Title

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

Permalink

https://escholarship.org/uc/item/58b0z7bc

Journal

Frontiers of Biogeography, 15(3)

Authors

Giraldo-Kalil, Laura J.
Pinilla-Buitrago, Gonzalo E.
Lira-Noriega, Andrés
et al.

Publication Date

2023

DOI

10.21425/F5FBG59528

Supplemental Material

https://escholarship.org/uc/item/58b0z7bc#supplemental

Peer reviewed

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

Laura J. Giraldo-Kalil[1,2] (iD), Gonzalo E. Pinilla-Buitrago[3,4] (iD), Andrés Lira-Noriega[5] (iD), Francisco Lorea-Hernández[6] (iD) and Juan Núñez-Farfán[1*] (iD)

[1]Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México (UNAM), Ciudad de México, México;

[2]Posgrado en Ciencias Biológicas, Unidad de Posgrado, Circuito de Posgrados, Universidad Nacional Autónoma de México (UNAM), Ciudad de México, México;

[3]Department of Biology, City College of New York, City University of New York, New York, NY, USA;

[4]PhD Program in Biology, The Graduate Center, City University of New York, New York, NY, USA;

[5]CONACYT Research Fellow, Red de Estudios Moleculares Avanzados-Instituto de Ecología, A. C., Xalapa, Veracruz, México;

[6]Departamento de Biodiversidad y Sistemática, Instituto de Ecología, A.C., Xalapa, Veracruz, México.

*Correspondence: J. Núñez-Farfán, farfan@unam.mx

Abstract

Edaphic specialization is considered to promote ecological differentiation among closely related species of *Damburneya* (Lauraceae) occurring in sympatry. However, little is known about the effects of soil and other key environmental factors like climate on the ecological 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 whose distributions span Central America and Mexico. 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 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 previous reports of wide ecological plasticity of *Damburneya salicifolia* based on its distribution and leaf trait variation, as it occurred in 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 niches do not necessarily reflect past evolutionary processes but rather the current environmental variation across the geographical ranges of the species. 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.

Resumen

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 el clima sobre el nicho ecológico 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* cuyas distribuciones abarcan Centroamérica y México. Realizamos modelos de nicho ecológico con MaxEnt utilizando tres conjuntos de datos ambientales: climáticos, edáficos y una combinación de ambos para caracterizar los nichos de las especies y las áreas idóneas para su distribución. Además, se cuantificó el solapamiento y se hicieron pruebas de similitud de nicho 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 *Damburneya salicifolia* basados en su distribución y su variación foliar, ya que se encuentra en ambientes más secos y con 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 están restringidas de forma similar por el clima y toleran amplia variación edáfica, lo que apoya el papel potencial del suelo 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.

Highlights

- The niches of *Damburneya* species were highly and similarly affected by climate, particularly by precipitation, suggesting that water availability is a major constraint to their distribution.

- Conversely, edaphic niche divergence among these closely related sympatric species was mostly explained by the large edaphic variation across distribution areas indicating a wide plant tolerance to soil variation rather than edaphic specialization.

- Against predictions of niche conservatism on closely related species, we detected niche divergence between the sister species *Damburneya ambigens* and *D. gentlei*, in agreement with previous findings of divergence in trait-based leaf functional strategies.

- *Damburneya salicifolia* displays a wide tolerance to climatic and edaphic variation in line with its high plasticity, as shown by its local trait variation and occurrence in disturbed areas and several types of forests, raising questions about the physiological differences potentially underlying niche differentiation in *Damburneya*.

- Models presented here point environmental restrictions to *Damburneya* species' distribution and constitute potential guides for planning future fieldwork, sampling, and data collection, particularly for poorly studied species like *Damburneya colorata.*

Introduction

The niche of species encompasses the ecological conditions and resources necessary to maintain viable 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). Niche similarity could limit coexistence if closely related species occurring in sympatry exploit environmental resources in the same way. Alternatively, 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 and Roughgarden 1985, Chesson 2000, Wright 2002, Silvertown 2004, Adler et al. 2013). This coexistence 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 the environmental constraints to their distribution is not yet well understood in several plant groups and particularly in highly diverse ecosystems like tropical forests.

Ecological niches can be described through environmental scenopoetic variables (i.e., those independent of the focal species) which vary at large scale across the geographic areas occupied by the species and likely constrain species distribution. The niches assessed in this way, rather than focusing on biotic interactions and local processes of the focal species, are termed "Grinnellian niches" (Grinnell 1917, Hutchinson 1957, 1978, Chase and Leibold 2003, 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 methods and applications for ENMs; for instance, model predictions of species' environmental niches can be spatialized to obtain potential distribution models, which are cartographic representations of geographic areas suitable for the 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 those 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 is a critical determinant of vegetation types and life forms and affects plant morphological, physiological, and functional variation (Holdridge 1947, Harrison et al. 2010); for example, temperature and precipitation are tightly linked to processes like evapotranspiration and water cycling (Fisher et al. 2009). Soils also have important effects on 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 and water 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) and 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 to what extent, and in which environmental dimensions, their niches differ. The genus includes 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 within one of the two Eocene cooling periods (50 – 48 Ma and 40 –36 Ma, respectively; Trofimov et al. 2016). Diversification occurred in Mesoamerica, likely in tropical forests of southern Mexico and Guatemala (Rohwer and Kubitzki 1993). Despite all *Damburneya* species being mainly bird dispersed, sympatric species (i.e., occurring in the same geographic area) differ in their local distribution along elevational gradients, suggesting that ecological differentiation could underlie spatial sorting. Edaphic, elevational, 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 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 and 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, such as *D. salicifolia,* are thought to have given rise to several species of more restricted distributions, such as *D. colorata,* via ecotypic differentiation (Rohwer 1993, Rohwer and Kubitzki 1993). However, we note that the particular examples given, *D. salicifolia* and *D. colorata,* 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 elevational 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 also by their responses to other environmental factors (e.g. climate, light, herbivory; 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 below 1000 m and 300 m a.s.l., 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). In contrast 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). Finally, there are few records of *D. colorata*, a species restricted to tropical
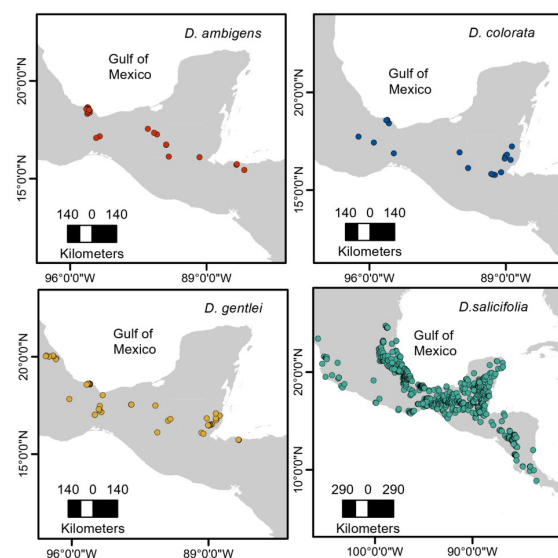

Figure 1. Maps of occurrence data of four *Damburneya* species employed to perform ecological niche models (ENMs) with MaxEnt. a) *Damburneya ambigens*:33 records, b) *D. colorata*: 20 records, c) *D. gentlei*: 53 records d) *D. salicifolia*: 697 records. The points show the location of collected samples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

                3

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 could expect greater niche similarity and overlap as species are more closely related. However, differences in local leaf trait variation and geographic distribution within this genus 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 and climate data, and a combination of both sets of environmental variables to assess their relevance for 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.

Materials and 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 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 unpublished). 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 were determined in herbaria by specialists, and excluded observation-only records. Occurrence data were searched using 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. Outlier data with incoherent distributional properties (e.g., in the desert, water bodies, very high elevations, 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 or to georeference records lacking coordinates. 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). 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. 2001) that intercepted species occurrence points. A 1 km buffer was added to the resulting polygons to avoid occurrence points 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 distributions. All environmental variables encompass the whole study area where the studied species occur, from Mexico to Panama (the coordinates of study area are: top: 28.805836226; left: -110.898210379; right: -77.648210379, bottom: 6.07250289266); 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 includes 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

     4

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. It 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. It 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 are rasters with 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.

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 those other variables because of its relationship to both soil texture and cation exchange capacity (Sollings 1998, Weil 2017). Furthermore, we prioritized those climatic variables encompassing annual periods, such as mean annual temperature and precipitation (Bio 1 and Bio 12, respectively), since these variables are considered important drivers of plant distribution (Morecroft and Paterson 2006) and trait variation (Wright et al. 2004). Temperature and precipitation seasonality (Bio4 and Bio 15) were included, as these variables describe departures from annual values. Other variables that represent extreme values (e.g., Bio 5, Bio 6, Bio 10, Bio 11, Bio 16, and Bio 17) and show high VIF values were not included.

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 points, we applied the Jackknife random partition method for *D. colorata* (n = 20; 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 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. S1, S2, and S3). 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 components 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 the statistical significance of niche overlap. Species' niches were considered more similar than expected by chance 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

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

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 provided greater contributions 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 had a higher contribution 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. The environmental suitability of most species increased with mean annual precipitation, and cation exchange capacity. Overall, environmental suitability was high at warm annual mean temperatures (20-25°C) but decreased with higher temperatures. Furthermore, it was high in environments with acidic soils (pH < 6), high soil water availability (>20%), and low precipitation seasonality, particularly for *D. ambigens* and *D. gentlei*, and decreased with annual precipitation below 2000 mm and more than 40% of soil clay (Fig. 2).

On the other hand, some response curves of *D. salicifolia* differed from those of the other species, reflecting potential differences in the tolerance to environmental variation. For instance, the environmental suitability for this species encompassed a wider pH range (from 4 to 8); it was high at neutral pH and dropped in slightly alkaline soils (Fig. 2). In addition, it increased with higher precipitation of

the driest month, higher temperature and precipitation seasonality, and was relatively higher for annual precipitation values below 2000 mm/ year than in the other species, suggesting that *D. salicifolia* tolerates drier environments and a wide range of variation of temperature and precipitation (Fig. 2).

Suitable areas predicted from potential distribution models 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 opposite 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. S4, S5, and S6).
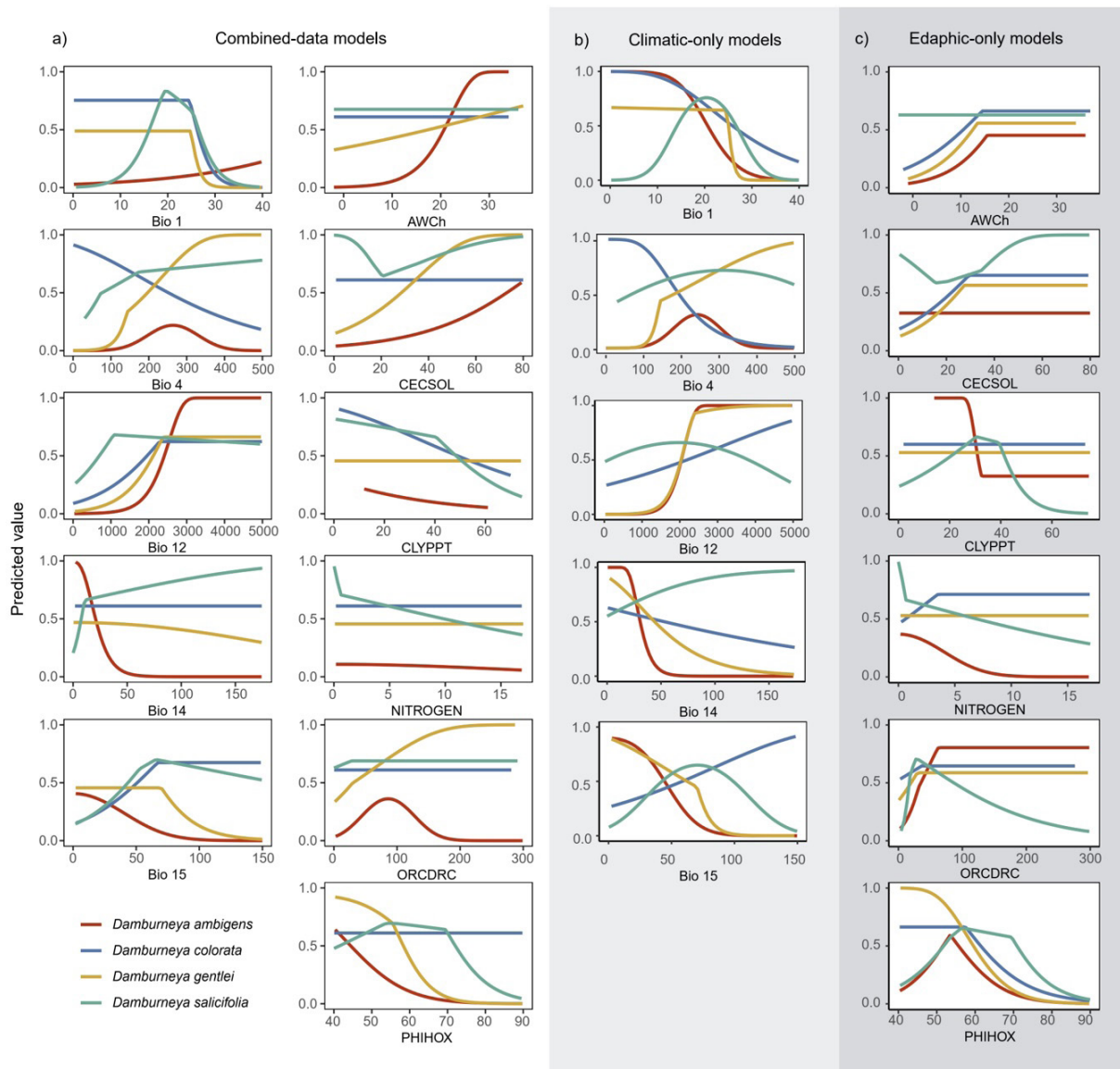
Figure 2. Response curves based on ecological niche models for four *Damburneya* species. The curves show the ranges of environmental variation favorable to species distributions and were based on models built with a combination of a) climatic and edaphic data, b) climatic-only, and c) edaphic-only datasets. Species are shown in different 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.

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, acid soil pH, and small variation of the amount of precipitation throughout the year 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
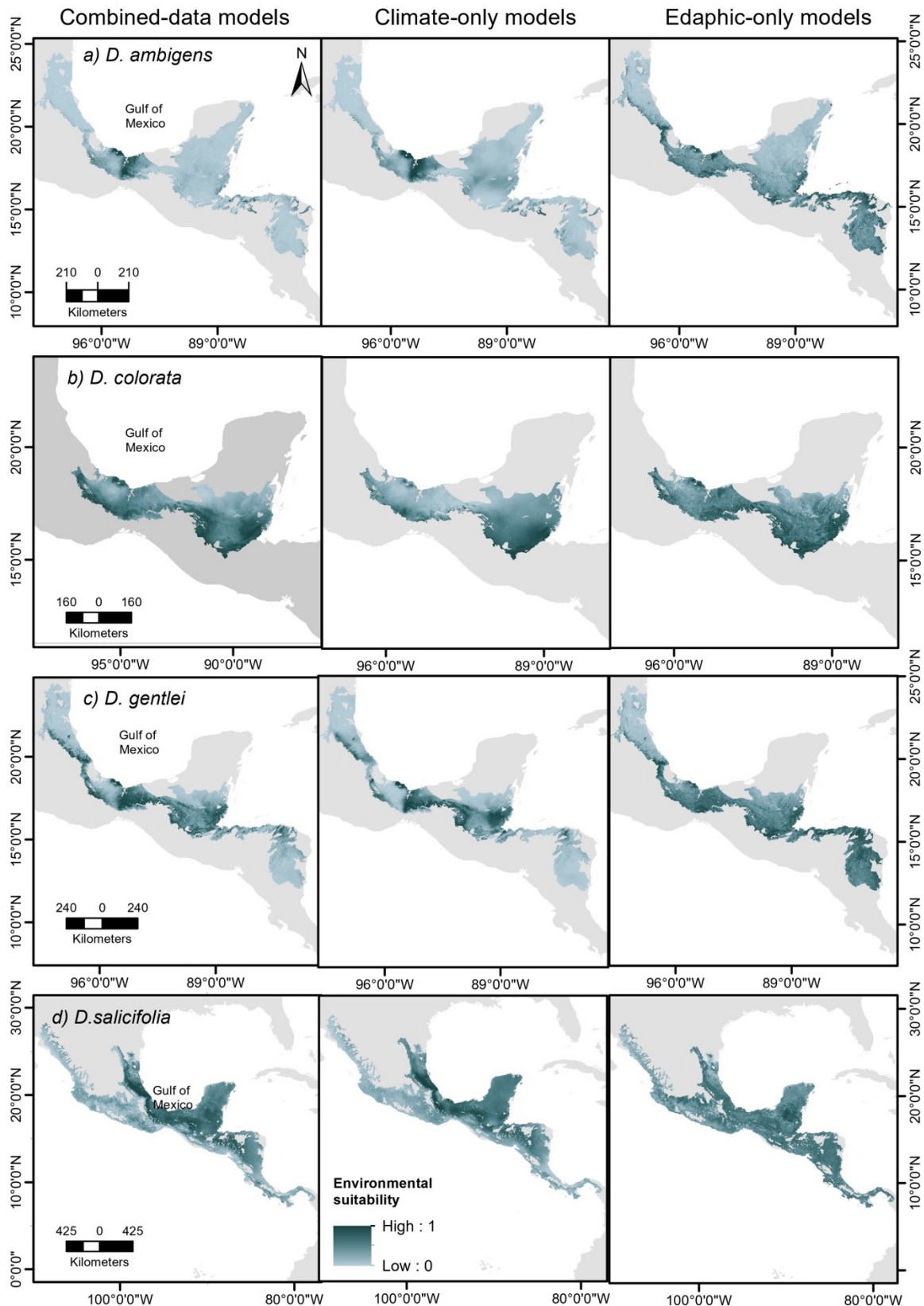
Figure 3. Geographic projection of niche models of four *Damburneya* species. Based on the environmental variables used to build the models, they were classified as combined-data models (combining climatic and edaphic variables, left column), climatic-only (center), and edaphic-only. The maps of each 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), light blue areas are the less suitable, and dark blue the most suitable areas.

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 (Schoener'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***

a divergence in physiological tolerances and likely underlies its wide distribution. In addition to humid tropical forests (rainforests and cloud forests), *D. salicifolia* can occur in drier 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), such as 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* is found across a wide edaphic range and even occurs in zones with alkaline soil pH (Fig. 2), including 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*. Moreover, we must acknowledge the influence of sample size on niche models. The large sample size of *D. salicifolia* reflected the wider environmental tolerance of this species; however, we do not know the extent to which the other *Damburneya* species are undersampled or their niches underestimated. Hence, more field observations and experiments are necessary to test the assumption that *D. salicifolia* has a greater physiological tolerance to edaphic and climatic variation.

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, and Fig. 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 elevational gradient in the San Martín Tuxtla volcano 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 (Giraldo-Kalil et al. 2022); the leaves of *D. salicifolia* seemed to require a lower phosphorus investment per nitrogen biomass unit, suggesting a plastic and efficient nutrient use. Furthermore, the higher soil nutrient availability, the higher leaf nutrient concentrations in 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 the 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 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, elevations, 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). It is thought that widespread plastic species tolerating a broad range of ecological conditions like *D. salicifolia* lead to locally specialized ecotypes with more specific environmental requirements. In turn, those ecotypes evolved into narrowly distributed species that likely remained in their differentiation sites like *D. colorata.* Eventually, closely related species, featuring ecological differentiation, 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, while 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 these topics. 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 of their interactions (e.g., soil water content might depend on precipitation and temperature), or because of their indirect effects on other unmeasured biotic or abiotic factors (e.g., abundance of dispersers; Wiens, 2011).

Furthermore, common methodological issues affecting ENMs must be recognized. Species occurrence records can be biased because they were not systematically collected in a single study but retrieved and collated from several sources and unrelated studies. Another bias comes from accessibility since easily accessible areas served by 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 the fact that 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 differences in the spatial scales governing variation in these environmental factors can be critical to consider (Sollins 1998, Thuiller 2013, Beauregard and De Blois 2014, Diekmann et al. 2015). However, several studies have found both edaphic and climatic variables to have relevance to species distributions at local (Phillips et al. 2003, Condit et al. 2013, Diekmann et al. 2015) and broad scales (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 edaphic variables at broad geographical scales (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 there are no such relationships, but because they may 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 in explaining 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, providing a starting point to understand the limitations to their establishment, and assessing 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

    13

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, von 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 sizes 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 drier 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

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 on 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

Supplemental Material

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

Appendix S1. 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.

References

Adler, P.B., Fajardo, A., Kleinhesselink, A.R. & Kraft, N.J.B. (2013) Trait-based tests of coexistence mechanisms. Ecology Letters, 16,1294–1306. https://doi.org/10.1111/ele.12157

Aerts, R. & Chapin III, F.S. (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Advances in Ecological Research, 30, 1–67. https://doi.org/10.1016/S0065-2504(08)60016-1.

Aguilar-Romero R., Pineda-Garcia F., Paz H., González-Rodríguez A. & Oyama, K. (2017) Differentiation in the water-use strategies among oak species from central Mexico. Tree Physiology, 37, 915-925. https://doi.org/10.1093/treephys/tpx033

Aguirre-Gutiérrez, J., Serna-Chavez, H.M., Villalobos-Arambula, A.R., Pérez de la Rosa, J.A. & Raes, N. (2015) Similar but not equivalent: ecological niche comparison across closely-related Mexican white pines. Diversity and Distributions, 21, 245–257. https://doi.org/10.1111/ddi.12268

Alkishe, A., Cobos, M. E., Osorio-Olvera, L., & Peterson, A. T. (2022). Ecological niche and potential geographic distributions of *Dermacentor marginatus* and *Dermacentor reticulatus* (Acari: Ixodidae) under current and future climate conditions. Web Ecology, 22, 33–45. https://doi.org/10.5194/we-22-33-2022

Alvarez, F., Morandi, P.S., Marimon-Junior, B.H., Exavier, R., Araújo, I., Mariano, L.H., Muller, A.O., Feldpausch, T.R., & Marimon, B.S. (2022) Climate defined but not soil-restricted: the distribution of a Neotropical tree through space and time. Plant and Soil, 471, 175–191. https://doi.org/10.1007/s11104-021-05202-6

Anderson, R.P. & Martínez-Meyer, E. (2004) Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. Biological Conservation, 116, 167–179. https://doi.org/10.1016/S0006-3207(03)00187-3

Austin, M.P. & Van Niel, K.P. (2011) Impact of landscape predictors on climate change modelling of species distributions: a case study with *Eucalyptus fastigata* in southern New South Wales, Australia. Journal of Biogeography, 38, 9–19. https://doi.org/10.1111/j.1365-2699.2010.02415.x

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., & Villalobos, F. (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecological Modelling, 222, 1810–1819. https://doi.org/10.1016/j.ecolmodel.2011.02.011

Beauregard, F. & De Blois, S. (2014) Beyond a climate-centric view of plant distribution: edaphic variables add value to distribution models. PLoS ONE, 9,e92642. https://doi.org/10.1371/journal.pone.0092642

Bertrand, R., Perez, V. & Gégout, J.C. (2012) Disregarding the edaphic dimension in species distribution models leads to the omission of crucial spatial information under climate change: the case of *Quercus pubescens* in France. Global Change Biology, 18, 2648–2660. https://doi.org/10.1111/j.1365-2486.2012.02679.x

Broennimann, O., Di Cola, V. & Guisan, A. (2021) ecospat: spatial ecology miscellaneous methods. R package. Version 3.2. Available at: https://cran.r-project.org/package=ecospat

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., et al. (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography, 21, 481–497. https://doi.org/10.1111/j.1466-8238.2011.00698.x.

Brown C., Burslem D.F.R.P, Illian J.B, et al. (2013) Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. Proceedings of the Royal Society B, 280, 20130502. https://doi.org/10.1098/rspb.2013.0502

Campbell, L.P., Luther, C., Moo-Llanes, D., Ramsey, J.M., Danis-Lozano, R. & Peterson, A.T. (2015) Climate change influences on global distributions of dengue and chikungunya virus vectors. Philosophical Transactions of the Royal Society B, 370, 20140135. https://doi.org/10.1098/rstb.2014.0135

Campo, J., Oliva, F.G., Navarrete, A. & Siebe, C. (2016) Almacenes y dinámica del carbono orgánico en ecosistemas forestales tropicales de México. Terra Latinoamericana, 34, 31–38. Available at: https://doaj.org/article/0020e3e6479c4c3c87ca958755fddd1f

Cavender-Bares, J. & Pahlich, A. (2009) Molecular, morphological, and ecological niche differentiation of sympatric sister oak species, *Quercus virginiana* and *Q. Geminata*

(Fagaceae). American Journal of Botany, 96, 1690-1702. https://doi.org/10.3732/ajb.0800315

Chacón de Rieger, I.M. & Fournier. O. L. (1987) Distribución del género *Nectandra* (Lauraceae) en Costa Rica. Revista de Biologia Tropical, 35, 155–157. Available at: https://revistas.ucr.ac.cr/index.php/rbt/article/view/24217

Chanderbali, A.S., van der Werff, H. & Renner, S.S. (2001) Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. Annals of the Missouri Botanical Garden, 88, 104–134. https://doi.org/10.2307/2666133

Chase, J.M. & Leibold, M.A. (2003) Ecological niches. Linking classical and contemporary approaches. University of Chicago Press, Chicago, USA.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics, 31, 343–366.

Condit, R., Engelbrecht, B.M.J., Pino, D., Pérez, R. & Turnera, B.L. (2013) Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. Proceedings of the National Academy of Sciences USA, 110, 5064–5068. https://doi.org/10.1073/pnas.1218042110

Corlett, R.T. & Primack, R.B. (2011) Tropical rain forests. An ecological and biogeographical comparison (2nd edn). Wiley-Blackwell, Oxford, UK.

Coudun, C., Gégout, J.C., Piedallu, C. & Rameau, J.C. (2006) Soil nutritional factors improve models of plant species distribution: an illustration with *Acer campestre* (L.) in France. Journal of Biogeography, 33, 1750–1763. https://doi.org/10.1111/j.1365-2699.2005.01443.x

Daza-Mendizabal, R. (1998) Caracterización dendrológica y ecológica de la familia Lauraceae en el bosque de la Montaña de Uyuca, Zamorano, Honduras.Universidad Zamorano. Honduras. Professional thesis. Available at: https://bdigital.zamorano.edu/bitstream/11036/2614/3/T831.pdf

de Kok, R. (2020a) *Damburneya ambigens*, the IUCN Red List of Threatened Species 2020: e.T146610634A146651525. Available at: https://dx.doi.org/10.2305/IUCN.UK.2020-1.RLTS.T146610634A146651525.en. (Accessed: January 21, 2021).

de Kok, R. (2020b) *Damburneya gentlei*, the IUCN Red List of Threatened Species 2020: e.T146611071A146651540. Available at: https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T146611071A146651540.en. (Accessed: January 21, 2021).

de Kok, R. (2020c) *Damburneya salicifolia.*, the IUCN Red List of Threatened Species 2020: e.T146611340A146651565. Available at: https://dx.doi.org/10.2305/IUCN.UK.2020-1.RLTS.T146611340A146651565.en. (Accessed: January 21, 2021).

Di Cola, V., Broennimann, O., Petitpierre, B., et al. (2017) ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography, 40, 774–787. https://doi.org/10.1111/ecog.02671

Diekmann, M., Michaelis, J. & Pannek, A. (2015) Know your limits - the need for better data on species responses to soil variables. Basic and Applied Ecology, 16, 563–572. https://doi.org/10.1016/j.baae.2015.08.010

DiMiceli, C., Carroll, M., Sohlberg, R., Kim, D., Kelly, M. & Townshend, J. (2015) MOD44B MODIS/Terra Vegetation Continuous Fields Yearly L3 Global 250m SIN Grid V006. Data set. NASA EOSDIS Land Processes DAAC. Available at: https://doi.org/10.5067/MODIS/MOD44B.006

Dormann, C.F., Elith, J., Bacher, S., et al. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography, 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Vittoz, P. & Guisan, A. (2013) Improving the prediction of plant species distribution and community composition by adding edaphic to topo-climatic variables. Journal of Vegetation Science, 24, 593–606. https://doi.org/10.1111/jvs.12002

Edwards R.D., Crisp M. D. & Cook L. (2013) Niche differentiation and spatial partitioning in the evolution of two Australian monsoon tropical tree species. Journal of Biogeography, 40, 559-569. https://doi.org/10.1111/jbi.12027

Elith, J., Phillips, S.J., Hastie, T. & Dudík, M., Chee Y.E. & Yates C.J. (2011) A statistical explanation of MaxEnt for ecologists. Diversity and

Distributions, 17, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Elith, J., Graham C.H., Anderson R.P., et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129-151. https://onlinelibrary.wiley.com/doi/10.1111/j.2006.0906-7590.04596.x

Escobar, L.E., Lira-Noriega, A., Medina-Vogel, G. & Townsend Peterson, A. (2014) Potential for spread of the white-nose fungus (*Pseudogymnoascus destructans*) in the Americas: use of Maxent and NicheA to assure strict model transference. Geospatial Health, 9, 221–229. https://doi.org/10.4081/gh.2014.19

FAO (Food and Agriculture Organization of the United Nations) (2020) Global Forest Resources Assessment 2020: main report. Rome, Italy. https://doi.org/10.4060/ca9825en

Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology, 37, 4302-4315. https://doi.org/10.1002/joc.5086

Figueiredo, F.O.G., Zuquim, G., Tuomisto, H., Moulatlet, G.M., Balslev, H. & Costa, F.R.C. (2018) Beyond climate control on species range: The importance of soil data to predict distribution of Amazonian plant species. Journal of Biogeography, 45, 190–200. https://doi.org/10.1111/jbi.13104

Fisher, J.B., Malhi, Y., Bonal, D., et al. (2009) The land-atmosphere water flux in the tropics. Global Change Biology, 15, 2694–2714. https://doi.org/10.1111/j.1365-2486.2008.01813.x

Flores-Delgadillo, L., Sommer-Cervantes, I., Alcalá-Martínez, J.R. & Álvarez-Sánchez, J. (1999) Estudio morfogenético de algunos suelos de la región de Los Tuxtlas, Veracruz, México. Revista Mexicana de Ciencias Geológicas, 16, 81–88. Available at: http://rmcg.geociencias.unam.mx/index.php/rmcg/article/view/1064

García-Licona, J., Esparza-Olguín, L. & Martínez-Romero, E. (2014) Estructura y composición de la vegetación leñosa de selvas en diferentes estadios sucesionales en el Ejido el Carmen II, Calakmul, México. Polibotánica, 38(1405–2768), pp. 1–26.

Giraldo-Kalil, L.J. & Núñez-Farfán, J. (2022): Patterns of leaf trait variation underlie ecological differences among sympatric tree species

of *Damburneya* in a tropical rainforest. figshare. Dataset. https://doi.org/10.6084/m9.figshare.20452599.v4

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

Grinnell, J. (1917) The niche-relationships of the California Thrasher. The Auk, 34, 427–433. https://doi.org/10.2307/4072271

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. Ecological Modelling, 135, 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Gutiérrez-García, G. & Ricker, M. (2011) Climate and climate change in the region of Los Tuxtlas (Veracruz, Mexico): a statistical analysis. Atmósfera, 24, 347–373. Available at: https://www.scielo.org.mx/scielo.php?script=sci_arttext&pid=S0187-62362011000400001

Harrison, S.P., Prentice, I.C., Barboni, D., Kohfeld, K.E., Ni, J. & Sutra, J.P. (2010) Ecophysiological and bioclimatic foundations for a global plant functional classification. Journal of Vegetation Science, 21, 300–317. https://doi.org/10.1111/j.1654-1103.2009.01144.x

Hengl, T., De Jesus, J.M., Heuvelink, G.B.M., et al. (2017) SoilGrids250m: global gridded soil information based on machine learning, PLoS ONE, 12, 1-40. https://doi.org/10.1371/journal.pone.0169748

Hijmans, R.J. (2021) terra: spatial data analysis. R package.Version 1.3-22. Available at: https://cran.r-project.org/package=terra

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2020) dismo: species distribution modeling. R package. R package. Version 1.3-3. Available at: https://cran.r-project.org/package=dismo

Holdridge, L.R. (1947) Determination of world plant formations from simple climatic data source. Science, 105, 367–368. https://doi.org/10.1126/science.105.2727.367

Hutchinson, G.E. (1957) Concluding remarks. Cold Spring Harbor Symposia on quantitative biology, 22, 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Hutchinson, G.E. (1978) An introduction to population ecology. Yale University Press, New Haven, Connecticut, USA.

Instituto Nacional de Estadística y Geografía de México —INEGI —, Consejo Nacional para el Conocimiento y Uso de la Biodiversidad — CONABIO — & Intituto Nacional de Ecología (2008) Ecorregiones Terrestres de México. Mapa, Escala 1:1000000. México. Available at: http://geoportal.conabio.gob.mx/metadatos/doc/html/ecort08gw.html

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996) A global analysis of root distributions for terrestrial biomes. Oecologia, 108, 389–411. https://doi.org/10.1007/BF00333714

Kass J.M., Vilela B., Aiello-Lammens, M.E., Muscarella R., Merow C. & Anderson R.P. (2018). Wallace: a flexible platform for reproducible modeling of species niches and distributions built for community expansion. Methods in Ecology and Evolution. 9, 1151–1156. https://doi.org/10.1111/2041-210X.12945

Kass, J.M., Muscarella, R., Galante, P.J., Bohl, C.L., Pinilla-Buitrago, G.E., Boria, R.A., Soley-Guardia, M., & Anderson, R.P. (2021) ENMeval 2.0: redesigned for customizable and reproducible modelling of species' niches and distributions. Methods in Ecology and Evolution, 12:1602–1608. https://doi.org/10.1111/2041-210X.13628

Kass J.M., Pinilla-Buitrago G.E., Paz A., et al. (2023) Wallace 2: a shiny app for modeling species niches and distributions redesigned to facilitate expansion via module contributions. Ecography, 2023, e06547. https://doi.org/10.1111/ecog.06547

Laso Bayas, J.C., See, L., Georgieva, I., et al. (2022) Drivers of tropical forest loss between 2008 and 2019. Scientific Data, 9, 1–8. https://doi.org/10.1038/s41597-022-01227-3

Lorea-Hernández, F.G. (2002) La familia Lauraceae en el sur de México: diversidad, distribución y estado de conservación. Boletín de la Sociedad Botánica de México, 71, 59–70. Available at: https://www.redalyc.org/articulo.oa?id=57707104

MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist, 101, 377–385. https://doi.org/10.1086/282505

Martin, M. P., Peters C. M., Asbjornsen H., & Ashton M. S. 2021. Diversity and niche differentiation of a mixed pine–oak forest in the Sierra Norte, Oaxaca, Mexico. Ecosphere 12, e03475. https://doi.org/10.1002/ecs2.3475

Martínez-Ramos, M. (2006) Aspectos ecológicos de la selva húmeda en la región Lacandona: perspectivas para su estudio y conservación. In: Manejo, Conservación y Restauración de Recursos Naturales en México: Perspectivas desde la Investigación Científica. (ed. by K. Oyama and A. Castillo), pp. 279–292, Siglo XXI, UNAM, México.

Martínez-Ramos, M., Anten, N.P.R. & Ackerly, D.D. (2009) Defoliation and ENSO effects on vital rates of an understorey tropical rain forest palm. Journal of Ecology, 97, 1050–1061. https://doi.org/10.1111/j.1365-2745.2009.01531.x

McPherson, J.M., Jetz, W. & Rogers, D.J. (2004) The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? Journal of Applied Ecology, 41, 811–823. Available at: https://doi.org/10.1111/j.0021-8901.2004.00943.x

Merow, C., Smith, M.J. & Silander, J.A. (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography, 36, 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

Mod, H.K., Scherrer, D., Luoto, M. & Guisan, A. (2016) What we use is not what we know: environmental predictors in plant distribution models. Journal of Vegetation Science, 27, 1308–1322. https://doi.org/10.1111/jvs.12444

Morecroft, M. D. & Paterson, J.S. (2006) Effects of temperature and precipitation changes on plant communities. In: Plant growth and climate change. (ed. by J.I.L. Morison and Michael D. Morecroft), pp. 146-165. Blackwell Publishing Ltd, Ames, Iowa, USA. https://doi.org/10.1093/aob/mcm188

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M. & Anderson, R.P. (2014) ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models . Methods in Ecology and Evolution, 5, 1198–1205. https://doi.org/10.1111/2041-210x.12261

Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K. & Toxopeus, A.G. (2014) Where is positional uncertainty a problem for species distribution modelling? Ecography, 37, 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x

Navarrete-Segueda, A., Martínez-Ramos, M., Ibarra-Manríquez, G., Vázquez-Selem, L. & Siebe, C. (2018) Variation of main terrestrial carbon stocks at the landscape-scale are shaped by soil in a tropical rainforest. Geoderma, 313, 57–68. https://doi.org/10.1016/j.geoderma.2017.10.023

Ochoa-Zavala, M. , Osorio-Olvera L., Cerón-Souza, I., Rivera-Ocasio E., Jiménez-Lobato, V. & Núñez-Farfán, J. (2022) Reduction of genetic variation when far from the niche centroid: prediction for mangrove species. Frontiers in Conservation Science, 2:795365. https://doi.org/10.3389/fcosc.2021.795365

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., et al. (2001) Terrestrial ecoregions of the world: a new map of life on earth. BioScience, 51, 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Ortiz-Rodríguez, A.E., Ramírez-Barahona, S., González Hernández, D. & Lorea-Hernández, F. (2018) Past climatic fluctuations are associated with morphological differentiation in the cloud forest endemic tree *Ocotea psychotrioides* (Lauraceae). Plant Systematics and Evolution, 304, 607–617. https://doi.org/10.1007/s00606-018-1492-5

Pacala, S.W., & J. Roughgarden. (1985). Population experiments with the *Anolis* lizards of St. Maarten and St. Eustatius. Ecology, 66,129–141. https://doi.org/10.2307/1941313

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography, 12, 361–371. https://doi.org/10.1046/j.1466-822X.2003.00042.x

Peterson, T.A. (2011) Ecological niche conservatism: a time-structured review of evidence. Journal of Biogeography, 38, 817-827. https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2699.2010.02456.x

Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. Science, 285, 1265–1267. https://doi.org/10.1126/science.285.5431.1265

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. & Araújo, M.B. (2011) Ecological niches and geographic distributions. Princeton University Press, Princeton, NJ, USA.

Phillips, O.L., Núñez Vargas, P., Monteagudo, A.L., Cruz, A.P., Zans, M.E.C., Sánchez, W.G., Yli-Halla, M., Rose, S. (2003) Habitat association among Amazonian tree species: a landscape-scale approach. Journal of Ecology, 91, 757–775. https://doi.org/10.1046/j.1365-2745.2003.00815.x

Phillips, S.J., Dudík, M. & Schapire, R.E. (2022) Maxent software for modeling species niches and distributions. Available at: http://biodiversityinformatics.amnh.org/open_source/maxent/

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling, 190, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E. & Blair, M.E. (2017) Opening the black box: an open-source release of Maxent. Ecography, 40, 887–893. https://doi.org/10.1111/ecog.03049

Poggio, L., De Sousa, L.M., Batjes, N.H., Heuvelink, G.B.M., Kempen, B., Ribeiro, E. & Rossiter, D. (2021) SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. Soil, 7, 217–240. https://doi.org/10.5194/soil-7-217-2021

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.r-project.org/

Roa-Fuentes, L.L., Templer, P.H. & Campo, J. (2015) Effects of precipitation regime and soil nitrogen on leaf traits in seasonally dry tropical forests of the Yucatan Peninsula, Mexico. Oecologia, 179, 585–597. https://doi.org/10.1007/s00442-015-3354-y

Rodríguez-Sánchez, E., Giraldo-Kalil, L.J. & Núñez-Farfán, J. (2022) Diversity of insects associated to the fruits of four tree species of Lauraceae from Los Tuxtlas region, Mexico: an annotated and illustrated taxonomic list. Revista Mexicana de Biodiversidad, 93, e934178. https://doi.org/10.22201/ib.20078706e.2022.93.4178

Rodríguez-Sánchez, F. & Arroyo, J. (2008) Reconstructing the demise of Tethyan

plants: climate-driven range dynamics of *Laurus* since the Pliocene. Global Ecology and Biogeography, 17, 685–695. https://doi.org/10.1111/j.1466-8238.2008.00410.x

Rodríguez-Sánchez, F., Guzmán, B., Valido, A., Vargas, P. & Arroyo, J. (2009) Late Neogene history of the laurel tree (*Laurus* L., Lauraceae) based on phylogeographical analyses of Mediterranean and Macaronesian populations. Journal of Biogeography, 36, 1270–1281. https://doi.org/10.1111/j.1365-2699.2009.02091.x

Rohwer, J.G. (1993) Lauraceae: *Nectandra*. Flora Neotropica. New York Botanical Garden Press, New York, New York, USA.

Rohwer, J.G. & Kubitzki, K. (1993) Ecogeographical differentiation in *Nectandra* (Lauraceae), and its historical implications. Botanica Acta, 106, 88–99. https://doi.org/10.1111/j.1438-8677.1993.tb00342.x

Rzedowski, J. (2006) Vegetacion de México. Primera Edición digital. México: Comision Nacional para el Conocimiento y Uso de la Biodiversidad.

Shivaprakash, K. N., Rajanna, J. M., Gunaga, S. V., Ravikanth, G., Vasudeva, R., Shaanker, R. U., & Dayanandan, S. (2022). The flooded habitat adaptation, niche differentiation, and evolution of Myristicaceae trees in the Western Ghats biodiversity hotspot in India. Biotropica, 54, 1349–1362. https://doi.org/10.1111/btp.13078

Sillero, N., Arenas-Castro, S., Enriquez-Urzelai, U., Vale, C.G., Sousa-Guedes, D., Martínez-Freiría, F., Real, R., & Barbosa, A.M. (2021) Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. Ecological Modelling, 456, 109671. https://doi.org/10.1016/j.ecolmodel.2021.109671

Silvertown, J. 2004. Plant coexistence and the niche. Trends in Ecology and Evolution, 19, 605–611. https://doi.org/10.1016/j.tree.2004.09.003

Simões, M., Romero-Alvarez, D., Nuñez-Penichet, C., Jiménez, L. & Cobos, M.E. (2020) General theory and good practices in ecological niche modeling : a basic guide. Biodiversity Informatics, 15, pp. 67–68. https://doi.org/10.17161/bi.v15i2.13376

Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters, 10, 1115–1123. https://doi.org/10.1111/j.1461-0248.2007.01107.x

Soberón, J. & Peterson, T.A. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics, 2, 1–10. https://doi.org/10.1093/wber/lhm022

Sollins, P. (1998) Factors influencing species composition in tropical lowland rain forest: does soil matter? Ecology, 79, 23–30. https://doi.org/10.1890/0012-9658(1998)079[0023:FISCIT]2.0.CO;2

Sommer-Cervantes, I., L. Flores-Delgadillo, & M. Gutiérrez-Ruiz. (2003) Caracterización de los suelos de la Estación de Biología Tropical Los Tuxtlas. In: Ecología del suelo en la selva tropical húmeda de México (ed. by J. Álvarez-Sánchez and E. Naranjo-García), pp. 17– 69. Instituto de Ecología, A.C., Instituto de Biología, Facultad de Ciencias, UNAM., Xalapa, México.

Sri-Ngernyuang, K., Kanzaki, M., Mizuno, T., et al. (2003) Habitat differentiation of Lauracaceae species in a tropical lower montane forest in northern Thailand. Ecological Research, 18, 1–14. https://doi.org/10.1046/j.1440-1703.2003.00539.x

Srinivas, S.G. & Krishnamurthy, Y.L. (2019) Altitude and ecological distribution of genus *Litsea* (Lauraceae) in Western Ghats of Karnataka, India. Journal of Tropical Forestry and Environment, 9, 108–119. https://doi.org/10.31357/jtfe.v9i2.4473

Syphard, A.D. & Franklin, J. (2010) Species traits affect the performance of species distribution models for plants in southern California. Journal of Vegetation Science, 21, 177–189. https://doi.org/10.1111/j.1654-1103.2009.01133.x

Thuiller, W. (2013) On the importance of edaphic variables to predict plant species distributions - limits and prospects. Journal of Vegetation Science, 24, 591–592. https://doi.org/10.1111/jvs.12076

Trofimov, D., Rudolph, B. & Rohwer, J.G. (2016) Phylogenetic study of the genus *Nectandra* (Lauraceae), and reinstatement of *Damburneya*. Taxon, 65, 980–996. https://doi.org/10.12705/655.3

Trofimov, D., De Moraes, P.L.R. & Rohwer, J.G. (2019) Towards a phylogenetic classification of the *Ocotea* complex (Lauraceae): classification principles and reinstatement of *Mespilodaphne*. Botanical Journal of the

Linnean Society, 190, 25–50. https://doi.
org/10.1093/botlinnean/boz010

Tsuneki, S., Kato, H. & Murakami, N. (2014)
Ecological and genetic differentiation in
Persea boninensis (Lauraceae) endemic to
the Bonin (Ogasawara) Islands. Plant Species
Biology, 29, 16–24. https://doi.org/10.1111/
j.1442-1984.2012.00383.x

van der Werff, H. (1992) Substrate preference of
Lauraceae and ferns in the Iquitos area, Peru.
Candollea, 47, 11–20.

Velazco, S.J.E., Galvão, F., Villalobos, F. & De Marco
Júnior, P. (2017) Using worldwide edaphic
data to model plant species niches: An
assessment at a continental extent. PLoS ONE,
12, 1–24. https://doi.org/10.1371/journal.
pone.0186025

von Thaden, J.J., Laborde, J., Guevara, S. & Venegas-
Barrera, C.S. (2018) Forest cover change
in the Los Tuxtlas Biosphere Reserve and
its future: the contribution of the 1998
protected natural area decree. Land Use Policy,
72, 443–450. https://doi.org/10.1016/j.
landusepol.2017.12.040

von Thaden, J.J., Laborde, J., Guevara, S. & Mokondoko-
Delgadillo, P. (2020) Dinámica de los cambios
en el uso del suelo y cobertura vegetal en la
Reserva de la Biosfera Los Tuxtlas (2006-
2016) Revista Mexicana de Biodiversidad,
91, e913190. https://doi.org/10.22201/
ib.20078706e.2020.91.3190

Warren, D.L. & Seifert, S.N. (2011) Ecological niche
modeling in Maxent: the importance of model
complexity and the performance of model
selection criteria. Ecological Applications, 21,
335–342. https://doi.org/10.1890/10-1171.1

Warren, D.L., Glor, R.E. & Turelli, M. (2008)
Environmental niche equivalency versus
conservatism: Quantitative approaches
to niche evolution. Evolution, 62, 2868–
2883. https://doi.org/10.1111/j.1558-
5646.2008.00482.x

Warren, D.L., Glor, R.E. & Turelli, M. (2010)
ENMTools: a toolbox for comparative studies
of environmental niche models. Ecography, 33,

607–611. https://doi.org/10.1111/j.1600-
0587.2009.06142.x

Weil, R.R. & Brady, N.C. (2017) The nature and
properties of soils (15th edn). Pearson
Education, Boston, Massachusetts, USA.

Wiens, J.J. (2011) The niche, biogeography
and species interactions. Philosophical
Transactions of The Royal Society B, 366,
2336–2350. https://doi.org/10.1098/
rstb.2011.0059

Wiens, J.J. & Graham, C.H. (2005) Niche
conservatism: integrating evolution, ecology,
and conservation biology. Annual Review
of Ecology, Evolution, and Systematics, 36,
519–539. https://doi.org/10.1146/annurev.
ecolsys.36.102803.095431

Wiens, J.J., Ackerly, D.D., Allen, A.P., et al. (2010)
Niche conservatism as an emerging principle
in ecology and conservation biology.
Ecology Letters, 13, 1310–1324. https://
doi.org/10.1111/j.1461-0248.2010.01515.x

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., et al. (2008)
Effects of sample size on the performance of
species distribution models. Diversity and
Distributions, 14, 763–773. https://doi.
org/10.1111/j.1472-4642.2008.00482.x

Wright, I.J., Reich, P.B., Westoby, M., et al. (2004) The
worldwide leaf economics spectrum. Nature,
428, 821–827. https://doi.org/10.1038/
nature02403

Wright S.J. (2002) Plant diversity in tropical forests: a
review of mechanisms of species coexistence.
Oecologia, 130,1-14. https://link.springer.
com/article/10.1007/s004420100809

Zuquim, G., Costa, F.R.C., Tuomisto, H., Moulatlet, G.M.
& Figueiredo, F.O.G. (2020) The importance
of soils in predicting the future of plant
environmental suitability in a tropical forest.
Plant and Soil, 450, 151–170. https://doi.
org/10.1007/s11104-018-03915-9