



SPATIAL INTERACTIONS IN NOVEL HOST-PLANTS OF THE BLUE MORPHO IN MEXICO †

[INTERACCIONES ESPACIALES EN NUEVAS PLANTAS HOSPEDERAS DE LA MORPHO AZUL EN MÉXICO]

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SUMMARY

Background. Plants in the neotropical region provide different ecological services and sustain entomofauna biodiversity. The butterfly, *Morpho helenor montezuma*, has high economic value worldwide, derived from recreational activities. To enhance its sustainable use, it is important to know the spatial relationship of this species with its host-plants. **Objective.** To estimate the potential geographical areas in Mexico of three host-plants: *Bauhinia divaricata*, *Andira inermis* and *Pterocarpus rohrii* and their spatial relationship with *M. helenor montezuma*. **Methodology.** Distribution models of the species were generated using MaxEnt, employing predictive variables based on temperature and precipitation, and records of presence data. Subsequently, a joint analysis of layers was performed to determine the overlap in the distributions. **Results.** The models were appropriate as the area under the curve ranged from 0.86 to 0.96. The broadest potential host-plant distribution was for *B. divaricata* (30%), followed by *A. inermis* (21%) and *P. rohrii* with 7% of the country. In general, the joint distribution of the plant species is neotropical, and can be found in Veracruz, Tabasco, Chiapas and Oaxaca. **Implications.** The knowledge of the distributions of the plants allows their prioritization for conservation management and entomotourism. **Conclusion.** The joint distribution of *B. divaricata* against that of *M. helenor montezuma* had the greatest overlap (61%), with regard to the type of climate the highest concordance was found with *P. rohrii*. Pertinence to entomotourism and conservation planning is discussed. **Keywords:** Entomotourism; Fabaceae; plant-butterfly relationship; species distribution modelling; sustainable management.

RESUMEN

Antecedentes. Las plantas en la región neotropical suministran diferentes servicios ecológicos y sostienen la biodiversidad de la entomofauna. La mariposa *Morpho helenor montezuma*, posee un alto valor económico a nivel mundial, derivado de actividades recreacionales. Para favorecer su aprovechamiento sustentable, es importante conocer la relación espacial de esta especie con sus plantas hospederas. **Objetivo.** Estimar el área geográfica potencial en México de tres plantas hospederas: *Bauhinia divaricata*, *Andira inermis* y *Pterocarpus rohrii* y su relación espacial con la distribución de *M. helenor montezuma*. **Metodología.** Los modelos de distribución para las especies fueron generados con MaxEnt, se utilizaron variables predictoras basadas en temperatura y precipitación, y registros de datos de presencia. Posteriormente, se realizó un análisis conjunto de capas para conocer el traslape en las distribuciones. **Resultados.** Los modelos fueron apropiados, el área bajo la curva osciló entre 0.86 a 0.96. La distribución potencial más amplia de las hospederas la tuvo *B. divaricata* (30%), le siguió *A. inermis* (21%) y *P. rohrii* con 7% del país. En general, la distribución conjunta de las especies de plantas es neotropical y se pueden encontrar en Veracruz, Tabasco, Chiapas y Oaxaca. **Implicaciones.** El conocimiento de las distribuciones de las plantas permite su priorización para fines de manejo de conservación y entomoturismo. **Conclusión.** La distribución conjunta de *B. divaricata* con la de *M. helenor montezuma* tuvo el mayor traslape (61%). En relación al tipo de clima, la mayor concordancia se encontró con *P. rohrii*. La pertinencia para entomoturismo y planeación de conservación se discute. **Palabras claves:** Entomoturismo, Fabaceae, relación planta-mariposa, modelado de distribución de especies, manejo sustentable.

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INTRODUCTION

The neotropical region of Latin America is abundant in tropical tree species, which constitute the arboreal and shrub layer of the evergreen, subperennifolia and deciduous forests of the Mexican transition zone (Morrone, 2014). Here, we study the distribution of three species of the family Fabaceae: *Andira inermis* (W. Wright) Kunth ex DC. E and *Pterocarpus rohrii* Vahl and *Bauhinia divaricata* (L.). These plants provide environmental services such as oxygen and soil erosion control, have medicinal properties and their wood is used as a construction material. In addition, they serve as refuge and food for the lepidoptero fauna, among which stands out for its economic and ornamental importance the blue morpho, *Morpho helenor montezuma* Guenée, 1859 (Gálvez-Ruiz et al., 2013, Lopez-Collado et al., 2016).

Species of tropical butterflies exist as part of the range of natural resources available for human use in Mexico for aesthetic or ornamental purposes. The states of Chiapas, Oaxaca and Veracruz have high species richness, endemism, and production, within their high diversity of ecosystems and landscapes (Bousquets-Llorente et al., 2006, 2014). The most studied butterfly families are the Lycaenidae, Papilionidae, Pieridae, Riodinidae and the Nymphalidae, of which the last contains 10 subfamilies, 130 genera and 413 species (Lamas, 2000, Zhang et al., 2018). Some species of this family have economic value, such as *M. helenor*, which is highly demanded on the national and international markets; commercially, this species is highly prized in the state of Veracruz for its iridescent blue color and size (Cotrina, 2008, Lopez-Collado et al., 2016). The estimated potential surface area with bioclimatic factors favoring *M. helenor* is 23% of the national territory (Jacinto-Padilla et al., 2017), which benefits ecotourism activities (Parque Ecológico Xcaret, 2019, El Parque y Mariposario Yéé lo Beé, 2019), as well as the elaboration of crafts and accessories for sale at tourist sites (Jacinto-Padilla et al., 2017). Currently, the genus *Morpho* contains approximately 30 species and several subspecies, and the larvae are polyphagous, feeding on plants of different species and families. The Fabaceae, Convolvulaceae and Menispermaceae predominate as the families with the greatest number of host-plant species (Ehrlich and Raven, 1964, Ramírez-García et al., 2014, Robinson, 2010, Vásquez-Bardales et al., 2017, Young, 1975), which favors modelling over a wide geographic space containing appropriate climatic conditions for their growth and survival. Wild *M. helenor* larvae predominantly feed on *A. inermis*, *B. divaricata*, *Lonchocarpus oliganthus* F. J. Herm., *Mucuna urens* (L.), and *P. rohrii* (Suvák, 2015, Vega-Araya, 2011, García-García, G., Colegio de Postgraduados. Personal communication, September 27, 2017).

In addition to serving as host-plants for the blue morpho, these species fulfill different medicinal, ecological and agronomic functions. For example, *B. divaricata* has anti-diabetic, anti-inflammatory, antimicrobial and anti-oxidant properties (Barragán et al., 2010, Mendes and Bogle, 2015, Tostes et al., 2019). The species *A. inermis* is used as a shade tree in coffee plantations to facilitate nitrogen fixation and erosion control (Prado et al., 2018), and in carbon capture (Chen and Goh, 2017). This species also provides ecological services where the flowers provide nectar and pollen for bee communities in Costa Rica and the fruits serve as food for bats and weevils (genus *Cleogonus*) (Frankie et al., 2009, Janzen et al., 2018, Pennington et al., 2018). Ethno-botanically, this plant has been used in traditional medicine as a vermifuge and purgative (Da Silva et al., 2000). The host-plant species *P. rohrii* is also used in ethno-botany because of its anti-microbial activity (Kloucek et al., 2007), and the genus is of global importance in the wood industry because its red pigments are used as dyes in textiles, medicine and food (Arunkumar and Joshi, 2014).

Studies on the joint distribution of interacting species tend to be oriented towards the conservation of biodiversity and its functions in threatened environments, mainly due to the diverse plant-lepidoptera ecological interactions, including herbivory, predation, pollination and dispersion (Koi, 2017, Patel et al., 2017, Simonetti and Devoto, 2018, Zhang et al., 2018). An example of this latter relationship is that of the monarch butterfly *Danaus plexippus* (L.), from which the occurrence and abundance of eggs and larvae in several host-plant species in the genus *Asclepias* have been recorded spatially and temporally (Brower et al., 2018). Another research interest address the role of generalization in the distribution of host-plants and butterflies (Hardy and Otto, 2014). Generalization is explained by scarceness, inconsistency and unreliability in food resources (Wiklund and Friberg, 2009) and by evolution in larva and adult traits of some neotropical *Adelpha* spp. that lead to a diversification in the use of plant resources (Ebel et al., 2015). Species distribution modeling has been applied to study the effect of climate change on the distribution of *Arícia morronensis*, an endemic butterfly in Spain and its host-plants and to *Abies religiosa* and *Danaus plexippus* in Mexico (Sáenz-Romero et al., 2012; Zarzo-Arias et al., 2019). In the case of lepidopterans, its interaction with humans through reserves, protected areas or natural parks, may lead to conflicts of different kinds regarding the management of biodiversity (Esquivel-Rios et al., 2014; Putri, 2016). Therefore, our objective was to estimate the potential distribution in Mexico of *B. divaricata*, *A. inermis* and *P. rohrii* and their spatial interaction with *M. helenor montezuma*, regarding the fitness of the environmental conditions

as related to entomotourism activities (Lemelin, 2015) and the practical management of these species on a wide area scale (Sofaer et al., 2019).

MATERIALS AND METHODS

Selection of the host-plants and butterfly species

Due to its aesthetic value (Lopez-Collado et al., 2016), *M. helenor montezuma* was chosen as the target species, including three reported host-plant species: *A. inermis*, *B. divaricata* and *P. rohrii*. The records of presence of these species in Mexico were compiled from different databases: UNIBIO (2019), LIFEMAPPER (2019), GBIF (2019), CONABIO (2019), and Cruz-Salas (2011). The geo-referenced points were spatially projected to verify their location and eliminate duplicate records. Table 1 presents the records used to calculate the potential species distribution. In the case of *M. helenor*, its distribution at the species level is already known (Jacinto-Padilla et al., 2017), but was updated with new presence records (Table 1) at the sub-species level of *M. helenor montezuma*. In the present study, the analysis was oriented to the host-plants and the distribution of the butterfly served to make a comparative host-plant x host analysis.

Table 1. Class, family, species and number of presence records analyzed to generate the potential distribution models for the host-plant species and the blue morpho in Mexico.

Class	Family	Species	Records
Dicotyledon	Fabaceae	<i>Bauhinia divaricata</i>	1789
Dicotyledon	Fabaceae	<i>Andira inermis</i>	353
Dicotyledon	Fabaceae	<i>Pterocarpus rohrii</i>	140
Insecta	Nymphalidae	<i>Morpho helenor montezuma</i>	391

Selection of bio-climatic variables

Based on 19 variables, including precipitation and temperature, downloaded from the Worldclim database (Hijmans et al., 2005, Fernández-Eguiarte et al., 2010), a principal coordinate analysis (PCoA) was performed with the values extracted from the records of presence for *B. divaricata*, *A. inermis*, *P. rohrii* and

M. helenor montezuma. These values were processed to assess the similarity among the variables using the Hellinger h dissimilarity index (Wilson, 2011), and a 2D Cartesian space was then constructed to visualize similarities and exclude variables with high similarity ($1-h > 0.7$). The purpose of this selection process was to construct parsimonious models to maximize the dissimilarity among the predictor variables and reduce the interdependence between them. In the case of *M. helenor montezuma*, the PCoA analysis made it possible to construct a more parsimonious model by reducing the number of bioclimatic variables to four (Table 2, Fig.1) in relation to the model previously estimated by Jacinto-Padilla et al. (2017). Here, three variables are related to temperature and one to precipitation; values that can occur in summer and winter (warm and cold seasons), or periods of rain and drought. These layers can be related to biological phases of rest, such as in winter when hibernation or diapause occurs, while during summer conditions are favorable for population development (Jacobo-Cuellar et al., 2005, Logarzo and Gandolfo, 2005, Nokelainen et al., 2018, Posledovich et al., 2017). For the host-plants, the bioclimatic variables selected as predictors were the same for all three species (Table 2, Fig. 1).

Table 2. Bioclimatic variables selected as predictors to generate the potential distribution models of *B. divaricata*, *A. inermis*, *P. rohrii* and *M. helenor montezuma* in Mexico.

Bio-climatic variable code	Variable name	Target Species
BIO 01	Annual average temperatura	Host-plant
BIO 07	Annual temperature range for Mexico	Host-plant
BIO 12	Annual precipitation	Host-plant
BIO 15	Seasonal precipitation (coefficient of variation)	Host-plant
BIO 16	Precipitation during the most rainy period	Host-plant
BIO 17	Precipitation during the most dry period	Host-plant
BIO 02	Mean maximum and minimum temperature	Butterfly
BIO 04	Seasonal temperatura	Butterfly
BIO 11	Average temperature of the coldest season	Butterfly
BIO 19	Precipitation during the coldest season	Butterfly

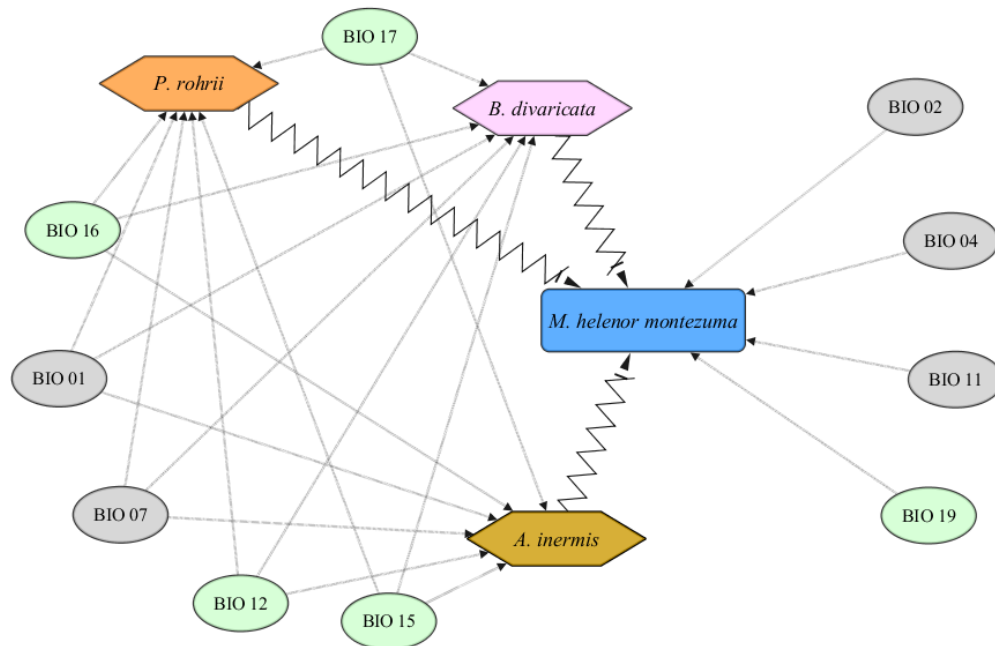


Fig. 1. Acyclic network shows the types of predictive bio-climatic variables (green ellipses are for precipitation and gray are for temperature) selected to generate the potential distribution models of the host-plants (hexagons) and the blue morpho (blue rectangle). The zigzag lines correspond to the overlap of the host-plants with *M. helenor montezuma*.

Distribution model generation, their spatial overlap and type of climate

The distribution models of each species were constructed separately with the program Maximum Entropy Species Distribution Modelling (MaxEnt), v 3.4.1 (Phillips et al., 2017). Data were entered as bioclimatic layers (Fig. 1) and records of the presence of the three host-plant species and the blue morpho, projected for all of Mexico, were used (Table 1). The basic configuration parameters were: a 30% random test percentage, a regulation multiplier of 1, a maximum number of 10,000 background points, cross validation, and a logistic output format. The Area Under the Curve (AUC) was used to measure the goodness of fit of the models. Subsequently, to facilitate visualization and interpretation, the distribution maps were simplified to presence-absence maps with a cut-off of 0.2 (Jacinto-Padilla et al., 2017), and the percentages of the potential geographical distribution for Mexico were calculated. The overlap between the distribution of plant species A with that of the blue morpho B was calculated as $100 * (A \cap B) / (A \cup B)$. To visualize the joint spatial distribution of the three host-plant species, each binary raster layer was smoothed with a local filter to remove the noise and vectorized. We also calculated the temperature and

precipitation ranges within the potential distribution of the host-plants and the blue morpho. To do so, we extracted a random sample without replacement of 140 points in the presence records for each species and plotted them in 3D along with the bioclimatic variables BIO 01, BIO 12 and BIO 17 due to their relevance and not presenting correlations. In addition, for each model of potential distribution, the most dominant climate types were obtained based on the Köppen global classification (Rubel and Kottek, 2010). Analyses were performed with R v3.6.2 (R Core Team, 2019), Mathematica v11.3 (Wolfram Research, 2019) and maps were generated using Quantum GIS v3.10 (QGIS Development Team, 2019).

RESULTS AND DISCUSSION

Host-plant distributions and their spatial overlap with the blue morpho

Among the host-plant potential distribution models, *B. divaricata* covered the largest area of the country (30%), extending from the northern Gulf of Mexico to the Yucatan Peninsula and the Pacific coast (Fig. 2). Second was *A. inermis* with 21%, with its distribution extended towards the northern Pacific coast and part of the southern Gulf of Mexico (Fig. 3). Finally, *P. rohrii* covered only 7% in the southern part of the country

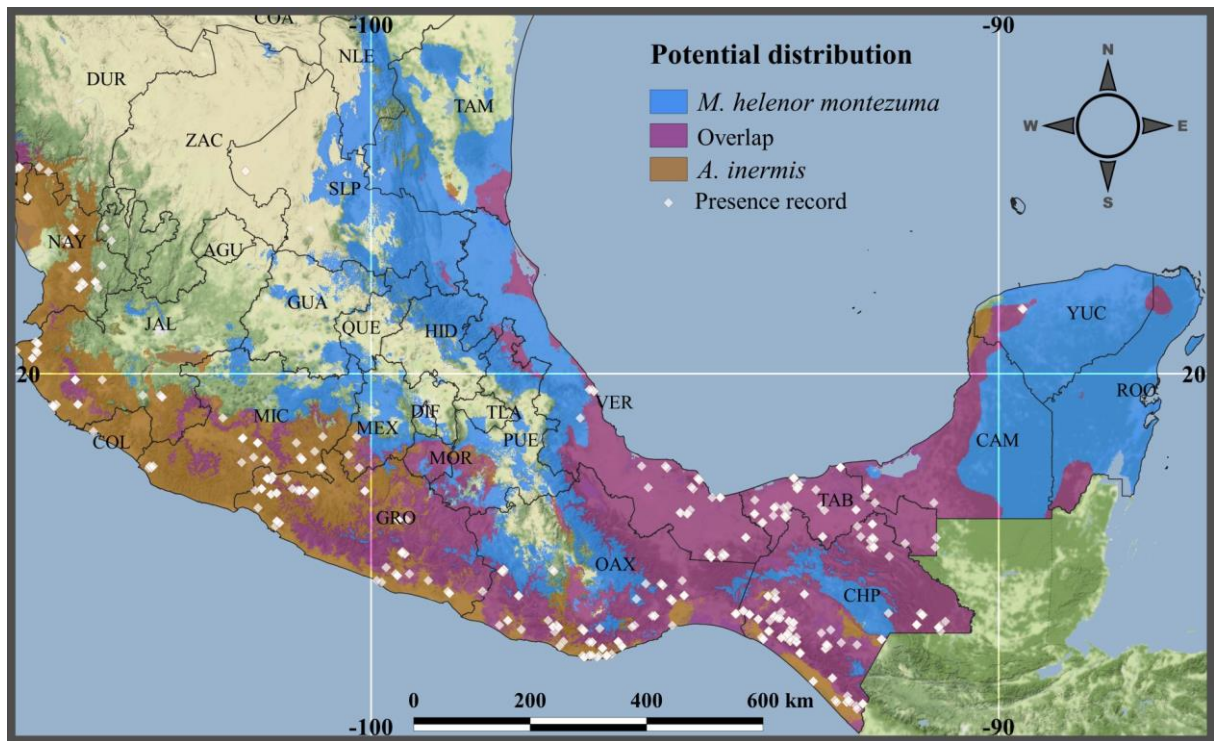


Fig. 3. Potential distribution areas, where brown corresponds to *A. inermis*, violet represents the overlap with *M. helenor montezuma* and blue represents the blue morpho. Diamonds represent presence points of *A. inermis*.

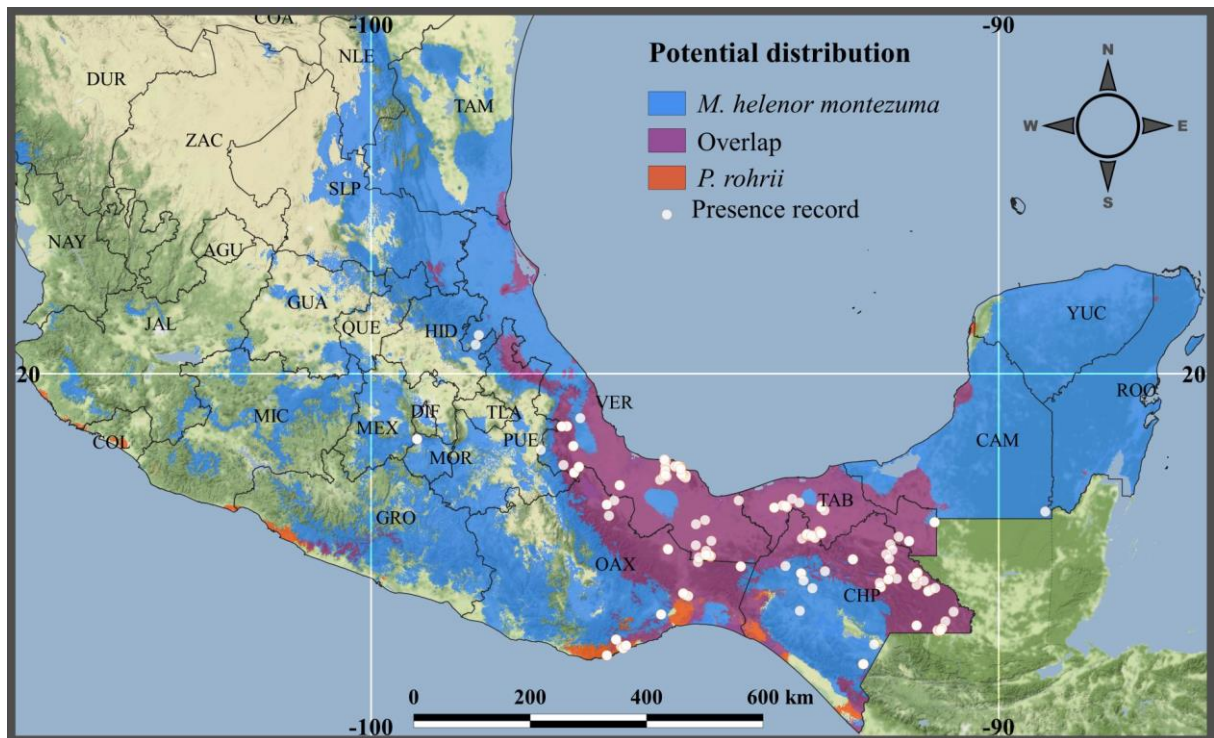


Fig. 4. Potential distribution areas, where orange corresponds to *P. rohrii*, violet represents the overlap with *M. helenor montezuma* and blue represents the blue morpho. Circles represent presence points of *P. rohrii*.

Fig. 5 shows the joint distribution of the host-plant models, where the three species converge in southern Veracruz, Tabasco, Campeche, Chiapas and Oaxaca

due to similar bioclimatic conditions. Here, the first and last two states are considered to have the highest tropical butterfly species richness (Llorente-Bousquets

et al., 2014). However, *B. divaricata* and *A. inermis* extend and overlap along the Pacific coast, concordant with the occurrence of records for the sub-species *M. helenor Octavia* Bates and *M. helenor guerrensis* Le Moutl & Réal (Luis-Martínez et al., 2016, Vargas-Fernández et al., 2008), therefore, these plant species could serve as a source of food. Consequently, it is recommended to implement effective and sustainable management measures to help conserve the blue morpho and its habitat. This may occur by recording sightings made by trained eco-tourists; this is important since most people will have to make such observations at distance, without capturing specimens. Also, by using zoo breeding facilities for entomotourism activities to benefit tourists who are not well trained in identification.

Fig. 6 shows the 3D distribution of a sample without replacement of the presence records of the host-plants and the blue morpho. For the mean annual temperature (variable BIO 01, Table 2), among the three host-plants the values ranged between 15 and 30 °C. As for variable BIO 12 (precipitation), for *B. divaricata* values ranged between 800 to 2000 millimeters per year. The extreme value layer (variable BIO 17), which refers to the precipitation during the driest season of the year, can support this plant species with just 20 to

200 millimeters per year. Thus, it is a plant species that tolerates drought and a variety of habitats ranging from secondary vegetation, low deciduous forest, intermediate sub-deciduous forest and sub-evergreen forest. In addition, nectar-bearing flowers attract insects including butterflies of the genus *Papilio*, and the leaves of many species are recommended as forage in grazing systems during drought and along hedgerows / living fences (Avendaño-Reyes and Acosta-Rosado, 2000, Cab-Jiménez et al., 2015). Yet, *A. inermis* requires conditions similar to *B. divaricata*, except that its average annual precipitation range extends over 4000 millimeters, its habitat is limited to intermediate sub-evergreen forest, it is part of the composition of tropical riparian forest, and has qualities as a pioneer species for regeneration in areas of abandoned crops (Rodríguez-Sosa et al., 2018, Zimmerman et al., 2000). In contrast, *P. rohrii* requires rainfall of approximately 1000 to 5000 millimeters and during the dry season at least 200 to 400 millimeters, confirming its distribution in climates that are more humid and in high evergreen or evergreen forests. Yet, unlike *B. divaricata* that requires little water to survive, this species tolerates flooded soils or wetlands, where its seeds during dry periods can germinate and repopulate these lands (Kloucek et al., 2007).

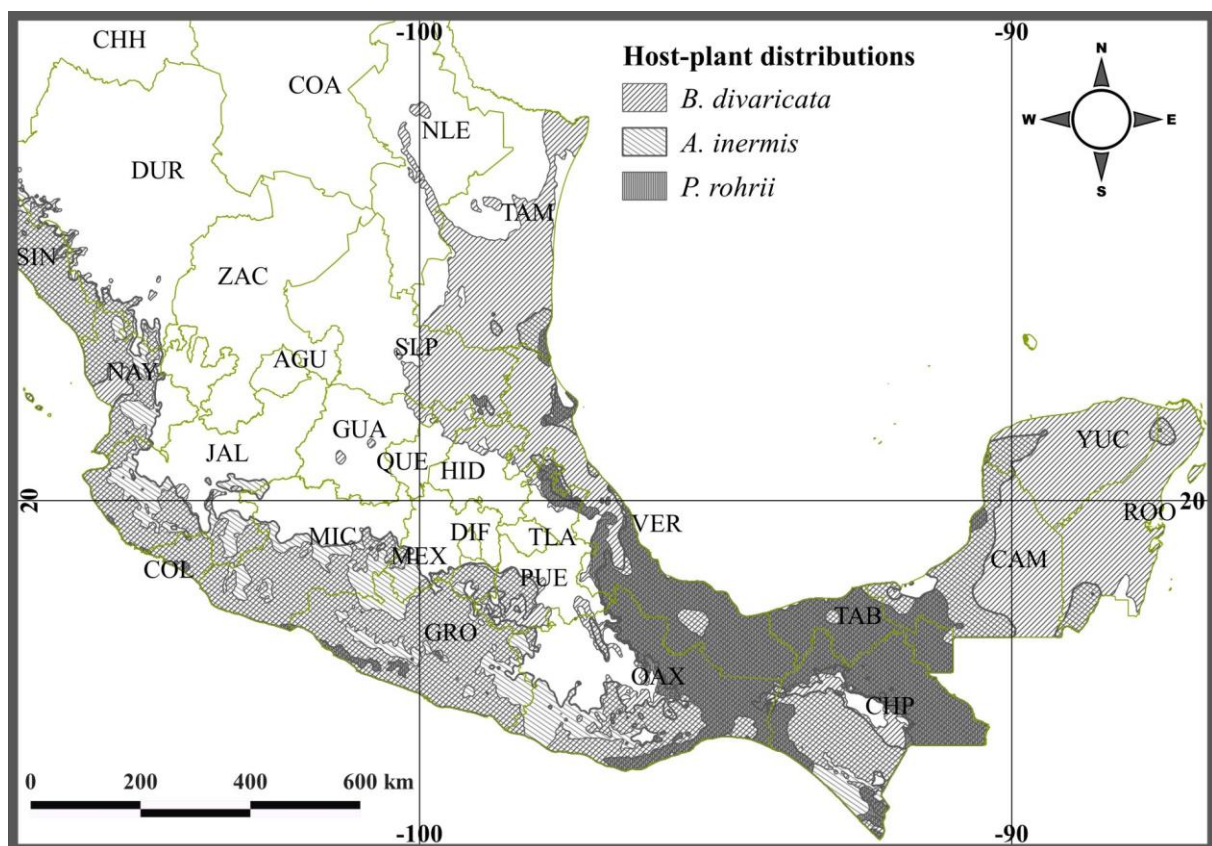


Fig. 5. Overlap of the potential distribution areas of *B. divaricata* (inclined lines to the right), *A. inermis* (inclined lines to the left) and *P. rohrii* (solid gray).

Finally, the distribution of *M. helenor montezuma* falls within the bioclimatic conditions of the three selected host-plants (blue circles), with greater occurrence from 20 to 28 °C, having 1000 to 4000 millimeters of average annual rainfall, and capable of withstanding a dry season receiving only 100 to 400 millimeters of rain. These results strengthen the conclusion that the blue morpho is present at some stage of its biological cycle throughout the year in tropical climates, provided that one of its three host-plants is present. As suggested by Williams (2008) and Kocsis and Hufnagel (2011), temperature and precipitation directly affect butterfly distribution. The higher spatial overlap and similar range values of the bioclimatic variables between this insect with *B. divaricata* suggest they have close bioclimatic requirements.

The percentages of the climate types that predominate in the modelled potential distribution areas of the host-plants and the blue morpho according to the Köppen world classification (Rubel and Kottek, 2010) are presented in Fig. 7. Warm sub-humid temperatures

prevail with rains during summer (Aw), favoring *B. divaricata* (70%), *A. inermis* (59%) and *M. helenor montezuma* (36%), followed by warm humid temperatures with rains during summer (Am) favoring *P. rohrii* (47%) and *M. helenor montezuma* (34%). The third most abundant climate condition was humid warm with rainfall throughout the year (Af) which benefits the distribution of *P. rohrii* (26%) while other climates have similar values for the four species. However, the climate types obtained for each species coincide with the neotropical distribution of Fig. 5 and the overlap between the layers for *B. divaricata* and *A. inermis* along the Gulf and Pacific coasts, both of which have lowland forest and intermediate sub-evergreen vegetation. A similar situation exists with the range of precipitation shown in Fig. 6, where the three host-plant species require summer rains so that the blue morpho can coexist. This suggests a greater potential area of bioclimatic conditions favorable for the natural reproduction of *M. helenor montezuma*, increasing the habitat diversity of this butterfly species (Barranco-León et al., 2016).

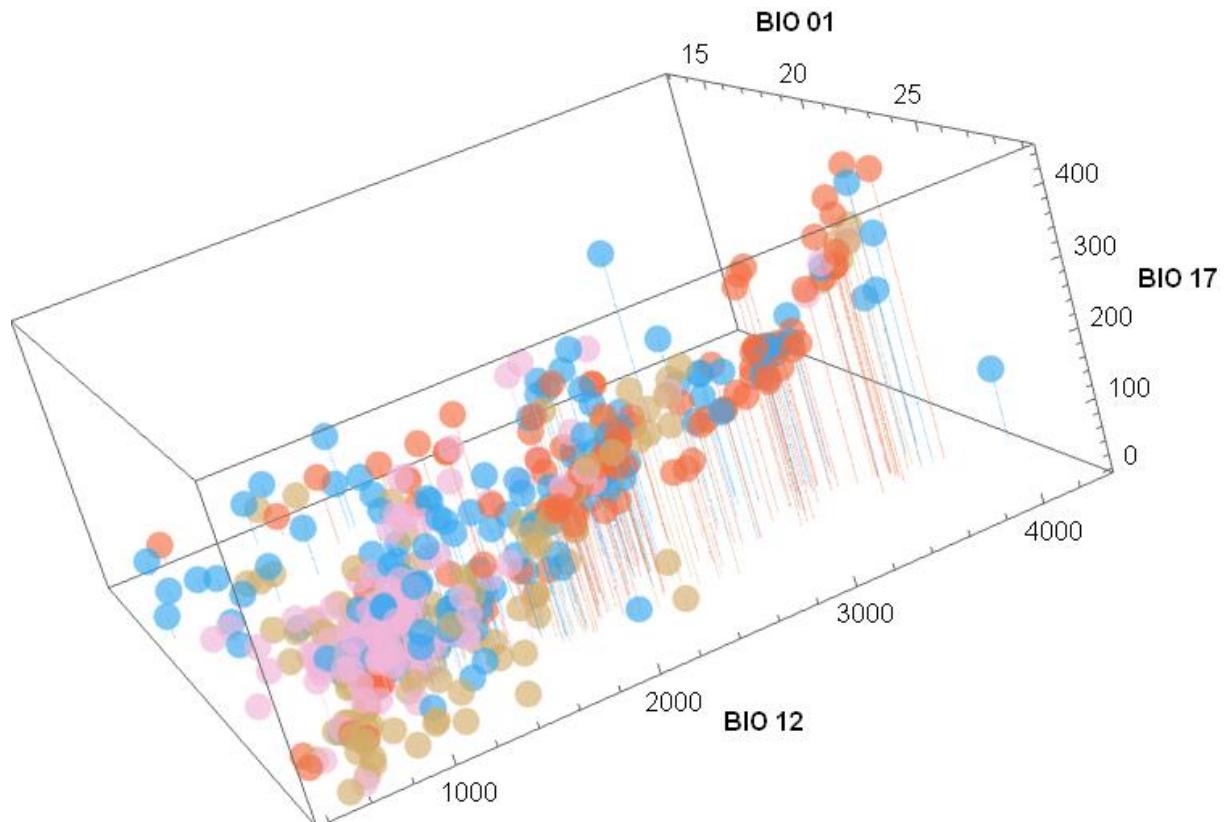


Fig. 6. 3D representation of a sample of 140 records of the presence of the host-plants *B. divaricata* (pink circles), *A. inermis* (brown circles), *P. rohrii* (orange circles), and the blue morpho *M. helenor montezuma* (blue circles), based on bioclimatic variables BIO 1, BIO 12 and BIO 17 that directly affect its spatial distribution.

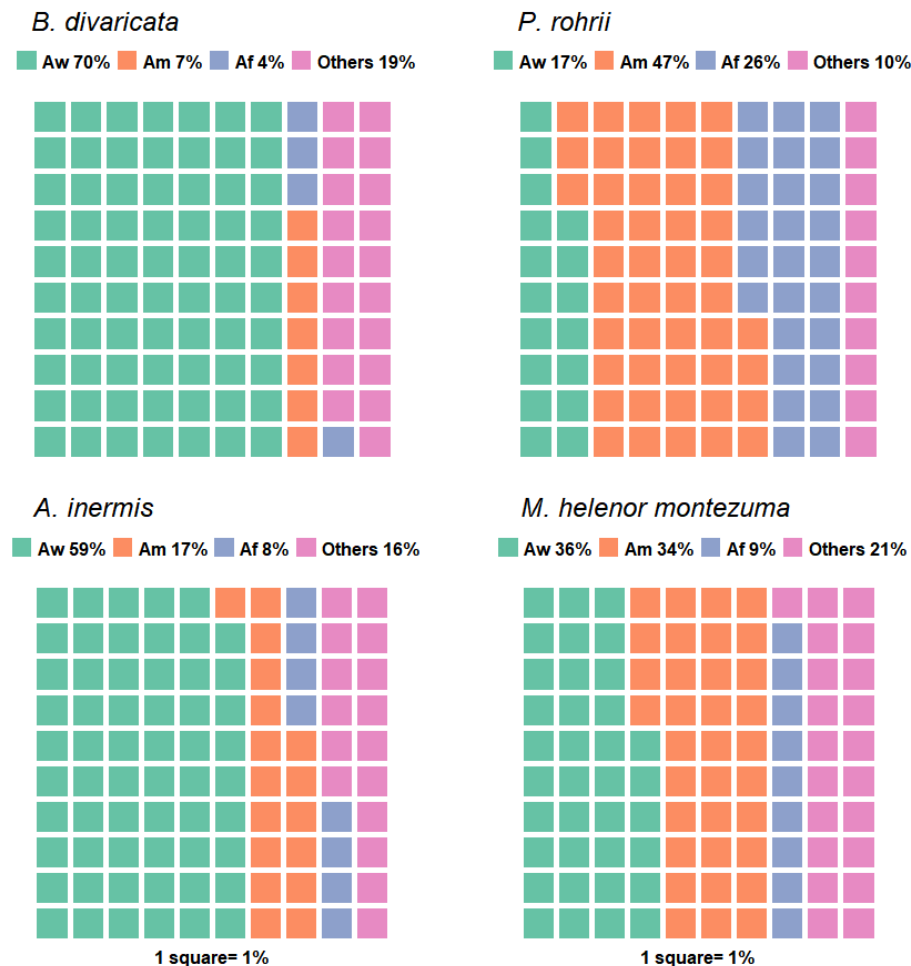


Fig. 7. Waffle graphs showing the percentages of the types of climates that predominate in the models of potential distribution of *B. divaricata*, *A. inermis*, *P. rohrii* and *M. helenor montezuma* based on the Köppen classification.

Our results are similar to those presented by Zarzo-Arias et al. (2019) related to the butterfly *Aricia morronensis* and five host-plants, however, they built an additive composite interaction model representing the simultaneous overlap of the butterfly and its hosts. Here, we could determine the individual butterfly-plant interaction and the similarities in the spatial and bioclimatic space. As *M. helenor* is a polyphagous insect, we could not find a close spatial/ bioclimatic relationship with any of its host-plant, coinciding with the findings of the butterfly *Melitia cinxia* and its host-plant, for which the study found a broad spatial relationship (Van Nouhuys et al., 2003). On the other hand, while our analysis provided with some basic information regarding the joint distribution of the plants and the blue butterfly, other factors like dispersal processes possibly affect the distribution of the plants. For example, bats feed on seeds of *A. inermis* (Janzen et al., 1976), ants (*Paraponera clavata*) are associated to *P. rohrii* (Perez et al., 1999) and birds and rodents feed on *B. divaricata* (Alderete-Chavez et al., 2011), all of them can contribute to their dispersal (Garcia et al., 2000). Thus, our findings are

limited by the modeling approach. Alternative, mechanistic models that account for dispersal mechanism can take into account the potential effect of this process, and provide with further information on the spatial interaction between the butterfly and its host-plants (Descombes et al., 2016; Van Nouhuys et al., 2003).

Table 3. AUC values of the distribution models of the host-plants and the blue morpho.

Species	AUC	AUC
	Training	Test
	70%	30%
<i>Andira inermis</i>	0.91	0.91
<i>Bauhinia divaricata</i>	0.86	0.87
<i>Pterocarpus rohrii</i>	0.96	0.95
<i>Morpho helenor montezuma</i>	0.89	0.89

Model validation

Table 3 shows the values of the area under the curve for modelled species, where the predictive power for both the host-plants and the blue morpho ranged between 0.86 and 0.96 for the training models and between 0.87 and 0.95 for the test models. In general, this indicates that the number of bioclimatic variables used is sufficient to construct models with a high level of predictability.

CONCLUSIONS

The potential distribution of *B. divaricata* was the greatest, followed by *A. inermis* and *P. rohrii*. All three host-plant species presented a neotropical distribution similar to the blue morpho and converged on the states of Veracruz, Tabasco, Chiapas and Oaxaca, where *B. divaricata* obtained an overlap of 61%, suggesting that it shares similar bioclimatic conditions that *M. helenor montezuma*. On the other hand, *P. rohrii* obtained the least overlap with the butterfly but preferred the same temperature and precipitation. The most frequent climate types connected with the distribution of the host-plants and the blue morpho are (in decreasing order): Aw, Am and Af. As habitats, these are present in the tropics as lowland deciduous forest, intermediate sub-deciduous forest, intermediate sub-evergreen forest, high evergreen forest, and secondary vegetation. This research provides relevant information to the potential geographic areas for management of these host-plants of the blue morpho and the preservation of its habitat. Importantly, *M. helenor montezuma* and its host-plants are not on the list of protected species in Mexico, yet they are exposed to effects from climate change and it is essential to contribute positively to their management and preservation in order to conserve biodiversity. Thus, the current potential distributions of the blue morpho and its host-plants will set the stage for future projections and reinforce the implementation of strategies in their use in current and future conservation efforts.

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Compliance with ethical standards. Do not apply.

Data availability. Data are available with Jose Lopez-Collado, jlopez@colpos.mx upon request.

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