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Evidence of niche shift in *Schistocerca piceifrons* and identification of potential colonization zones in Mexico in the face of climate change

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ABSTRACT

Objective: *Schistocerca piceifrons piceifrons* is a species that significantly impacts agriculture and threatens food security, making it essential to conduct studies that assess areas susceptible to invasion in Mexico. This study aimed to examine the climatic niche of *S. piceifrons piceifrons* and to identify potential invasion zones in Mexico under climate change scenarios.

Design/Methodology: A niche overlap analysis was conducted to detect variations in niche occupancy by *S. piceifrons piceifrons* in Costa Rica and Mexico. Additionally, a niche modeling approach was implemented to identify new areas at risk of invasion in Mexico under projected climate change conditions.

Results: Findings reveal that the species exhibits variations in its climatic niche across the regions it inhabits in Mexico and Costa Rica. The niche model predicts that, for the 2021-2040 period, suitable habitat availability for *S. piceifrons piceifrons* will expand, particularly in the tropical dry forest and tropical moist forest ecoregions.

Implications: Exploring climatic niche variation in *S. piceifrons piceifrons* provides valuable insights into its invasive potential. Niche modeling further enables the identification of high-risk zones for future invasions in Mexico.

Conclusions: This study contributes to assessing the invasion potential of *S. piceifrons piceifrons* and identifying new areas at risk of colonization. These findings serve as a strategic tool for guiding decision-making and prioritizing control measures against one of the most significant agricultural pests in Mexico and Central America.

Keywords: *S. piceifrons piceifrons*, climatic niches, climate change, invasion, agriculture.

INTRODUCTION

The Central American locust, *Schistocerca piceifrons piceifrons* (Walker, 1870), has posed a significant threat to human societies for millennia (Flores-Granados, 2011). At low population densities, individuals are solitary and harmless; however, under favorable environmental conditions, populations can surge and form swarms composed of millions of individuals capable of migrating long distances within days, causing severe damage to agriculture and livestock systems (Barrientos-Lozano *et al.*, 2021). According to Trujillo (1975), a single swarm can consume an estimated 26 tons of plant material per day. Globally, locusts are responsible for affecting approximately 0.2% of total crop production (Latchininsky & Sivanpillai, 2010). In this context, pest outbreaks represent one of the most pressing biotic challenges for farmers worldwide and remain a central topic of discussion in contemporary agricultural and environmental policy (Simberloff *et al.*, 2013; Skendžić *et al.*, 2021). Global food demand is expected to rise significantly due to population growth, which is projected to reach 10 billion people by 2050 (Tilman *et al.*, 2011; Zelaya-Molina *et al.*, 2022). Consequently, yield losses caused by pest insects pose a serious threat to food security (Culliney, 2014), and this issue is likely to intensify as climate change alters the distribution and dynamics of phytophagous insects (Trnka *et al.*, 2007). The reproduction, survival, dispersal, and population dynamics of pest species are ultimately influenced by their interactions with abiotic variables such as climate, as well as biotic factors including natural enemies, competitors, vectors, and mutualists (Prakash *et al.*, 2014). These interactions can be interpreted through the concept of the ecological niche, defined as the set of biotic and abiotic conditions under which a species can persist and maintain stable population sizes (Hutchinson *et al.*, 1957; Hill & Terblanche, 2014). Accordingly, some authors argue that climate change may generate new ecological niches, facilitating the establishment and spread of pest species into previously uncolonized geographic regions (FAO, 2020).

The ecological niche is typically approached from two perspectives: (1) the fundamental niche, determined by a species' genetic and physiological traits, and (2) the realized niche, shaped by constraints such as interspecific competition (Pearman *et al.*, 2008). Species distribution has been evaluated through two main conceptual frameworks: niche conservatism the tendency of species to retain ancestral ecological traits (Wiens & Graham, 2005) and niche shift, which refers to any alteration in the position of a species' fundamental or realized niche (Broennimann *et al.*, 2007), or both (Pearman *et al.*, 2008). These frameworks are critical to understanding how climate change may affect species distributions and are particularly relevant for designing and implementing adaptive pest management strategies under shifting environmental conditions. In light of the above, and considering that both Mexico and Central America contain permanent breeding areas of *S. piceifrons piceifrons*, and that invasive species are capable of undergoing niche shifts and adapting rapidly to newly colonized environments (Pearman *et al.*, 2008; Broennimann *et al.*, 2007; Da Mata *et al.*, 2010), the present study investigates potential shifts in the realized niche of *Schistocerca piceifrons piceifrons* and its potential range expansion in Mexico under climate change scenarios. Generating this type of information is essential for the development of informed strategies aimed at controlling this pest under emerging environmental conditions.

MATERIALS AND METHODS

Occurrence rate

A total of 720 geographic records of *Schistocerca piceifrons piceifrons* distribution in Mexico and Central America were obtained from the Global Biodiversity Information Facility (GBIF) online platform. According to Hijmans and Elith (2013), databases sourced from platforms like GBIF lack standardized sampling methodologies, making thorough cleaning and filtering especially important. Accordingly, using the R statistical software (version 4.4.0, R Core Team, 2024) and the "dismo" package (Hijmans *et al.*, 2017), we verified the geographic projections of each record and removed duplicates. Coordinates were also checked through visual inspection (Hijmans *et al.*, 1999), and sampling bias was evaluated by subsampling the geographic records (Hijmans and Spooner, 2001; Phillips *et al.*, 2009). Records with unreliable coordinates based on the known distribution of the species were excluded from the database, resulting in a total of 92 validated geographic records for the study area. From this information, six distribution zones were identified: Northern Costa Rica (Zone 1) with 20 records, Yucatán (Zone 2) with eight records, Chiapas-Oaxaca (Zone 3) with 31 records, Southwestern Tabasco (Zone 4) with 11 records, Southeastern Veracruz (Zone 5) with eight records, and San Luis Potosí-Tamaulipas (Zone 6) with 14 records (Figure 1).

Climatic variable selection

Meteorological data for the study area were obtained from the WorldClim database at a 30 arc-seconds resolution. This online database includes 19 bioclimatic variables derived from monthly averages (1970-2000) of temperature and precipitation (Fick & Hijmans, 2017). To reduce collinearity error, a Pearson correlation matrix ($r<0.7$) was generated

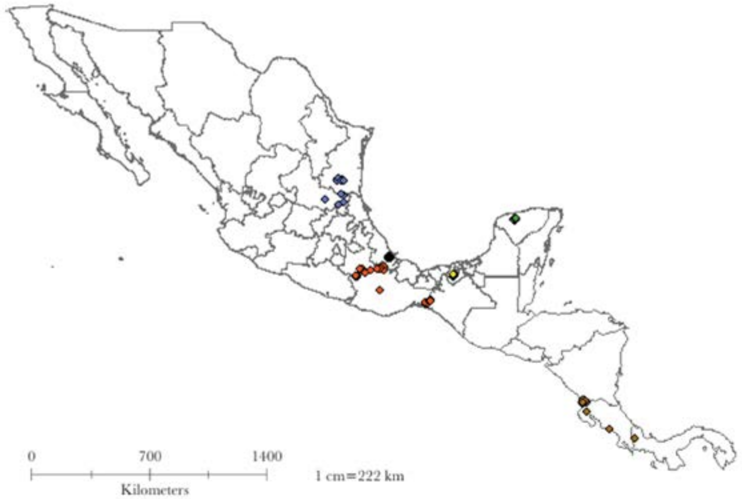

Figure 1. Zone 1: brown dots; Zone 2: green dots; Zone 3: orange dots; Zone 4: yellow dots; Zone 5: black dots; and Zone 6: purple dots.

using R statistical software. This process aimed to eliminate variables providing redundant information. The selected variables were: Annual Mean Temperature (bio1), Mean Diurnal Range (bio2), Temperature Seasonality (bio4), Annual Precipitation (bio12), Precipitation of Wettest Month (bio13), Precipitation of Wettest Quarter (bio16), Precipitation of Driest Quarter (bio17), and Precipitation of Warmest Quarter (bio18). In general, the bivariate correlation analysis was conducted by overlaying the 19 climatic variables on species occurrence records. In our case, climate data were assigned to 10,000 geographically random points across the species' distribution area to avoid excluding zones with relevant (non-redundant) climatic information (Becerra-López *et al.*, 2016). This approach is based on the premise that climate influences the broader contours of species distributions (Araújo & Peterson, 2012). Therefore, the appropriate selection of climatic variables plays a crucial role in understanding the geographic distribution of species (Ward, 2007).

Climatic niche overlap

A principal component analysis (PCA) was implemented following the approach proposed by Broennimann *et al.* (2012) to assess niche equivalency and similarity between the area occupied by *S. piceifrons piceifrons* in Costa Rica and the regions it occupies in Mexico. This method compares the environmental conditions available to a species within a defined background extent with its observed occurrences, and calculates the available environmental space defined by the first two PCA axes. It corrects for sampling bias using a uniform kernel density function (Broennimann *et al.*, 2012). Niche overlap was quantified using Schoener's D metric (Schoener, 1970), which ranges from 0 (no overlap) to 1 (complete overlap). Additionally, based on the documented south-to-north invasion pathway of *S. piceifrons piceifrons* in the Americas (Trujillo, 1975; Bredo, 1985), we measured niche stability (proportion of the niche occupied in Costa Rica overlapping with that in Mexico), niche unfilling (partial occupation of the Costa Rican niche in the Mexican area), and niche expansion (colonization of new environmental conditions relative to its Costa Rican distribution). We also assessed niche equivalence and similarity between regions of occurrence in Mexico.

Climatic niche modeling

To represent the potential distribution of *S. piceifrons piceifrons* in Mexico, the MaxEnt model (version 3.4.1k; Phillips *et al.*, 2024) was used. Prior to this, model calibration was performed in R using the ENMeval package (Muscarella *et al.*, 2014), incorporating the selected climatic variables and the known distribution of the species in Mexico and Costa Rica. The calibrated model was evaluated using the corrected Akaike Information Criterion (AICc) (Warren & Seifert, 2011; Muscarella *et al.*, 2014). The resulting model was projected for Mexico using MaxEnt (version 3.4.1), under both current climate conditions and future projections based on the ACCESS-CM2 model for the 2021-2040 period, using Shared Socioeconomic Pathway (SSP) 585. A total of 100 replicates were run (Dambach & Rödder, 2011), generating an ecological niche model represented as a habitat suitability map under both current and future climatic conditions for *S. piceifrons piceifrons*. For both scenarios, the relative importance of each bioclimatic variable was assessed based on the average of the percentage contribution and permutation importance values obtained from the niche model (Anadón *et al.*, 2015).

RESULTS AND DISCUSSION

Both the climatic niche equivalency and similarity tests between the areas occupied by *S. piceifrons piceifrons* in Costa Rica and those in Mexico yielded non-significant results, with p-values greater than 0.05 ($P>0.05$), indicating no significant difference in the climatic environments where the species is present. Similarly, the results for niche stability, niche unfilling, and niche expansion also showed values greater than 0.05. Additionally, when comparing niche equivalency and similarity among the regions occupied by the species within Mexico, significance values were again above 0.05 ($P>0.05$) (Table 1, Figure 2).

Table 1. Niche equivalency and similarity, measured in terms of niche overlap (Schoener's D) and statistical significance (P). X→Z: From the area occupied in Costa Rica to the area occupied in Mexico; Z→X: From the area occupied in Mexico to the area occupied in Costa Rica.

	Equivalence	**Similarity**		**Expansion**	**Stability**	**Empty**
		X→Z	**Z→X**			
Zone 2	D=0	P=1	P=1	0.93	0	0.92
	P=1					
Zone 3	D=0.00	P=0.37	P=0.33	0.45	0	0.98
	P=1					
Zone 4	D=0	P=1	P=1	0.95	0	0.98
	P=1					
Zone 5	D=0	P=1	P=1	0.98	0	0.99
	P=1					
Zone 6	D=0	P=1	P=1	0.99	0	0.99
	P=1					

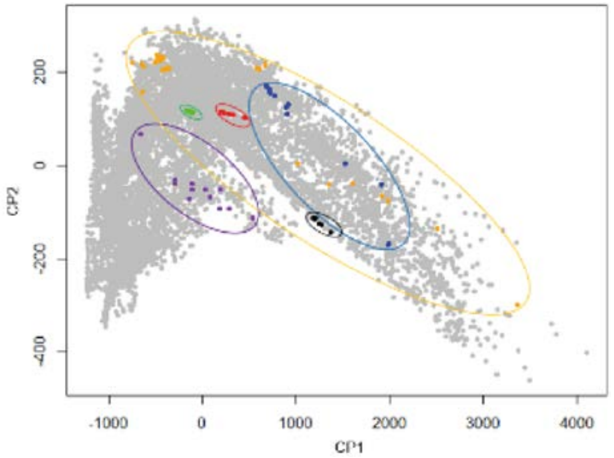

Figure 2. Distribution of *S. piceifrons piceifrons* in climatic space; gray dots indicate the climatic space across the geographic zones of Costa Rica and Mexico, while colored dots represent the areas occupied by the species within the climatic context. Blue dots: species distribution in the climatic space of Zone 1; green dots: Zone 2; orange dots: Zone 3; black dots: Zone 4; red dots: Zone 5; purple dots: Zone 6.

The model was built using a calibration with a regularization multiplier (beta multiplier) of 2, indicating medium complexity; a background of 10,000 geographic points; and a 10% random test partition. The feature classes used for the model were linear (L), quadratic (Q), product (P), threshold (T), and hinge (H); redundant points were removed per pixel using the "Remove duplicates" function. The model generated for current climate conditions achieved an average Area Under the Curve (AUC) of 0.95, while the projection model for the 2021-2040 period achieved an average AUC of 0.97. These values indicate strong model performance, with low commission errors and accurate identification of all reported localities of *S. piceifrons piceifrons* in Mexico and Costa Rica. The climatic variables with the greatest influence on identifying high climatic suitability areas for the species under current conditions were: bio2, bio4, bio16, and bio13. Under the projected climate scenario for 2021-2040, the most influential variables were bio4, bio2, bio1, and bio13 (Table 2).

For Mexico, the highest habitat suitability for this species under current climatic conditions was predicted in the Tropical Dry Forest and Tropical Moist Forest ecoregions, which border the Gulf of Mexico and the Pacific Ocean. This includes the states of Yucatán, Campeche, Tabasco, Veracruz, Tamaulipas, Chiapas, Oaxaca, Guerrero, Michoacán, Jalisco, Nayarit, and Sinaloa, respectively. Additionally, zones of high suitability were identified within the Great Plains ecoregion; within this ecoregion, the areas with the greatest habitat availability for *S. piceifrons piceifrons* are central Nuevo León, southern Tamaulipas, southern San Luis Potosí, northeastern Guanajuato, northern Querétaro, and central Hidalgo. The Temperate Sierra ecoregion in southern states also showed areas of high habitat suitability. In contrast, regions showing intermediate or moderate suitability were found within Temperate Sierra and North American Desert ecoregions in the states of Coahuila, Durango, Zacatecas, and Aguascalientes. Meanwhile, the climate-projection model for the period 2021-2040 indicates that habitat availability for *S. piceifrons piceifrons* is predicted to increase in the Tropical Dry Forest and Tropical Moist Forest ecoregions (Figure 3).

The results from the niche equivalency test between the climatic niche occupied by *S. piceifrons piceifrons* in Costa Rica and those occupied in Mexico indicate that the values

Table 2. The importance values of climatic variables in the identification of suitable areas for the presence of the species *S. piceifrons piceifrons* are shown under current climate conditions and the time period 2021-2040.

Variables	Niche Model Current Climate			Climate Niche Model Time period 2021-2040		
	Percentage of contribution	Permutation value	Relative value	Percentage of contribution	Permutation value	Relative value
bio1	10.6	8.7	14.95	16.1	13.5	22.85
bio2	31.5	24.6	43.8	27.3	16.9	35.75
bio4	27.7	19.3	37.3	29.3	23.7	41.15
bio12	3.4	3	4.9	0.3	2.6	1.6
bio13	9.7	12.8	16.1	11.6	15.4	19.3
bio16	6	20.1	16.05	7.3	14.9	14.7
bio17	6.4	8.2	10.5	5.2	11.1	10.75
bio18	4.8	3.4	6.5	3	2	4

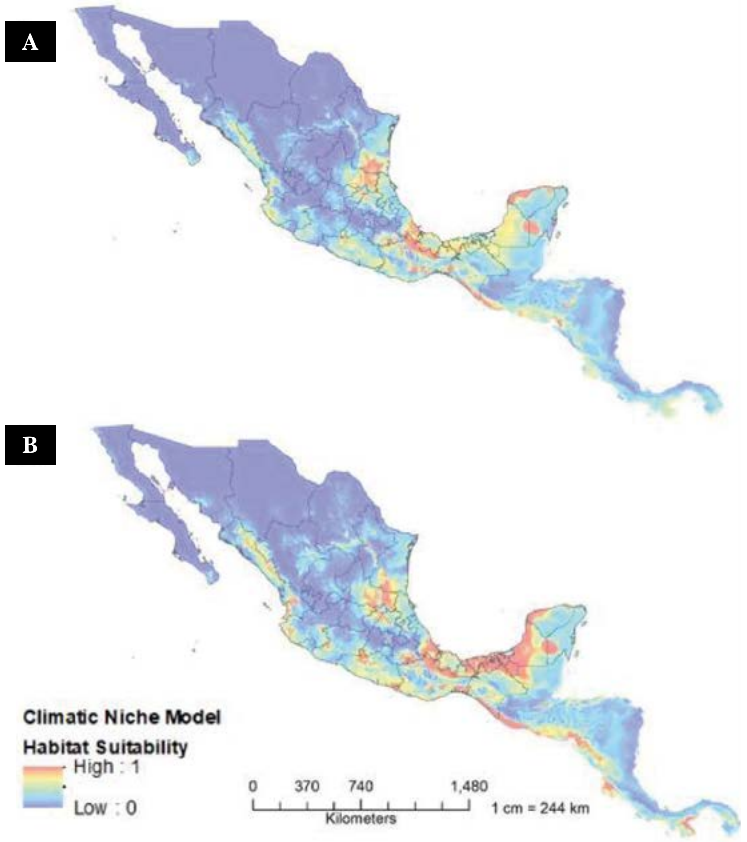

Figure 3. The availability of habitat for the species *S. piceifrons piceifrons* in Mexico is presented under current climate conditions (A) and under the climate projection corresponding to the time period 2021-2040 (B), considering the shared socioeconomic trajectory (SSP) 585.

of D did not show statistically significant differences. Therefore, there is no evidence to reject the null hypothesis of niche equivalency (Warren *et al.*, 2008), which allows us to interpret the evaluated niches as ecologically equivalent. Regarding the similarity test, the null hypothesis proposed by Broennimann *et al.* (2012) states that if the observed overlap exceeds 95% of simulated values, then the species occupies environments in both ranges that are more similar than expected by chance. This test is stringent because it only considers climatic similarity valid when significance is attained in both directions (native *vs.* invaded and invaded *vs.* native) (Warren *et al.*, 2008). Considering this criterion and given that in all comparisons the p-values were greater than 0.05 we reject the null hypothesis of climatic similarity between the niche occupied in Costa Rica and those occupied in Mexico by *S. piceifrons piceifrons*. This indicates that there is no climatic similarity between them. Likewise, no climatic similarity was detected among the five regions in Mexico where the species is present. These findings provide evidence that *S. piceifrons piceifrons* is capable of occupying climatically distinct niches throughout its range, supporting the hypothesis that some species may undergo niche shifts along their colonization routes (Da Mata *et al.*, 2010; Lauzeral *et al.*, 2011). From this perspective, analyzing the niche dynamics inherent to biological invasions becomes crucial (Glennon *et al.*, 2014; Guisan *et al.*, 2014). In this case, our results show zero niche stability when comparing the Costa Rican distribution with its Mexican distribution; according to Strubbe *et al.* (2015), niche stability is defined as the proportion of the exotic niche overlapping with the native niche.

From this standpoint, it is possible to assert that the niches occupied in Mexico by the species are different from those in Costa Rica. Moreover, as noted by Broennimann *et al.* (2012) and Guisan *et al.* (2014), the absolute values of "equivalency" and "similarity" have limited biological meaning unless niche shifts are dissected in terms of their driving processes, namely "niche unfilling" and "niche expansion." According to Petitpierre *et al.* (2012), "niche unfilling" refers to partial filling of the native niche within the invaded area, while "niche expansion" signifies colonization of novel environmental conditions relative to the species' native range. Based on these definitions, our results indicate high niche expansion in Zones 2, 4, 5, and 6, suggesting that in Mexico *S. piceifrons piceifrons* is exploiting climatic niches different from those used in Costa Rica. According to Broennimann *et al.* (2007), this could imply shifts in the species' fundamental niche driven by evolutionary processes. However, given that our data are correlative, it is not possible to distinguish between niche change resulting from physiological tolerance evolution and changes driven by other factors such as competition or predation (Soberón & Peterson, 2011). Thus, physiological studies are necessary to elucidate the principal mechanisms underpinning the observed realized-niche variation. Additionally, "niche unfilling" values were high across all Mexican zones occupied by *S. piceifrons piceifrons*. "Niche unfilling" represents the portion of the native niche not overlapped by the invaded range (Guisan *et al.*, 2014), and according to Strubbe *et al.* (2015), species recently introduced into few locations tend to exhibit greater niche unfilling compared to those with longer colonization histories and broader distributions.

This pattern suggests that many suitable habitats remain uncolonized. Under this criterion, *S. piceifrons piceifrons* may face a high expansion risk in Mexico, as high niche unfilling values imply a large amount of potentially colonizable habitat. According to our niche-modeling results, the greatest invasion risk is predicted for the Tropical Dry Forest, Tropical Moist Forest, and Great Plains ecoregions. This encompasses primarily the states of Yucatán, Campeche, Tabasco, Veracruz, Tamaulipas, Chiapas, Oaxaca, Guerrero, Michoacán, Jalisco, Nayarit, Sinaloa, Nuevo León, San Luis Potosí, Guanajuato, Querétaro, and Hidalgo. Areas with moderate habitat suitability were identified within Temperate Sierra and North American Desert ecoregions in Coahuila, Durango, Zacatecas, and Aguascalientes. However, given that the species' niche is not static and may expand, contract or shift it is plausible that *S. piceifrons piceifrons* could adapt to environmental changes generated by climate change, thereby increasing its invasion capacity under scenarios where competitors, predators, or pathogens are absent.

CONCLUSIONS

In conclusion, this study provides a robust assessment of the invasion potential of *S. piceifrons piceifrons* and identifies new potential invasion zones in Mexico. The results constitute a crucial tool for decision-making and prioritization of control measures against one of the most significant agricultural pests in Mexico and Central America.

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