

Anticipating Pest Expansion Under Climate Change: Ecological Risks of *Scyphophorus acupunctatus* to Agave Species in Mexico

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Abstract

Climate change is reshaping species distributions worldwide, with severe consequences for biodiversity and ecosystem services. In Mexico, the agave weevil (*Scyphophorus acupunctatus*), an invasive pest of ecologically and economically important agave species, threatens both wild populations and cultivated systems. In this study, we used ecological niche modeling to assess the present and future distributions of the agave weevil and seven economically and culturally significant agave species (*Agave americana*, *A. tequilana*, *A. salmiana*, *A. angustifolia*, *A. cupreata*, *A. karwinskii*, and *A. potatorum*) for the period 2041–2060. We projected shifts in species distributions and evaluated the potential overlap between the weevil and its host plants using bioclimatic variables and two shared socioeconomic pathways (SSPs). Our findings revealed divergent responses, indicating that suitable habitats for some agave species may decline due to climate change; conversely, the range of *S. acupunctatus* is likely to expand, particularly under high-emission scenarios. Niche overlap analysis predicted increased co-occurrence between the weevil and economically critical species such as *A. tequilana* and *A. americana*, posing heightened risks to the tequila and mezcal industries. These findings highlight the need for integrated pest management strategies, including biological control, habitat conservation, and sustainable agricultural practices, to mitigate the risks associated with pest expansion. This study provides critical information for conservation planning and adaptive management. By conserving agave biodiversity and promoting climate-resilient practices, we can protect the livelihoods of communities dependent on the agave industry and preserve the cultural heritage associated with these emblematic plants.

Introduction

Climate change is recognized as a key driver of biological invasions, particularly due to its influence on the geographic distribution and population dynamics of pest species (Deustch et al. 2018, Skendžić et al. 2021). Increases in global temperature, altered precipitation regimes, and the frequency of extreme weather events are reshaping habitat suitability for both native and nonnative species (Estay et al. 2009; Deutsch et al. 2018; Finch et al. 2021; Battisti and Larson 2023). The global average surface temperature has increased by 0.19 to 0.21°C per decade since the mid-20th century due to anthropogenic activity and greenhouse gas emissions (Hansen et al. 2006; Levinson and Fettig 2014). This trend, along with extreme weather events, is altering the distribution and behavior of agricultural pests, creating new ecological niches, and enabling pest invasions into formerly unsuitable areas (Estay et al. 2009; Finch et al. 2021; Battisti and Larson 2023). These environmental shifts may not only enable range expansions of agricultural pests into new regions but also enhance their settlement potential by weakening host resistance and altering ecological interactions (Rao et al. 2022).

The Agave weevil (*Scyphophorus acupunctatus*) is a xylophagous insect that damages wild and farmed agave species in México. Although their area of origin remains unclear (Viviano et al. 2024), they are considered endemic to the arid and semiarid zones of Mexico and Central America. Its geographic range has increased as a result of anthropogenic activities, including the cultivation of *Agave tequilana* and inadequate agricultural practices, such as the mismanagement of agave plant residues (Ruiz-Montiel et al. 2017; Recéndiz-De la Mora et al. 2024). The weevil larvae bore into agave cores, causing internal decay, reduced growth, and plant death, leading to substantial yield losses (Cuervo-Parra et al. 2019; Rodríguez et al. 2020). The recorded losses ranged from 24.7–72% in agave crops (Solis-Aguilar et al. 2001). Furthermore, volatile compounds released during plant tissue fermentation attract the weevil, turning agricultural residues into infestation hotspots (Arista-Carmona et al. 2024). These factors, combined with the widespread use of agrochemicals, have exacerbated pest populations in agave plantations, extending the distribution of the weevil (Rodríguez et al. 2020).

The genus *Agave* includes more than 200 species, 74% of which are endemic to Mexico, making it one of the genera with the highest species diversity in the country's native flora; thus, it plays a fundamental role in the plant communities of arid and semiarid regions (Eguiarte et al. 2013). These plants contribute to soil maintenance; provide shelter and microhabitats for insects, birds, and mammals (Torres-García et al. 2019, Trejo-Salazar et al. 2023); and are essential in pollination networks (Trejo-Salazar et al. 2016; Borbón-Palomares et al. 2018). They are also important ornamental plants worldwide (Eguiarte et al. 2021). Agaves are the main supply for industries such as tequila and mezcal production, which drive local economies and preserve centuries-old artisanal traditions (Alducin-Martínez et al. 2023). Moreover, agave species are an integral part of local agroforestry systems and are used in the production of food, beverages, and fiber, which highlights their cultural and economic importance (Torres-García et al. 2020).

Despite the growing recognition of these risks, the combined effects of climate change and pest expansion on agave species habitats have not been fully explored. Specifically, there is limited understanding of how changing climatic conditions influence the distribution and interactions between the agave weevil and its host plants. This knowledge gap is critical, as the agave weevil is a significant threat to the species needed to produce tequila and mezcal (Rodríguez et al. 2020; Arista-Carmona et al. 2023). Addressing this gap is

essential for developing adaptive management strategies to mitigate the environmental and economic impacts of climate change on pest expansion. Ecological niche models (ENMs) have emerged as tools for predicting species distributions under changing environmental conditions. By integrating climatic, environmental, and biological data, ENMs can project how species ranges may change in response to factors such as temperature and precipitation (Araújo et al. 2019; Franklin, 2023). These models are particularly valuable for anticipating the spread of invasive species, identifying at-risk areas, and informing proactive management strategies (Sunny et al. 2024). However, their application in agave ecosystems and agave weevils has been limited, highlighting the need for further research.

This study assessed the current and future potential distributions of seven economically important and traditional agave species and the agave weevil under climate change scenarios for 2041–2060. Using ENMs, we projected species distributions and evaluated the potential overlap between the weevil and agave species under two shared socioeconomic pathways (SSPs). Our findings provide critical insights into the impacts of climate change on agave ecosystems, identify areas at risk of pest infestation, and inform conservation, pest management, and sustainable agricultural strategies. By addressing these challenges, we aim to safeguard agave biodiversity and support the livelihoods of communities dependent on agave-based industries.

Methods

Occurrence records

To assess the future distribution of the agave weevil, we obtained occurrence records of seven economically and culturally significant agave species distributed in Mexico: *Agave americana* (white maguey), *A. tequilana* (tequila agave), *A. salmiana* (pulque agave), *A. angustifolia* (sprat maguey), *A. cupreata* (agave papalote), *A. karwinskii* (candelilla), and *A. potatorum* (tobalá). Records were obtained from the Global Biodiversity Information Facility (GBIF), Comisión Nacional de la Biodiversidad (CONABIO; <http://www.conabio.gob.mx/informacion/gis/>), field visits conducted by the authors between 2021 and 2022, and recent publications (Fig. 1). We avoid sampling bias in the distribution models by applying spatial filtering with the thin function of the spThin package (Aiello-Lammens et al. 2015), discarding presence points within a 1 km radius. The final set of presence data was used for species distribution modeling.

Modeling Ecological Distribution

To model the present and future potential distributions of *Scyphophorus acupunctatus* and *Agave* species, we used maximum entropy analysis in Maxent 3.4.1 (Philips et al. 2006). We obtained bioclimatic layers from WorldClim Project 2 (Fick and Hijmans, 2017). The bioclimatic variables were selected based on the variance inflation factor (VIF) to avoid overparameterization and collinearity among layers using the USDM package (Naimi et al. 2014). The final set of layers included the variables annual mean diurnal range (bio2), mean temperature of the wettest quarter (bio8), mean temperature of the driest quarter (bio9), precipitation of the wettest month (bio13), precipitation of the driest month (bio14), precipitation seasonality (bio15), precipitation of the warmest quarter (bio18), and precipitation of the coldest quarter (bio19).

Before constructing the species distribution models (SDMs), we identified the optimal parameter set to obtain the most parsimonious model using the ENMeval package (Muscarella et al. 2014). Model evaluation included the area under the curve (AUC) test, which measures discriminatory capacity, where higher values indicate better distinction between test locations and background points (Peterson et al. 2011). In addition, we used the corrected Akaike information criterion (AIC) for small samples (AICc) to assess both model fit and complexity, selecting the model with the lowest AICc value as the best model (Warren and Seifert, 2011).

To derive the evaluation metrics, we generated 50,000 random points to serve as background data. We partitioned the occurrence records using the "block" method, which divides the data based on latitude and longitude lines, creating four bins with an equal number of records. Both occurrence and background points were assigned to one of the four bins according to their geographic position relative to these dividing lines (Muscarella et al. 2014).

Model complexity was estimated based on the regularization multiplier (RM) and feature classes in Maxent. We tested 10 RM values ranging from 1 to 5, in increments of 0.5, and six feature classes—linear (L), quadratic (Q), product (P), threshold (T), and hinge (H)—using the ENMeval package (Muscarella et al. 2014). The final models were constructed in Maxent and implemented in the Dismo package (Hijmans et al. 2017). Model performance was evaluated using partial receiver operating characteristic (ROC) curves.

Statistical significance was assessed through null distributions in the EcoNicheS package (Sunny et al. 2025), applying 1000 iterations and a 5% error rate. The AUC significance was estimated using 1000 bootstraps, with 50% of the data used as training locations. All analyses and models were performed in R (R Core Team 2024).

Present and Future Species Distribution Models Under Climate Change Scenarios

To generate future potential distribution maps, we used bioclimatic layers from the CNRM-CM6-1-HR and MPI-ESM1.2-HR climate change scenarios for the years 2040–2060, available in WorldClim Project 2 (Fick and Hijmans 2017). These scenarios, based on the Coupled Model Intercomparison Project Phase 6 (CMIP6), are among the most suitable for inferring relevant climatological aspects in the study area and are appropriate for species distribution studies in Mexico (López-Díaz et al. 2022). We selected the shared socioeconomic pathways (SSPs) SSP245 (middle of the road), which represents moderate environmental degradation with some improvements in resource and energy use, and SSP585 (fossil-fueled development), which is characterized by intensive fossil fuel use and increased emissions (O'Neill et al. 2017).

As in the present-day models, the model parameters were optimized using ENMeval (Muscarella et al. 2014), and the models were evaluated using AUC and AICc. The RM values and feature class combinations were tested in the same manner as before. The final models were built in Maxent and implemented in Dismo (Hijmans et al. 2017). The resulting distribution maps were reclassified into binary presence–absence maps using the 10th percentile training presence threshold, excluding the lowest 10% probability values (Radosavljevic and Anderson 2014). These maps were subsequently used to assess changes in potential distribution in terms of climate suitability gains and losses following Phillips and Dudík (2008).

Niche Similarity and Equivalence

To evaluate the distribution of *S. acupunctatus* and its potential overlap with *Agave* species under climate change scenarios, we used principal component analysis (PCA) as proposed by Broennimann et al. (2012). This method compares the environmental conditions available for a species within a region with its observed presence records, calculating the available environmental space defined by the first two PCA axes. It corrects for sampling bias by considering the available environmental space through kernel density smoothing of presence data. To assess niche overlap and determine whether niches are significantly different, we compared the niches of *S. acupunctatus* with those of the focal *Agave* species, estimating niche equivalence and similarity. Niche equivalence was tested using the Hellinger-based I metric. This metric determines whether niche overlap remains consistent when presence records are randomly reassigned between species. Schoener's D metric was utilized to assess niche similarity. Both metrics range from 0 to 1, where 0 indicates no similarity and 1 indicates high similarity. For this study, D or I values close to 1 suggest a high overlap between the pest and host distributions, indicating a greater risk of infestation (Broennimann et al. 2012).

Results

Potential Distribution

The present and future potential distributions of *S. acupunctatus* and *Agave* species based on bioclimatic variables are illustrated in Fig. 2. The results indicate strong model performance, with AUC values > 0.85. Consequently, the model predictions were regarded as reliable according to the partial ROC calculation at the 0.05 significance level (Supplementary information 1). The distribution models indicate cases of both expansion and contraction in suitable areas for the focal species under future climate scenarios. For *S. acupunctatus*, an expansion of the suitable regions was projected in all analyzed narratives for the 2041–2060 period, ranging from a 5.2% increase (MPI-ESM-585) to a 16.4% increase (CNRM-CM6-245). Conversely, *A. tequilana* and *A. salmiana* are projected to undergo reductions in suitability, ranging from 0.9–28% and 3.1–7.6%, respectively, under both climate scenarios. *A. cupreata* is predicted to undergo a substantial reduction (-26.1% to -35%) in response to both trajectories of the CNRM-CM6 scenario (Table 1). The climatic suitability area for *A. tequilana* spans an area of 730,814.2 km², which constitutes 37% of Mexico's total land area (Table 1). This makes it the species with the greatest climatic suitability. The distribution of this species is primarily concentrated in the western region of the country, with its northern limit defined by the Sierra Madre Occidental (SMO). Toward the Gulf of Mexico, its potential distribution decreases, with further constraints imposed by the central Mexican deserts and xeric regions (the Sonoran Desert and central Mexican shrublands of the Altiplano) and the southern limit defined by the Sierra Madre de Oaxaca. *Agave angustifolia* exhibits a similar distribution pattern but also encompasses a suitable area within the Yucatán Peninsula in southeastern Mexico. *Agave*

americana, on the other hand, is found between the Sierra Madre Oriental and Occidental, extending southward into the mountainous regions of Oaxaca and Chiapas. The climatic suitability areas for *A. salmiana* are located between the SMO, the Trans-Mexican Volcanic Belt (TMB), and the central regions of Oaxaca and Chiapas. *A. cupreata* is distributed primarily from Michoacán in the Bajío dry forests across the western TMB toward the Sierra Madre del Sur and the pine-oak forests of the Chiapas highlands. *A. karwinskii* exhibits a more limited climatic suitability area (26,781.5 km²), predominantly restricted to the Balsas dry forests and xeric regions of Oaxaca.

Table 1

Current and future potential distribution areas for *S. acupunctatus* and *Agave* species in Mexico. The table displays the area in square kilometers (km²) and the percentage of loss or gain in climatic suitability for the focal species.

Species	Historical (km ²)	CNRM 245 (km ²)	% Change	CNRM 585 (km ²)	% Change	MPI-ESM 245 (km ²)	% Change	MPI-ESM 585 (km ²)	% Change
<i>S. acupunctatus</i>	421,968.30	491,227.90	14.10%	448,880.70	6.40%	452,551.10	7.20%	443,944.80	5.20%
<i>A. americana</i>	700,174.20	722,820.90	3.20%	753,494.80	7.60%	789,211.20	12.70%	691,924.10	-1.2%
<i>A. angustifolia</i>	636,999.90	653,262.40	2.60%	641,860.50	0.80%	605,390.60	-5.0%	596,001.50	-6.4%
<i>A. cupreata</i>	137,055.50	101,309.60	-26.1%	88,771.10	-35.2%	139,640.60	1.90%	124,696.50	9.00%
<i>A. karwinskii</i>	26,781.50	21,774.50	-18.7%	43,279.10	38.10%	30,857.50	15.20%	38,052.90	42.00%
<i>A. potatorum</i>	66,420.50	63,877.60	-3.8%	82,032.00	23.50%	60,565.80	-8.8%	82,919.80	24.80%
<i>A. salmiana</i>	217,523.80	201,050.60	-7.6%	210,772.40	-3.1%	210,576.30	-3.2%	206,113.40	-5.2%
<i>A. tequilana</i>	730,814.20	526,032.30	-28.0%	723,903.70	-0.9%	572,992.00	-21.6%	602,451.70	-17.6%

Key Variables Contributing to the Models

The distribution of the species in the study area was influenced primarily by the variability in precipitation and temperature fluctuations (SI 2). For *S. acupunctatus*, bio8, bio15, and bio19 together account for 70% of the explanation of the distribution of the species under both present and future climatic conditions. In contrast, the distribution of *A. americana* was predominantly explained by bio2, bio8, and bio19 (> 75%). For *A. cupreata*, the present distribution was influenced by bio13 (> 30%), followed by bio8 and bio15 under the CNRM-CM6-585 and MPI-ESM 1.2-585 scenarios. Conversely, under the middle-of-the-road scenario (ssp245), bio8, bio13, and bio19 are projected to shape their future distributions. For *A. karwinskii*, bio15 and bio19 will continue to be the predominant influencing factors (> 70%). *A. potatorum* was influenced by bio8, bio15, and bio19 across all the analyzed scenarios. Similarly, for *A. salmiana*, bio8 was the most significant variable (> 50%), followed by bio19 (SI 2). In the context of prevailing circumstances, *A. tequilana* is predominantly influenced by bio15 (31%), bio13 (27.9%), and bio9 (17%), a tendency that persists under the fossil fuel development scenario. Conversely, under the middle-of-the-road scenario, bio13, bio14, and bio9 are projected to emerge as the predominant influencing factors. Presently, bio15 is the main factor influencing *A. angustifolia* distribution (> 28%). For the period from 2041–2060, bio13 (> 30%) is projected to have the most significant influence under the CNRM-CM6 and MPI-ESM-245 scenarios, whereas bio13 and bio9 are projected to be the most relevant under CNRM-CM6 and MPI-ESM 1.2-585.

Niche Equivalence and Similarity

The niche overlap analysis between *S. acupunctatus* and seven *Agave* species revealed a consistent pattern of low equivalence and similarity during the present period (1970–2017). The D and I indices were generally less than 0.5 and lacked evidence of statistical significance ($p \geq 0.1$), suggesting a low degree of ecological matching between the pest and host species under the current conditions. However, under projected climate change scenarios for the period 2041–2060, particularly in the MPI-ESM-245 and CNRM-245 trajectories, there is a notable shift in this trend. Here, significantly high values of equivalence with *A. americana* were observed ($D = 0.6-0.63$; $I = 0.8-0.89$; $p < 0.05$). Furthermore, the CNRM-585 scenario demonstrated important overlap in terms of similarity ($I = 0.7$; $p = 0.03$), although it did not reach statistical equivalence. Conversely, species such as *A. cupreata*, *A. karwinskii* and *A. potatorum* exhibited low values of overlap ($D < 0.1$), with no statistical significance observed in any scenario (Table 2).

Table 2

Niche overlap between *Scyphophorus acupunctatus* and seven *Agave* species under present (1970–2017) and future (2041–2060) climate scenarios. Equivalency and similarity tests were calculated using Schoener's D and Hellinger's-based I indices. The values in parentheses indicate p values obtained from 100 permutations. Significant overlaps ($p < 0.05$) are indicated in bold.

Scenario	Species overlap	Equivalency		Similarity	
		D (p value)	I (p value)	D (p value)	I (p value)
1970–2017	<i>S. acupunctatus</i> vs. <i>A. americana</i>	0.4 (0.8)	0.5 (1)	0.4 (0.1)	0.5 (0.1)
	<i>S. acupunctatus</i> vs. <i>A. angustifolia</i>	0.2 (1)	0.3 (1)	0.2 (0.2)	0.3 (0.2)
	<i>S. acupunctatus</i> vs. <i>A. cupreata</i>	0 (1)	0.1 (1)	0 (0.2)	0.1 (0.1)
	<i>S. acupunctatus</i> vs. <i>A. karwinskii</i>	0 (1)	0.1 (1)	0 (0.3)	0.1 (0.2)
	<i>S. acupunctatus</i> vs. <i>A. potatorum</i>	0 (1)	0.2 (1)	0 (0.2)	0.2 (0.2)
	<i>S. acupunctatus</i> vs. <i>A. salmiana</i>	0.1 (1)	0.2 (1)	0.1 (0.2)	0.2 (0.2)
	<i>S. acupunctatus</i> vs. <i>A. tequilana</i>	0.2 (1)	0.4 (1)	0.2 (0.2)	0.4 (0.2)
2041–2060	<i>S. acupunctatus</i> vs. <i>A. americana</i>	0.63 (0.03)	0.89 (0.01)	0.63 (0.6)	0.89 (0.3)
CNRM-245	<i>S. acupunctatus</i> vs. <i>A. angustifolia</i>	0.26 (1)	0.40 (1)	0.26 (0.2)	0.40 (0.2)
	<i>S. acupunctatus</i> vs. <i>A. cupreata</i>	0.02 (1)	0.14 (1)	0.02 (0.3)	0.14 (0.2)
	<i>S. acupunctatus</i> vs. <i>A. karwinskii</i>	0.02 (1)	0.14 (1)	0.02 (0.3)	0.14 (0.3)
	<i>S. acupunctatus</i> vs. <i>A. potatorum</i>	0.10 (1)	0.28 (1)	0.10 (0.1)	0.28 (0.07)
	<i>S. acupunctatus</i> vs. <i>A. salmiana</i>	0.34 (1)	0.56 (1)	0.34 (0.07)	0.56 (0.06)
	<i>S. acupunctatus</i> vs. <i>A. tequilana</i>	0.44 (1)	0.55 (1)	0.44 (0.11)	0.55 (0.14)
2041–2060	<i>S. acupunctatus</i> vs. <i>A. americana</i>	0.26 (0.8)	0.48 (0.8)	0.26 (0.22)	0.48 (0.20)
CNRM-585	<i>S. acupunctatus</i> vs. <i>A. angustifolia</i>	0.14 (1)	0.32 (1)	0.14 (0.28)	0.32 (0.22)
	<i>S. acupunctatus</i> vs. <i>A. cupreata</i>	0.1 (1)	22 (1)	0.1 (0.19)	22 (0.17)
	<i>S. acupunctatus</i> vs. <i>A. karwinskii</i>	0.07 (1)	0.24 (1)	0.07 (0.18)	0.24 (0.16)
	<i>S. acupunctatus</i> vs. <i>A. potatorum</i>	0.15 (1)	0.34 (1)	0.15 (0.22)	0.34 (0.29)
	<i>S. acupunctatus</i> vs. <i>A. salmiana</i>	0.27 (1)	0.5 (1)	0.27 (0.12)	0.5 (0.12)
	<i>S. acupunctatus</i> vs. <i>A. tequilana</i>	0.11 (1)	0.29 (1)	0.11 (0.21)	0.29 (0.21)
2041–2060	<i>S. acupunctatus</i> vs. <i>A. americana</i>	0.6 (0.03)	0.8 (0.01)	0.63 (0.6)	0.89 (0.3)
MPI-ESM-245	<i>S. acupunctatus</i> vs. <i>A. angustifolia</i>	0.42 (1)	0.53 (1)	0.42 (0.7)	0.53 (0.7)
	<i>S. acupunctatus</i> vs. <i>A. cupreata</i>	0.02 (1)	0.13 (1)	0.42 (0.2)	0.13 (0.2)
	<i>S. acupunctatus</i> vs. <i>A. karwinskii</i>	0.02 (1)	0.14 (1)	0.02 (0.2)	0.14 (0.2)
	<i>S. acupunctatus</i> vs. <i>A. potatorum</i>	0.06 (1)	0.21 (1)	0.06 (0.2)	0.21 (0.2)
	<i>S. acupunctatus</i> vs. <i>A. salmiana</i>	0.34 (1)	0.56 (1)	0.34 (0.1)	0.56 (0.1)
	<i>S. acupunctatus</i> vs. <i>A. tequilana</i>	0.5 (1)	0.6 (1)	0.5 (0.08)	0.6 (0.09)
2041–2060	<i>S. acupunctatus</i> vs. <i>A. americana</i>	0.5 (0.7)	0.7 (0.7)	0.5 (0.07)	0.7 (0.03)
MPI-ESM-585	<i>S. acupunctatus</i> vs. <i>A. angustifolia</i>	0.4 (1)	0.6 (1)	0.4 (0.1)	0.6 (0.1)
	<i>S. acupunctatus</i> vs. <i>A. cupreata</i>	0 (1)	0.2 (1)	0 (0.2)	0.2 (0.2)
	<i>S. acupunctatus</i> vs. <i>A. karwinskii</i>	0.1 (1)	0.3 (1)	0.1 (0.1)	0.3 (0.1)

Scenario	Species overlap	Equivalency		Similarity	
		D (p value)	I (p value)	D (p value)	I (p value)
	<i>S. acupunctatus</i> vs. <i>A. potatorum</i>	0.1 (1)	0.3 (1)	0.1 (0.2)	0.3 (0.1)
	<i>S. acupunctatus</i> vs. <i>A. salmiana</i>	0.1 (1)	0.3 (1)	0.1 (0.2)	0.3 (0.1)
	<i>S. acupunctatus</i> vs. <i>A. tequilana</i>	0.4 (1)	0.6 (1)	0.4 (0.1)	0.6 (0.2)

PCA of the species bioclimatic space demonstrated that PC1 contributed > 45% and that PC2 contributed > 19% under both current and future conditions. The density of occurrence of the different scenarios and SSP is illustrated in Fig. 3. During the historical period (1970–2000), overlap between the pest and *Agave* species was scarce and localized, with a well-differentiated density of presence. However, under the projected climate change scenarios (CNRM and MPI-ESM, SSP 245 and 585), a general trend of increasing spatial overlap was observed, particularly with *A. americana*, *A. tequilana*, and *A. salmiana*. These species exhibited overlap in terms of the density of occurrence with *S. acupunctatus*, particularly under the SSP245 trajectory. The increase in projected overlap in bioclimatic space was mainly concentrated in species of high economic value, in contrast to *A. angustifolia*, *A. karwinskii*, *A. potatorum*, and *A. cupreata*, which indicates that the low density of occurrence overlaps with *S. acupunctatus* in the environmental space, with little overlap visible throughout the scenarios.

Discussion

In this study, we evaluated the effects of climate change on the distribution and niche overlap of *Scyphophorus acupunctatus* (agave weevil) as well as its potential expansion, which poses a significant threat to agave crops in Mexico. This study assessed how changes in regional climatic conditions could affect the distribution of agave species and their interactions with the agave weevil. The predictive models for the present and future distributions developed in this study demonstrated strong performance, with AUC values exceeding 0.85, thus confirming the reliability of the predictions (Guisan and Thuiller 2005). The findings of the present study suggest that environmental and economic pressures on key agave species will continue to intensify under climate change, particularly for those species most heavily exploited for agricultural and beverage production. This emphasizes the necessity of implementing adaptive management strategies to mitigate the impacts of climate change and ensure the sustainability of agave ecosystems and associated industries.

Projected Pest Expansion and Climatic Threats to Agave-Based Agroecosystems

S. acupunctatus exhibited an expansion in distribution across all evaluated climate scenarios, thereby corroborating prior findings that anticipated an increase in suitable areas for its establishment on a global scale (Viviano et al. 2024). In Mexico, its presence has been documented primarily in the central-southern region, reported in at least five biomes, and is expanding into northern states (Recéndiz-De la Mora et al. 2024). Projections from future scenarios, specifically MPI-ESM5-8.5 and CNRM-ESM2-4.5, indicate the potential expansion of *S. acupunctatus* into regions currently cultivated by *A. americana* and *A. tequilana*, driven by rising temperatures and changing precipitation patterns. These agave species are particularly susceptible to infestation, increasing the risk of economic damage in cultivation areas (Cuervo-Parra et al. 2019). However, the magnitude of this expansion was more pronounced under the SSP-245 scenario, while under SSP-585, the increase was less significant. Consequently, the impact of these interactions with their host species may be less pronounced under extreme climate change conditions.

The findings of this study indicate that *Agave* species are likely to experience elevated temperatures and an increased risk of droughts, particularly in arid regions and areas exhibiting high agave presence. This assertion is corroborated by both observed and modeled changes in the country's climatic conditions under shared socioeconomic pathways, which demonstrate a trend toward increased aridification (Beck et al. 2023). The analysis of the distribution ranges of the analyzed species indicated both expansions and reductions in their distribution ranges under these climate scenarios. This highlights the importance of ecological and evolutionary adaptations in *Agave* species to cope with predicted climatic conditions (García-Moya et al. 2011), especially given the expansion of arid and semiarid zones in Mexico (Beck et al. 2023).

At present, *A. tequilana* occupies the most extensive area of climatic suitability and is predominantly located in western Mexico, thus highlighting its significant commercial value and propagation. However, projections indicate that its distribution may undergo substantial reductions across the four evaluated climate scenarios, with SSP-245 posing a particularly notable threat. This contrasts with the recent increase in cultivated areas of the species in Mexico (Martínez et al. 2003). It is anticipated that prolonged droughts and water scarcity in arid regions, associated with reduced precipitation, could further restrict the distribution of this species across Mexico (Torres-García et al. 2020, Alducín-Martínez et al. 2022). However, nonclimatic factors such as reproduction rates, maturation time, interactions with pollinators (Gómez-Ruiz and Lacher Jr, 2019), and pest pressures, including the agave weevil, also play a role in shaping its distribution. The distribution of *A. tequilana* will depend not only on climate but also on its reproduction and propagation methods in the agricultural industry.

Climatic Determinants of Agave Weevil Distribution and Establishment

The distribution of the agave weevil is primarily constrained to areas where monthly temperatures are lower during the wettest quarters of the year (bio8), typically between May and October. These findings are consistent with those documented in previous studies, which reported increased weevil abundance during the rainy season, with a peak in May (Figueroa-Castro et al. 2013; Pedraza-Méndez et al. 2024). Furthermore, areas with low precipitation during the coldest quarters were identified as key factors for weevil establishment. Studies on *S. acupunctatus* abundance have shown increases in individual numbers during the dry season between January and June, reaching their peak in March and April (Solis-Aguilar et al. 2001; Figueroa-Castro et al. 2013; Rodríguez and Navarrete-Heredia, 2017). Conversely, the presence of humid conditions and well-irrigated plantations has been observed to foster the establishment of the weevil (Davis et al. 2017).

We recognize important critical factors of environmental variables such as humidity, temperature, and precipitation in shaping the distribution patterns of agave species. In México, annual precipitation cycles are distinctly pronounced, occurring primarily from May to October (Perdigón-Morales et al. 2018). These climatic conditions determine the species' tolerance to moisture and heat, as well as their capacity to adapt to fluctuations in rainfall patterns and water availability during pivotal stages of their life cycle (Kearney and Porter, 2009). The analysis of models and socioeconomic trajectories in Mexico revealed that climatic variables, including the temperature of the wettest quarter (bio8), precipitation of the coldest quarter (bio19), and precipitation seasonality (bio15), account for 70% of the distribution of the agave weevil. This highlights the importance of water resources and species adaptation to regional climatic conditions (Hernández- Hernández et al. 2014, Davis et al. 2021).

Effect of Climate Change on Niche Overlap

Our findings demonstrated an increase in niche overlap between *S. acupunctatus* and *Agave* species under high-emission scenarios (MPI-ESM5-8.5), indicating that, in the absence of mitigation and adaptation measures, agave crops could suffer significant losses due to pest expansion. Consequently, interactions with host species may be affected by extreme climate change conditions. A greater overlap under the analyzed SSPs also indicated a greater risk of invasion into the distribution areas of the most widely cultivated agave species, particularly under MPI-ESM-585. Our findings revealed that the highest degree of niche overlap was among *A. americana*, *A. angustifolia*, and *A. tequilana*, suggesting that these species may be particularly susceptible to the expansion of the climatic niche of the agave weevil. This effect could be attributed to rising temperatures and reduced precipitation in arid regions under climate change conditions. These results also support previous studies that predicted the expansion of *S. acupunctatus* into the habitats of *Agave* species in Mexico (Viviano et al. 2024).

Species such as *A. cupreata*, *A. karwinskii*, and *A. potatorum* demonstrated limited ecological niche affinity, considering the minimal overlap observed in the analyzed trajectories. These findings suggest that these species have no overlapping historical ecological niches and are unlikely to do so in the future, likely due to differences in climatic tolerances (Broenniman et al. 2012). On the other hand, we suggest that the agricultural practices associated with the studied *Agave* species closely influence the distribution of *S. acupunctatus*. The agave weevil has thus far been found to be most prevalent in species that are important to agriculture and industry (Recéndiz-De la Mora et al. 2024). Alternatively, the overlap of niches with economically important species may be indicative of increased sampling efforts in agriculturally dominant and economically developed regions, which in turn may influence species distribution patterns and introduce sampling biases (Guisan and Thuiller, 2005). Consequently, the lower niche overlap with the distribution of these species could be attributed to the management of less commercially exploited agaves, which are frequently associated with local, low-intensity use practices. These findings suggested that the overlap analysis points to lower densities of agave weevils in areas where agave species of lesser commercial value are found. This observation is further supported by the notion that such management practices may be associated with traditional agroecological approaches, which have been demonstrated to

enhance the natural control of pest-insect invasions in heterogeneous landscapes (Rusch et al. 2016; Rodríguez et al. 2020; Dittmer et al. 2023; Altieri et al. 2024).

Ecological, Economic, and Management Implications of Pest Expansion in Agave Ecosystems

The findings of this study underscore the potential ecological consequences of climate change and the propagation of *S. acupunctatus* in Mexico. The anticipated declines in the distribution ranges of essential species such as *Agave americana*, *A. tequilana*, and *A. salmiana*, coupled with the proliferation of the pest, pressure not only agave biodiversity but also the economic sustainability of dependent industries such as tequila and mezcal production, as well as sociocultural dynamics in areas where agaves are integral to local traditions (Arellano-Plaza et al. 2022). This finding is particularly relevant in central Mexico, where agaves exhibit diverse practical and traditional applications (Delgado-Lemus et al. 2014). In the case of economically important species, industry practices and mitigation measures adopted in response to climate change will have a significant impact on agave production in Mexico, similar to the impact observed for agricultural crops (Lobell et al. 2008).

Climate change may stress agave plants, reducing their resistance to pest infestations and further exacerbating the threat to agave-dependent industries (Stewart 2015). Without appropriate mitigation measures, the region will suffer from the direct effects of climate change (Lotze-Campen and Schellnhuber 2009), as factors such as the abundance of natural enemies of pest species and crop yield are linked to the composition of the surrounding landscape (Karp et al. 2018). We recommend early monitoring to identify the pest's presence and implement control measures to lessen the likelihood of *S. acupunctatus* attacks on plantations. Furthermore, integrated pest management should use biological control methods (natural enemies), culture methods (crop rotation, removal of infected residues), and chemical methods (selective insecticides) to regulate pest populations. In addition, the integration of agroecological practices for endemic species with limited distributions will help mitigate the effects of the weevil. Specifically, for species used in beverage production, adopting sustainable practices that reduce the negative effects of monocultures and promote pollination will be essential (Alducín-Martínez et al. 2023).

Among agave plantations, clonal propagation adds additional pressure due to the loss of genetic diversity, which, in addition to pest pressure, could limit the ability of species to adapt to changing environmental and climatic conditions (Eguiarte et al. 2021, Figueredo-Urbina et al. 2021). Conversely, wild agave populations exhibit greater genetic diversity than cultivated plants, mainly in response to the presence of pollinators such as bats (Ruiz Mondragón et al. 2023). Moreover, unmanaged ecosystems or those under traditional management maintain populations of insects and pathogens through the dynamics of the trophic network and habitat conditions (Harvey et al. 2023). Therefore, the management of agave plantations and wild populations should prioritize the conservation of native vegetation and complex landscapes that are climatically suitable for pollinator species to ensure the continuity of the pollination process (Zizumbo-Villarreal et al. 2013, Trejo-Salazar et al. 2016, Gómez-Ruiz and Lacher Jr. 2019).

The introduction of *S. acupunctatus* to areas where it has not previously been observed poses a considerable risk, as it has the potential to become a pest that could impact both economically important *Agave* crops and traditionally harvested species. The impacts of this pest could include direct damage to plants, reduced productivity, and increased management costs. Among the recommended mitigation measures are early monitoring and the implementation of alert systems to detect the presence of the agave weevil in both natural populations and crops and the implementation of alert systems. Biological control through natural enemies, such as larval predators and parasitoids, or entomopathogenic fungi, such as *Beauveria bassiana*, could serve as a viable option to counteract *S. acupunctatus* populations (Cuervo-Parra et al. 2019). Furthermore, the increasing overlap between the distribution areas of *S. acupunctatus* and agave crops under high-emission scenarios (e.g., MPI-ESM5-8.5) represents a significant risk to agricultural production, particularly in regions with a designation of origin.

To mitigate the impacts of this phenomenon, it is crucial to implement integrated pest management strategies, promote sustainable agricultural practices, and strengthen both in situ and ex situ conservation efforts, as well as assisted migration processes. These actions will not only protect *Agave* biodiversity but also ensure the economic sustainability of communities and industries that rely on these resources.

Conclusion

The findings of this study emphasize the potential ecological consequences of climate change and the expanding range of *Scyphophorus acupunctatus* in Mexico. The projected reduction in suitable habitats for key *Agave* species, coupled with the increasing

overlap between agave cultivation areas and the pest's potential range, underscores the urgency of implementing adaptive management strategies. In the absence of intervention, the projected consequences for biodiversity, including the disruption of essential ecological interactions such as pollination and the jeopardization of the economic sustainability of industries reliant on agave, such as tequila and mezcal production, are profound. To mitigate these threats, an integrated approach that combines habitat conservation, sustainable agricultural practices, and proactive pest management is crucial. The enhancement of biological control measures, the promotion of genetic diversity within Agave populations, and the fostering of ecosystem resilience will serve to enhance the capacity of both natural and cultivated populations to withstand environmental pressures. The adoption of climate-smart agricultural strategies, including assisted migration and diversified cropping systems, could help safeguard agave-dependent economies and cultural traditions. Addressing the challenges posed by climate change and *S. acupunctatus* expansion requires coordinated efforts among researchers, policymakers, and industry stakeholders. By prioritizing sustainable practices and conservation initiatives, it is possible to protect Agave ecosystems while ensuring the long-term viability of the communities and industries that depend on them.

Declarations

Competing interest and funding

The authors declare that they possess no competing interests and have no pertinent financial or nonfinancial interests to report. R-BH and GIS-R have received grants from Secretaría de Ciencia, Humanidades, Tecnología e Innovación (SECIHTI): CVU 458597 and 239732.

Author Contribution

Author Contribution Statement RB-H and GIS-R conceptualized and designed the study; GIS-R collected field data; RB-H analyzed the data and wrote the manuscript; ACG, JLN-H and AS validated and edited the text. All the authors reviewed and approved the final manuscript.

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Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author upon request.

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Figures

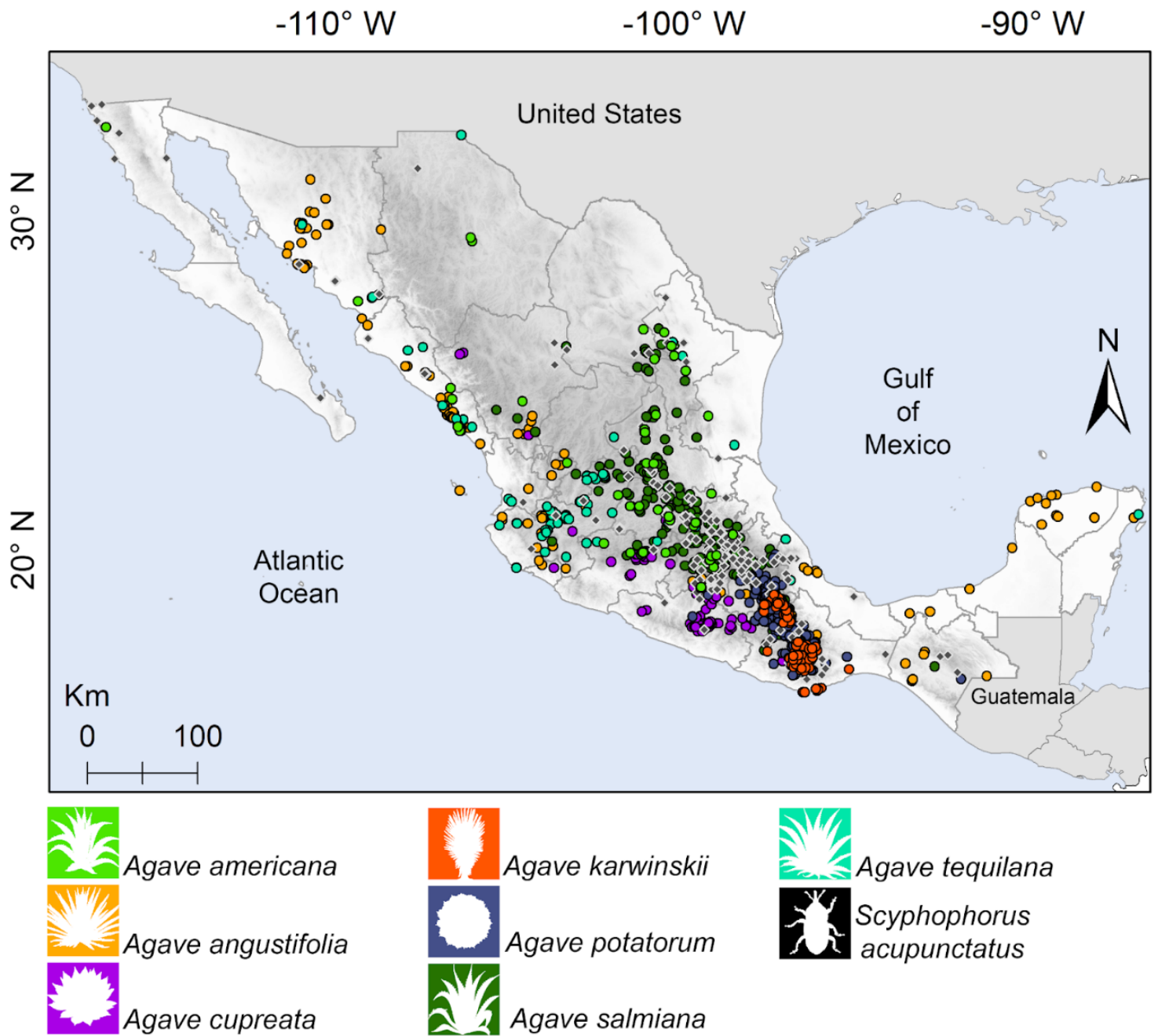


Figure 1

The distribution of the species of the genus *Agave* and the agave weevil studied in this work in Mexico.

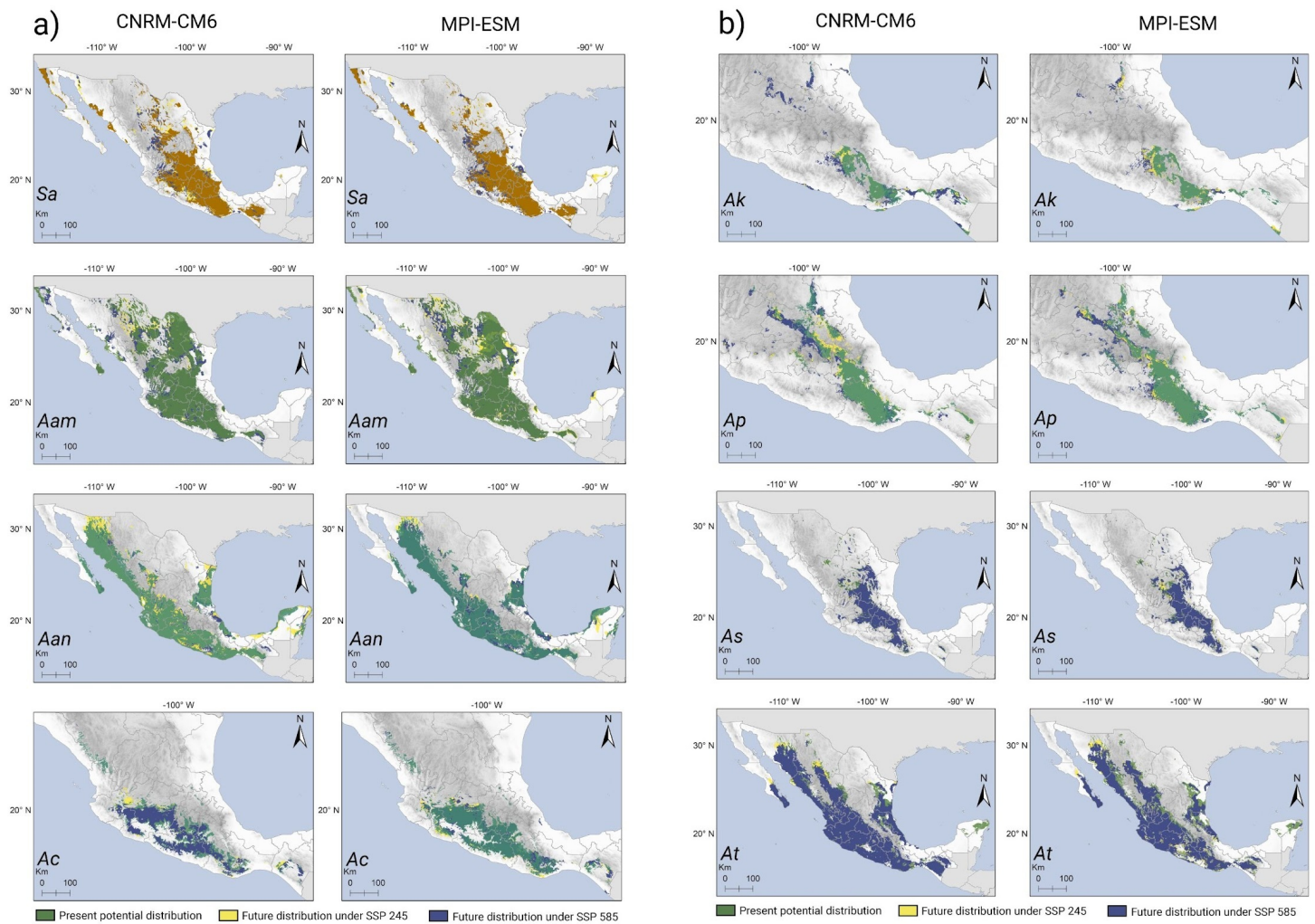


Figure 2

Projected areas suitable for the species, highlighting shifts in their distributions under the analyzed climate scenarios and pathways. The species abbreviations used are as follows: Aam (*Agave americana*), Aan (*Agave angustifolia*), AC (*Agave cupreata*), Ak (*Agave karwinskii*), Ap (*Agave potatorum*), As (*Agave salmiana*), At (*Agave tequilana*) and Sa (*Scyphophorus acupunctatus*).



S. acupunctatus



Agave species

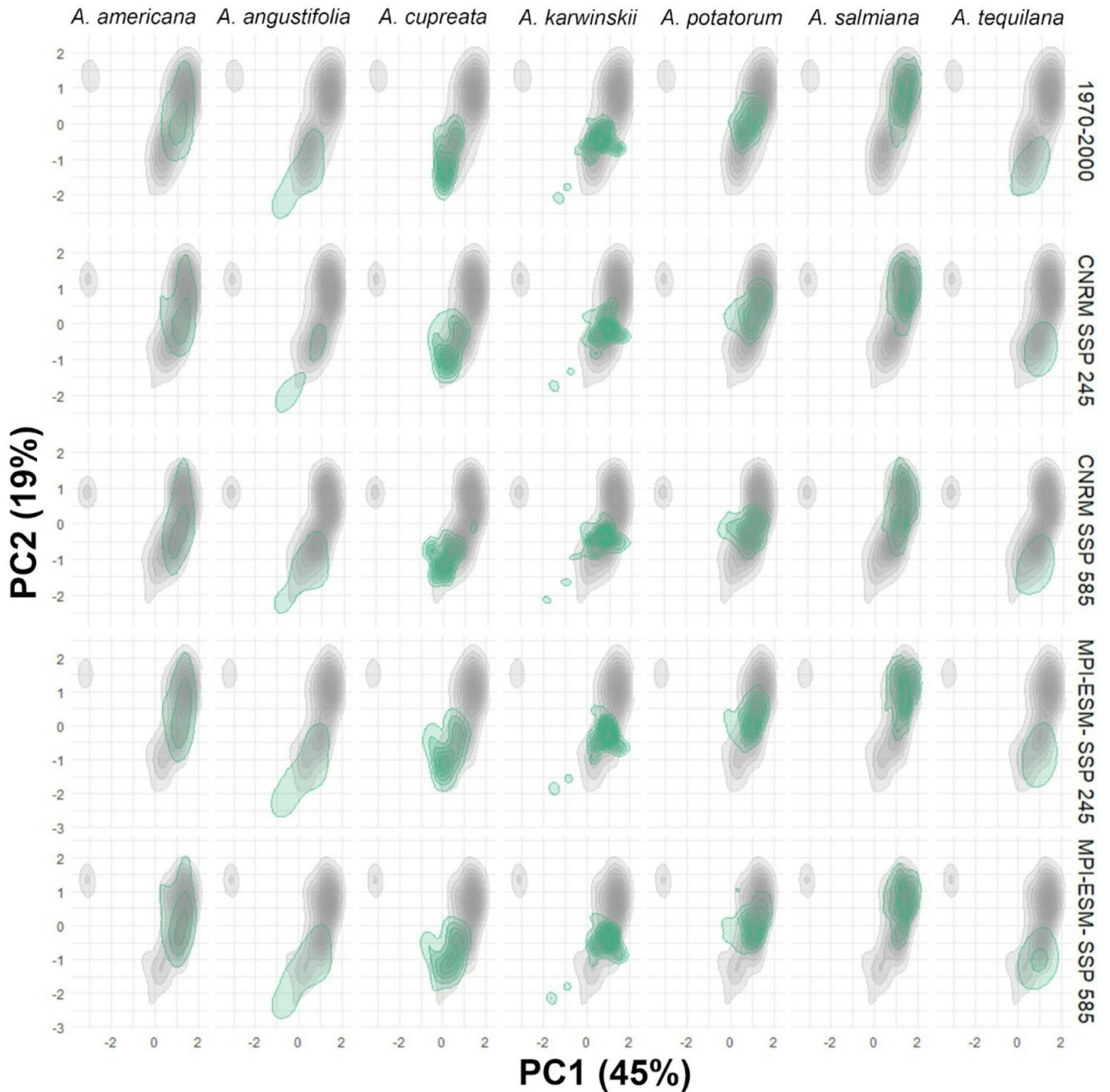


Figure 3

Presence density and overlap of the bioclimatic space of *S. acupunctatus* and Agave species. The figure illustrates changes in niche overlap based on presence density under different analyzed periods and shared socioeconomic pathways.

Supplementary Files

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- [SI1.pdf](#)
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