con poca variación anual, temperaturas cálidas, y un ambiente de sotobosque sombreado, cuya variación lumínica depende, en gran medida, de la apertura de claros. A esto se suman los efectos de las interacciones bióticas como la dispersión de semillas por aves y mamíferos, los efectos de la depredación de semillas, el ataque de herbívoros y patógenos y la alta competencia intraespecífica entre plántulas. Las conclusiones puntuales fueron:

- Las especies de *Damburneya* aquí estudiadas tienen un nicho climático Grinnelliano similar y conservado, mientras que presentan diferencias en sus nichos edáficos, lo que sugiere que pueden tolerar mayor variación de las propiedades físicas y químicas del suelo, que de las variables climáticas como la precipitación (y, por ende, la disponibilidad de agua). Su distribución parece estar particularmente limitada por las condiciones climáticas y edáficas de las selvas húmedas tropicales.
- A diferencia de las demás especies, *D. salicifolia* tolera mayor variabilidad climática (p. ej. climas más secos y con estacionalidad más pronunciada) y edáfica (p. ej. suelos más alcalinos), además tiene una amplia variación de rasgos funcionales foliares, lo que sugiere que esta especie es relativamente plástica, y tolerante a un mayor rango de condiciones ambientales que las otras especies del género.
- La variación edáfica puede promover diferencias en la distribución de las especies de *Damburneya* a escala continental, y potencialmente también a escala local; además, puede generar respuestas diferenciales de la variación funcional foliar entre especies.
- La variación de rasgos funcionales foliares puede dar una base causal para entender la divergencia ecológica entre especies de *Damburneya* a lo largo de gradientes ambientales.

- A pesar de su cercanía filogenética, *D. ambigens* y *D. gentlei* difieren en sus nichos Grinnellianos y en sus estrategias funcionales foliares, lo que sugiere que, aun coocurriendo en simpatría, son diferencialmente afectadas por las mismas condiciones ambientales.
- Además de la variación edáfica, otros factores que varían con la elevación en la zona de estudio tales como el clima, la disponibilidad de luz y agua, pueden explicar tanto la variación funcional foliar de los árboles adultos, como la supervivencia y el vigor de las plántulas.
- Más allá del efecto independiente de estas variables, debe considerarse su interacción para entender de forma integral la medida en que la variación ambiental afecta el vigor de las plántulas, su supervivencia, y la variación foliar en los estadios juvenil y adulto.
- El ataque de herbívoros y patógenos sobre las plántulas de *D. ambigens* y *D. salicifolia* fue considerablemente mayor en las zonas altas que en las zonas bajas, en dónde la mortalidad fue, no obstante, mayor.
- No encontramos evidencias directas de diferenciación del nicho de regeneración dadas por la elevación, el suelo, o el ataque de enemigos naturales; sin embargo, probablemente el tamaño de la semilla puede explicar diferencias en el reclutamiento de plántulas entre especies ya que fue determinante para el vigor y la supervivencia de las plántulas y tuvo un valor adaptativo en las condiciones ambientales más adversas.
- Se requieren más estudios para entender a fondo el reclutamiento de plántulas de las especies, que a la fecha ha sido poco investigado para *D. gentlei*, *D. colorata*, y *D. salicifolia.* Así mismo, se requiere en general un monitoreo a las poblaciones silvestres de las especies investigadas.
- El análisis de los efectos de la variación ambiental sobre las especies de *Damburneya*, en varias escalas espaciales y etapas del ciclo de vida, permite tener una perspectiva más integral para entender las causas potenciales de las diferencias y similitudes entre las especies.

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Apéndices

En esta sección se incluyen los resúmenes de tres manuscritos relacionados con el efecto potencial de la depredación de semillas sobre la germinación, y con la diversidad de insectos asociados a los frutos de las especies de *Damburneya* investigadas en esta tesis, incluyendo la descripción de dos especies nuevas. Dichos insectos emergieron de los frutos colectados para el establecimiento de los experimentos del capítulo 3. Si bien estos anexos no se incluían formalmente dentro de los objetivos principales de esta tesis, constituyen información novedosa y relevante sobre la historia natural de las plantas y los insectos, que han sido muy escasamente estudiados. Todos los manuscritos fueron redactados durante la realización de esta tesis, dos de ellos fueron publicados y el tercero continúa en proceso de edición para su envío a una revista científica. Dado que los artículos son extensos, únicamente anexo aquí los resúmenes de estos trabajos, para su consulta en las correspondientes revistas científicas. Estos tres trabajos han sido liderados por Edna Rodríguez Sánchez, quién es la primera autora de dichas publicaciones y realizó junto a mí gran parte de este trabajo durante su servicio social de licenciatura. Gracias a su complicidad y a su trabajo duro, y a la colaboración de muchas personas dentro y fuera de México, la mayoría de estos trabajos ya fue publicada.

Apéndice 1.

Diversidad de insectos asociados con los frutos de cuatro especies de Lauraceae de la región de Los Tuxtlas, México: una lista taxonómica comentada e ilustrada.

Publicado en: *Revista Mexicana de Biodiversidad*, 93(2022): e934178
https://doi.org/10.22201/ib.20078706e.2022.93.4178

Instituto de Biología UNAM

Revista Mexicana de Biodiversidad

Revista Mexicana de Biodiversidad 93 (2022): e934178

RMB Revista Mexicana de Biodiversidad

Ecology

Diversity of insects associated with the fruits of four tree species of Lauraceae from Los Tuxtlas region, Mexico: an annotated and illustrated taxonomic list

Diversidad de insectos asociados a los frutos de cuatro especies arbóreas de Lauraceae de la región de Los Tuxtlas, México: un listado taxonómico anotado e ilustrado

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Received: 22 September 2021; accepted: 24 February 2022

Abstract

Besides recruitment and dispersal, fruits are key resources for the maintenance of insect communities. This study is focused on the insects inhabiting the fruits of 4 wild Lauraceae species. Although the trees of this family are important elements of tropical forests, their interaction with insects, especially in association with fruits, remains poorly studied in wild tree species. Our study aims to characterize the diversity of insects associated with fruits of *Damburneya ambigens*, *Damburneya gentlei*, *Damburneya salicifolia*, and *Nectandra turbacensis*, in the rainforest of Los Tuxtlas, Veracruz. We present an illustrated taxonomic list of species, annotated with a comprehensive review of the insects' natural history and their interactions with Lauraceae species. We reared 54 insect species from approximately 6,500 fruits, some of which represent potential new species and records for Mexico. Insect species diversity was high and differed between Lauraceae species. The reared insects comprise a wide variety of distributional ranges, feeding types, and habitats. This research provides novel information about the interactions among insects and fruits of Lauraceae and the complexity of their trophic networks in tropical rainforests. Furthermore, it evidences the importance of wild fruits as resources for insect communities.

Keywords: *Damburneya*; *Nectandra*; Neotropical; Parasitoids; Saprophagous; Seed predators; Tropical rainforest

Apéndice 2.

Dos nuevas especies del género de avispas *Bracon* (Braconinae) de la región de Los Tuxtlas en Veracruz, México, criadas a partir de los frutos de tres especies de Lauraceae.

Publicado en: *Zootaxa* 5162 (1): 067-077. https://doi.org/10.11646/zootaxa.5162.1.4

Zootaxa 5162 (1): 067–077
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5162.1.4
http://zoobank.org/urn:lsid:zoobank.org:pub:F3F2E742-6E2D-4F00-BA70-7CB4ED3EBBAE

Two new species of the braconid wasp genus *Bracon* (Braconinae) from Los Tuxtlas region in Veracruz, Mexico, reared from fruits of three species of Lauraceae

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Abstract

Two new species belonging to the braconid genus *Bracon* (Braconinae) are described from the tropical rainforest of Los Tuxtlas in the state of Veracruz, Mexico, *B. laurae* **sp. nov.** and *B. rosamondae* **sp. nov.** These species are morphologically similar and were reared from fruits of three Lauraceae species, *Damburneya ambigens, D. salicifolia* and *Nectandra turbacensis*. However, comparison of their DNA barcoding locus and a fragment of the nuclear ribosomal 28S gene confirmed their allospecificity. These two species share a number of morphological features with the two described Neotropical *Bracon* species that are known to be phytophagous (seed predators), *B. phytophagus* Quicke and *B. zuleideae* Perioto & Lara. We therefore propose a new species-group for the above four species, the *B. phytophagus* Quicke species-group, and suggest that the two newly described species also have a phytophagous feeding strategy.

Key words: tropical rainforest, insect-fruit association, phytophagy, Neotropics, Ichneumonoidea

Apéndice 3.

Depredación pre-dispersión por parte de insectos de semillas de tres especies simpátricas de
Lauraceae en una selva húmeda tropical

Artículo en preparación.

Pre-dispersal insect seed predation of three sympatric Lauraceae species in a tropical rainforest

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Abstract

Pre-dispersal seed predation (PDSP) by insects can impact plant populations by reducing plant fitness. The outcomes of this complex interaction can be simultaneously determined by several traits and dynamics of plants and seed predators. Here, we characterized PDSP by insects, its relationship with seed size and its potential impact on seedling recruitment of three sympatric species in the Lauraceae family, in a lowland tropical rainforest of Mexico. The extent of PDSP varied between trees, populations, and species. Although 76% of the seeds were predated, only 50% suffered embryo damage. The incidence of the seed damage was negatively associated with seed size, and the incidence of embryo damage was positively related to the damage intensity. We found five species of insect seed predators, with *Heilipus albomaculatus* and *Pagiocerus frontalis* being the most abundant. Both species can exert the same magnitude of seed damage despite their huge differences in body size. Seed size can explain, in part, damage incidence and intensity and predators' abundance. Furthermore, the abundance of *P. frontalis* increased with seed size. Likely, predator species have divergent attack dynamics on each Lauraceae species. Our results point that potential effects of PDSP on plant fitness depend on damage intensity, seed size, and abundance and consumption preferences of predator species.

Key words: *Damburneya, Nectandra,* Los Tuxtlas, *Pagiocerus frontalis, Heilipus albomaculatus*