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Tomicus species (Coleoptera: Curculionidae: Scolytinae) as an Invasive Threat to Mexico's Forests Using Ecological Niche Modeling

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ABSTRACT

Scolytine bark beetles from the genus *Tomicus* (Coleoptera: Curculionidae: Scolytinae) are among the most important forestry pests globally, known for their ability to establish themselves in new environments and pose a risk to native forest ecosystems. These beetles are considered non-native to the Americas. However, *Tomicus piniperda* L., commonly known as the pine shoot beetle, has recently invaded North America, and specimens of *T. minor* Hart have been identified in the United States. Their potential for establishment in Mexico continues to increase. A proactive approach to assessing the risk of invasive species involves ecological niche modeling. Using bioclimatic variables, species distribution data, an entropy-based algorithm, and modeling tools, the ecological niches of 3 *Tomicus* species were determined and mapped across Mexico. The findings indicated that *Tomicus destruens* could potentially be established in limited and scattered regions in the Altiplano Norte biogeographic province and a separate area in the province of Tamaulipeca. In contrast, *T. minor* showed a high probability of suitability in the biogeographic provinces of Baja California, California, Sonorense, Altiplano Norte, Altiplano Sur, Tamaulipeca, and certain regions in the eastern Eje Volcánico. No suitable environmental conditions for *T. piniperda* were identified in Mexico. Additional factors, including specific ecological requirements, host tree preferences, and interactions with native fauna, are explored concerning the possible establishment of *T. minor* in the country. This research holds substantial significance, as Mexico is recognized as one of the world's most important regions for pine diversity, with key pine biodiversity hotspots.

Keywords: Mexican biogeographic provinces, Ecological niche, Invasive species, Pine shoot beetles

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Introduction

Mexico is recognized as a megadiverse nation [1], where its rich plant life, abundance, and distribution patterns are shaped by the interaction of Neotropical and Nearctic elements [2]. Additionally, the geological history and formation of the country's mountain systems have played a crucial role in the dispersal of forests across different regions [3].

The family Pinaceae has found in Mexico the necessary geographic complexity, climatic conditions, and evolutionary space to thrive. The country serves as a center for Pinus diversity and radiation [4], with at least 23 species classified as endemic [5, 6]. A total of 49 Pinus species have been documented across Mexico, covering nearly the entire national territory, except for the tropical lowlands of Tabasco and Yucatán [5]. However, forested areas are diminishing each year due to various economic (poverty), social (population increase, migration), political (government policies), and climatic (drought, climate change) factors [7, 8]. As a result, 21 *Pinus* species are currently classified as threatened or under special protection [5, 9].

Coniferous forests face an additional challenge beyond economic, social, political, and climatic pressures— the threat posed by invasive species, particularly insect pests [10]. Among these arthropods, certain species within the genus *Tomicus* (Coleoptera: Curculionidae: Scolytinae) have become notable for their ability to colonize new environments and for the damage they inflict on native forest populations, either directly or indirectly.

Tomicus species are associated with Pinaceae (primarily Pinus) [11] and include eight recognized species: *T. puellus* Reitter, *T. pilifer* Spessivtsev, *T. brevipilosus* Eggers, *T. destruens* Woll., *T. minor* Hart., *T. armandii* Li & Zhang, *T. piniperda* L., and *T. yunnanensis* (Kirkendall & Faccoli). These beetles have been identified as significant forestry pests in multiple regions worldwide [11]. While *T. brevipilosus*, *T. armandii*, *T. puellus*, *T. pilifer*, and *T. yunnanensis* are primarily confined to central, southwestern, and eastern China [11], *T. minor*, *T. destruens*, and *T. piniperda* have a broader geographic range and are considered particularly important in forestry management [11].

The common pine shoot beetle, *T. piniperda*, is regarded as a highly destructive Scolytinae pest with a broad Eurasian range and an established presence in North America [12]. This beetle has been found to affect Christmas tree farms [13] and continues to spread rapidly across Canada and the U.S. due to its remarkable adaptability [14]. In its native environment, *T. piniperda* often coexists with the lesser pine shoot beetle, *T. minor*. When both species infest the same tree, their combined attack can compromise the tree's defenses, making it more vulnerable to damage [15]. There have been reports of *T. minor* being intercepted in the United States from areas outside its native distribution [16]. Although some researchers classify it as a secondary pest, *T. minor* poses a notable threat to *Pinus* species in China [17].

Confined in the Mediterranean Basin and the Macaronesian Islands [17, 18], *Tomicus destruens* is recognized as a major pest of Mediterranean pine forests [19]. Generally, *Tomicus* species invade the trunks and branches of Pinus trees, leading to deformities in foliage and reducing their commercial quality. Large-scale infestations can either directly kill the trees or weaken them, increasing their susceptibility to secondary infestations that ultimately result in their decline due to stress.

Mexico imports significant quantities of Christmas pines from the United States and Canada, with 25,859 metric tons recorded in 2014 [20]. The movement of plant materials facilitates the introduction of harmful pests that could pose a risk to native flora and impact the local timber industry. Domestically, *Pinus* plays a crucial role in the forestry sector, accounting for 75.1% of the country's annual wood production [21].

Given this context, this study employs ecological niche modeling to assess the potential climate suitability for three *Tomicus* species (Coleoptera: Curculionidae: Scolytinae) that have been classified as invasive in other parts of the world. The goal is to generate data that could assist Mexican phytosanitary authorities in making informed management decisions [22], whether through targeted monitoring, sampling efforts, or the implementation of preventive control measures.

Materials and Methods

Distribution record of Tomicus spp. and Pinus spp

Data on the distribution of three *Tomicus* species (*T. piniperda*, *T. minor*, and *T. destruens*) were gathered from scientific publications and the Global Biodiversity Information Facility (GBIF) database [14, 15, 17, 19, 23-27].

Model calibration

To ensure data quality, best practices for handling distributional records were applied. Duplicate entries were removed, and to minimize spatial autocorrelation, records within a 10 km radius of each other were filtered out using the 'spThin' package in RStudio® ver. 3.3.

For *T. minor*, the initial dataset contained 3,825 records, which were refined to 747 after processing. Of these, 561 (75%) were allocated for model training, while 186 (25%) were reserved for evaluation. *T. piniperda* had an initial set of 5,504 records, which was reduced to 1,357 following data refinement, with 1,018 (75%) used for training and 339 (25%) for model assessment. In the case of *T. destruens*, the original dataset included 237 records. After applying data cleaning protocols, the final dataset comprised 145 records, with 109 (75%) used for training and 36 (25%) for evaluation.

The accessible area (M) for each species was defined based on its dispersal capacity [28], following the BAM framework (M = species accessibility, B = biotic factors, A = abiotic factors) [28]. These areas were mapped using global biogeographic ecoregions [29] in QGIS ver. 3.16.11®. 19 bioclimatic variables were obtained from www.worldclim.org at a spatial resolution of 2.5 minutes; however, variables 8, 9, 18, and 19 were excluded due to inconsistencies in pixel values **(Table 1)** [18].

Table 1. Bioclimatic variables were used for the ecological niche model calculation of three *Tomicus* species (Coleoptera: Curculionidae: Scolytinae).

Bioblimatic variable
BIO1 = Annual Mean Temperature
BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3 = Isothermality (BIO2/BIO7) (×100)
BIO4 = Temperature Seasonality (standard deviation ×100)
BIO5 = Max Temperature of Warmest Month
BIO6 = Min Temperature of Coldest Month
BIO7 = Temperature Annual Range (BIO5-BIO6)
BIO10 = Mean Temperature of Warmest Quarter
BIO11 = Mean Temperature of Coldest Quarter
BIO12 = Annual Precipitation
BIO13 = Precipitation of Wettest Month
BIO14 = Precipitation of Driest Month
BIO15 = Precipitation Seasonality (Coefficient of Variation)
BIO16 = Precipitation of Wettest Quarter
BIO17 = Precipitation of Driest Quarter

A Spearman correlation analysis was conducted using the NicheToolBox (http://shiny.conabio.gob.mx:3838/nichetoolb2/), an exploratory tool for ecological niche modeling (ENM) designed to remove correlated environmental variables (MNE) [30]. The uncorrelated variables were then selected to create two separate variable sets.

Candidate models were developed in RStudio® ver. 3.3 using the 'kuenm' package, a tool designed for the advanced creation of ecological niche models using Maxent [31]. A total of three hundred ten candidate models were generated using the kuenm_cal function from the 'kuenm' package, which combines various regularization multipliers, environmental predictor sets, and entity classes. For each variable set combination, Maxent generated two models: one using the occurrence data points and another using the training data occurrences [32]. The feature class combinations included linear (L), quadratic (Q), product (P), threshold (T), and hinge (H), while the regularization multiplier values were 0.5, 1, 2, 3, and 4. Each model was used to assess the environmental suitability of the species based on the selected variables.

Evaluation of ecological niche models

The candidate models were assessed using the kuenm_ceval function within the 'Kuenm' package in RStudio® ver. 3.3. This process helps identify the most accurate models, considering both their prediction performance and complexity, while prioritizing models that show statistical importance [33]. Partial ROC analysis was used to compare the models against random expectations to identify those with better predictive power [33]. Afterward, the omission rate criterion was applied to refine the models further. In the final step, models with statistically significant results, low omission rates, and delta AICc values under 2 were selected for further use [32].

Results and Discussion

Models' quality

Ecological niche modeling in invasive species research involves using species occurrence data from one area to develop models, which are then applied to other regions where the species might not yet be invasive [28]. To support the hypothesis of environmental suitability, we chose models that exhibited strong statistical performance **(Table 2)**, with omission rates at or below 5% and delta AICc values under 2 [28, 32].

Table 2. Statistically evaluated best models for *Tomicus* (Coleoptera: Curculionidae: Scolytinae) species, employed for ecological niche modeling.

Species	Model	Partial ROC	Omission the rate of 5%	AICc	Delta AICc	W_AICc	Number of parameters
T. minor	M_4_F_pt_Set_02	0.02	0.049	17450.033	0	0.99996812	16
T. piniperda	M_1_F_lqpt_Set_01	0	0.024	32079.290	0	0.38921386	96
T. destruens	M_1_F_lq_Set_01	0	0.029	2787.7524	0	0.99934317	10

Bioclimatic variables for modeling ecological niches

The ecological models for the species examined were determined by a unique set of bioclimatic variables **(Table 3)**, which correspond to the environmental conditions that influence their natural geographical range. Based on global biogeographic regions [34], T. *destruens* is typically found in the Oriental region, extending into the Palearctic and reaching the Saharo-Arabian transition zone, marking its southernmost habitat [11]. *T. minor* and *T. piniperda*, however, exhibit a similar distribution pattern, originating from the Chinese transition zone and expanding throughout the Oriental and Palearctic regions [11]. *T. piniperda*, however, requires a broader set of bioclimatic variables than *T. minor*.

The ecological models for each species were mainly shaped by three to four bioclimatic factors, contributing 71.9%, 97.1%, and 78.3% of the model's definition for *T. destruens*, *T. minor*, and *T. piniperda*, respectively **(Table 3)**. For *T. destruens*, the most important variables were related to precipitation and temperature, such as bio14 (Precipitation of the driest month), bio15 (Precipitation seasonality), and bio2 (Annual mean diurnal range). *T. minor*, in comparison, was more influenced by precipitation variables, with bio1 (Annual mean temperature), bio7 (Annual temperature range), and bio16 (Precipitation of the wettest quarter) being the key factors. *T. piniperda*'s ecological profile was defined by bio1 (Annual mean temperature), bio5 (Maximum temperature of the warmest month), and bio4 (Temperature seasonality, indicating yearly temperature fluctuations).

Table 3. Bioclimatic factors were incorporated into the final ecological niche modeling for the three *Tomicus* species (Coleoptera: Curculionidae: Scolytinae).

T. destruens		***T. minor***		***T. piniperda***	
Bioclimatic variable	**Percent contribution**	**Bioclimatic variable**	**Percent contribution**	**Bioclimatic variable**	**Percent contribution**
Bio 14	30.9	Bio 1	49.4	Bio 1	19.8
Bio 15	22.0	Bio 7	33.9	Bio 5	28.6
Bio 2	19.0	Bio 16	13.8	Bio 4	14.6
Bio 4	15.0	Bio 15	2.9	Bio 2	15.3
Bio 1	5.2			Bio 3	9.8
Bio 5	3.5			Bio 12	7.0
Bio 12	3.4			Bio 15	4.8
Bio 3	1.0				

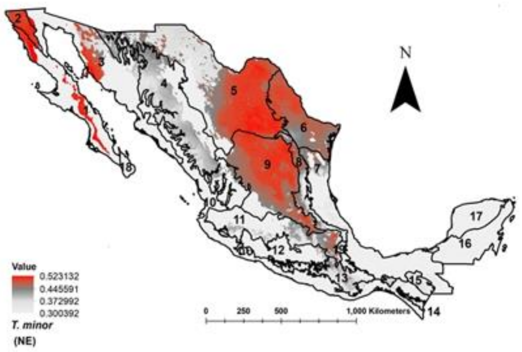
Environmental suitability

The calculated environmental availability varied for the three species, with differences arising from the settings used in the modeling software. Maxent offers three extrapolation options: free extrapolation, no extrapolation, and extrapolation with clamping. In this study, free extrapolation was not employed because it allows for an unrestricted extension of projections into the study area. The no extrapolation option restricts the model's response to zero if the environmental conditions in the projection area are more extreme than those in the calibration region [32]. As a result, only *T. minor* and *T. destruens* showed environmental availability in Mexico, while *T. piniperda* lacked sufficient data to extrapolate its environmental suitability. However, this does not rule out Mexico's potential environmental suitability for *T. piniperda*, as the inclusion of additional geographical data in the future could enhance model accuracy.

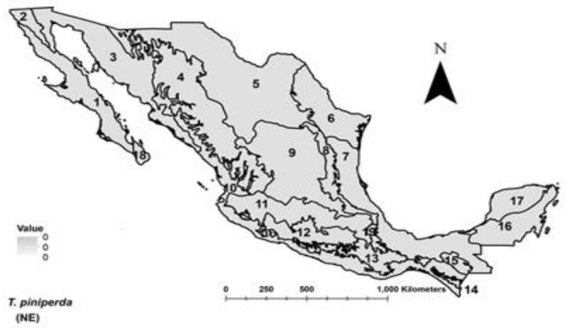
When extrapolation with clamping was applied, the model's response in areas with environmental conditions differing from those in the calibration region was limited to the extremes observed at the edges of the calibration area [32]. Using this setting, all three species demonstrated a potential for temporary survival in Mexico's environmental conditions.

Under the no extrapolation setting, the *T. destruens* model indicated optimal environmental suitability in a small, dispersed region in northeastern Mexico, with additional areas of moderate suitability in the Altiplano Norte and Tamaulipeca biogeographic provinces **(Figure 1a)**. Lower levels of environmental suitability were also projected in these areas, particularly in the Tamaulipeca region **(Figure 1a)**.

a)



b)



c)

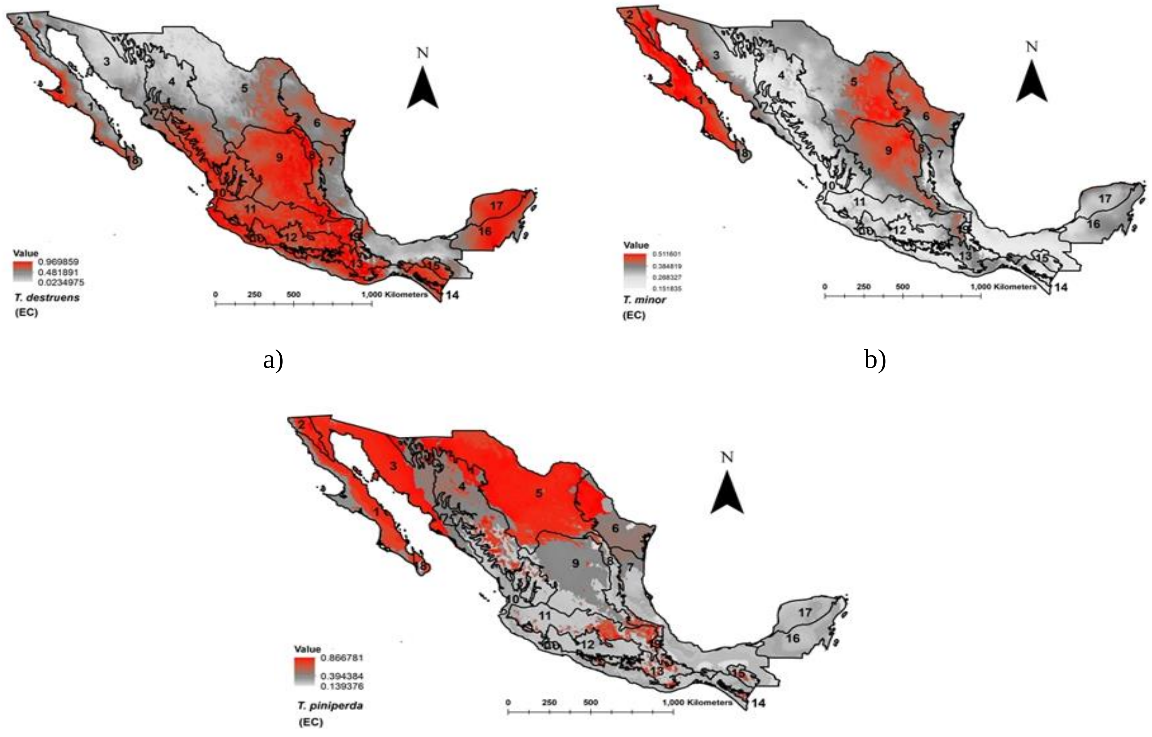
Figure 1. Ecological niche models for three *Tomicus* species (Coleoptera: Curculionidae: Scolytinae) mapped onto the biogeographic provinces of Mexico [35], using the Maxent model with the no Extrapolation setting. Panels show: a) *T. destruens*, b) *T. minor*, and c) *T. piniperda*. The following biogeographic regions are marked: 1. Baja California, 2. California, 3. Sonorense, 4. Sierra Madre Occidental, 5. Altiplano Norte, 6. Tamaulipeca, 7. Golfo de México, 8. Sierra Madre Oriental, 9. Altiplano Sur, 10. Costa del Pacífico, 11. Eje Volcánico, 12. Depresión del Balsas, 13. Sierra Madre del Sur, 14. Soconusco, 15. Los Altos de Chiapas, 16. Peten, 17. Yucatán, 18. Del Cabo, 19. Oaxaca.

T. minor displayed the largest area of environmental suitability in Mexico in this research **(Figure 1b)**, with suitable regions covering the Baja California biogeographic province, the entire California province, the northwestern part of Sonorense, central sections of Altiplano Norte and Altiplano Sur, the northwestern part of Tamaulipeca, and smaller zones within eastern Eje Volcánico. Lower suitability was noted in the Sierra Madre Occidental, Altiplano Norte, Eje Volcánico, Altiplano Sur, Sierra Madre del Sur, Sierra Madre Oriental, Sonorense, and northern Golfo de México.

In the case of *T. piniperda*, environmental suitability could not be calculated for Mexico **(Figure 1c)**.

When the extrapolation-clamping setting was applied, the environmental suitability of *T. destruens* expanded significantly, especially in central Mexico **(Figure 2a)**. Now, suitable areas were identified in Costa del Pacífico, Baja California, Los Cabos, southern Sonorense, southern Sierra Madre Occidental, most of Eje Volcánico, Depresión del Balsas, eastern Altiplano Norte, Altiplano Sur, Sierra Madre del Sur, isolated spots in Tamaulipeca and Golfo de México, most of Yucatán, Peten, Soconusco, and Los Altos de Chiapas.

For *T. minor*, the environmental suitability projections were generally similar between the two modeling settings **(Figures 1b and 2b)**, although there were notable changes. The suitability now fully covered Baja California, while some contraction was observed in Altiplano Sur, Altiplano Norte, and Tamaulipeca. Environmental suitability remained in northern Golfo de México and portions of Eje Volcánico. In Sonorense, the projections reshaped, expanding and contracting along its eastern areas and increasing towards the California boundary **(Figures 2a and 2b).**



a) b)

c)

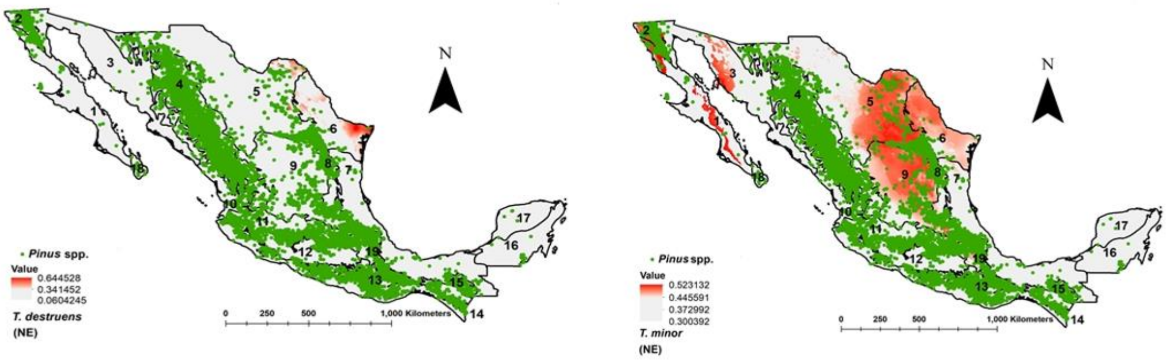
Figure 2. Projected ecological niche models for three *Tomicus* species (Coleoptera: Curculionidae: Scolytinae) across Mexican biogeographic provinces [35], utilizing the Maxent Extrapolation-Clamping setting. a) *Tomicus destruens*, b) *T. minor*, and c) *T. piniperda*. The regions are as follows: 1. Baja California, 2. California, 3. Sonorense, 4. Sierra Madre Occidental, 5. Altiplano Norte, 6. Tamaulipeca, 7. Golfo de México, 8. Sierra Madre Oriental, 9. Altiplano Sur, 10. Costa del Pacífico, 11. Eje Volcánico, 12. Depresión del Balsas, 13. Sierra Madre del Sur, 14. Soconusco, 15. Los Altos de Chiapas, 16. Peten, 17. Yucatán, 18. Del Cabo, 19. Oaxaca.

The environmental suitability for *T. piniperda* under the Extrapolation and Clamping setting shows a dramatic shift, expanding from no suitable areas **(Figure 1c)** to encompass significant portions of northern and central Mexico, as well as some southern regions **(Figure 2c)**. The suitability now covers the entire Altiplano Norte, California, Los Cabos, Baja California, and Sonorense biogeographic provinces. It also extends into parts of western Tamaulipeca, northern Altiplano Sur, scattered areas in Sierra Madre Occidental, Sierra Madre Oriental, Eje Volcánico, Sierra Madre del Sur, Oaxaca, and includes sections of Soconusco and Altos de Chiapas biogeographic provinces **(Figure 2c)**.

The notable expansion in suitable areas under this model suggests a substantial difference in projections for *T. piniperda* and *T. destruens*. Given the considerable differences in the results from the Extrapolation plus Clamping setting, it is crucial to approach the interpretation of these models carefully. As previously mentioned, extrapolation and clamping rely on environmental data from the edges of the calibration zone, which could lead to projections that do not accurately represent regions with contrasting environmental conditions [28, 32]. Consequently, we decided to prioritize the No Extrapolation results for further analysis in this manuscript.

Ecological niche and Pinus distribution in Mexico

Although *T. destruens* is projected to occur sporadically in northeastern Mexico, it is unlikely to pose a significant threat to the diversity of Pinus species in the region **(Figure 3a)**. The Tamaulipeca biogeographic province, where this species was projected, does not show a high density of Pinus records. The diversity and abundance of *Pinus* gradually increase near the boundaries between the Altiplano Norte and Tamaulipeca provinces, where environmental suitability is limited. *T. destruens* is a univoltine species and typically infests various *Pinus* species from the Mediterranean ecosystem, including *P. brutia*, *P. canariensis*, *P. halepensis*, *P. nigra*, *P. pinaster*, *P. pinea*, and *P. radiata* [11, 20]. The presence and concentration of monoterpenes in these hosts are key factors influencing host selection by this scolytine beetle within its native range [19]. This insight presents an opportunity to investigate the composition, concentration, and distribution of monoterpenes in Mexican Pinus species as a preventive measure for identifying potential or susceptible host trees.



a) b)

Figure 3. Ecological niche models for *Tomicus destruens* (a) and *T. minor* (b) (Coleoptera: Curculionidae: Scolytinae), projected onto the Mexican biogeographic provinces [35], using the Maxent No Extrapolation setting along with Pinus distribution data. Panel a) represents the model for *T. destruens*, and panel b) shows that for *T. minor*. The biogeographic provinces are as follows: 1. Baja California, 2. California, 3. Sonorense, 4. Sierra Madre Occidental, 5. Altiplano Norte, 6. Tamaulipeca, 7. Golfo de México, 8. Sierra Madre Oriental, 9. Altiplano Sur, 10. Costa del Pacífico, 11. Eje Volcánico, 12. Depresión del Balsas, 13. Sierra Madre del Sur, 14. Soconusco, 15. Los Altos de Chiapas, 16. Peten, 17. Yucatán, 18. Del Cabo, 19. Oaxaca.

A different outlook emerges for *T. minor*, which exhibits the broadest environmental suitability among the *Tomicus* species examined, expanding its potential to interact with conifer species **(Figure 3b)**. Nevertheless, caution is necessary when interpreting these results for three key reasons: a) the ecological behavior of *T. minor*, b) its host preferences, and c) the local pine shoot insect community. *T. minor* is recognized as a less aggressive pine shoot beetle [36], typically a secondary colonizer after *T. piniperda* infestations, and it has a fragmented distribution [11], preferring weakened trees (e.g., those with significant needle loss, around 80%) [37]. In its native regions, *T. minor* targets a variety of pines, including *P. cembra*, *P. brutia*, *P. densiflora*, *P. halepensis*, *P. koraiensis*, *P. leucodermis*, *P. mugo*, *P. pallasiana*, *P. nigra*, *P. pinea*, *P. pinaster*, *P. pythiusa*, *P. rotundata*, *P. strobus*, *P. sylvestris*, *P. tabuliformis*, *P. thunbergiana*, and *P. yunnanensis* [11]. However, these pine species are absent in Mexico [6]. While this may seem reassuring for Mexico's pine diversity, should *T. minor* invade, there would be a wide array of potential host species, which could lead to changes in its host selection preferences. Scolytines are capable of infesting and completing their lifecycle in new host species that are related to their ancestral ones, as seen with *Xyleborus glabratus*, which now feeds on new Lauraceae species in North America [38]. Local insect competition for pine resources could also limit host availability for *Tomicus* species. Species such as *Eucosma sonomana* and *Rhyacionia neomexicana* (Tortricidae), which are widely distributed across Mexico and are considered significant pine shoot pests, might compete with *T. minor* for pine resources [39]. This competition could act as an ecological barrier. For a successful invasion of *T. minor* into Mexico, environmental suitability alone would not suffice. Two other conditions would likely be necessary: host stress and *T. piniperda* infestation. The 1st condition is already being met, as severe droughts have affected northern Mexico since 1994 [40], significantly impacting the survival of Mexican Pinus species [41]. Drought stress is known to facilitate the invasion of wood-boring beetles [41]. The 2nd condition, however, is not yet present—*T. piniperda* does not currently thrive in Mexico.

Based on our findings, *T. piniperda* appears to be the least likely species to invade among those analyzed. While it tends to favor higher altitudes and wetter climates [42] and has a broader host range, including species such as *P. brutia*, *P. densifloris*, *P. cembra*, *P. funebris*, *P. halepensis*, *P. leucodermis*, *P. koraiensis*, *P. mugo*, *P. pentaphylla*, *P. nigra*, *P. peuce*, *P. pinaster*, *P. pythusa*, *P. pinea*, *P. radiata*, *P. sylvestris*, *P. strobus*, *P. thunbergiana*, and *P. tubaeformis* [11, 39], the species struggles to find suitable environmental conditions in Mexico, reducing its invasive potential. As noted previously, the success of *T. minor* depends on that of *T. piniperda*, but since *T. piniperda* fails to identify viable habitats, this limits the likelihood of *T. minor* successfully invading as well.

The study of environmental suitability for foreign forest pests is expanding, especially considering local phytosanitary concerns. It is crucial to analyze and interpret data to identify potential areas where environmental conditions may support pest establishment. Moving forward, various management strategies should be implemented to curb the invasion and spread of these pine shoot beetles. These strategies should include monitoring drought conditions and their effects on Pinus populations [43], tracking adult populations of *T. piniperda* and *T. minor* [23], and enforcing quarantine inspections at international borders [44].

Conclusion

The ecological niche modeling for 3 *Tomicus* species (Coleoptera: Curculionidae: Scolytinae) was performed and mapped across the Mexican biogeographic provinces. Environmental suitability was successfully calculated for *T. destruens* and *T. minor* using the no extrapolation setting, whereas no suitable areas were identified for *T. piniperda*. The results suggest that the *Pinus* (Pinaceae) diversity in Mexico is likely not at significant risk from potential invasions by these beetles.

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