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Potential distribution of *Drosophila suzukii* (Diptera: Drosophilidae) in relation to alternate hosts in Mexico

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Abstract

The spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), is one of the most important pests of berry crop production in Mexico. The purpose of this research was to model the potential distribution of *D. suzukii* in the Mexico relative to 4 non-crop hosts using Maximum Entropy Ecological Niche Modeling. Spotted wing drosophila records were collected from a survey conducted in commercial blackberry plots and non-cultivated areas between 2013–2015. The data for the presence of non-crop hosts in the country and the bioclimatic variables used in the modeling were obtained from the Global Biodiversity Information Facility and WorldClim websites, respectively. For climatic variable selection, a principal component analysis on climatic variables was conducted prior to the MaxEnt modeling. The results demonstrate that the potential distribution of spotted wing drosophila was primarily in central Mexico. However, other suitable locations in the southeastern portion of the country were identified, which were not previously known. Likewise, the joint modeling depicted areas of coincidence between the spotted wing drosophila distribution and 4 alternating non-crop hosts commonly distributed in the berry-producing region, which includes the states of Michoacán, Jalisco, Guanajuato, and Mexico. This joint modeling of the potential distribution of spotted wing drosophila and non-crop hosts partly explains how the populations of the pest sustain themselves during seasons of low or no commercial berry production in Mexico.

Key Words: spatial distribution; MaxEnt; invasive pests

Resumen

Drosophila suzukii (Matsumura) (Diptera: Drosophilidae) es una de las plagas más importantes en cultivos de berries en México. El objetivo de esta investigación fue modelar la distribución potencial de *D. suzukii* en México en presencia de cuatro hospederos no cultivados utilizando el modelado de Nicho Ecológico mediante el método de Máxima entropía incluido en MaxEnt. Los registros de *Drosophila suzukii* fueron recolectados de una muestreo realizado en parcelas comerciales de zarzamora y áreas no cultivadas durante 2013–2015. Los datos de la presencia de los hospederos no cultivados en el país y las variables bioclimáticas utilizadas en el modelado se obtuvieron de los sitios web del Global Biodiversity Information Facility y WorldClim, respectivamente. Para la selección de variables, previo al modelo de MaxEnt se realizó un análisis de componentes principales sobre variables climáticas. Los resultados mostraron que la distribución potencial de *D. suzukii* estuvo en el centro de México y áreas específicas del sureste del país, no reportados previamente. Del mismo modo, el modelado conjunto mostró las áreas de coincidencia entre la distribución de *D. suzukii* y cuatro hospederos alternos no cultivados comúnmente distribuidos en la región productora de berries, incluyendo los estados de Michoacán, Jalisco, Guanajuato y México. Esta modelación de la distribución potencial de *D. suzukii* hospederos potenciales no cultivados explica en parte cómo las poblaciones de la plaga se mantienen en temporadas de baja o no producción comercial de berries en México.

Palabras Clave: distribución espacial; MaxEnt; plaga invasora

Drosophila suzukii (Matsumura) (Diptera: Drosophilidae), commonly known as the spotted wing drosophila, is one of the most important invasive pests in the world because of its wide range of hosts, mostly soft-skinned fruit crops (Asplen et al. 2015). The ability of *D. suzukii* to adapt to different environmental conditions and hosts has enabled it to invade tropical and subtropical areas in both hemispheres as has been recently reported (dos Santos et al. 2017).

The presence of *D. suzukii* in Mexico was first reported in 2011 (NAPPO 2011), and it is currently considered a quarantine pest because of its potential to cause a severe economic loss in host crops, which have great economic importance. These crops include blackberries, raspberries, strawberries, and blueberries. Therefore, this pest is under surveillance by the Mexican government (SENASICA 2015).

Several cultivated and non-cultivated hosts of *D. suzukii* have been previously reported (Berry 2012; Lee et al. 2015; Poyet et al. 2014; Poyet et al. 2015; CABI 2016; Kenis et al. 2016). Recent studies under laboratory conditions in Mexico (unpublished) indicate that black cherry (*Prunus serotina* subsp. *capuli* (Cav.) McVaugh [Rosaceae]), yellow mombin (*Spondias mombin* L. [Anacardiaceae]), wild blackberry (*Rubus adenotrichos* Schltd [Rosaceae]), and cultivated and non-cultivated guava (*Psidium guajava* L. [Myrtaceae]) represent alternate hosts for *D. suzukii*. These studies have shown that in hosts such as guava and yellow mombin the insect can complete its life cycle in 15 d in both hosts in laboratory conditions (23 ± 2) (Rebollar-Alviter, unpublished data) which indicates that they favor the sustainability of the populations during the seasons where commercial berry crops are not in production (Rebollar-Alviter et al.

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2015). These non-crop species are widely distributed in the tropical and subtropical regions of Mexico (Rzedowski & Calderón de Rzedowski 1999; Rzedowski & Calderón de Rzedowski 2005; Jaiswal & Jaiswal 2005; Cruz & Gutiérrez 2010). Additionally, the species inhabit the same geographical space and are frequently associated with the commercial production areas of berry crops.

Obtaining knowledge of the potential distribution of an invasive species is useful for planning and decision-making for public plant health policies. In this regard, different algorithms for modeling ecological niches have been published that use presence and absence data or only presence in conjunction with environmental variables in a particular zone (Phillips et al. 2006; Franklin 2009; Peterson et al. 2011). Maximum Entropy Ecological niche modeling with the MaxEnt algorithm is one of the most popular methodologies for modeling species distribution (Phillips et al. 2006; Booth et al. 2014).

The MaxEnt algorithm estimates a target probability distribution by searching for the distribution of the probability of maximum entropy (close to uniform distribution) subject to a set of constraints that represents incomplete information regarding the target distribution (Phillips et al. 2006). The available information regarding this distribution is the set of environmental variables known as characteristics. Additionally, expected constraints of each characteristic must correspond to their mean values of the sample (the sample mean for a set of sampling points has been extracted from the destination distribution) (Phillips et al. 2006; Cruz-Cárdenas et al. 2014a).

The ecological niche modeling with the MaxEnt algorithm has been used to estimate the potential distribution of different invasive species (Václavík & Meentemeyer 2009; Elith 2014; Hill & Thomson 2015; Jarnevich & Young 2015). Additionally, the potential distribution of insect species of economic importance, such as *Lobesia botrana* Den. and Schiff. (Lepidoptera: Tortricidae), beneficial and harmful insects for grapes (Fiaboe et al. 2012), and *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Rhynchophoridae) in palm trees (Lv et al. 2011; Hoffmann & Thomson 2013), has previously been reported. In addition, *Phenacoccus solenopsis* (Tinsley) (Hemiptera: Pseudococcidae) in cotton (Fand et al. 2014) and *Diaphorina citri* Kuwayama (Hemiptera: Liviidae) in citrus (López-Collado et al. 2013) have been studied. Recently, Biber-Freudenberger et al. (2016) estimated the potential distribution of *Bactrocera invadens* Drew, Tsuruta & White (Diptera: Tephritidae), *Ceratitis cosyra* (Diptera: Tephritidae), and *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in Africa. A common objective for these studies was the ability to generate scenarios for the purpose of planning and designing more efficient strategies for the management of these pests at different spatial scales.

In addition to modeling the distribution of invasive species, it is important also to consider their relationship with their potential hosts. Barredo et al. (2015) determined the potential distribution of *Hylobius abietis* L. (Coleoptera: Curculionidae) and *Cameraria ohridella* Deschka & Dimić (Lepidoptera: Gracilariidae) in 5 species of trees. They considered the vulnerable areas as those that could be occupied by both the insect pests and the host. The shared areas were divided into 4 categories: (a) habitat not suitable for the insect, (b) suitable habitat for the insect and no host presence, (c) adequate habitat for the insect and presence of the host, and (d) habitat not suitable for the insect but with host presence. This categorization allowed the precise identification of changes in the habitat suitable for insects for each host studied.

Damus (2009) estimated the potential distribution of *D. suzukii* in North America with MaxEnt modeling by using the invaded area and the native area in southeastern Asia. In this context, the European and Mediterranean Plant Protection Organization (EPPO 2010) estimated the potential distribution of *D. suzukii* at a global scale with an emphasis on Europe based on the parameters published by Damus (2009).

More recently dos Santos et al (2017) also modeled the global distribution of *D. suzukii* using MaxEnt and GARP (Genetic Algorithm for Rule-set). However, modeling the potential distribution of *D. suzukii* with the presence of alternate hosts has not been published.

Mexico has an annual production of 596,592 tons of berries (blackberry, raspberry, blueberry, and strawberry) in an area of 29,721 ha (SIAP 2016). This production results in an income greater than 805 million dollars with an annual growth rate of approximately 29.8%. Given the accelerated growth and the opening of new berry production areas in Mexico, it is useful to model the potential distribution of *D. suzukii* in the presence of non-host crops. The purpose of this research was to determine the potential distribution of *D. suzukii* in Mexico, given scenarios that include the presence of wild blackberry, yellow mombin, black cherry, and guava using Ecological Niche Modeling with the MaxEnt algorithm.

Materials and Methods

RECORDS FOR THE PRESENCE OF SPOTTED WING DROSOPHILA IN CULTIVATED AND NON-CROP HOSTS

Records of *D. suzukii* were obtained from a trap route defined mainly by commercial blackberry production areas and neighboring sites with presence of non-crop hosts, such as wild grape, wild blackberries, nance (*Byrsonima crassifolia* (L.) Kunth [Malpighiaceae]), yellow mombin, and guava. The data were collected from 3 sampling routes (Los Reyes, Ziracuaretiro, and Tacámbaro) in the state of Michoacán between 2013 and 2015. A total of 150 traps was placed along these routes in the main blackberry-producing zone. Each trap consisted of a 1 L clear plastic cup with 0.5 cm diam side holes (Lee et al. 2012) containing 200 mL of apple cider vinegar (Clemente Jacques®) and a few drops of dishwashing soap as an attractant and drowning solution, which was changed every 14 d. To extend the sampling points of *D. suzukii* beyond the target zone in state of Michoacán, additional data were provided by the Plant Health Committees for the states of Michoacán, Jalisco, Colima, and Guanajuato. These data are the result of *D. suzukii* sampling conducted during an official program on “Phytosanitary Management of Spotted Wing Drosophila” in 2015 and 2016 (Table 1).

Table 1. Number of records documenting the presence of *Drosophila suzukii* and non-crop hosts used in MaxEnt modeling potential distribution.

Species	Source of data	Total of records
<i>Drosophila suzukii</i>	UACH-CRUCO ¹	150
	CESAVEMICH ²	1,306
	CESAVEJAL ³	107
	CESAVECOL ⁴	81
	CESAVEG ⁵	34
<i>Rubus adenotrichos</i>	UACH-CRUCO	30
	GBIF	71
<i>Spondias mombin</i>	UACH-CRUCO	14
	GBIF	309
<i>P. serotina</i> var. <i>capuli</i>	GBIF	159
<i>Psidium guajava</i>	UACH-CRUCO	10
	GBIF	437

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³Jalisco State Plant Health Committee
⁴Colima State Plant Health Committee
⁵Guanajuato State Plant Health Committee.

The data for the presence of wild blackberry, yellow mombin, black cherry, and guava were obtained from the Global Biodiversity Information Facility (www.gbif.org). Additionally, data from field sampling during 2013 to 2015 in the areas surrounding commercial blackberry production were included in the analyses.

SELECTION OF ENVIRONMENTAL VARIABLES

Worldclim's bioclimatic variables (<http://www.worldclim.org>) were used in the analysis (Hijmans et al. 2005). WorldClim consists of a set of data layers generated from the interpolations of monthly average weather data from meteorological stations around the world with a 30-s arc of grid resolution (often referred to as 1 km²). The variables included total monthly and average monthly precipitation, and minimum and maximum temperatures, to generate 19 bioclimatic variables (O'Donnell & Ignizio 2012).

A principal component analysis was performed with the 19 WorldClim variables for points that contained records of the presence of *D. suzukii* in order to reduce variable redundancy and the existence of multicollinearity (Graham 2003; Cruz-Cárdenas et al. 2014b). A data matrix of 19 columns (values of the environmental variables) and N rows was created, which corresponds to the observations or locations with the presence of *D. suzukii* and the non-crop hosts under study. The proportion of variance explained by each component in the principal component analysis, eigenvalues, and eigenvectors were obtained with Minitab (Ver. 17 Minitab Inc. State College, Pennsylvania, USA). The number of components was determined by using the Cliff criterion, retaining components with eigenvalues accounting for 70% or more of the total variance (Cliff 1987). The correlation between the original variables and the selected components was estimated according to Pla (1986). The discrimination of the climatic variables was completed by quantifying the proportion of the variance explained by each original variable on the components selected by the sum of squares of the correlation between original variables and the selected components. The variables that contributed less than 80% to the variance were excluded from the modeling. Given the large number of *D. suzukii* records in some of the sampled areas, a grid of 6 × 6 km was generated, which considered only 1 record within each grid. For the non-crop hosts under study, the spatial distribution of the records was wider, and no modifications were made.

MODELING THE POTENTIAL DISTRIBUTION OF *DROSOPHILA SUZUKII* AND NON-CROP HOSTS

Modeling of the potential distribution of *D. suzukii* and non-crop hosts (*R. adenotrichos*, *S. mombin*, *P. serotina* var. *capuli* and *P. guajava*) was performed with the MaxEnt algorithm (Phillips et al. 2006). Previously, the environmental variables were selected as indicated above, and the records for presence of non-crop hosts were obtained.

The settings used for the MaxEnt modeling for *D. suzukii* and non-crop hosts were set to default (Phillips & Dudík 2008; Cruz-Cárdenas et al. 2014a; Jarnevich & Young 2015). The cumulative output format was used as a prediction for conditions suitable for the species above a threshold (Phillips 2009). This output was obtained in the ASCII format, which was later input in ArcGIS ver. 10.3 (Esri Inc. Redlands, California, USA) for editing and processing the resulting maps that display the potential distribution of each species. The criterion used as a threshold from which *D. suzukii* was considered present was the *maximum test sensitivity plus specificity* (Liu et al. 2005) which was also applied by Barredo et al. (2015). For the non-crop host species, the *ten percentile training* presence was used, i.e., ten percent of the records fell outside of the potential area and were those with an atypical environment, not

included in the niche (Scheldeman & van Zonneveld 2011) and which 90% of the points of presence were within the potential range. In order to evaluate the performance of the 5 models that were generated in the MaxEnt algorithm, we used the receiver operating characteristic analysis. The receiver operating characteristic curve evaluates the configuration of a model regarding omission and commission errors through a single number independent of any threshold choice (Phillips et al. 2006). The shared common area between the pest and the non-crop hosts under study was estimated according to the presence or absence categorization proposed by Barredo et al. (2015).

Results

SELECTED CLIMATIC VARIABLES AND *DROSOPHILA SUZUKII* RECORDS

Table 2 displays the environmental variables identified by principal component analysis for each species that was analyzed. According to the contribution to the variance in the selected components, the average temperature in the coldest quarter (bio11) was the variable with the highest contribution to the presence of *D. suzukii*. For wild blackberry, yellow mombin, and guava, mean annual temperature (bio1) was the variable with the highest contribution to the variance, and for black cherry the average temperature in the hottest quarter (bio10) was the variable that contributed the most to the variance presence data.

The reduction in the number of records of presence using a 6 × 6 km grid enabled us to obtain a model for the potential distribution of *D. suzukii*. This approach permitted a better model fit than with the original data given its spatial aggregation for the main berry-producing states of central and western Mexico (Michoacán, Jalisco, and Colima). Of the 1,680 records initially obtained, 135 were used in the final MaxEnt modeling.

Based on the receiving operator characteristic curve, the performance of the models was better than the random distribution. In all cases, the area values under the curve were higher than 0.9. These results indicate that the area predicted by the resulting models for the species have a higher sensitivity and a lower specificity, which classifies them as excellent (Swets 1988).

POTENTIAL DISTRIBUTION OF *DROSOPHILA SUZUKII* AND NON-CROP HOSTS

Figure 1 depicts the potential distribution of *D. suzukii* in Mexico. The state of Jalisco had the highest probability of favorable environmental conditions for the pest (Table 3) followed by the states of Michoacán and Oaxaca. For wild blackberry, the potential distribution indicated that this host is distributed mainly in the mountainous zone of Mexico, in the Sierra Madre Occidental, the Transverse Volcanic Belt, part of the Gulf Coastal Plain, and in a portion of the Sierra Madre del Sur. In this latter region, the state of Oaxaca contained the greatest area, followed by the states of Michoacán and Jalisco. Yellow mombin was associated more with tropical environments in Mexico, such as the Yucatán Peninsula and the Gulf coast of Mexico, and it was associated less with areas in the Pacific coast. Black cherry was distributed in the mountainous areas, similar to wild blackberry, and it extended more northward, but covered a considerable area in the central portion of the country. Finally, guava was distributed mainly in the tropical areas of the Gulf and the Pacific coasts, but it also occupied areas of temperate zones, although to a lesser extent (Fig. 2).

Table 2. Selected environmental variables by principal component analysis. Values correspond to variance contribution of each variable to the selected component.

Variable	<i>Drosophila suzukii</i>	<i>Rubus adenotrichos</i>	<i>Spondias mombin</i>	<i>Prunus serotina</i> subsp. <i>capuli</i>	<i>Psidium guajava</i>
Annual Mean Temperature (Bio1, °C)	0.96	0.99	0.98	0.95	0.99
Isothermality (Bio3)	0.85				
Temperature Seasonality (Bio4)	0.84				
Max Temperature of Warmest Month (Bio5)	0.88	0.89		0.89	0.86
Min Temperature of Coldest Month (Bio6, °C)	0.97	0.95	0.95	0.83	0.89
Mean Temperature of Wettest Quarter (Bio8, °C)	0.83	0.96	0.89	0.98	0.93
Mean Temperature of Driest Quarter (Bio9, °C)	0.94	0.96	0.89	0.91	0.88
Mean Temperature of Warmest Quarter (Bio10, °C)	0.96	0.97	0.91	0.98	0.94
Mean Temperature of Coldest Quarter (Bio11, °C)	0.98	0.99	0.94	0.84	0.86
Annual Precipitation (Bio12, mm)	0.85	0.81	0.86	0.89	0.90
Precipitation of Wettest Month (Bio13, mm)	0.82				
Precipitation of Driest Month (Bio14, mm)			0.82	0.81	0.80
Precipitation of Wettest Quarter (Bio16, mm)	0.85			0.80	
Precipitation of Driest Quarter (Bio17, mm)			0.87	0.89	0.82
Precipitation of Coldest Quarter (Bio19, mm)			0.86		
Number of significant variables	12	8	10	11	10

^aEnvironmental variables coded as Bio1 to Bio19 as indicated in <http://www.worldclim.org/bioclim>



Fig. 1. Potential distribution *Drosophila suzukii* in México based on MaxEnt modeling.

Table 3. Potential distribution of *Drosophila suzukii* and non-crop host species per state of Mexico (km²) estimated with MaxEnt modeling.

State	Total state area	<i>Drosophila suzukii</i>	<i>Rubus adenotrichos</i>	<i>Spondias mombin</i>	<i>Prunus serotina</i> subsp. <i>capuli</i>	<i>Psidium guajava</i>
Aguascalientes	5,559	2,115			4,794	167
Baja California	73,515	1,886			35	
Baja California Sur	73,971				2,429	
Campeche	57,277			54,293		55,138
Ciudad de México	1,486	1,446	917		1,484	434
Chiapas	73,612	11,829	15,265	51,339	6,176	50,024
Chihuahua	246,973		2,816		13,701	3,753
Coahuila	150,671				580	
Colima	5,753	4,178	322	1,184	776	5,575
Durango	122,131	1,340	13,016	25	53,483	10,399
Guanajuato	30,340	19,318	4,067	142	25,161	13,691
Guerrero	63,565	36,062	11,621	28,223	6,017	41,412
Hidalgo	20,655	9,822	3,614	3,497	14,304	9,206
Jalisco	77,966	63,492	20,017	11,416	47,537	56,155
México	22,227	21,218	14,472	2,084	18,349	8,748
Michoacán	58,296	54,433	25,064	12,955	26,848	44,242
Morelos	4,859	4,780	1,036	1,426	1,134	4,586
Nayarit	27,817	12,879	2,857	6,367	10,397	22,976
Nuevo León	63,559				6,119	4,463
Oaxaca	93,960	44,079	32,458	41,258	37,551	73,691
Puebla	34,152	17,548	8,289	5,109	18,858	20,515
Querétaro	11,589	5,240	1,665	1,108	8,110	4,829
Quintana Roo	44,556			40,922		41,552
San Luis Potosí	60,500	330	75	10,498	4,460	17,830
Sinaloa	56,804		1,045	639	1,783	27,092
Sonora	180,841	18			758	2,704
Tabasco	24,695			22,968		15,190
Tamaulipas	79,426			6,819	4,462	35,431
Tlaxcala	3,974	1,996	1,423		3,948	689
Veracruz	71,461	2,009	4,063	57,078	5,172	48,120
Yucatán	39,426			34,910		35,031
Zacatecas	74,480	7,784	221		29,199	2,702
Total (National)	1,956,095	323,800	164,322	394,261	353,620	656,346

DISTRIBUTION OF *DROSOPHILA SUZUKII* IN THE PRESENCE OF NON-CROP HOSTS

The presence probability thresholds selected for each species allowed calculation of estimates of the potential distribution of *D. suzukii* in relation to non-crop hosts (Table 4). The area shared by *D. suzukii* and non-crop host species, based on the categorization by Barredo et al. (2015) is presented in Figure 2. Of the total area predicted for potential distribution of *D. suzukii*, 72% coincided with the presence of *P. guajava*, 59% with *P. serotina* var. *capuli*, 35% with *R. adenotrichos*, and 17% with *S. mombin*. The results also indicated that of the area predicted for *R. adenotrichos*, 69% was shared with the area predicted for *D. suzukii*. Likewise, the corresponding values for *P. serotina* subsp. *capuli*, *P. guajava*, and *S. mombin* were 54, 36, and 14%, respectively.

Discussion

Drosophila suzukii has been reported to attack a large number of cultivated and non-cultivated hosts (Berry 2012; Lee et al. 2015; Poyet et al. 2014; CABI 2016). This study demonstrates that the suitable habitat for *D. suzukii* distribution in Mexico is concentrated mainly in the central and western region of the country, including certain areas of the states of Oaxaca, Chiapas, and Baja California (Ensenada Municipality).

Previously, preliminary modeling demonstrated a similar distribution of *D. suzukii* in the northwestern and central portions of Mexico (SENASICA 2013; LaNGIF 2014), but the parameters and data sources for the modeling were not reported.

The principal component analysis allowed a priori reduction for the number of environmental variables to be used in the MaxEnt modeling for the potential distribution of the species studied, which facilitated the reduction of overfitting the models (Cruz-Cárdenas et al. 2014a). In this regard, the temperature of the coldest month was the variable that explained the most variance for the *D. suzukii* distribution data. Wiman et al. (2014) and Tochen et al. (2015) indicated that temperature and relative humidity were the most influential factors that affected physiology, survival, fecundity, reproduction, behavior, and the population dynamics of *D. suzukii*. Adult mortality rate was reported to increase when temperatures were below 10 °C (Dalton et al. 2011).

The determination of the potential distribution of *D. suzukii* in Mexico are consistent with the known distribution of the pest, especially in the central and western regions. Additionally, the results indicate additional favorable conditions for the development of this invasive species in areas in the southeastern portion of Mexico, such as certain zones in the states of Chiapas and Oaxaca in which the production of berries is nonexistent or incipient. The MaxEnt modeling for 4 non-crop hosts showed the areas potentially suitable for the development of *D.*

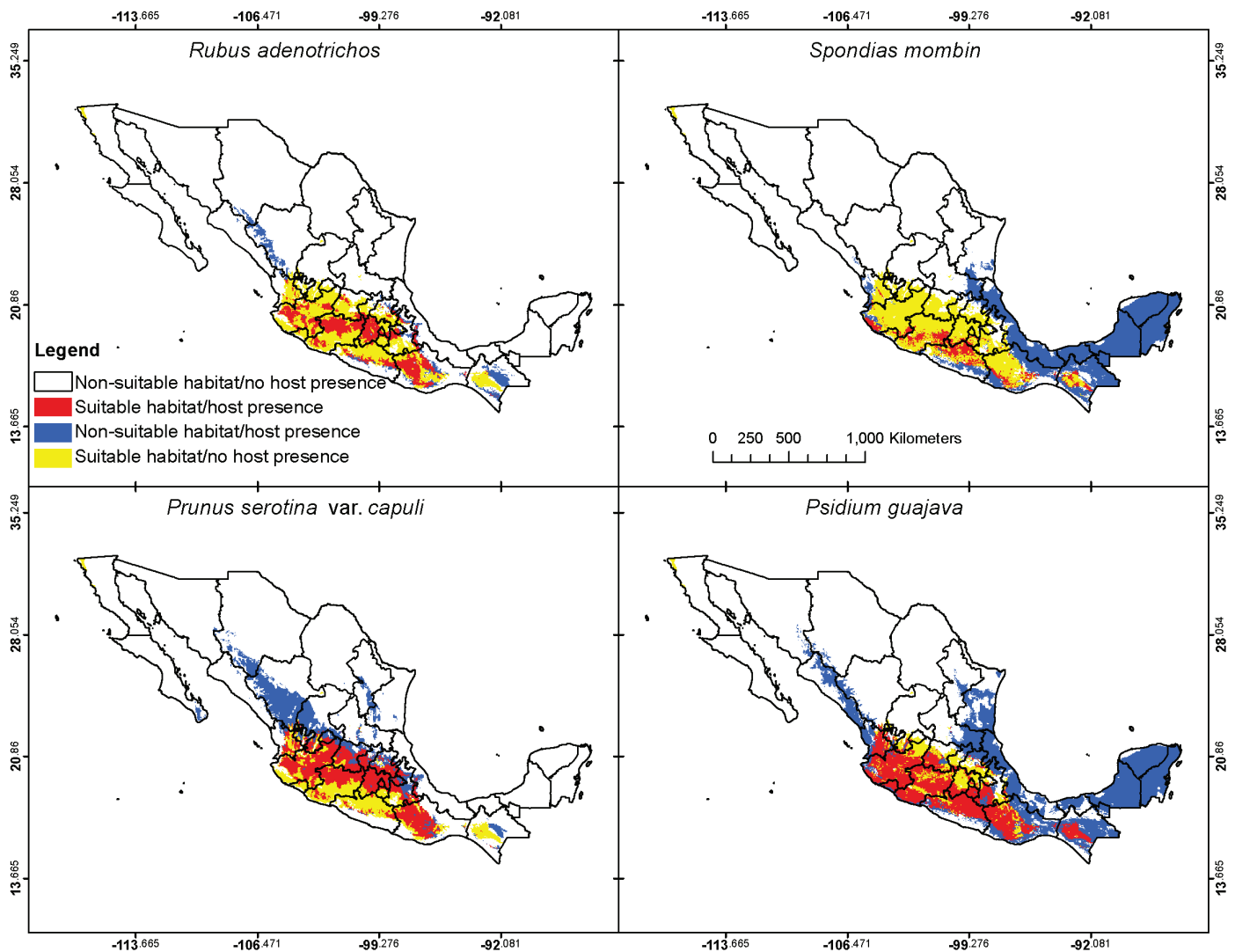


Fig. 2. Potential distribution of *Drosophila suzukii* in relation to four noncrop hosts; in white, non-suitable habitat and non-crop host presence; in blue suitable habitat for the non-crop host but non-suitable habitat *D. suzukii*; in yellow suitable habitat *D. suzukii* but not for the non-crop host and in red color suitable habitat for *D. suzukii* and for the non-crop host.

suzukii. The potential distribution of wild blackberry is consistent with that described by Rzedowski and Calderón de Rzedowski (2005), which reported that the presence of this host was mainly in the temperate zones of the Pacific coast. Yellow mombin distribution was similar to that previously reported (Avitia et al. 2003; Cruz & Rodríguez 2010; Arce-Romero et al. 2017), and its distribution is mainly in the coastal zones of the Yucatan peninsula and the state of Veracruz, although it has been found to a lesser extent on the Pacific coast of Mexico. Additionally, potential distribution of black cherry was similar to that previously reported (Fresnedo-Ramírez et al. 2011). Our results on the potential distribution of guava were generally similar to that previously described by Jaiswal and Jaiswal (2005), but the distribution was different in locations with temperate conditions. This difference could be because during the construction of the model we included records of the host presence above 2,000 m above sea level, generally considered as temperate climate compared to places with similar latitude but with low elevations.

Taken together, these results indicate that wild blackberry, yellow mombin, black cherry, and guava have a wide distribution in Mexico. Interestingly, the areas with a greater probability of distribution of these hosts coincided with the highest probability of *D. suzukii* dis-

tribution in the central and western zones of Mexico. This is also the region with the highest production of berry crops in the country. This coincidence of the presence of alternate hosts in the areas most favorable for *D. suzukii* development could partly explain the maintenance of the population of this pest during the seasons when commercial production is limited or non-existent (Jul to mid-Sep). During these summer months, yellow mombin, black cherry, wild blackberry, and guava are in full production, and they provide food, shelter, and suitable hosts for reproduction of *D. suzukii* in the absence of commercial berry production.

In summary, our results indicate that *D. suzukii* has a wide potential distribution in Mexico, confirming reports from the field, and our results add new potential zones of occurrence not previously reported. Likewise, our results depict the area with the greatest potential distribution in relation to 4 non-crop hosts, which partly explains the capacity for the survival and sustainability of the *D. suzukii* populations during the periods free from commercial production of berries (during the summer). These results will be useful for decision-making regarding the expansion of sampling and pest monitoring areas in the current and potential new areas for berry production in Mexico.

Table 4. Potential distribution of *Drosophila suzukii* in relation to 4 non-crop host species per state (Km²) based on MaxEnt modeling.

State	<i>Rubus adenotrichos</i>	<i>Spondias mombin</i>	<i>Prunus serotina</i> subsp. <i>capuli</i>	<i>Psidium guajava</i>
Aguascalientes			1,845	167
Ciudad de México	879a [*]		1,449	433
Chiapas	573	5,125	378	12,067
Colima	322	867	674	4,168
Durango	4		415	708
Guanajuato	4,064		17,231	11,050
Guerrero	8,392	16,834	5,512	32,693
Hidalgo	2,099		9,085	2,241
Jalisco	19,897	7,203	43,505	50,288
México	14,189	2,071	17,710	8,747
Michoacán	25,064	12,331	27,412	41,768
Morelos	1,031	1,419	1,128	4,526
Nayarit	1,930	763	7,277	11,249
Oaxaca	25,237	8,673	33,238	36,966
Puebla	4,991	802	10,761	11,153
Querétaro	1,037		5,246	1,132
San Luis Potosí			111	115
Tlaxcala	1,015		2,001	615
Veracruz	1,926	40	2,008	796
Zacatecas	188		5,256	2,147
Total of shared area	112,835	56,128	192,241	233,028
Proportion (%) in relation to host ^y	69	14	54	36
Proportion (%) in relation to <i>D. suzukii</i> ^z	35	17	59	72

^{*}Estimated shared area between *D. suzukii* and 4 non-crop hosts per state.
^yProportion (%) of estimated shared area of *D. suzukii* (nationwide) in relation to each non-host crop. Total of estimated area for *D. suzukii* is shown in Table 3.
^zProportion (%) of estimated shared area of each non-host crop in relation to the total (nationwide) estimated area for *D. suzukii*. Total of estimated area for non-crop hosts is shown in Table 3.

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