



Risk analysis for *Anastrepha suspensa* (Diptera: Tephritidae) and potential areas for its biological control with *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) in the Americas

Geovani da Silva Santana^{a,*}, Beatriz Ronchi-Teles^a, Cícero Manoel dos Santos^b,
Philipe Guilherme Corcino Souza^c, Priscila Kelly Barroso Farnezi^c,
Victoria Libertad de Assis Paes^b, Marcus Alvarenga Soares^c,
Ricardo Siqueira da Silva^c

^a Instituto Nacional de Pesquisa da Amazônia, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil

^b Universidade Federal do Pará R. Cel. José Porfírio, 030 - Recreio, Altamira, PA, 68371-030, Brazil

^c Universidade Federal dos Vales de Jequitinhonha e Mucuri. Rodovia MGT 367 – Km 583, n° 5000 - Alto da Jacuba, Diamantina, MG, 39100-000, Brazil

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ABSTRACT

The Caribbean fruit fly *Anastrepha suspensa* (Diptera: Tephritidae) is a polyphagous pest causing economic losses in Central America, the Caribbean and South Florida. The parasitoid wasp *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) is the main parasitoid of *A. suspensa* in biological control programs. In this study, by modeling with CLIMEX software, climatically suitable areas were projected according to historical climate data. Areas with overlapping optimal climatic suitability for the joint establishment of the pest and parasitoid were mapped, indicating large areas with host presence in North, Central, and South America, with cold stress being the main climatic factor limiting distribution for both species. Tropical regions have the most potential for invasion, with optimal suitability in many areas. Through the projected distributions, this study can target quarantine strategies in areas most susceptible to invasion and establishment of the pest in each country. In addition, classical biological control with the parasitoid in areas with climatic suitability is also recommended.

1. Introduction

Many species of fruit flies (Diptera: Tephritidae) are invasive pests of horticultural crops worldwide because of their climatic adaptability, host range, and high reproduction [1]. *Anastrepha suspensa* (Lower, 1862), better known as the Caribbean fruit fly, is a polyphagous species that attack about 100 temperate, subtropical, and tropical climate plants [2,3]. The pest has preference for guava (*Psidium guajava*), jambo (*Syzygium jambos*), peach (*Prunus persica*), surinam cherry (*Eugenia uniflora*), and mature *Citrus* spp [4,5].

The current occurrence of *A. suspensa* includes the entire Caribbean region, the coast of Mexico, and southern and central Florida [5]. The first infestation probably occurred in Key West, Florida (USA) in 1931 from collected adults, allowing the identification of guava

* Corresponding author.

E-mail addresses: geovanibtt@gmail.com (G. da Silva Santana), ronchibr@gmail.com (B. Ronchi-Teles), cmanoel@ufpa.br (C.M. dos Santos), philipe.corcino@gmail.com (P.G.C. Souza), priscila.farnezi@ufvjm.edu.br (P.K.B. Farnezi), ricardo.siqueira@ufvjm.edu.br (R.S. da Silva).

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as the main host. In 1936, the population became extinct through biological control programs promoted by the State Plant Board of Florida and the United States Department of Agriculture [3,4]. In 1965, 14,000 adults of *A. suspensa* were captured in Dade County (Miami), representing a new infestation after 30 years of eradication [6].

Because they lay their eggs inside the fruit, most fruit flies are pests that cause failure and damage the quality of the infested fruits [7,8]. The larvae consume the fruit flesh, leading to early ripening, fruit drop, and rotting [9]. An attacked fruit may have oviposition perforations, but it can be difficult to identify these or any other damage indicators in the early stages of an infestation [5]. Because of their direct impact and quarantine requirements set by importing countries, the presence of specific pest species restricts access to international markets [10].

More than one strategy is used for fruit fly management. Each method has its requirements and may not be suitable for all cases [7]. Biological control with parasitoids has been the most researched control strategy [11]. The parasitoid *Diachasmimorpha longicaudata* (Ashmead, 1905) (Hymenoptera: Braconidae) is ideal for biological control programs due to its ability to be mass-reared on artificial diet and its high reproductive rate with rapid doubling [12]. Oviposition of *D. longicaudata* occurs on fruit fly larvae in infested fruit. The parasitoid larvae feed internally and emerge from fly pupae in the soil [13,14].

A biological control program was established with the *A. suspensa* infestation in 1965 in Florida by importing 11 species of parasitoids. In the following years, the release of the parasitoids *D. longicaudata* and *Doryctobracon areolatus* (Szépligeti, 1911) decreased *A. suspensa* populations in Florida by 40% [15,16]. The *D. longicaudata* has become established in areas determined in biological control programs in the Caribbean, Pacific Islands, South Florida, and Central and South American countries [4,17].

Predictive technologies, such as species distribution models (SDMs), allow for risk assessment and possible changes in species distribution and are an important component in pest control [18,19] SDMs include ANUCLIM/BIOCLIM, CLIMATE, CLIMEX, DOMAIN, GARP, HABITAT, and MaxEnt [20].

CLIMEX is often used to estimate the impact of climate change on species, as it correlates climate and biological parameters to project niches on a temporal and spatial scale [21,22]. The potential distribution can be examined in advance, and guidance can be provided to implement control measures for the target species [23].

The objective of this study was to estimate the distribution potential of *A. suspensa* and the parasitoid *D. longicaudata* for the identification of ecologically suitable overlapping sites for the recommendation of classical biological control in case of invasion.

2. Material and methods

2.1. Occurrence data

The occurrence points of *A. suspensa*, *D. longicaudata* and the main host crops of the pest *P. guajava*, *S. jambos*, *P. persica*, *E. uniflora* and *Citrus* spp. were obtained from the databases of the Global Biodiversity Information Facility (GBIF) (www.gbif.org) and the Center for Agriculture and Bioscience International (www.cabi.org) and complemented with field work published in scientific articles [3,6,24–32]. We found 35 occurrences of *A. suspensa* and 51 for *D. longicaudata*, of which 33 were from sites where the parasitoid was released but there was no establishment confirmation, and 18 with confirmation.

Inquiries were made for synonyms of *A. suspensa* as *Anastrepha longimaculata* (Greene, 1934), *Anastrepha unipuncta* (Seín, 1933), and *Trypeta suspensa* (Loew, 1862). Synonyms for *D. longicaudata* include *Biosteres compensans* (Silvestri, 1916), *Biosteres longicaudatus* (Ashmead, 1905), *Diachasmimorpha chocki* (Fullaway, 1953), *Diachasmimorpha formosana* (Fullaway, 1926), *Diachasmimorpha novocaledonica* (Fullaway, 1953), *Diachasmimorpha taiensis* (Fullaway, 1953) and *Opius longicaudatus* (Ashmead, 1905).

The accuracy of the occurrence points obtained for *A. suspensa* and *D. longicaudata* was verified to affirm its veracity with the locality related through Google Maps (www.google.com/maps).

2.2. Meteorological data

Historical data from 1961 to 1990 (30 years centered on 1975) from Climond 10's spatial resolution were used as they have good spatial resolution and high quality. These data have five climate variables: average monthly maximum temperature, average monthly minimum temperature, average monthly precipitation, and relative humidity at 9 a.m. and 3 p.m. [33].

2.3. Climex

CLIMEX is a simulation model that dynamically represents the structure of complex systems, such as the seasonal phenology of a species and its behavior over time through climate information [34,35] CLIMEX version 4.0 (Hearne software, Melbourne, Australia) was used for the analyses. We used the Compare Locations function to predict the potential distribution of areas with climatic suitability for *A. suspensa* and *D. longicaudata*.

CLIMEX simulates species distribution using the growth index (GI) and the stress index (SI) [35]. The Annual Population Growth Index (GIA) describes the potential for population growth during favorable climatic conditions as measured by the temperature (TI) and humidity (MI) indices [35–37]. The SI index addresses the species' ability to survive as measured by the quantity of cold stress (CS), heat stress (HS), wet stress (WS), and dry stress (DS) [23].

The final result, which is the suitability for the presence of the target species in a given location, is represented by the ecoclimatic index (EI), which incorporates the GI and SI plus the degree days per generation (PDD). Ranging on a scale from 0 to 100, EI near 0 indicates climatic unsuitability for species survival in a given region, while $EI \geq 30$ represents high climatic suitability for the long-

term survival of a species [35]. Values near 100 indicate optimal suitability for species introduction and establishment. For the present work, the range of EI was defined as $EI = 0$ (unsuitable), $0 < EI < 30$ (suitable), and $EI \geq 30$ (ideal).

2.4. CLIMEX parameter adjustment

The parameters were set based on the pest and parasitoid's current known distribution and thermal requirements as found in the literature. The parameters for lowest soil moisture threshold (SM0), lower optimum soil moisture (SM1), upper optimum soil moisture (SM2) and upper soil moisture threshold (SM3) were adjusted for humid tropical climate [35] based on the preferences of average temperature greater than 18 °C and 1500 mm annual precipitation for *A. suspensa* [5,9] and *D. longicaudata* for their successful introductions over the last century in tropical and subtropical climate against fruit flies belonging to the genus *Anastrepha* [15,38] (Table 1).

The lower temperature limit (DV0), lower optimum temperature (DV1), upper optimal temperature (DV2), and upper temperature limit (DV3) were defined based on scientific experimental work (Table 1). For *A. suspensa*, the temperature limits for development were set at 15 °C (DV0) and 34 °C (DV3) [39]; the optimal range for development was set between 18 °C (DV1) [5,40] and 28 °C (DV2) [41]. The heat stress temperature limit (TTHS) cold stress temperature limit (TTCS) and cold degree-day threshold (DTCS) were set at 40.56 °C [42], 11 °C and 15 °C days, respectively [39]. The number of degree days required to complete a generation was determined to be 152.6 °C [39].

The parameters for *D. longicaudata* were determined by Ndlela et al. (2021), who determined temperature thresholds for the parasitoid, porting DV0 = 10 °C, DV1 = 15 °C, DV2 = 25 °C, DV3 = 33.7 °C, TTHS = 35 °C, and PDD = 333.33. The DTCS value was set at 25 °C days and TTCS was set 7.33 °C [43].

For the other stress indices, the model was fitted for *A. suspensa* and *D. longicaudata* based on [35] recommendations for tropical humid climates (Table 1).

3. Results

3.1. Distribution potential of *A. suspensa* and *D. longicaudata*

The distribution potential for *A. suspensa* (Fig. 1) and *D. longicaudata* (Fig. 2) shows climatic suitability in the Caribbean, Central, North, and South America with suitable and ideal areas. *A. suspensa* presents areas with ideal climatic suitability distributed in Argentina, Brazil, Bolivia, Colombia, Costa Rica, Cuba, Florida (USA), Guatemala, Guyana, French Guyana, Honduras, Nicaragua, Panama, Paraguay, Peru, Dominican Republic, Suriname, and Venezuela. These regions may be suitable for the pest to establish a population and spread rapidly. Climate-suitable areas in Central America present a threat of invasion due to their proximity to areas where the pest occurs.

The areas with ideal climatic suitability for *D. longicaudata* (Fig. 2) are smaller than *A. suspensa*. The highest concentration of ideal-suitable regions is found in Guatemala, Nicaragua, Dominican Republic, French Guiana, Venezuela, Colombia, Brazil, Paraguay, and Argentina.

The current distribution of *A. suspensa* and *D. longicaudata* was validated based on areas where there is an establishment of the species in Central America (Figs. 1A and 2A) and South America (Fig. 2B). The modeling showed high consistency with the geographic

Table 1
CLIMEX parameter values used for modeling *A. suspensa* and *D. longicaudata*.

Index	Parameters	Value	
		<i>A. suspensa</i>	<i>D. longicaudata</i>
Moisture	SM0 = lower soil moisture threshold	0.35 ^a	0.35 ^a
	SM1 = lower optimum soil moisture	0.7 ^a	0.7 ^a
	SM2 = upper optimum soil moisture	1.5 ^a	1.5 ^a
	SM3 = upper soil moisture threshold	2.5 ^a	2.5 ^a
Temperature	DV0 = lower temperature limit	15 °C	10 °C
	DV1 = lower optimum temperature	18 °C	15 °C
	DV2 = upper optimum temperature	28 °C	25 °C
	DV3 = upper temperature limit	34 °C	33.7 °C
Cold stress	TTCS = cold stress temperature limit	11 °C	7.33 °C
	DTCS = degree-day threshold	15 °C days	25 °C days
	DHCS = stress accumulation rate	-0.001 week ⁻¹	-0.02 week ⁻¹
Heat stress	TTHS = heat stress temperature limit	40.56 °C	35 °C
	THHS = stress accumulation rate	0.0002 week ⁻¹	0.0002 week ⁻¹
Wet stress	SMWS = soil moisture threshold	2.5 ^a	2.5 ^a
	HWS = stress accumulation rate	0.002 week ⁻¹	0.002 week ⁻¹
Dry stress	SMDS = Dry Stress Threshold	0.25 ^a	0.2 ^a
	HDS = Dry Stress Rate	-0.01 ^a	-0.005 ^a
Degree days	PDD = degree days per generation	152.6 °C days	333.33 °C days

^a Estimated soil moisture indices, with values ranging from 0 (dry) to 1, are given without units (field capacity).

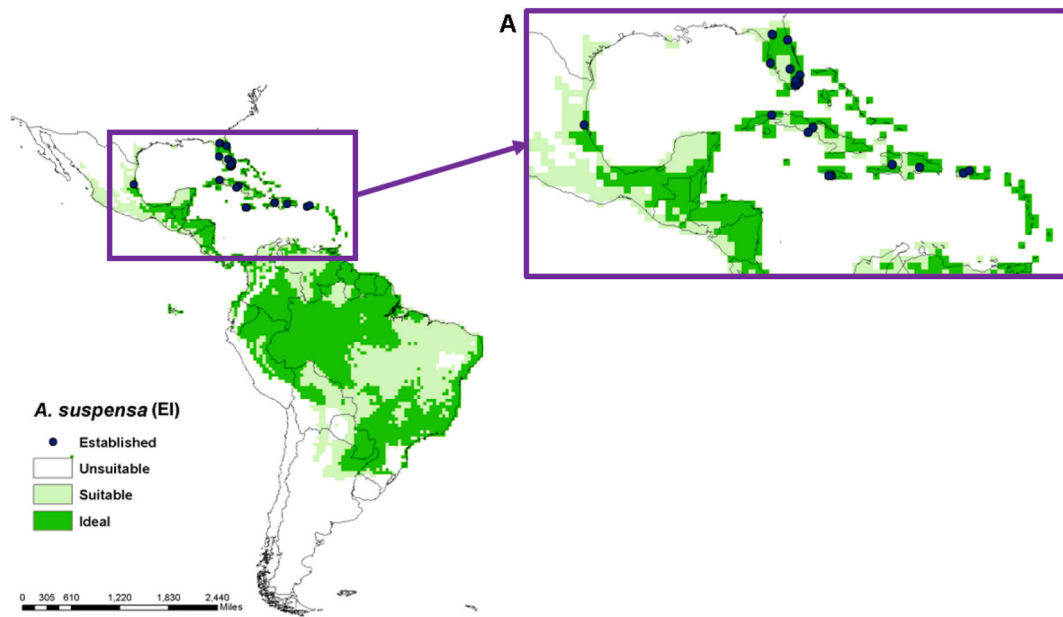


Fig. 1. Potential distribution of *Anastrepha suspensa* predicted by CLIMEX for the Americas and validation with current occurrence points (A).

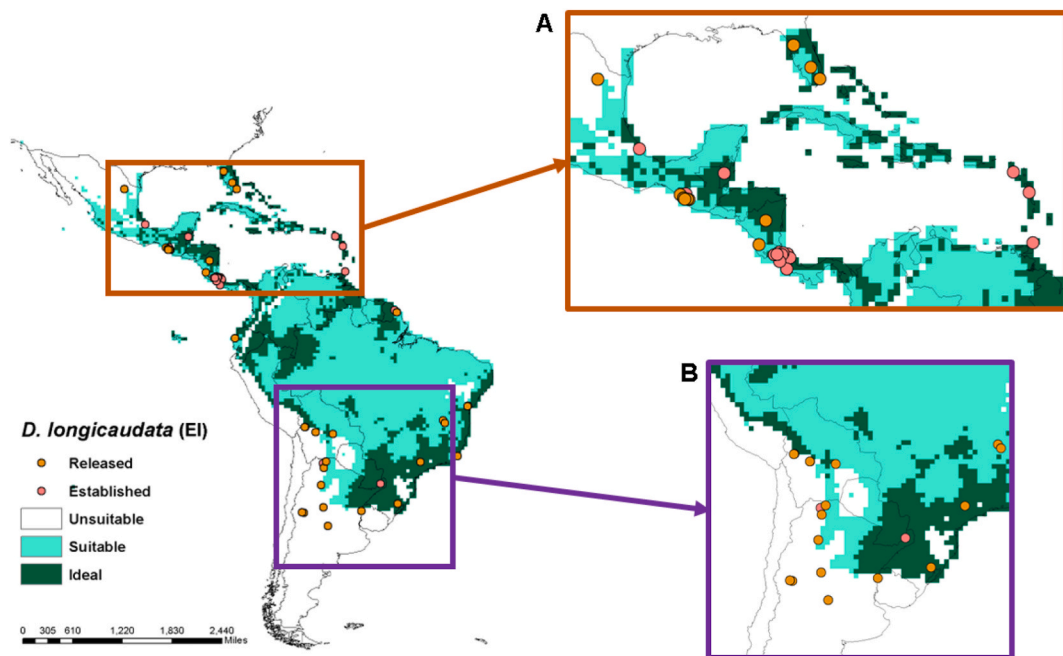


Fig. 2. Potential distribution of *Diachasmimorpha longicaudata* predicted by CLIMEX for the Americas and validation with establishment points in the Caribbean, Central and South America (A and B).

distribution; all occurrence points were located within the projected distribution.

3.2. Distribution limiting climatic variables for *A. suspensa* and *D. longicaudata*

The factors limiting the distribution of *A. suspensa* (Fig. 3A and B) and *D. longicaudata* (Fig. 4A and B) in many regions of North and South America are associated with cold, heat, and drought stress. Cold stress is the main limiting factor for both species, especially in North America and countries such as Chile, Argentina, and coastal Peru. Drought stress is more present in the United States, Mexico,

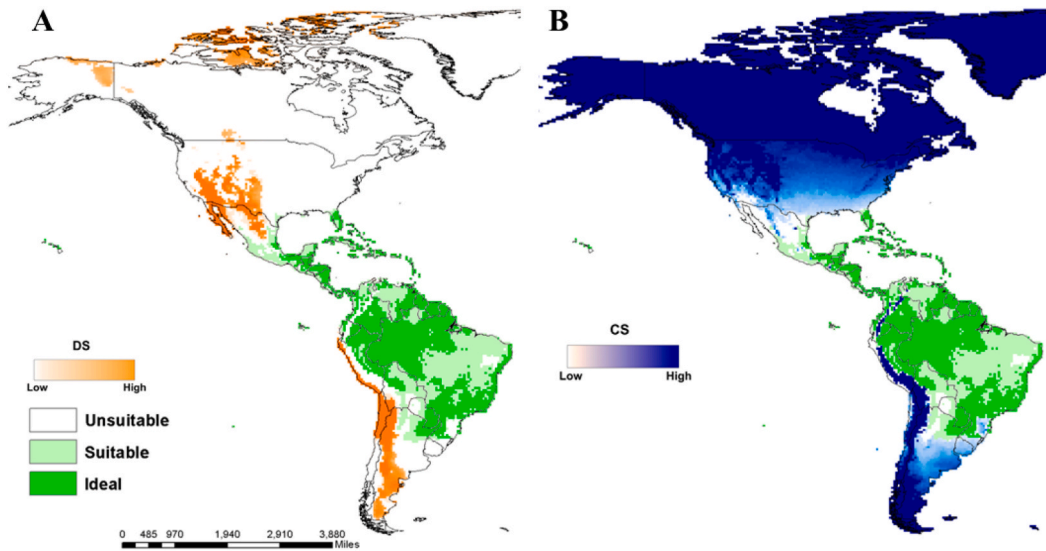


Fig. 3. The dry stress (DS) and cold stress (CS) for *Anastrepha suspensa* projected by CLIMEX on the American continent (A and B).

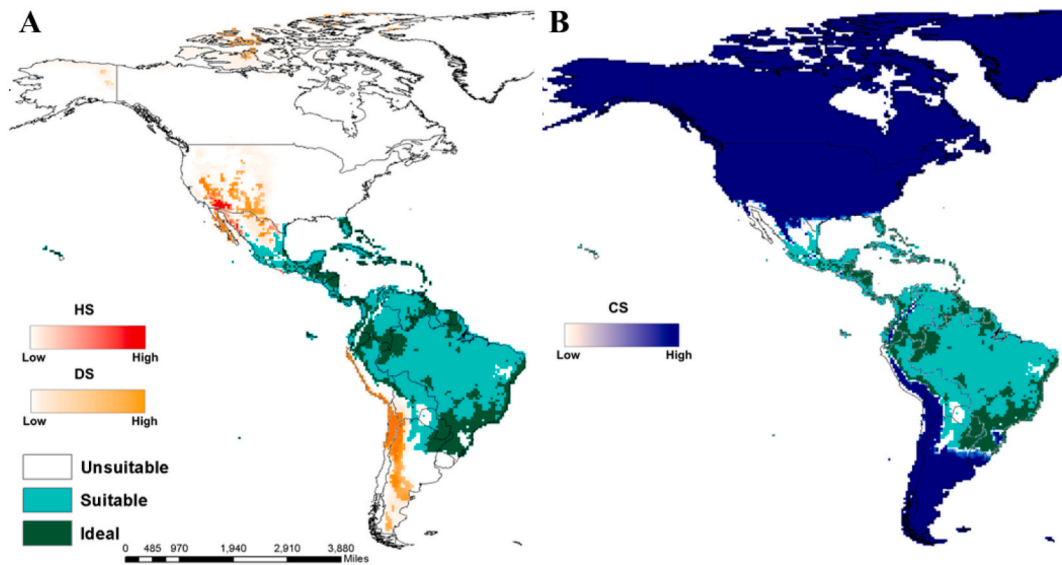


Fig. 4. The dry stress (DS) and cold stress (CS) for *Diachasmimorpha longicaudata* projected by CLIMEX on the American continent (A and B).

Chile, Peru, and Argentina for *A. suspensa* and *D. longicaudata*. Heat stress was identified for *D. longicaudata* (Fig. 4A) in the southwestern United States and northern Mexico.

3.3. Development and propagation potential of *A. suspensa* and *D. longicaudata*

The GIA map for *A. suspensa* (Fig. 5A) and *D. longicaudata* (Fig. 6A) shows regions favorable for potential development throughout the year, and regions with potential in the Caribbean, Central and South America. The midwestern and northeastern regions of the United States show migratory potential in favorable periods for both species.

Under ideal conditions, *A. suspensa* can reach 36.29 generations throughout the year (Fig. 5B). The most prone regions are found in northern Brazil, Colombia, Guatemala, Nicaragua, and Venezuela, the entire Caribbean region and Florida. Other areas of South America have the potential for up to 27 generations.

The parasitoid *D. longicaudata* (Fig. 6B) exhibits potential for up to 21 generations in the Caribbean, Central America, and the tropical Amazon region of South America. These regions are more prone to long-term establishment, with the potential for multiple annual generations.

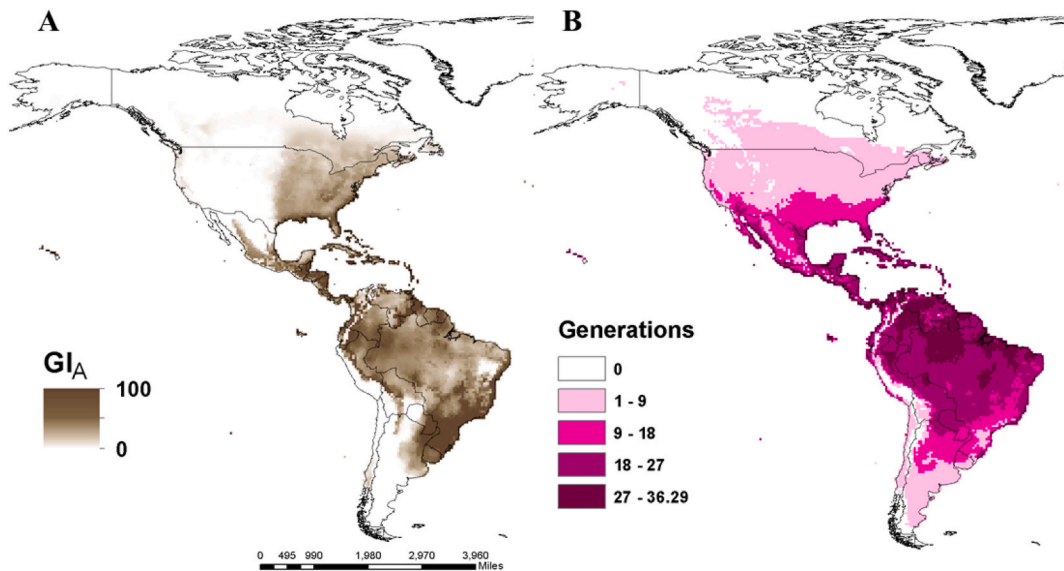


Fig. 5. A: Annual growth index (GI_A), and annual number of generations (B) for *Anastrepha suspensa* by CLIMEX on the American continent.

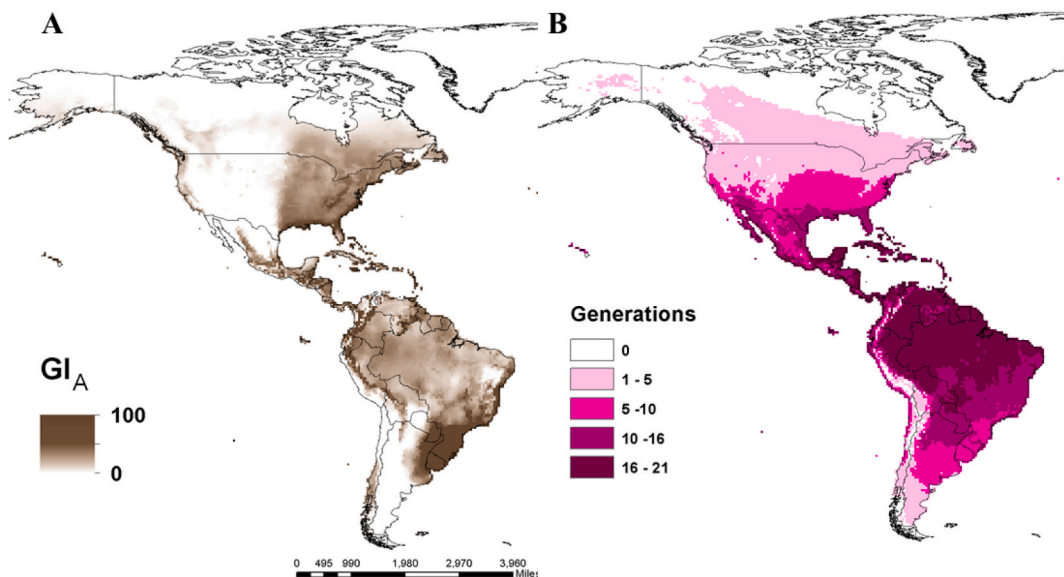


Fig. 6. A: Annual growth index (GI_A), and annual number of generations (B) for *Diachasmimorpha longicaudata* by CLIMEX on the American continent.

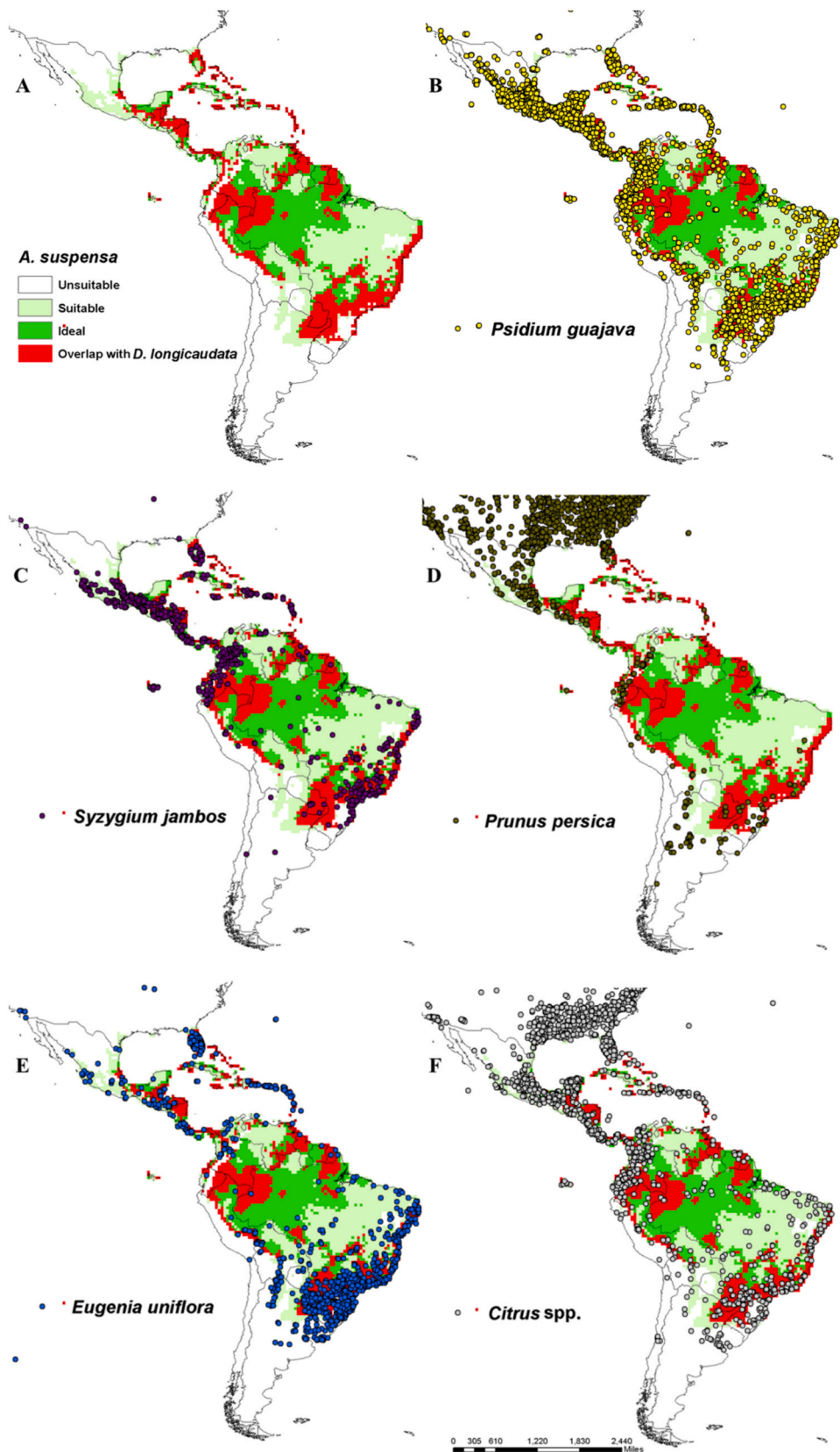
3.4. Areas with classic biological control potential

According to the projection of ideal overlapping areas between the two species (Fig. 7A), *A. suspensa* and *D. longicaudata* can coexist in regions of the Caribbean, North America, Central and South America.

In North America, the model indicates Florida and, the northeastern region and coastline with the Atlantic Ocean have the greatest potential for areas of overlap in the United States. In Mexico, Tamaulipas, Vera Cruz, Puebla, and Chiapas are ideal for the joint establishment of *A. suspensa* and *D. longicaudata*. These regions have all major hosts (Fig. 7A–F).

Also, all major hosts (Fig. 7A–F) occur in Central America. The model indicates that overlapping areas with ideal climatic suitability are present in almost all of its territory, except of El Salvador, which did not show optimal suitability overlap.

In the Caribbean, all regions have areas of overlap. Jamaica and the Bahamas have the occurrence of *P. guajava* (Fig. 7B), *S. jambos* (Fig. 7C), and *Citrus* spp. (Fig. 7F) and suitability throughout their territory. Cuba and the Dominican Republic have small areas of overlap and occurrence of all major hosts, with *P. persica* occurring to a lesser extent.



(caption on next page)

Fig. 7. Overlapping optimal areas of the potential distribution models of *Anastrepha suspensa* and *Diachasmimorpha longicaudata* (A) in crops of *Psidium guajava* (B), *Syzygium jambos* (C), *Prunus persica* (D), *Eugenia uniflora* (E) and *Citrus* spp. (F) for the Caribbean, North America, Central and South America.

The *A. suspensa* does not occur in South America but has potential distribution and the presence of significant hosts for almost all countries in suitable and ideal areas. In Brazil, the areas of overlap between *A. suspensa* and *D. longicaudata* were located in the north in the states of Acre, Amazonas, Amapá, Pará, and Rondônia, with *Citrus* spp. (Fig. 7F), *E. uniflora* (Fig. 7E), and *P. guajava* (Fig. 7B). In the central-western and southern regions, in the states of Minas Gerais, Paraná, Santa Catarina, São Paulo, and Rio Grande do Sul, the greatest number of *Citrus* spp., *E. uniflora*, *P. persica* (Fig. 7D), *P. guajava*, and *S. jambos* (Fig. 7C) are concentrated in overlapping areas. Small areas of ideal suitability for both species are also present in the coastal region with the presence of the main hosts.

Paraguay's eastern region presents ideal establishment potential for *A. suspensa* and *D. longicaudata*. Also, it has occurrences of the main hosts (Fig. 7A–F), emphasizing *Citrus* spp., *E. uniflora*, and *P. guajava* due to the highest number of occurrences.

Argentinian mesopotamia has the establishment of *D. longicaudata* (Fig. 2B) and areas with potential overlap with *A. suspensa*. The most abundant hosts are *P. guajava* and *E. uniflora*, but all major hosts occur (Fig. 7A–F).

The Amazonian regions of Ecuador, Colombia, and Peru exhibit ideal climatic suitability and coincide with occurrences of *P. guajava*, *Citrus* spp., and *S. jambos*. Other countries like Guyana, French Guiana, Suriname, and Venezuela have regions overlapping *A. suspensa* and *D. longicaudata* mainly in border areas with the presence of the main hosts, except *P. persica*, occurring only in French Guiana.

4. Discussion

The potential distribution of *A. suspensa* and *D. longicaudata* was estimated using CLIMEX. We identified the overlap of climatically ideal areas, the stress factors that limit the distribution of the species, and the development and number of annual generations. The results were consistent through cross-validation between current occurrence and predicted distribution. In this context, our study indicates the success of a biological control program with *D. longicaudata* in the case of a possible invasion of *A. suspensa*.

In North and South America locations, *A. suspensa* and *D. longicaudata* lack conditions for establishment because they are species adapted to tropical and subtropical climates [4,15]. *Anastrepha suspensa* is restricted to Central America and the Caribbean, but there is a risk of migration and establishment in South America due to the proximity of sites with climatically suitable occurrences and areas. At the same time, North America is limited by areas affected by drought and cold stresses (Fig. 3A–B), but it may have migratory potential during periods of the year favorable for development (Fig. 5A–B).

Fluctuations in temperature, rainfall, and constant winds are factors that hinder the establishment of *D. longicaudata* [29,30]. For example, dry and cold stresses may have restricted the establishment of *D. longicaudata* in Argentina after releases in Entre Ríos, Jujuy, Province of Córdoba, Tucumán [31], San Juan and San Miguel de Tucumán [30], regions that are outside the predicted potential distribution (Fig. 2B) and with drought and cold stress rates (Fig. 4). However, in Misiones and Salta, *D. longicaudata* became established after deliberate introductions (Oroño and Ovruski, 2007; Schliserman et al., 2003), areas with climatic suitability predicted by CLIMEX (Fig. 2B).

The modeling indicates that the likelihood of *A. suspensa* expanding its distribution is high due to the abundance of climatically suitable areas and host plants available throughout the projection. *A. suspensa* has been observed attacking *E. uniflora*, *P. guajava*, *P. persica*, *S. jambos*, and *Citrus* spp. in Florida [4,25,44,45]. The Americas account for about 45% of the world's guava production [46], most of it being produced in Central and South America [47]. *A. suspensa* has been causing problems on *P. guajava* for several decades in South Florida [4,48].

In South America, there are no reports of the presence of *A. suspensa*, but significant damage could be caused if the pest were introduced. According to the modeling, these areas have ideal potential that could present risks to agricultural production in case of invasion. For example, the municipality of Casa Branca, state of São Paulo, in southeastern Brazil is the largest orange producer in the world [49].

In the absence of natural enemies, invasive pest insects arrive in new environments and rapidly increase in numbers in newly invaded areas. The use of insecticides against *A. suspensa* adults in infested orchards will not control larvae in fruits or on the ground [50], and sterile insect techniques and destruction of *A. suspensa* infested fruits are not observed in large commercial orchards because of high labor costs [51,52].

The population of *A. suspensa* can be reduced through chemical control using attractive baits [9] and biological control with parasitoid wasps. Because *D. longicaudata* has been established in countries in the Caribbean, Central, and South America, introducing it to countries with similar climatic suitability may be an effective control method if *A. suspensa* is introduced.

Studies show that *D. longicaudata* attacks *A. suspensa* larvae on all its main fruit hosts [24,45] and can establish itself without compromising pre-existing trophic relationships [53]. It can be recommended to use it together with other parasitoid species such as *Doryctobracon crawfordi* (Viereck, 1911) and *D. areolatus*, since at the competition level, the two controls together become more effective than separately [24,54].

CLIMEX is used as a species distribution model. However, the model has limitations that must be taken into consideration. The modeling was performed without using non-climate variables such as disease presence, biotic interactions, and host availability. Therefore, the species' metabolism may change with climate changes [55].

In addition to analyses based on historical temperature records, it is important to consider the influences of climate change on the

distribution and invasive potential of pests belonging to the Tephritidae Family [56–59]. For instance, the impact of climate change on the future distribution of *Anastrepha grandis* (Macquart, 1846) is expected to result in a potential expansion of its range due to rising temperatures [58]. These studies highlight the importance of incorporating considerations about climate change into future studies on the distribution of *A. suspensa* and its overlap with the control species *D. longicaudata*. Climatically ideal areas should have intensified quarantine policies in product and host surveillance and monitoring with traps to prevent the occurrence of *A. suspensa*. However, this study may provide guidelines for preventing *A. suspensa* in areas with climatic suitability and hosts, as this method has been used to predict the possibility of using biological control measures on pest species [60] and, as an alternative, the use of *D. longicaudata* as a control in overlapping areas.

5. Conclusions

The American continent has areas suitable for *A. suspensa* and *D. longicaudata*. The potential for the establishment of *A. suspensa* in areas where the species is absent in countries that produce the main hosts, such as Guatemala, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, French Guiana, Suriname, Brazil, Peru, Bolivia, Paraguay and Argentina, indicates a risk of the pest invasion. The parasitoid *D. longicaudata* showed climatic suitability and areas with optimal overlap with the pest in large North, South, and Central America areas.

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Ethical guidelines

Ethics approval was not required for this research.

Declarations

Author contribution statement

Geovani Santana: conceived and designed the experiments; performed the experiments; Wrote the paper.

Geovani Santana, Ricardo da Silva, Beatriz Ronchi-Teles, Cícero dos Santos and Marcus Alvarenga: Analyzed and interpreted the data.

Geovani Santana, Ricardo da Silva, Beatriz Ronchi-Teles, Cícero dos Santos, Marcus Alvarenga, Victoria Paes, Priscila Farnezi and Philipe Souza.: Contributed reagents, materials, analysis tools or data.

Data availability statement

Data will be made available on request.

Additional information

No additional information is available for this paper.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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