

## Stored-Product

# Predicted range expansion of *Prostephanus truncatus* (Coleoptera: Bostrichidae) under projected climate change scenarios

Rachel R. Harman<sup>1,\*</sup>, William R. Morrison III<sup>1</sup>, Dalton Ludwick<sup>2,3</sup>, Alison R. Gerken<sup>1</sup>

<sup>1</sup>USDA, Agricultural Research Service, Center for Grain and Animal Health Research, 1515 College Ave, Manhattan, KS 66502, USA, <sup>2</sup>Department of Entomology, Texas A&M AgriLife, 10345 Highway 44, Corpus Christi, TX, 78406, USA, <sup>3</sup>Plant Genetics Research Unit, USDA, Agricultural Research Service, 205 Curtis Hall, University of Missouri, Columbia, MO 65211, USA \*Corresponding author, mail: [rachel\\_harman@outlook.com](mailto:rachel_harman@outlook.com)

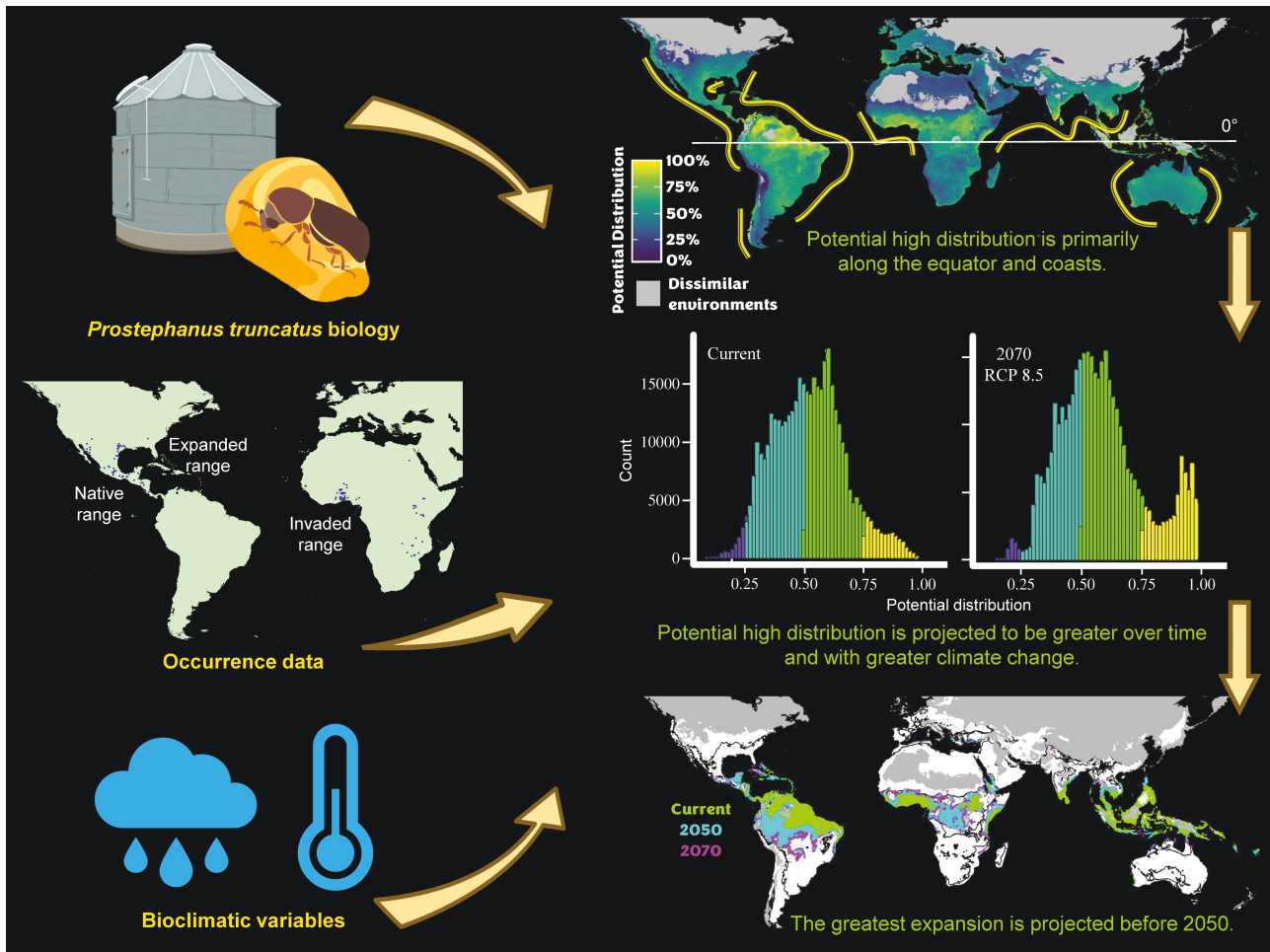
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The larger grain borer (*Prostephanus truncatus* [Horn] [Coleoptera: Bostrichidae]) is a wood-boring insect native to Central America and adapted to stored maize and cassava. It was accidentally introduced to Tanzania and became a pest across central Africa. Unlike many grain pests, *P. truncatus* populations can establish and move within forests. Consequently, novel infestations can occur without human influence. The objectives of our study were to (i) develop an updated current suitability projection for *P. truncatus*, (ii) assess its potential future distribution under different climate change scenarios, and (iii) identify climate variables that best inform the model. We used WALLACE and MaxEnt to predict potential global distribution by incorporating bioclimatic variables and occurrence records. Future models were projected for 2050 and 2070 with Representative Concentration Pathways (RCPs) 2.6 (low change) and 8.5 (high change). Distribution was most limited by high precipitation and cold temperatures. Globally, highly suitable areas (> 75%) primarily occurred along coastal and equatorial regions with novel areas in northern South America, India, southeastern Asia, Indonesia, and the Philippines, totaling 7% under current conditions. Highly suitable areas at RCPs 2.6 and 8.5 are estimated to increase to 12% and 15%, respectively, by 2050 and increase to 19% in 2070 under RCP 8.5. Centroids of highly suitable areas show distribution centers moving more inshore and away from the equator. Notably, the result is a range expansion, not a shift. Results can be used to decrease biosecurity risks through more spatially explicit and timely surveillance programs for targeting the exclusion of this pest.

**Key words:** stored product, movement, ecological niche model, risk prediction, invasive species

## Graphical Abstract



## Introduction

Long-distance trade and travel have promoted the spread of destructive invasive species across the globe (Turner et al. 2021). Despite management implementation, insect pests are a threat that can lead to substantial economic damage (Bradshaw et al. 2016). In particular, invasive insects cause \$120 + billion USD in damage each year (Pimentel et al. 2005). Insect pests also contribute to postharvest commodity loss, such as during on- and off-farm storage, transportation, processing, marketing, and delivery to the end consumers. *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae), the larger grain borer, is one of the few invasive stored product insect pests that are on quarantine or watch lists and is actively being monitored on the borders of Europe, the USA, and Oceania (Quellhorst et al. 2021, Adler et al. 2022).

*Prostephanus truncatus* is a generalist wood-boring insect endemic to Mexico and Central America (Hodges 1986, Nansen et al. 2004), where it adapted to maize. The insect is a landscape-level pest, meaning it can switch habitats from woody hosts to postharvest commodities at food facilities (Borgemeister et al. 1998, Nansen et al. 2004). Maize on the cob can become infested with *P. truncatus* while it is still in the field, and infestations can continue in both the field and storage (Golob and Hanks 1990). Infestations can readily occur as male *P. truncatus*, like other Bostrichidae, release aggregation pheromones at food sources, promoting immigration into food storage facilities (Hodges et al. 1984). Higher densities in an area and/or poor-quality food patches are likely to prompt

aggregating species such as *P. truncatus* to leave a current food patch and increase population spread (Altwegg et al. 2013). The native range of *P. truncatus* has expanded in the last several decades, with known collections in the USA from Texas, New Mexico, Florida, and Georgia (Supplementary Table S1).

A severe outbreak of the pest occurred in sub-Saharan Africa in 1981 (Hodges 1983). The proposed mechanism of the outbreak was a human-mediated introduction to Tanzania through grain shipments during a 1970s refugee and grain supply crisis. *Prostephanus truncatus* quickly spread throughout the equatorial region of Africa (see Quellhorst et al. 2021 for review), likely aided by the insect's life history of dispersing through and residing in natural forested and non-agriculture habitats. Major outbreaks have been reported in the eastern African countries, Kenya and Mozambique. A second introduction into West Africa, specifically Togo, resulted in a population spread to Benin, Ghana, and Nigeria (Krall 1984, Krall and Favi 1986). Smaller outbreaks have been reported in countries surrounding these (Supplementary Table S1) resulting in widespread damage to stored grain.

Furthermore, the economic loss due to *P. truncatus* in its African-invaded region is staggering. Grain loss by weight is estimated at 34–40% during a 3-month storage period (Boxall 2002). In addition, *P. truncatus* adapted to dried cassava (*Manihot esculenta*), a versatile crop that is grown for human and animal consumption as well as to make products such as glue, paper, and medicine (Hodges et al. 1985, FAO and IFAD 2000). Mean weight losses from infestations

are estimated to be 52–74% for fermented and unfermented cassava root (Hodges et al. 1985). These losses are substantial considering that 90% of the stored maize in Africa is for human consumption, and grains often provide up to 60% of the daily caloric intake for people in low- and middle-income countries (Awika 2011). Thus, informed surveillance and management that is both timely and spatially specific is essential for intercepting *P. truncatus* populations to limit the spread of this destructive grain pest.

Predicting the distribution of a pest through models that use bioclimatic variables under projected climate change can promote timely pest control as well as reduce surveillance costs and labor (Gerken and Morrison 2022). Species distribution models (SDMs) utilize environmental factors, often bioclimatic variables, in relation to population locations to estimate species' niches and project distributions across space (Gerken and Morrison 2023). Arthur et al. (2019) utilized the SDM platform MaxEnt to estimate the current potential distribution of *P. truncatus*. The authors concluded that much of the tropical region of the western hemisphere and Asia could support *P. truncatus* populations if the species were introduced; thus, these areas should be vigilantly monitored. Although this study provided important information for management practices at the time, rapid changes in climate variables will likely change the potential distribution of the species.

SDMs have used non-stored product insect occurrence data to estimate insect species' range shifts due to climate change of invasives (e.g., Song et al. 2021, Aidoo et al. 2022, Della Rocca and Milanesi 2022, Lee et al. 2023) and a diverse collection of native species (e.g., Hosni et al. 2022, Lis et al. 2022, Goodman et al. 2023). However, the impact of climate change on stored product pests is often overlooked because of the assumption that the insects occur in environmentally mediated storage facilities and, thus, are not influenced by the outside climate. However, there are likely several major impacts of climate change on stored product insects, including altered microclimates at food facilities, which can be tied to decreased generation times, elevated damage and contamination potential, greater abundance of species, greater need for external inputs, and altered integrated pest management tactic efficacy (Terblanche et al. 2015, Gerken and Campbell 2022, Gerken and Morrison 2023).

The movement of *P. truncatus* has been recorded to occur from forests to agricultural areas, including stores of grain (Scholz et al. 1997, Borgemeister et al. 1998). A total of 27 of 84 tested native and agroforestry tree taxa were found to be suitable as feeding and breeding hosts for *P. truncatus* (Nang'ayo et al. 2002). This suggests that *P. truncatus* is subject to climatic variables for a significant portion of its life history, similar to other landscape insect species (e.g., invasive Argentine ant, *Linepithema humile* [Mayr] [Hymenoptera: Formicidae] (Roura-Pascual et al. 2011), and the Japanese beetle, *Popillia japonica* [Newman] [Coleoptera: Scarabaeidae]; Della Rocca and Milanesi 2022).

To characterize how climate change may affect *P. truncatus*, we performed a SDM using the modeling algorithm MaxEnt via the WALLACE platform to (i) develop an updated current global suitability projection for *P. truncatus* based on newly gathered historical museum records from the USA, (ii) assess the potential future distribution of *P. truncatus* under low Representative Concentration Pathway (RCP 2.6) and high (RCP 8.5) climate change scenarios for 2050 and 2070 to detect areas for potential invasion, and (iii) identify climate variables that best inform the model. These models that identify areas at high risk of invasion can lead to proper monitoring to prevent further incursion and may thus strengthen biosecurity protocols.

## Methods

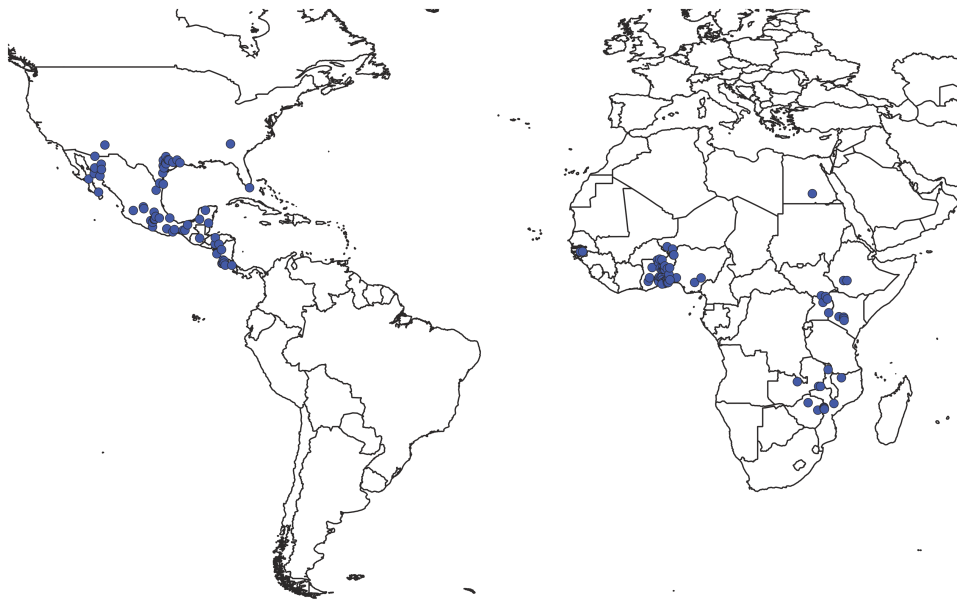
We used the software WALLACE v2.0.4, an open-source graphical user interface (GUI) platform that runs an R-script workflow in the background. It additionally implements MaxEnt to create species distribution maps (Kass et al. 2023a). MaxEnt estimates the potential suitability of an area for a species based on environmental data at occurrence locations and across a study area in given buffer zones as “background” environmental data (Phillips et al. 2004, 2006). The model can further project to future conditions given different climate change models and the RCPs. The information is converted into a scale that estimates potential suitability for the species. MaxEnt is a popular modeling tool for presence-only data and has been noted to have better prediction performance than similar models (Elith et al. 2011, Yackulic et al. 2013). Several R packages were used by WALLACE throughout the methods including spThin (Aiello-Lammens et al. 2015), Rmarkdown (Allaire et al. 2023), rgdal (Bivand et al. 2023), Ecospat (Broennimann et al. 2023), adehabitatHR (Calenge et al. 2023), ade4 (Chessel et al. 2004, Dray and Doufour 2007, Bougeard and Dray 2018, Thioulouse et al. 2018), terra and dismo (Hijmans et al. 2023), shiny (Kass et al. 2023A), ENMeval (Kass et al. 2023B), sp (Pebesma and Bivand 2005), maxnet (Phillips 2021), Knitr (Xie 2014, 2015, 2023, Boettiger 2021), and rmarkdown (Xie et al. 2018, 2020).

## Occurrence

Our species dataset consisted of occurrences of *P. truncatus* amassed from Arthur et al. (2019) as a baseline. We searched or inquired with the University of Kansas (KU) Biodiversity Institute and Natural History Museum and the Kansas State University Museum of Entomological and Prairie Arthropod Research but found no records of *P. truncatus*. However, we additionally received location information for confirmed *P. truncatus* specimens from the Louisiana State Arthropod Museum, Texas A&M University Insect Collection, California Academy of Sciences Entomology Collection, and Florida State Collection of Arthropods. Lastly, we acquired occurrence records from the Global Biodiversity Information Facility (GBIF; GBIF.org 2023). Before modeling, we processed the occurrences by filtering out points lacking coordinate or environmental information, in duplicate, and museum specimens in areas vastly outside of the native or introduced ranges, likely representing interceptions. This resulted in 71 points in the Americas and 77 in Africa (Fig. 1). The occurrence data were spatially thinned by 10 km to reduce the effects of sampling bias to 130 total occurrence locations (Kiedrzyński et al. 2017).

## Predictor Variables

We utilized the bioclimatic data from the WorldClim database version 2.1 (Fick and Hijmans 2017) at a spatial resolution of 2.5 arc-min (~4.6 km at the equator). A total of 19 bioclimatic variables (Table 1) derived from global temperature and precipitation values were incorporated. These variables are commonly used in SDMs to model current and future potential distribution (e.g., Arthur et al. 2019, Goodman et al. 2023, Singh et al. 2023). As some of the bioclimatic variables are calculated with the same data (e.g., BIO7 is the difference between BIO5 and BIO6), there is potential for multicollinearity, and the likelihood of an overfitted model is high (Heikkinen et al. 2006). Thus, to improve the accuracy of the model, we (i) generated an SDM model with all 19 bioclimatic variables using WALLACE with methods described below in section “Distribution Projections,” (ii) performed a pairwise Pearson correlation analysis of all variables from the top-performing model that was



**Fig. 1.** Map of the 148 documented occurrence points used for the species distribution modeling in this study. The map is focused on northern Central America and Africa.

**Table 1.** The 19 bioclimatic variables from WorldClim. Those marked with a star and bolded were retained after removing highly correlated variables (Pearson  $r \geq 0.70$ )

Variable and Description
BIO1 = Annual mean temperature
BIO2* = Mean diurnal range (mean of monthly (max temp—min temp))
BIO3* = Isothermality (BIO2/BIO7) ( $\times 100$ )
BIO4 = Temperature seasonality (standard deviation $\times 100$ )
BIO5* = Max temperature of warmest month
BIO6* = Min temperature of coldest month
BIO7 = Temperature annual range (BIO5—BIO6)
BIO8* = Mean temperature of wettest quarter
BIO9 = Mean temperature of driest quarter
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
BIO18* = Precipitation of warmest quarter
BIO19* = Precipitation of coldest quarter

selected by the area under the curve (AUC), and (iii) removed 1 variable from each highly correlated pair when  $r \geq 0.70$  (Supplementary Figure S1). We used a jackknife test and response curves produced by MaxEnt and WALLACE, respectively, to decide which variable to keep in the final model based on its contribution to the model. The jackknife test ranks variables' importance by their contribution to the suitability model. Contribution is measured as information gained when the variable is added in isolation as well as information lost when it is removed (Miller 1974). The response curves show the relationship between the modeled suitability and the predictor environmental variables when other variables are at their median (Elith and Graham 2009). WALLACE does not calculate response

curves for variables that add zero information to the model. Hence, both tests, in tandem, inform what ranges within important bioclimatic variables most promote or limit potential suitability and distribution. We additionally considered the biological relevance of *P. truncatus*. In total, 10 of the nineteen variables were retained (Table 1), and an updated SDM was generated.

We projected future bioclimatic data using the Community Climate System Model version 4 (CCSM4 model), a coupled climate model that simulates the Earth's climate system with 5 separate models representing the atmosphere, ocean, land, land-ice, and sea-ice, and 1 central coupler component to project climate scenarios to the past or future (National Center for Atmospheric Research 2020). We modeled *P. truncatus* potential distribution under 2 RCP scenarios, one estimating low (RCP 2.6) and the other high (RCP 8.5) climatic change, as well as projected both RCP scenarios to near-(2050) and long-term (2070) timescales. The RCPs are greenhouse gas concentration trajectories introduced by the Intergovernmental Panel on Climate Change (IPCC) to describe possible climate change scenarios. An RCP of 8.5 estimates an environment in which no efforts to change greenhouse gas emissions were made whereas an RCP of 2.6 reflects very stringent mitigation efforts (Meinshausen et al. 2011).

### Niche Space

We used principal component analysis (PCA) within WALLACE to visualize if the endemic populations within the Americas and the invaded African regions were similar in Hutchinsonian niche space. The niche space included the 10 bioclimatic variables retained after removing highly correlated variables. An ordination plot was created with Mahalanobis distances between the occurrence points, which gives equal weight to all environmental predictors. We calculated a *P*-value to determine whether the overlap in niche space was significantly similar ( $P \leq 0.05$ ) using WALLACE. In addition, a niche overlap metric, overlap D (Schoener 1968), was measured using WALLACE. Overlap D is an index of niche overlap ranging from 0 to 1, with 1 representing an exact ratio of the density of occurrences to the density of the background environment. As the niche spaces

of populations within the native and invasive range were not significantly different (see section “Results”), we pooled all data together to create final species distribution maps.

### Distribution Projections

The settings used in WALLACE were selected as follows. To select the background extent, point buffers with a 2° buffer were created around the occurrence points. Point buffers limit the area from which the 50,000 background data points are collected to areas most likely sampled for the specific species’ presence. This increases the precision of MaxEnt as the model relates occurrence point environments to the environment across the buffered study area as the “background” (Pearson 2007). The occurrence data were partitioned into training and testing groups using a block ( $k = 4$ ) spatial partition, which creates 4 groups corresponding to spatial rectangles ( $k = 4$ ) based on longitude and latitude, which is appropriate for projecting into future scenarios (Muscarella et al. 2014).

Model selection was performed in WALLACE with the following settings to calculate an appropriate level of complexity. The feature classes selected included L, H, Q, LQ, and LQH (L = linear, H = hinge, and Q = quadratic). Model complexity was limited by a regularization multiplier of 1–4 with a step size of 1. This provided 32 models with each feature and multiplier combination. The model was additionally clamped to match the upper or lower values found in the study area. Clamping removes predictions of high suitability outside of the known environmental variable ranges, which can inflate forecasts (Pearson 2007). Corrected Akaike information criterion and AUC of receiver operator characteristic were used to determine the top models. Current distributions of the top 4 models were mapped and visually analyzed for biological accuracy (e.g., if distributions were predicted in the desert or arctic habitats). The top AUC selected model, hinge with a regularization multiplier of 3, was used.

The jackknife test was performed in the stand-alone MaxEnt program using the same settings used in WALLACE to ascertain the percent contribution of each variable in the SDM. Response curves were created in WALLACE to show the predicted suitability across the range of values of each bioclimatic variable (Elith and Graham 2009). A table and figure were compiled (see section “Results”).

Maps of current and future climate scenarios (2050 and 2070 projections at RCPs 2.6 and 8.5) were created in WALLACE, and raster information was imported into R (R Core Team 2023). Five potential distribution maps were created using a scale of 0–1.0, with numbers representing environmental suitability, with 1.0 being highly suitable, and, thus, the potential that *P. truncatus* populations could establish at the pixel point. In addition, multivariate environmental similarity surface (MESS) maps were created in WALLACE for the present time period. MESS calculates the similarity of the environment in the projected zone compared to the occurrence and background data. The map was converted to a binary similar–dissimilar scale, and dissimilar areas ( $\leq 0$ ) on the species distribution maps were covered to disallow the interpretation of areas with extrapolation uncertainty. The packages terra, raster, rgdal, ggplot2, and dplyr, sp were used to create the maps (Pebesma and Bivand 2005, Bivand et al. 2013, Wickham 2016, Bivand et al. 2023, Hijmans 2023a, 2023b, Wickham et al. 2023).

### Movement of High Distribution Category

The potential distribution for all 5 projections was categorized into 4 classes: low ( $< 0.25$ ), poor (0.25–0.499), moderate (0.5–0.749), and high suitability ( $\geq 0.75$ ). Chi-square goodness-of-fit tests were

performed in R to test for significant differences between class levels, compared to the current projection or 2050 as a null hypothesis. A centroid was calculated for highly suitable areas in 6 regions that showed geographically distinct potential populations, including North America, Central/South America, western Africa, eastern Africa, western Asia, and eastern Asia, and was plotted for each of the 5 projections in QGIS (version 3.32.0). The latitude and longitude for each centroid were used to measure the distance between each time period and climate change scenario. Two-tailed *t*-tests were performed in R to test for significant differences between distances. Maps were created in QGIS to interpret the change in high suitability for both the low and high climate change scenarios (RCPs 2.6 and 8.5, respectively). Histograms of suitability were created in R using ggplot2 (Wickham 2016).

## Results

### Niche Space

The PCA niche model resulted in a significant overlap of niche space (Schoener  $D = 0.77$ ;  $P = 0.03$ ) between the occurrence data in the endemic North American and the invaded African populations (Fig. 2). As the niche space was significantly similar, the occurrence data were pooled for further analyses.

### Response Curves

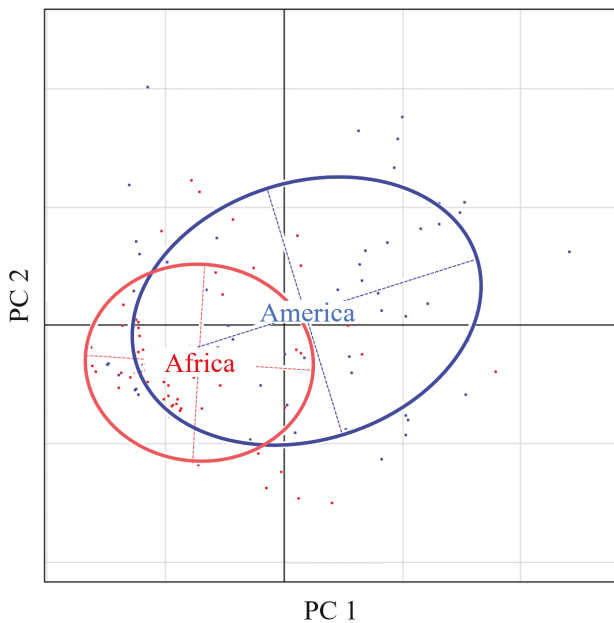
The 3 bioclimatic variables that most contributed to the model and thus most influenced *P. truncatus* distribution included precipitation in the coldest quarter, minimum temperature of the coldest month, and precipitation of the warmest quarter according to the jackknife analysis (Table 2). The contribution of these 3 bioclimatic variables together accounts for 95.1% of the variation in the data. Other variables, such as precipitation of the wettest quarter, mean temperature of the wettest quarter, and isothermality, added little information to the model. The remaining variables did not provide substantial information or influence *P. truncatus* distribution (Table 2).

The shape of the response curves indicated that *P. truncatus* primarily inhabits areas with medium to low precipitation and/or high temperature. Very low temperatures and great amounts of precipitation reduced suitability (Fig. 3).

### Distribution Projections

Under present-day conditions, highly suitable land area for *P. truncatus* covers 7.2% of the projected globe (not including the MESS layer, Fig. 4). These areas are primarily tropical, subtropical, and coastal areas (Fig. 5A). Outside of the native and invaded ranges, highly suitable areas were projected in much of northern South America, India, southeast Asia, Indonesia, and the Philippines. Poor and low suitability are primarily areas that are more polar, desert, mountainous, and inshore.

Overall, the amount of highly suitable areas is estimated to increase with future climate change. Under low climate change, RCP 2.6, highly suitable areas are estimated to be 11.6% of the projected world in 2050 and 11.3% in 2070 (Fig. 4). However, under a high climate change regime, RCP 8.5, highly suitable areas are estimated to increase to 15.1% and 19% in 2050 and 2070, respectively (Fig. 4). The area of poor and low suitability areas is projected to decrease with climate change and time (Fig. 4). The proportion of the 4 suitability types under low climate change is not significantly different between the current and 2050 ( $\chi^2 = 2.57$ ;  $df = 1$ ;  $P = 0.46$ ), current and 2070 ( $\chi^2 = 2.3$ ;  $df = 1$ ;  $P = 0.51$ ), or 2050 and 2070 low climate



**Fig. 2.** Principle component analysis (PCA) of the niche overlap between the endemic North American and invaded African population of *P. truncatus* showing occurrence data points within each.

**Table 2.** List of the bioclimatic variables that added the most to the model and thus more greatly impacted *P. truncatus* distribution

Variable	Percent contribution	Permutation importance
Precipitation of coldest quarter	51.7	44.2
Min. temperature of coldest month	37.4	17.3
Precipitation of warmest quarter	6	21.6
Precipitation of wettest quarter	3	12.1
Mean temperature of wettest quarter	1.8	2.3
Isothermality	0.1	2.5
Precipitation of driest quarter	≈0	0
Precipitation seasonality (coefficient of variation)	≈0	0
Max. temperature of warmest month	≈0	0
Mean diurnal range (mean of monthly (max temp—min temp))	0	0

change scenarios ( $\chi^2 = 0.01$ ;  $df = 1$ ;  $P = 0.99$ ). The proportions of suitability types under high climate change were not significantly different between current and 2050 ( $\chi^2 = 5.71$ ;  $df = 1$ ;  $P = 0.13$ ) nor between 2050 and 2070 ( $\chi^2 = 1.32$ ;  $df = 1$ ;  $P = 0.73$ ). However, there was a significant difference between current and high climate change conditions in 2070 ( $\chi^2 = 11.4$ ;  $df = 1$ ;  $P = 0.01$ ).

The future species distribution maps show that highly mountainous and desert areas remain at low suitability levels, and the highly suitable areas encroach further inland and to the polar regions (Fig. 5B–E). Centroids of the highly suitable areas for both climate change scenarios distinctly shift in each projected continent (Figs. 6 and 7). North American centroids moved northward and slightly west toward the USA. Western African centroids move eastward along the coast, whereas eastern African centroids move southward and more inland. Eastern and western Asia centroids move distinctly northward, away from the coast.

The distance between centroids was 4.1 times greater between current and 2050 ( $2.11^\circ \pm 0.47$  SE apart) than 2050 and 2070

( $0.52^\circ \pm 0.14$  SE apart) for low climate change ( $T = 3.57$ ;  $df = 5$ ;  $P = 0.016$ ). Similarly, under high climate change, the distance between current and 2050 centroids ( $3.15^\circ \pm 0.60$  SE apart) was 3.6 times greater than between 2050 and 2070 ( $0.88^\circ \pm 0.17$  SE apart;  $T = 3.70$ ;  $df = 5$ ;  $P = 0.013$ ). The distance between the centroids was not significantly different between low and high climate change scenarios between current and 2050 ( $T = 2.43$ ;  $df = 5$ ;  $P = 0.059$ ) or 2050 and 2070 ( $T = 2.11$ ;  $df = 5$ ;  $P = 0.088$ ), although high climate change scenarios tended to move more.

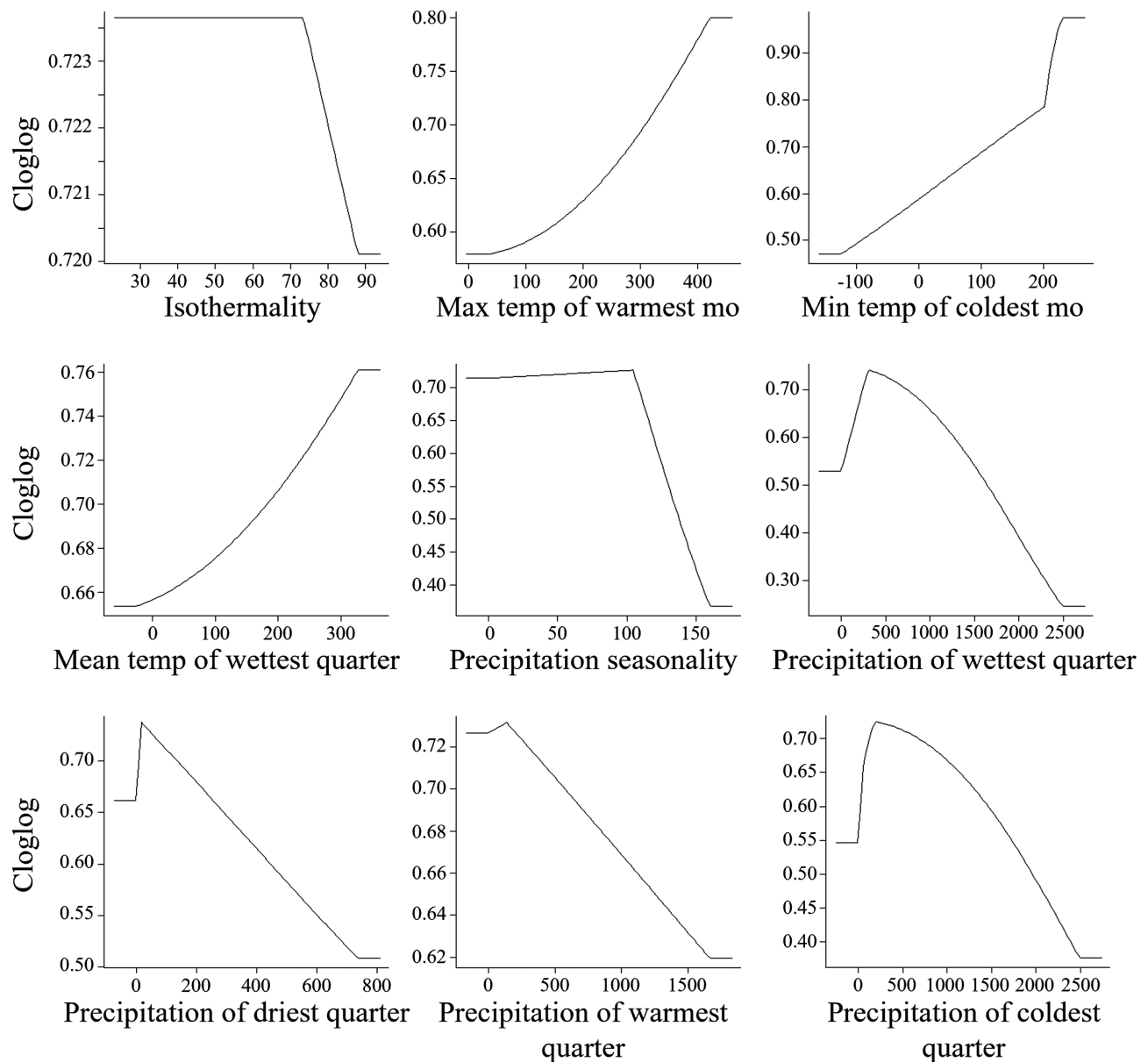
## Discussion

As shown in the present study, the potential distribution of the devastating stored product pest species, *P. truncatus*, is expected to increase significantly under future climate change. This work contributes to the growing understanding of SDMs for stored-grain pests (Arthur et al. 2019, Kim et al. 2020, Lee et al. 2020, Zhao et al. 2023). *Prostephanus truncatus* is vulnerable to bioclimatic changes and is an excellent species for understanding the effects of larger changes in climate. Overall, the models show that extremes in precipitation and temperature limit the potential distribution of *P. truncatus*. Importantly, the greatest increase in suitable areas for *P. truncatus* establishment is expected by 2050, not 2070. This expansion is projected to move further away from the equator and coastal zones, allowing for potential distribution more inland and in currently cooler environments. This includes currently unoccupied areas of India, southeastern Asia, and Oceania modeled as highly suitable even under current climates.

Changes in temperature and precipitation are highly influenced by climate change. *Prostephanus truncatus* distribution was primarily negatively impacted by low minimum temperatures and extreme precipitation levels, which reflects the native tropical and subtropical habitats of *P. truncatus* (Quellhorst et al. 2021). A species adapted to the warmth of the equator would be unaccustomed to cold temperatures below the species' developmental threshold, which can induce stress, coma, and mortality (Sinclair et al. 2003). For *P. truncatus* eggs, larvae, and pupae, the lower developmental temperatures have been measured at 11.4, 14.6, and 13.1 °C, respectively (Subramanyam and Hagstrum 1991), whereas adults can survive temperatures as low as  $-15^\circ\text{C}$  for 30 min (Machekano et al. 2017). In addition, low temperatures may negatively impact *P. truncatus* flight (Nansen et al. 2004) and potentially restrict their distribution in areas with low minimum temperatures more than predicted.

Precipitation is expected to become more variable with climate change (Araya-Osses et al. 2020). Changes in precipitation affect herbivorous insects by impacting the plant communities and, thus, what is available for the species to consume as natural refugia in the landscape (Pincebourde and Woods 2012). Although *P. truncatus* is a specialist in maize and cassava after harvest, outside storage facilities, it prefers tree species corresponding to subtropical climates (Nang'ayo et al. 2002). Changes in precipitation may allow the expansion of agriculture in areas that were previously too dry (Parry 1990) or can change the composition of crops altogether (Gerken and Morrison 2022), further providing hospitable land for *P. truncatus* populations. However, extreme variability could also leave once fertile areas barren due to drought, although irrigation may reduce plant stress in these agricultural landscapes. In addition, precipitation influences humidity, an important environmental factor for insect fecundity, diapause, and survivorship (Chapman et al. 2013).

The response curves indicate that suitability is greater in hot and consistent environments, similar to its native subtropical

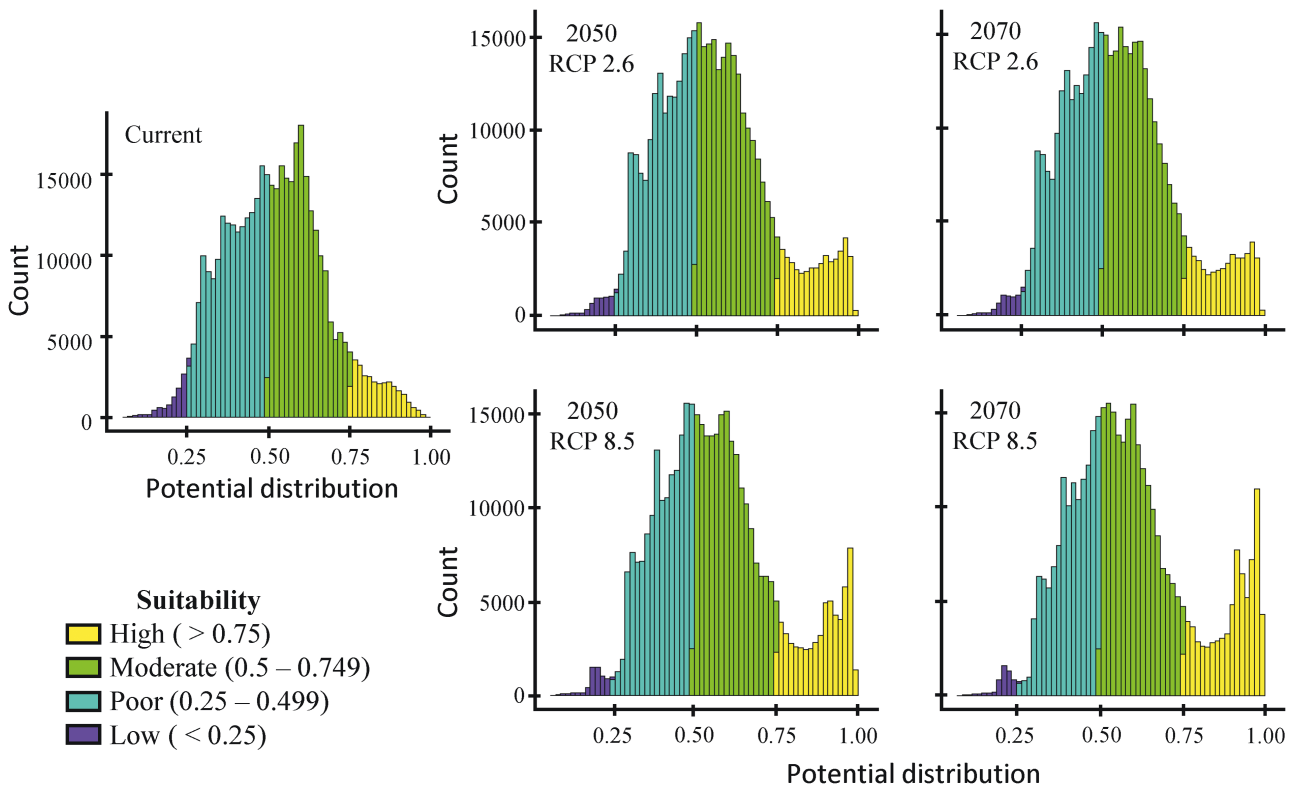


**Fig. 3.** Response curves for the 9 bioclimatic variables maintained in the model after removing correlated variables with  $r \geq 0.70$  designated by the Pearson test. The response curve for mean diurnal range was not created as it was not incorporated into the model.

regions. *Prostephanus truncatus* has been noted to flourish at higher temperatures than most stored product insects and is often reared at 32 °C compared to other species' optimal temperatures of 28–30 °C (Quellhorst et al. 2020). Climate change is predicted to increase global mean temperatures by 2–7 °C by the end of the century (Allison et al. 2009), which may increase survival during overwintering, shorten generation time, and alter community interactions (Skendžić et al. 2021). However, high temperatures did not contribute much to the model (e.g., the maximum temperature of the warmest month), nor did measurements of temperature range, which only contributed 0.01% through isothermality. This indicates that the drivers influencing *P. truncatus* distribution are not necessarily the variables that make an area suitable but rather those that do not.

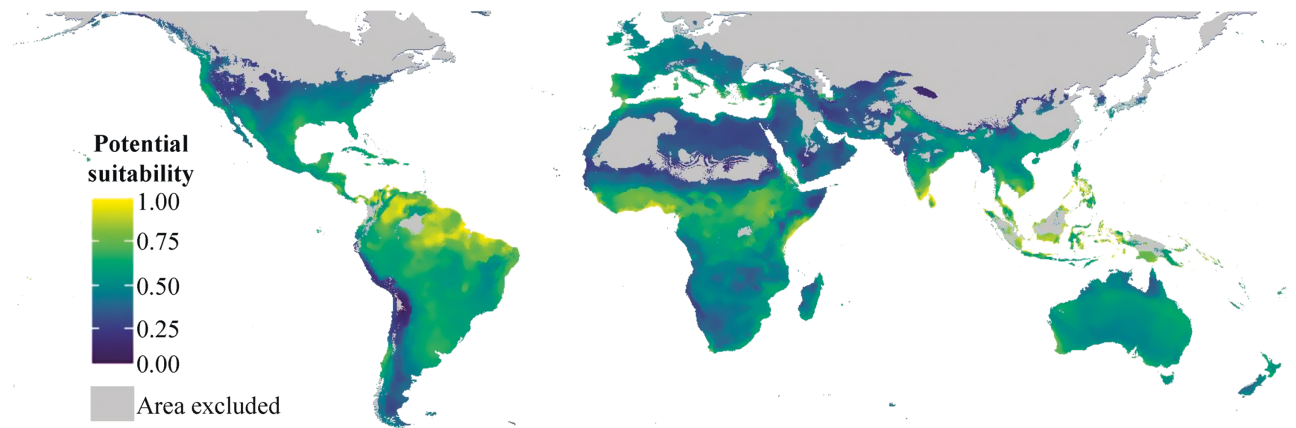
Similar environmental trends were noted by Arthur et al. (2019), who also extrapolated *P. truncatus* distribution using only MaxEnt and current environmental variables. Notably, this article did not

include several occurrence points in the southern United States from natural history collections, which we have now provided here as new information. It also did not explicitly take climate change into account. The climatic variables in that study included isothermality, maximum temperature of the warmest month, minimum temperature of the coldest month, and annual precipitation, which were included in both the American and African projections (trained separately). Of these, only annual precipitation was not included in our model, although several other measurements of precipitation were. The authors do not state the percent contribution of the variables to the model; however, based on their suitability maps, the bioclimatic variables drove the suitability similarly. The potential distribution projected by Arthur et al. (2019) is reflected in our current distribution of this study as the tropics, subtropics, equatorial regions, and islands with much coastline were highly suitable. However, our model's additional United States data greatly increased suitable areas and included substantially more of North America, Africa, Europe,



**Fig. 4.** Histogram of the number of pixels within each map (count; size = 2.5 arc-min) by suitability projection. A corresponding summary table details the percent of the area for each suitability category for current and future global projections. Categories from left to right include low (< 0.25), poor (0.25–0.499), moderate (0.5–0.749), and high ( $\geq 0.75$ ) suitable bioclimatic areas.

A



**Fig. 5.** Continuous potential distribution maps of *P. truncatus* in current time (A), 2050 RCP 2.6 (B), 2070 RCP 2.6 (C), 2050 RCP 8.5 (D), and 2070 RCP 8.5 (E). The continuous scale has 1.0 as the greatest suitability and 0.0 as the least suitable for population survival. Solid areas indicate land excluded from modeling as not suitable for *P. truncatus* survival derived from the MESS layer overlays.

and Asia. Arthur and colleagues projected current distributions of highly suitable areas ( $> 80$  suitability) in just 3.5% of the projected area, which is much smaller than the 7% highly suitable areas ( $> 75$  suitability) in our projected areas. Clearly, the additional data in the expanded native range greatly influenced the SDM and revealed more areas where monitoring is necessary, particularly when climate change is considered. This highlights the importance of monitoring and surveillance efforts.

Climate change is anticipated to increase the severity and frequency of extreme climatic events, promoting stronger ecological responses in species than historically reported (Filazzola et al. 2021). For *P. truncatus*, the greatest potential distribution expansion is expected to occur between present conditions and 2050, not between 2050 and 2070. This was unexpected as we hypothesized that changes would continue at a similar or even greater rate as time passed. Temperatures are projected to increase by 1.0–1.5 °C

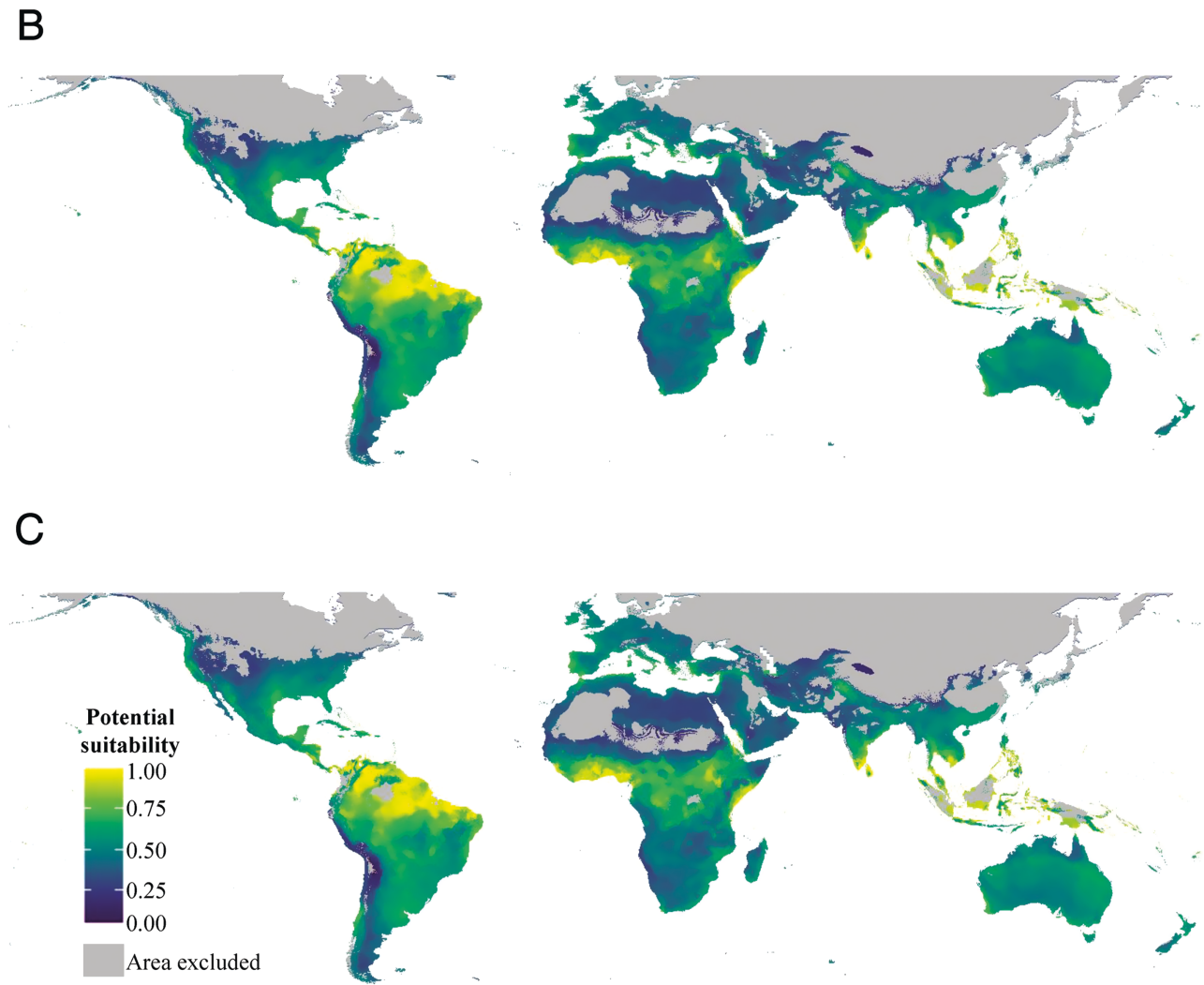


Fig. 5. Continued

by 2050 (Christensen et al. 2007), which is much smaller than the expected changes by 2100. The 2017 U.S. Climate Science Special Report estimated that if changes were made by 2050 to reduce carbon emissions, temperatures are more likely to increase by 2.4–5.9 °C warmer rather than predicted extremes of 10.2 °C by the end of the century. However, the greatest changes in *P. truncatus* distribution are predicted even before this potential 2050 turn-around point. Expectedly, greater changes in potential distribution are predicted under high rather than low climate change scenarios. The two RCPs, 2.6 and 8.5, were selected as they were the lowest and highest levels of possible greenhouse gas emissions projected by the IPCC, providing extreme scenarios that bracket the range of response. Potential distribution expansion toward the poles under climate change has been noted with several tropical and subtropical species (Chen et al. 2011) and is often associated with either declining or stable populations at the equator.

Similar to several other forest insects (e.g., *Dendroctonus frontalis* [Zimmermann] [Coleoptera: Scolytinae] and *Chorisonneura fumiferana* [Clemens] [Lepidoptera: Tortricidae]) and agricultural insects (e.g., *Diuraphis noxia* [Kurdjumov] [Hemiptera: Aphididae], *Schizaphis graminum* [Rondani] [Hemiptera: Aphididae]; see Battisti and Larsson 2015 for review), the change is a range expansion, not

a range shift, as there seemed to be no visible contraction in range in any currently suitable areas for *P. truncatus*. This suggests that the initial changes in precipitation and temperature are enough to quickly promote suitability and thus expand *P. truncatus* range to new areas. Further increasing temperatures and variability in rainfall after 2050 will likely have less of an impact on range expansion, as these were not as important to the final model.

However, climate change has often been reported to negatively impact non-pest insect species, such as bees, dragonflies, damselflies, and butterflies (Thomas et al. 2006, Kerr et al. 2015, Soroye et al. 2020). The insect declines are due, in part, to the lack of tolerance to new extremes (see review by Filazzola et al. 2021). Climate-related cues are often used for the development of insects as well as other taxa used for food, such as plants, which may not withstand climate change (Terblanche et al. 2015). However, insects with a higher potential to move long distances, be phenotypically more plastic, or more likely to undergo microevolutionary change may thrive in future climatic scenarios (Pulido and Berthold 2004, Kokko and López-Sepulcre 2006). In addition, insects that have adapted to a strongly modified anthropogenic landscape, such as agricultural fields or postharvest storage, may experience more limited adverse effects (Battisti and Larsson 2015). *Prostephanus truncatus* has

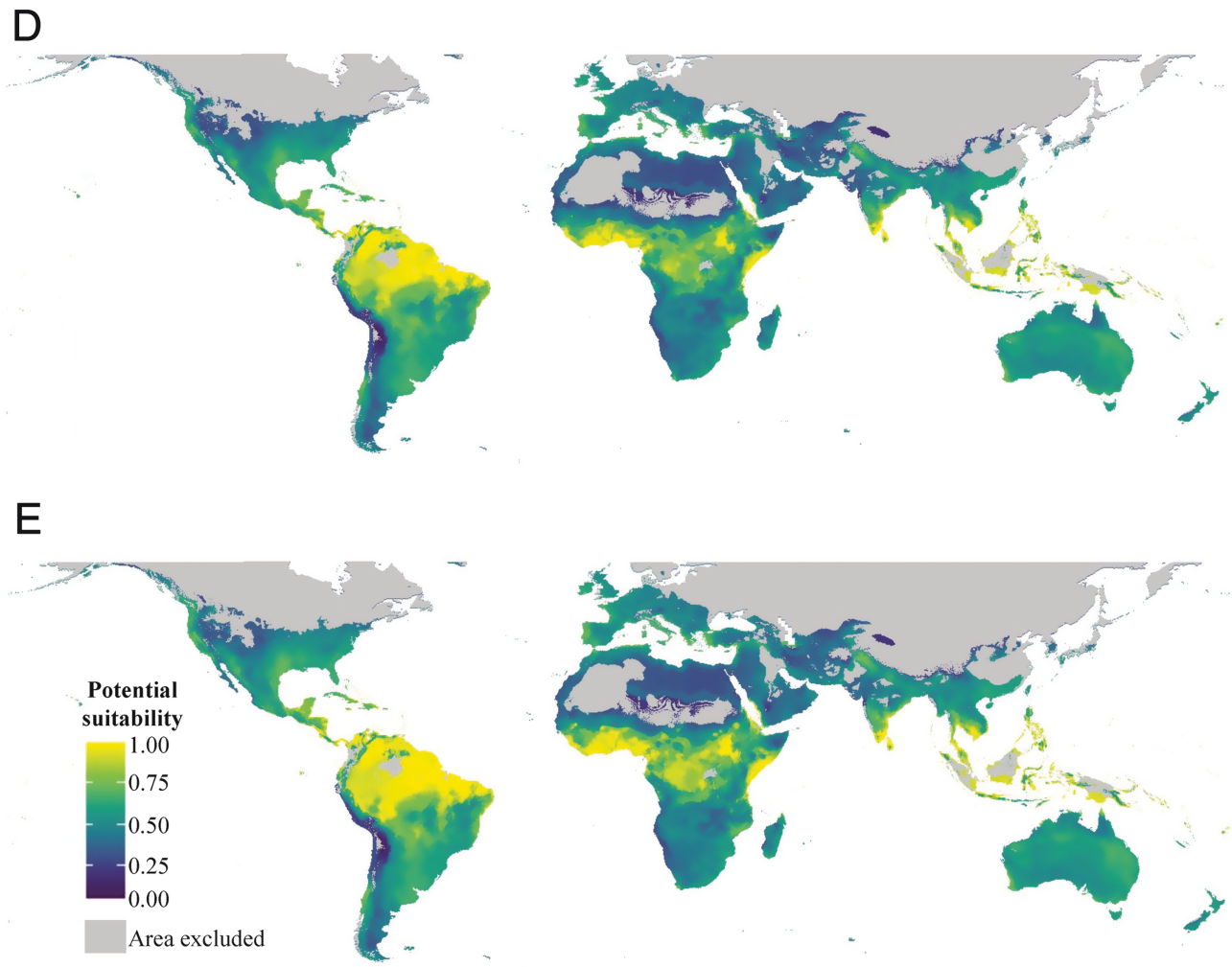


Fig. 5. Continued

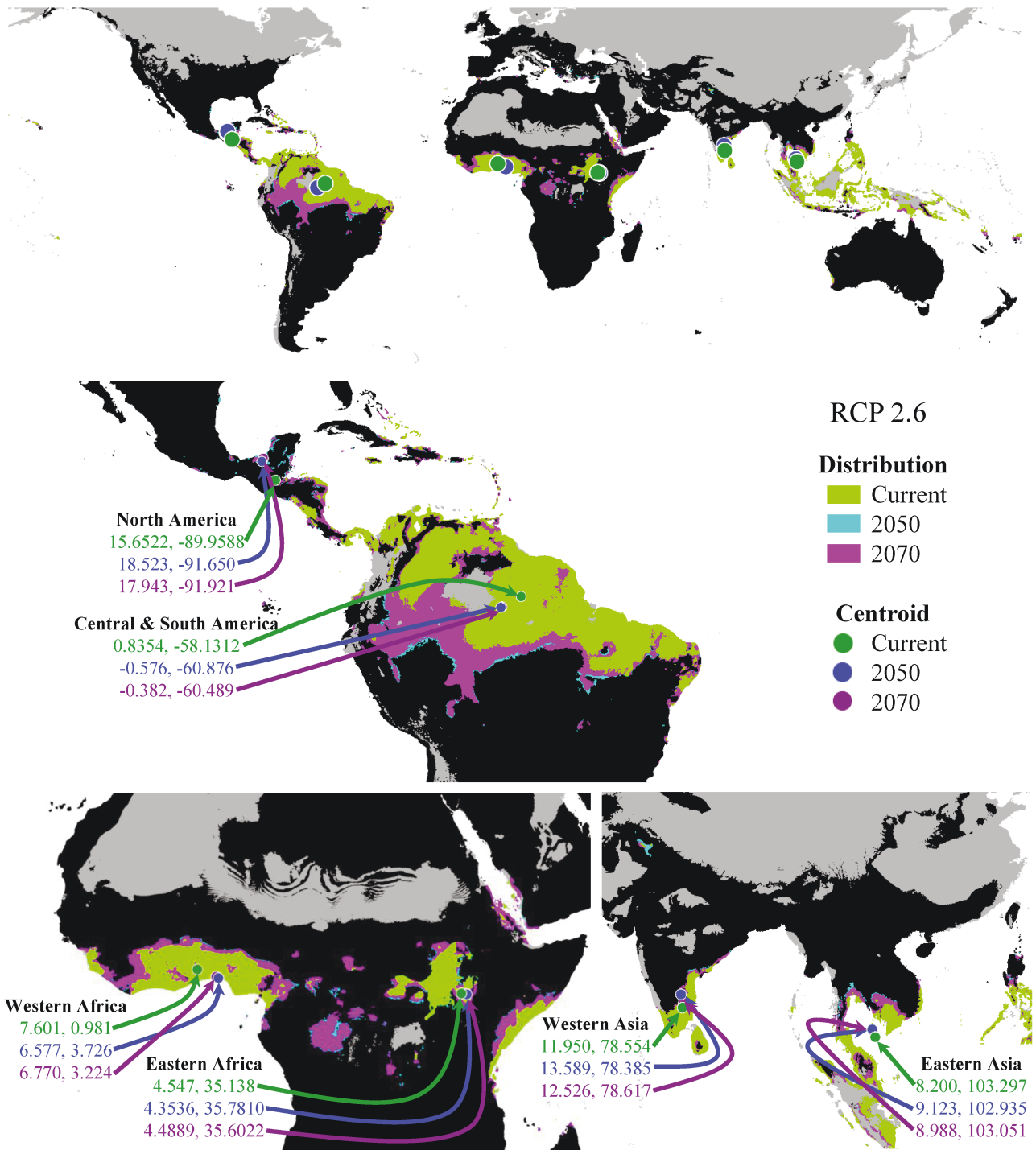
several of these life-history traits suitable for climate change, which may further promote its potential distribution.

Notably, while we have focused here on only highly suitable areas (75–100% suitability), moderately suitable areas (50–75% suitability) have a high likelihood of supporting populations, while making up nearly half of the global area, and remaining relatively constant in area among SDMs (0.4% difference) if not location. Numerically, the increase in highly suitable areas was due to decreases in poor suitability areas (10.5% difference) and, to a much lesser extent, low (1% difference) suitability areas. The centroids of the projected highly suitable areas were estimated to shift, on average, 2.11–3.15° by 2050 in high and low climate change scenarios, respectively. This equals 23.4–35 km in the next 27 years. On average, ranges of terrestrial plants and animals have shifted or expanded northward by 6.1 km per decade (Thuiller 2007). If the populations can persist at the edge of the highly suitable areas, then the expansion of *P. truncatus* is expected to be much greater than the terrestrial taxa average. Interestingly, despite a significant change in suitability levels, the centroids of highly suitable areas did not significantly differ in distance when comparing climate change scenarios or time frames. However, there was a distinct trend as centroids moved more inland and toward polar regions in 4 of the 6 high suitability areas. In the invaded region, the western African area centroids moved eastward along the coast, whereas the eastern area moved

inland and toward the equator. We expect the potential northward movement to be greatly limited by the Sahara Desert and the surrounding desert biome, which likely lacks the precipitation needed to sustain populations, according to the bioclimatic response curves.

However, in the native range of Central and South America, the high potential distribution area is expected to greatly expand north into the United States and further inland and south into more of South America. In the United States, *P. truncatus* is an Animal and Plant Health Inspection Service (APHIS)-designated species-of-concern, and there are currently few species records. The greatest amount of monitoring should be along the border with Mexico and the southern coast. However, much of the Corn Belt, ranging from the Great Plains through Ohio, becomes more moderately suitable with climate change. Established populations within this area will pose a great threat to the US economy as the country is the largest producer of corn with 32% of the global supply in 2023 (USDA-NASS 2024).

Other countries are also bioclimatically suitable for *P. truncatus* populations. For example, much of northern South America, the southern coastal areas of India and eastern Asia as well as the majority of Indonesia and the Philippines are highly suitable, even under current climates. Currently, there are no records of established populations within these areas. However, these areas are global leaders in maize production. For example, Brazil (10%), China

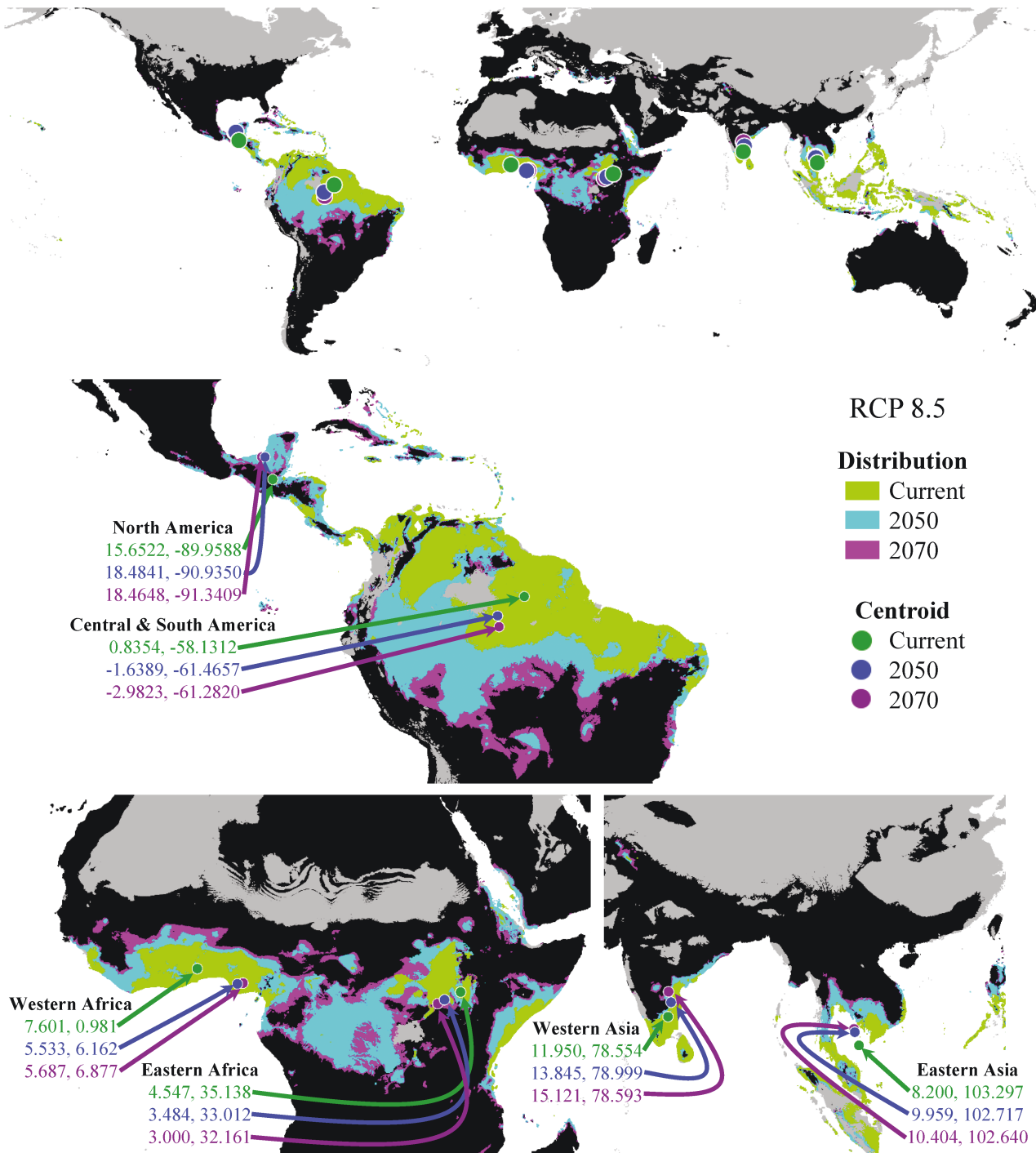


**Fig. 6.** The potential distribution map for the 6 geographic areas with potential high suitability for *P. truncatus* (> 0.75) with centroid points for current, 2050, and 2070 under low climate change (RCP 2.6) projections.

(23%), and India (3%) produced a greater percentage of the world's maize production than native Mexico (2%), with Indonesia and the Philippines (1% of global production each) close behind (USDA-NASS 2024). In addition, Thailand, Indonesia, and Brazil are the top producing countries of cassava after the invaded country of Nigeria (Sen Nag 2017). Thus, great economic loss is expected in these highly suitable countries if *P. truncatus* becomes established. Geographic barriers, such as the Arabian Sea and Pacific Ocean, should keep the insects from these countries; consequently, the most feasible

introduction path is via human transport. Thorough monitoring in these areas must be maintained.

As the greatest expansion is predicted to occur by 2050 in both the low and high climate change scenario, trapping and monitoring for the pest needs to happen soon and should be targeted along the coast and within shipping ports. Ideally, surveillance of *P. truncatus* should occur in both forested habitats and maize stores since it can move between both. Commonly used monitoring methods have been summarized in Quellhorst et al. (2021), with trapping using a 4-funnel Lindgren trap



**Fig. 7.** The potential distribution map shows the 6 geographic areas that are highly suitable for *P. truncatus* (> 0.75) with centroid points of current, 2050, and 2070 under high climate change (RCP 8.5) projections.

or sticky cards and a *P. truncatus* pheromone lure. A reliable monitoring network may provide early detection of this pest as it encroaches on borders. In addition, it is known that *P. truncatus* can bore into wooden pallets; thus, an increased ability to identify the species by port personnel in high-risk areas would be helpful. A comprehensive surveillance and exclusion protocol for this pest may be warranted.

Timely surveillance programs and management of *P. truncatus* will be important in limiting damage incurred by this devastating stored grain pest. Introduction of the pest into Asia, Europe, and Oceania along the coast via shipping will likely result in established

populations if the insect is not quarantined. Future studies on *P. truncatus* distribution should include landscape features, such as forest and agricultural cover, as well as the biology of the insect, such as dispersal kernels and flight phenology. In addition, at least for studies of the endemic population, evaluating how the main highly effective predator of *P. truncatus*, *Teretriosoma nigrescens* (Lewis) (Coleoptera: Histeridae), is moving in response to climate and how it may be interacting with this biosecurity threat may be of importance. This study showcases the need to act swiftly and precisely to limit the potential destruction of this devastating stored product pest.

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## Author Contributions

Rachel Harman (Conceptualization [equal], Data curation [equal], Formal analysis [lead], Methodology [lead], Project administration [lead], Validation [lead], Writing—original draft [lead], Writing—review & editing [equal]), William Morrison (Conceptualization [equal], Data curation [equal], Formal analysis [supporting], Funding acquisition [equal], Methodology [equal], Project administration [equal], Resources [equal], Supervision [equal], Validation [equal], Writing—original draft [equal], Writing—review & editing [equal]), Dalton Ludwick (Data curation [equal], Resources [equal], Validation [equal], Writing—review & editing [equal]), and Alison Gerken (Conceptualization [equal], Formal analysis [supporting], Funding acquisition [equal], Methodology [equal], Project administration [equal], Resources [equal], Supervision [equal], Validation [equal], Writing—original draft [equal], Writing—review & editing [equal])

## Data Availability

We will upload the occurrence data details and the r code used onto the Ag Data Commons platform once the website is available to do so.

## Supplementary Material

Supplementary material is available at *Journal of Economic Entomology* online.

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