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Changes in the potential distribution of the guava fruit fly *Anastrepha striata* (Diptera, Tephritidae) under current and possible future climate scenarios in Colombia

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Abstract

Climate change has affected the geographical distributions of most species worldwide; in particular, insects of economic importance inhabiting tropical regions have been impacted. Current and future predictions of change in geographic distribution are frequently included in species distribution models (SDMs). The potential spatial distributions of the fruit fly *Anastrepha striata* Schiner, the main species of agricultural importance in guava crops, under current and possible future scenarios in Colombia were modeled, and the establishment risk was assessed for each guava-producing municipality in the country. SDMs were developed using 221 geographical records in conjunction with nine scenopoetic variables. The model for current climate conditions indicated an extensive suitable area for the establishment of *A. striata* in the Andean region, smaller areas in the Caribbean and Pacific, and almost no areas in the Orinoquia and Amazonian regions. A brief discussion regarding the area's suitability for the fly is offered. According to the results, altitude is one of the main factors that direct the distribution of *A. striata* in the tropics. The Colombian guava-producing municipalities were classified according to the degree of vulnerability to fly establishment as follows: 42 were high risk, 16 were intermediate risk, and 17 were low risk. The implementation of future integrated management plans must include optimal spatial data and must consider environmental aspects, such as those suggested by the models presented here. Control decisions should aim to mitigate the positive relationship between global warming and the increase in the dispersal area of the fruit fly.

Introduction

Climate change is expected to cause shifts in the geographical distribution of species as a result of the rearrangement of climate zones (Beever and Belant, 2016). Hence, the magnitude of the associated impacts is projected to be higher in some regions than in others. The Latin American and Caribbean region is one of the most vulnerable areas to climate change; most of the species living there are endemic or restricted to a specific tropical ecosystem (CEPAL, 2015). Consequently, they are more susceptible to the effects of global warming because of their particular physiology and phenological qualities, which are typically adapted to narrow ecological niches (Sheldon, 2019). It is anticipated that poikilothermic organisms, such as insects, whose body temperature varies according to the surrounding weather, will be strongly influenced by a volatile climate (Régnière *et al.*, 2012). Temperature, precipitation, and other climatic parameters can directly affect the ecological interactions of insect pests; for instance, the increase in heat in the tropics allows species to colonize higher elevations and extend their geographical distributions upslope (Freeman *et al.*, 2018). Furthermore, climate warming resulting from increasing levels of greenhouse gases (GHGs) in the Earth's atmosphere could have a significant and highly uncertain impact on the development, distribution, and population density of agricultural insect pests (Lehmann *et al.*, 2020).

Predictions of geographical distribution changes relating to global warming are frequently included in species distribution models (SDMs) (Guisan and Zimmermann, 2000). These models use associations between environmental variables, such as temperature, precipitation, and geographical records of species to identify the environmental conditions under which reproductive populations can be established (Peterson *et al.*, 2011). SDMs have multiple applications in conservation, ecology, evolution, epidemiology, and invasive species management studies (Peterson, 2006). In an agricultural context, SDMs allow the assessment of the potential dispersal of exotic and invasive species to crops (Villacide and Corley, 2003; Beckler *et al.*, 2005; Campo *et al.*, 2011), while also permitting the implementation of control and eradication programs and monitoring of these biological agents. SDMs can also assist in the selection of cultivatable areas and the declaration of phytosanitary problem-free zones (Anderson and Martínez-Meyer, 2004; Parra *et al.*, 2004; Phillips *et al.*, 2006; Aluja and Mangan, 2008). The advantages of these models make their use appropriate in making decisions to mitigate the effects of insect pests.

Fruit flies of the Neotropical genus *Anastrepha* include more than 300 species, many of which are of economic importance in the Americas and some of them of quarentenarian importance (Castañeda *et al.*, 2010; Tigrero and Norrbom, 2020). The guava fruit fly (GFF), *Anastrepha striata*, is one of the quarentenarian species in the genus (EPPO, 2021). This species is widespread in America from the USA to Brazil, infesting 37 species belonging to 23 genera and 17 families; however, the most important host belongs to the Myrtle family (Myrtaceae) (Norrbom, 2004; Gallo-Franco *et al.*, 2017). All surveys of fruit flies carried out in Colombia reported *A. striata*, but georeferenced and documented records have only been done in six of 32 Colombian departments (Castañeda *et al.*, 2010). In contrast to other countries, in Colombia, surveys have shown that the altitudinal distribution ranges from 16 to 2400 m (Martínez and Serna, 2005; Castañeda *et al.*, 2010; Gallo-Franco *et al.*, 2017). Further studies related to this species biology are lacking, only some regarding distribution range; sexual behavior (Pérez-Staples and Aluja, 2004), pheromones (Cruz-López *et al.*, 2015), host use (Saavedra-Díaz *et al.*, 2017), and genetic structure (Gallo-Franco *et al.*, 2017) have been carried out. The distribution of fruit fly species in Colombia is also related to the presence of its primary host plant (Castañeda *et al.*, 2010). *A. striata* is mainly associated with Myrtaceae; this family encompasses nearly 180 species in Colombia, distributed across all vegetation type communities and altitudinal gradients, being species adapted to very humid lowlands and to highland paramo (Parra, 2014). According to Saavedra-Díaz *et al.* (2017), fruit flies in Colombia do not use the same fruit or host in the same region, i.e., host partitions. This species has been reported on guava crops, turning into a plague with significant negative impacts on fruit production (Insuasty *et al.*, 2007; Martínez-Alava, 2007; Castañeda *et al.*, 2010).

In Colombia, guava is one of the top five species of economic importance and is a significant crop in Colombian agriculture as an essential product of small and intermediate producers (Agronet, 2018). The damage caused by *A. striata* can be devastating; total losses of 90% of the crop have been documented in recent decades (Núñez *et al.*, 2004). The potential distribution of fruit flies as part of pest management has been considered in the United States (Sequeira *et al.*, 2001), Europe (Godefroid *et al.*, 2015), and globally for *Anastrepha obliqua* (Fu *et al.*, 2014). In Colombia, integrated pest management (IPM) against fruit flies has been proposed by governmental institutions (Instituto Colombiano de Agropecuario [ICA], 2016); however, none of these initiatives have included potential distribution or spatial distribution modeling. The aim of this study was to model the potential distribution of *A. striata* and to assess the establishment risk in Colombia under current and possible future climate change scenarios. The resulting maps and data may provide a broad geographical perspective for decision-making in area-wide and local fruit fly management for guava crops and could be informative about the behavior of the species in other countries.

Materials and methods

Geographical records

Geographic records of *A. striata* were compiled from specimens deposited at the following entomological collections: Colección Entomológica de la Universidad de Antioquia, Medellín, Antioquia, Colombia (CEUA), Colección Entomológica de la Universidad Nacional de Colombia, Sede Palmira, Valle del Cauca, Colombia (CEUNP), Colección Taxonómica Nacional Luis María Murillo, ICA Tibaitatá, Mosquera, Cundinamarca, Colombia (CTNI), Colección Entomológica Forestal Universidad Distrital Francisco José de Caldas, Bogotá, Cundinamarca, Colombia (EF-UDFJC), Colección de Insectos del Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Boyacá, Colombia (IAVH), Colección de Insectos del ICA Palmira, Valle del Cauca, Colombia (ICA-P) Colección de Zoología, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Sede Bogotá, Cundinamarca, Colombia (ICN), Museo Entomológico 'Francisco Luis Gallego', and Universidad Nacional de Colombia, Sede Medellín, Antioquia, Colombia (MEFLG); secondary sources, including articles and databases, were also used (Supplementary Table S1). For an adequate geographical interpretation, a figure with the maps of the administrative boundaries ('Departments,' as they are locally known in Colombia), natural regions, digital elevation models, and the location of some geographical features is referred to throughout the text (fig. 1).

Climatic information

Bioclimatic variables were gathered from the WorldClim 1.4 climate data archive (Hijmans *et al.*, 2005; table 1) in the form of 19 bioclimatic data layers, summarizing potentially relevant climate dimensions at a 30 arc-second (1 km) spatial resolution. The data were derived from monthly precipitation and temperature values, appropriate to the biological requirements of *A. striata* in terms of temperature, precipitation, seasonal trends, and extreme or limiting environmental factors (Hijmans *et al.*, 2005). Bioclimatic data layers incorporating global climate change were calculated using a general circulation model (GCM) for different scenarios. The MIROC5 Global Climate model was selected to include variation and uncertainty among climate change mathematical simulations (Yañez-Arenas *et al.*, 2016). The years 2050 and 2070 were considered as future time slices under two emission scenarios: representative concentration pathways (RCPs) 2.6 and 8.5. They were consistent with a wide range of possible changes in future anthropogenic (i.e., human-caused) GHG emissions and aimed to represent their atmospheric concentrations in different scenarios (Ward *et al.*, 2012). RCP 2.6 presumes that global annual GHG emissions (measured in CO_2 equivalents) peak between 2010 and 2020, with emissions declining substantially thereafter (Meinshausen *et al.*, 2011). Under RCP 8.5, emissions continue to rise throughout the 21st century (Meinshausen *et al.*, 2011).

An essential element in the development of ecological niche models is the hypotheses of areas (M) that have been accessible to the species (Barve *et al.*, 2011). Based on the presence records and the terrestrial ecoregions of the world proposed by the World Wildlife Foundation (Olson *et al.*, 2001), the area M was estimated to calibrate the model. Charted Colombian administrative boundaries (fig. 1) were used as the area for the final projection model. According to the variable contributions calculated by the jackknife analysis and the Pearson correlation coefficients,

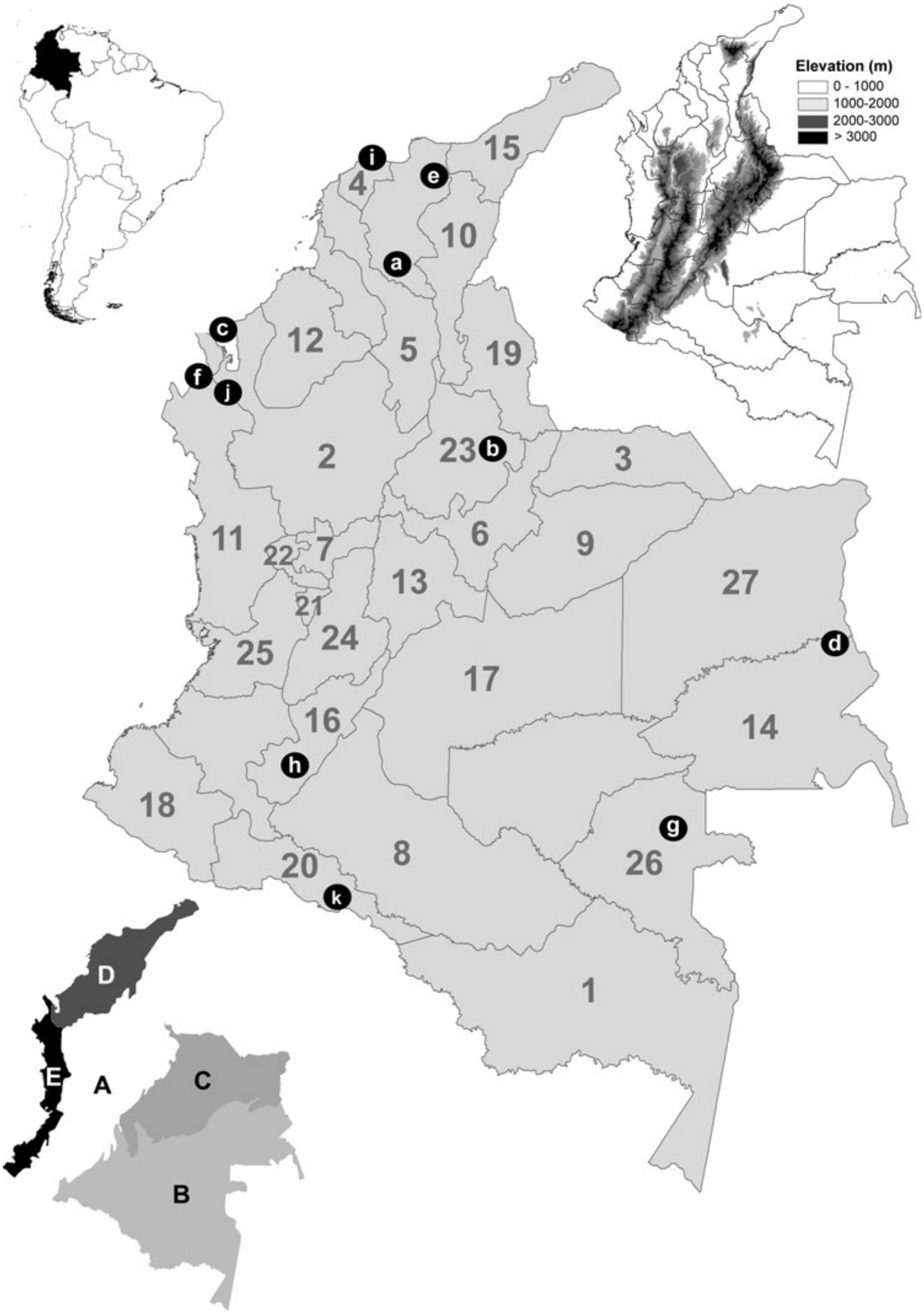

Figure 1. Location of Colombia in South America (top left). Digital elevation map (top right) in m. Map of administrative boundaries (center) (number of each department in gray) (1) Amazonas; (2) Antioquia; (3) Arauca; (4) Atlántico; (5) Bolívar; (6) Boyacá; (7) Caldas; (8) Caqueta; (9) Casanare; (10) Cesar; (11) Chocó; (12) Córdoba; (13) Cundinamarca; (14) Guainia; (15) Guajira; (16) Huila; (17) Meta; (18) Nariño; (19) Norte de Santander; (20) Putumayo; (21) Quindío; (22) Risaralda; (23) Santander; (24) Tolima; (25) Valle del Cauca; (26) Vaupes; (27) Vichada. Referenced localities are indicated with black dots and white letters. (a) Depresión Momposina; (b) Cañon del Chicamocha; (c) Golfo de Uraba; (d) Inirida interfluvial region; (e) Sierra Nevada de Santa Marta; (f) Serrania del Darien; (g) Vaupes River; (h) Valle de Laboyos; (i) Salamanca National Park; (j) Los Katios National Park; (k) La Paya National Park. Five natural regions (bottom left) (IGAC, 2021) (A) Andes; (B) Amazon; (C) Orinoquia; (D) Caribbean; and (E) Pacific.

variables were selected to be retained for further evaluations. If two variables had a correlation of >|0.8|, the highly contributing variable was preferred over the other (Raghavan *et al.*, 2019). In the current and future models, nine bioclimatic variables were used (table 1).

Model design

The potential distribution model was generated with a maximum entropy algorithm incorporated in MaxEnt v.3.3.3k (Phillips *et al.*, 2006). The partial receiver operating characteristic (pROC) statistics were applied for only the current model to the 50% subset of occurrences left out before model calibration for testing. pROC was chosen as a significance test in light of critiques of the appropriateness of traditional ROC approaches (Peterson *et al.*, 2008). This metric was used to test the statistical significance of ecological niche model predictions. A value of 1.0 was equivalent to the performance of a random classifier. These results were based on 100 bootstrap replicates, and statistical significance was assessed by bootstrapping and comparison with a random classifier ratio of 1.0, according to the significant sensitivity of this algorithm to particular parameter settings. A detailed model selection exercise was conducted using the ENMeval R package. This provided an automated method to execute MaxEnt models across a user-specified range of regularization multiplier (RM) values and feature combinations (FCs)

Table 1. Bioclimatic variables used in modeling the potential distribution for *A. striata* in Colombia

Code	Environmental variable	Percent contribution	No. of correlated variables
Bio1	Annual mean temperature	4.9	3
Bio3	Isothermality (BIO_2/BIO_7) (×100)	23.3	2
Bio4	Temperature seasonality (standard deviation × 100)	7.5	4
Bio5	Max temperature of warmest month	6.5	3
Bio6	Min temperature of coldest month	13.3	4
Bio11	Mean temperature of coldest quarter	5.1	1
Bio12	Annual precipitation	21	2
Bio14	Precipitation of driest month	5.8	3
Bio15	Precipitation seasonality (coefficient of variation)	8.3	1

(Muscarella *et al.*, 2014). The RM range was set from 0.5 to 4.0 in increments of 0.5, and three FCs, i.e., linear (L); linear and quadratic (LQ); linear, quadratic, and product (LQP); linear, quadratic, product, and threshold (LQPT); linear, quadratic, product, threshold, and hinge (LQPTH), were employed, resulting in 45 possible combinations of features and RMs (Muscarella *et al.*, 2014). The fine-tuned MaxEnt models were made by seeking the lowest delta value of Akaike's information criterion, which was corrected for small sample sizes (AICc) among the candidate models, reflecting both model goodness-of-fit and complexity to provide the most conservative results (Basanta *et al.*, 2019). The model with the lowest delta AICc score was selected; it had a parameterization of RM of 2.0 and an LQHP FC and exhibited good predictive performance.

A total of ten model replications were implemented through bootstrapping tools. The medians were used through repetitions as a final niche estimation (Altamiranda-Saavedra *et al.*, 2017). A final set of models was built using the 'logistic' output and 10,000 background points (Barbet-Massin *et al.*, 2012). All models were converted to binary using a threshold of training omission rate with an error rate of $E = 5\%$. The threshold selection methods were based on lower threshold values, i.e., with a broader distribution of suitable habitat and close to zero omission errors. To predict variations in the spatial distribution, the expansion and contraction in the dispersion area were estimated through pairwise ranking between the two binary distribution models (current and future distribution models) through the SDMtoolsbox tool in ArcGIS 10.3. The range of median values was calculated across all models for RCPs 2.6 and 8.5, and the estimated variance among models was considered as a measure of uncertainty using ArcGis 10.3 (Peterson *et al.*, 2018). Finally, to assess the model's transferability, a variance partitioning approach was used to compare the estimates of environmental suitability in the SDM prediction maps on a pixel-by-pixel basis across different maps and to characterize the proportion of variance in the estimates of suitability attributable to individual factors (Diniz-Filho *et al.*, 2009). As Supplementary material, all models are available to download in the .*KMZ* format (Supplementary Material 2).

Current risk of establishment of A. striata *in municipalities*

A preliminary list of 75 guava-producing municipalities was generated by consulting annual reports from the ICA (Instituto Colombiano Agropecuario) Phytosanitary Surveillance and Epidemiology Technical Division (ICA, 2020). The area at risk for *A. striata* establishment was measured as the percentage of suitable space in the current potential distribution model by each municipality using ArcGIS 10.3. Consequently, the 75 districts were classified in the following way: units with coverage below 33% were considered low vulnerability; those with coverage between 33 and 66% had intermediate vulnerability; and those with coverage above 66% had high vulnerability.

Results

A total of 211 geographical records of *A. striata* were collected at elevations ranging from 6 to 3044 m (fig. 2a); most were located in the Andean region (fig. 1A) (Colombian natural regions; IGAC, 2021). The percentage contribution of the bionomical variables is shown in table 1. The final model for current environmental conditions showed an extensive suitable area for *A. striata* establishment, mainly in the Andean region (fig. 1A). There was less establishment risk in the Caribbean (fig. 1D) and Pacific regions (fig. 1E), and it was almost nonexistent in the Orinoquia (fig. 1C) and Amazonian regions (fig. 1D). Despite the notable absence of suitable areas in the Amazonian region, the current model (fig. 2a) included the interfluvial areas of the Inírida, Guainía, and Vaupés rivers (fig. 1, localities d, g), the surrounding jurisdiction of Mitú in Vaupes (fig. 1g -26), southwestern Putumayo (fig. 1-20), and the western area of La Paya National Natural Park (fig. 1, locality k) as suitable for *A. striata* establishment. Omission errors were evidenced in locations such as Leticia in southern Amazonas (fig. 1-1), southwestern Putumayo (fig. 1-20), Orinoquian localities (northeastern Vichada [fig. 1-27] and northern Arauca [fig. 1-3]), and the Caribbean of central Guajira (fig. 1-15). The currently unsuitable areas for the establishment of *A. striata* (fig. 2a) were as follows: the Caribbean region, a large part of the xerophytic formations in northern Guajira (fig. 1-15), areas of Salamanca National Park (fig. 1, locality i), the Depresión Momposina (fig. 1, locality a), Sierra Nevada de Santa Marta (fig. 1, locality e), and swamp complexes in eastern Cordoba (fig. 1-12). The areas above the 2050 m elevation along the Andean region were also unsuitable, including all high-altitude areas of the Andean paramos complex (fig. 1A), the foothills of western Norte de Santander (fig. 1-19), eastern Boyacá (fig. 1-6), and Cundinamarca (fig. 1-13), and the surrounding areas of El Cañon de Chicamocha (fig. 1, locality b) and Valle de Laboyos in Huila (fig. 1, locality h). Extensive areas of tropical rainforest (TRF) in the Pacific and Amazon (fig. 1B, E) were deemed unsuitable, as were the savannas in the Orinoquia region (fig. 1C).

Potential distribution under climate change scenarios

Significant levels of uncertainty in climate change models were found, especially in the Andean region (fig. 3). An increase in the area suitable for *A. striata* establishment was observed in all climate change scenarios (fig. 4a–d). This result was more

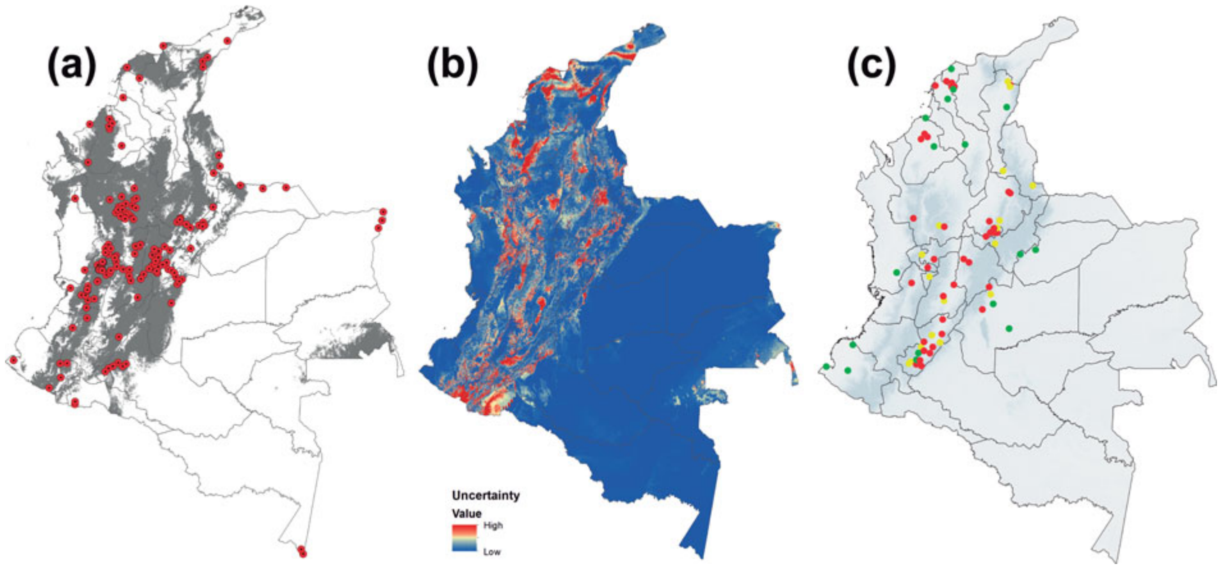

Figure 2. (a) Potential distribution of *A. striata* in Colombia for the current environmental conditions (suitable areas in gray); red dots are the localities of the compiled geographical records. (b) Uncertainty of models in the range of median values of GCMs for *A. striata*. The color scale represents the degree of variance (blue: low; red: high). (c) Locations of guava-producing municipalities and their vulnerability category for *A. striata* establishment under the current climatic scenario (red: high; yellow: intermediate; green: low).

pronounced in the most pessimistic GHG emission scenario (RCP 8.5) for both temporal projections in 2050 and 2070 (fig. 4b, d). According to the analysis of predicted changes in suitable habitat and the associated potential distributions, the greatest extent of the possible area increase for *A. striata* was predicted under the RCP 8.5 scenario by 2050 (fig. 4b) with an increased area of 520,071 km^2 (table 2). Remarkably, this expansion was predicted to occur mainly in the Amazonian natural region (fig. 1b), including the departments of Caquetá (fig. 1-8), Amazonas (fig. 1-1), Vaupés (fig. 1-26), Guainía (fig. 1-14), and Putumayo (fig. 1-20). In contrast, RCP 2.6 predicted reductions in the area (i.e., contraction area) by 2050, with a potential decrease of more than 52,808 km^2 (table 2). This effect was especially distinct in the northern area of the Pacific region, specifically in the Chocó department (figs 1-11 and 4a).

Current risk of establishment of A. striata *in municipalities*

Forty-eight guava-producing municipalities in Colombia are located in the Andean region (fig. 1A), 18 in the Caribbean region (fig. 1D), 8 in the Pacific region (fig. 1E), and 6 in the Orinoquia region (figs 1C and 2c). Of these municipalities, 56% were categorized as highly vulnerable to the establishment of *A. striata*; 21% had intermediate vulnerability, and 23% had low vulnerability (fig. 2c and table 3).

Discussion

This study was the first regional (northwest South America) study to use ecological niche modeling to assess the potential distribution of a fruit fly species of economic importance under global climate change scenarios. Additionally, this study was the first to consider the risk of pest establishment according to administrative boundaries to configure regional policies and decision-making. The results showed that in Colombia, (i) under the current environmental model, the suitable areas for the establishment of *A. striata* were located mainly in the Andean region, with some risk areas in the Caribbean region and to a lesser extent in the Pacific, Orinoquia, and Amazonian regions. High-spatial alignment with geographical records has been recently reported by Rodriguez *et al.* (2018). (ii) The climate change models showed an increase in suitable areas for the establishment of *A. striata* in response to global warming, and (iii) high-environmental suitability for the establishment of populations was evidenced in the guava-producing municipalities in Colombia. Distribution patterns of fruit flies should be influenced by host distribution, natural enemies, other fruit fly species, and/or climate conditions. Our results indicated that *A. striata* currently inhabits a significant portion of Colombian territory, probably because of its thermal physiological plasticity (Baker *et al.*, 1944) and all abovementioned faunistic interactions acting together.

Data on Colombian GFF hosts are widely lacking; however, species of Myrtaceae, its main hosts, could be found through a wide altitudinal range (Parra, 2014); due to the effect of the host on insect distribution (Castañeda *et al.*, 2010; Salazar-Mendoza *et al.*, 2021), *A. striata* may use the available host species according to altitude. In Colombia, guava is parasitized by *A. striata*, *A. obliqua*, Anastrepha *fraterculus* s.l., and *Anastrepha ornata* (Núñez *et al.*, 2004; Castañeda *et al.*, 2010; Saavedra-Díaz *et al.*, 2017). However, Saavedra-Díaz *et al.* (2017) found that, in the studied ecosystems, two species of *Anastrepha* do not use the same resource, and guava parasitization by *A. obliqua* is accidental; only GFF was the Tephritid fly in guava. An uncommon species, *A. ornata*, had been reared from guava (Castañeda *et al.*, 2010), but it is scarce and only occurs at high altitudes. The other two species, *A. striata* and *A. fraterculus* s.l., are frequently found on guava; however, they showed altitudinal separation. Núñez *et al.* (2004) found that at 1700–1900 m, more than 90% of flies from guava were *A. striata*, and fewer were *A. fraterculus*, but the opposite trend was observed in coffee crops. *A. fraterculus* were primarily obtained from infested Myrtaceae collected at over 2000 m altitude, and GFF

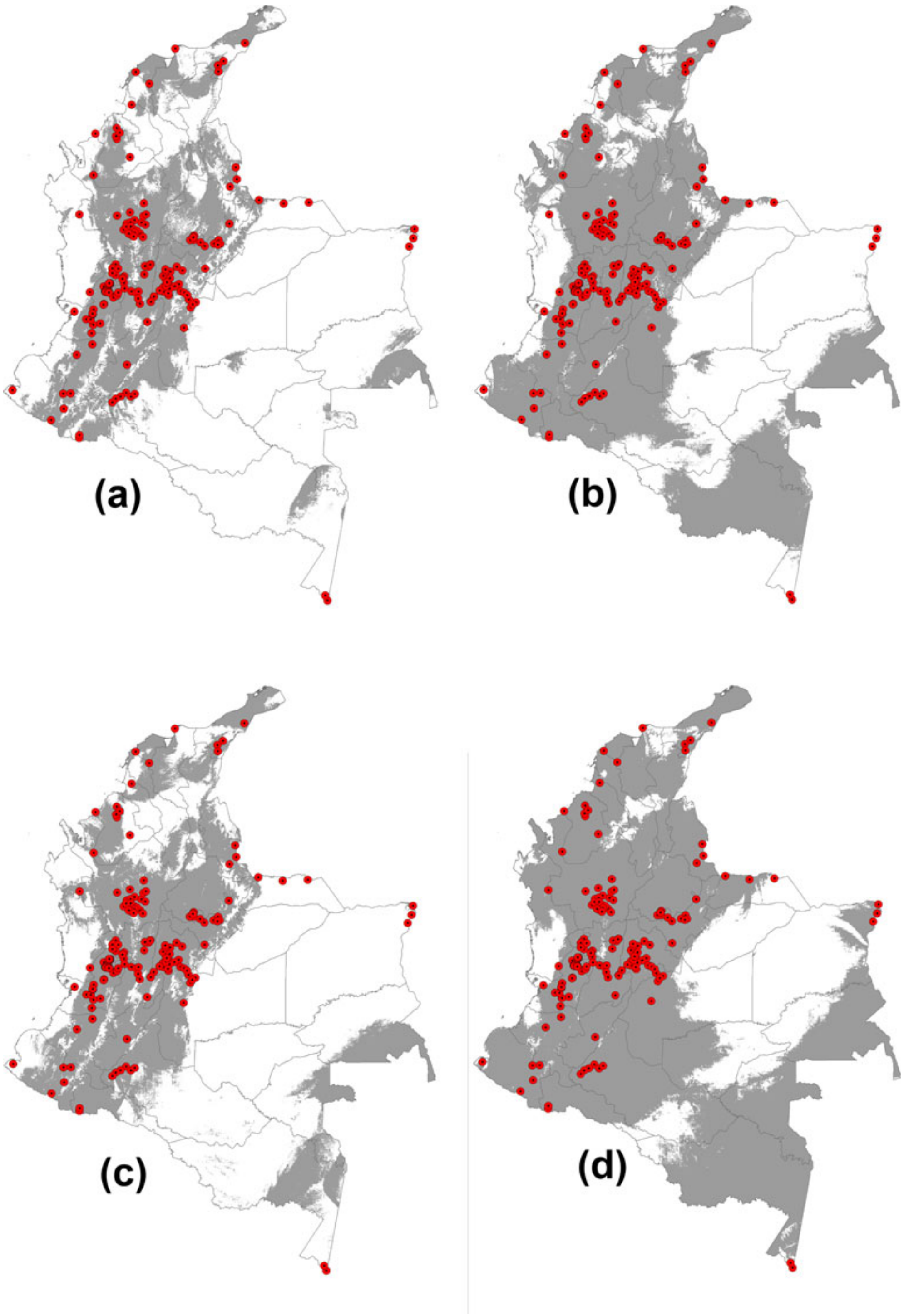

Figure 3. Potential distribution of *A. striata* in Colombia based on climate change scenarios: (a) 2050 under RCP 2.6, (b) 2050 under RCP 8.5, (c) 2070 under RCP 2.6, and (d) 2070 under RCP 8.5.

under 1000 m. Among the GFFs collected and referred to by Castañeda *et al.* (2010) from traps over 2000 m specimens of *A. striata* were scant (N.A. Canal, unpublished data). Among 16 species collected from traps, Salazar-Mendoza *et al.* (2021) found the same three fruit fly species from guava in the altitudinal transect in Peru, with *A. fraterculus* predominant in lowlands and *A. striata* in highlands. Among species in the *A. fraterculus* complex, those from lowlands in Peru were different from those from highlands in Peru, Ecuador, and Colombia (Hernández-Ortiz *et al.*, 2015).

In Colombia, fruit fly species may be in places with very low variability in weather conditions, thus exhibiting hierarchical competition. There is a competitive displacement from the host to the less adapted species (Duyck *et al.*, 2004) due to being genetically adapted to climatic conditions, i.e., the host is not the main factor for geographical distribution; it is the weather.

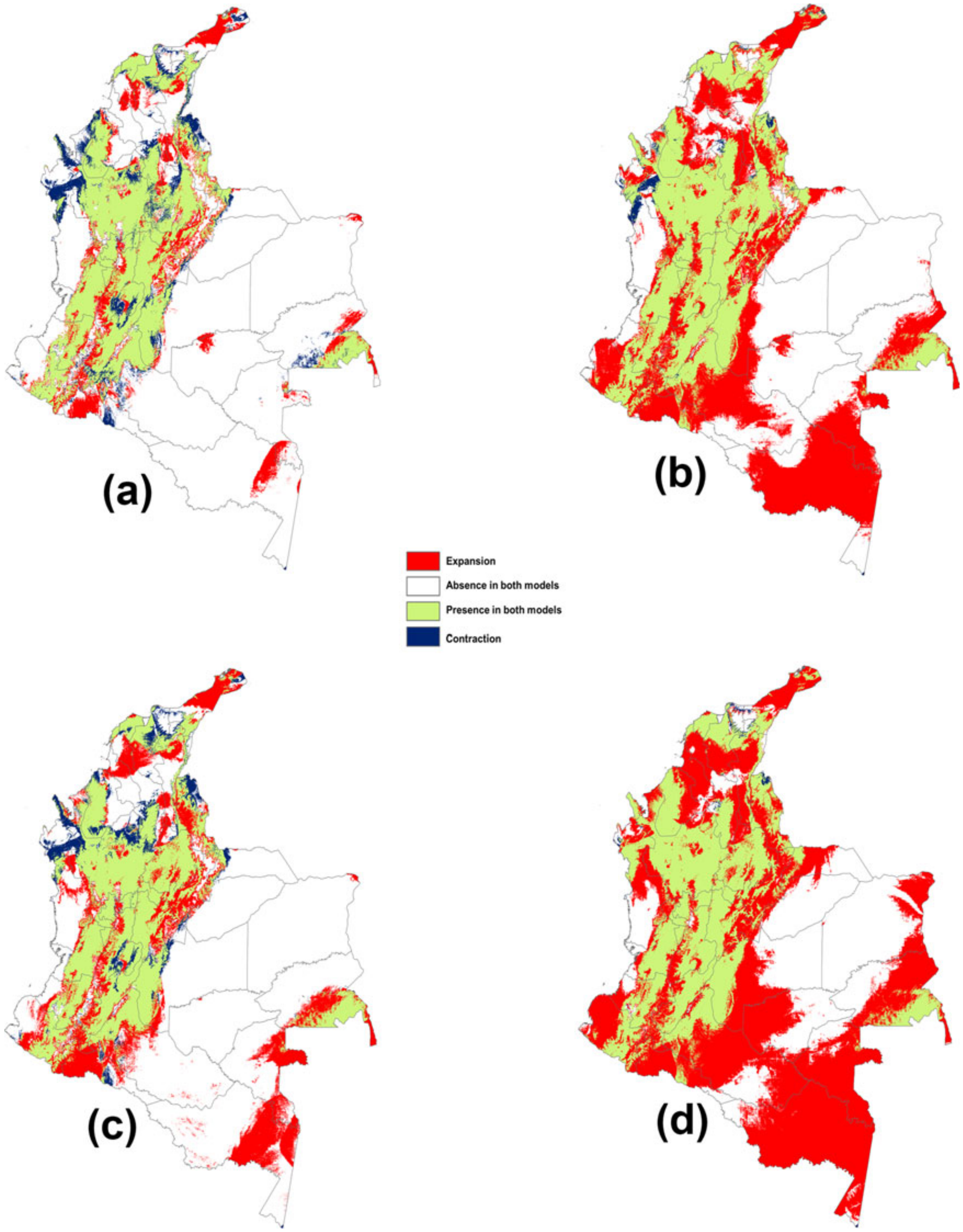

Figure 4. Changes in suitable climatic spaces for *A. striata* and the potential distributions between current and future conditions in Colombia: (a) current vs. time 2050 under RCP 2.6, (b) current vs. 2050 under RCP 8.5 (c) current vs. 2070 under RCP 2.6, and (d) current vs. 2070 under RCP 8.5.

Under scenarios of climatic change in temperate regions, fruit flies could be moved to similar Colombian behaviors. Natural enemies could affect fruit fly distribution. Surveys reporting parasitoids, such as the fruit-infesting Tephritid in Colombia, were summarized by Ruíz-Hurtado *et al.* (2013) and Cruz-B *et al.* (2017). Data have shown that parasitism is low, similar to other countries, and a high species turnover according to the altitudinal range, i.e., parasitoids are adapted to weather conditions, but fly species are not. Similar conclusions were found by Salazar-Mendoza *et al.* (2021) in an altitudinal transect from Peru where parasitism was similar among altitudes, but parasitoid richness was different. Other biological factors could affect fruit fly populations, but they are largely unknown around the world. From the biological point of view, Colombian weather conditions are stable throughout the year in the same place, and there are differences only by altitude variation; in GFF and perhaps other fruit

Table 2. Changes in the potential distribution area (km^2) of *A. striata* in Colombia between different climatic scenarios

Model	Expansion	Absence in both	Presence in both	Contraction
Current/MIROC5-2050-RCP26	98,611	730,745	253,462	52,808
Current/MIROC5-2050-RCP85	369,239	460,118	297,437	8834
Current/MIROC5-2070-RCP26	187,860	641,497	265,375	40,895
Current/MIROC5-2070-RCP85	520,071	309,285	303,298	2972

fly species and insect species, weather must be the principal factor for distribution. Thus, models developed in this paper reflect *A. striata* behavior and can act as a guide for other countries under climatic scenarios.

Our omission errors may be the result of the retrieved geographical record attributes of *A. striata*, which were mainly based on two sources: the first came from five departmental initiatives (control programs) (Castañeda *et al*., 2010) and the second came from sporadic records of specimens deposited in entomological collections. These data show the lack of comprehensive surveys of fruit flies in Colombia; systematic collections were carried out mainly in the mountain ecosystem, and data from the eastern plains and Amazonian and Pacific regions are scarce (Herrera-Buitrago *et al*., in prep.). Optimal biological data are a crucial aspect for good results in distribution models. Despite these circumstances, the current distribution model coincided with previous information, which showed that guava fruit flies were common in Colombia, as summarized by Rodriguez *et al.* (2018); additionally, the results of the statistical validation of the model under the current environmental conditions showed adequate statistical support.

The most influential variables of *A. striata* occurrence were temperature- and precipitation-related variables (table 1). These results aligned with those of Porter *et al.* (1991). The models also indicated the absence of flies in cold localities at high altitudes, such as paramo ecosystems; the paramo is distributed along the top of the Andean ranges (fig. 1a) and the upper Sierra Nevada de Santa Marta (fig. 1, locality e). Despite the existence of Myrtaceae in these altitudinal floors, in samplings carried out in these ecosystems, *A. striata* was not collected (N.A. Canal, unpublished data). This suggests that the absence of *A. striata* in paramo may be because it does not adapt physiologically to these ecosystems.

Additionally, very humid regions with high-precipitation levels (TRFs), such as the Serrania del Darien (fig. 1, locality f) and most forested areas of the Pacific (fig. 1E) and Amazonian region (fig. 1B), were identified as having low suitability for the flies. The area suitable for *A. striata* in the Pacific region was mainly located in northern Chocó (figs 2A and 1-11) in extensive areas bordering Golfo de Uraba (fig. 1, locality c) and in a small area in the Nariño department (fig. 1-18). However, the map indicates suitability in the interfluvial area of the Inírida (fig. 1, locality d), Guainía, and Vaupés rivers and the surroundings of the jurisdiction of Mitú (fig. 1, locality g) in the Orinoquia and Amazonian regions. The establishment of *A. striata* must be interpreted cautiously since the precarious conditions of the soils, where it is common to find rocky outcrops and floristic associations of monocotyledons (Hernández-Camacho and Sanchez-Páez, 1992), provide unfavorable conditions for *A. striata*'s host plants. However, bionomic and scenopoetic variables that were not assessed may positively affect the occurrence of source populations (Peterson *et al*., 2011).

The models under climate change scenarios with an increase in temperature expanded the geographic area suitability, as evidenced here for *A. striata* in Colombia (fig. 4). This behavioral response may be evidenced in species limited by low temperatures, where the increase in warmth in the occurrence area may shift the geographical range toward cold regions (Fu *et al*., 2014). Although the presence probability decreased in the Pacific region, it could be the result of climatic effects due to proximity to the coastal zone, where the general climatic conditions are remarkably unstable (Martínez-Ardila *et al*., 2005). Changes in climatic variables, such as precipitation regimes, can cause contractions in the spatial distribution (Martínez-Freiría *et al*., 2016). Our results agreed with those of Fu *et al.* (2014), who demonstrated that climate change expanded the potential distribution of the fruit fly *A. obliqua* (Macquart, 1835) toward the poles but decreased the distribution in northwestern Australia and northern sub-Saharan Africa due to climate stress caused by marine climate effects.

Notably, the potential distributions of species depend not only on weather conditions but also on dispersal capacity, host availability, the effects of ecological relationships (Peterson *et al*., 2011), and species physiology (Gamaliel *et al*., 2020). The estimation of these aspects is especially critical for species of economic importance (Lira-Noriega *et al*., 2013; Reyes and Lira-Noriega, 2020). This information is difficult to model with climate change scenarios, and even current biotic interaction data are challenging to include (Peterson *et al*., 2011). This study faced a poor understanding of the basic bionomic parameters of *A. striata* (Cruz-López *et al*., 2015) due to insufficient local data to infer ecological and distributional patterns in *A. striata* populations (Canal, 2010; Castañeda *et al*., 2010). The current and future ecological interactions of *A. striata* in Colombia are still enigmatic and lead to additional challenges for integrated management. Nevertheless, we offered an additional tool never before considered in Colombian fruit agriculture. The most significant proportion of potential areas predicted by climate change scenario models for the expansion of *A. striata* occurred in the Amazonian region (fig. 4b, d). This could be related to accelerated deforestation rates, which are caused primarily by the presence of illicit crops and the expansion of the agricultural frontier (Vieira, 2019); these activities could promote *A. striata* establishment (Aluja *et al*., 2003).

Due to the economic importance of *A. striata*, knowledge on the autoecology and variables determining its geographic distribution are essential on the local scale (Castañeda *et al*., 2010); this information provides crucial feedback for implementing effective IPM programs (Martínez-Ardila *et al*., 2005). Under the current environmental and climatic conditions, the *A. striata* distribution is intimately associated with guava crops. The predominance of

Table 3. List of guava-producing municipalities and their respective risk category for the establishment of *A. striata* according to the area deemed suitable by the ecological niche model under current climate conditions in Colombia

Natural region	Department	Municipality	Suitable area (%)	Category of vulnerability
Andean	Antioquia (fig. 1-2)	Carmen de Viboral	54.2	Intermediate
		Cocorná	95.4	High
		Urrao	86.8	High
	Boyacá (fig. 1-6)	Moniquirá	98.4	High
		Ráquira	60.8	Intermediate
	Caldas (fig. 1-7)	Manizales	71.8	High
	Cundinamarca (fig. 1-13)	Guaduas	93.7	High
		Guayabetal	82.5	High
		Sasaima	97.5	High
	Huila (fig. 1-16)	Acevedo	97.6	High
		Aipe	91.2	High
		Algeciras	49.0	Intermediate
		Garzón	77.0	High
		Gigante	83.9	High
		Isnos	37.1	Intermediate
		La Argentina	15.5	Low
		La Plata	38.5	Intermediate
		Nátaga	66.7	High
		Pital	75.1	High
		Pitalito	79.2	High
		Rivera	86.7	High
		Saladoblanco	29.5	Low
		San Agustín	36.5	Intermediate
		Teruel	41.4	Intermediate
		Timaná	87.3	High
	Norte de Santander (fig. 1-19)	Toledo	65.3	Intermediate
	Quindío (fig. 1-21)	Calarcá	96.3	High
	Risaralda (fig. 1-22)	Belén de Umbría	59.8	Intermediate
		Pereira	89.6	High
	Santander (fig. 1-23)	Albania	98.6	High
		El Guacamayo	50.3	Intermediate
		Girón	85.7	High
		Güepsa	35.9	Intermediate
		Jesús María	99.4	High
		Landázuri	67.0	High
		Lebrija	80.4	High
		Puente Nacional	89.0	High
		Vélez	90.4	High
	Tolima (fig. 1-24)	Coello	89.1	High
		Coyaima	61.1	Intermediate
		Ortega	86.0	High
	Valle del Cauca (fig. 1-25)	Bolívar	86.0	High

(*Continued*)

Table 3. (*Continued.*)

Natural region	Department	Municipality	Suitable area (%)	Category of vulnerability
Caribbean	Atlántico (fig. 1-4)	Manatí	81.5	High
		Repelón	70.6	High
		Santa Lucía	92.6	High
		Suan de la Trinidad	85.7	High
		Tubará	5.0	Low
	Bolívar (fig. 1-5)	Achí	11.1	Low
		Calamar	6.3	Low
		Cartagena	87.1	High
		San Juan Nepomuceno	1.4	Low
	Cesar (fig. 1-10)	Becerril	32.8	Low
		La Paz Robles	71.4	High
		San Alberto	39.6	Intermediate
		San Diego	47.2	Intermediate
		Valledupar	59.4	Intermediate
	Córdoba (fig. 1-12)	Cereté	94.6	High
		Montería	98.9	High
		Pueblo Nuevo	2.3	Low
		San Antero	14.4	Low
		San Carlos	86.6	High
Orinoquía	Casanare (fig. 1-9)	Chámeza	18.7	Low
		Yopal	0.6	Low
	Meta (fig. 1-17)	Acacías	60.7	Intermediate
		Lejanías	90.2	High
		Puerto Rico	0.0	Low
		San Martín	6.9	Low
Pacific	Chocó (fig. 1-11)	Sipí	19.7	Low
	Nariño (fig. 1-18)	Barbacoas	3.6	Low
		Santa Bárbara	5.4	Low
		Tumaco	9.5	Low
	Valle del Cauca (fig. 1-25)	Ansermanuevo	85.1	High
		Jamundí	84.1	High
		Pradera	67.1	High
		Roldanillo	98.1	High

A. striata and guava crop interactions, the high vulnerability of the guava-producing municipalities to the potential occurrence of *A. striata*, and its presence in a large area, principally in the Andes (fig. 2c and table 3), make it difficult to effectively establish IPM strategies based on a single local initiative. The use of the data offered here concerning each municipality may be used to configure national policies based on area-wide management (Bouyer *et al*., 2021).

Furthermore, the estimated distributions for *A. striata* according to climate change scenarios for 2050 and 2070 will not modify this outlook and are trending toward expansion. Importantly, the data presented here have established a clear and present risk to the spread of this fly of economic importance, emphasizing that these risks will only worsen in the face of climate change. Action should be taken to ensure optimal guava productivity. The selection and cultivation of cultivars adapted to environments unsuitable for *A. striata*, as well as the selection of fly-resistant varieties, present promising opportunities. Alternative approaches employing chemical ecology and trophic relationship studies could represent useful improvements for GFF management in Colombia. Finally, it would be desirable to establish transnational policies to enhance the monitoring of fruit fly pests in areas where eradication techniques, such as low prevalence areas and sterile males use, are unlikely.

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