

Research Paper

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Maximum Entropy (MaxEnt) as extreme distribution indicator of two Neotropical fruit fly parasitoids in irrigated drylands of Argentina

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Abstract

The figitid *Ganaspis pelleranoi* and the braconid *Doryctobracon areolatus* (Hym: Braconidae, Opiinae) are wide-ranging (from Florida, USA to Argentina) fruit fly parasitoids with tropical and subtropical distribution with a wet and temperate climate. In Argentina, both parasitoid species are thought to be restricted to the subtropical rainforests of the northwest and northeast, locally known as ‘Yungas’ and ‘Paranaense’ forests, respectively. However, these species recently have been recorded at the Monte and Thistle of the Prepuna eco-region, an arid region of central-western Argentina. Despite the extreme environmental conditions, anthropic artificial irrigation seems to be playing a fundamental role in fostering the presence and persistence of these species. Maximum Entropy (MaxEnt) models were developed to assess the suitability of these areas to harbor both species. The present work is a first approach to identify suitable areas for the distribution of these two fruit fly biological control agents in the American continent; based on 19 bioclimatic variables. Furthermore, the models resulting from including the new records in the ‘Monte’ eco-region suggest that local populations may become adapted to particular micro-environmental conditions generated by artificial irrigation. Models revealed that these artificial oases are suitable for *G. pelleranoi* but seem to be unsuitable for *D. areolatus*. This first and new approach to the area suitability of these species invites to produce models that reflect actual distribution including more records of presence in oases with similar conditions, thus decreasing the bias of the model generated by over reliance on areas with higher humidity (forest), which correspond to the distribution known before the inclusion of the new records.

Introduction

In Argentina, *Anastrepha fraterculus* (Wiedemann) (South American Fruit Fly) and *Ceratitidis capitata* (Wiedemann) (Mediterranean fruit fly) (Diptera: Tephritidae) are by far the most economically important fruit fly species recorded (Aruani *et al.*, 1996). *Ceratitidis capitata* is native to Africa and has a wide distribution, covering many tropical, subtropical, and temperate regions of the world (De Meyer *et al.*, 2002). *Ceratitidis capitata* was introduced to Argentina either accidentally via Buenos Aires, infesting peaches in 1905 (Vegiani, 1952) or by dispersing naturally from Brazil (Gonzalez, 1978). The species *A. fraterculus* is native to South America. It is distributed from Mexico to Argentina. However, morphological and genetic evidence indicates that this putative species is actually a complex of at least seven cryptic species (Steck, 1991; Hernandez-Ortiz *et al.*, 2012). Not all the species within this complex are pests (Aluja *et al.*, 2003). In Argentina, *A. fraterculus* is mainly distributed in regions with tropical and subtropical climates (Ovruski *et al.*, 2003).

Tritrophic interactions among plants, herbivores, and natural enemies have always been of interest in view of the need to integrate host plant resistance and biological control into arthropod pest management (Tscharrntke and Hawkins, 2002). Within the natural enemies’ complex, parasitoids are critical members of multitrophic food webs, and have a significant influence on ecological community structure and diversity (Godfray *et al.*, 1994). Similar to other insects, environmental temperature is essential in determining the dynamics of parasitoid populations, as well as the distribution in their suitable habitats (Walther *et al.*, 2002). The bioclimatic envelope, which refers to the multidimensional climatic conditions of an area, is not necessarily the same for a parasitoid as for its host or hosts (van Baaren *et al.*, 2010). Fully congruent

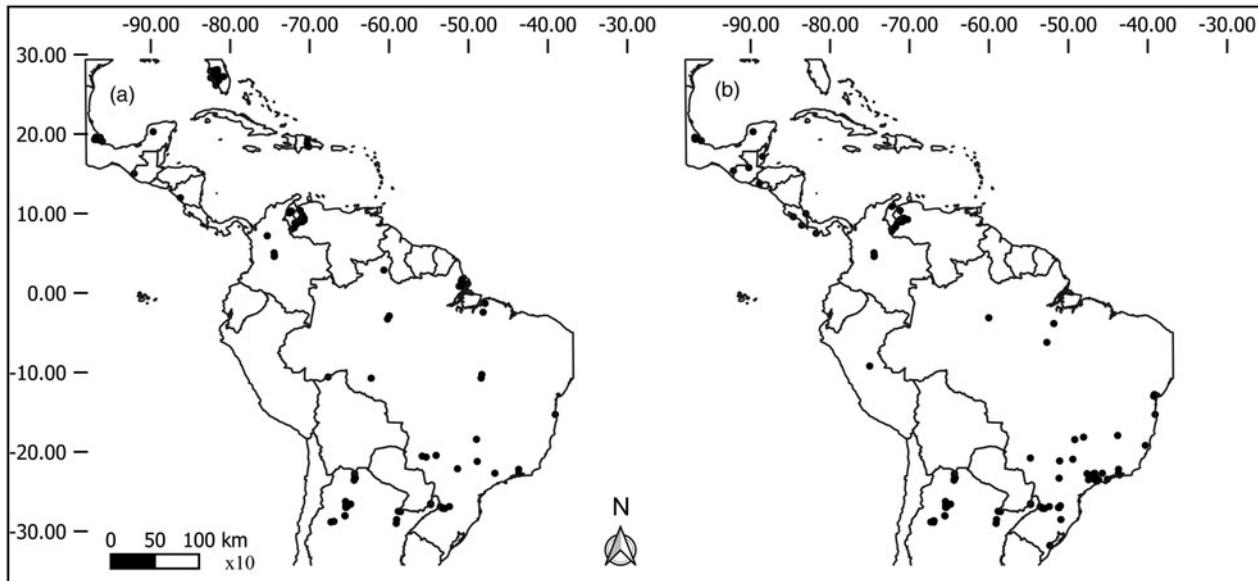


Figure 1. Maps of American distribution recorded for (a) *G. pelleranoi*, and (b) *D. areolatus*, including the new records from La Rioja province, Argentina.

host-parasitoid distributions appear to be rare and climate effects are the most likely explanation for the absence of specialized parasitoids throughout their host distribution (Hance *et al.*, 2007; Thomson *et al.*, 2010). An example of an interesting multitrophic biological system is clearly represented by tephritid fruit flies attacking economically important host fruits. A wide diversity of natural enemies, especially parasitoids, have been associated with frugivorous tephritids (Hoffmeister and Vidal, 1994; Garcia *et al.*, 2020). Many parasitoid species have mostly been used as biocontrol agents against tephritid pests of fruit crops worldwide (Dias *et al.*, 2018; Garcia *et al.*, 2020). Within sympatric fruit fly parasitoid assemblages in tropical and subtropical areas, several species have exhibited different environmental requirements, which have enabled interspecific coexistence (López *et al.*, 1999; Sivinski *et al.*, 2000; Schliserman *et al.*, 2016). Of all Neotropical parasitoid species associated with tephritid fruit flies, 24% are widely distributed, 22% are more regionally distributed, and 53% are only known from a single location (Ovruski *et al.*, 2000; Sivinski *et al.*, 2000).

Ganaspis pelleranoi (Brèthes) (Hym: Figitidae, Eucoilinae) and *Doryctobracon areolatus* (Hym: Braconidae, Opiinae) are two parasitoid species native from the Neotropical region (Aluja *et al.*, 2009) widely distributed throughout the American Continent (Ovruski *et al.*, 2000) (fig. 1). Both are koinobiont solitary larval-pupal endoparasitoids and primarily attack several species of true fruit flies (Tephritidae) in the genus *Anastrepha*. Both parasitoid species exhibit potential for biological control of fruit flies, given their relatively fast adaptation to laboratory conditions (Aluja *et al.*, 2009) and the fact that they can be mass-produced on irradiated host larvae (Cancino *et al.*, 2009). Thus, assessments of the suitability of areas for the potential distribution of these species might help developing or improving biological control or integrated pest management programs.

In Argentina, both parasitoid species are thought to be restricted to the subtropical rainforests of the northwest and northeast, locally known as 'Yungas' and 'Paranaense' forests, respectively (Schliserman *et al.*, 2010, 2016). In those subtropical forests, both hymenopterans were recorded attacking the two fruit

fly species of economic importance (Ovruski and Schliserman, 2012).

Fruit flies developing in commercial fruit orchards and backyard trees from species introduced were widely spread after American Spanish colonization. The introduction of exotic commercial fruit species combined with artificial irrigation in semi-arid or arid areas is often the source of environmental disturbances that encourage the establishment and spread of invasive arthropod species, such as the exotic tephritid *C. capitata*, and enable the expansion of the distributional range of generalist native insect species, such as *A. fraterculus* and their associated parasitoids (Schliserman *et al.*, 2014). Such expansion of frugivorous invasive species may influence the distribution patterns at other trophic levels, for instance, natural enemies, as is the case of the parasitoids. Thus, environmental changes have probably been playing a role in the presence registered of the parasitoids species recorded in the Monte eco-region.

In 1998, *G. pelleranoi* and *D. areolatus* were recorded at the semi-arid eco-region commonly known as Northwest Monte and Thistle of the Prepuna (Ovruski, 2002) (Monte eco-region). This site has very different climatic conditions than northern Argentina's subtropical forests (Morello *et al.*, 2012). The authors who found both parasitoid species in the eco-region mentioned above did not consider them as established. Instead, they suggested that the findings might have been the consequence of the accidental introduction or transport of fruit infested with fruit fly larvae and subsequently parasitized by *G. pelleranoi* and *D. areolatus* from other fruit-growing areas of Argentine (Ovruski, 2002). Due to the arid climate of the Monte eco-region, fruit crops and backyard orchards are limited by artificial irrigation, conforming oases in a desert matrix that allow both pestiferous tephritid flies presence (Guillen and Sanchez, 2007). This anthropic alteration could also be playing a role in the establishment and permanence of the parasitoid species.

Different methods have been used to empirically assess the species' distribution by correlating observed field distributions to environmental predictor variables (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005). In such cases, data on species

distribution can consist of species presence only, presence-absence, coming from empirical studies of species abundance, or natural history collections (Graham *et al.*, 2004). Climate is a driver of biotic systems, affecting individual fitness, population dynamics, species distribution, abundance, ecosystem structure, and function. Regional variation in climatic regimes produces selective pressures that may result in the evolution of locally adapted physiologies, morphological adaptations (e.g., color patterns, surface textures, body shapes, and sizes), and behavioral adaptations (e.g., foraging strategies and breeding systems). The two most common biological responses to climate variables are spatial and temporal changes in population dynamics (Parmesan *et al.*, 2000).

Many living organisms' distribution ranges are primarily limited by climatic variables (Messenger, 1959; Grace, 1987; Cooper, 1995). Entomologists accept weather and climate as dominant drivers of insects' behavior, abundance, and distribution (Messenger, 1959). A bio-climate modeling approach can still provide a valid first approximation to the potential insects' species distribution (Pearson and Dawson, 2003).

Considering the above, some new records out of a knowledge on species distribution could affect the suitable areas of distribution predicted by models.

In the last years, *G. pelleranoi* and *D. areolatus* were re-recorded at four localities of La Rioja province, belonging to the Northwest Monte and Thistle of the Prepuna. To corroborate the potential suitability of these oases for the permanence of both parasitoids, Species Distribution Models (SDM) using 'maximum entropy' (MaxEnt) (Phillips *et al.*, 2018) at a continental scale were run. MaxEnt is a helpful technique for predicting species' geographical distribution based on the most critical environmental conditions (Phillips *et al.*, 2004, 2006). The algorithm is deterministic and converges to the maximum entropy probability distribution (Berger *et al.*, 1996; Phillips *et al.*, 2006; Baldwin, 2009), establishing the relationship between species records at specific sites and their environmental and spatial characteristics (Elith *et al.*, 2011). If the area has sufficient food resources (fruit fly larvae) to support the parasitoid populations, the environmental variables should be the only limiting factors influencing these species' presence or annual permanence. MaxEnt could elucidate the probability of these artificial 'oases' to harbor both *G. pelleranoi* and *D. areolatus* in this semi-arid eco-region of Argentina. Two possible scenarios could result: models will show as unsuitability of these oases for these species, supporting the idea of the accidental introduction from actual distribution areas, and the second, that the models may include these 'oases' as a suitable area of distribution. In this last case, it is possible to consider these oases as new areas for the species distribution.

Methods

Model data sources

Datasets were elaborated from two source types, the first, from field collections in new distribution areas, and the second from scientific literature. The methods for obtaining the records are detailed below.

New distribution areas and collecting methods

The new records correspond to five study sites (Aminga, Los Molinos, Anjullón, San Pedro, Santa Veracruz), located in the

Monte and Thistle of the Prepuna eco-region (Monte eco-region), in the northwest of Argentina, La Rioja province). The native vegetation is characterized by xerophytic shrubs dominated by Zygophyllaceae, such as the genus *Larrea*, associated with the species of the genus *Prosopis* (Fabaceae) reduced in size. The fruit-growing areas are restricted to irrigated valleys shaping real oases, isolated from each other by wide desert plains, or high elevation mountains, where no native host plants for the economically important fruit fly species are found (Ovruski, 2002). Altitude ranges from 1000 to 3500 m.a.s.l. The climate is continental, with a wide annual variation in temperature and atmospheric pressure. The temperature fluctuates between -9°C (June–July) and 42°C (November–February). Rainfall is scarce, concentrated in summer (i.e., December–March), and fluctuates annually between 60 and 120 mm (Morello *et al.*, 2012).

Parasitoid presence for new localities was accessed through a collection of fruit infested by tephritids (Los Molino's locality), and direct parasitoids adult's collection by manual aspirator (other four localities).

According to the following plan, fruits were sampled: five American plum trees (*Prunus americana* Marsh, Rosaceae) from six orchards. A total of ten fruits were collected from individual trees, five directly from canopies, and five from the ground every week from December 2015 to January 2016. *Prunus americana* was chosen because it hosts both *A. fraterculus* and *C. capitata* fruit flies species. Each sample was placed in a plastic crate ($48 \times 28 \times 15$ cm) with slotted bottom and piled up over another plastic crate of the same size but with a non-perforated bottom lined with 3 cm sterilized sand as the pupation medium. Both crates were covered with an organdy lid. The second crate method was used to prevent the mix of sand and fruit, fungal growth, and bacterial contamination. Samples were kept in the darkroom for 20 days. The sand was sifted weekly to collect fly pupae, which were transferred into plastic cups (6.5 cm diameter, 8.5 cm deep) filled with sterilized moist vermiculite as the pupation medium and covered with a piece of organdy lid to allow breathing of pupae. The number of emerging parasitoids and flies was recorded, and non-emerged pupae were dissected to corroborate the presence of a fly or a parasitoid. Parasitism is a biological parameter that allows comparing the incidence of a fruit fly parasitoid on the pest tephritid species among different host fruit species or study sites, and also, throughout fruiting seasonality (Ovruski *et al.*, 2004; Schliserman *et al.*, 2016). Here the percentage of parasitism was calculated as follows:

$$\% \text{ of parasitism} = \frac{N_p}{N_{pu}} \times 100$$

where N_p is the total number of parasitized pupae (emerged + non-emerged), and N_{pu} is the total number of fruit fly pupae (parasitized and non-parasitized).

Adult parasitoids were collected using a manual aspirator in the other four localities studied (Aminga, Anjullón, San Pedro, and Santa Veracruz).

Collection was carried out from December 2016 to January 2017, December 2017 to January 2018, and December 2018 to January 2019 in the plum orchards.

Collected parasitoids and fruit fly adults were identified by the senior author. Voucher specimens were placed in the entomological collection of Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja (CRLAR), Anillaco, La Rioja, Argentina.

Dataset of species distribution and bioclimatic layers

Data sources for both *G. pelleranoi* and *D. areolatus* distribution extracted from the scientific literature are presented in Appendix 1 (Supplementary Material), covering mainly tropical and subtropical America, from Florida (USA) to northern Argentina. This area matches the native distributional range of tephritid species of the genus *Anastrepha* Schiner (Aluja and Norrbom, 1999), the native host of both parasitoids studied. All localities recorded represent only presence points.

Two data subsets were elaborated for each species under study; the first includes only data recorded in the scientific literature (DS1). The second is the literature data plus the new records at the Monte eco-region in La Rioja province (DS2), Argentina, here termed as new records.

The Wallace R-based GUI application for ecological modeling was used (Kass *et al.*, 2018) to clean the distribution dataset to avoid duplication of point records. The module Spatial Thin implements the R package spThin, which removes localities that record less than a specified geographic distance from other localities (Aiello-Lammens *et al.*, 2015); the distance used was 2 km.

Images were used as bioclimatic data layers for model development, based on a quasi-mechanistically statistic down-scaling global circulation model output temperature and precipitation estimates of the ERA-Interim climatic reanalysis to a high resolution of 30 arcsec (~1 km) (Karger *et al.*, 2017, 2018). Bioclimatic variables represent annual trends (e.g., mean annual temperature, annual precipitation), seasonality (e.g., temperature and precipitation annual range), and extreme or limiting environmental factors (e.g., the temperature of the coldest and warmest month; precipitation of wet and dry quarters) (table 1).

The bioclimatic layers were cut to cover the maximum extension of the two species distribution knowing (−98.233, −34.683; −36.800, 29.383, SRC = EPSG: 4326 – WGS 84 – Geographic).

MaxEnt models

The open-source MaxEnt (3.4.1) (Phillips *et al.*, 2018) was used to predict the suitability of the geographical areas for *G. pelleranoi* and *D. areolatus* presence through the American continent, between latitude 29° north and 34° south.

Four models were conducted, two for *G. pelleranoi*, one with DS1 (DS1-Gp) and the other with DS2 (DS2-Gp), and in the same way, two for *D. areolatus*, one for each dataset (hereafter named DS1-Da and DS2-Da).

Comparisons were made within each species, not between them. All models were run using the same parameters to corroborate differences produced only by datasets.

The background used for MaxEnt corresponds to a maximum of 10.000 random points within the species distribution extent (−98.233, −34.683; −36.800, 29.383, SRC = EPSG: 4326 – WGS 84 – Geographic). The software was run with the following parameters: random-seed for the test; cross-validate as replicate type and ten replicates performed; ten percentile training presence as threshold rule; 1000 maximum iterations; and the beta multiplier setting in 0.5 to minimize any possible overfitting. The feature type was set in auto feature for all the model runs and both species, considering that all the datasets contain more than 80 records (Elith *et al.*, 2011). Furthermore, Morales *et al.* (2017)

Table 1. Chelsa bioclimatic variables are derived from min., max., and mean temperature, and mean precipitation values

Code	Bioclimatic variables	Units
BIO1	Annual mean temperature	°C
BIO2	Mean diurnal range (mean of monthly (max temp – min temp))	°C
BIO3	Isothermality (BIO2/BIO7) × 100	°C
BIO4	Temperature seasonality	SD × 100
BIO5	Max temperature of warmest month	°C
BIO6	Min temperature of coldest month	°C
BIO7	Temperature annual range (BIO5–BIO6)	°C
BIO8	Mean temperature of wettest quarter	°C
BIO9	Mean temperature of driest quarter	°C
BIO10	Mean temperature of warmest quarter	°C
BIO11	Mean temperature of coldest quarter	°C
BIO12	Annual precipitation	mm
BIO13	Precipitation of wettest month	mm
BIO14	Precipitation of driest month	mm
BIO15	Precipitation seasonality	CV
BIO16	Precipitation of wettest quarter	mm
BIO17	Precipitation of driest quarter	mm
BIO18	Precipitation of warmest quarter	mm
BIO19	Precipitation of coldest quarter	mm

They represent annual trends (e.g., mean annual temperature, annual precipitation), seasonality (e.g., annual range in temperature and precipitation), and extreme or limiting environmental factors (e.g., the temperature of the coldest and warmest month and precipitation of the wet and dry quarters). A quarter is three months period (1/4 of the year) (<https://climate.org/bioclim/>).

concluded that sample size does not affect the output results between models using default settings and by models with parameters defined by users.

The AUC values were used to measure model fitting, comparing models resulting from both studied datasets. The variable importance was generated by jackknife, and the logistic output format was selected. Those variables with more than 10% of contribution were considered significant.

Visualization, map development, and measuring of suitable areas' extensions were worked with Qgis 3.18.2 version GNU software (Qgis.org, 2021). The extensions of suitable areas are expressed in km². Binary maps were developed using the ten percentile training presence's logistic threshold, calculated as the average value of the ten replicates performed for cross-validation.

Results

The parasitoid *G. pelleranoi* was recorded in the four localities throughout the three seasons sampled. Eight specimens (five females and three males) were recovered from *A. fraterculus* pupae coming from fruits sampled at Los Molino's locality. Furthermore, 32, 26, 54, and 6 specimens were collected with manual aspirators from Los Molinos, Anjullón, San Pedro, and Santa Veracruz localities during the 2016/2017 and 2017/2018 fruiting seasons.

While in the case of *D. areolatus*, only two females were recorded from a fruit sampled in Los Molinos (only on season 2016/2017), no direct observation occurred. During the other two seasons, no parasitoids of this species were recorded.

The percentage of parasitism was 0.71 and 0.17% for *G. pelleranoi* and *D. areolatus*, respectively.

The search for data on distribution with geographical information of the two hymenopteran species resulted in 39 scientific papers scrutinized between the years 1981 and 2013, no results were found in the GBIF international online databases for records of *G. pelleranoi*, and only two unpublished data points were recorded for *D. areolatus* from 1984 (not included in the database used here). For *G. pelleranoi* and *D. areolatus* 98 and 123 geographical distribution points were recovered, respectively, from the scientific literature. After cleaning, datasets ended with the following record numbers: DS1-Gp = 98, DS2-Gp = 103 (fig. 1a), DS1-Da = 123, DS2-Da = 125 (fig. 1b).

Models from datasets of both species showed an excellent fitting. For *G. pelleranoi*, the models presented an AUC value of 0.916 ± 0.015 and 0.918 ± 0.023 (mean \pm standard error) for DS1-Gp and DS2-Gp respectively; and for *D. areolatus*, the values were 0.931 ± 0.025 and 0.930 ± 0.026 (mean \pm standard error) respectively for DS1-Da and DS2-Da.

Incorporating the five new record points from La Rioja, for *G. pelleranoi* (DS2), and two points for *D. areolatus* (DS2) produced different models than those resulting from the DS1. Suitable areas of distribution generated by MaxEnt showed differences using the different datasets (Supplementary files S1–8, georeferenced maps for GIS visualization). For *G. pelleranoi*, the suitable distribution area suffered a reduction in 4,714,936 km², 30.55% less using DS2-Gp. On the other hand, the suitable distribution area of *D. areolatus* was increased by 21.64%, corresponding to 1,140,028 km² more using DS2-Da (table 2). Figure 2 shows the substantial reduction in the suitable area for the distribution of *G. pelleranoi*, using DS1-Gp (fig. 2a) and DS2-Gp (fig. 2b). Differences between maps for *D. areolatus* were less evident, but it was possible to show an increasing suitable area along the Andean mountains (Bolivia, Peru, Ecuador, and Colombia) and Venezuela, when using DS1-Da (fig. 2d) and DS2-Da (fig. 2e). Figure 2c and f show the differences between maps generated for each dataset and parasitoid species, the differences represent the areas added or eliminated when the DS2 is used for modeling; from them it is possible to show that the incorporation of the new records to the datasets affects with more intensity the suitable areas for distribution of *D. areolatus* (fig. 2f) than for *A. pelleranoi* models (fig. 2c).

In the case of *G. pelleranoi* at a regional scale (Fig. 3a), the suitable area predicted by the model resulting from DS1-Gp did not include the new record points from La Rioja (fig. 3b); instead, the

model produced with DS2-Gp shows the new record points into the suitable area predicted (fig. 3c).

The maps generated for *D. areolatus* with DS1-Da show the new record points out of the suitable area, as in the case of *G. pelleranoi* (fig. 3d), but with DS2-Da, the suitable area includes one of the points, and the other excluded of this area (fig. 3e).

From the 19 variables used for modeling distribution, only four climatic variables attained more than 10% of the contribution to the models for both species; these were: temperature of the wettest quarter (Bio8), precipitation of the driest month (Bio14), precipitation of driest quarter (Bio17), and precipitation of coldest quarter (Bio19).

The different datasets (DS1 and DS2) modified the percentage of contribution of the bioclimatic variables. These modifications were observed both in the values and in the order of importance of the variables for *G. pelleranoi*. However, in the case of *D. areolatus*, differences were only observed on values.

Model for *G. pelleranoi* with DS1-Gp shows that bio14 (38.2%) and bio19 (18.8%) were the most critical variables. While using DS2-Gp, the variables with the largest contribution to the model were bio08 (11%) and bio17 (25%). Instead, both models for *D. areolatus* had bio17 and bio 19 as the bioclimatic variables of importance (more than 10%), but it was possible to appreciate differences in values. Model using DS1-Da attained 27.9 and 28.7% values for bio17 and bio19, respectively, while the model using DS2-Da shows values of 33.9 and 18.7% for the same variables (table 3).

Appendix 2 show graphical results of jackknife of test gain, AUC and regularized training gain, for both species and datasets, and for the 19 bioclimatic variables used.

Discussion

The fruit fly parasitoids *G. pelleranoi* and *D. areolatus* are widely distributed throughout the American continent, but most records are from tropical and subtropical rainforests. Thus, both species' southernmost natural distribution range in Argentina occurs in the Paranaense subtropical rainforest of central-eastern, latitude -32.26 (Ovruski *et al.*, 2008). In this study, both parasitoid species were found in the Monte eco-region at Argentina's central-west desert, outside their putative natural distributional range. This finding raises the possibility that these two species are already established in this environment (Monte eco-region) despite the extreme weather conditions. This statement is supported by the first record of these two parasitoid species in 1998 in the eco-region mentioned above (Ovruski, 2002) and the recent record reported in this study, with no previous evidence of these species in other semi-arid or arid regions of the American continent. Recently, Vanoye-Eligio *et al.* (2017) found well-established populations of the Mexican fruit fly in highland semi-arid regions of Mexico, where they report associated populations of the braconid parasitoid *Doryctobracon crawfordii* (Viereck). These findings suggest that some fruit fly parasitoid species can track their hosts after range expansion and adapt to extreme and, at times novel areas, this is the case of environments in artificially irrigated areas.

Almarinez *et al.* (2021) present a bioclimate-based maximum entropy model for the parasitoid *Comperiella calauanica* Barrion from the Philippines, with good results using the 19 bioclimatic variables. Using these same 19 variables, our MaxEnt models for the parasitoids *G. pelleranoi* and *D. areolatus* constitute the first approximation to the suitable distribution areas for these

Table 2. The predicted suitable area in square kilometers for both species *G. pelleranoi* and *D. areolatus*, using dataset without new records (DS1-Gp and DS1-Da) and including the new records (DS2-Gp and DS2-Da)

Species	Datasets	Predicted area (km ²)
<i>G. pelleranoi</i>	DS1-Gp	6,788,619
<i>G. pelleranoi</i>	DS2-Gp	2,073,683
<i>D. areolatus</i>	DS1-Da	5,265,887
<i>D. areolatus</i>	DS2-Da	6,405,915

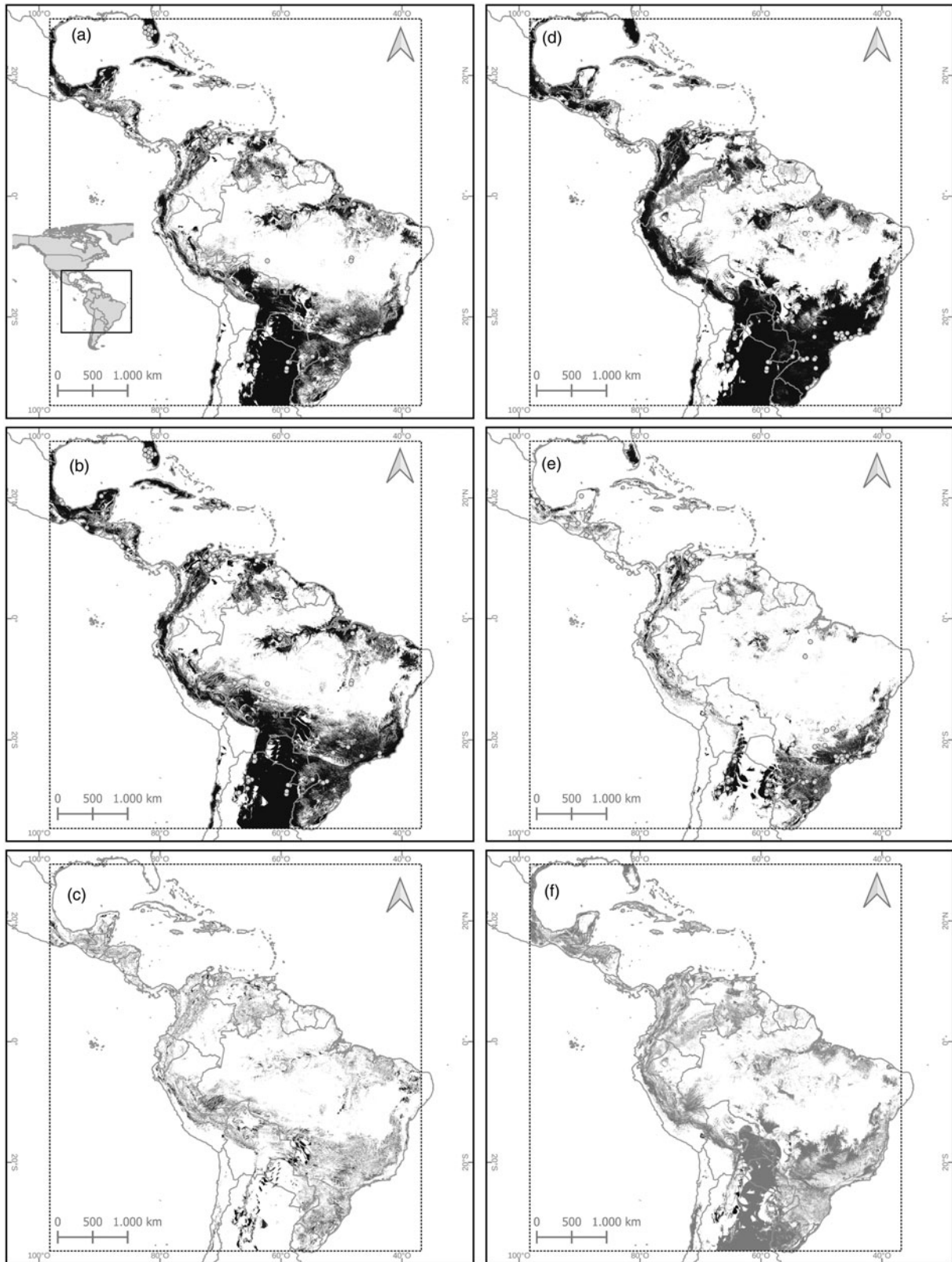


Figure 2. (a) Binary maps for suitable distribution areas using the DS1-Gp; and (b) using the DS2-Gp datasets for *G. pelleranoi*; (c) map showing the difference in areas between maps (a) and (b) added areas in black and subtracted areas in gray; (d) binary maps for suitable distribution areas using DS1-Da; and (e) using DS2-Da datasets for *D. areolatus*; (f) map showing the difference in areas between maps (d) and (e) added areas in black and subtracted areas in gray. Gray circles represent the record points and dashed line the background boundaries.

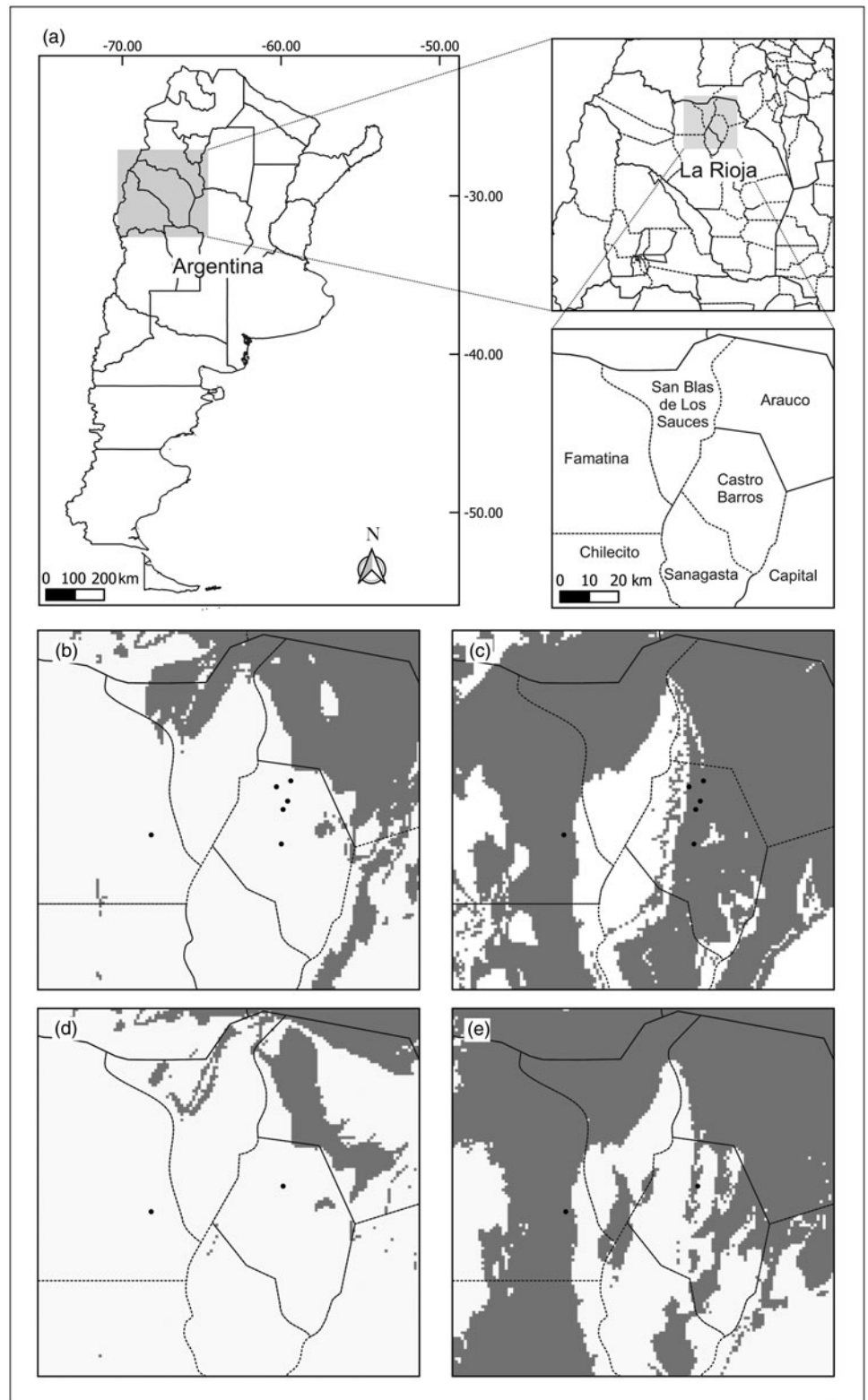


Figure 3. (a) Location of La Rioja province in Argentina and the specific sites where the new records were obtained; (b) suitable distribution areas using the DS1-Gp, and (c) using the DS2-Gp for *G. pelleranoi*; (d) suitable distribution areas using DS1-Da; and (e) using DS2-Da for *D. areolatus*. Black points correspond to the new distribution records for both species; suitable areas are shown in grey and unsuitable areas in white.

species. Results here suggest a distribution expansion at least for one of these species (*G. pelleranoi*).

Considering that parasitoid distributions were modeled using the same parameter to run MaxEnt, and the same set of bioclimatic layers, with the only difference in the datasets used (DS1 and DS2 for each parasitoid), it is possible to ensure

that, in this case, the addition of the new record points was sufficient to change the results. The critical changes recorded between models could result only if the few new records contribute essential information to the model without these points. If the information contained in the bioclimatic variables for these new points added in DS2 falls within the average values expected by

Table 3. Percentage of contribution (% of cont.) and permutation importance (Perm. Import.) of the 19 environmental variables used for modeling distribution for both datasets (DS1 and DS2) of *G. pelleranoi* and *D. areolatus* distribution records

Variable	<i>G. pelleranoi</i> DS1-Gp		<i>G. pelleranoi</i> DS2-Gp		<i>D. areolatus</i> DS1-Da		<i>D. areolatus</i> DS2-Da	
	% of cont.	Perm. Import.	% of cont.	Perm. Import.	% of cont.	Perm. Import.	% of cont.	Perm. Import.
bio 01	4.4	2.1	4.4	5.4	2.2	2.3	1.6	2.2
bio 02	1.1	1.5	1.9	2.3	1.4	8.1	1.6	8.3
bio 03	2.1	2.4	3.5	4.3	7.8	6.3	7.3	4.7
bio 04	0	0.2	1.1	1.3	0.3	0.7	1.2	1.6
bio 05	0.2	1.7	3.3	6	0.6	0.9	0.7	1
bio 06	1.7	15.1	1.8	2.6	2.2	14	2.2	17.3
bio 07	7.9	18.5	6.4	22.3	4.2	2.7	6.7	5.4
bio 08	9.8	1.8	11	6	2.6	1.3	3	3.2
bio 09	0.4	0	1.3	1.5	3.7	0.6	4.9	3
bio 10	3	3.6	5.1	2.2	1.1	0.8	1.9	0.8
bio 11	1.8	3.6	8.2	3.4	1.3	1.7	1.4	1.7
bio 12	1.7	3.4	1.5	2.2	1.2	2.3	1.4	4.3
bio 13	1.9	1	2.7	3.3	6.2	3.9	5	4.4
bio 14	38.2	12	8.7	2.9	0.9	2.2	2.2	3.6
bio 15	1.1	7	2.1	8.9	6.2	16.5	4.8	15.4
bio 16	5	4.7	9.2	6.6	0.6	1.3	0.8	0.9
bio 17	0.6	6.4	25	13.9	27.9	18.8	33.9	13.4
bio 18	0.2	1.5	1.4	2.2	1	2.6	0.7	0.3
bio 19	18.8	13.5	2	2.7	28.7	12.9	18.7	8.5

The numbers in bold show the percentage of contribution higher than 10%.

a model with DS1, the results would not show significant differences.

Model differences due to incorporating the new records into the datasets showed that the oases from La Rioja province are suitable for *G. pelleranoi* distribution, indicating that the information provided for the environmental variables at these new record points was enough to produce deviance in the results. This last fact supports the idea that the maps incorporating the new records represented a better potential distribution area for *G. pelleranoi*. Its presence could be due to natural distribution or an accidental historical introduction with a posterior establishment at these oases.

In the case of *D. areolatus*, the conclusion is more complex. The oases from La Rioja do not seem to be a potential distribution area for neither of the two datasets used (DS1-Da and DS2-Da). Moreover, the low number of records and adult captures only occurred during one of the three sampled years, according to the results obtained here for the species.

Such finding highlights that potential distribution models based exclusively on climatic variables (mainly temperature and precipitation) could underestimate the prediction of suitable areas of distribution. One of the reasons is the challenge of incorporating artificially irrigated areas and humid microclimatic conditions within arid regions in models. Concerning this, Vanoye-Eligio *et al.* (2017) found no correlation between climatic variables and fly population peaks, which were more related to particular host plants existence in suitable microclimates. A

situation like this could be necessary for the distribution range of entomophagous insects. This emphasizes on the need to searching the entomophagous insects even out of the putative distribution; especially at the limit points of its known distribution.

The Monte eco-region is characterized by sizeable thermal amplitude, scarce precipitation, and low relative humidity (Morello *et al.*, 2012). These conditions would not be favorable for the occurrence of *G. pelleranoi*, yet this species can enter diapause to overcome stressful environmental periods (Ovruski *et al.*, 2015). Facultative diapause allows a given genotype of the insect population to attain a better emergence distribution over time, thereby enabling progeny to reproduce under more suitable environmental conditions or during periods of greater host abundance (Menu *et al.*, 2000). Therefore, diapause might be an essential biological mechanism determining *G. pelleranoi* persistence in the Monte eco-region.

However, this physiological mechanism may be one of the various strategies that insects display to overcome harsh conditions. For example, Vanoye-Eligio *et al.* (2017) report that the fruit fly *A. ludens* pupates under moist leaf litter generated in gullies and creeks by its host plant *Casimiroa pubescens*; this behavior can also contribute to survival. Finally, parasitoid populations in the Monte could have become adapted to arid climates. For example, desiccation resistance is more significant in the desert inhabiting species *Drosophila mojavensis* and *D. nigrospiracula* than the cosmopolitan *D. melanogaster* and *D. pseudobscura* (Matzkin *et al.*, 2007). There is a considerable variation in

desiccation resistance, and the trait can be rapidly selected within a population (Hoffmann and Harshman, 1999). This resistance is known for the tephritid fly *Anastrepha ludens* (Tejeda *et al.*, 2016) and could be similar for parasitoids associated with this and other species in the same genus.

This new approximation to the extreme distribution of *G. pel-leranoi* leaves a gateway to ecological studies in order to corroborate the factors involved that allow this parasitoid to establish itself in arid climate areas. Comparing physiological and behavioral traits between dryland and subtropical populations of parasitoids could foster understanding of desiccation resistance and perhaps facilitate rearing of parasitoids tailored to perform in particular environments (Hill and Terblanche, 2014), in concordance with the recent interest in the potential of native Neotropical parasitoids to control fruit crop pests (Sivinski *et al.*, 1997; Ovruski *et al.*, 2000; Aluja *et al.*, 2009).

This result also highlights the importance of maintaining good record points of this species and insects in general. In some cases, records only represent country distribution levels, but local georeferenced points are essential for modeling more accurate species distribution maps. The online databases have scarce records despite the well-recorded distribution in the scientific bibliography and the large quantity of biological material conserved in scientific collections, this agrees with the problems stated by Rangarajan *et al.* (2011) that propose integrating journals and biological databases.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0007485322000013>.

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