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Ants (Hymenoptera: Formicidae) in a temperate ecosystem from La Malinche National Park, Mexico

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Abstract

The formicofauna of temperate Mexican ecosystems have been studied poorly. The objective of this study was to document the number of ant species in the protected natural area of La Malinche National Park, which features a temperate ecosystem in central Mexico. Furthermore, this study serves to update the list of species for Tlaxcala State in this area of the country. During 2015 to 2016, samples were collected along six 400 m linear transects in oak forest and agricultural land (2,700, 2,800, and 2,900 masl), using pitfall traps, baits with either protein or sugar, and hand collection from plants (where ants were foraging for floral nectar, extrafloral nectar, or honeydew). Twenty-three ant species belonging to 14 genera, 11 tribes, and 4 subfamilies were collected in La Malinche National Park. One genus (*Brachymyrmex* Mayr [Hymenoptera: Formicidae]), 7 species in the park, and 5 species in Tlaxcala State were new collection records. In pitfall traps, 23 species were recorded, where *Dorymyrmex insanus* Buckley, *Formica densiventris* Viereck, *Lasius mexicanus* Wheeler, and *Brachymyrmex musculus* Forel (all Hymenoptera: Formicidae) were collected exclusively from agricultural land. *Temnothorax brevispinosus* MacKay and *Stenamma huachucanum* Smith (both Hymenoptera: Formicidae) were collected exclusively in the oak forest, whereas 17 species were recovered from both habitats. Nine species were recorded from either protein or sugar baits; *Formica propatula* Francoeur and *Temnothorax texanus* Wheeler (both Hymenoptera: Formicidae) were recorded only in tuna baits, and with the remainder of the species collected with tuna and honey. Seven ant species were recorded from hand collections on plants. We have increased the number of ant species in Tlaxcala State from 53 to 58 (28 of which are present in La Malinche National Park). This faunal survey demonstrated that there is a great diversity of ant species in this temperate ecosystem. It is urgent to document the diversity of formicofauna in these types of ecosystems because they may possibly be the first to be negatively affected by climate change.

Key Words: Tlaxcala State; Formicinae; Myrmicinae; oak forest; agricultural land; protected natural area

Resumen

La formicofauna de los ecosistemas templados ha sido pobremente estudiada. El objetivo de este estudio fue documentar el número de especies de hormigas en el área natural protegida del Parque Nacional La Malinche, que cuenta con un ecosistema templado en el centro de México. Además, este estudio actualiza la lista de especies de hormigas para el Estado de Tlaxcala en esta área del país. Durante 2015 y 2016, las muestras fueron colectadas a lo largo de seis transectos lineales de 400 m en bosque de encino y campo de cultivo (2.700, 2.800, y 2.900 m sobre el nivel del mar), usando trampas pitfall, cebos con proteína o azúcar, y colecta manual sobre plantas (donde las hormigas estaban forrajeando néctar floral, néctar extrafloral, o honeydew). Veintitres especies de hormigas pertenecientes a 14 géneros, 11 tribus, y 4 subfamilias fueron colectadas en el Parque Nacional La Malinche. Un género (*Brachymyrmex* Mayr [Hymenoptera: Formicidae]), 7 especies en el Parque Nacional La Malinche, y 5 especies en el estado de Tlaxcala fueron nuevos registros. En trampas pitfall, 23 especies fueron colectadas, de éstas, *Dorymyrmex insanus* Buckley, *Formica densiventris* Viereck, *Lasius mexicanus* Wheeler, y *B. musculus* Forel (todas Hymenoptera: Formicidae) fueron exclusivamente colectadas del campo de cultivo. *Temnothorax brevispinosus* MacKay y *Stenamma huachucanum* Smith (ambas Hymenoptera: Formicidae) fueron exclusivamente colectadas en el bosque de encino, mientras que 17 especies se registraron en ambos hábitats. Nueve especies fueron colectadas con cebos de proteína o azúcar; *Formica propatula* Francoeur y *Temnothorax texanus* Wheeler (ambas Hymenoptera: Formicidae) fueron registradas solo en cebos de atún, y el resto de las especies fueron registradas en cebos de atún y miel. Siete especies fueron registradas a partir de la colecta manual sobre las plantas. Hemos incrementado el número de especies de hormigas conocidas en el estado de Tlaxcala de 53 a 58 (28 de las cuales están presentes en el Parque Nacional La Malinche). Este estudio de fauna demostró que hay una gran diversidad de especies de hormigas en este ecosistema templado. Es urgente documentar la diversidad de formicofauna en estos tipos de ecosistemas porque ésta puede ser posiblemente la primera en ser afectada negativamente por el cambio climático.

Palabras Clave: estado de Tlaxcala; Formicinae; Myrmicinae; bosque de encino; campo de cultivo; área natural protegida

Ants (Hymenoptera: Formicidae) are a very diverse and widely distributed group of organisms, being absent only from Greenland, Iceland, and Antarctica (Keller & Gordon 2009). Ecologically, they play an important role as ecosystem engineers because they are important

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in nutrient cycling, bioturbation, and pedogenesis (Arcila & Lozano-Zambrano 2003). In addition, ants interact in a variety of ways with other organisms in antagonistic or mutualistic manners. Antagonistically, they can function as plant herbivores. For example, in the case of leaf cutters, ants of the tribe Attini (Formicidae: Myrmicinae) harvest leaves not for their own consumption but as substrates to grow the fungus on which they feed. Leaf cutters are the primary consumers in terrestrial ecosystems in the New World, and their impact on vegetation is greater than any herbivore taxa (Beattie & Hughes 2009). This group can act as mutualists where they grow and feed on the fungus they are producing; although they consume part of the mycelium, the fungus relies exclusively on the ants for propagation and reproduction (Vásquez-Bolaños & Quiroz-Rocha 2013). Also, ants that defend plants against herbivores in exchange for the nectar that the plants produce from extrafloral nectaries can be considered mutualists (Beattie & Hughes 2009). Furthermore, those ants that act as seed dispersants are similarly regarded as mutualists (Rico-Gray & Oliveira 2007; Salazar-Rojas et al. 2012). For all of these reasons ants can be used as bioindicators (Arcila & Lozano-Zambrano 2003). Approximately 13,000 species of ants occur worldwide (Vázquez-Bolaños 2015). For Mexico, the most recent taxonomic review indicates that there are 927 present in the country belonging to 93 genera and 11 subfamilies, with the Myrmicinae subfamily being the most represented with 51.5% of the species (Vázquez-Bolaños 2015).

However, there are still knowledge gaps regarding the taxonomy of ants in Mexico. These knowledge gaps occur because identification to the species level often is difficult and complex; additionally the number of taxonomic specialists is lacking (Vázquez-Bolaños 2015). Generally, there appears to be a geographic bias in the sampling of this group of insects. Ants have been more studied in the tropics than temperate or arid areas of Mexico (Hinojosa Ontiveros et al. 2015). This is partly because, like other groups of organisms, ant diversity follows a latitudinal and altitudinal pattern, with most ant species occurring at lower forest elevations and tropical latitudes (Ward 2000). Studies in temperate ecosystems have shown differential composition in ant functionality when compared with tropical ecosystems. For example, cold climate specialists are an important component of temperate ecosystems (Andersen 1997, 2000; Cuautle et al. 2016) followed by Myrmicine generalists in low land tropics (Andersen 2000). Whereas tropical climate specialists are dominated by Dolichoderinae in arboreal tropical rainforests, Myrmicinae generalists and subordinate Camponotini are important dominant elements as well (Andersen 2000). It has been reported that cold climate specialists could be the first ant group negatively affected by climate change because they are associated with low temperature environments (Ellison 2012). Because of this, knowledge of ant communities in temperate ecosystems has become vitally important because changes in its abundance or richness could be the first warning of the effect of global warming, and changes in the way we manage natural resources should be implemented.

Rojas (2001) reported that Tlaxcala, Querétaro, Aguascalientes, and the state of Mexico were areas with the least ant diversity; however, it is believed that this is merely the result of having been poorly studied. Velasco Corona et al. (2007) recorded *Liometopum apiculatum* Mayr (Formicidae: Dolichoderinae) from Tlaxcala while Vásquez-Bolaños (2011) reported *Formica retecta* Francoeur (Formicidae: Formicinae) and *Pogonomyrmex barbatus* Smith (Formicidae: Myrmicinae) from the same city. Vásquez-Bolaños & Quiroz-Rocha (2013) reported that 14 states of Mexico, including Tlaxcala, did not have a local myrmecofauna survey. Later, Vásquez-Bolaños (2015) reported 14 species (5 subfamilies, 14 genera) for Tlaxcala State. Eleven of those reported species were state records as a result of the study by Landero-Torres et al. (2014) conducted in the Botanical Garden of Tizatlán, Tlaxcala. In a subsequent study, Landero-Torres et al. (2015) recorded 9 more species from Tlaxcala State (6 municipalities), including *Pheidole ceres* Wheeler (Formicidae: Formicinae), which was the first ant species reported for the Natural Protected Area, La Malinche National Park. Subsequently, Dubovikoff & Coronado-Blanco (2017) recorded 20 species for Tlaxcala State (7 municipalities) of which 8 species were collected in La Malinche National Park. Later, Castillo-Guevara et al. (2019) reported 4 new species in La Malinche National Park. Finally, Dáttilo et al. (2019) has reported 9 species in La Malinche National Park. As a result of the above studies, 53 species, 23 genera, 16 tribes, and 7 subfamilies were reported for Tlaxcala State. Despite the importance of La Malinche National Park as a protected area in a temperate ecosystem, a formicid fauna survey has been conducted in the area. The objective of this study was to update the fauna list of Formicidae species for the state of Tlaxcala, Mexico, by adding to the species inventory present in La Malinche National Park. The information, reported herein, contributes particularly to the knowledge of formicofauna of Tlaxcala and Mexico, and temperate ecosystems in general.

Materials and Methods

STUDY SITE

The study was conducted at La Malinche National Park, Tlaxcala, Mexico, with a total area of 46,093 ha (19.2333°N, 98.0333°W; 2,300–4,461 masl). Approximately 17,500 ha of the protected area of the park is comprised of coniferous and oak remnant forests surrounded by a landscape of human-induced grasslands, i.e., *Festuca tolucensis* H.B.K., *Muhlenbergia macroura* (Kunth), and *Stipa ichu* (Ruiz & Pav.) Kunth (all Poaceae), that usually is subjected to prescribed burning for thinning of the cultivation areas and secondary succession vegetation. The park is in the Mexican Transition Zone, a biogeographic province that was proposed by Halffter (2008) for insects and other groups. In this transition zone, there are Nearctic and Neotropical biota. Within the Mexican Transition Zone, there are a series of mountains and volcanoes that constitute the Trans-Mexican Volcanic Belt, in which La Malinche National Park is included. The Trans-Mexican Volcanic Belt is characterized as a route of dispersion for northern fauna to the mountains as a result of the many volcanic events present in this area. This situation has resulted in a high rate of change in species composition (i.e., beta diversity) in this area (Moctezuma et al. 2016). Mean annual precipitation is 800 mm; the rainy season is between Jun and Oct, and mean annual temperature is 15 °C (Lara 2006; Villers et al. 2006).

Our study was conducted in 7.68 ha of preserved transitional oak forest located within La Malinche National Park (i.e., *Quercus rugosa* Née, *Quercus crassipes* Humb. & Bonpl., *Quercus laurina* Bonpl., *Quercus crassifolia* Bonpl., and *Quercus dysophylla* Benth. [all Fagaceae]) that included hedgerows, rainfed agriculture (i.e., maize crops), and agricultural land used for grazing livestock outside La Malinche National Park, with an elevation range between 2,700 to 2,900 masl. At each elevation range (2,700, 2,800, and 2,900 masl) we established 3 paired 400 m linear transects, spaced at least 500 m apart, that included a transect in an oak forest and agricultural land (i.e., 1 transect pair at each altitudinal step). The separation between paired transects from each elevation range was at least 1.5 km. Ant samples were collected in each of these transects using 3 collection methods: pitfall traps, protein or sugar baits, and hand collection from plants where ants foraged for floral or extrafloral nectar as well as honeydew sources. To avoid interference between sampling methods, collections were performed on different d of the mo.

Pitfall Traps

The pitfall traps consisted of plastic cups (Reyma®, Reyma Group, Ecatepec, Mexico State, Mexico) (10 cm high) that contained 70 mL of propylene glycol. Traps were placed during the dry season (Mar 2015 and Apr 2016) and rainy season (Jul 2015 and Sep 2016). In each transect, 20 traps were placed 20 m apart (20 traps per transect × 6 transects × 2 seasons = 240 traps total). Trap contents were collected 96 h after placement. Captured ants were stored in 70% ethanol and transferred to the laboratory for identification.

Baits

Bait collections were conducted during Apr and Sep 2015. Bait stations were placed every 10 m along the linear transects described earlier. Each sampling point consisted of paired Petri dishes (at < 10 cm apart) with baits as attractants (placed in the center of the Petri dish). Two types of baits were used: 0.5 mL of commercial honey (Carlota®, Herdez, Mexico City, Mexico) diluted with 50% water, and 0.5 g of commercial tuna (Dolores®, Pinza Group, Mexico City, Mexico). For each transect, there were 9 sampling points with 18 Petri dishes. Each mo, 108 Petri dishes were placed (2 vegetation types × 3 transects × 9 sampling points × 2 types of bait), for a total of 648 Petri dishes. Baits were placed ad libitum in the center of each Petri dish. Weather permitting, Petri dishes were placed in the first pair of transects at 9:00 AM, the second pair of transects at 11:00 AM, and in the third at pair at 1:00 PM, and remained in place for 4 h each. The order of placement of Petri dishes in transects was alternated each mo. Ants from collections were stored in 70% ethanol and transferred to the laboratory for identification.

Hand Collection from Plants

For each transect, hand collection of ants from plants was conducted every mo from Jun 2015 to Jul 2016 on d with mild weather conditions. Walking counts were performed from 8:00 AM to 1:00 PM beginning from a different transect and different vegetation type each time to avoid sample location bias. Observers recorded individual ants showing some type of interaction with any plant at a parallel distance no more than 10 m from the center line of the transect. Each observed specimen was collected with an entomological aspirator or forceps and preserved individually in capped 1.5 mL Eppendorf® Safe-Lock™ Axygen® microcentrifuge tubes (Corning Inc., Corning, New York, USA) containing 70% alcohol.

Ants were identified using the taxonomic keys of Mackay & Mackay (1989) following the classification proposed by Vásquez-Bolaños (2019). Identification also was aided by myrmecology specialists from the Entomology Laboratory of the Institute of Ecology AC (J. E. Valenzuela-González), University of Quebec, in Chicoutimi; the Department of Fundamental Sciences (A. Francoeur); and the University Autonoma of Guadalajara (M. Vásquez-Bolaños). A reference collection of ants collected in the study was created and later integrated into the Entomological Collection (Formicidae) of the Institute of Ecology AC, Xalapa, Veracruz, Mexico (IEXA; Reg. SEMARNAT: Ver. IN.048.0198), and the Entomology Laboratory of the University of Las Americas Puebla, San Andrés Cholula, Puebla, Mexico.

Results

In La Malinche National Park, a total of 11,064 ants were collected that included workers, soldiers, and queens from pitfall traps; 3,498 ants collected from protein or sugar baits, and 1,053 ants collected from plants. Twenty-three ant species belonging to 14 genera, 11 tribes, and 4 subfamilies were recorded (Table 1). One genera (*Brachymyrmex*), 7 species (in La Malinche National Park: *Dorymyrmex insanus* [Buckley], *Camponotus pudorosus* Emery, *Formica pacifica* Francoeur, *Formica propatula* [Francoeur], *Lasius mexicanus* Wheeler, *Brachymyrmex musculus* Forel, and *Crematogaster lineolata* [Say] [all Hymenoptera: Formicidae]) (Table 1) and 5 species (in Tlaxcala: *D. insanus*, *F. pacifica, L. mexicanus*, *B. musculus*, and *C. lineolata*) (Table 2) were new records. Formicinae and Myrmicinae were the subfamilies most represented with 11 and 10 species, respectively, while Dorylinae and Dolichoderinae were represented by only 1 species each. According to the sampling method used, all species were recorded in pitfall traps, 9 species were collected on baits, and 7 species were hand collected from plants.

All species were present in both environments in pitfall traps, except for *D. insanus*, *Formica densiventris* Viereck (Hymenoptera: Formicidae), *L. mexicanus*, and *B. musculus*, which were recorded only from agricultural land, while *Temnothorax brevispinosus* Mackay and *Stenamma huachucanum* Smith (both Hymenoptera: Formicidae) were recorded only in oak forest (Table 1). *Formica propatula* and *Temnothorax texanus* Wheeler (Hymenoptera: Formicidae) were collected from the tuna bait, whereas 6 species were recorded from both types of baits, with only 3 unidentified *Camponotus* specimens collected exclusively with honey (Table 1).

We found representatives of the following functional groups (based on the criteria of Andersen 2000): cold-climate specialists (*Lasius latipes* Walsh, *L. mexicanus*, *Lasius niger* (L.), *T. brevispinosus*, *Temnothorax punctithorax* Mackay, *T. texanus*, and *S. huachucanum*), opportunists (*D. insanus*, *F. densiventris*, *F. pacifica*, *F. propatula*, *F. retecta*, and *Myrmica mexicana* Wheeler), generalized Myrmicinae (*Pheidole chalca* Wheeler, *Pheidole soritis* Wheeler, *C. lineolata*, and *Monomorium minimum* [Buckley]), tropical climate specialists (*Neivamyrmex pilosus* Smith, *B. musculus*, and *Solenopsis picea* Emery), subordinate Camponotini (*Camponotus picipes pilosulus* Emery and *Camponotus pudorosus* Emery), and hot-climate specialists (*Myrmecocystus melanoticus* Wheeler) (all Hymenoptera: Formicidae).

Discussion

Tlaxcala is a small state in central Mexico (4,016 m^2), and ant collections have been carried out in only 12 of the 60 municipalities that comprise it: Tlaxco, Tizatlán, Huamantla, Nanacamilpa, Tepetitla, Tlaxcala, Xaloztoc, Zacatelco, Tzompantepec, Teacalco, Apizaco, and Tetlanohcan. Of the representative vegetation types present in Tlaxcala, the oak forest and agricultural land ants had not been sampled until recent studies by Castillo-Guevara et al. (2019) and Dáttilo et al. (2019) in the La Malinche National Park. Prior to these studies, Landero-Torres et al. (2015) reported on the first ant species on record (*P. ceres*) in La Malinche National Park, but recorded from pine and oyamel forest at 3,086 masl. Later, Dubovikoff & Coronado-Blanco (2017) recorded 20 ant species for Tlaxcala State, of which 8 species were collected in La Malinche National Park (*Formica browni* Francoeur, *F. densiventris*, *Formica moki* Wheeler, *F. retecta*, *Pheidole calens* Forel, *T. brevispinosus*, *T. punctithorax*, and *Stenamma ignotum* Branstetter) (all Hymenoptera: Formicidae). Recently Castillo-Guevara et al. (2019) reported 4 species from La Malinche National Park, where *C. p. pilosulus* and *M. minimum* were new records. *Formica retecta* and *M. mexicana* were reported previously by Dubovikoff & Coronado-Blanco (2017), but from outside La Malinche National Park. More recently, Dáttilo et al. (2019) reported 9 species for La Malinche National Park: *P. soritis* Wheeler, *P. chalca* Wheeler, *M. melanoticus*, *L. niger*, *L. latipes* Walsh, *S. picea*, *Neivamyr-*

Table 1. Inventory of ant species collected in La Malinche National Park in Tlaxcala, Mexico, by [1]Vásquez-Bolaños (2011); [2]Landero-Torres et al. (2015); [3]Vásquez-Bolaños (2015); [4]Dubovikoff & Coronado-Blanco (2017); [5]Castillo-Guevara et al. (2019); [6]Dáttilo et al. (2019). Abbreviations: OF = oak forest, AL = agricultural land, P = pitfall trap, B = bait, HB = honey bait, TB = tuna bait, HCP = hand collection from plants. Mexico distribution ant species (Vásquez-Bolaños 2015). **Camponotus pudorosus* and *Formica propatula* had been reported for Tlaxcala State, but not specifically in La Malinche National Park.

FORMICIDAE Latreille, 1809	Vegetation types	Collecting techniques	Distribution
DOLICHODERINAE Forel, 1878			
Leptomyrmecini Emery, 1913			
Dorymyrmex Mayr, 1866			
Dorymyrmex insanus (Buckley, 1866)	AL	P	BC, BCS, CHIH, DGO, HGO, NAY, NL, PUE, QRO, QR, SIN, SON, TAMPS, VER, YUC
DORYLINAE Leach, 1815			
Dorylini Ashmead, 1905			
Neivamyrmex Borgmeier, 1940			
Neivamyrmex pilosus Smith, 1858[6]	AL, OF	P	
FORMICINAE Latreille, 1809			
Camponotini Forel, 1878			
Camponotus Mayr, 1861			
Camponotus picipes pilosulus Emery, 1925[5,6]	AL, OF	P	
Camponotus pudorosus Emery, 1925[4]*	AL, OF	P, HCP	
Formicini, Latreille, 1809			
Formica Linnaeus, 1758			
Formica browni Francoeur, 1973[4]			
Formica densiventris Viereck, 1903[4]	AL	P	
Formica moki Wheeler, 1906[4]			
Formica pacifica Francoeur, 1973	AL, OF	P, HB, TB, HCP	VER
Formica propatula Francoeur, 1973[2,4]*	AL, OF	P, TB, HCP	
Formica retecta Francoeur, 1973[4,6]	AL, OF	B	
Lasiini Ashmead, 1905			
Lasius Fabricius, 1804			
Lasius latipes Walsh, 1863[6]	AL, OK	P, HB, TB	
Lasius mexicanus Wheeler, 1917	AL	P	HGO, PUE, VER
Lasius niger Linnaeus, 1758[6]	AL, OF	P	
Myrmecocystus Wesmael, 1838			
Myrmecocystus melanoticus Wheeler, 1914[6]	AL, OF	P	
Plagiolepidini Ashmead, 1905			
Brachymyrmex Mayr, 1868			
Brachymyrmex musculus Forel, 1899	AL	P	DGO, HGO, MOR, PUE, VER
MYRMICINAE Lepeletier, 1835			
Attini Smith, 1858			
Pheidole Westwood, 1839			
Pheidole calens Forel, 1901[4]			
Pheidole ceres Wheeler, 1904[2]			
Pheidole chalca Wheeler, 1914[6]	AL, OF	P	
Pheidole soritis Wheeler, 1908[6]	AL, OF	P, HB, TB	
Crematogastrini Forel, 1893			
Crematogaster Lund, 1831			
Crematogaster lineolata Say, 1836	AL, OF	P, HCP	CHIH, HGO, NL, TAMPS
Temnothorax Mayr, 1861			
Temnothorax brevispinosus MacKay, 2000[4]	OF	P	
Temnothorax punctithorax MacKay, 2000[4,6]	AL, OF	P, HB, TB, HCP	
Temnothorax texanus Wheeler, 1903[6]	AL, OF	P, TB	
Myrmicini Lepeletier de Saint-Fargeau, 1835			
Myrmica Latreille, 1804			
Myrmica mexicana Wheeler, 1914[4,5,6]	AL, OF	P, HB, TB, HCP	
Solenopsidini Forel, 1893			
Monomorium Mayr, 1855			
Monomorium minimum (Buckley, 1867)[5,6]	AL, OF	P, HB, TB, HCP	
Solenopsis Westwood, 1840			
Solenopsis picea Emery, 1896[6]	AL, OF	P	
Stenammini Ashmead, 1905			
Stenamma Westwood, 1839			
Stenamma huachucanum Smith, 1957[6]	OF	P	
Stenamma ignotum Branstetter, 2013[4]			

Mexico state abbreviations: BC = Baja California, BCS = Baja California Sur, CHIH = Chihuahua, DGO = Durango, HGO = Hidalgo, MEX = Estado de México, MOR = Morelia, NAY = Nayarit, NL = Nuevo León, PUE = Puebla, QRO = Querétaro, QR = Quintana Roo, SIN = Sinaloa, SON = Sonora, TAMPS = Tamaulipas, VER = Veracruz, YUC = Yucatán.

Table 2. Inventory of ant species in Tlaxcala State, Mexico. Ant species marked with an asterisk (*) were collected in La Malinche National Park during the current study.

FORMICIDAE Latreille, 1809	References
DOLICHODERINAE Forel, 1878	
Leptomyrmecini Emery, 1913	
Dorymyrmex Mayr, 1866	
Dorymyrmex insanus (Buckley, 1866)*	
Dorymyrmex bicolor Wheeler, 1906	Landero-Torres et al. 2014; Vásquez-Bolaños 2015; Dubovikoff & Coronado-Blanco 2017
Dorymyrmex smithi Cole, 1936	Dubovikoff & Coronado-Blanco 2017
Linepithema Mayr, 1866	
Linepithema dispertitum (Forel, 1885)	Landero-Torres et al. 2014; Vásquez-Bolaños 2015
Tapinomini Emery, 1913	
Liometopum Mayr, 1861	
Liometopum apiculatum Mayr, 1870	Velasco Corona et al. 2007; Vásquez-Bolaños 2011, 2015; Dubovikoff & Coronado-Blanco 2017
Tapinoma Foerster, 1850	
Tapinoma litorale Wheeler, 1905	Dubovikoff & Coronado-Blanco 2017
Tapinoma melanocephalum (Fabricius, 1793)	Landero-Torres et al. 2014; Vásquez-Bolaños 2015
DORYLINAE Leach, 1815	
Dorylini Ashmead, 1905	
Labidus Jurine, 1807	
Labidus coecus (Latreille, 1802)	Landero-Torres et al. 2014; Vásquez-Bolaños 2015
Neivamyrmex Borgmeier, 1940	
Neivamyrmex pilosus Smith, 1858*	Dáttilo et al. 2019
ECTATOMMINAE Emery, 1895	
Ectatommini Emery, 1895	
Gnamptogenys Roger, 1863	
Gnamptogenys strigata (Norton, 1868)	Landero-Torres et al. 2014; Vásquez-Bolaños 2015
FORMICINAE Latreille, 1809	
Camponotini Forel, 1878	
Camponotus Mayr,1861	
Camponotus atriceps (Smith, 1858)	Landero-Torres et al. 2014; Vásquez-Bolaños 2015
Camponotus picipes pilosulus Emery, 1925*	Castillo-Guevara et al. 2019; Dáttilo et al. 2019
Camponotus planatus Roger, 1863	Landero-Torres et al. 2015
Camponotus pudorosus Emery, 1925*	Dubovikoff & Coronado-Blanco 2017
Formicini, Latreille, 1809	
Formica Linnaeus, 1758	
Formica browni Francoeur, 1973	Dubovikoff & Coronado-Blanco 2017
Formica densiventris Viereck, 1903*	Dubovikoff & Coronado-Blanco 2017
Formica moki Wheeler, 1906	Dubovikoff & Coronado-Blanco 2017
Formica pacifica Francoeur, 1973*	
Formica propatula Francoeur, 1973*	Landero-Torres et al. 2015; Dubovikoff & Coronado-Blanco 2017
Formica pulla Francoeur,1973	Dubovikoff & Coronado-Blanco 2017
Formica retecta Francoeur, 1973*	Vázquez-Bolaños 2011, 2015; Dubovikoff & Coronado-Blanco 2017; Castillo-Guevara et al. 2019; Dáttilo et al. 2019
Formica xerophila Smith, 1939	Dubovikoff & Coronado-Blanco 2017
Lasiini Ashmead, 1905	
Lasius Fabricius, 1804	
Lasius latipes Walsh, 1863*	Dubovikoff & Coronado-Blanco 2017; Dáttilo et al. 2019
Lasius mexicanus Wheeler, 1917*	
Lasius niger Linnaeus, 1758*	Dáttilo et al. 2019
Lasius sitiens Wilson, 1955	Dubovikoff & Coronado-Blanco 2017
Myrmecocystus Wesmael, 1838	
Myrmecocystus melanoticus Wheeler, 1914*	Dáttilo et al. 2019
Plagiolepidini Ashmead, 1905	
Brachymyrmex Mayr, 1868	
Brachymyrmex musculus Forel, 1899*	
Paratrechina Motschoulsky, 1863	
Paratrechina longicornis (Latreille, 1802)	Landero-Torres et al. 2014; Vásquez-Bolaños 2015
MYRMICINAE Lepeletier, 1835	
Attini Smith, 1858	
Atta Fabricius, 1818	
Atta mexicana (Smith, 1858)	Landero-Torres et al. 2014; Vásquez-Bolaños 2015
Pheidole Westwood, 1839	
Pheidole azteca Wilson, 2003	Landero-Torres et al. 2015

Table 2. (Continued) Inventory of ant species in Tlaxcala State, Mexico. Ant species marked with an asterisk (*) were collected in La Malinche National Park during the current study.

FORMICIDAE Latreille, 1809	References
Pheidole calens Forel, 1901	Dubovikoff & Coronado-Blanco 2017
Pheidole ceres Wheeler, 1904	Landero-Torres et al. 2015; Vásquez-Bolaños 2015
Pheidole chalca Wheeler, 1914*	Dáttilo et al. 2019
Pheidole deceptrix Forel, 1899	Landero-Torres et al. 2015
Pheidole hirtula Forel, 1899	Landero-Torres et al. 2014; Vásquez-Bolaños 2015
Pheidole hyatti Emery, 1895	Dubovikoff & Coronado-Blanco 2017
Pheidole nitidicollis Emery, 1896	Landero-Torres et al. 2015
Pheidole polymorpha Wilson, 2003	Dubovikoff & Coronado-Blanco 2017
Pheidole tepicana Pergande, 1896	Landero-Torres et al. 2015
Pheidole soritis Wheeler, 1908*	Dáttilo et al. 2019
Crematogastrini Forel, 1893	
Crematogaster Lund, 1831	
Crematogaster lineolata Say, 1836*	
Crematogaster opaca Mayr, 1870	Dubovikoff & Coronado-Blanco 2017
Temnothorax Mayr, 1861	
Temnothorax brevispinosus MacKay, 2000*	Dubovikoff & Coronado-Blanco 2017
Temnothorax manni (Wheeler, 1914)	Dubovikoff & Coronado-Blanco 2017
Temnothorax punctithorax MacKay, 2000*	Dubovikoff & Coronado-Blanco 2017; Dáttilo et al. 2019
Temnothorax texanus Wheeler, 1903*	Dáttilo et al. 2019
Myrmicini Lepeletier de Saint-Fargeau, 1835	
Myrmica Latreille, 1804	
Myrmica mexicana Wheeler, 1914*	Dubovikoff & Coronado-Blanco 2017; Castillo-Guevara et al. 2019; Dáttilo et al. 2019
Myrmica striolagaster Cole, 1953	Dubovikoff & Coronado-Blanco 2017
Ponogomyrmecini Ward, Brady, Fisher & Schultz, 2014	
Pogonomyrmex Mayr, 1868	
Pogonomyrmex barbatus Smith, 1858	Vásquez-Bolaños 2011, 2015
Solenopsidini Forel, 1893	
Monomorium Mayr, 1855	
Monomorium ebenium Forel, 1891	Landero-Torres et al. 2014; Vásquez-Bolaños 2015
Monomorium minimum (Buckley, 1867)*	Castillo-Guevara et al. 2019; Dáttilo et al. 2019
Solenopsis Westwood, 1840	
Solenopsis geminata (Fabricius, 1804)	Landero-Torres et al. 2014; Vásquez-Bolaños 2015
Solenopsis picea Emery, 1896*	Dáttilo et al. 2019
Stenammini Ashmead, 1905	
Stenamma Westwood, 1839	
Stenamma huachucanum Smith, 1957*	Dáttilo et al. 2019
Stenamma ignotum Branstetter, 2013	Dubovikoff & Coronado-Blanco 2017
PONERINAE Lepeletier, 1835	
Ponerini Lepeletier, 1835	
Odontomachus Latreille, 1804	
Odontomachus leticeps Roger, 1952	Landero-Torres et al. 2015
PSEUDOMYRMECINAE Smith, 1952	
Pseudomyrmecini Smith, 1952	
Pseudomyrmex Lund, 1831	
Pseudomyrmex pallidus (Smith, 1855)	Landero-Torres et al. 2015

mex pilosus Smith, *T. texanus*, and *S. huachucanum* (all Hymenoptera: Formicidae).

Our study is the first taxonomic faunal survey conducted exclusively at La Malinche National Park using 3 collection methods over a period of 2 yr. This fact makes it the most recent complete study conducted in the area. Ant species recorded in La Malinche National Park and Tlaxcala State belonged to the following functional groups: cold-climate specialists (7 species), opportunists (6 species), generalized Myrmicinae (4 species), tropical climate specialists (3 species), subordinate Camponotini (2 species), and hot-climate specialists (1 species). As expected, cold-climate specialists were the best represented group in this temperate high-altitude ecosystem. Opportunist species were the second functional group in terms of number of species. This is interesting given that this functional group is associated with sites with high levels of disturbance and stress; although some of these species are found only on agricultural land (*D. insanus* and *F. densiventris*), the majority were found in both vegetation types. The generalized Myrmicinae, which are associated with warm, open environments, were found in both vegetation types, although numerically they were better represented in agriculture land (Castillo-Guevara et al. 2019). Of the 23 species of ants recorded in our study, 2 cold-climate specialist species were exclusively present in the oak forest, whereas 4 species that were opportunists, cold-climate specialists, and tropical climate specialists were collected exclusively from agricultural land (Table 1). Cold-climate

specialists that were found only in the oak forest, such as T*. brevispinosus* and *S. huachucanum*, could be used as positive bioindicators for monitoring this protected natural area. The functional groups that were present in both vegetation types were cold-climate specialists, generalized Myrmicinae opportunists (with 4 species in each group), subordinate Camponotini, tropical climate specialists (with 2 species in each group), and hot-climate specialists (with 1 species). Whereas the *Formica* genus is represented by a great diversity of species, our survey reported only 4 species. We also collected representatives from the *Fusca* group, which are considered opportunist species (*F. densiventris*, *F. pacifica*, *F. propatula*, *F. retecta*) from both vegetation types.

Our study updates and lists new records in La Malinche National Park for 7 species belonging to 6 genera. Overall, we recorded 28 ant species of 14 genera, 11 tribes, and 5 subfamilies for the La Malinche National Park (Table 1). It is necessary to carry out systematic sampling in other vegetation types in La Malinche National Park. This work increases the number of known species of Tlaxcala State (Table 2), in addition to the 53 species previously reported by Landero-Torres et al. (2015), Vásquez-Bolaños (2015), Dubovikoff & Coronado-Blanco (2017), Castillo-Guevara et al. (2019), and Dáttilo et al. (2019). Studies on ants in Tlaxcala State have begun only fairly recently. The first report of 1 ant species, *Liometopum apiculatum* Mayr (Hymenoptera: Formicidae) (Velasco Corona et al. 2007), was published in 2007; Vásquez-Bolaños (2011) reported *Pogomyrmex barbatus* Smith and *F. retecta*. Later, Landero-Torres et al. (2014) further reported 11 ant species, and Vásquez-Bolaños (2015) recently published 14 ant species. That same yr, Landero-Torres et al. (2015) reported 9 new ant species for Tlaxcala State, and Dubovikoff & Coronado-Blanco (2017) reported 20 new ant species. Castillo-Guevara et al. (2019) reported 2 new species; more recently Dáttilo et al. (2019) reported 8 new ant species in Tlaxcala State. The updated number of species for Tlaxcala State now increases to 58 species, belonging to 24 genera, 16 tribes, and 7 subfamilies.

After the present study, Tlaxcala State now can be compared, with respect to the number of reported ant species, with the states of Durango (60 species) and Puebla (61 species). Ant diversity in Tlaxcala State now is superior to 10 Mexican states: Estado de México (16), Guanajuato (16), Querétaro (17), Distrito Federal (18), Zacatecas (21), Michoacán (36), Campeche (37), Colima (40), Sinaloa (48), and Coahuila (51) (Ríos-Casanova 2014), all of which are far larger in geographical area compared with Tlaxcala State. These data suggest that there is still a large gap to cover with respect to ant diversity in such a megadiverse country as Mexico.

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