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Actual and potential distribution of five regulated avocado pests across Mexico, using the maximum entropy algorithm

Andrea Luna[1], Víctor López-Martínez[1,], Nidia Bélgica Pérez-De la O[1], Daniel Jiménez-García[2], Robert W. Jones[3], Álvaro Castañeda-Vildozola[4], and César Ruiz-Montiel[5]*

Abstract

Mexican avocado producers face phytosanitary barriers that limit the ability to ship avocados to foreign markets due to concerns about invasion by unwanted pests. The principal regulated pests are the big avocado seed weevil, *Heilipus lauri* Boheman; the small avocado seed weevils *Conotrachelus aguacatae* Barber and *C. perseae* Barber; the branch borer weevil, *Copturus aguacatae* Kissinger (all Coleoptera: Curculionidae); and the avocado seed moth, *Stenoma catenifer* Walsingham (Lepidoptera: Elachistidae). In Mexico, distribution information of these pests is largely based on a slow integration of the geographic data. This study was conducted to determine the potential distribution of these 5 insect pests in Mexican avocado-growing areas by using the maximum entropy algorithm. Distributional data of these insects were obtained from scientific literature, databases, and field collection, and incorporated into the MaxEnt model using 19 global climatic variables and elevation data. Distributional models for Mexico, and geographic interaction with avocado-growing areas of the country, were calculated. *Conoctrachelus aguacatae*, *C. perseae*, *Copturus aguacatae*, and *H. lauri* showed similar environmental suitability patterns in Mexico, with a potential distribution from central to southern Mexico. High suitability was projected principally in the Trans-Mexican Volcanic Belt and surrounding biogeographic provinces. *Stenoma catenifer* exhibited an irregular environmental suitability pattern, with preference for western Mexico. Altitude, isothermality, and seasonality of precipitation were the variables that most influenced potential distribution of analyzed species. Geographic interaction with avocado-growing areas ranged from wider (*Conoctrachelus aguacatae*, *C. perseae*, *Copturus aguacatae*, and *S. catenifer*) to narrow or irregular (*H. lauri*), but the last species has the potential to invade new geographic areas. For the first time, the geographic distribution of these 5 insect pests was determined based on environmental suitability and their geographic interaction with avocados. These data could support development of management strategies throughout the country, and help focusing surveys and control tactics.

Key Words: ecological niche; seed avocado borer; branch avocado borer; distribution modeling; Mexican biogeographic provinces

Resumen

Los productores de aguacates de México se enfrentan a barreras fitosanitarias que limitan la capacidad de enviar aguacates a los mercados extranjeros debido a la preocupación por la invasión de plagas no deseadas. Las principales plagas reguladas son el gran gorgojo de semilla de aguacate, *Heilipus lauri* Boheman; los pequeños gorgojos de la semilla de aguacate *Conotrachelus aguacatae* Barber y *C. perseae* Barber; el gorgojo de la rama, *Copturus aguacatae* Kissinger (todos Coleoptera: Curculionidae); y la polilla de la semilla del aguacate, *Stenoma catenifer* Walsingham (Lepidoptera: Elachistidae). En México, la información de distribución de estas plagas se basa en gran medida en una lenta integración de los datos geográficos. Se realizó este estudio para determinar la distribución potencial de estas 5 plagas insectiles en las áreas de cultivo de aguacates de México utilizando el algoritmo de máxima entropía. Los datos de distribución de estos insectos se obtuvieron de la literatura científica, bases de datos y recolección de campo, y se incorporó al modelo MaxEnt utilizando 19 variables climáticas globales y datos de elevación. Se calcularon los modelos de distribución para México y la interacción geográfica con las áreas productoras de aguacate para el país. *Conoctrachelus aguacatae*, *C. perseae, Copturus aguacatae* y *Heilipus lauri* mostraron patrones de idoneidad ambiental similares en México, con una posible distribución desde el centro hasta el sur de México. La alta aptitud se proyectó principalmente en el Cinturón Volcánico Transmexicano y en las provincias biogeográficas circundantes. *Stenoma catenifer* exhibió un patrón de idoneidad ambiental irregular, con preferencia por el oeste de México. La altitud, la isoterma y la estacionalidad de la precipitación fueron las variables que más influyeron en la distribución potencial de las especies analizadas. La interacción geográfica con las áreas de cultivo de aguacate varió de más ancha (*Conotrachelus aguacatae*, *C. perseae*, *Copturus aguacatae* y *S. catenifer)* a estrecha o irregular (*H. lauri)*, pero

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la última especie tiene el potencial de invadir nuevas áreas geográficas. Por primera vez, se determinó la distribución geográfica de estas 5 plagas de insectos basándose en la idoneidad ambiental y su interacción geográfica con los aguacates. Estos datos podrían apoyar el desarrollo de estrategias de manejo en todo el país y en las encuestas de enfoque de ayuda y tácticas de control.

Palabras Clave: nicho ecológico; barrenador de aguacate; broca del aguacate de la rama; modelado de distribución; provincias biogeográficas mexicanas

Mexico is the principal producer of avocado, *Persea americana* Mill. (Lauraceae), with 1,520,695 t harvested in 521,037 ha in 2014 (SIAP 2015). Avocados are consumed mainly as fresh fruits, but they are used in the oil, cosmetic, soap, and shampoo industries (Yahia & Woolf 2011). Fruit consumption is highly recommended due to their nutritional characteristics and their capacity to maximize the absorption and conversion of lipids to vitamin A (Dreher & Davenport 2013; Kopec et al. 2014).

Current trends indicate constant growth for the export market, but countries such as the USA have implemented phytosanitary barriers to minimize the risk of unwanted pest introduction (Stout et al. 2004; Hoddle & Parra 2013). These technical barriers can limit or reduce market access for Mexican avocados (Peterson & Orden 2008).

The insect pests of concern are 4 species of weevils and 1 moth species: the big avocado seed weevil, *Heilipus lauri* Boheman; the small avocado seed weevils *Conotrachelus aguacatae* Barber and *C. perseae* Barber; the branch borer weevil, *Copturus aguacatae* Kissinger (all Coleoptera: Curculionidae); and the avocado seed moth, *Stenoma catenifer* Walsingham (Lepidoptera: Elachistidae) (Peña 1988; Castañeda-Vildózola et al. 2007, 2013; Palacios-Torres et al. 2011).

Powerful modeling methods and tools that integrate distribution data and climatic variables are widely used to predict, at the global, country, or local scale, the actual and potential distribution of insect pests (Guisan & Thuiller 2005). The final result is the integration of maps wherein the presence or absence of a particular species is predicted (Gevrey & Worner 2006). These predictions can serve as the basis for planning future monitoring, management, and control strategies. However, for quarantine pests in Mexico, distribution data are largely based on traditional sampling efforts. Environmental suitability maps could be an important tool to support technical and political decisions related to pest management. To contribute in the development of pest risk assessments for fruit culture in Mexico, we applied the maximum entropy algorithm to assess the role of bioclimatic factors in determining the geographic distribution of 5 important insect pest species of avocado, and their interaction with commercial avocado-growing areas.

Materials and Methods

OCCURRENCE RECORDS FOR QUARANTINE PESTS

The distributional data for *Conotrachelus aguacatae*, *C. perseae*, *Copturus aguacatae*, *H. lauri*, and *S. catenifer* were obtained from the literature (Champion 1902–1906; Barber 1923; Gibson & Carrillo 1959; Kissinger 1957; Muñiz 1959, 1970; Acevedo et al. 1972; Whitehead 1979; Cabrera & Salazar 1991; Romero et al. 1996; Coria-Ávalos 1999; Velázquez 2001; Castañeda-Vildózola et al. 2007, 2009, 2012, 2013, 2015; Castañeda 2008; Francia 2008; Urías-López & Salazar-García 2008; Hoddle et al. 2011; Palacios-Torres et al. 2011; Castillo et al. 2012; Soto et al. 2013; Payán-Arzapalo et al. 2015; Vázquez et al. 2016), from collection data provided by the Mexican phytosanitary federal agency Servicio Nacional de Sanidad, Inocuidad y Calidad Agroalimentaria (SENASCA), and by field collections conducted by the authors in Morelos, Puebla, and Veracruz. Also, infested fruits were collected for weevil adult emergence under laboratory conditions, and species were determined using the keys published by Barber (1919, 1923), García-Arellano (1975), Whitehead (1979), and Castañeda-Vildózola et al. (2007).

Pest distribution records were incorporated into an Excel© spreadsheet, then the distributional data were reviewed using a gazetter (INEGI 2015) or were georeferenced with Google Earth® v 7.1.2.2041 (Google Inc., USA) (López-Martínez et al. 2016a). Geographic coordinates were expressed in decimal degrees (i.e., 21.5164, −104.8942). The final database included 178 records for *Conotrachelus aguacatae*, 39 records for *C. perseae*, 122 records for *H. lauri*, 53 records for *S. catenifer*, and 14,786 records for *Copturus aguacatae* (data are available from the authors upon request). The number of records included was considered accurate for calculating species distribution models (Van Proosdij et al. 2015).

SPECIES DISTRIBUTION MODEL

We used the maximum entropy algorithm in MaxEnt version 3.3.3 (Phillips et al. 2006) to model various scenarios of potential spread of the avocado pests in Mexico, using default settings with logistic output. Nineteen global climatic variables were downloaded from WorldClim (2015) with 30 arc-second resolution and 90 m resolution elevation data used in the model (Table 1). These bioclimatic variables represent current environmental conditions (1950–2000), are available on global scale, and have finer spatial resolutions. The outcome of the model is quantification of habitat suitability for the species as a function of the input variables (Phillips & Dudík 2008).

MODEL EVALUATION

Niche model performance was evaluated with the area under the curve (AUC) index (Hernandez et al. 2006; Phillips & Dudík 2008), and were classified according to Swets (1988): AUC 0.90–1.00 = excellent; 0.80–0.89 = good; 0.70–0.79 = fair; 0.60–0.69 = poor; 0.50–0.59 = fail. The Optimal Cutoff Point (PCO) was determined based on the more stringent threshold within MaxEnt (10 percentile training presence). The importance of individual environmental factors for the development of the model was evaluated using the built-in Jackknife.

PREDICTION AND DISTRIBUTION MAPS

The global environmental layers were projected in the biogeographic provinces of Mexico, and each modeling ecosystem was interpreted (Guisan & Thuiller 2005). Geographic interactions (the likelihood that the habitat would be suitable for coexistence; López-Martínez et al. 2016b) of the 5 avocado pests and avocado-growing areas in Mexico (SIAP 2015) were calculated with IDRISI 17.0 (Clark Labs, Clark University, USA). For map production, the software ArcMap® 10.3.1. (ESRI Inc., USA) was used. Biogeographic provinces are according to Morrone (2014a); regions and transition zones are based on Morrone (2015).

Results

ENVIRONMENTAL SUITABILITY

Four of the 5 insect species under consideration displayed similar environmental requirements. *Conotrachelus aguacatae*, *C. perseae*, *Copturus aguacatae*, and *H. lauri* were predicted to occupy similar geographic areas. Only *S. catenifer* displayed potential to occupy different areas.

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Table 1. Analysis of the contribution (%) of 19 bioclimatic and 1 topographic variables[a] to the environmental suitability model of 5 avocado pests in Mexico.

Variable	*Conotrachelus aguacatae*	*Conotrachelus perseae*	*Copturus aguacatae*	*Heilipus lauri*	*Stenoma catenifer*
Altitude	34.50	39.21	15.56	30.28	15.32
Annual mean temperature	0.44	0.35	0.13	0.00	0.24
Mean diurnal range	0.15	0.23	14.35	0.03	2.54
Isothermality	29.41	16.21	31.01	11.24	25.19
Temperature seasonality	4.83	10.23	2.96	19.03	5.41
Maximum temperature in warmest month	0.16	0.00	0.01	0.47	0.04
Minimum temperature in coldest month	4.68	0.04	0.17	0.00	0.71
Temperature annual range	0.21	0.00	0.11	0.02	2.34
Mean temperature in wettest quarter	0.28	0.00	0.02	0.06	0.00
Mean temperature in driest quarter	0.08	0.00	0.09	0.57	0.00
Mean temperature in warmest quarter	0.00	0.00	1.02	0.00	0.02
Mean temperature in coldest quarter	0.15	0.00	0.36	0.12	0.40
Annual precipitation	0.08	1.64	0.25	0.02	2.79
Precipitation in wettest month	0.01	10.46	6.40	0.01	6.31
Precipitation in driest month	5.84	3.64	0.64	4.19	4.96
Precipitation seasonality	8.69	4.99	18.22	16.45	14.65
Precipitation in wettest quarter	2.89	0.03	2.64	9.60	0.00
Precipitation in driest quarter	1.70	0.25	0.01	0.02	3.72
Precipitation in warmest quarter	1.39	7.23	2.92	0.74	3.51
Precipitation in coldest quarter	4.44	5.43	3.05	7.04	11.58

[a]WorldClim version 1.4 (release 3), sources: www.worldclim.org; Hijmans et al. (2005), O'Donnell & Ignizio (2012).

Conotrachelus aguacatae had high environmental suitability in the model output for the central-western region of Trans-Mexican Volcanic Belt province, adjacent areas of Mexican Plateau and Trans-Mexican Volcanic Belt provinces, adjacent areas of Balsas Basin and Trans-Mexican Volcanic Belt provinces, across Sierra Madre del Sur, adjacent areas of Balsas Basin and Sierra Madre Oriental, and central Sierra Madre Oriental biogeographic provinces (Fig. 1A). Medium environmental suitability was calculated in the south-central Mexican Plateau, south of Tamaulipeca, across adjacent areas of Sierra Madre Occidental and the Mexican Pacific Coast, across Sierra Madre Oriental, the eastern Trans-Mexican Volcanic Belt, across Sierra Madre del Sur, and Chiapas biogeographic province. Low environmental suitability was projected in the Mexican Pacific Coast, northern Tamaulipeca, northern Mexican Plateau, northern Sierra Madre Occidental, eastern Sonora, and isolated areas in Baja California. No environmental suitability was calculated in California and Yucatan provinces. Actually, there are no records of this weevil from south of Sierra Madre Occidental in Jalisco or Zacatecas, Sierra Madre del Sur in Oaxaca, Sierra Madre Oriental in San Luis Potosi, and Chiapas provinces; future collections in these regions are needed to confirm this prediction.

For *C. perseae*, the highest environmental suitability included the Trans-Mexican Volcanic Belt, and adjacent areas of the Trans-Mexican Volcanic Belt with Sierra Madre Occidental, Mexican Pacific Coast, Mexican Plateau, Balsas Basin, Sierra Madre del Sur, and Sierra Madre Oriental provinces. Other areas with high environmental suitability were calculated in an irregular east-west strip (Fig. 1B). Medium environmental suitability was projected in Sierra Madre Occidental, southern Mexican Plateau, central-northern Sierra Madre Oriental, eastern Balsas Basin, southern Sierra Madre del Sur, Chiapas, and isolated areas in Tamaulipeca, Veracruzana, Mexican Pacific Coast, and Baja California. Minimal environmental suitability was projected for isolated areas in Sonora, Mexican Plateau, northern Sierra Madre Occidental, Mexican Pacific Coast, Tamaulipeca, central and southern Veracruzana, eastern Balsas Basin, and Yucatan provinces. According to our model, we predict the potential collection of *C. perseae* in the western Trans-Mexican Volcanic Belt in Jalisco, Estado de México, Distrito Federal, Morelos, and Tlaxcala, in southern Sierra Madre Occidental in Zacatecas, and in many isolated areas along the Mexican Pacific Coast. We expect future records of this species for Guerrero and more reports for Oaxaca in Sierra Madre del Sur.

High environmental suitability for *Copturus aguacatae* was calculated in the central-eastern area of Trans-Mexican Volcanic Belt province, adjacent areas of Trans-Mexican Volcanic Belt with Mexican Pacific Coast, Sierra Madre Occidental, Mexican Plateau, Balsas Basin, and Sierra Madre Oriental provinces; and central-eastern regions of Sierra Madre del Sur, adjacent areas of Sierra Madre del Sur with Balsas Basin, and Mexican Pacific Coast provinces (Fig. 1C). Small isolated areas were projected along Sierra Madre Oriental and south-eastern Tamaulipeca provinces. Medium environmental suitability was calculated along Sierra Madre Occidental, southern Mexican Plateau, central and western areas in Trans-Mexican Volcanic Belt, Balsas Basin, adjacent areas of Balsas Basin with Mexican Pacific Coast, adjacent areas of Sierra Madre del Sur with Mexican Pacific Coast, Chiapas, and adjacent areas of Chiapas with Mexican Pacific Coast provinces. Low environmental suitability was projected in a small area south of Baja California, along Sonora, northern and eastern Sierra Madre Occidental, central Mexican Plateau, areas across Mexican Pacific Coast, Chiapas, Veracruzana, and Yucatan provinces. We expect future reports for this species in Guerrero and Oaxaca for Sierra Madre del Sur, Hidalgo and San Luis Potosi for Sierra Madre Oriental, and Chiapas province.

Heilipus lauri had high environmental suitability in central and southern areas of Trans-Mexican Volcanic Belt, adjacent areas of Trans-Mexican Volcanic Belt with Balsas Basin, and Mexican Plateau, eastern areas of Sierra Madre del Sur, adjacent areas of Sierra Madre del Sur with Mexican Pacific Coast, and small areas in central Sierra Madre Oriental (Fig. 1D). Medium environmental suitability was calculated across Trans-Mexican Volcanic Belt, western, northern, and eastern areas of Sierra Madre del Sur, eastern areas of Balsas Basin, Chiapas, and western areas of Yucatan provinces. Low environmental suitability was projected in areas of Sierra Madre Occidental, south-central Mexican Plateau, Sierra Madre Oriental, central-eastern Mexican Pacific Coast, central Veracruzana, and Chiapas provinces. No environmental suit-

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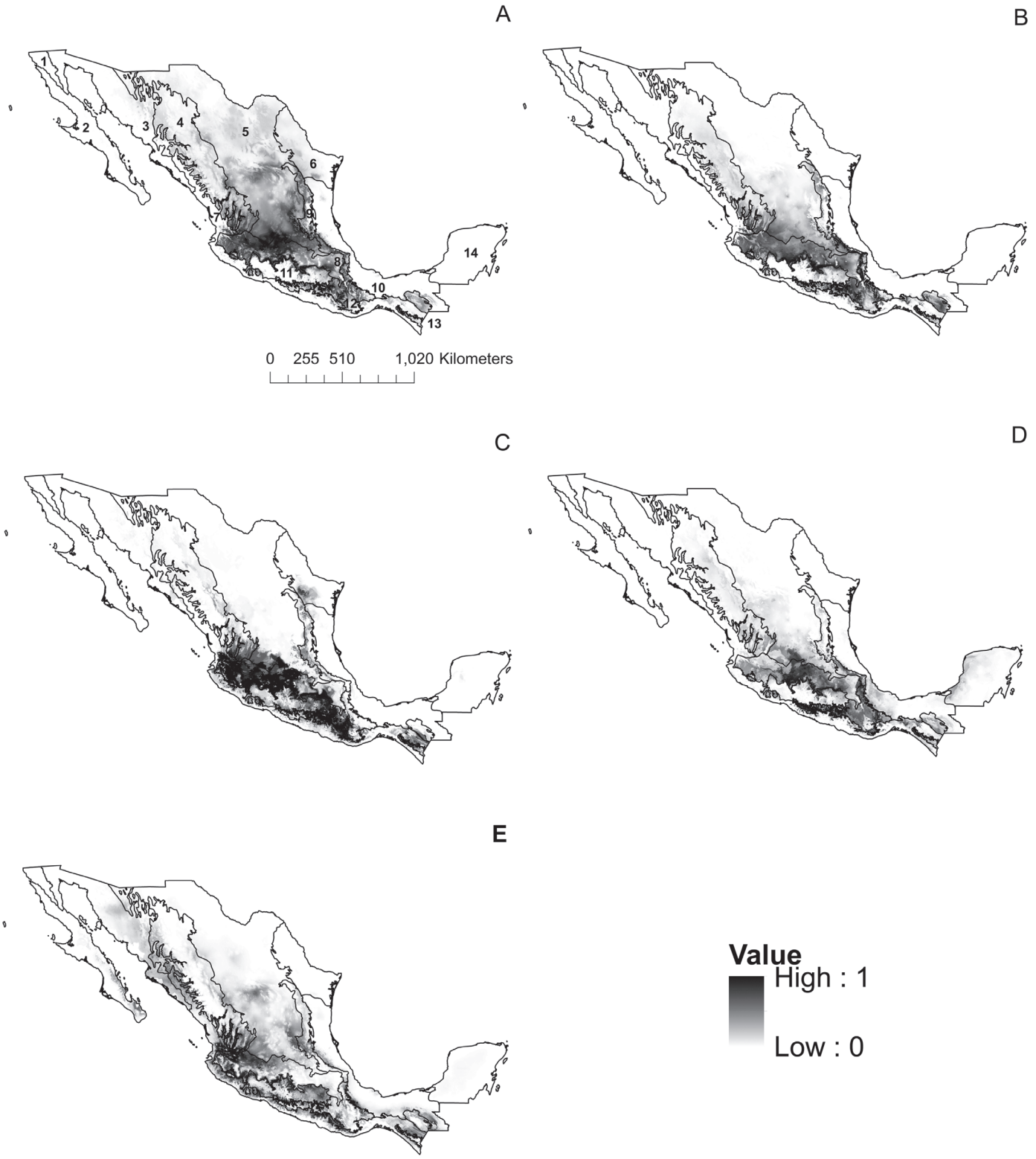


Fig. 1. Potential distribution of 5 insect pests of quarantine importance in Mexican avocados, based on ecological niche modeling. A) *Conotrachelus aguacatae*; B) *Conotrachelus perseae*; C) *Copturus aguacatae*; D) *Heilipus lauri*; and E) *Stenoma catenifer*. Current and potential distribution in Mexico was projected according to biogeographic provinces (Morrone 2005, 2014a), 1 = Baja California, 2 = California, 3 = Sonora, 4 = Sierra Madre Occidental, 5 = Mexican Plateau, 6 = Tamaulipeca, 7 = Mexican Pacific Coast, 8 = Trans-Mexican Volcanic Belt, 9 = Sierra Madre Oriental, 10 = Veracruzana, 11 = Balsas Basin, 12 = Sierra Madre del Sur, 13 = Chiapas, 14 = Yucatan. Scale values: 0 = absence, 1 = presence.

ability was calculated in California, Baja California, Sonora, and Tamaulipeca provinces. For big avocado seed weevil, we expect more reports in the future for Sierra Madre del Sur in Guerrero and possibly Oaxaca. Michoacán in Trans-Mexican Volcanic Belt had appropriate environmental suitability for this weevil, but no records for this species have been documented in these areas.

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Stenoma catenifer exhibited an irregular environmental suitability pattern (Fig. 1E), with high environmental suitability projected mainly in western Mexico, in adjacent areas of Mexican Pacific Coast, Sierra Madre Occidental, and Trans-Mexican Volcanic Belt provinces. Other areas with high suitability were found along adjacent areas of Trans-Mexican Volcanic Belt with Balsas Basin, Mexican Pacific Coast with Sierra Madre del Sur, and Sierra Madre del Sur with Veracruzana provinces. Medium environmental suitability was calculated south of Baja California, southern Sonora, northern and southern Mexican Pacific Coast, central and southern Mexican Plateau, central areas of Trans-Mexican Volcanic Belt, Balsas Basin, central and eastern Sierra Madre del Sur, and adjacent areas of Chiapas and Veracruzana provinces. Low environmental suitability was calculated in central Baja California, northern Sonora, central Sierra Madre Occidental, northern and southern Mexican Plateau, a small area in Tamaulipeca, northern, eastern and southwestern Sierra Madre Oriental, central Veracruzana, and areas in Balsas Basin, Sierra Madre Oriental, and Chiapas. No environmental suitability was projected in California, Tamaulipeca, and Yucatan provinces. Future records from Trans-Mexican Volcanic Belt could be expected for Jalisco, Michoacán, Estado de México, Morelos, and Puebla, Sierra Madre Occidental in Zacatecas, and Mexican Pacific Coast in Nayarit, Guerrero, Oaxaca.

MODEL VALIDATION

Performance of all models was considered excellent, with values ranging from 0.92 to 0.99 (*Conotrachelus aguacatae* = 0.99, *C. perseae* = 0.99, *Copturus aguacatae* = 0.92, *H. lauri* = 0.99, and *S. catenifer* = 0.99). For the species studied herein, altitude, isothermality (evenness of temperatures), and seasonality of precipitation were the variables that most influenced the potential distribution of these insects (Table 2). These variables measure changes in environmental conditions throughout the year (Aguilar & Lado 2012). For *Conotrachelus aguacatae*, these 3 variables contributed 72.6% in the calculated model. For *C. perseae*, these variables were complemented with temperature seasonality and precipitation in wettest month, thus contributing 76.1% in the model. For *Copturus aguacatae*, mean diurnal range was an additional important factor, and together with the other 3 variables accounted for 79.1% in the predicted model. For *H. lauri*, the 3 variables plus temperature seasonality contributed 77.0% in the calculated model. For *S. catenifer*, the 3 variables plus precipitation in the coldest quarter contributed 66.7% in the predicted model.

GEOGRAPHIC INTERACTION

According to our study, *Conotrachelus aguacatae* has a wide potential distribution in the country, and with geographic interaction that could involve avocado-growing areas in Aguascalientes, Chiapas, Colima, Durango, Estado de México, Guanajuato, Guerrero, Hidalgo, Jalisco, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Veracruz, and Zacatecas (Table 2; Fig. 2A).

Table 2. Potential geographic distribution (ha) of 5 insect pests of quarantine importance in Mexico by federal entity.

Federal entity	*Conotrachelus aguacatae*	*Conotrachelus perseae*	*Copturus aguacatae*	*Heilipus lauri*	*Stenoma catenifer*
Aguascalientes	0.00	0.00	0.00	0.00	7,125.84
Baja California	0.00	0.00	0.00	0.00	0.00
Baja California Sur	0.00	0.00	0.00	0.00	275,506.66
Campeche	0.00	0.00	0.00	464.73	0.00
Chiapas	344,673.78	976,085.18	0.00	266,831.73	2,459,189.36
Chihuahua	0.00	0.00	0.00	0.00	0.00
Coahuila	6,428.75	0.00	0.00	0.00	0.00
Colima	31,369.19	31,136.82	5,421.83	464.73	324,148.27
Distrito Federal	0.00	24,630.62	1,394.19	0.00	0.00
Durango	238,715.64	133,764.41	0.00	0.00	260,015.71
Guanajuato	2,037,602.98	7,977.84	77.45	1,161.82	281,005.95
Guerrero	587,029.80	833,413.47	103,711.95	1,222,546.29	2,552,057.65
Hidalgo	459,229.41	318,958.80	0.00	0.00	224,076.69
Jalisco	2,558,408.94	772,921.28	962,065.86	37,410.66	3,002,534.66
Mexico	320,817.71	572,158.48	83,418.80	284,491.42	395,639.03
Michoacán	1,302,479.63	856,882.26	918,071.54	338,322.49	1,905,542.57
Morelos	97,360.66	98,754.85	57,781.27	98,367.57	239,954.92
Nayarit	450,941.75	390,062.29	215,711.57	0.00	1,080,649.13
Nuevo Leon	460,003.96	20,912.79	0.00	0.00	30,207.37
Oaxaca	2,237,513.77	2,966,130.91	307,650.40	1,310,612.38	2,308,772.17
Puebla	694,846.86	710,337.81	106,190.51	129,426.94	1,016,129.30
Queretaro	781,596.22	81,327.52	4,647.29	0.00	227,639.61
Quintana Roo	0.00	0.00	0.00	0.00	0.00
San Luis Potosi	562,786.45	39,501.94	0.00	0.00	1,356,775.43
Sinaloa	9,217.12	52,746.71	0.00	0.00	164,359.05
Sonora	0.00	0.00	0.00	0.00	0.00
Tabasco	77.45	0.00	0.00	0.00	8,287.66
Tamaulipas	361,946.20	7,977.84	0.00	0.00	408,496.53
Tlaxcala	18,279.33	7,048.39	0.00	0.00	0.00
Veracruz	444,900.27	514,609.58	0.00	96,121.39	533,586.00
Yucatan	0.00	0.00	0.00	65,526.75	0.00
Zacatecas	4,260.01	0.00	0.00	0.00	220,436.31
Total	14,010,485.88	9,417,339.79	2,766,142.67	3,851,748.90	19,282,135.86

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Conotrachelus perseae showed a similar distribution pattern as *C. aguacatae*, but potentially covers a greater number of production areas (Table 2; Fig. 2B).

Copturus aguacatae has a narrow distribution in comparison with both small avocado seed weevils, but it could affect avocado production areas from Nayarit, through central Mexico, to Chiapas. Northern production areas, including Baja California, Veracruz, and Yucatan peninsula, are practically free of this species (Table 2; Fig. 2C).

It seems that *H. lauri* has a restricted distribution in the country, with isolated populations in commercial avocado plantations from Estado de México, Guerrero, Jalisco, Michoacán, Morelos, Oaxaca, Puebla, and Veracruz (Table 2; Fig. 2D).

Stenoma catenifer is projected to have the widest geographic distribution across the country, from Baja California Sur, central Mexico to Chiapas (Table 2; Fig. 2E), and from Nuevo Leon, and San Luis Potosi joining with Veracruz growing areas. However, avocado production areas in Yucatan seem to be inadequate for *S. catenifer*.

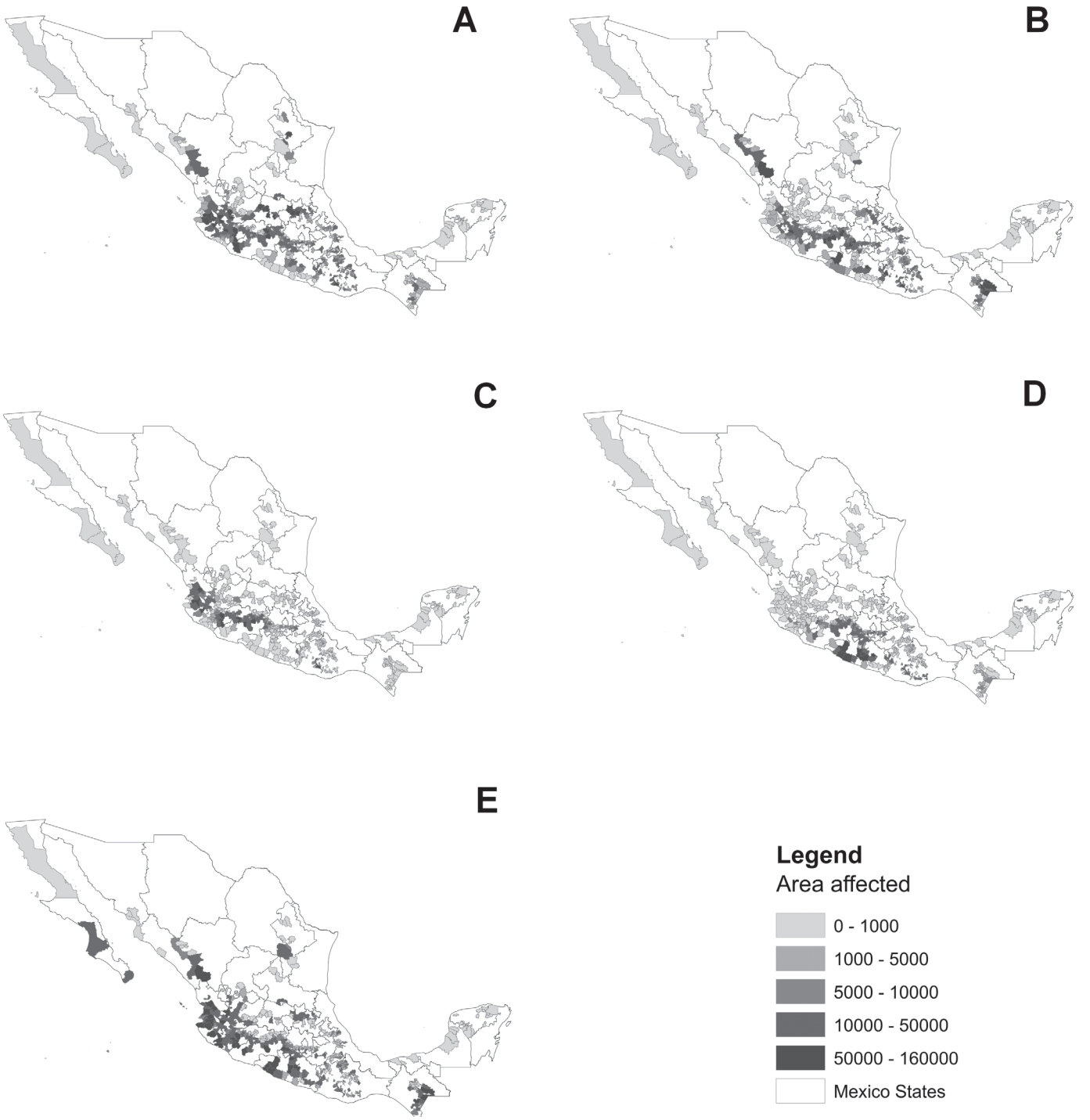


Fig. 2. Geographic areas in Mexico where both the insect pest and avocados are found. Shading indicates hectares affected. A) *Conotrachelus aguacatae*; B) *Conotrachelus perseae*; C) *Copturus aguacatae*; D) *Heilipus lauri*; and E) *Stenoma catenifer*.

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Discussion

The distribution of species calculated herein coincides with a typical Mexican Transition Zone species (Halffter 1974) and with a Neotropical dispersal pattern (Morrone 2015). The Mexican Transition Zone is considered by Morrone (2014b) as an area of natural endemism for Curculionoidea, where agricultural pests can coevolve with their host (López-Martínez et al. 2016a). It seems that the Mexican Plateau acts as a natural barrier reducing the dispersion of these species to the Nearctic region. However, there are different levels of penetration for these species in Mexican Plateau province, with *Conotrachelus aguacatae* and *C. perseae* reaching the maximal potential distribution range including the Mexican Transition Zone in southern Sierra Madre Occidental, Sierra Madre Oriental, and Mexican Plateau. *Stenoma catenifer* is classified similarly as a Mexican Transition Zone species with a Neotropical dispersal pattern, but in this case, the dispersal pattern is deeply influenced by the Mexican Pacific Coast, with a potential for populations with Nearctic dispersal pattern in Baja California and Sonora provinces.

A natural barrier that likely limits species dispersion is the Mexican geography with several volcanic systems extending across the country, each of which differs in extent, origin, and orientation. The Sierra Madre Occidental volcanic province is extensive, of middle Tertiary origin, running from the southwestern United States to central Mexico (Ferrari et al. 1999). The Trans-Mexican Volcanic Belt is an east–west system, a 1,200 km long, 100 km wide, active, continental volcanic arc (Ego & Ansan 2002). The Sierra Madre Oriental is an eastern, 800 km long, 80 to 100 km wide mountain system, with peaks higher than 2,500 m (Eguiluz et al. 2000). Sierra Madre del Sur is a Pacific marginal mountain system, 1,100 km long, with maximal peaks from 2,600 to 3,200 m (Lugo-Hubp 1990). But in the connection areas of Sierra Madre Occidental, Sierra Madre Oriental, Trans-Mexican Volcanic Belt, and Sierra Madre del Sur, there are valleys and depressions with wide ranges in extent and altitudes. Here is where these orographic elements show 2 effects on regulated avocado pests: creating environmental conditions for natural existence of insects in high altitudinal ranges (≤2,300 m), but limiting dispersion (i.e., *H. lauri* from Morelos to Michoacán) across physical barriers and into lowlands (<1,000 m).

Avocado is a native fruit in the tropical and subtropical regions of North and South America, with 3 general ecological races: Mexican, Guatemalan, and West Indian (Ayala & Ledesma 2014). This fruit has a deep and old interaction with humans in the Neotropics (Galindo-Tovar et al. 2008). Dispersion of avocado in America was in a north–south direction, with diversity increased by Mesoamerican cultures (Galindo-Tovar et al. 2008). In addition, it is possible to hypothesize a host–pest coevolutionary relationship, with dispersion of the insects following production by Mesoamericans, or more contemporary producers. An additional explanation for the distribution pattern of avocado seed weevils could be the fruit dispersion by large herbivores (fruit consumption and undamaged seed excretion) (Wolstenholme & Whiley 1999).

Altitude is positively associated with the potential distribution of pests of quarantine importance for Mexican avocados, indicating a preference for high altitudes. Ecologically, when a species has a broad altitudinal range, its probabilities for finding suitable environments are high (Harabiš & Dolný 2010). Importantly, this variable is considered as an easy metric for characterizing habitat in the field (Chunco et al. 2013). For *Conotrachelus aguacatae* and *H. lauri*, the probability of finding this species increases at 1,500 m altitude. The niche suitability for *C. perseae* and *Copturus aguacatae* starts at lower altitudes, about 1,000 m, and increases between 2,000 and 4,000 m. *Stenoma catenifer* showed only a minor influence of this variable on its distribution, with a strong probability of collecting it only in areas with altitudes ranging between 1,000 and 1,500 m.

Day-to-night temperature oscillations relative to the annual oscillations (isothermality) (O'Donell & Ignizio 2012) is an important weather element in determination of environmental suitability for all species studied herein. This phenomenon was also reported for some other insect pests in Mexico (López-Martínez et al. 2016b).

Avocado fruit growth in Mexico takes 8 to 9 mo, and 2 fruit seasons are recorded in commercial orchards (Cossio-Vargas et al. 2008; Rocha-Arroyo et al. 2011). The principal period of precipitation coincides with fruit harvest (Rocha-Arroyo et al. 2011). The combination of these elements (fruit maturity and rain) seems to be an important factor affecting emergence, mating, host selection (fruit or wood), and oviposition in these avocado pests.

The Mexican avocado industry faces strong phytosanitary pressure from the native avocado pests. The national phytosanitary agency (SENASICA) and local farmers implement local, regional, and national inspections, and pest control measures (cultural, biological, and chemical options) to reduce pest populations (Sangerman-Jarquin et al. 2014). These efforts have resulted in the establishment of pest-free avocado areas (Thiébaut 2010; Martín 2016). However, according to this work, these areas are under constant threat from avocado pest invasions emanating in surrounding production areas.

Potential expansion of the infested areas is a major concern of the avocado industry in Mexico. *Conotrachelus aguacatae* and *C. perseae* are principally distributed in central Mexico. However, these species could also inhabit nearby areas, especially orchards with low pest control technology, or live on wild hosts. For species with irregular or patchy distribution (*H. lauri* and *S. catenifer*), eradication of these species from avocado-growing regions may be a logical priority.

Environmental suitability, as determined by this study, could be the basis to conduct systematic sampling studies to determine the definite distribution of these species in selected entities such as Nuevo Leon for *S. catenifer*, and Michoacán for *H. lauri*. Currently, there are no data to confirm or deny the presence or absence of *S. catenifer* in Nuevo Leon (Jorge Luis Morales Marín, Comite Estatal de Sanidad Vegetal de Nuevo Leon, Mexico), but the apparent environmental suitability suggests that natural invasion or accidental introduction could occur. The same situation applies to *H. lauri* in Michoacán.

Finally, Mexico is a place with commercial and wild avocado distributed throughout the country and with a traditional culture of small backyard orchards; for now, the role of these native and backyard trees in avocado pest dispersion is still poorly known. Recently, Castañeda-Vildózola et al. (2013) and Palacios-Torres et al. (2011), reported that backyard orchards may act as reservoirs, allowing natural interactions among different avocado seed borers, as has been reported for *H. lauri* with *C. perseae* and *H. lauri* with *S. catenifer.* Also, anthropogenic activities such as commerce could facilitate continuous dispersion of these pests into new agroecosystems. Further research is needed to examine these assumptions.

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