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Artículo

Environmental niche stability of *Panstrongylus geniculatus* (Hemiptera: Reduviidae) across historical and future climate scenarios

Estabilidad del nicho ambiental de *Panstrongylus geniculatus* (Hemiptera: Reduviidae) en escenarios climáticos históricos y futuros

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Abstract

Panstrongylus geniculatus is one of the most widely distributed triatomine species in the Americas and an important vector of *Trypanosoma cruzi*, the causative agent of Chagas disease. This study evaluated changes in the environmental suitability of *P. geniculatus* under historical, current, and future climate scenarios across the Americas using ecological niche modeling. A total of 347 occurrence records and bioclimatic variables were used to calibrate ecological niche models in kuenm, which were subsequently projected to the Last Glacial Maximum, the current climate, and future conditions (2061–2080) under the RCP4.5 and RCP8.5 scenarios. The variables contributing most to the final model were maximum temperature of the warmest month (Bio5), temperature seasonality (Bio4), and precipitation of the wettest month (Bio13). Model projections indicated broad, relatively stable areas of environmental suitability throughout the Neotropical region, with localized contractions in central Brazil and expansions in northern Mexico, Argentina, and Uruguay. Comparisons among temporal scenarios showed limited changes in environmentally suitable areas, with expansion and contraction areas remaining below 4% of the modeled extent. These results suggest that the climatic niche of *P. geniculatus* has remained relatively stable across the evaluated historical and future scenarios. The persistence of environmentally suitable areas highlights the importance of maintaining long-term entomological surveillance and vector monitoring under changing climatic conditions.

Keywords: biogeography, climate projections, disease vectors, Maxent, species distribution.

Resumen

Panstrongylus geniculatus es una de las especies de triatominos con mayor distribución en el continente americano y un importante vector de *Trypanosoma cruzi*, agente causal de la enfermedad de Chagas. Este estudio evaluó los cambios en la idoneidad ambiental de *P. geniculatus* bajo escenarios climáticos históricos, actuales y futuros en las Américas mediante la modelación del nicho ecológico. Se utilizaron 347 registros de ocurrencia y variables bioclimáticas para calibrar modelos de nicho ecológico en *kuenm*, los cuales fueron posteriormente proyectados al Último Máximo Glacial, al clima actual y a condiciones futuras (2061–2080) bajo los escenarios RCP4.5 y RCP8.5. Las variables con mayor contribución al modelo final fueron la temperatura máxima del mes más cálido (Bio5), la estacionalidad de la temperatura (Bio4) y la precipitación del mes más húmedo (Bio13). Las proyecciones del modelo indicaron áreas ambientalmente adecuadas amplias y relativamente estables en toda la región Neotropical, con contracciones localizadas en el centro de Brasil y expansiones en el norte de México, Argentina y Uruguay. Las comparaciones entre escenarios temporales mostraron cambios limitados en las áreas ambientalmente adecuadas, con expansiones y contracciones inferiores al 4 % del área modelada. Estos resultados sugieren que el nicho climático de *P. geniculatus* se ha mantenido relativamente estable en los escenarios históricos y futuros evaluados. La persistencia de áreas ambientalmente adecuadas resalta la importancia de mantener programas de vigilancia entomológica y monitoreo vectorial a largo plazo frente a las condiciones climáticas cambiantes.

Palabras clave: biogeografía, proyecciones climáticas, vectores de enfermedades, Maxent, vigilancia vectorial.

Introduction

Triatomines are hematophagous insects of the order Hemiptera and the family Reduviidae. They are recognized as biological vectors of the protozoan parasite *Trypanosoma cruzi* (Kinetoplastida: Trypanosomatidae) (Chagas, 1909), the etiological agent of Chagas disease (Solis-Medina et al., 2020). This parasitic infection affects blood and multiple tissues and may lead to progressive and irreversible cardiac damage (Storeno & Milei, 1994).

Panstrongylus geniculatus (Hemiptera: Reduviidae) (Latreille, 1811) one of the most widely distributed triatomine species in the Americas, occurring from southern Mexico to Argentina (Vivas et al., 2021). Its broad distribution has been associated with both the dispersion of its vertebrate hosts and its ability to occupy a wide variety of dry and humid ecotopes (Gorla & Noireau, 2017; Wolff & Castillo, 2000). This adaptability enables de species to persist under diverse environmental conditions, with habitat and climatic factors acting as major determinants of its geographic distribution (Ríos-Muñoz et al., 2021; Sánchez-Hernández, 2021).

Although species distribution models (SDMs) and ecological niche models (ENMs) are often used interchangeably, they represent distinct conceptual approaches and address questions differently (Melo-Merino et al., 2020). SDMs are represented in geographic space, while ENMs are presented in ecological space (Rangel & Escalante, 2008). ENMs provide the theoretical foundation for SDMs and, along with biogeography, species ecology, evolutionary theories, and other factors, facilitate the development of accurate SDMs (Franklin, 2023).

Among the different niche concepts proposed in the ecological literature, we adopt the definition introduced by Joseph Grinnell (1917), in which niche represents the “the smallest distribution unit of a species in which it can maintain its instinctive or structural limitations”. Under suitable niche conditions, populations are able to survive, reproduce, and contribute genetic material to future generations (Mota-Vargas et al., 2019; Peterson, 2003). Using species occurrence records together with climatic variables, ENMs can identify environmentally suitable conditions and provide an approximation of the species’ potential geographic distribution under

current and alternative climatic scenarios (Tineo-González et al., 2021).

Characterizing the environmental niche occupied by *P. geniculatus* under past, present, and future climatic scenarios enables the comparison of environmentally suitable areas across time, from the Pleistocene to the present and from the current conditions to projected climates for 2061–2080 under contrasting greenhouse gas (GHG) emission scenarios. Such analyses provide a framework for evaluating the potential persistence and geographic redistribution of suitable environmental conditions across the species' range. In turn, these projections can inform decision-making on climate adaptation, vector surveillance, and public health, while contributing to the Sustainable Development Goals associated with climate action, health, and well-being established in the 2030 United Nations Agenda (Organización de las Naciones Unidas, 2020; Rodríguez et al., 2019).

Based on the current knowledge of the natural history and ecology of *P. geniculatus,* we hypothesize that its geographic distribution is primarily determined by climatic conditions, particularly the maximum temperature of the warmest month and precipitation patterns, together with habitat suitability linked to vegetation types and ecotopes, and the availability of vertebrate hosts.

Methods

Data preparation

Occurrence records of *P. geniculatus* were obtained from the Global Biodiversity Information Facility (GBIF) open-access biodiversity data repository (last accessed: 22 October 2021; 1,472 records; https://doi.org/10.15468/dl.9gyrzd).

Records were filtered by excluding those lacking geographical coordinates, duplicate records, records unsupported by scientific literature or originating from non-academic sources, and records exhibiting spatial autocorrelation. After data cleaning, the final dataset comprised 347 occurrence records (*Supp_P.geniculatus*).

Considering that *P. geniculatus* disperses both passively through vertebrate hosts and actively by flight during the adult stage, spatial clustering of occurrence records could bias model calibration. To reduce this effect, spatial thinning was performed by retaining a single occurrence within each 10-km neighborhood using the *spThin* package (Aiello Lammens et al., 2019; Castillo & Wolff, 2020). This procedure reduced spatial autocorrelation while maintaining consistency with the spatial resolution of the environmental predictors.

Selection of bioclimatic variables

Bioclimatic variables were obtained from WorldClim 2.1 (Fick & Hijmans, 2017) at a spatial resolution of 30 arc-seconds (approximately 1 km). Variables Bio14 (Precipitation of the driest month) and Bio15 (Precipitation seasonality) were excluded because of their documented inconsistency among General Circulation Models (GCMs) (Varela et al., 2015).

Three alternative sets of predictor variables were evaluated. The first set of variables contributed up to 70% of the model gain, according to the Maxent jackknife test. The second comprised the least correlated variables, selected using Pearson's correlation analysis (correlation ≥ 0.8 or ≤ 0.8) after assessing data normality with the Shapiro–Wilk test (Díaz-Vallejo et al., 2024). The third included all bioclimatic variables except Bio14 and Bio15 (Table 1).

Ecological niche modeling

Ecological niche models were developed in R using the *kuenm* package (Cobos et al., 2019), which automates calibration, evaluation, and projection based on the Maxent algorithm (Phillips et al., 2006).

The calibration area, representing the biologically accessible region for the species, was defined by overlaying the ecoregions proposed by Olson et al. (2001) with the occurrence records of *P. geniculatus.* Candidate models were evaluated according to three selection criteria: statistical significance, an omission rate below 5%, and the lowest corrected Akaike Information Criterion (AICc). Models meeting all three criteria were retained for final projections under past, present, and future climatic scenarios.

Environmental suitability maps

Continuous suitability outputs were converted to binary maps using the training presence threshold with an allowable omission error of 5%. This threshold reduces the influence of potentially erroneous occurrence records and provides a conservative estimate of environmentally suitable areas (Peterson et al., 2017).

Changes in environmentally suitable areas

Changes in environmentally suitable areas among climatic scenarios were assessed using SDM ToolBox version 2.0, an ArcGIS extension that automates spatial analyses for ecological and evolutionary applications (Brown, 2014). The "Distribution Changes Between Binary SDMs" tool was used to compare binary suitability maps among scenarios and generate maps depicting areas of stability, expansion, and contraction in environmental suitability for *P. geniculatus* (Brown, 2017).

Extrapolation risk assessment

Model extrapolation risk was evaluated using the Multivariate Environmental Similarity Surface (MESS; Elith et al., 2010) analysis. This metric quantifies the environmental similarity between projection areas and the environmental conditions represented by the calibration data. Negative MESS values indicate novel environmental conditions outside the range observed in the training dataset. Although MESS does not detect changes in correlations among predictor variables, it identifies areas where model projections require extrapolation beyond the environmental space used for model calibration (Elith et al., 2010; Elith et al., 2011).

Results

Model calibration

A total of 357 candidate models were generated for the calibration area. Only two models satisfied the predefined selection criteria, and the one with the lowest ΔAICc value was selected as the final model. This model used a regularization multiplier of 0.9, linear, quadratic, and product feature classes, and the second predictor set (M_0.9_F_lqp_Set2; Table 2).

The variables contributing the most to model performance were Bio5 (Maximum temperature of the warmest month), Bio4 (Temperature seasonality), and Bio13 (Precipitation of the wettest month) (Table 3). Since Bio5 showed the highest contribution and its response curve exhibited a biologically consistent pattern, model projections were generated using clamping to limit extrapolation beyond the range of environmental conditions represented in the calibration dataset.

Environmental suitability maps and MESS analysis

The current climate projection identified environmentally suitable areas extending from southern Mexico through Central America and much of South America to northern Argentina and Chile (Figure 1A). The MESS analysis indicated the highest extrapolation risk in western Brazil, Peru, Venezuela, and the Guianas, with additional localized areas in Bolivia (Figure 1B).

Under the past MIROC climate scenario, environmentally suitable areas were reduced in Bolivia and in portions of central Brazil and southern Venezuela (Figure 2A). The corresponding MESS analysis indicated an extensive risk of extrapolation across northern and central South America (Figure 2B).

Future projections under the MIROC model showed similar spatial patterns under both climate scenarios. Environmentally suitable areas were absent from large portions of central and western Brazil and southern Venezuela, whereas suitable areas persisted or appeared in northern Chile (Figures 2C and 2E). The highest extrapolation risk was concentrated in southeastern Brazil, with smaller areas identified in the Guianas and Bolivia (Figures 2D and 2F).

Changes in environmentally suitable areas

Comparison between the past and current MIROC scenarios revealed expansions of environmentally suitable areas in the montane forests of northern Mexico, western Colombia, the temperate steppe of southern Argentina, and transitional zones between

herbaceous savannas and subtropical dry forests in northern Uruguay (Figure 3). In contrast, contractions were primarily concentrated within the tropical rainforest of central Brazil and in small areas of herbaceous savanna in Venezuela. In both scenarios, environmentally suitable areas were predominantly distributed throughout tropical and subtropical regions (Figure 3).

Comparison of the current climate with the optimistic future MIROC scenario showed expansions along the western coast of North America, portions of the subtropical rainforest of the southeastern United States, and several regions of Argentina, Uruguay, and western Brazil (Figure 4). Areas of contraction were concentrated mainly within the tropical forest of central Brazil (Figure 4). Overall, environmentally suitable areas remained predominantly distributed across tropical and subtropical regions (Figure 4).

The comparison between the current climate and the pessimistic future MIROC scenario showed localized expansions throughout the continent, particularly in Argentina, Uruguay, and Paraguay (Figure 5). Contractions were concentrated in the central and eastern portions of the Brazilian rainforest. Despite these spatial changes, environmentally suitable areas remain largely restricted to the Neotropical region, with additional suitable areas along the west coast of North America (Figure 5).

Quantitative comparisons among temporal transitions indicated limited changes in the extent of environmentally suitable areas (Figure 6). Across all comparisons, expansion areas did not exceed 3.5% of the study area, whereas contraction areas remained below 4%. Although the proportion of unsuitable areas remained consistently high, the proportion of suitable areas showed little variation among scenarios, indicating overall stability in the modeled distribution of *P. geniculatus* throughout the evaluated temporal periods (Figure 6).

Discussion

Our results indicate that the maximum temperature of the warmest month (Bio5) was the most influential predictor of the ecological niche model of *P. geniculatus*, followed by temperature seasonality (Bio4) and precipitation of the wettest month (Bio13). The predominance of temperature-related variables is consistent with the ectothermic physiology of insects, whose development, survival, reproduction, dispersal, and population dynamics are strongly regulated by ambient temperature (Lazzari, 1991; Mellanby, 1939; Schilman & Lazzari, 2004; de la Vega & Schilman, 2015). These results are also consistent with the broad environmental range reported for *P. geniculatus*, which has been recorded from sea level to approximately 4,000 m a.s.l., under a wide range of thermal (–3.9–34.3°C) and precipitation conditions (up to 4,000 mm/year) (Rabinovich & Feliciangeli, 2015; Reyes-Lugo, 2009; Vivas et al., 2021).

Previous ecological niche models for *P. geniculatus* in Colombia identified altitude, precipitation seasonality (Bio15), and isothermality (Bio3) as the variables with the greatest explanatory power (Parra et al., 2016). Although the relative importance of predictors varies across studies, both analyses consistently highlight the combined influence of temperature and precipitation on the species' environmental suitability. Such differences are expected because variable contributions depend on the geographic extent, environmental gradients, occurrence data, and modeling strategy used.

In regions characterized by a marked alternation between rainy and dry periods, the recurrence of dry conditions appears to enhance environmental suitability. The seasonality of precipitation (the clustering of rainy seasons) is related to thermal seasonality and humidity, with atmospheric circulation patterns affecting the distribution of precipitation across different seasons of the year (Barton et al., 2019; Ward & Aukema, 2019). Low precipitation seasonality may reduce environmental suitability for *P. geniculatus*, whereas high precipitation seasonality may favor the presence of suitable areas, as this species requires warm, humid environments to establish itself (Funes et al., 2009).

The potential ecological breadth distribution of *P. geniculatus* is probably associated not only with its tolerance to diverse climatic conditions but also with its ecological flexibility. The species exploits a wide variety of vertebrate hosts and occupies multiple natural

habitats, including different food sources, because it can feed on a broad range of vertebrates with broad distributions. This adaptability allows it to inhabit burrows, palm trees, and tree nest cavities, or palm trees, thereby expanding its trophic niche compared to other hematophagous species that have specific dietary specializations and whose distribution patterns are mainly limited by the presence of their hosts (Castillo et al., 2019; Reyes-Lugo, 2009). This versatility likely reduces dependence on a narrow set of environmental conditions or host species, facilitating persistence across heterogeneous landscapes throughout the Neotropics.

Comparisons between the Last Glacial Maximum and the present indicate relatively limited changes in the spatial extent of environmentally suitable areas. Although localized contractions and expansions were identified, the overall distribution remained continuous across much of the Neotropical region. These results suggest that the environmental niche of *P. geniculatus* has remained comparatively stable despite major climatic oscillations since the late Pleistocene. However, these projections represent changes in environmental suitability rather than historical population dynamics or realized distributions.

Most contractions in environmental suitability occurred in regions characterized by marked environmental heterogeneity (Cayuela, 2012), whereas expansions were concentrated mainly in tropical and subtropical dry forests (Miles et al., 2006). These spatial patterns likely reflect differences in the distribution of suitable climatic conditions among scenarios rather than direct effects of vegetation or land-cover changes, which were not included as predictor variables in the models.

Future climate projections also indicate relatively limited changes in the extent of environmentally suitable areas. Under both optimistic and pessimistic scenarios, the species retained a broadly continuous distribution throughout the Neotropics, with localized areas of expansion and contraction. The small proportional changes observed among scenarios suggest that the climatic niche of *P. geniculatus* is comparatively robust to the range of climatic conditions represented by the evaluated projections.

Temperature is expected to influence insect physiology, dispersal, and survival under future climates (Bozinovic, 2019). Since flight activity in triatomines is temperature dependent (Child, 2007; Reyes-Lugo, 2009), shifts in thermal conditions could modify dispersal opportunities in some regions while reducing environmental suitability in others. Nevertheless, the ecological niche models developed here evaluate changes in climatic suitability rather than demographic responses, dispersal dynamics, or local extinction processes. Consequently, these mechanisms remain hypotheses that require validation through physiological and field-based studies.

Although the effects of climate change on vector-borne diseases remain uncertain, our projections suggest that environmentally suitable areas for *P. geniculatus* are likely to persist across much of its current range under future climate scenarios. Given the epidemiological importance of this species as a vector of *Trypanosoma cruzi*, the persistence of climatically suitable areas highlights the need to maintain long-term entomological surveillance and vector monitoring, particularly in regions where suitability is projected to remain stable or increase (Mikery-Pacheco et al., 2023; Peterson et al., 2017; Vivas et al., 2021).

Conclusions

Ecological niche models indicate that *P. geniculatus* has maintained a broad extent of environmentally suitable areas from the Last Glacial Maximum to the present, with only limited spatial changes. Likewise, future climate projections suggest relatively minor changes in the distribution of suitable environments, while maintaining broad connectivity throughout the Neotropical region.

These findings support the hypothesis that the climatic niche of *P. geniculatus* is comparatively stable across the evaluated temporal scenarios. Nevertheless, the projections represent potential environmental suitability rather than realized distributions and should therefore be interpreted as estimates of climatic suitability. The projected persistence of suitable areas underscores the importance of continued ecological and epidemiological surveillance, as environmental

conditions favorable for this vector are likely to remain widespread under future climate scenarios.

Authors' contributions

Camilo Rivera-Pacheco: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Software; Visualization; Writing – original draft.
Carolina Montaño: Investigation; Validation; Writing – review & editing.

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Table 1. Bioclimatic variables included in each predictor set used for ecological niche modeling of *Panstrongylus geniculatus*. Bio14 and Bio15 were excluded from all predictor sets because of their documented inconsistency among General Circulation Models.

Bioclimatic variables	Code	Set 1	Set 2	Set 3
Annual Mean Temperature	Bio1	×		×
Mean Diurnal Range	Bio2	×	×	×
Isothermality	Bio3			×
Temperature Seasonality	Bio4	×	×	×
Max Temperature of Warmest Month	Bio5	×	×	×
Min Temperature of Coldest Month	Bio6		×	×
Temperature Annual Range	Bio7		×	×
Mean Temperature of Wettest Quarter	Bio8			×
Mean Temperature of Driest Quarter	Bio9			×
Mean Temperature of Warmest Quarter	Bio10			×
Mean Temperature of Coldest Quarter	Bio11	×		×
Annual Precipitation	Bio12	×		×
Precipitation of Wettest Month	Bio13		×	×
Precipitation of Driest Month*	Bio14			
Precipitation Seasonality*	Bio15			
Precipitation of Wettest Quarter	Bio16		×	×
Precipitation of Driest Quarter	Bio17			×
Precipitation of Warmest Quarter	Bio18		×	×
Precipitation of Coldest Quarter	Bio19			×

Table 2. Performance statistics of candidate ecological niche models that satisfied the predefined model selection criteria. Model names indicate the regularization multiplier (M), feature classes (F), and predictor set used during model calibration.

Model	Mean partial ROC ratio	Partial ROC	Omission rate (5%)	AICc	Δ AICc	Number of parameters
M_0.9_F_lqp_Set2	1.061	0.000	0.041	7293.581	0.000	17
M_1_F_lp_Set2	1.058	0.000	0.041	7294.424	0.843	16

Table 3. Percent contribution of environmental variables to the final Maxent model.

Environmental predictor	Code	Contribution (%)
Max Temperature of Warmest Month	Bio5	39.2
Temperature Seasonality	Bio4	17.8
Precipitation of Wettest Month	Bio13	15.6
Precipitation of Wettest Quarter	Bio16	8.6
Min Temperature of Coldest Month	Bio6	8.4
Temperature Annual Range	Bio7	4.1

Figure 1. Current ecological niche model for *Panstrongylus geniculatus*. **A)** Binary projection of environmentally suitable areas in the Americas under current climatic conditions; the continuous model output was converted into suitable/unsuitable areas using the training presence threshold with 5% omission. Yellow circles indicate the occurrence records used for model calibration. **B)** Multivariate Environmental Similarity Surface (MESS) under current climatic conditions, relative to the calibration dataset. MESS is a unitless index: negative values (red) indicate environmental conditions outside the range of the calibration data (novel conditions, i.e. extrapolation risk), whereas values ≥ 0 (blue) indicate analogous conditions; the black line marks MESS = 0. The map extent corresponds to the full projection area (the Americas); the calibration area, defined by the ecoregions containing occurrence records, is smaller (see Methods).

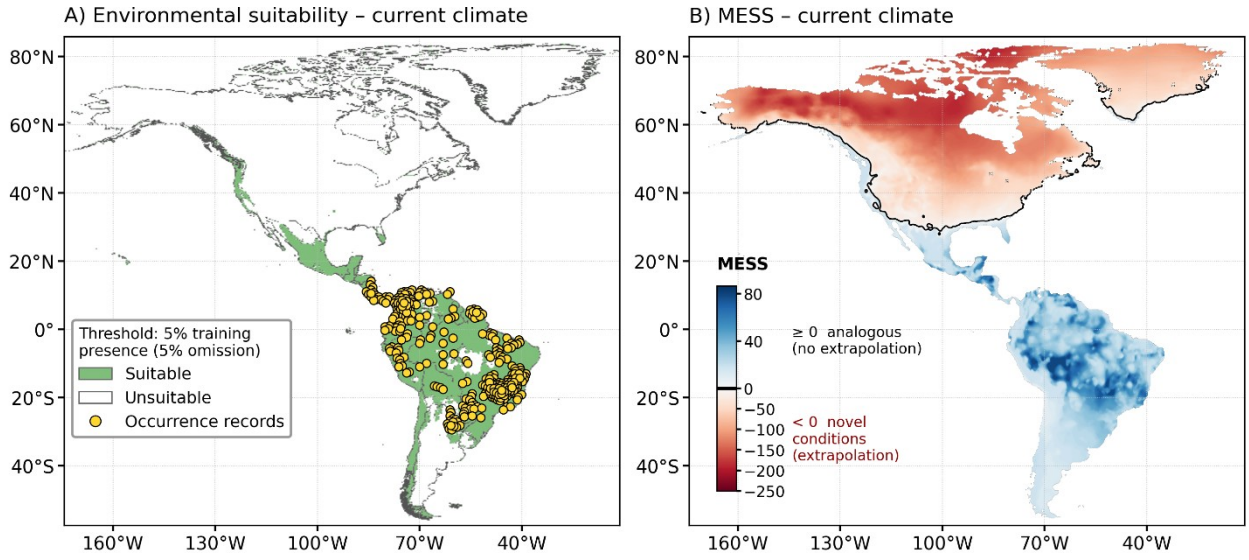

Figure 2. Binary projections of environmentally suitable areas (a, c, e) and corresponding Multivariate Environmental Similarity Surfaces (MESS; b, d, f) for *Panstrongylus geniculatus* under the MIROC general circulation model (GCM): Last Glacial Maximum (LGM, ~21 ka; a, b), 2061–2080 under SSP2-4.5 (c, d) and 2061–2080 under SSP5-8.5 (e, f). Binary maps were obtained with the training presence threshold with 5% omission; yellow circles are the occurrence records used for calibration. All MESS maps share the same colour scale and value range; negative values (red, delimited by the black MESS = 0 line) indicate novel conditions and therefore extrapolation risk.

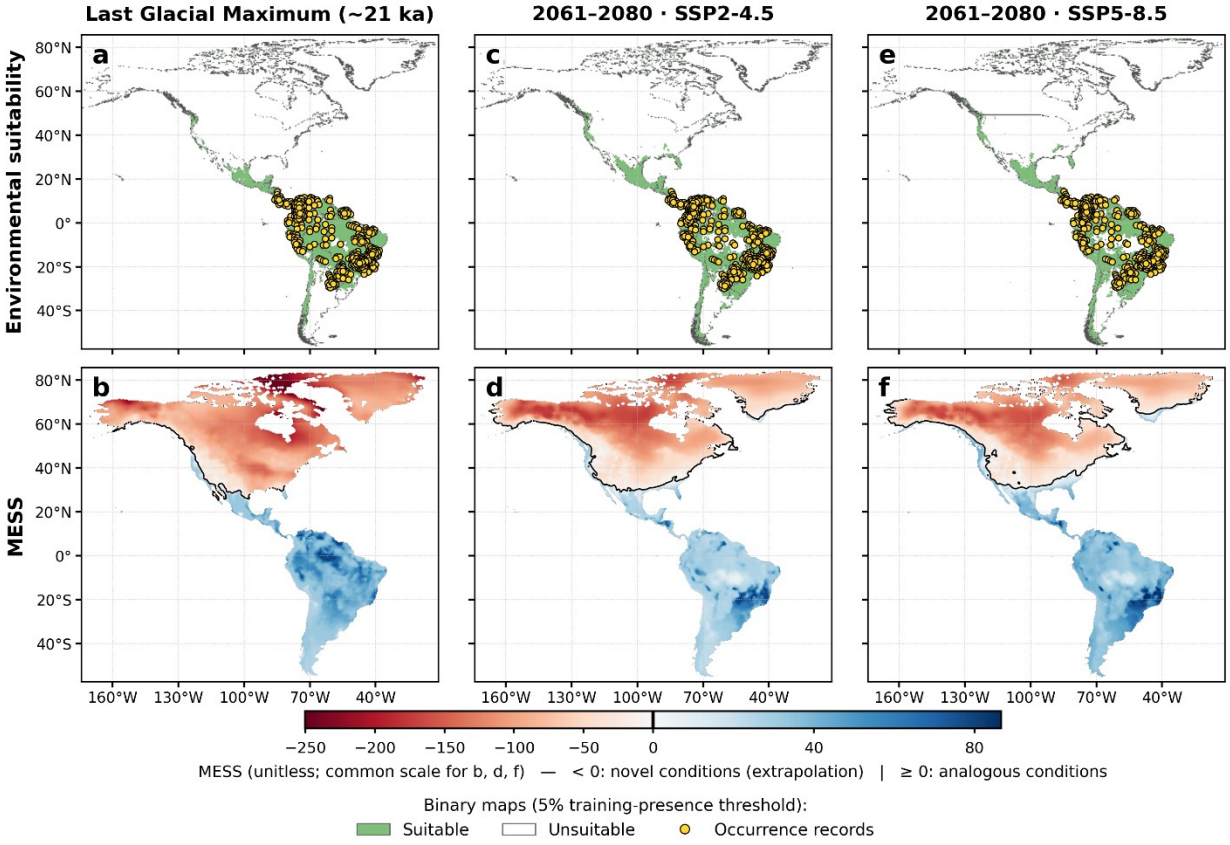

Figure 3. Changes in environmental suitability for *Panstrongylus geniculatus* between the Last Glacial Maximum (LGM, ~21 ka) and the current climate under the MIROC general circulation model (GCM), obtained by overlaying the corresponding binary maps (training presence threshold with 5% omission). Blue: gain of environmental suitability; red: loss of environmental suitability; beige: environmental suitability maintained in both scenarios; white: unsuitable in both scenarios. Yellow circles show the occurrence records used for model calibration, included as a reference to locate the areas of change relative to the documented distribution of the species. Categories refer to environmental suitability and not to observed changes in the geographic range of the species. The same colour scheme is used in Figures 3–5; the corresponding percentages are shown in Figure 6.

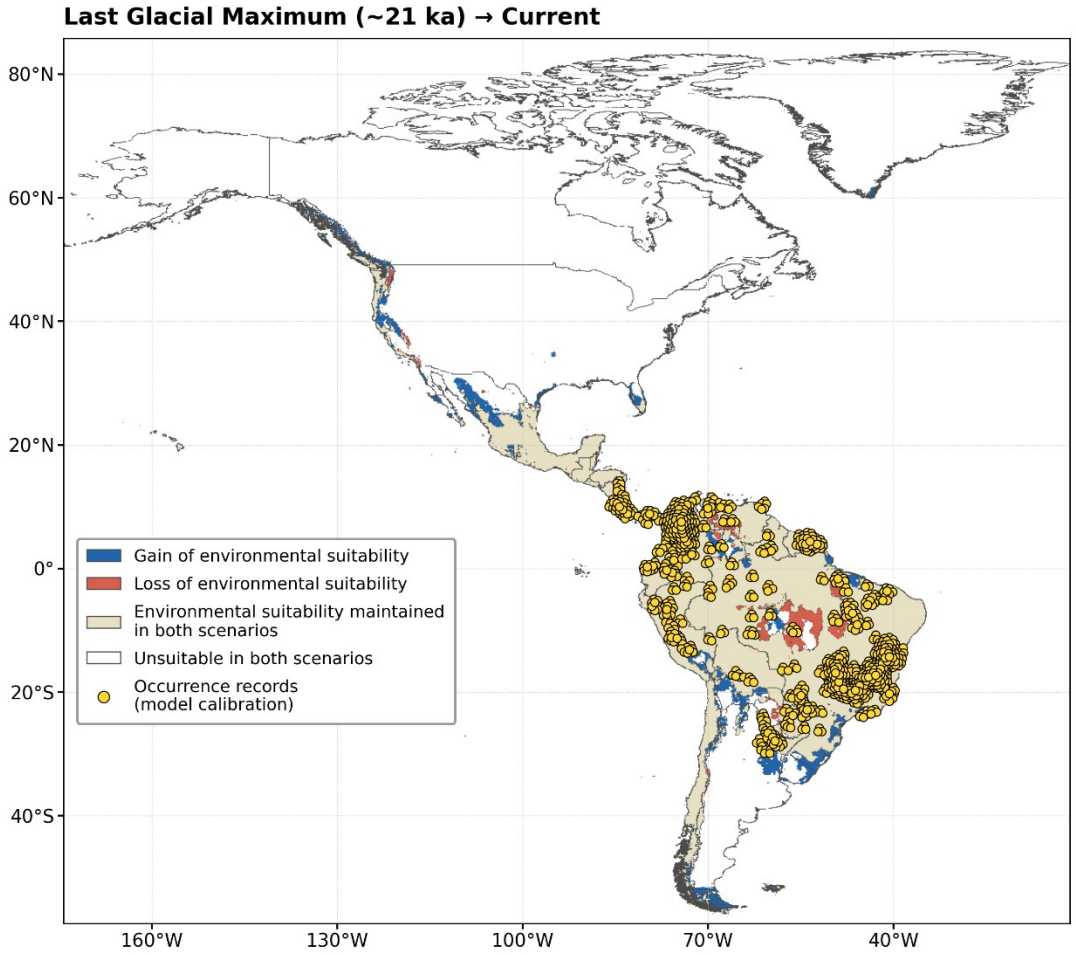

Figure 4. Changes in environmental suitability for *Panstrongylus geniculatus* between the current climate and the future climate for 2061–2080 under SSP2-4.5 under the MIROC general circulation model (GCM), obtained by overlaying the corresponding binary maps (training presence threshold with 5% omission). Blue: gain of environmental suitability; red: loss of environmental suitability; beige: environmental suitability maintained in both scenarios; white: unsuitable in both scenarios. Yellow circles show the occurrence records used for model calibration, included as a reference to locate the areas of change relative to the documented distribution of the species. Categories refer to environmental suitability and not to observed changes in the geographic range of the species. The same colour scheme is used in Figures 3–5; the corresponding percentages are shown in Figure 6.

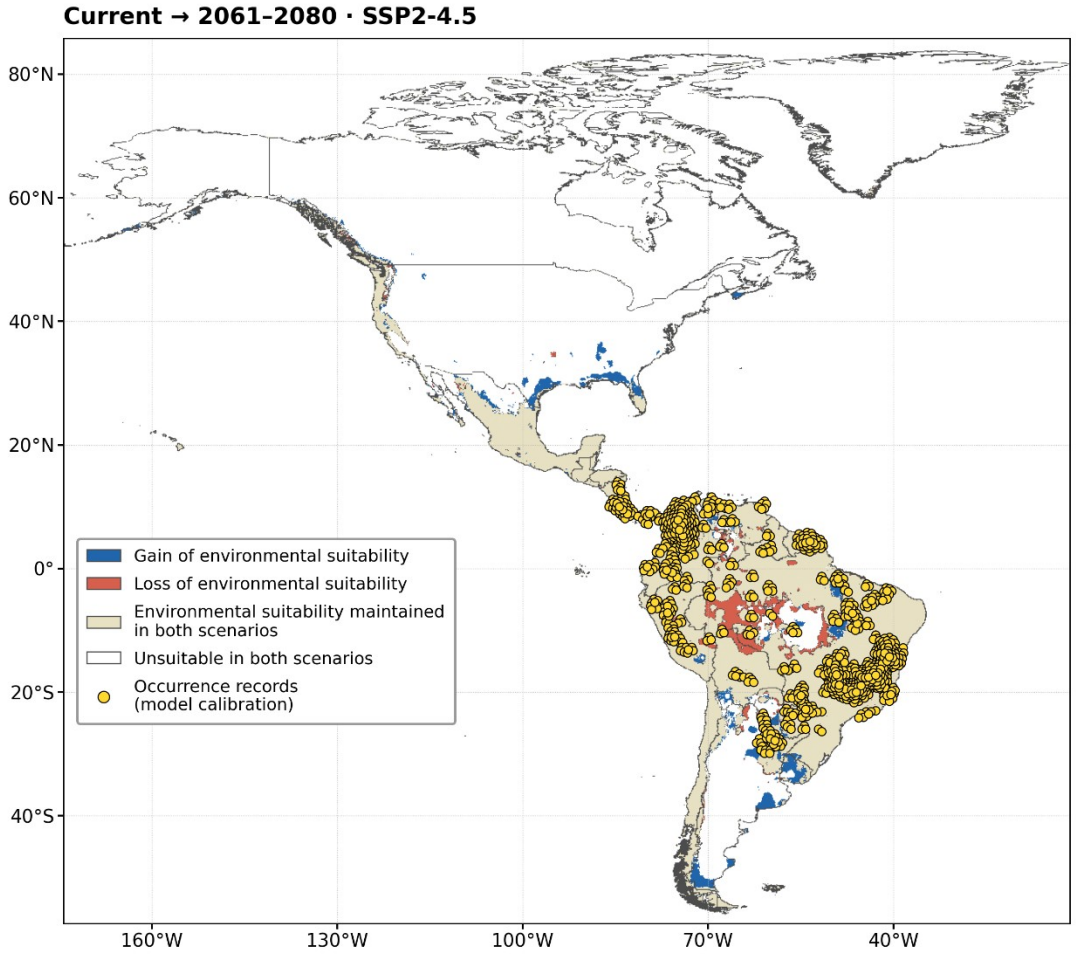

Figure 5. Changes in environmental suitability for *Panstrongylus geniculatus* between the current climate and the future climate for 2061–2080 under SSP5-8.5 under the MIROC general circulation model (GCM), obtained by overlaying the corresponding binary maps (training presence threshold with 5% omission). Blue: gain of environmental suitability; red: loss of environmental suitability; beige: environmental suitability maintained in both scenarios; white: unsuitable in both scenarios. Yellow circles show the occurrence records used for model calibration, included as a reference to locate the areas of change relative to the documented distribution of the species. Categories refer to environmental suitability and not to observed changes in the geographic range of the species. The same colour scheme is used in Figures 3–5; the corresponding percentages are shown in Figure 6.

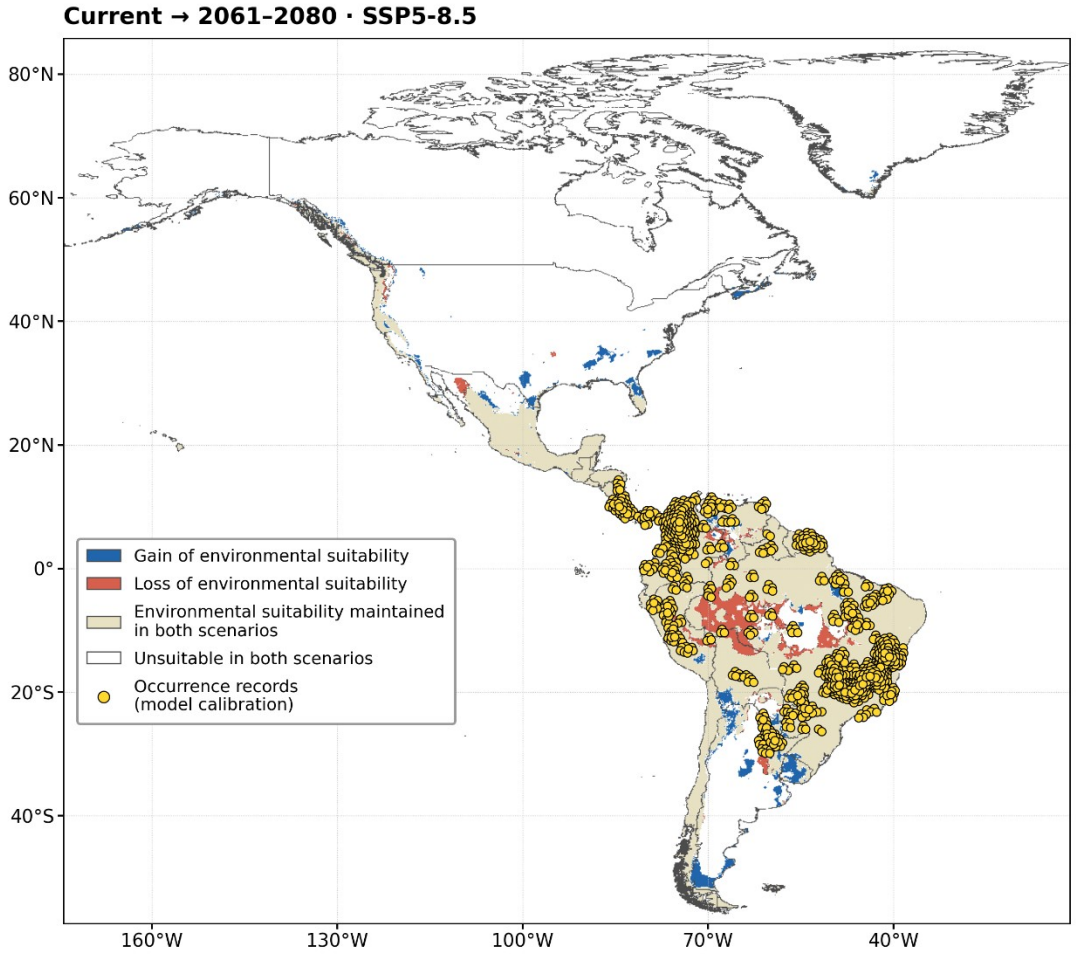
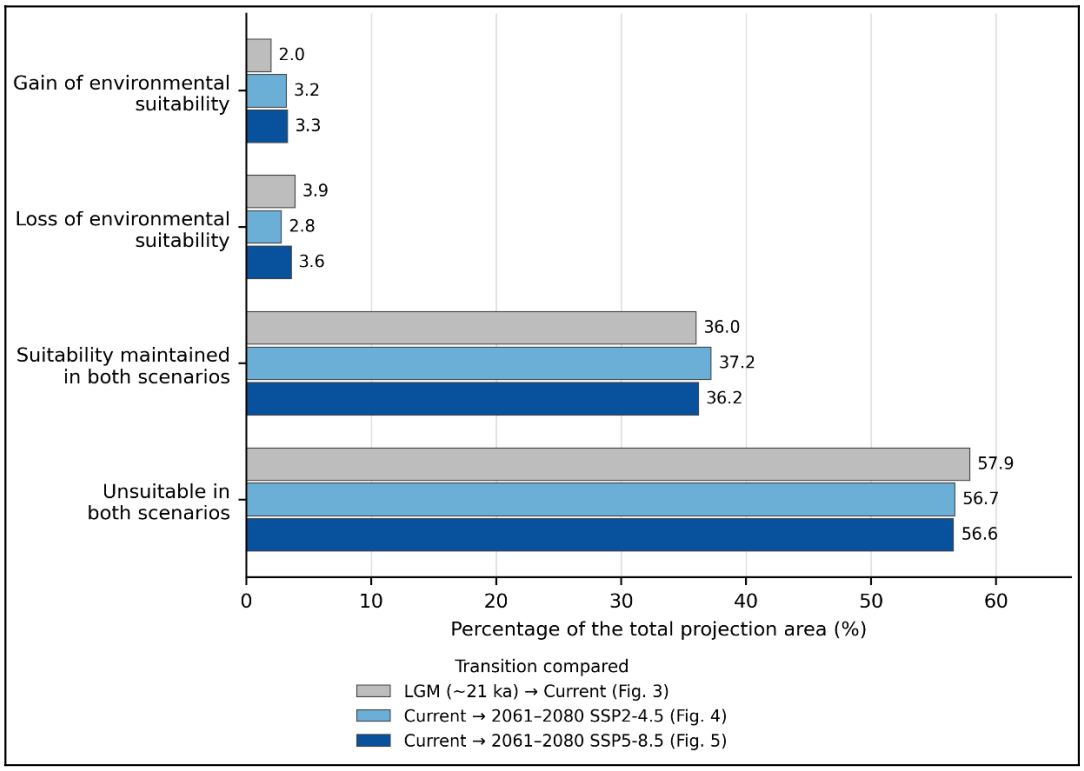
Figure 6. Percentage of the total projection area (the Americas) in each category of change in environmental suitability for *Panstrongylus geniculatus* under the MIROC general circulation model, for the transitions LGM (~21 ka) → current (Figure 3), current → 2061–2080 SSP2-4.5 (Figure 4) and current → 2061–2080 SSP5-8.5 (Figure 5). Values were computed from the same binary layers and classification used in Figures 3–5; for each transition the four categories sum to 100%.