

Biogeographical evaluation and conservation assessment of arboreal leafhoppers in the Mexican Transition Zone biodiversity hotspot

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Abstract

Aims: Mexico harbours a diverse fauna comprising more than 1,400 leafhopper species, 60% of which appear to be strictly endemic, with many apparently restricted to particular habitats and host plants. The aims of this study were to identify areas of high species richness and endemism, and determine the biogeographic affinities of species in the diverse arboreal tribe Athysanini to provide data useful for conservation prioritization.

Location: Mexico.

Methods: A data set of 643 historical occurrence records based on authoritatively identified specimens from museums, recent fieldwork, literature and digital repositories was analysed. Analyses of species richness and areas of endemism were conducted using geographic information systems.

Results: A total of 164 species belonging of 50 genera were included, of which 145 species of 31 genera are considered to be endemic. The Mexican state of Guerrero yielded the most species records (48%). The highest numbers of taxa and endemic species were concentrated along the Mexican Transition Zone (MTZ) within which the Trans-Mexican Volcanic Belt (TVB) province had the most species records. Endemicity analyses showed two different geographical patterns but similar species richness weights with overlapping values over the MTZ. Distribution across vegetation types was not uniform, with most athysanine species concentrated in the dry tropical forest (65%). Species were documented at elevations between sea level and 3,200 m a.s.l. with three altitudinal preference classes. Conservation assessments applying IUCN criteria categorized a majority of species (145) as endangered or critically endangered. **Main conclusions:** Our findings suggest that most identified areas of high species richness throughout the territory have predominantly endemic taxa. Distributional patterns found are non-random, influenced by richness and endemism values over the TVB province and in the MTZ with a variable dispersion among species. Data highlight a greatly threatened status by habitat loss, remarking an urgent need for an improved conservation framework.

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KEYWORDS

Auchenorrhyncha, Cicadellidae, distribution, endangered species, Mexico, sap-sucking insects

1 | INTRODUCTION

Studies of biodiversity and biogeography are key to understanding the historical processes that led to present distributions of species and natural communities, and also to delineating areas of high endemism in need of conservation prioritization (Morrone, 2019; Sanmartín et al., 2001, 2012; Slatyer et al., 2007). The Americas harbour a diverse biota including many species that appear to require unique or specific environmental conditions (Ceballos & Ehrlich, 2006; Marques et al., 2006; Pinkus-Rendón et al., 2006; Sanchez & Parmenter, 2002; Sánchez-González & López-Mata, 2005; Tovar-Sanchez, 2009). Zones with high biodiversity and endemism occur throughout North America and South America (Van Jaarsveld et al., 1998). In North America, there are eight recognized biodiversity hotspots between the Nearctic and Neotropical regions and two of these occur in Mexico (Brooks et al., 2006; Myers et al., 2000; Norman, 2003).

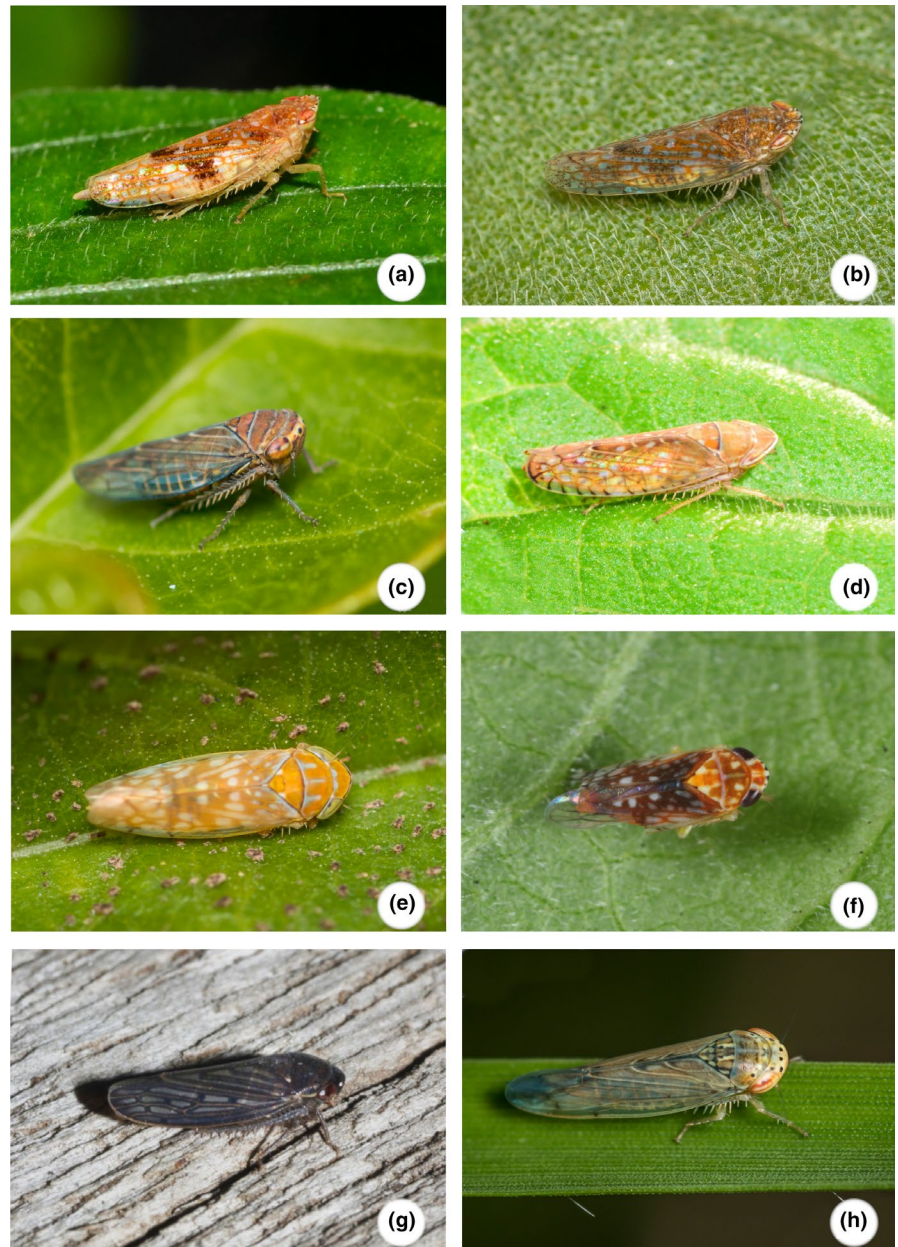
Mexico is a megadiverse country with 1.9 million km² of land area (CONABIO, 2020), 15 physiographic provinces, 17 floristic provinces representing ten vegetation types (Rzedowski, 1978, 2006), 11 morphotectonic provinces (Ferrusquilla-Villafranca, 1993), six ecological zones (Toledo & Ordoñez, 1993) and 44 terrestrial ecoregions (Olson et al., 2001). Mexico also spans two major biogeographic regions (Nearctic and Neotropical) (Morrone, 2001, 2005, 2014) and encompasses a large area where the biota of the two regions mix: the Mexican Transition Zone (MTZ) (Halffter & Morrone, 2017). Fourteen smaller biogeographical provinces have also been delimited in Mexico (Morrone, 2017, 2019) and subsequently corroborated by biogeographical analysis of various groups including birds (Blancas-Calva et al., 2010), mammals (Escalante et al., 2004), reptiles (Salinas et al., 2019), plants (Contreras-Medina et al., 2007; Salinas-Rodríguez et al., 2018), freshwater fishes (Huidobro et al., 2006) and arthropods (Arriaga et al., 2012; Bizuet-Flores et al., 2015; Morrone, 2006). The MTZ is of particular interest because it harbours a mixture of Neotropical and Nearctic taxa with a wide range of environmental tolerances (Bryson et al., 2011; Corona et al., 2009; Gutiérrez-Ortega et al., 2018; Marshall & Lieberr, 2000; Morrone & Márquez, 2001). Its geographical boundaries extend from the dry south-western United States through Mexico to the wet forests of northern Nicaragua. In Mexico, this region includes the Chiapas Highlands (CH), the Sierra Madre Occidental (SMOc), the Sierra Madre Oriental (SMOr), the Sierra Madre del Sur (SMS), and the Trans-Mexican Volcanic Belt (TVB) biogeographical provinces as categorized by Morrone (2010, 2017, 2019) and Morrone et al. (2017). The highly variable geology, topography and climate of Mexico have played important roles in limiting species distributions and yielding high levels of biodiversity and endemism (Esquerré et al., 2019; Morrone, 2010; Rzedowski, 1978).

Cicadellidae, commonly known as leafhoppers, is one of the ten largest insect families worldwide. Within the order Hemiptera, it is the most species-rich family with more than 23,500 described species (Dmitriev, 2003; S. H. McKamey, pers. comm.) and is widespread and abundant in all major geographical regions (Bartlett et al., 2018). Of the nineteen cicadellid subfamilies, Deltocephalinae is the largest, comprising 39 tribes, of which Athysanini is the largest and most widespread with 228 genera and 1,123 species (Zahniser & Dietrich, 2013). These insects feed on a wide variety of angiosperms and gymnosperms and many species appear to be highly specialized on particular plant genera or species (Dietrich, 2009; Hamilton & Whitcomb, 2010). They are abundant insects that occur in all places inhabited by vascular plants and are easily sampled using conventional methods (e.g. sweeping, light traps). Thus, they are useful as indicators of overall biodiversity and habitat quality (Biedermann et al., 2005; Wallner et al., 2013).

Compared with many other insect groups, the leafhopper fauna of Mexico is relatively well studied. In Mexico, ~1,426 species of Cicadellidae are recorded, most belonging to the subfamily Deltocephalinae and nearly 11% are in the tribe Athysanini (Zanol, 2008). Prof. Dwight DeLong and colleagues from Ohio State University collected leafhoppers intensively during the 1930s and 40s and described numerous genera and species, a large proportion of which appear to be endemic and highly threatened by modern anthropogenic activities (DeLong, 1943, 1945, 1980; DeLong & Hershberger, 1948; Pinedo-Escatell et al., 2016). More recent field work by the authors has yielded many additional occurrence records. All these data combined provide an opportunity to examine patterns of biogeography and endemism in the Mexican leafhopper fauna for conservation proposes.

Endemic Mexican forest-dwelling arboreal leafhopper genera and species are mostly placed in the tribe Athysanini, which is polyphyletic according to recent phylogenetic analyses (Zahniser & Dietrich, 2013; Lu et al., unpublished data). However, these analyses also suggest that the New World genera of this tribe belong to a single lineage that also includes the smaller endemic New World tribes Bahitini, Pendarini, and Scaphytopiini. Thus, this lineage could be used as an indicator of biogeographic relationships among New World forest ecosystems. Although host plant data for individual species of this group remain incomplete, available data suggest that many species and genera are highly host specific and some alternate between woody and herbaceous hosts during different life stages, tying them closely to particular habitat types and plant communities. Available occurrence data also indicate that many genera and species have narrow geographic ranges in Mexico and are associated with particular types of forest (Pinedo-Escatell et al., unpublished data). This raises concerns about the conservation status of endemic Mexican leafhoppers, particularly in the notably threatened forests that predominate in the Mexican Transition Zone where

FIGURE 1 Mexican Athysanini leafhopper included in the study. a, *Acunasus luteus* (Michoacán). b, undescribed species of *Acunasus* (Querétaro). c, undescribed species of *Jaacunga* (Querétaro). d, *Mesamia* sp. (Michoacán). e, undescribed Athysanini (Querétaro). f, *Stoneana marthae* (Oaxaca). g, *Duocrassana longula* (Yucatán). h, *Ollarianus* sp. (Querétaro). Photo credits: a and d by Ricardo Arredondo T.; b-c, e and h by Felix Fleck (<https://www.felixfleckonline.com/>); f by Adilson Pinedo-Escatell; g by Juan Cruzado



diversity and endemism appear to be highest. Recent studies of terrestrial arthropods in general suggest that this crucial component of global biodiversity is threatened by habitat destruction and other human activities (Hallmann et al., 2017; Kunin, 2019; Sánchez-Bayo & Wyckhuys, 2019). Thus, concerted efforts are needed to identify areas comprising exceptionally diverse or endemic biota in need of protection.

A first step towards understanding historical biogeography and present status of Mexican forest-dwelling leafhoppers is presented here via analyses of species richness, areas of endemism and geographical affinities. Previous studies of global leafhopper biogeography have revealed some general patterns of relationships between the faunas of the Nearctic and Neotropical regions (Krishnankutty et al., 2016; Wang et al., 2017; Xue et al., 2020; Zahniser & Dietrich, 2015), but none examined New World biogeographic patterns in detail or considered the unique fauna of the Mexican

Transition Zone (MTZ) as either a potential distributional bridge or a centre of origin for these sap-sucking insects. Understanding the biogeographical affinities of this leafhopper tribe in combination with a broader phylogenetic and ecological framework might help to comprehend the evolutionary processes that promoted their diversity, current distributions and conservation basis.

2 | MATERIAL AND METHODS

2.1 | Geographical setting

The project focussed on the Mexican landscapes between 14°–32°N latitude and 86°–117°W longitude, spanning the Nearctic and Neotropical biogeographical zones of the country. The varied topography and climate support a diverse terrestrial biota which includes

both northern and southern elements (Halffter & Morrone, 2017). The north-south trending mountain ranges provide a natural corridor between regions (Valdez et al., 2006).

2.2 | Insect model

We selected the diverse leafhopper tribe Athysanini (Cicadellidae: Deltocephalinae) (Figure 1) because genera and species of this group exhibit a strong association with native forests and vegetation occurring in Mexico (Aguilar-Pérez et al., 2019; DeLong & Hershberger, 1948). Most Mexican athysanine taxa apparently are endemic and confined to particular native forest types, many of which are endangered habitats (Pinedo-Escatell et al., unpublished data). These taxa are mostly specialized and rarely occur in multiple habitats. Relatively few species of this group are geographically widespread.

2.3 | Distributional data compilation

A complete georeferenced occurrence data set of all known Athysanini leafhopper taxa inhabiting Mexico was included (Appendix S1 and S3). Data were obtained from openly available electronic repositories such as Global Biodiversity Information Facility (GBIF.org) and iNaturalist (iNaturalist.org), in addition to records from specialized taxonomic literature and specimen holdings in the following entomological collections: Colección Nacional de Insectos del Instituto de Biología, Mexico (CNIN), Colección de Auchenorrhyncha de J. Adilson Pinedo Escatell, Mexico (CAJAPE), Colección de Insectos del Instituto de Fitosanidad del Colegio de Postgraduados, Mexico (CEAM), C. A. Triplehorn Collection, USA (OSUC), Illinois Natural History Survey, USA (INHS), and National Museum of Natural History, USA (NMNH). Additional records were obtained through field work by the authors over the past 25 years. Methodologies used vary among collectors from the 1920s until the present but most commonly employed sweep nets, light traps, malaise traps and entomological aspirators. Data comprising all species records from different collections, methods and times were compiled into a single data set (matrix) and analysed as a whole. Of the gathered information, taxonomic identification and locality records collected for each individual species were mapped and corrected when necessary, using ArcGIS 9.3 (ESRI, 2008) and Google Earth (Google, 2015). Ambiguous locations and doubtful records (i.e. cases where either the locality or species identification was uncertain) were omitted. Because most historic collections of insects were made haphazardly, collecting intensity is difficult to assess and has presumably varied among Mexican states. Thus, available historic data may be biased to some unknown extent by variation in sampling effort among regions of Mexico. Nevertheless, given our focus on a particular group of leafhoppers largely limited to tropical and montane forests, which have been intensively sampled in the past as well as

through our own recent efforts, we expect the available occurrence data for Athysanini to provide a reasonably accurate reflection of the actual distributional patterns of this group in Mexico.

2.4 | Richness and endemism

To evaluate richness and endemism patterns, $0.5^\circ \times 0.5^\circ$ grid cells were superimposed over a Mexican territory polygon (Escalante et al., 2007). We calculated leafhopper species richness using all available records for (1) Mexican political divisions, (2) biogeographical regions/provinces, (3) per grid cell and (4) elevation classes. These calculations were also made for endemic species only. Both weighted endemism (WE) (Laffan et al., 2013; Linder, 2001) and corrected weighted endemism (CWE) (Laffan & Crisp, 2003) were calculated.

The WE formula ($WE = \sum t_l \in TL (r_{tl}/R_{tl})$) expresses scores of all species attributes (TL) in one grid cell; r refers to a single species value (t_l) recorded per cell over R , which is the summation of WE values found in different grid cells over the studied area. Calculations follow taxa at level t_l , with one taxon at the highest taxonomic level ($=0$, tribe Athysanini) and the lowest level being species ($t_l = 1$) (for details see Aragón-Parada, 2018). CWE is calculated by dividing the WE value per species by total species number. Analyses were run using Biodiverse (Laffan et al., 2010). Species richness as a function of elevation was analysed by using categorical taxa occurrence points grouped into classes spanning 500 m a.s.l. Analyses and figures were plotted using R (Development Core Team, 2016).

2.5 | Biogeographical distribution

Biogeographical affinities of the tribe Athysanini were inferred under the concept of biogeographic regionalization proposed by Morrone et al. (2017) considering three major regions: Nearctic, Neotropical and the MTZ with their respective 14 provinces. Vegetation preference was also included following criteria of Rzedowski (1978, 2006). Elevation range data for each genus and species were also analysed. Map layouts were built by using QGIS (QGIS Development Team, 2015) with open-access territorial land schemes generated by the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO, 2019).

2.6 | Conservation assessment

Conservation status was estimated using the geographical distribution known for each individual species with extent of occurrence (EOO) and the area of occupancy (AOO) calculated using convex polygons and grid cells of 2×2 km to measure and obtain values in accordance with the categories and criteria established by the IUCN Red List of Threatened Species (IUCN, 2012). Geostatistical data were processed using GeoCat (Bachman et al., 2011).

3 | RESULTS

3.1 | Georeferenced data

A total of 643 geographical records for Athysanini (Figure 2) were compiled representing 164 species and 50 genera (Table 1; Appendix S1). Eighty percent of taxa had valid names while the remaining 20% are new to science. Of the taxa recorded, 145 species (88%) and 31 genera (63%) are strictly endemic to Mexico (Appendix S2) whereas 19 species occur either to the north or south of Mexico. Guerrero state had the largest number, 199, of occurrence records followed by Michoacán, Estado de Mexico and Jalisco (72–59 records). Remaining states had fewer than 50 records.

3.2 | Species richness by political distribution

Species richness was calculated for 23 Mexican states. The state of Guerrero had the highest species richness, harbouring 78 species (48%) and 36 genera (72%). Michoacán, Hidalgo and Jalisco followed with 36 (30%), 26 (16%) and 26 (16%) species and 16 (32%), 14 (28%) and 13 (26%) genera, respectively. In contrast, Chihuahua, Zacatecas and Baja California Sur had the lowest species richness

values with one species each. The state with the most endemic species was also Guerrero which had 71 species (49%) recorded, followed by Michoacán with 32 species (22%) (Figure 3). Nine states had no species records.

3.3 | Species richness of biogeographical regions and provinces

The Nearctic and Neotropical regions with their respective natural bridge, the MTZ, all showed distinctive patterns of biogeographical affinity for the arboreal leafhopper tribe Athysanini. The MTZ region showed the highest species richness (NS) and endemic species richness (ES) with 140 and 87 species, respectively. The Neotropical region showed higher richness in genera (40 taxa) but lower species richness, and the Nearctic region accounted for 23 species and ten genera (Figure 4).

Twelve biogeographic provinces of the 14 recognized in Mexico had species occurrence records (Figure 5). Species richness was not homogeneous. The Transvolcanic Belt (TVB) had the most genera and species (24/73) (Figure 6) followed by the Balsas Basin (BB) with 24/73 (Figure 7), while the Baja Californian (BC) province had the lowest diversity with 1/1 (Figure 8). On the other hand, the BB

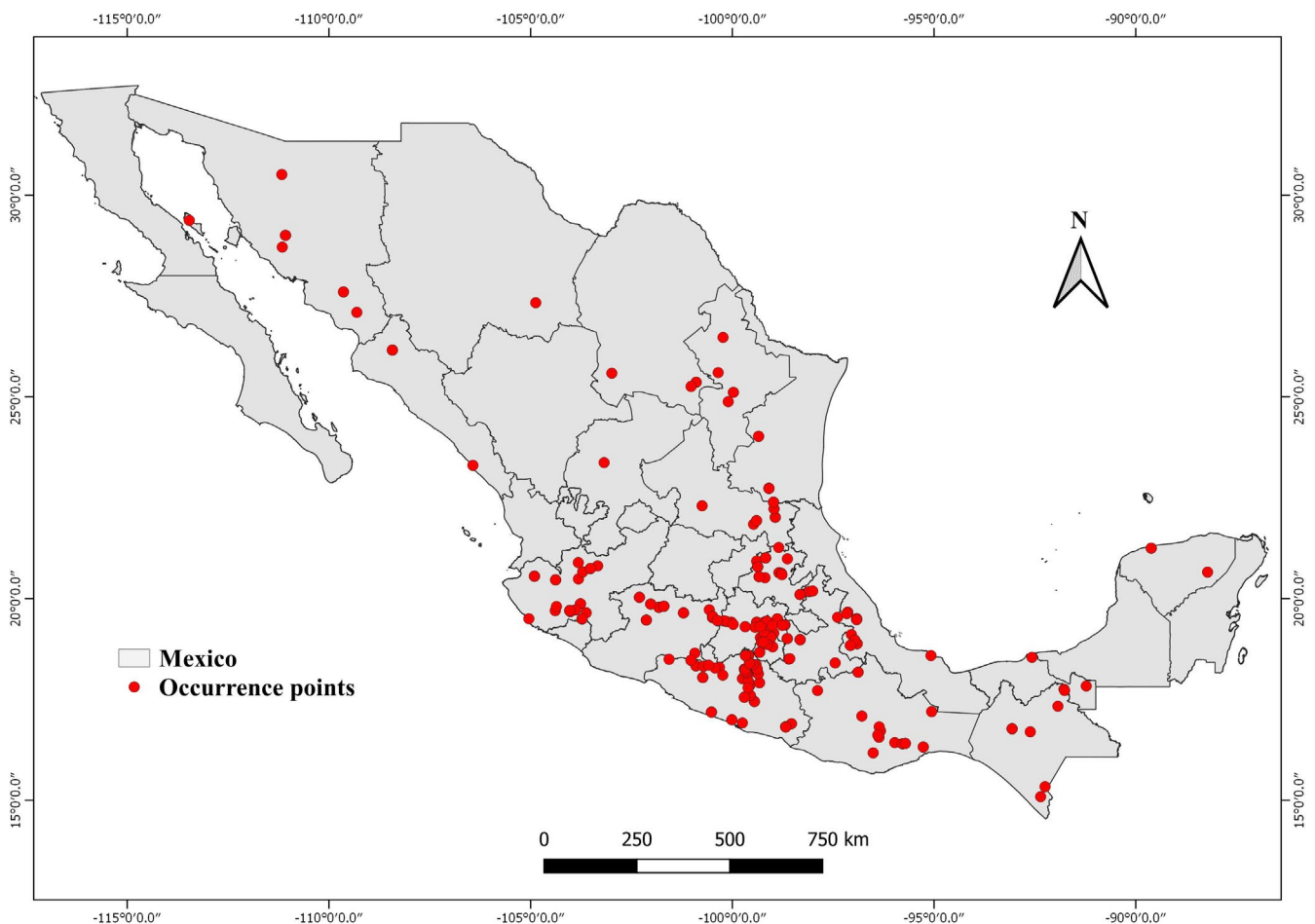


FIGURE 2 Leafhopper occurrence points included in this study

province has the highest genus diversity, 33, substantially more than the other provinces. The richest province for endemic species (ES) was the TVB with 69 species, followed by the BB with 67 species and the SMS with 24 species (Figure 5). The Californian (C) and SMOc provinces had no species recorded.

3.4 | Species richness and endemism by grid cell

Among the 848 grid cells of $53.3 \times 53.3 \text{ km}^2$, 91 cells had species records. Twenty-four percent of cells had 21 to 70 species and the remaining 76% had lower species richness. 54% of cells fell in the Neotropical region followed by the MTZ and Nearctic regions with 34% and 12%, respectively. All cells with 11–40 species were located along the MTZ. The centre of Mexico had higher cell numbers (42%) than northern or southern areas. The nine richest cells with

51–70 species were placed among the TVB, BB and SMS provinces. Two cells with 61–70 species were located in the state of Guerrero, centre of the BB. Two additional cells with 51–60 species were situated between the TVB and BB. Of the remaining cells, 12 contained 1–10 species and 22 cells had 21–30 species (Figure 9).

The WE index recovered a pattern congruent to that obtained by richness analysis. Cells with high values were located in the centre of Mexico (Figure 10a). Three cells with highest values (40.1–45) are placed over Guerrero, lying at the centre of the BB province. Surrounding these latter cells, other less rich cells had values ranging between 10.1 and 40.0. Analysis of CWE showed a different pattern, with the five cells having the highest endemism values dispersed across the territory of Mexico (Figure 10b). Western central Mexico had the richest areas with values ranging between 0.41 and 0.8. Both endemism indexes, WE and CWE, have overlapping cells with high endemism along the MTZ. Areas with medium or low endemism are dispersed in several biogeographical provinces.

TABLE 1 Number of taxa recovered by geographical region

Variable	Total	MTZ	Neotropical	Nearctic
NS	164	140	131	23
NG	50	29	40	10
ES	145	87	81	11

Abbreviations: ES, endemic species; NG, number of genera; NS, number of species.

3.5 | Vegetation and elevation

Species richness by vegetation type was not uniform. The Tropical Dry Forest (TDF) had the highest richness, with 107 species, representing 65% of the total. The Oak-Pine Forest (OPF) had 89 species (52.4%) followed by the Xerophytic Shrubs (XS) with

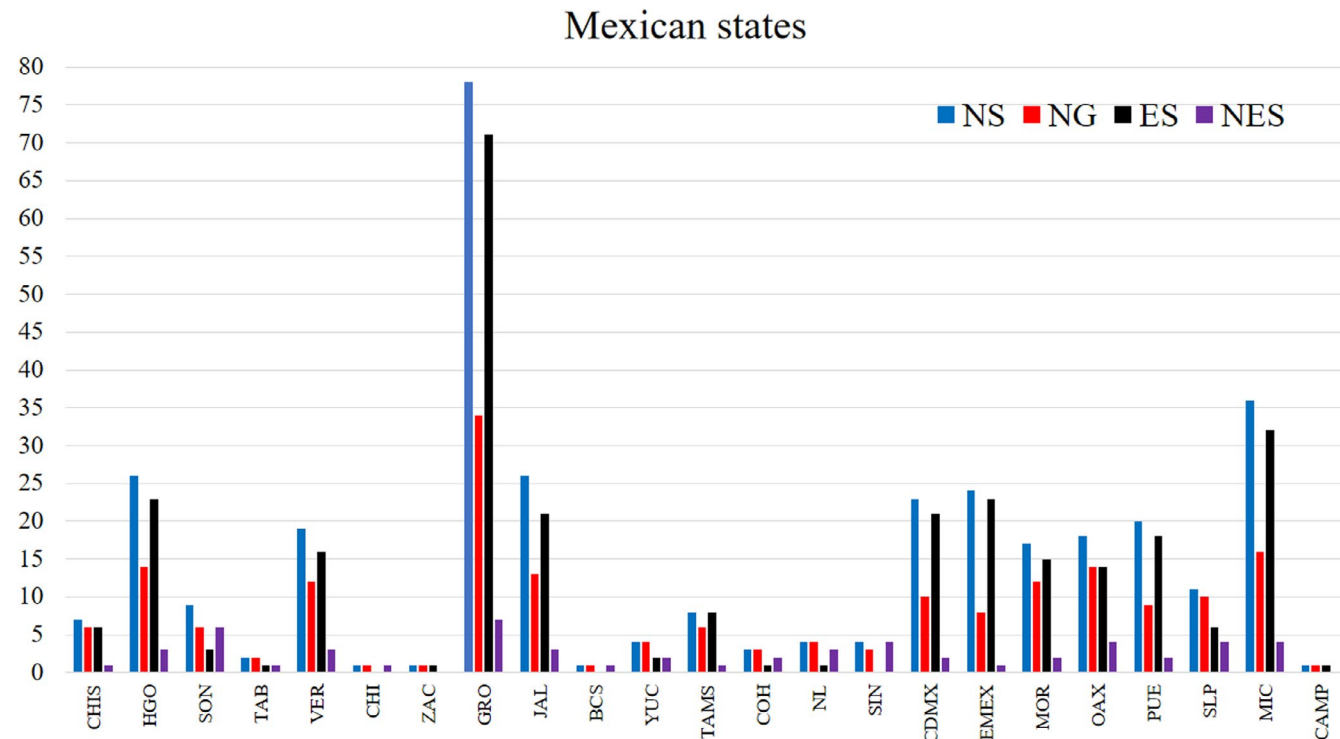


FIGURE 3 Species richness of Athysanini leafhoppers by Mexican political divisions. Total species (NS), total genera (NG), total endemic species (ES) and total non-endemic species (NES). Mexican states displayed: Chiapas (CHIS), Hidalgo (HGO), Sonora (SON), Tabasco (TAB), Veracruz (VER), Chihuahua (CHI), Zacatecas (ZAC), Guerrero (GRO), Jalisco (JAL), Baja California Sur (BCS), Yucatán (YUC), Tamaulipas (TAMS), Coahuila (COH), Nuevo León (NL), Sinaloa (SIN), Ciudad de México (CDMX), Estado de México (EMEX), Morelos (MOR), Oaxaca (OAX), Puebla (PUE), San Luis Potosí (SLP) and Michoacán (MIC)

FIGURE 4 Species richness of Athysanini leafhoppers by major biogeographical regions. Total endemic species (ES), total genera (NG) and total species (NS); Mexican Transition Zone (MTZ)

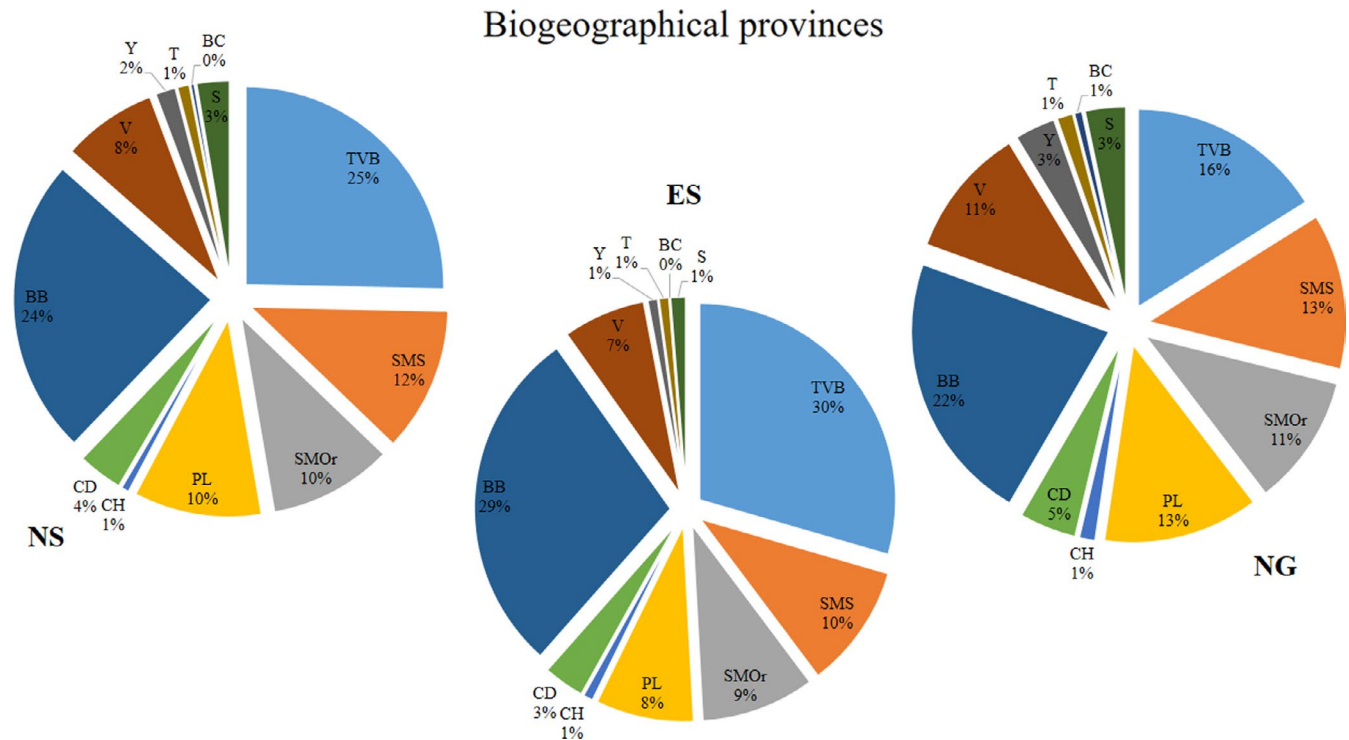
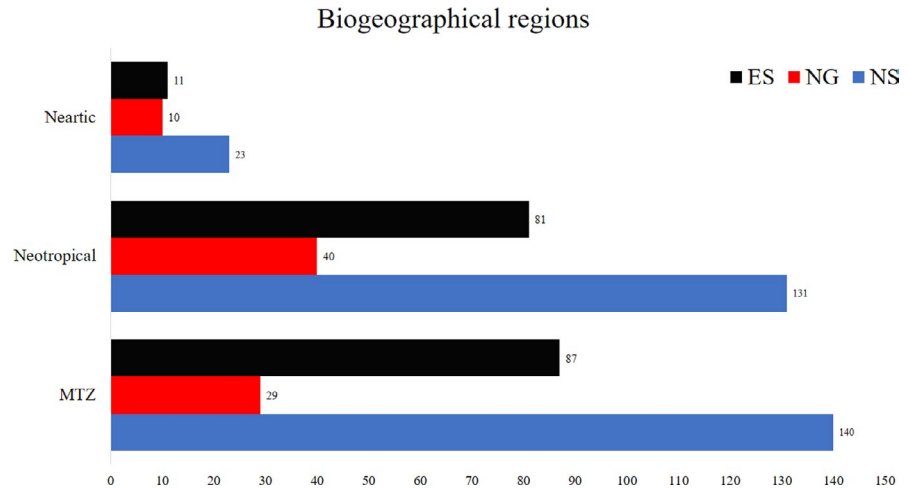


FIGURE 5 Species richness of Athysanini leafhoppers by biogeographical provinces. Total species (NS), total endemic species (ES) and total genera (NG). Percentages are proportions of total present in each province. Biogeographical provinces displayed: Trans-Mexican Volcanic Belt (TVB), Sierra Madre del Sur (SMS), Sierra Madre Occidental (SMOc), Sierra Madre Oriental (SMOr), Pacific Lowlands (PL), Chiapas Highlands (CH), Chihuahuan Desert (CD), Balsas Basin (BB), Veracruz (V), Yucatan Peninsula (Y), Tamaulipas (T), Baja Californian (BC) and Sonoran (S)

18 species (10.9%). Of the remaining observations, 12 (7.3%), 9 (5.4%) and 2 (1.2%) species were recorded in the Mountain Cloud Forest (MCF), Evergreen Forest (EF) and Thorn Forests (TF), respectively.

Athysanini leafhoppers were found to occur between sea level and 3,200 m a.s.l. Most taxa (63%) occur between 350 and 1,600 m a.s.l. Endemic taxa were most prevalent below 1,300 m a.s.l. with few species found at low elevation (below 350 m a.s.l.), and few others with wider tolerance of higher elevations while non-endemic taxa were found along the entire altitudinal range (Figure 11).

3.6 | Conservation status

Applying IUCN criteria to 145 Mexican athysanine leafhopper species (Appendix S2) suggests that most of the evaluated species meet the criteria for listing under one of the protected categories. Based on available data, 57 species met the criteria to be included in the Endangered (EN) category while 88 species were assessed as Critically Endangered (CR). By contrast, the categories Least Concern (LC) and Data Deficient (DD) included relatively few species (Figure 12).

4 | DISCUSSION

Identification of areas of high species richness and endemism (biodiversity hotspots) requires not only measurement of species richness but also reliable data on species distributions with regard to both geography and habitat (Myers et al., 2000; Norman, 2003). No similar studies have been attempted on this insect group but the present results strongly suggest that forest leafhoppers are useful indicators of threatened faunas and habitats (Arriaga et al., 2012; Bizuet-Flores et al., 2015; Blancas-Calva et al., 2010; Contreras-Medina et al., 2007; De-Nova et al., 2012; Escalante et al., 2004; Halffter & Morrone, 2017; Huidobro et al., 2006; Morrone, 2006, 2017, 2019; Salinas et al., 2019; Salinas-Rodríguez et al., 2018). Similar studies should be conducted in other regions to provide a more comprehensive conservation assessment of the global leafhopper fauna. Unfortunately, Mexico is one of the few tropical countries where the leafhopper fauna has been relatively well studied with extensive historical as well as recent occurrence data available. Our analysis of available data for the leafhopper tribe Athysanini indicates that, in Mexico, this group is not only highly endemic but also greatly threatened by habitat loss (Pinedo-Escatel et al., unpublished data).

These data may be useful for further conservation assessment and planning.

Based on 164 Athysanini species identified from Mexico, the diversity of Athysanini in this country appears to be similar to that of other megadiverse Neotropical countries such as Peru, Bolivia and Brazil (Zanol, 2008), although the latter countries may not have been sampled as intensively for this group of insects. Levels of endemism in Athysanini appear to be higher in Mexico. Most recorded Mexican leafhopper species are not shared with neighbouring countries to the south or north (79%) and only 20 of the athysanine species recorded are widely distributed beyond Mexican boundaries. Distribution patterns of this leafhopper tribe are non-random, with richness and endemism highest in the TVB province and, more broadly, in the MTZ. Guerrero state had more taxa (48%) and records (31%) than any other Mexican state.

Endemism is a scale-dependent biogeographic concept (Daru et al., 2020) but consistent patterns can often be discerned by examining multiple unrelated groups of species. We identify an important hotspot with a high degree of endemism and species richness in the centre of the BB province which might be prioritized for conservation. This region is home to several

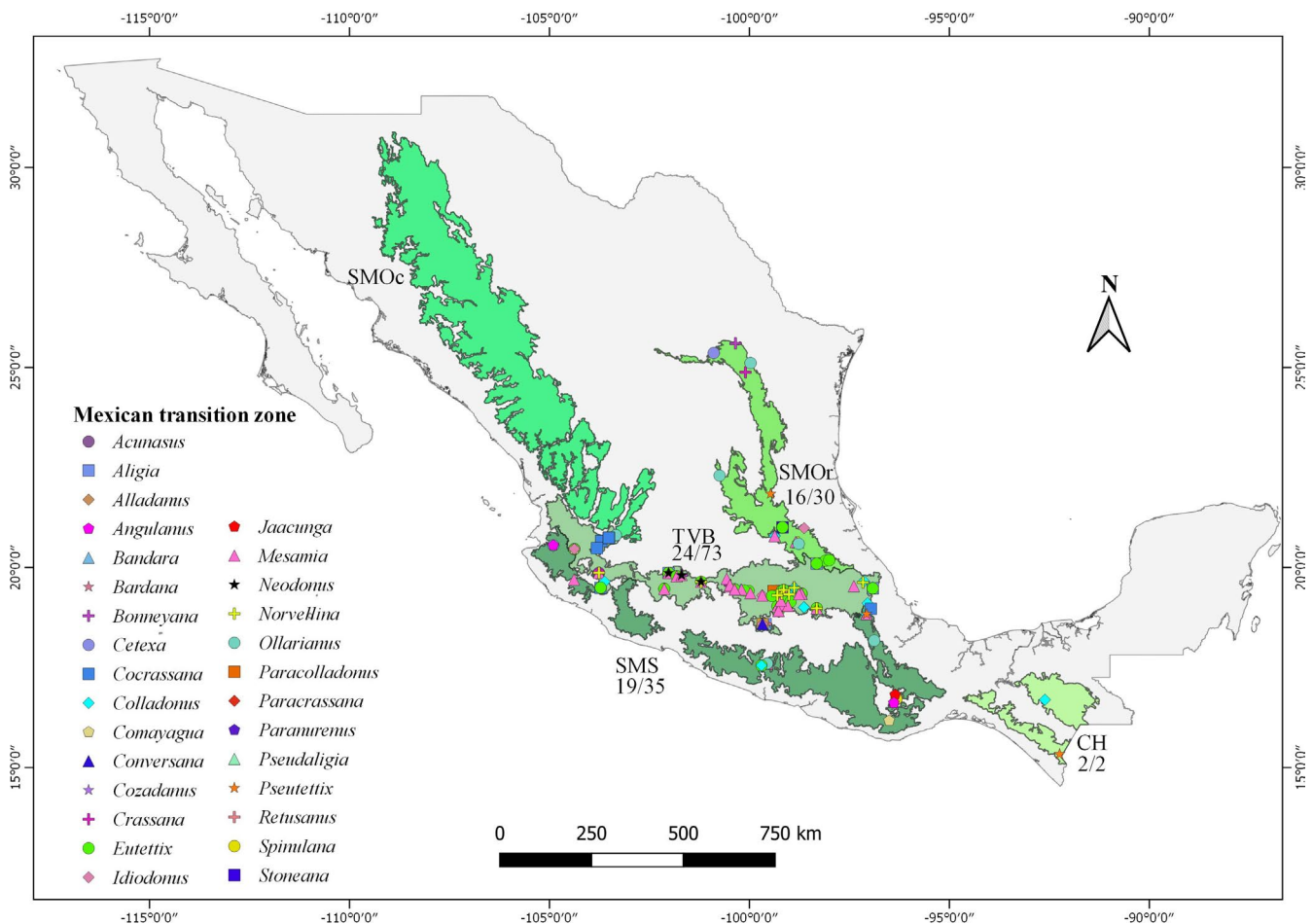


FIGURE 6 Biogeographical provinces of the Mexican Transition Zone: Trans-Mexican Volcanic Belt (TVB), Sierra Madre del Sur (SMS), Sierra Madre Occidental (SMOc), Sierra Madre Oriental (SMOr) and Chiapas Highlands (CH). Numbers below province abbreviations show genera/species number recorded

endemic, monotypic genera (*Dampfiana* DeLong & Hershberger, *Arthucephalus* DeLong, *Sobara*, *Deltorynchus* DeLong, *Excavanus* DeLong, *Costamia* DeLong, *Paracolladonus* Nielson, etc.). Few other arthropod taxa are known to show similar distributional patterns (Arriaga et al., 2012; Halffter et al., 2019), but patterns of distribution in endemic plant species are similar in this region (De-Nova et al., 2012). Additional, hotspots occur in the transitional region of the TVB province, home to several additional small genera with few species, including *Pseudaligia* Kramer & DeLong, *Cozadanus* DeLong & Harlan, *Crassana* DeLong & Hershberger, *Retusanus* DeLong, and *Usanus* DeLong. Most endemic Mexican Athysanini occur in the TVB (30%) consistent with patterns exhibited by some other taxa (Contreras-Medina et al., 2007; Huidobro et al., 2006). As a natural biogeographical unit representing the largest mountain system that extends transversely across Mexico (Mastretta-Yanes et al., 2015), the TVB is the link among niches, habitats and vegetation from other provinces recognized in the MTZ. Detailed phylogenetic analyses are needed to elucidate the patterns of relationships between endemic leafhopper taxa in this region with those of the surrounding Nearctic and Neotropical zones. We predict such studies will show that this region is not

only a “crossroads” between north and south but also a cradle of phyletic diversity.

WE analysis recovered 48 grid cells located in the MTZ with the highest weighted endemism. Ruiz-Sánchez et al. (2020) reported a similar distribution pattern for endemic woody plants. Results of CWE analysis vary in proportion but had a similar pattern with more higher-value cells located in the MTZ than in the Neotropical or Nearctic regions. Rodríguez et al. (2018) and Halffter et al. (2019) identified the MTZ as a zone evidencing biotic interchange between the Nearctic and Neotropical region with a wide range of environments offering variable ecological niches, inherent for conservation in several plants or animal taxa. Although several regions of Mexico, including the Chihuahuan, Coahuilan and Zacatecas semiarid zones, remain poorly sampled, because they are dominated by grasslands and other open habitats they are not expected to harbour large numbers of forest-dwelling species. Further sampling in poorly accessible wooded regions of southern or western states such as Jalisco, Michoacán, Guerrero and Oaxaca might be expected to change proportions of endemic species (see Figure 5 in Pinedo-Escatel et al., unpublished data). As mentioned above, our results should be interpreted with caution because sampling for leafhoppers in Mexico has

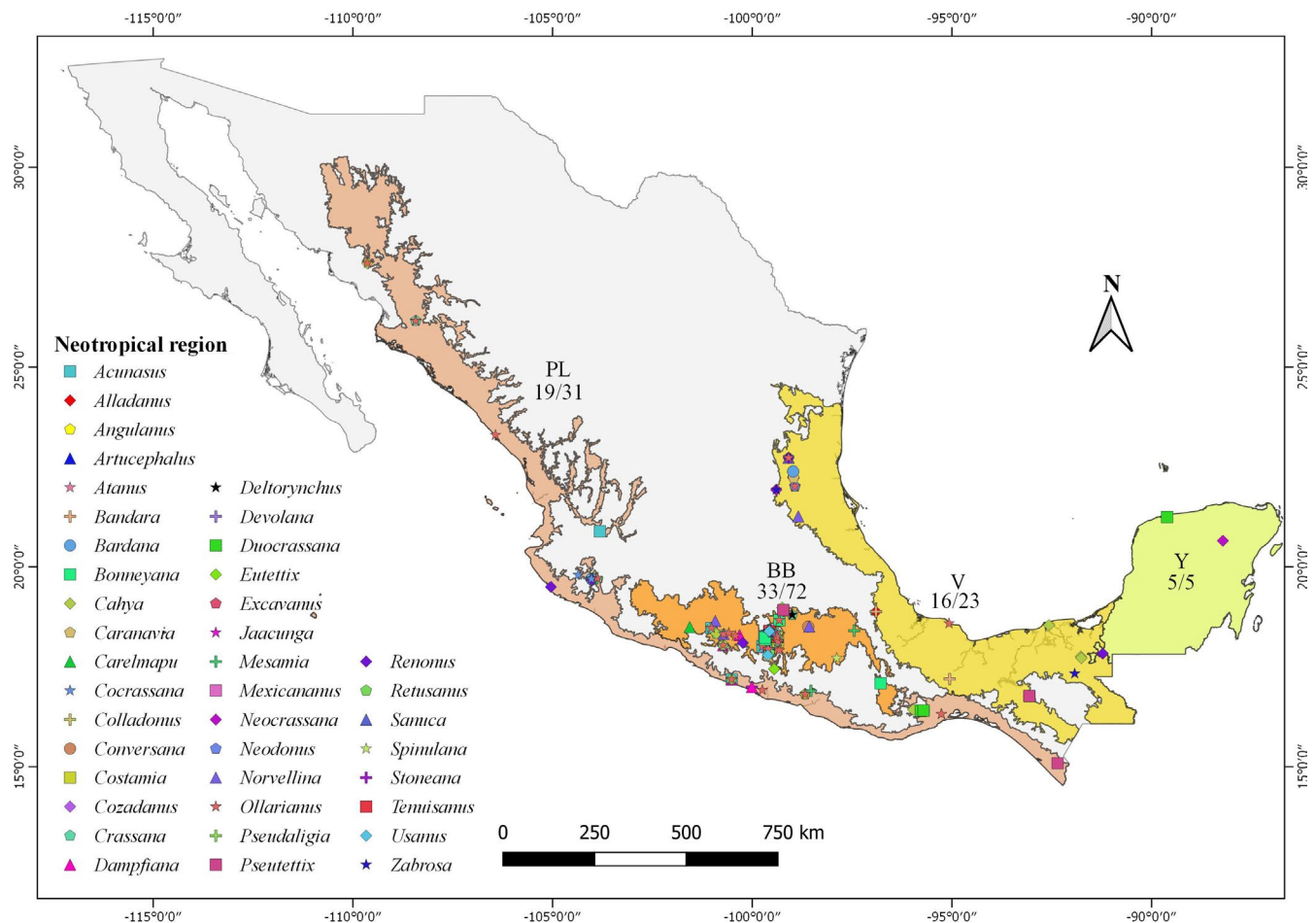


FIGURE 7 Neotropical biogeographical provinces of Mexico: Pacific Lowlands (PL), Balsas Basin (BB), Veracruz (V) and Yucatan Peninsula (Y). Numbers below province abbreviations show genera/species number recorded

been uneven, with some species-rich areas targeted by collectors repeatedly and other areas largely ignored.

Fidelity of leafhopper species to particular forest types appears to be variable among forests of Mexico. Pinedo-Escatell et al. (unpublished data) provided an overview of Athysanini inhabiting the seasonally dry tropical forest and showed that this forest type is inhabited mostly by endemic genera. According to Aguilar-Pérez et al. (2019) and Pinedo-Escatell and Dietrich (2020) as well as the present results, the dry forest harbours 65% of athysanine species richness, more than in other forests in Mexico. A few more widespread genera, for example *Mesamia* Ball, *Norvellina* Ball, *Eutettix* Van Duzee, *Zabrosa* Oman and *Comayagua* Linnavuori & DeLong inhabit multiple types of vegetation and are more dispersed geographically to the north and south (Hamilton & Whitcomb, 2010). Most studied species also exhibit distinct preferences in elevation. Half of the endemic and Neotropical taxa occurred between sea level and 1,300 m a.s.l. Montane taxa including 20% of the remaining endemic seem to be restricted to high elevations between 1,300 and 2,300 m. a.s.l. with a small species group in low elevations. The remaining species showed broader tolerance over the entire range of elevation from sea level to 3,500 m a.s.l. Leafhopper elevation ranges in Mexico had not

been evaluated previously but some possible patterns were noted by DeLong (1946).

Continuing a trend begun in the 1920s, recent field work in Mexico has led to discovery of new leafhopper species and genera (Appendix S1; Aguilar-Pérez et al., 2019; Pinedo-Escatell et al., 2016). Ongoing surveys will continue to fill gaps in knowledge of this diverse insect fauna. Undoubtedly diversity is substantially higher than indicated by previous studies (Zanol, 2008; Pinedo-Escatell et al., unpublished data; Mariño-Pérez et al., 2012) and efforts are needed to sample additional regions and habitat types, particularly those threatened by human activities and not covered by previous surveys. Unfortunately, the region remains poorly evaluated with regard to conservation priorities although a growing body of evidence accentuates the need for further efforts to conserve endangered habitats in this area.

As often observed in other arthropods (Corona et al., 2009; Pinkus-Rendón et al., 2006), most of the species treated in this study are restricted geographically. Nevertheless, 20 of the athysanine species collected are more widespread as in certain grass-feeding leafhoppers, for example Chiasmini and Stenometopiini (Zahniser & Dietrich, 2013). These taxa belong to four genera, *Caranavia* Linnavuori, *Comayagua*, *Neocrassana* Linnavuori and *Zabrosa*,

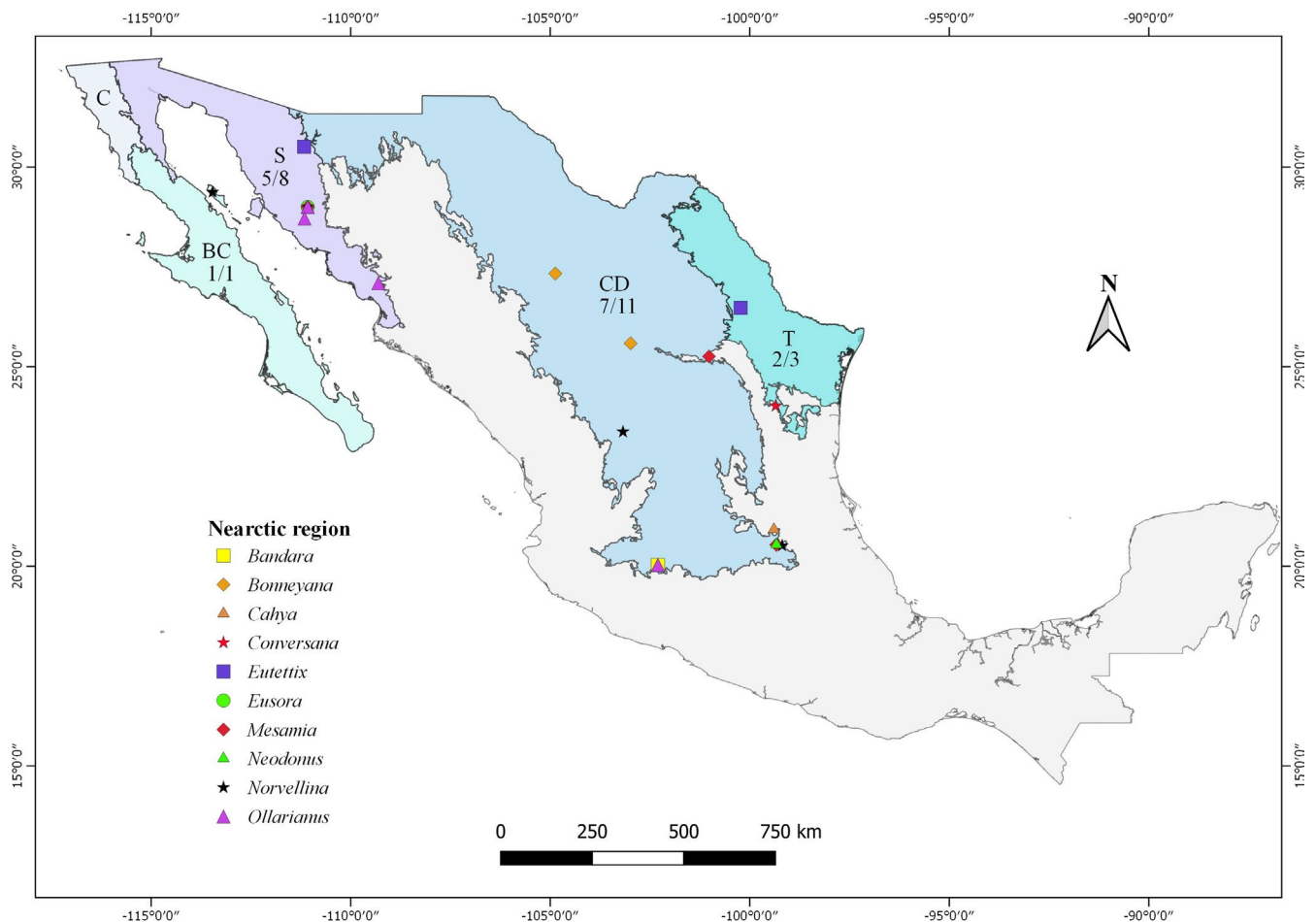


FIGURE 8 Nearctic biogeographical provinces of Mexico: Chihuahuan Desert (CD), Tamaulipas (T), Baja Californian (BC) and Sonoran (S). Numbers below province abbreviations show genera/species number recorded

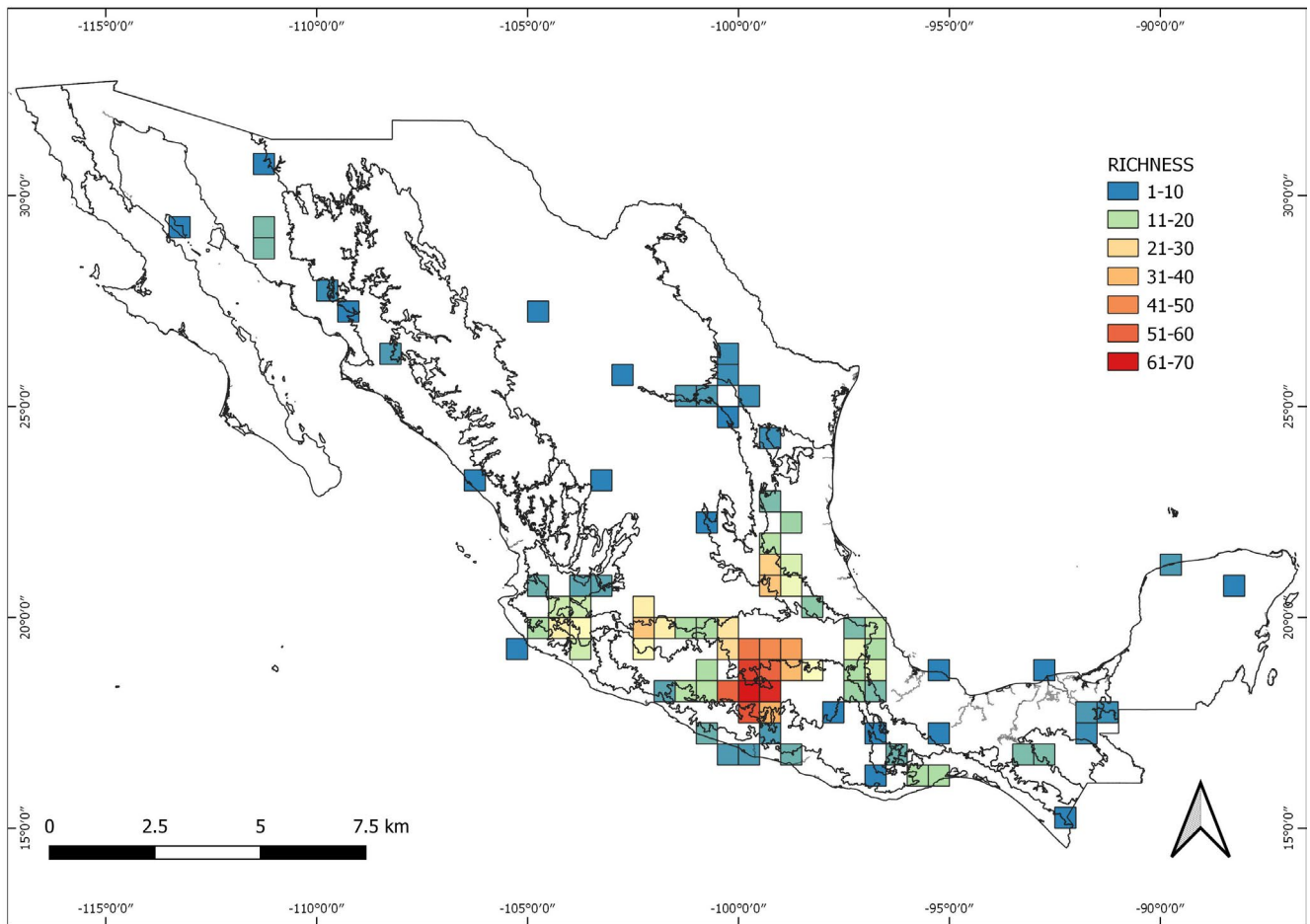


FIGURE 9 Map of species richness by grid cell

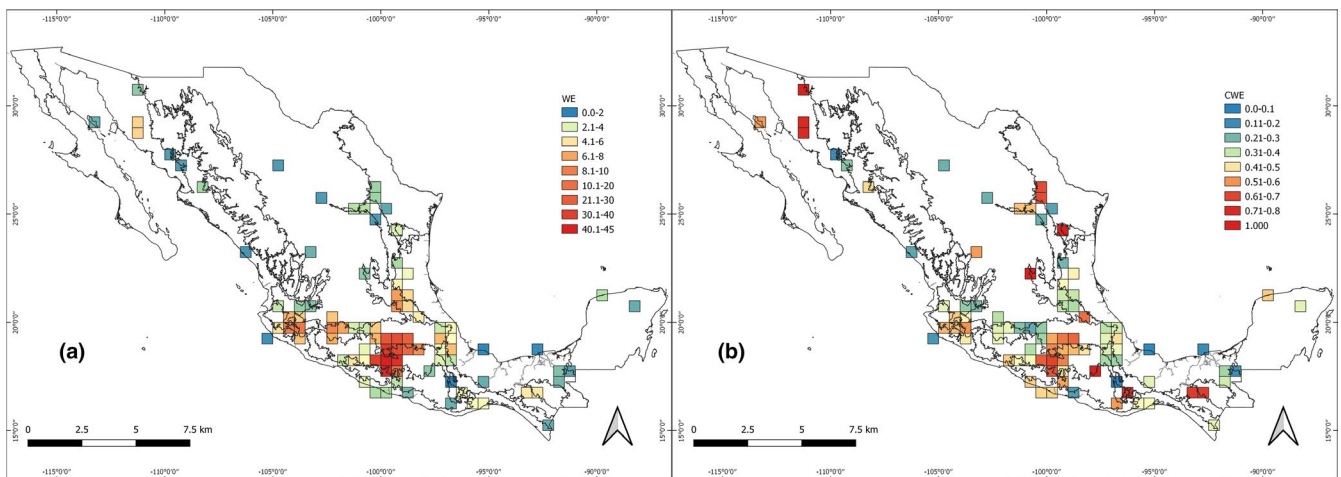


FIGURE 10 Maps of species richness by endemism criterion. WE: weighted endemism (a) and CWE: corrected weighted endemism (b)

recorded in this study for the first time in Mexico. The first three of these were previously known from the southern Neotropical region, while *Zabrosa* includes one species previously recorded from the southern USA. Distributions of athysanine leafhoppers in this study ranged from 33° to 25°N latitude, but the largest concentration of species (63) occurred between 17° and 21°N. For most of

these species, this is the first comprehensive assessment of available data on distribution and habitat.

Although an ongoing "insect apocalypse" has been highlighted in the recent conservation literature, accompanied by calls to preserve and protect insect biodiversity, very few insect species have, so far, been included on official lists of threatened or endangered

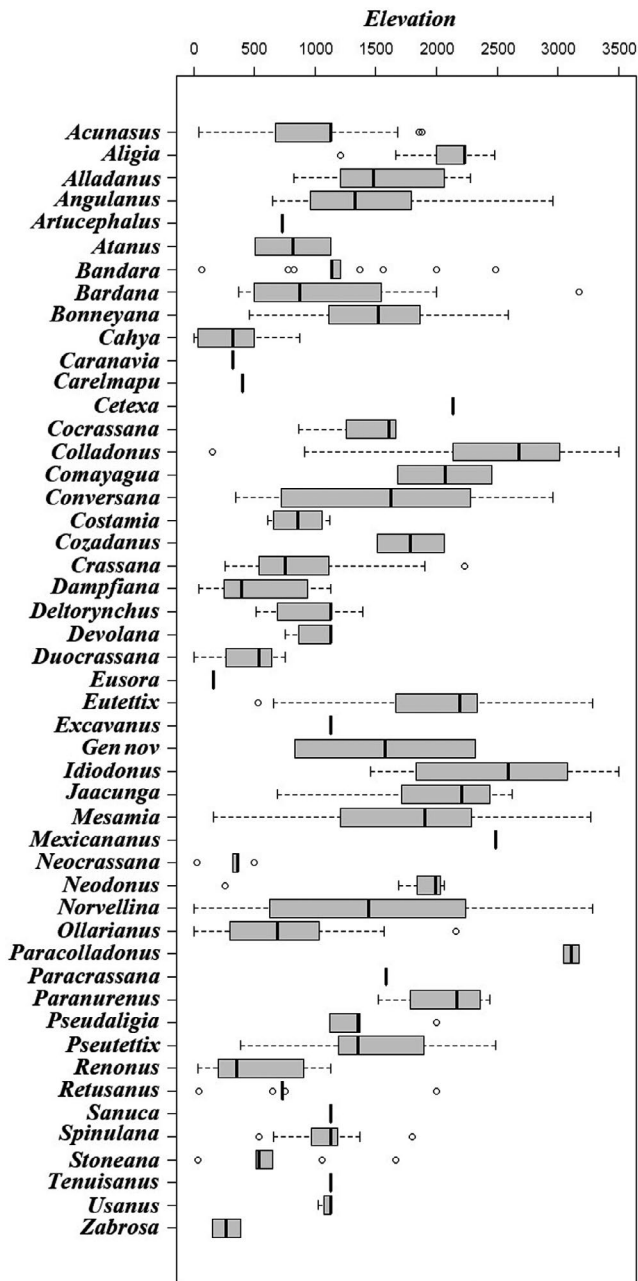


FIGURE 11 Elevation ranges for genera of Mexican Athysanini

species, mostly because most insect species are considered “data deficient.” Globally, only 13 species of leafhoppers have been placed in a risk category on the IUCN red list of threatened species. Seven species are considered critically endangered (CR), three species are endangered (EN), two species are vulnerable and the last two are near threatened (IUCN, 2012). None of these species occur in the Americas. Our assessment of endemic Mexican athysanine leafhoppers using current IUCN criteria indicates that most endemic Mexican species of this tribe satisfy the criteria for listing as either EN or CR on the IUCN red list. 60% of these species inhabit the MTZ region, 39% have a Neotropical distribution and nearly 30% of these inhabit threatened habitats. These results

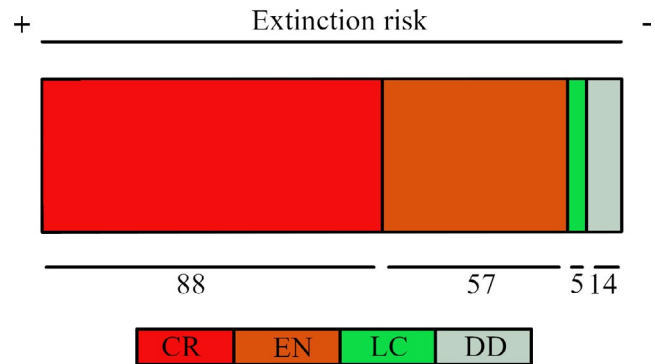


FIGURE 12 Red list status of Mexican Athysanini species. Number indicate species number in such risk category. IUCN categories displayed: Critically Endangered (CR), Endangered (EN), Least Concern (LC) and Data Deficient (DD)

highlight the urgent need for an improved conservation framework in the Americas.

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CONFLICT OF INTEREST

The authors declare that they have no known competing interests that could have appeared to influence the work reported in this paper.

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DATA AVAILABILITY STATEMENT


Additional information of records, species and distribution of Mexican leafhoppers are fully available on request.

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BIOSKETCH

The research team works on identifying rich diversity areas and high degrees of leafhopper endemism. Aims to generate basis data for the inclusion of species endangered to UAIC red list inhabiting tropical relict ecosystems. This research is one of the multidisciplinary studies that fulfil conservation decision-making on these key important insect family as indicator of healthy habitats.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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