

# The risk of invasion by angiosperms peaks at intermediate levels of human influence



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## Abstract

Biological invasions are a growing threat to biodiversity. The control and eradication of exotic species established in earnest are of limited success despite high financial investments. Anticipating biological invasions based on species' suitabilities is a cost-effective strategy given it helps identifying areas where exotic species can prosper, which can then translate in improving management and conservation efforts. Based on information from 191 invasive angiosperm species worldwide, we used ecological niche models to identify areas at high risk of invasion (cumulative predicted distribution of invasive species) in Mexico. Further, we explored the importance of bioclimatic and human influence variables as drivers of the distribution of invasive species and analyzed the status of the currently recognized priority conservation sites in Mexico. We found that areas with intermediate human activity scores had a high risk of invasion. Additionally, we found that many of the current priority conservation sites in Mexico had a high risk of invasion. Our findings contribute to disentangling the factors that drive environment susceptibility to invasions and urge management strategies to minimize the impacts of biological invasions in priority conservation sites.

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## Introduction

Invasive species are a major threat to biodiversity worldwide (Clavero & García-Berthou, 2005; Richardson & Pyšek, 2008). The risk of invasion by exotic species has increased in recent decades in strong association with human activities (Hulme, 2009). Controlling and eradicating biological invasions is costly (Pimentel et al., 2005) and complex. Populations of invasive species usually have high

demographic rates, and local species rapidly evolve ecological dependencies with invasive species (Kolar & Lodge, 2001), integrating complex networks of interactions (e.g., Carneiro et al., 2008; Lopezaraiza-Mikel et al., 2007). Cases that have been successful in controlling biological invasions are restricted to those that attacked the invasions in their earliest stages (Simberloff, 2013). Ecological niche modeling (ENM) tools have been used to predict biological invasions of plants (Thuiller et al., 2005), animals (Martínez-Morales et al., 2010), and pathogenic fungi (Escobar et al., 2014). In addition to climatic conditions, species' distributions can also be influenced by processes

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like freezing vulnerability (Wheeler et al., 2014) and carbon limitation (Wheeler et al., 2016). Additionally, human influence like population density (McGeoch et al., 2010), density of roads (del-Val et al., 2015), land use (Beauséjour et al., 2015), habitat disturbance (Macdougall et al., 2014), and distance to trade hubs (Bellard et al., 2016), can influence the establishment of exotic species.

Angiosperms form part of the culinary, ornamental, and indigenous medical traditions around the world, and many species are reported as synanthropes (Carretero, 2010). Therefore, the extent and depth of human activities may be a driver of invasiveness in this group of plants (Klein et al., 2007). Furthermore, the convergence of biotic regions, such as the Nearctic and Neotropical regions in Mexico, in addition to an inherently high biodiversity (Halffter & Morrone, 2017), likely has different effects on the potential distribution of invasive species across the country. Nonetheless, there is a shortage of knowledge on the potential spatial distribution of threatening invasive species and their drivers in Mexico. Improving our knowledge about the risk of angiosperm invasion in the country could help to explain how biological invasions vary across ecological and human-induced gradients.

In this study, we used ENM to spatially describe the invasion risk of angiosperms across continental Mexico and break it down at the biogeographic province level. We also analyzed threats for over 2000 terrestrial priority conservation sites identified for the country (Koleff et al., 2009). Because the intensity and density of human activities are widely known to promote biological invasions from diverse taxa across vast regions (Bellard et al., 2016), we hypothesized that the human influence would be an important driver of species distributions and that the probability of a species being present would be higher in areas with greater human influence. Additionally, since most exotic or invasive angiosperm species in Mexico are from the Old World (Villaseñor & Espinosa-García, 2004), we expected that biogeographic provinces more climatically similar to Europe, Africa, and Asia would show a high risk of invasion.

## Materials and methods

### Data collection

Of the 210 invasive angiosperm species identified as major threats to biodiversity in Mexico (Semarnat Secretaría del Medio Ambiente y Recursos Naturales, 2016), 140 already occur in the country. Most of these species are native to Europe, Asia, and Africa (Appendix A: Table 1). We downloaded occurrence data for the 210 species, including native and invaded regions, from the following four databases using the ‘spocc’ package in R (Chamberlain, 2020): (1) Global Biodiversity Information Facility; (2) Berkeley Ecoinformatics Engine; (3) Biodiversity Information Serving Our Nation; and (4) Integrated Digitized Biocollections.

We also downloaded records from the database on Mexican biodiversity (SNIB) curated by CONABIO (<http://www.snib.mx/>). We used only species with more than 30 records (Wisniewski et al., 2008); thus, we generated niche models for 192 of 210 candidate species.

### Environmental data

We used 19 bioclimatic variables and the global human influence index (GHII). Bioclimatic variables consist of combinations of temperature and precipitation to represent more biologically meaningful physiological extremes. We used the WorldClim database version 2.1 (Hijmans et al., 2005; <http://www.worldclim.org/>) at a 10 min spatial resolution. GHII is a worldwide map of human influence (GHII version 2, <http://sedac.ciesin.columbia.edu>), summarizing information on human population pressure, human access, human land use, and infrastructure. The range of GHII was between 0 and 72. The highest values of GHII characterize the world’s largest cities (New York, Mexico City, São Paulo, and London), while the lowest values are found in highly conserved sites (Sanderson et al., 2002). To match the spatial resolution of the bioclimatic layers, GHII was scaled down from 0.5 min grid cells to 10 min using the bilinear interpolation method in the R package ‘raster’ (Hijmans & van Etten, 2012).

### Study area and species information

Mexico still maintains a large portion of land with low impact from human activities, especially in the more deserts and mountainous regions (González-Abraham et al., 2015). The most recent official spatial land use data available for Mexico (INEGI, 2016) indicates that around 34% of Mexico is covered by primary and secondary forests, 29% by scrub vegetation, and 24% by agriculture and pasture for livestock. In accordance with this data, 50% of Mexican territory has GHII values lower than 15.69, and the highest GHII value for the country is 53.52 at the 10 min spatial resolution used in this study.

Some of the 192 angiosperm species considered in this study are also considered aggressive invasives in other countries, e.g., *Abrus precatorius*, *Arundo donax*, and *Pennisetum purpureum* (CABI, 2021). Among the species with more occurrences in Mexico, several are grasses, such as *Eleusine indica*, *Dactyloctenium aegyptium*, and *Cenchrus ciliaris* (Appendix A: Table 2), which are species with great dispersal capacity and history of human use (CABI, 2021). Some of the species were not yet present in Mexico but were included in the study due to their level of damage to biodiversity reported in other countries. For instance, some mistletoes (*Arcetobium*) are known to cause great economic and ecological impact to agroecosystems (CABI, 2021).

## Ecological niche models: selection and evaluation

Ecological niche models were generated using minimum volume ellipsoids, a method that generates an ellipsoid representing the species niche, and values closer to the niche centroid correspond to regions of the environmental space with higher suitability for the species. Before model calibration, we eliminated variables using a threshold  $> 0.8$  of Spearman's correlation coefficient. Then, we selected the best model for each species, based on the omission rate value and statistical significance, using three variables per species. To evaluate the models, we generated binary potential distribution maps for each species by using a threshold that maximizes the true skill statistic (TSS). Then, we divided presence records into calibrating (70%) and testing data (30%). Lastly, we evaluated the models using two methods, the partial ROC (Peterson et al., 2008), and the TSS (Allouche et al., 2006). The pseudo-absence points for the TSS were generated using the R package 'dismo' (Hijmans et al., 2017) and everything else was done using the R package 'ntbox' (Osorio-olvera et al., 2020).

## Angiosperms: invasion risk, variable importance, and response curves

We obtained a surface of cumulative risk probabilities by summing the suitability rasters of each modeled species, and then we rescaled the raster to range between zero and one. We assessed the variable importance using two methods: (1) counting the number of times a variable was selected in the best model, and (2) estimating a  $z$ -score to determine if models with a particular variable had a lower or higher omission rate than models without this variable. The  $z$ -score formula was  $z = (x - \mu) / \sigma$ , where  $x$  is the omission rate of a model with the target variable, and  $\mu$  and  $\sigma$  are the mean and standard deviation of the omission rate, respectively, from models without this variable. Lastly, we generated a response curve for all species using generalized additive models for all variables to identify the pattern of suitability distribution along each variable gradient.

## Invasion risk distribution in terrestrial priority conservation sites and biogeographic provinces

To evaluate the distribution of the invasion risk in Mexico, we spatially summarized the cumulative suitability values for all studied species across Mexican biogeographic provinces (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), 1997) and the priority sites for terrestrial biodiversity conservation (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), 2008). The priority sites for conservation were defined using information about species distributions, conservation status, biodiversity threatening variables, and natural vegetation types and

cover (Urquiza-haas et al., 2009). To evaluate the distribution of the invasion risk in Mexico, we calculated the mean invasion risk for each province and conservation priority site and then plotted its distribution in the three categories of prioritization, along with its density distribution.

Then, to determine if invasion risk distribution in the Mexican biogeographic provinces is related to the climatic similarity regarding the continents of origin of most of these exotic species, we obtained the climatic information for each of the Old World continents and compared their climatic centroid with the climatic centroid of the Mexican biogeographic provinces. Hence, we first summarized the climatic variability using principal component analysis (PCA) for the 19 bioclimatic variables considering Mexico and the three Old World continents. Second, we used the function 'cov\_center' (Osorio-olvera et al., 2020) to obtain the climatic centroid coordinates for those regions. Third, we used the 'vegan' package (Oksanen et al., 2019) to calculate the Euclidean distance between the climatic centroids from the Old World continents and the 19 provinces from Mexico. Finally, we performed a GLM using the mean invasion risk value for each province as the dependent variable and the climatic distance from Africa, Asia, and Europe as independent variables, allowing for interactions between these variables.

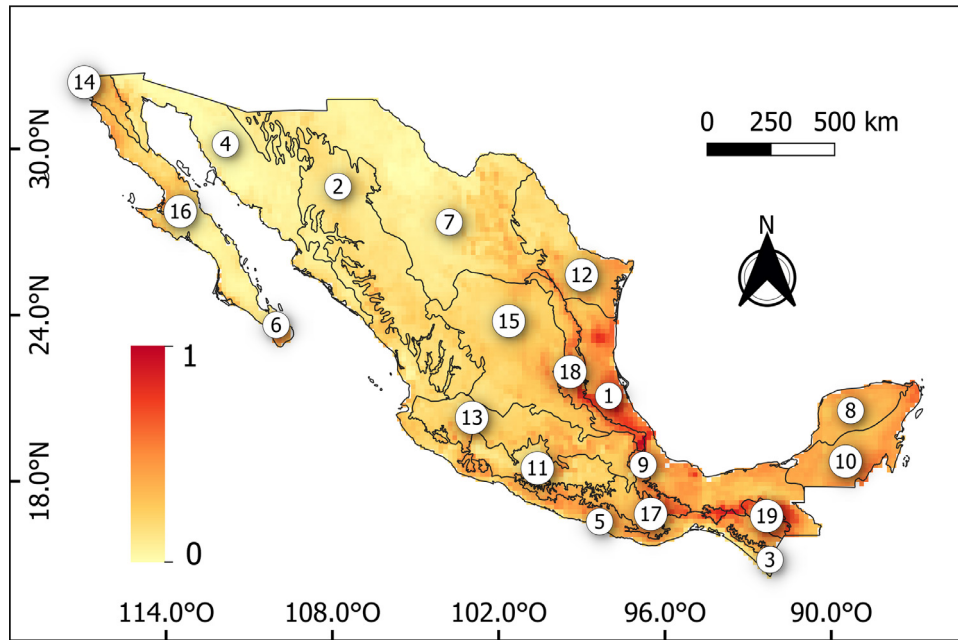
To determine if our results would be affected if we only used the best models (based on TSS), we separated the species' models into five groups, considering their TSS value ( $0.4 < \text{TSS} < 1$ ,  $0.5 < \text{TSS} < 1$ ,  $0.6 < \text{TSS} < 1$ ,  $0.7 < \text{TSS} < 1$ ,  $0.8 < \text{TSS} < 1$ ), and then, we used these groups to generate the invasion risk map, response curves, and variable importance, similar to the method we previously used for all species. Finally, to determine how the trends from the distribution of the individual species differed from the summarized map, we used the individual maps to calculate the standard error and minimum and maximum value of the invasion risk using a 95% confidence interval.

## Results

Exotic and invasive angiosperms actually or potentially occurring in continental Mexico showed varying degrees of suitability across the country's territory. The summary distributional ranges of invasives showed a higher invasion risk along the Gulf of Mexico and northern and southern Pacific coast (Fig. 1). The most important variables for invasive species potential distribution were annual mean temperature, mean diurnal range of temperature, and GHII (Fig. 2). Additionally, areas with intermediate human influence were the ones at higher risk of angiosperm invasion (Fig. 3B).

## Distribution of angiosperm invasion risk

The majority (191 out of 192) of ecological niche models were statistically significant (Appendix A: Table 1). The

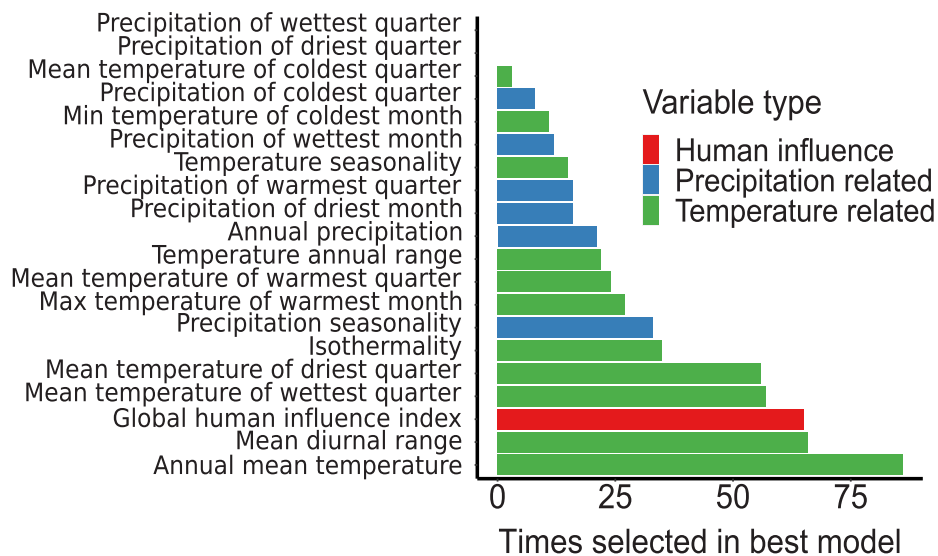


**Fig. 1.** Angiosperm invasion risk distribution across Mexico. The scale of the index ranges from 0 (least invasion risk) to 1 (highest invasion risk), and the division and number correspond to each of the 19 biogeographic provinces in Mexico: (1) Golfo de México; (2) Sierra Madre Occidental; (3) Soconusco; (4) Sonorense; (5) Costa del Pacífico; (6) Del Cabo; (7) Altiplano Norte (Chihuahuense); (8) Yucatan; and (9) Oaxaca; (10) Petén; (11) Depresión del Balsas; (12) Tamaulipeca; (13) Eje Volcánico; (14) California; (15) Altiplano Sur (Zacatecano-Potosino); (16) Baja California; (17) Sierra Madre del Sur; (18) Sierra Madre Oriental; and (19) Los Altos de Chiapas.

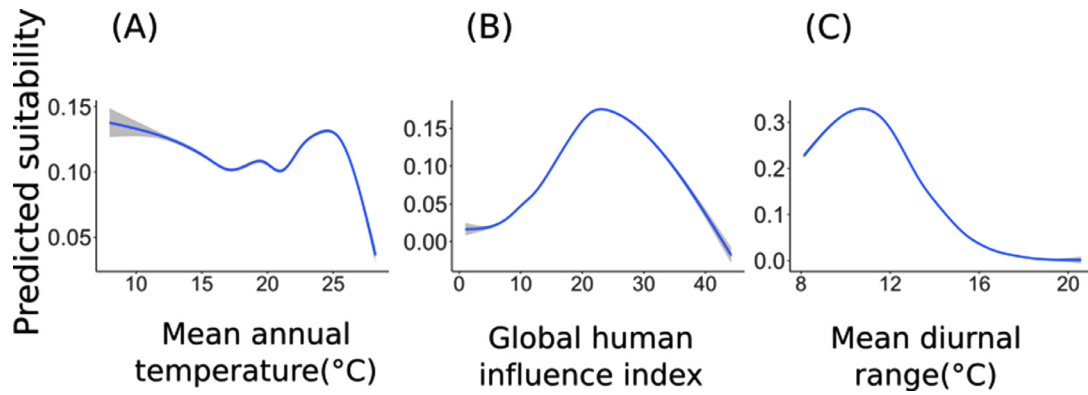
potential risk of invasion by angiosperms in Mexican biogeographic provinces was uneven. Invasion risk was higher in 'Los Altos de Chiapas,' 'Soconusco,' 'Oaxaca,' 'Golfo de México,' and 'Sierra Madre Oriental' and lower in 'Altiplano Norte,' 'Sierra Madre Occidental,' 'Sonorense,' and 'Baja California' provinces (Appendix A: Table 2). Biogeographic provinces with a higher risk of invasion were mostly mountainous regions (e.g., 'Sierra Madre Oriental' and 'Los Altos

de Chiapas'), while the more desertic regions had lower invasion risk values (e.g., 'Sonorense' and 'Altiplano Norte') (Fig. 1). The same invasion risk pattern was detected for different thresholds of TSS (Appendix A: Fig. 1), and when we consider a 95% confidence interval among all species distribution maps (Appendix A: Fig. 2).

Additionally, the potential risk of invasion in Mexican biogeographic provinces was not affected by the climatic



**Fig. 2.** Number of times that a variable was selected in the best model for a species using omission rate as a criterion to select the best model.



**Fig. 3.** Relationship between predicted suitability and the three variables selected most frequently in the best ecological niche models for 191 invasive angiosperm species: (A) Mean annual temperature (bio1); (B) Global human influence index; (C) Mean diurnal range.

similarity of the provinces with Asia and Africa, but we found a significant effect with climatic distance between the provinces and Europe (Fig. 4, Table 1).

We found that invasion risk was also unevenly distributed along the priority conservation sites. Most sites had intermediate invasion risk values, but the highest values were concentrated in extreme conservation-priority areas (Fig. 5).

### Importance of environmental variables to predict invasion risk

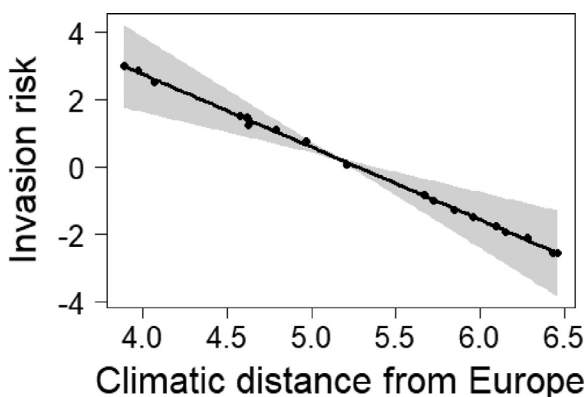
We found that annual mean temperature was the most important variable in determining the species distribution ranges, followed by mean diurnal temperature range and GHII index. The least important variables were precipitation of the wettest quarter and precipitation of the driest quarter (Fig. 2). Of the variables that contributed to models with lower omission rates, six were related to temperature and

three to precipitation and GHII (Fig. 6). GHII remained one of the most important variables in the groups separated by the TSS thresholds (Appendix A: Table 3).

The relationship between predicted suitability for each species and the 20 variables had different response curve shapes (Fig. 3 and Appendix A: Fig. 3). For example, areas with a higher risk of invasion tended to have a higher mean annual temperature (Fig. 3A), lower mean diurnal temperature range (Fig. 3C), and intermediate GHII (Fig. 3B). The response pattern for GHII remained the same for all groups separated by the TSS threshold (Appendix A: Fig. 4).

### Discussion

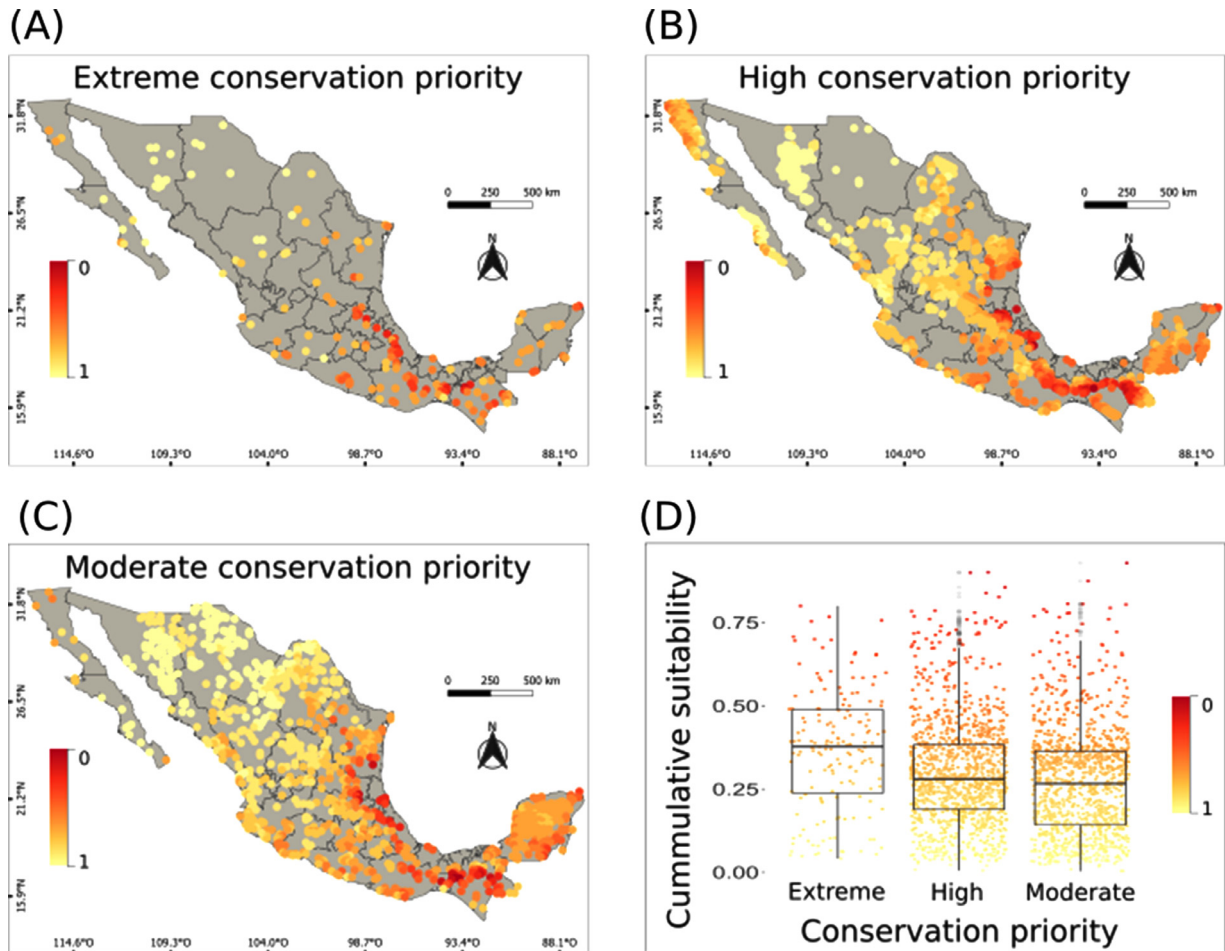
We found that the invasion risk of 191 angiosperm species differs among the country’s biogeographic provinces and conservation priority sites. In addition, we showed that the invasion risk was high in areas with intermediate anthropization levels, high mean annual temperature, and narrow mean diurnal temperature range. The regions that were identified as most vulnerable to invasion by angiosperms (i.e., near the Gulf of Mexico) were also those that



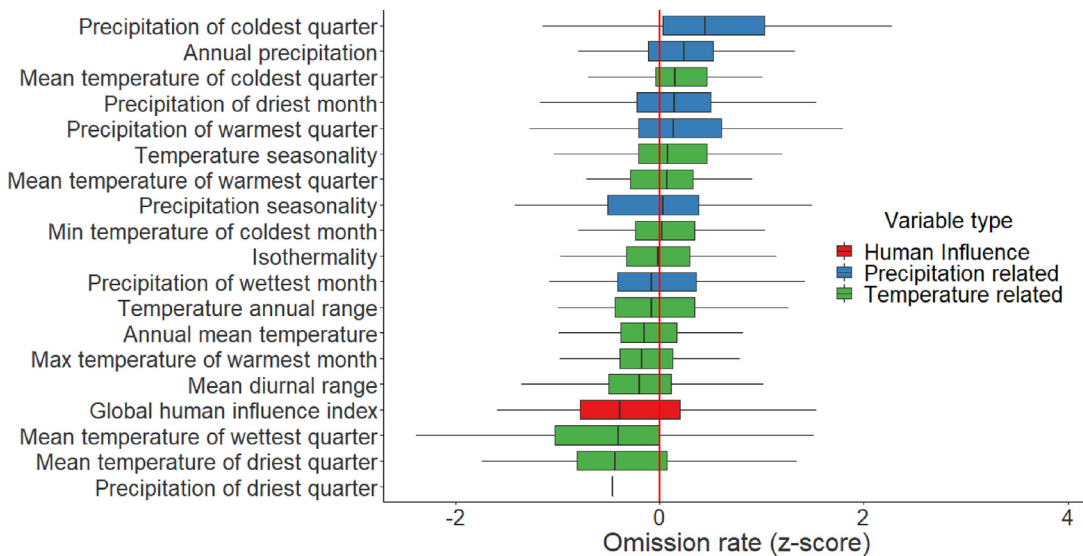
**Fig. 4.** Relationship between climatic distance from Europe and invasion risk for the 19 Mexican biogeographic provinces. Climatic distance corresponds to the Euclidean distance between the centroids (based on the first three principal components from 19 bioclimatic variables) for each of the biogeographic provinces and the centroid from Europe (estimate = -3.049, *p*-value = 0.00147).

**Table 1.** Results from the generalized linear model using invasion risk as a response variable and distance between Old World continents and Mexican biogeographic province climatic centroids as independent variables. The only significant variable is highlighted in bold.

Variables (distance from)	Estimate	Standard error
Africa	-1.08018	1.08112
Asia	1.39416	0.85007
<b>Europe</b>	<b>-3.04952</b>	<b>0.72480</b>
Africa:Asia	-0.11838	0.45461
Africa:Europe	0.26731	0.24854
Asia:Europe	0.23496	0.11499
Africa:Asia:Europe	-0.02831	0.05800



**Fig. 5.** Geographic and density distribution of angiosperm invasion risk across priority conservation sites in Mexico (classification according to Koleff et al., 2009). (A) Geographic distribution of invasion risk in extreme priority sites. (B) Geographic distribution of invasion risk in high priority sites. (C) Geographic distribution of invasion risk in moderate priority sites. (D) Density distribution of invasion risk in extreme, high, and moderate priority sites. The scale of the index ranges from 0 (least invasion risk) to 1 (highest invasion risk).



**Fig. 6.** Boxplots for omission rate z-scores for models with each of the 20 variables.

are vulnerable to other exotic taxa (e.g., [Ramírez-Ortiz et al., 2020](#)). Several regions that were identified in our study as regions with low invasion risk were classified as high risk for angiosperm invasion in a previous study ([del-Val et al., 2015](#)). Such divergence could be caused by the difference in the methodological approaches used. We focused on the environmental suitability for each plant species, while [del-Val et al. \(2015\)](#) used traits that can make an environment more susceptible to invasion (e.g., population and road density, vegetation type, and land use) as a measure of environmental invasibility. Nonetheless, both studies highlighted that the Pacific coast, the Gulf of Mexico, and Baja California have a higher risk of invasion by angiosperms, and those regions should receive more attention from research and conservation standpoints.

Low-to-medium levels of disturbance may favor biological invasion by angiosperms (e.g., [Dodd et al., 2016](#)), and the distribution of exotic plants tends to correlate positively with different anthropogenic variables, such as distance to airports and human population density ([Bellard et al., 2016](#)). However, our findings suggest that the risk of invasion decreases below or above certain levels of GHII. Some evidence shows that moderate and short-term disturbances can trigger biological invasions by temporarily reducing or suspending competition for key resources to the advantage of latent propagules of exotic species ([Davis & Pelsor, 2001](#)), and the availability of propagules of exotic species is thought to increase with anthropogenic influence ([Davis et al., 2016](#)). Therefore, while we expected a positive relationship between GHII and invasion risk, our findings suggest that in highly anthropized areas, environmental conditions are no longer suitable for the establishment of most exotic species, lowering the risk of invasion.

The higher risk of invasion in areas with less variation in temperature throughout the day can be explained because temperature stability is positively related to plant species richness ([Gao & Liu, 2018](#)), and wider temperature ranges can have stronger negative effects on invasive plants than on native ones ([Chen et al., 2017](#); [He & He, 2020](#)). Additionally, mean annual temperature is positively related to plant species richness ([Gao & Liu, 2018](#)), and it is possible that invasive plant species can perform better than native species in higher temperatures ([Hou et al., 2014](#)). Therefore, the importance of mean annual temperature and mean diurnal temperature range in predicting exotic and invasive species distribution is supported by previous studies. The distribution of the risk of invasion in the biogeographic regions could be explained by the environmental similarity between the native range from the species used in this study (mostly Eurasia) and the mountainous biogeographic regions from Mexico. [Jiménez-Valverde et al. \(2009\)](#) found a high environmental correlation between North America and Eurasia using the same bioclimatic variables used in our study, and our results highlight the role of environmental conditions in the native area for predicting the invasion risk of angiosperms in Mexico.

Changes in microhabitat characteristics can influence species establishment, survival, and distribution ([Correa et al., 2020](#); [Cortés et al., 2014](#); [Gentili et al., 2020](#); [Little et al., 2016](#); [Sedlacek et al., 2015, 2016](#); [Zellweger et al., 2020](#)); thus, generalizations cannot always accurately describe local processes ([Pichancourt et al., 2019](#)). Therefore, conservation projects should consider results from niche models cautiously, especially when using climate change scenarios (e.g., [Buisson et al., 2010](#); [Jetz et al., 2007](#); [Sinclair et al., 2010](#)). This is mostly because niche models make strong assumptions that are not always met in reality, such as that observed species distributions are in equilibrium with their environment ([Yackulic et al., 2015](#)), thus overestimating the effect of climate change ([Botkin et al., 2007](#)), in part because niche models frequently represent the realized niche, not the fundamental niche ([Loehle & LeBlanc, 1996](#)).

Selecting among the various modeling techniques and model complexity to estimate ecological niches and their performance is a crucial step in any risk or biodiversity assessment ([Cobos et al., 2019](#)). In this study, we followed key recommendations, such as implementing a variable selection method as suggested by ([Cobos et al., 2019](#)), and we also used complementary evaluation methods to AUC ([Lobo et al., 2008](#)). We also performed a sensitivity analysis based on evaluation metrics (TSS threshold; see Appendix A: Fig. 1). Another recommendation we evaluated was that of eliminating species with few records since low sample sizes could potentially affect species distribution predictions ([Wisniewski et al., 2008](#)). However, the elimination of the six species with less than 30 records did not impact the overall trend of results and the observed pattern was consistent with the suitable regions for this large set of (actual or potential) invasive angiosperms.

## Conclusions and perspectives

In this study, we identified that the risk of exposure to exotic angiosperm invasion is higher in regions at intermediate levels of GHII, suggesting that high anthropization imposes a strong filter not only on native but also exotic species and contradicts our original hypothesis. The most important variables for the potential distribution of exotic angiosperms to Mexico were annual mean temperature, mean diurnal range of temperature, and GHII. Mexican areas of extreme priority for conservation are particularly at risk, corroborating the need to focus on those sites for conservation and preventing invasions.

This study aimed to present emerging potential invasion patterns for angiosperms and the strong anthropogenic influence associated with it. Ecological niche modeling can help guide the search for introduced species in invasion management ([Fois et al., 2018](#); [West et al., 2016](#)), and future research should elucidate the importance of the different components of GHII separately, as well as other variables from hyperspectral imagery and machine learning

approaches (Garzon-Lopez & Lasso, 2020; Leitão & Santos, 2019; Tito et al., 2020). These risk assessments should also be done considering particularities that can drastically change across spatial and temporal scales (e.g., habitat or biotic interactions) of plant communities in the context of biological invasions. For example, recent efforts in that direction have been made in the ‘páramo,’ with efforts to better understand the plant community (Peyre et al., 2015, 2018) and how it can be affected by climate change and other natural or anthropogenic pressures (Peyre et al., 2020; Quesada-Román et al., 2020; Valencia et al., 2020). Additionally, studies on climate change should consider processes that can lead to alterations in the environment, such as ‘shrubification’ (Myers-Smith et al., 2011) and ‘thermophilization’ (Gottfried et al., 2012), and the role that invasive species play in them. Future studies should also consider each species distribution separately and look at unexpected downslope and neutral range shifts that can be caused by climate change or anthropogenic modifications that can cause competition release (Lenoir et al., 2010) and facilitate biological invasions. Therefore, it is always important to consider the role of abiotic (e.g., soil nutrient conditions, see Sedlacek et al., 2014; Reverchon & Méndez-Bravo, 2021) and biotic (Bueno & Llambí, 2015; Mora et al., 2019; Wheeler et al., 2015) mechanisms, which can mediate the complex network of interactions established between native and exotic plants (Llambí et al., 2018).

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.12.005.

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