

Current Knowledge of *Leishmania* Vectors in Mexico: How Geographic Distributions of Species Relate to Transmission Areas

Camila González, Eduardo A. Rebollar-Téllez, Sergio Ibáñez-Bernal, Ingeborg Becker-Fausser, Enrique Martínez-Meyer, A. Townsend Peterson, and Víctor Sánchez-Cordero*

Departamento de Zoología, Instituto de Biología, and Centro de Ciencias de la Complejidad, Universidad Nacional Autónoma de México, Mexico City, Mexico; Laboratorio de Entomología Médica, Departamento de Zoología de Invertebrados, Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, Nuevo León, Mexico; Instituto de Ecología, AC Red Ambiente y Sustentabilidad, Xalapa, Veracruz, Mexico; Laboratorio de Inmunoparasitología, Facultad de Medicina, Universidad Nacional Autónoma de México, Hospital General de México, Mexico City, Mexico; Biodiversity Institute, The University of Kansas, Lawrence, Kansas

Abstract. Leishmaniasis are a group of vector-borne diseases with different clinical manifestations caused by parasites transmitted by sand fly vectors. In Mexico, the sand fly *Lutzomyia olmeca olmeca* is the only vector proven to transmit the parasite *Leishmania mexicana* to humans, which causes leishmaniasis. Other vector species with potential medical importance have been obtained, but their geographic distributions and relation to transmission areas have never been assessed. We modeled the ecological niches of nine sand fly species and projected niches to estimate potential distributions by using known occurrences, environmental coverages, and the algorithms GARP and Maxent. All vector species were distributed in areas with known recurrent transmission, except for *Lu. diabolica*, which appeared to be related only to areas of occasional transmission in northern Mexico. The distribution of *Lu. o. olmeca* does not overlap with all reported cutaneous leishmaniasis cases, suggesting that *Lu. cruciata* and *Lu. shannoni* are likely also involved as primary vectors in those areas. Our study provides useful information of potential risk areas of leishmaniasis transmission in Mexico.

INTRODUCTION

Studies of ecological and geographic patterns of occurrence of vector-borne diseases are relevant for understanding modes of parasite transmission.¹ Recent research in ecological niche modeling, integrating point occurrence data with digital environmental maps, provides a useful and powerful framework for understanding the eco-epidemiologic geography of zoonotic diseases because their transmission cycles involve different sylvatic (enzootic) and domestic reservoir and vector species, each responding to environmental variation, according to its own ecological niche.^{2–6} The ecological niche is defined as the set of environmental conditions in which species can maintain populations without immigrational subsidy, and provides a framework for testing hypotheses regarding roles of environmental variables in shaping distributional patterns of species and evaluating how different species' ecological niches relate to one another.^{3,7}

An interesting and complex disease system from the point of view of the variety of species involved in the transmission cycle and public health relevance are the leishmaniasis, a group of diseases with different clinical manifestations, caused by parasites transmitted by sand fly vectors (Diptera: Psychodidae: Phlebotominae) among mammal reservoir hosts. Vectors and reservoir hosts may differ depending on the geographic region.^{8–11}

In the New World, insect vectors known to be responsible for *Leishmania* transmission to humans belong to the genus *Lutzomyia*. Although the taxonomy of sand flies has seen major changes in nomenclature after the proposal of Galati,¹² throughout this report we use the name *Lutzomyia* (*sensu*) in a more conservative sense.^{12,13} Most sand fly species are only

classified as suspected leishmaniasis vectors because ultimate proof of involvement is rather difficult to achieve.^{9,14,15}

In Mexico, at least for cutaneous leishmaniasis (CL), only one taxon, *Lutzomyia olmeca olmeca*, has been incriminated as a vector of this disease. Other species, such as *Lu. cruciata*, *Lu. shannoni*, *Lu. panamensis*, and *Lu. ylephiletor*, have recently been found infected with *Leishmania mexicana* in Campeche.^{16,17} Previous studies in Campeche documented *Lu. o. olmeca* as infected with *Leishmania*; *Lu. cruciata* was also found infected with similar parasites, although the particular *Leishmania* species could not be identified.¹⁸ *Lutzomyia cruciata* is a suspected leishmaniasis vector in Nicaragua and Belize, and its abundances at some collecting sites in the Yucatan Peninsula exceed those of the known vector species.^{19–23} Other species that feed on humans and that have been found infected with *Leishmania* in Central America include *Lu. panamensis*, *Lu. shannoni*, and *Lu. ylephiletor*.^{10,24} *Lutzomyia gomezi* has been found infected with *Leishmania panamensis* in Panama.^{25,26} In northern Mexico and the southern United States, sand fly species suspected of being involved in parasite transmission to humans are *Lu. diabolica* and *Lu. anthophora*.^{27,28} *Lutzomyia diabolica* is suspected of being a vector of *L. mexicana* and has been infected experimentally with *L. infantum*, and *Lu. anthophora* was able to transmit *L. mexicana* experimentally to mice.^{29–31}

Visceral leishmaniasis (VL) is caused by *L. infantum* (*L. chagasi*) and is transmitted in the New World to humans by *Lu. longipalpis* and *Lu. evansi*, which alternate their relevance as vectors depending on ecological characteristics of transmission focus.³² *Lutzomyia longipalpis* is generally considered the principal vector of *L. infantum* and is known to comprise a species complex distributed in the Neotropics from Mexico to Argentina.^{33–36} *Lutzomyia evansi* is distributed from Mexico to Colombia and Venezuela.^{26,34,37–40} In some localities in Colombia, this species acts as the main vector,³⁷ and in Costa Rica it is dominant when *Lu. longipalpis* shows low abundance.³⁸

In Mexico, the first clinically documented records of CL were from forested parts of the Yucatan Peninsula.^{41,42}

*Address correspondence to Víctor Sánchez-Cordero, Instituto de Biología, Departamento de Zoología, Universidad Nacional Autónoma de México, Circuito Exterior, Edificio Nuevo, Módulo C, Apartado, Postal 70–153, Mexico City DF 04510, Mexico. E-mail: victor@ibiologia.unam.mx

Currently, although cases are not reported by public health authorities, they are nonetheless a significant public health problem in the region. Cases of VL have been reported from the states of Chiapas, Puebla, Guerrero, Oaxaca, Morelos, and Tabasco,^{41,42} and several foci in the state of Chiapas and the Balsas River Basin are found in tropical dry forest areas (Becker I, Laboratorio de Inmunoparasitología, Universidad Nacional Autónoma de México and Ramsey J, Centro Regional de Investigación en Salud Pública, unpublished data).

Thus, in Mexico, knowing the ecology and geography of vector species involved in *Leishmania* transmission is of great relevance to public health because entomologic surveillance is one of the most important intervention strategies of vector-borne diseases. The official policy of the Mexican government public health agency regarding entomologic surveillance is Norma Oficial Mexicana sobre la Vigilancia Epidemiológica, Prevención y Control de las Enfermedades Transmitidas por Vector (PROY-NOM 032-SSA2-2000).

The aim of this study was to estimate likely distributions of all sand fly species with potential medical importance for leishmaniasis transmission in Mexico and to relate these distributions to known transmission areas. This comparison will enable assessment of whether current knowledge of vector diversity is likely to be complete. By this means, we identified vector species likely to be involved in *Leishmania* transmission cycles. Because leishmaniasis cases in Mexico have not been followed-up with research on local transmission, information regarding leishmaniasis etiology is scarce. Distributional maps on a national scale will facilitate understanding of the relative roles of different sand fly vector species. The ultimate aim is to identify high-risk areas and use this information for designing control and prevention strategies.

METHODS

Eleven sand fly species (*Lutzomyia*) of at least potential medical importance are found in Mexico. These species were selected based primarily on their vector status and public health relevance in nearby countries, and also on the findings obtained by different authors in recent years in Mexico. For CL, we included nine species: the proven vector *Lu. o. olmeca* and eight suspected vectors: *Lu. cruciata*, *Lu. shannoni*, *Lu. ylephiletor*, *Lu. gomezi*, *Lu. diabolica*, *Lu. ovallesi*, *Lu. panamensis*, and *Lu. anthophora*.^{10,16,20,22,24,26,28,30,43–48} For VL, we included the two known vectors, *Lu. longipalpis* and *Lu. evansi*.^{33,40}

A database summarizing known occurrences for these species in Mexico was assembled from a variety of sources, such as scientific publications,^{49–53} records of the entomologic collections of the Instituto de Diagnóstico y Referencia Epidemiológicos⁵⁴ and the Universidad Autónoma de Yucatán, and personal communications with Dr. Oscar Velasco-Castrejón (Departamento de Medicina Experimental, Universidad Nacional Autónoma de México). Geographic coordinates were added to each record on the basis of the Instituto Nacional de Estadística y Geografía 2000 locality database (www.inegi.gob.mx), Biogeomancer (www.biogeomancer.org), and Falling Rain Genomics, Inc. (Palo Alto, CA) (www.fallingrain.com).⁵⁵

Ecological niche modeling. We modeled ecological niches and estimated potential geographic distributions for each species by using the computer algorithms Genetic Algorithm for Rule-Set Prediction (GARP) and Maxent.^{56,57} We decided

to use both algorithms because the two methods have been widely used, although sometimes showing contrasts in performance:^{58–60} GARP often overpredicts potential distributions of species somewhat, and Maxent may overfit models and underpredict.^{57,59} Also, obtaining predictions using different methodologic approaches generally produces more reliable results than under a single approach.⁶¹

For those species with ≥ 13 available records, we divided occurrence points randomly into two pools: training data (80%) and testing data (20%). Models were built using training data, reserving the testing data for model evaluation; species with < 13 records were modeled using all available points as training data. Using GARP, we developed 100 replicate models for each species; the best subset was chosen considering an extrinsic omission measure for species with a test dataset and intrinsic omission measure for the rest, and soft omission threshold (20% of distribution) for all species. Models generated using Maxent were run choosing logistic output.⁶²

For all model outputs, we then used a threshold for presence that was set such that 90% of all occurrences on which the model was based were included in the predicted area (i.e., $E = 10\%$, in the terminology of Peterson⁸), and remaining areas were classed as absent. The areal extent of distributional areas was calculated in a geographic information system based on the number of pixels predicted as suitable.⁶ Testing data were overlaid on the binary outputs to evaluate which of the three output models (GARP, Maxent, and coincident areas between them) better fit to known vector distributions. We used a binomial test to evaluate statistical significance of predictions by comparing observed successes and failures with random expectations.⁶³

WorldClim climatic coverages used for modeling were chosen to minimize inter-variable correlations measured on the basis of 5,000 random points in Mexico.⁶⁴ We generated a correlation matrix in JMP 6.0 among all variables in the WorldClim dataset version 1.4 (approximately 1 km resolution; www.worldclim.org), and retained variables that were relatively uncorrelated ($r < 0.75$). The nine environmental variables chosen to build the models were mean diurnal range, isothermality, maximum temperature of warmest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, precipitation seasonality, precipitation of warmest quarter, and precipitation of coldest quarter from the WorldClim database. We also included slope, aspect, and topographic index from the Hydro-1K dataset.^{65,66}

Areas of public health importance. To define important areas for leishmaniasis transmission in Mexico, we used the states historically known to report cases of leishmaniasis, clipped with the Mexican ecoregions, to set geographic limits with ecological meaning.⁶⁷ Two transmission levels were set such that states with recurrent transmission had annual records for at least 15 consecutive years and states with occasional transmission had sporadic records obtained from the Sistema Único de Información para la Vigilancia Epidemiológica, Dirección General de Epidemiología, Secretaría de Salud. Predicted distributions for vector species were overlapped with the map produced depicting the areas of transmission to estimate the percentage of the distribution of each vector in recurrent and occasional transmission areas (Table 1).

Land use coverage. We used a land use map (www.conabio.gob.mx) to assess the presence of suitable forested areas for sand fly breeding sites and evaluated the percent of species'

TABLE 1
Percentage of *Lutzomyia* species potential distributions related to transmission level and land use coverage, Mexico

Species	Relation to transmission areas		Relation to land cover			Eco-epidemiologic traits			
	Occasional %	Recurrent %	Human settlements %	Crops and pastures %	Forested areas %	Infected	No. infected/no. collected (%), reference	Abundance	Vector ability
<i>Lu. cruciata</i>	17.35	60.41	0.58	39.45	59.96	Yes	1/128 (0.8) ¹⁷ 6/6 (100) ⁶⁵	High	Likely
<i>Lu. diabolica</i>	25.95	12.60	0.77	34.38	64.84	No			Suspected
<i>Lu. gomezi</i>	9.98	75.91	0.64	31.26	68.1	No			Suspected
<i>Lu. longipalpis</i>	44.40	26.65	0.66	39.02	60.32	No			Suspected
<i>Lu. olmeca</i>	8.31	81.84	0.57	37.84	61.6	Yes	1/453 (0.2) to 11/144 (7.6) ¹⁷ 6/38 (15.7) ⁶⁵	High	Confirmed
<i>Lu. ovallesi</i>	18.27	70.44	0.73	38.73	60.54	No			Suspected
<i>Lu. panamensis</i>	6.57	91.08	0.38	24.18	75.44	Yes	2/46 (4.3) ¹⁷	High	Likely
<i>Lu. shannoni</i>	16.46	66.24	0.57	39.27	60.16	Yes	3/56 (5.4) to 8/53 (15.1) ¹⁷ 2/7 (28.5) ⁶⁵	High	Likely
<i>Lu. ylephiletor</i>	14.49	62.42	1.03	32.46	66.51	Yes	1/8 (12.5) ¹⁷	Low	Likely

potential distribution in each of three land coverage types: human settlements, agriculture (including crops and pastures), and forested areas. In their sylvatic cycle, sand flies require humid and shadowed substrates provided by forested areas in which they lay eggs to ensure larval survival and development. This coarse-resolution land use map included only a broad classification of agriculture that did not enable identifying shadowed crops potentially providing similar suitable ecological conditions for sand flies; we considered crops and pasture as transformed areas.

RESULTS

In all, 172 presence records for *Leishmania* vector species in Mexico were assembled (Figures 1 and 2). Not surprisingly, we found that sampling of sand flies was focused in the southern parts of the country. Among states, sampling was most intense in Campeche (n = 86), Oaxaca (n = 47), and Quintana Roo (n = 40). In contrast, only single sampling localities were available for the states of Coahuila, Chihuahua, and Tamaulipas. The species most commonly obtained were *Lu. cruciata* (n = 102) and *Lu. shannoni* (n = 61), and only few records were available for *Lu. anthophora* (n = 2), *Lu. ylephiletor* (n = 3), *Lu. gomezi* (n = 3), and *Lu. evansi* (n = 1). *Lutzomyia o. olmeca*, the only demonstrated CL vector in Mexico, has been obtained at 29 localities, all in the southern part of the country. Overall, species richness of potential vectors was highest in southeastern Mexico, including the states of Veracruz, Tabasco, Campeche, and Quintana Roo (Figures 1 and 2).

Although GARP models predicted larger areas of potential distribution for six of the seven species modeled, Maxent models performed slightly better in terms of independent testing (Table 2). In general, GARP models had statistically significant predictions for all species except for *Lu. diabolica* and *Lu. longipalpis*, and Maxent was not significant only for *Lu. diabolica*. The areas of predicted distribution generated by both algorithms were also highly coincident for all species and were generally the same as the area predicted only with Maxent (i.e., the Maxent prediction was a subset of the GARP prediction). On the basis of these results, we decided to use only outputs generated by Maxent as predicted areas of potential distribution.

The potential distribution of *Lu. o. olmeca* was restricted to Campeche, Quintana Roo, Tabasco, southern Veracruz, and some areas in Chiapas and Yucatan. *Lutzomyia cruciata* was the species with the largest predicted area of potential distribution, ranging across the Yucatan Peninsula and the states of

Chiapas, Oaxaca, and Veracruz, and along the Pacific Coast north to Nayarit. Interestingly, *Lu. shannoni* showed a similar, although smaller, area of potential distribution compared with that of *Lu. cruciata*. The potential distribution of *Lu. panamensis* was restricted to the Yucatan Peninsula, southern Veracruz, and the Chontalpa region of Tabasco. *Lutzomyia ovallesi* had a small potential distributional area in Mexico restricted to Campeche and Quintana Roo (Figure 1). In northern Mexico, the most broadly distributed species was *Lu. diabolica*: its potential distribution reached the southern part of the United States, supporting the idea of its potential importance as a vector in Texas (Figure 1).²⁹

The Yucatan Peninsula has areas of recurrent leishmaniasis transmission (Figure 3). In those areas, the sand flies *Lu. olmeca*, *Lu. panamensis*, and *Lu. ovallesi* had almost 80% of their Mexican distributional areas (Figure 1 and Table 1). Widely-distributed vector species, such as *Lu. shannoni* and *Lu. cruciata*, were present in all transmission areas, and were dominant in regions with recurrent transmission. In general, all vector species were distributed in areas with recurrent transmission, except for *Lu. diabolica*, which appeared related only to areas of occasional transmission, corresponding to the cases reported from northern Mexico (Table 1). Interestingly, areas of recurrent transmission are concentrated in moist forest ecoregions, and occasional transmission areas were mainly distributed in the tropical dry forests and Tamaulipan mezquital ecoregions (Figure 4). We observed that sand fly species occur mainly in forested areas, although at least one-third of their potential distributions overlapped with crops and pastures, probably reflecting the fragmented nature of Mexican forests; only minimal overlap of sand fly species potential distribution with human settlements was observed (Table 1).

DISCUSSION

Studies of geographic and ecological distributions of vectors and cases of diseases offer powerful tools for identifying risk zones and exploring potential interactions between hosts, vectors, and parasites.^{2,3} Our results provide a baseline against which to improve research on *Leishmania* and their vectors in Mexico. Because one of the criteria set by the World Health Organization for linking species to disease transmission is that vector and reservoir geographic distributions must coincide with human case distributions,⁶⁸ our comparisons of modeled potential distributions enabled us to assess disease transmission in places where entomologic surveillance has scarcely been conducted.⁴

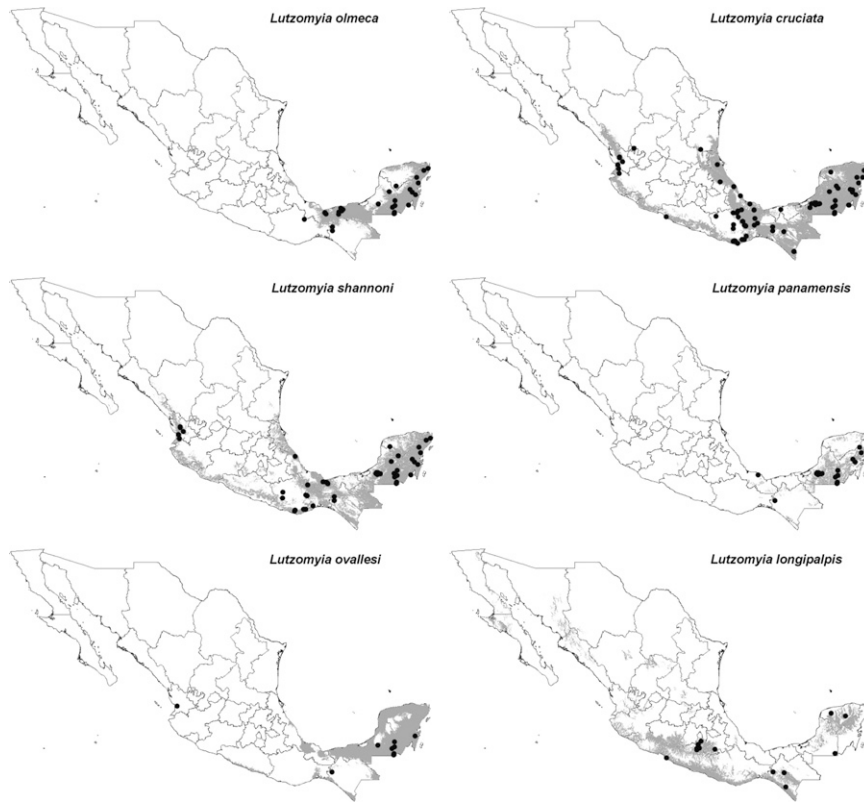


FIGURE 1. Ecological niche model-based distributional predictions for the species of *Lutzomyia* with known or potential medical importance in Mexico (gray). Black dots indicate species' known occurrence points. Non-significant models are not shown.

The distribution of the only proven CL vector in Mexico, *Lu. olmeca*, does not overlap all of the known CL cases in the country, suggesting that other sand fly species must be involved as vectors in those areas. On the basis of numbers of records and broad geographic distributions, we suggest that *Lu. cruciata* and *Lu. shannoni* would be the most suitable candidates: both are distributed broadly in southeastern Mexico and in the coastal lowlands. *Lutzomyia cruciata*, *Lu. shannoni*, *Lu. panamensis*, and *Lu. ylephiletor* have been found infected with *Leishmania*, although no studies on vector capacity of these species for disease transmission have been conducted in Mexico. The proportion of infected sand flies varied between species, places, and seasons (Table 1).^{17,69} Because *Lu. shan-*

noni occurs well north into the United States, incorporation of occurrences in the United States into next-generation models would be useful.⁷⁰ In this regard, *Leishmania mexicana* has also been found in the United States.⁷¹⁻⁷⁴

Leishmaniasis transmission in the states of Campeche and Quintana Roo is related to areas of moist forest, suggesting that infection is occurring by human proximity to areas with



FIGURE 2. Known occurrence points for non-modeled *Lutzomyia* species, Mexico.

TABLE 2
Area predicted and statistical significance of models from GARP and Maxent, and their coincidence, Mexico*

Algorithm	<i>Lutzomyia</i> species	Area predicted (km ²)	P	N (training data)
GARP	<i>Lu. cruciata</i>	703,980	6.04 × 10 ⁻⁶	82
	<i>Lu. diabolica</i>	669,718	0.331	11
	<i>Lu. longipalpis</i>	300,985	0.079	14
	<i>Lu. olmeca</i>	183,971	7.27 × 10 ⁻⁵	25
	<i>Lu. shannoni</i>	660,361	2.38 × 10 ⁻⁵	50
	<i>Lu. panamensis</i>	203,306	0.002	26
Maxent	<i>Lu. cruciata</i>	314,851	1.31 × 10 ⁻¹³	82
	<i>Lu. diabolica</i>	511,085	0.025	11
	<i>Lu. longipalpis</i>	171,022	0.001	14
	<i>Lu. olmeca</i>	123,742	1.30 × 10 ⁻⁷	25
	<i>Lu. shannoni</i>	253,205	4.10 × 10 ⁻⁸	50
	<i>Lu. panamensis</i>	53,263	1.58 × 10 ⁻⁷	26
Coincidence	<i>Lu. cruciata</i>	290,770	9.19 × 10 ⁻¹⁰	82
	<i>Lu. diabolica</i>	277,042	0.406	11
	<i>Lu. longipalpis</i>	83,335	0.006	14
	<i>Lu. olmeca</i>	98,055	3.26 × 10 ⁻⁶	25
	<i>Lu. shannoni</i>	218,944	9.79 × 10 ⁻⁹	50
	<i>Lu. panamensis</i>	37,096	0.006	26

*Models were performed by using 80% of point data (training data). The remaining 20% of occurrence data were overlapped on the predicted area, and a binomial table of presence/absence was built. Statistical significance of predictions was assessed by comparing observed successes and failures with random expectations and using a binomial test.

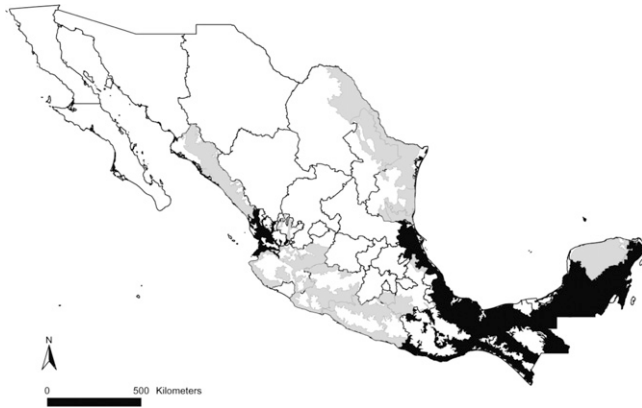


FIGURE 3. Leishmaniasis transmission areas in Mexico. Areas of recurrent transmission are in black, and areas of occasional transmission are in gray.

original vegetation coverage.^{10,75} A curious variation occurs in the state of Yucatan, where case incidence is low compared with the rest of the Peninsula, although the known reservoirs are present. The proven vector *Lu. olmeca* has been reported in this state, although its abundance is low compared with other sand flies in the area (e.g., *Lu. cruciata*). It is possible that the number of human cases caused by *Lu. o. olmeca* is minimal.⁷⁵

In Tabasco, most of the original vegetation coverage has been replaced, especially with cacao crops. In this region, *Lu. o. olmeca* has been identified as the primary vector, and clinical cases with a high prevalence of patients with diffuse CL have been recorded.⁷⁶ Areas with homogenous land coverage, such as crops, offer a less complex habitat where only disturbance-tolerant species can survive. Vector species with medical importance have shown to have the ability to establish populations in transformed areas after human interventions.⁷⁷ Our results showed a high proportion of potential distributions of species overlapping with transformed habitats, suggesting ample potential for domiciliation of the sand flies by shifting from a sylvatic to a peridomestic cycle. Clearly, landscape analyses along ecological gradients should be conducted to establish population dynamics of vectors and their impacts on parasite incidence and persistence.

In Nayarit, cases have been related to coffee plantations, and recent records of infected patients with *Lu. nia mexicana*



FIGURE 4. Ecoregions where leishmaniasis transmission is known to occur in Mexico. Moist forests are in black, Tamaulipan mezquital is in dark gray, and tropical deciduous forests are in light gray.

in the adjacent states of Durango and Sinaloa suggest a wider geographic range of the disease or a recent spread of the disease northwest.⁷⁸ Given their geographic distribution, vector species responsible for transmission in this region could include *Lu. shannoni*, *Lu. diabolica*, and *Lu. cruciata*.

Lutzomyia anthophora has been obtained only in north-eastern Mexico in the states of Nuevo Leon and Tamaulipas. Given the low number of records for *Lu. anthophora* in Mexico, ecological niche models could not be developed in this study. However, models based on collection points in the United States predict potential distributional areas for this vector in the states of Sinaloa, Sonora, and Baja California Sur in Mexico.⁷⁹ *Lutzomyia anthophora* is a non-anthropophilic feeder. Thus, although no human cases have been recorded in these states, sylvatic transmission may be occurring.⁷² The absence of an anthropophilic vector species provides a barrier for parasite transmission to humans. However, cases occurring along the Mexico–United States border area must be monitored carefully because other vector species can be incriminated in transmission of parasites to humans. For example, the spread of *Lu. diabolica* from the east would favor appearance of zoonotic transmission foci in the western states. Clearly, intensive monitoring of sand fly species along the Mexico–United States border is crucial for identifying potential risk areas of infection in the region, particularly in light of changing climates and shifting vector species distributions.⁷⁹

Little is known about VL in Mexico. The known vector *Lu. longipalpis* is distributed in tropical deciduous forests corresponding to areas of VL transmission. No parasite isolations from either vectors or reservoirs have been reported, and no surveillance has been undertaken by government health authorities. However, cases are known to occur and are likely underestimated because of limited access of rural communities to health services. Spread of VL has been documented in South America as a result of socio-environmental factors such as deforestation and human and domestic dog migration.^{80,81} The appearance of new foci in South America involve *Lu. longipalpis* as the principal VL vector and domestic dogs as reservoirs, as was assessed in the 2006 VL outbreaks in Brazil, Paraguay, and Argentina.⁸¹ These new transmission trends are leading increasingly to VL urbanization. Thus, we consider initiation of research on VL in Mexico to be of paramount importance.

Although leishmaniasis distribution and incidence in Mexico is likely underestimated, the general picture is one of focal regions with recurrent transmission. In Quintana Roo and Tabasco, where most cases have been historically reported, cases are usually related to areas with changing land use, suggesting the possibility of a domiciliation process. It is critical to evaluate the course of disease transmission under dynamic scenarios related to land use or climatic change.⁷⁹ More generally for leishmaniasis, given specific transmission areas in northern Mexico, the Balsas River Basin, the southeastern region, and the state of Nayarit, where particular species interactions seem to be occurring, we believe that different *Leishmania* strains are involved in different foci.

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Authors' addresses: Camila González, Centro de Ciencias de la Complejidad (C3), Universidad Nacional Autónoma de México, Torre de Ingeniería, Ciudad Universitaria, Mexico City 04510 DF, Mexico and Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Circuito Exterior, Edificio Nuevo, Módulo C, Apartado, Postal 70-153, Mexico City DF 04510, Mexico, E-mail: c.gonzalez2592@uniades.edu.co. Eduardo A. Rebollar-Téllez, Laboratorio de Entomología Médica, Departamento de Zoología de Invertebrados, Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, Ave. Universidad s/n, Ciudad Universitaria, Apartado, Postal 109-F, San Nicolás de los Garza, Nuevo León C.P. 66451, Mexico, E-mail: eduardo.rebollart1@uanl.edu.mx. Sergio Ibáñez-Bernal, Instituto de Ecología, AC Red Ambiente y Sustentabilidad, Carretera Antigua a Coatepec No. 351, El Haya, Xalapa, 91070, Veracruz, México, E-mail: sergio.ibanez@inecol.edu.mx. Ingeborg Becker-Fausser, Laboratorio de Inmunoparasitología, Facultad de Medicina, Universidad Nacional Autónoma de México, Hospital General de México, Dr. Balmis 148, Mexico City 06726 DF, Mexico, E-mail: becker@servidor.unam.mx. Enrique Martínez-Meyer and Víctor Sánchez-Cordero, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Circuito Exterior, Edificio Nuevo, Módulo C, Apartado, Postal 70-153, Mexico City DF 04510, Mexico, E-mails: emm@ibiologia.unam.mx and victor@ibiologia.unam.mx. A. Townsend Peterson, Biodiversity Institute, The University of Kansas, Lawrence, KS, E-mail: town@ku.edu.

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