Biol Invasions (2021) 23:1669–1680
https://doi.org/10.1007/s10530-020-02423-1

ALIEN FLORAS AND FAUNAS 8

Alien ants (Hymenoptera: Formicidae) in Mexico: the first database of records

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Received: 23 June 2020 / Accepted: 6 November 2020

Abstract The synthesis of comprehensive databases on the identity and distributions of alien organisms is a critical step to developing informed invasion management plans and identifying areas that are data-deficient. Here, we assembled all available records of alien ant distributions for Mexico, based on the literature, databases and unpublished data for a period ranging from 1855 to 2019; we compiled 967 records for 42 ant species non-native to Mexico, distributed across 438 localities. For the first time, we present mapped records and the distribution database of alien ants which is available through The Global Ant Biodiversity Informatics database at www.antmaps.org. The most commonly recorded species were *Paratrechina longicornis*, *Monomorium pharaonis* and *Anoplolepis gracilipes*. The states with the most records were Veracruz, Chiapas, Jalisco and Quintana Roo. The alien ants were most frequently encountered in urban areas (372 records) and in deciduous forest habitats (220). We provide summary of their distribution patterns and other related information useful for the control of these species in Mexico.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10530-020-02423-1) contains supplementary material, which is available to authorized users.

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Keywords Non-native · Ants · Distribution · Mexico · Invasions · Exotic

Introduction

Many ant species have been introduced to Mexico through human activities, including the five species considered in the 100 of the world's worst invasive species compiled by IUCN (Lowe et al. 2000; Cupul-Magaña 2009; Sánchez-Soto 2013). However, a limited number of studies document the distribution and effects of these species across the country (Cupul-Magaña 2009; Vásquez-Bolaños 2015a). Currently, no summary of introduced ant species records nor any evaluation of their impact at the country level exist. Here, we present all currently available records for the alien ants in Mexico, a country with a large environmental heterogeneity and high potential to host non-native species both from temperate and tropical zones. After providing an overview of the oldest records for each species, we then summarize their main distribution trends.

The displacement of native species of insects and other invertebrates is likely among the most detrimental effects of invasive ants in Mexico. They also disrupt the relationships among native plants and insects; reduce the quality of habitat for many vertebrates and plants; attack and kill the brood or juvenile individuals of both invertebrates and vertebrates species (e.g. reptiles, birds) (Allen et al. 2017); or have diverse negative impacts on agricultural production (Plentovich et al. 2009; Rosas-Mejía and Janda 2017, 2018). In urban areas, they are also known to act as vectors of diseases (Sánchez-Soto 2013), in particular within sensitive areas such as medical facilities. In some Mexican cities, the Home Infestation index by ants was reported up to 90% (Puerto Vallarta) of which 42% of records was represented by the alien ant *Tapinoma melanocephalum* (Cupul-Magaña 2009), suggesting that these ants can be important pests of the urban ecosystems in Mexico.

The introduction pathways of alien ants to Mexico have not been sufficiently evaluated (Del-Val et al. 2017). As is the case with other alien species or invasive ants in other countries, we presume that the main sources of introductions are with transport of commercial products, biological materials (e.g. plants), soil and related items. Mexico imports and exports large volumes of materials and products through various sources of transport, with many major port hubs located on both Atlantic and Pacific coasts. This makes Mexico not only an easy target of such invasions but also an important hub for the further spread of various alien species.

Currently, there is no established strategy for the prevention or management of invasive ants in Mexico which would be coordinated at the federative level. In order to provide data for the development of informed management decisions and to evaluate where more data are needed, we assembled all alien ant records for the country and made them publically available as part of the Global Ant Biodiversity database (GABI) (Guénard et al. 2017).

Materials and methods

We reviewed all the available literature with at least one alien species reported from Mexico, published between 1855 and 2019. The literature included articles in journals databased in ISI Web of Science and also non-indexed publications such as diploma theses, reports and regional species lists. We also included all records from outdoors and indoors available in public databases containing information on distribution of ants, including AntWeb.org, and GABI database at www.antmaps.org (Janicki et al. 2016; Guénard et al. 2017). The taxonomic status of the records was checked and updated whenever necessary, following the latest version of the Bolton's Ant Catalogue at AntCat.org (Bolton 2012). We also contacted myrmecologists and entomologists active in Mexico to contribute any unpublished records based on specimens for any alien ants. Furthermore, during the years 2016–2017, we hand collected specimens and distribution records for non-native ants from the

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states of Ciudad de México, Coahuila, Guanajuato, Nuevo León, Oaxaca, Puebla, Sinaloa, Tamaulipas and Veracruz. Collected samples were sorted, mounted and identified following the species keys available for the genera, or specialized keys for alien species. The complete list of literature and record sources is part of the database associated with this article (Supplementary data 1).

All records were formatted according to the GABI standards (Guénard et al. 2017) and included information such as unique identifying number, collection location, geographic location, habitat data and other related information. Some geographic coordinates were obtained secondarily from the locality references and labels of the specimens. For 165 records with only geographic region or state listed instead of specific locality or GPS, and with no other records for the region, the coordinates of the largest city in the region were used. The habitat type was obtained from the collecting information in the source literature and databases and synonymized with the latest vegetation and habitat reference maps for México (González and Smith 1998).

The occurrence records were mapped using ArcGIS (Software Gis) version 10.2. The cumulative numbers of species and records for the states and habitats were calculated in MS Excel, and R Studio version 1.1.453 (Team R studio 2015). The first records for the presence of each species in Mexico were obtained from the literature and our database. We used simple linear regression (Team R studio 2015) to analyze whether there's a correlation between the number of records and the number of alien species. To evaluate how the records of alien ants relate to overall sampling intensity of ants across the country, we used simple linear regression to compare it with records of native species assembled in the recent comprehensive overview (Dáttilo et al. 2019). We compared the numbers of records by state (20,745 records) and by habitat, whenever the original data allowed to match adequately the habitat type distinguished by both studies (14,992 records).

To ensure the compatibility of our data with other studies and taxa, we provide an overview of the categories distinguished for alien ants in Mexico. Our terminology follows the categories recommended by Blackburn et al. (2011), where 'alien' refers to any species which has been unintentionally or intentionally transported outside of its original range (Pyšek et al. 2004). In this study it is also synonymous with the term 'non-native' while the GABI database currently refers to alien ants with established populations outdoors as 'exotic'. As 'invasive' we refer to alien species which are established, with self-sustaining populations in the wild and their spread has been documented over larger areas within the country (Blackburn et al. 2011).

Results

We assembled 967 records for 42 ant species alien to Mexico, distributed across 438 localities (Fig. 1). Of these 607 were from literature, 282 from databases, 72 were provided by the collaborating researchers and 22 by the authors of this study (Table 1). Based on the distributional and life history data we can consider 30 species as invasive alien and 12 species in the broader category of non-invasive alien, likely in the process of establishment.

The most frequently recorded species were *Paratrechina longicornis* (175), *Monomorium pharaonis* (94) and *Anoplolepis gracilipes* (57). The states with the highest number of records were Veracruz (161), Chiapas (122), Jalisco (92) and Quintana Roo (71) (Fig. 1). While the number of documented alien species has been growing linearly for the past 60 years, the majority of distributional records originated during the last 20 years (Fig. 2). There was a strong positive correlation ($R^2 = 0.794$, $P = 0.000$) between the number of records and the number of alien species. The number of alien species records and the alien species richness were positively correlated with the number of records for native species, when categorized by state (alien records: $R^2 = 0.632$, $P = 0.000$; alien species richness: $R^2 = 0.272$, $P = 0.002$). When compared by habitat, there was no apparent relationship among the number of alien records or alien species richness and the sampling effort for native species (records: $R^2 = -0.04852$, $P = 0.61$; number of species: $R^2 = 0.017$, $P = 0.6146$). The numbers of records for each state and habitat are listed in Supplementary data 1. The majority of alien ant species (30) reported here should be also considered invasive. The status of 12 species cannot be confirmed without further targeted studies and these species are here considered only within the broader category non-invasive alien (non-native). The

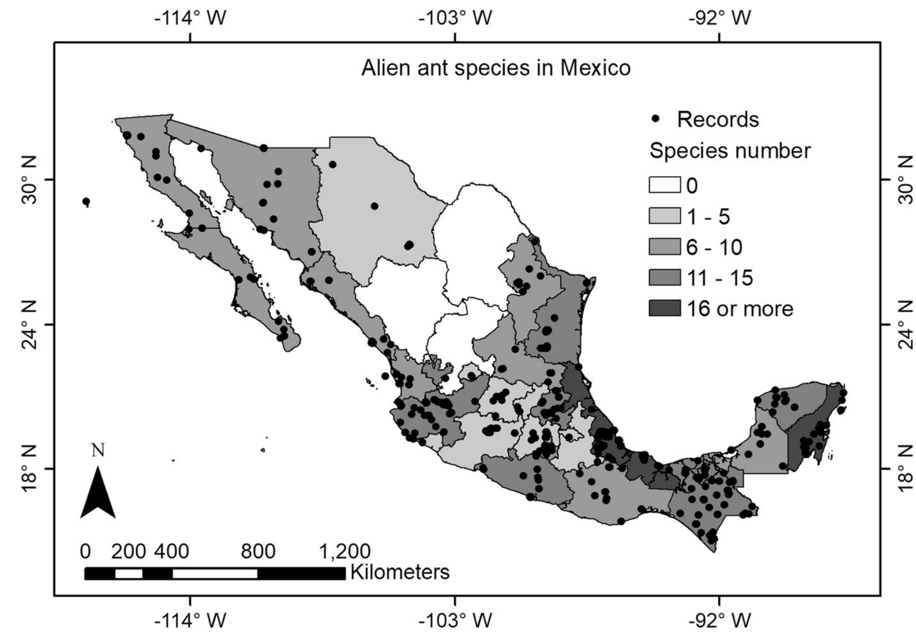

Fig. 1 Distribution records of 42 species of alien ants and number of alien species by state in Mexico

presence of invasive ants was also detected within 10 protected areas across Mexico.

The majority of alien species recorded belongs to the subfamily Myrmicinae (26), eight to Formicinae, four to Ponerinae and three to Dolichoderinae. The species with the highest number of Mexican state records were *P. longicornis* (25), *Monomorium pharaonis* (15) and *Cardiocondyla emeryi* (14) (Table 1). The earliest record for a non-native ant in Mexico dates from 1855 for *Tetramorium bicarinatum*, while the species documented as introduced the most recently were *Nylanderia flavipes* and *Trichomyrmex destructor* in 2017 and 2013 respectively (Table 1).

The localities from which alien ants were reported were assigned to 18 types of habitats, based on the collecting data and the vegetation maps (González and Smith 1998). The ants were most frequently encountered in urban areas (372 records) and in deciduous forest (220) (Fig. 3).

Discussion

This study presents the most complete dataset of records for alien ants in Mexico to date. With 42 species registered, this represents a considerable increase from the previously reported 32 species (Vásquez-Bolaños 2015b; Dáttilo et al. 2019). Considering the size, geographic span of the country, diversity of climate and the presence of subtropical and tropical regions, along with the intense commerce, it is likely that the actual number of alien species is higher or that more successful non-native ant species may be introduced in the future. For instance, the current number of alien ant species reported from Mexico is lower than the not so distant, but much smaller, state of Florida (57) (Deyrup 2003; Guénard et al. 2017).

Knowledge on alien ants in Mexico across the different states is somewhat related to the overall sampling efforts conducted on ants. Indeed, our results show that the intensity of sampling effort (number of records for native species) within states can hint on both the number of records and species richness of non-native ants. Other factors, however, here not considered, could also be important as the positive relationships between sampling efforts for native and non-native ants' records and richness was not particularly strong, as shown in the states of Veracruz de Ignacio de la Llave and Jalisco, which present the highest number of alien records, but not the highest numbers of native species records (Supplementary data 1). For instance, taxonomic efforts could be

Table 1 List of alien ant species with total number of records, number of states where they are reported, first record, source of the first record, and with habitat with the highest number of occurrences

Species	Records	States with reports	First record	Source	Habitat	Established in the wild + or within buildings *
FORMICIDAE Latreille, 1809						
DOLICHODERINAE Forel, 1878						
Linepithema humile	37	12	1965	Wetterer et al. (2009)	Urban zone	+
Linepitema iniquum	8	4	1901	Forel (1901a)	Urban zone	+
Linepithema micans	1	1	2009	Hernández-Ruiz et al. (2009)	Crop field	+
Tapinoma melanocephalum	46	12	1894	Pergande (1896)	Urban zone, deciduous forest, evergreen forest and pastureland	+*
FORMICINAE Latreille 1809						
Anoplolepis gracilipes	57	10	1893	Pergande (1894)	Urban zone	+
Brachymyrmex aphidicola	2	1	1965	Ortiz-Sepulveda et al. (2019)	N/A	
Camponotus maculatus	8	2	1913	Wheeler (1914)	Urban zone	*
Nylanderia bourbonica	6	2	1993	Quiroz-Robledo and Valenzuela-González (1993)	Urban zone and deciduous forest	+
Nylanderia fulva	15	3	1972	Kempf (1972)	Deciduous forest	+
Paratrechina longicornis	175	23	1859	Roger (1859)	Urban zone and deciduous forest	+*
Plagiolepis alluaudi	1	1	1993	Quiroz-Robledo and Valenzuela-González (1993)	Deciduous forest	+
PONERINAE Lepeletier de Saint-Fargeau, 1835						
Hypoponera ergatandria	9	4	1938	Wheeler (1938)	Urban zone	+
Hypoponera opaciceps	49	13	1901	Forel (1901a)	Urban zone and deciduous forest+	
Hypoponera punctatissima	21	11	1996	Johnson R. Personal database (2017)	Urban zone and deciduous forest	+
Odontomachus haematodus	49	13	1895	Pergande (1896)	Deciduous forest	+
MYRMICINAE Lepeletier de Saint-Fargeau, 1835						
Cardiocondyla emeryi	47	14	1922	Wheeler (1922)	Crop field and urban zone	+

Table 1 continued

Species	Records	States with reports	First record	Source	Habitat	Established in the wild + or within buildings *
Cardiocondyla mauritanica	5	3	1986	Rodríguez-Garza (1986)	Xerophytic scrub	+
Cardiocondyla minutior	14	7	1996	Wetterer (2014)	Deciduous forest	+
Cardiocondyla obscurior	13	2	2008	AntWeb (2017)	Secondary vegetation	+
Cardiocondyla venustula	20	4	2005	Gove et al. (2005)	Crop	+
Cardiocondyla wroughtonii	4	3	1987	Mackay (1995)	Urban zone	+
Crematogaster obscurata	7	2	1985	AntWeb (2017)	Crop field	+
Monomorium carbonarium	15	4	1989	Devall and Thien (1989)	Urban zone	+
Monomorium floricola	51	10	1888	Wetterer (2010)	Urban zone and deciduous forest	+*
Monomorium pharaonis	94	15	1889	Velasco (1889)	Urban zone and deciduous forest	+*
Monomorium subopacum	5	2	1979	Jeanne (1979)	Deciduous forest	+
Pheidole megacephala	14	5	1899	Forel (1899)	Pastureland and evergreen forest	+
Pheidole navigans	4	2	1901	Forel (1901b)	Deciduous forest	+
Solenopsis invicta	16	4	2004	Sanchez-Peña et al. (2009)	Xerophytic scrub	+
Strumigenys emmae	4	3	1993	Quiroz-Robledo and Valenzuela-González (1993)	Evergreen forest	+
Strumigenys membranifera	3	2	1988	Mackay et al. (1991)	Secondary forest	+
Strumigenys rogeri	2	1	1966	Wetterer (2012)	Urban zone	+
Tetramorium bicarinatum	13	3	1855	Forel (1899)	Evergreen forest	+
Tetramorium caldarium	6	3	1929	Wetterer and Hita-Garcia (2015)	Urban zone	+
Tetramorium insolens	1	1	2009	Vásquez-Bolaños and Quiroz–Rocha (2009)	Oak forest	+
Tetramorium lanuginosum	20	9	1974	AntWeb (2017)	Urban zone, deciduous forest and evergreen forest	+
Tetramorium lucayanum	5	2	1998	Rodríguez-Garza (1998)	Evergreen forest	+
Tetramorium simillimum	40	10	1909	Wheeler (1909)	Urban zone, deciduous forest and evergreen forest	+

Table 1 continued

Species	Records	States with reports	First record	Source	Habitat	Established in the wild + or within buildings *
Trichomyrmex destructor	2	2	2013	Sánchez-Soto (2013)	Urban zone, deciduous forest	+*
Wasmannia auropunctata	50	5	1901	Wheeler (1901)	Urban zone and deciduous forest	+*
Species in need of status verification						
Cardiocondyla nuda	25	8	2008	Rodríguez-Garza (2008)	Urban zone and deciduous forest disturbed	+
Nylanderia flavipes	3	1	2013	Rosas-Mejía et al. (2013)	Urban zone	+

another important parameter to consider as some studies provide information for morphospecies but not on nominal species, preventing the record of particular species. A second aspect, here considered, is the difference in sampling in function of the habitat types. Our results show that a disproportionate number of alien records and species originate from urban areas (372) despite the overall sampling effort being considerably lower in this type of habitat in comparison to other types such as forest habitats (Supplementary data 1). Thus, in Mexico, as for many other regions around the world (McIntyre 2000; Guénard et al. 2015; Leong et al. 2017) alien ants are particularly common and diverse within urban areas. This may be attributed to the combination of factors, such as their generalist life habits, affinities with high and regular disturbance levels, high propagule pressure and possibly reduced competition (Passera 1994; Holway et al. 2002a, b).

Many of the introductions are caused by humans via global transport. The trade has an important role in the rapid dispersion of species, and the marine ports of entry are often the main source areas for establishment and spread of alien and invasive species (Seebens et al. 2013). Regions with high per capita GDP and high population densities have higher established alien richness (Dawson et al. 2017). Port cities along the Gulf Coast of the United States play an important role in the introduction of numerous species of non-native ants into North America (Gochnour et al. 2019). For instance, in Veracruz de Ignacio de la Llave, the state with the highest number of the records, 14 records for eight different species were retrieved from an area less than 100 km from the main international port of entry located in the city of Veracruz.

Although some data from protected areas in Mexico exist, they are less frequent than the records from other areas. We attribute it to the lack of coordinated reporting of alien insects, rather than the absence of alien ants in these natural reserves. In the protected areas where alien species have been registered, there has been no reports so far of ecological dominance or negative effects caused by them (Varela-Hernández and Jones 2013). Similarly, the species *M. floricola*, *P. longicornis* and *C. obscurata* were reported from protected tropical dry and deciduous forests and from sand dune habitat.

Based on the recent review of information about alien ants in Mexico (Rosas-Mejía and Janda 2017, 2018), we can enlist the factors that promote

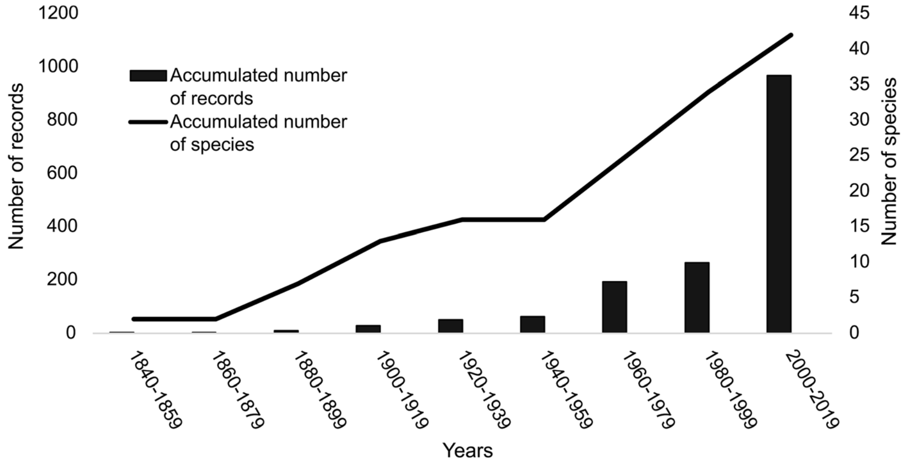

Fig. 2 The cumulative records and species richness for alien ants in Mexico from 1855 to 2019. The line shows number of species and the bars show numbers of records

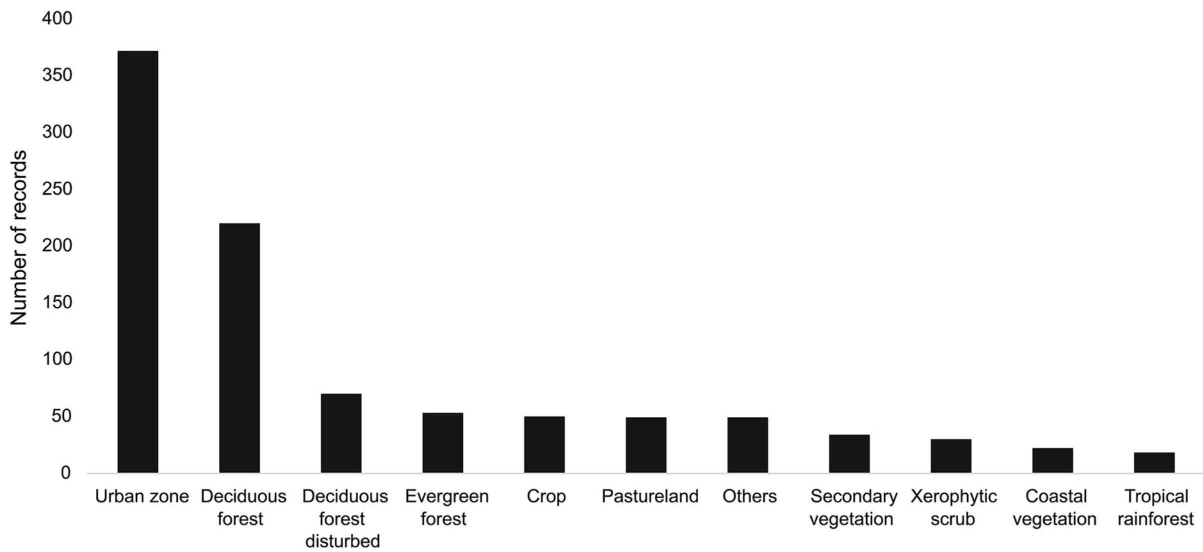

Fig. 3 Numbers of records from 18 habitats, 8 habitats with less than 10 records are combined in the category 'others' (oak forest, lowland wet forest, ornamental vegetation, coniferous forest, riparian vegetation, coastal vegetation, managed forest, tropical dry forest and mesophyll forest)

the establishment of their populations outside their native range. In particular: accidental transport mediated by humans, adaptation to anthropogenic environments, polygyny, polydomy, absence of interspecific aggression, generalized nesting and feeding habits, and mutualistic relationships with hemipteran (Suarez et al. 2010). Many of these traits have been well documented to contribute to success of invasive ants globally (Suarez et al. 2010), and we observe a similar pattern in Mexico.

The different types of impact are not necessarily linked. Some species can cause considerable economic and public health damage, directly affecting human activities and are often considered as pests (Rodríguez et al. 2016). Other species cause more of environmental damage as is the case of many invasive species. Among the alien ants reported in Mexico, the following species have the greatest ecological impact so far: *Pheidole megacephala, Solenopsis invicta, Linepithema humile, Wasmannia auropunctata, Anoplolepis gracilipes* and *Nylanderia fulva*. On the other hand, *Monomorium pharaonis* and *Tapinoma melanocephalum* are considered the most important pests. However, *Solenopsis invicta* fits well both categories and causes the strongest ecological and economic damage to humans in Mexico (Rosas-Mejía and Janda 2017). The other 23 species are not usually considered an urgent threat so far and they are not known to cause considerable harm to native species in their introduced ranges (Deyrup 2007; Wetterer 2012). Although there is sufficient evidence for considering many of alien ants documented here as invasive, in the case of *Brachyrmex aphidicola* and *W. auropunctata* the situation is less clear. *Brachymyrmex aphidicola* has been recently documented from few specimens collected in 1960's in central Mexico (Ortiz-Sepulveda et al. 2019), but information about its current status is missing. *Wasmannia auropunctata* is native to Central and South America and is also common in tropical habitats of south Mexico. Although it has been sometimes considered as alien to the whole country (e.g. Dáttilo et al. 2019), it is mostly based on political or biogeographical categorizations of Mexico. Here, we consider *W. auropunctata* as native to the tropical habitats at the south and east of the country, with its likely native range roughly corresponding to borders of Veracruz and Puebla. North of these states, where the ant fauna is mostly Nearctic, the species is treated in our database as invasive. Further genetic studies will be necessary to determine more precisely its native and introduced ranges in Mexico.

Nevertheless, it is also important consider the changes in distribution suggested by models developed for individual invasive ant species, incorporating suitable habitats information and predicted climate change. The global-level models proposed by Bertelsmeier et al. (2014) suggest, that 10 species may expand their range across the suitable habitats in Mexico under the current conditions. For example, the invasion potential for *S. invicta* includes all the states bordering the Gulf of Mexico and across the states on the Pacific coast to the north. This suggests a considerable expansion compared to the currently recorded situation, if the models are accurate.

The predicted distribution for invasive ants for 2080 varies greatly among the species, with some expanding (*S. invicta, Technomyrmex albipes*) and other diminishing their ranges (*A. gracilipes, L. humile, P. megacephala* and *W. auropunctata*) (Bertelsmeier et al. 2014). However, considering that the input data for these analyses were very limited for Mexico, it is necessary to update these models with the current situation and follow up with systematic monitoring efforts which will take into account the predicted optimal habitat conditions.

Future directions

The next steps for consolidating the monitoring and prevention of invasive ants in Mexico will be to improve the species identification process and to establish a coordinated network for fast sharing of data from the ports of entry. Furthermore, the systematic sampling across Mexico is needed to obtain actual information on species' distribution, as there are large parts of country with no data available (most of north and central Mexico). Focusing on areas of high biological importance (protected areas, regions with high endemism) should be a priority, as well as a detailed evaluation of the individual entry points. The agricultural, environmental and health sectors would greatly benefit from more detailed (or any) data in order to provide targeted treatments to the most affected areas. Regular and repeated monitoring is important, as many of the negative effects can be more easily detected at places with higher species abundance and over longer periods.

In effort to address the lack of information about the management of alien ants in Mexico, a risk analyses for eight species together with detailed information on their biology were recently published as part the National Strategy on Invasive Species in Mexico and the United Nations Development Program (Rosas Mejia and Janda 2017, 2018). However, much more coordinated effort is needed in order to provide effective prevention and management of alien ants in Mexico.

Acknowledgements We are grateful to John T. Longino, William Mackay, Aldo De la Mora Rodríguez and Luis Adrián Bonilla Ramírez for contributing the distributional data. The funding was provided by Consejo Nacional de Ciencia y Tecnología DICB No. 282471, Program CONACYT for Postdoctoral fellowships No. CVU 321229, by Universidad Nacional Autónoma de México PAPIIT IN206818, Czech Science Foundation (14-36098G), by Comisión Nacional para el Conocimiento y Uso de la Biodiversidad and by Program of United Nations for Development PNUD No. 89333. The suggestions and corrections from the two anonymous reviewers and P. Pyšek greatly improved the manuscript.

Author's contribution All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by MJ, MR-M. The first draft of the manuscript was written by MR-M. Map design and writing support MJA-M and MV-B. Data contributions and critical review of the work BG, EPE and AG. All authors read and approved the final manuscript.

Funding The funding was provided by Consejo Nacional de Ciencia y Tecnología DICB No. 282471, Program CONACYT for Postdoctoral fellowships No. CVU 321229, by Universidad Nacional Autónoma de México PAPIIT IN206818, Czech Science Foundation (14-36098G) and by Comisión Nacional para el Conocimiento y Uso de la Biodiversidad and the Program of the United Nations for Development PNUD No.89333, Japan Society for the Promotion of Science (No. 17K15180 to E.P.E.) and Japan Ministry of Environment (4-1904).

Availability of data and materials All data generated or analysed during this study are included in this published article. The data is available for consultation in supplementary Table 1.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Consent to participate All authors gave their consent to participate in the manuscript.

Consent for publication All authors reviewed the content of the manuscript and gave their consent to submit the document.

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