Potential geographic distribution and ecological niche of the insect order Megaloptera: the case of the nearctic-neotropical transition zone

Hugo A. Alvarez^{1*}, Miguel A. Rivas-Soto²

¹ Departamento de Biología, IINCINH, Instituto de Investigación en Ciencias-Naturales y Humanidades A.C. Puebla, Mexico.

² Campaña de Hábitats, OCEANA (ONG), CDMX, Mexico.

*Corresponding author e-mail: hugoalvarez01@gmail.com. ORCID: 0000-0001-6576-9425.

Current affiliation: Department of Zoology, University of Granada, Spain.

Abstract

The Megaloptera are an interesting, but relatively poorly studied group of insects. Among the new world Megaloptera, it is not known the effect of the nearctic-neotropical transition zone on their biogeographic distribution. Here we present potential geographic distributions based on ecological niche models of the species of Megaloptera from North America that occurred in the transition zone. Results suggested that the geographic range of Corydalinae (dobsonflies) in the transition zone is associated to mountainous formations and that most species favour for warm climates with higher precipitation rates. Climate types tend to be important for species that show narrow geographic ranges, but precipitation tends to be the most important variable to explain species dispersion. In addition, Chauliodinae (fishflies) and Sialidae (alderflies) may have no

relation with the transition zone. Overall, our models support the dispersion of dobsonflies from the neotropics to North America and explain the two endemisms in Mexico as the result of the formation of the transition zone.

Keywords: Biogeography, alderflies, dobsonflies, fishflies, GIS, ecological niche models.

Introduction

The Megaloptera are an interesting, but relatively poorly studied group of insects composed of two families, Sialidae (alderflies) and Corydalidae. The latter including the subfamilies Corydalinae (dobsonflies) and Chauliiodinae (fishflies). This insect order is composed of less than 350 species (Cover and Resh 2008; Cover and Bogan 2015). Megaloptera are holometabolous, with aquatic larvae and terrestrial pupae and adults (Cover and Bogan 2015). Larvae are highly sensitive to pollution (Maki et al. 1973; Tarter et al. 2010) and good bio-indicators of freshwater ecosystem health (Nair et al. 2015). The life cycle of most species ranges from one to two years, though some species live up to five years (Elliott 1996; Cover and Resh 2008; Álvarez 2012). Nevertheless, the adult lifespan is short, only one to two weeks (Hayashi 1999; Álvarez 2012; 2014; Cover and Bogan 2015). Adult dobsonflies are typically nocturnal (Cover and Resh 2008; Álvarez 2014; Álvarez et al. 2017a; 2017b; 2019), while many alderflies and fishflies are diurnal (Stange 1990; Elliott 1996; Anderson 2009).

The nearctic-neotropical transition zone is a valid biogeographic region in the north of the Americas where confluence the Nearctic and Neotropical regions and includes the mountainous provinces in the central portion of Mexico (Cuervo-Robayo et al. 2020). It has been proposed that

the heterogeneous nature of this zone may produce high rates of divergence and endemism (Espinosa et al. 2008). However, its mountainous form could be also a limit for the dispersion of neotropical species to the north and nearctic species to the south. This zone holds 9 valid species of the fauna of Megaloptera (Contreras-Ramos and Rosas 2014). Though, in the country 13 species of Megaloptera fauna have been recorded, i.e., the three known species of the genus *Platyneuromus* Weele, 1909 (Corydalinae) are mostly distributed across the south, in the state of Chiapas. Three species of the genus *Chloronia* Banks, 1908 (Corydalinae) are distributed in central and south-eastern Mexico. A single species of the genus *Neohermes* Banks, 1908 (Chauliodinae) is distributed in the north of the country. While a sole species of the genus *Ilyobius* Enderlein, 1910 (Sialidae) is restricted to south-eastern Mexico. Finally, five species of the genus *Corydalus* Latreille, 1802 (Corydalinae) are distributed across the country with different geographic ranges, mostly in the center and south of the country (see Alvarez 2012; Contreras-Ramos and Rosas 2014). Recently a study of Jiang et al. (2021) showed that the biogeographic evolution of the new world Megaloptera was prior to Pangea breakup with groups affected latter by the Eurogondwanan faunal interchange, suggesting different events of vicariance and divergence, and apparently, in North America several lineage distributions are compromised by the nearctic-neotropical transition zone. However, no studies have suggested a potential distribution hypothesis for the species of Megaloptera fauna to assess specifically the effect of this transition zone.

Aquatic insects with discreet ecological requirements, low vagility and disjunct distributions such as Megaloptera represent a valuable model for testing biogeographical hypotheses by

reconstructing their distribution patterns. In this study we describe a possible scenario of geographic ranges for the species of the order Megaloptera that occur in the nearctic-neotropical transition zone using niche models with the data available to date, aiming to understand biogeographical patterns and to propose new insights regarding the evolution and conservation of the order Megaloptera.

Materials and methods

As the nearctic-neotropical transition zone occurs in Mexico, we focus on the species of the order Megaloptera that occur in this country. We obtained records from the data base of Mexican Megaloptera (Contreras-Ramos 2000), in the Mexican National Biodiversity Information System (SNIB). This system belongs to the Mexican Commission for the Knowledge and Use of Biodiversity (CONABIO). Additionally, we extracted records from literature and empirical occurrence records, including only the register with three or more degrees of distance between them.

We made ecological niches models (ENM) using the software Maxent (Phillips et al. 2006). Maxent is a maximum entropy-based machine-learning method used for making predictions when incomplete data are available. The environmental data and species occurrence data are used together in ENM with the aim of creating models of potential distributions of species. Maxent estimates the probability distribution for a species' occurrence that is most spread out given the constraints derived from the available data (Phillips et al. 2004; Phillips et al. 2006). The technique has the advantage of using both categorical and continuous environmental data, detail

of prediction due to the continuous nature of the resulting models, and speed and simplicity of the software implementation.

We included in the models the accepted climates of Mexico and ecoregions (CONABIO), and the 19 climate variables of BIOCLIM data sets developed by Hijmans et al. (2005). BIOCLIM data sets characterize global climates using average monthly weather station data (available at different spatial resolutions). Bioclimatic variables are derived from the monthly temperature and rainfall values (biologically meaningful variables). The bioclimatic variables represent annual trends (e.g., mean annual) seasonality (e.g., annual range) and extreme or limiting environmental factors (e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters; being a quarter a period of three months i.e., 1/4 of the year). They are coded as follows: BIO1 = Annual Mean Temperature, BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp)), BIO3 = Isothermality (BIO2/BIO7) ($\times 100$), BIO4 = Temperature Seasonality (standard deviation $\times 100$), BIO5 = Max Temperature of Warmest Month, BIO6 = Min Temperature of Coldest Month, BIO7 = Temperature Annual Range (BIO5-BIO6), BIO8 = Mean Temperature of Wettest Quarter, BIO9 = Mean Temperature of Driest Quarter, BIO10 = Mean Temperature of Warmest Quarter, BIO11 = Mean Temperature of Coldest Quarter, BIO12 = Annual Precipitation, BIO13 = Precipitation of Wettest Month, BIO14 = Precipitation of Driest Month, BIO15 = Precipitation Seasonality (Coefficient of Variation), BIO16 = Precipitation of Wettest Quarter, BIO17 = Precipitation of Driest Quarter, BIO18 = Precipitation of Warmest Quarter, BIO19 = Precipitation of Coldest Quarter.

We also included three topographic variables from the project Hydro1K. These datasets were used in this study because they provide ready-to-use, geo-referenced hydrographic information for regional and global-scale watershed analysis and modelling and have been constructed to maximize the accuracy of hydrologic parameters.

Finally, models were made with 75% of data occurrence for standardization and 25% for validation. We consider as a potential occurrence when a model predicted 10% of the training occurrences. The niche model results were clipped in ArcMap 9.3 using the terrestrial ecoregions from WWF to reduce the over-prediction outside the natural habitat of these insects (Olson et al. 2001).

Results

We obtained nine significative ENM (AUC parameter upper to 0.95) for the species *Chloronia mexicana* Stitz, 1914, *Chloronia mirifica* Navás, 1925, *Chloronia pallida* (Davis), 1903, *Corydalus bidenticulatus* Contreras-Ramos, 1998, *Corydalus luteus* Hagen, 1861, *Corydalus magnus* Contreras-Ramos, 1998, *Corydalus peruvianus* Davis, 1903, *Corydalus texanus* Banks, 1903, and *Platyneuromus soror* (Hagen), 1861. Moreover, four species *Ilyobius mexicana* (Banks), 1901, *Neohermes filicornis* (Banks), 1903, *Platyneuromus honduranus* Navás, 1924, and *Platyneuromus reflexus* Glorioso and Flint, 1984, had not enough records to reach the 10 % of the training occurrences. This means that we produced only the distributions for the representatives of Corydalinae, but not for the representatives of Chauliodinae and Sialidae.

The predicted distributions of the species resulted primarily from environmental variables and terrestrial ecoregions, and overall, model distributions match with hydro-ecoregions.

Accordingly, of the 19 BIOCLIM variables, the variables that contributed the most to models were: temperature seasonality (BIO4), mean temperature of coldest quarter (BIO11), and mean temperature of coldest month (BIO6). In addition, table 1 summarizes the climates of Mexico that had higher incidence in the models for all species, and table 2 shows the climates that had higher incidence on the models for each species (from most to least). Overall, it can be extracted that semi-warm subtropical climate types had the highest incidence in almost all species followed by semi-warm tropical and semi-cold subtropical.

Specific distribution patterns based on modelling

Chloronia mexicana: The species was distributed in regions with semi warm and warm climates mostly, which show high temperatures and moderate to high rainfall (Table 2). Niche models data show that the geographic range of *C. mexicana* is associated to the Sierra Madre Oriental, the gulf coastal plain, the Balsas depression, the east section of the volcanic belt, the Sierra Madre de Oaxaca, the Tabasco plain, the south section of Yucatan platform and the north section of Chiapas highlands (Figure 1). Accordingly, this species will be related with 8 hydro-ecoregions, Quintana Roo – Motagua (202), Upper Usumacinta (174), Grijalva – Usumacinta (173), Coatzacoalcos (172), Papaloapan (171), Rio Balsas (169), Panuco (167), and partly reaching Sierra Madre del Sur (170) (Figure 1, Table 3).

Chloronia mirifica: The species was distributed in regions with tropical climates that show semi-warm to warm temperatures and high rainfall (Table 2). Niche models data show that the geographic range of *C. mirifica* is associated to the Sierra Madre de Oaxaca, the north section of the Sierra Madre de Chiapas and the Chiapas highlands, and a restricted area in Los Tuxtlas formation (Figure 1). Accordingly, this species will be related with 5 hydro-ecoregions, Quintana Roo – Motagua (202), Upper Usumacinta (174), Grijalva – Usumacinta (173), Coatzacoalcos (172), and Papaloapan (171) (Figure 1, Table 3).

Chloronia pallida: The species is endemic of Mexico, it was distributed in regions with semi warm climates, which show moderate to high temperatures and moderate rainfall (Table 2). Niche models data show that the geographic range of *C. pallida* is associated to the south section of the Sierra Madre Oriental, the volcanic belt, the east section of the Sierra Madre del Sur, the north section of Sierra Madre de Oaxaca and the north section of the Sierra Madre de Chiapas and the Chiapas highlands (Figure 1). Accordingly, this species will be related with 3 hydro-ecoregions, Chiapas – Fonseca (201), Sierra Madre del Sur (170), and Rio Balsas (169) (Figure 1, Table 3).

Corydalis bidenticulatus: The species is endemic of Mexico, it was distributed in regions with semi-warm to arid climates, which show high temperatures and moderate to low rainfall (Table 2). Niche models data show that the geographic range of *C. bidenticulatus* is associated to the Sierra Madre del Sur, the south section of the Sierra Madre Occidental, the pacific coastal lowlands, the volcanic belt and the Balsas depression (Figure 1). Accordingly, this species will be related with 8 hydro-ecoregions, Chiapas – Fonseca (201), Sierra Madre del Sur (170), Rio

Balsas (169), Ameca – Manantlan (168), Lerma – Chapala (165), Rio Santiago (164), Sinaloa (162), and partly reaching Coatzacoalcos (172) (Figure 1, Table 3).

Corydalis luteus: The species was distributed in regions with semi-warm to temperate climates, which show moderate rainfall (Table 2). Niche models data show that the geographic range of *C. luteus* is associated to the south section of gulf coastal plain, the Sierra Madre Oriental, the north of the Tabasco plain, part of the Balsas depression, the Chiapas highlands, the Sierra Madre de Chiapas and part of the Sierra Madre del Sur (Figure 1). Accordingly, this species will be related with 13 hydro-ecoregions, Quintana Roo – Motagua (202), Chiapas – Fonseca (201), Upper Usumacinta (174), Grijalva – Usumacinta (173), Coatzacoalcos (172), Papaloapan (171), Sierra Madre del Sur (170), Rio Balsas (169), Panuco (167), Rio San Juan (138), Rio Salado (137), Lower Rio Grande – Bravo (135), and partly reaching Lerma – Chapala (165) (Figure 1, Table 3).

Corydalis magnus: The species was distributed in regions with semi-cold to semi-warm climates, which show moderate low temperatures and moderate high rainfall (Table 2). Niche models data show that the geographic range of *C. magnus* is associated to the south section of the Sierra Madre Oriental, the volcanic belt, the east section of the Sierra Madre del Sur, the north section of Sierra Madre de Oaxaca, and the north section of the Sierra Madre de Chiapas and Chiapas highlands (Figure 1). Accordingly, this species will be related with 11 hydro-ecoregions, Quintana Roo – Motagua (202), Chiapas – Fonseca (201), Upper Usumacinta (174), Grijalva – Usumacinta (173), Coatzacoalcos (172), Papaloapan (171), Sierra Madre del Sur (170), Rio

Balsas (169), Ameca – Manantlan (168); Panuco (167), and Lerma – Chapala (165) (Figure 1, Table 3).

Corydalis peruvianus: The species was distributed in regions with semi-cold to warm climates, which show moderate rainfall (Table 2). Niche models data show that the geographic range of *C. peruvianus* is associated to the south section of the Sierra Madre Oriental and the gulf coastal plain, the volcanic belt, the mesa central, the Balsas depression, the Tabasco plain, the Chiapas highlands and the south section of Yucatan platform (Figure 1). Accordingly, this species will be related with 11 hydro-ecoregions, Quintana Roo – Motagua (202), Chiapas – Fonseca (201), Upper Usumacinta (174), Grijalva – Usumacinta (173), Coatzacoalcos (172), Papaloapan (171), Rio Balsas (169), Ameca – Manantlan (168); Panuco (167), Lerma – Chapala (165), and partly reaching Sierra Madre del Sur (170) (Figure 1, Table 3).

Corydalis texanus: The species was distributed in regions with semi-warm to semi-arid climates, which show moderate to low rainfall (Table 2). Niche models data show that the geographic range of *C. texanus* is associated to the Sierra Madre Occidental, the pacific coastal lowlands, the east and south section of the mesa del norte, the mesa central and the volcanic belt, the south section of the Sierra Madre Oriental, the Balsas depression, the east face of the Sierra Madre del Sur and a small section of the Sierra Madre de Chiapas (Figure 1). Accordingly, this species will be related with 18 hydro-ecoregions, Quintana Roo – Motagua (202), Chiapas – Fonseca (201), Upper Usumacinta (174), Grijalva – Usumacinta (173), Coatzacoalcos (172), Papaloapan (171), Sierra Madre del Sur (170), Rio Balsas (169), Ameca – Manantlan (168); Panuco (167), Llanos

El Salado (166), Lerma – Chapala (165), Rio Santiago (164), Mayran – Viesca (163), Sinaloa (162), Guzman – Samalayuca (161), Sonora (160), and Rio Conchos (134) (Figure 1, Table 3).

Platyneuromus soror: The species was distributed in regions with semi-warm/semi-cold to temperate climates, which show moderate rainfall (Table 2). Niche models data show that the geographic range of *P. soror* is associated to the west face and the south section of the Sierra Madre Oriental, the volcanic belt, and part of the mesa central, the north section of the Sierra Madre de Oaxaca, the Sierra Madre de Chiapas and the Chiapas highlands, and a restricted area in Los Tuxtlas formation (Figure 1). Accordingly, this species will be related with 14 hydro-ecoregions, Quintana Roo – Motagua (202), Chiapas – Fonseca (201), Upper Usumacinta (174), Grijalva – Usumacinta (173), Coatzacoalcas (172), Papaloapan (171), Rio Balsas (169), Ameca – Manantlan (168); Panuco (167), Llanos El Salado (166), Lerma – Chapala (165), Rio San Juan (138); Lower Rio Grande -Bravo (135), and partly reaching Sierra Madre del Sur (170) (Figure 1, Table 3).

Discussion

Our results suggested that the geographic range of Corydalinae (dobsonflies) in the nearctic-neotropical transition zone seems to be closely associated to mountainous formations, and that model distributions match with hydro-ecoregions (Abell et al. 2008). Accordingly, our results also show that most species favour for warm climates with higher precipitation rates. Climate types tend to be important for species that show narrow geographic ranges such as *C. magnus* with a preference for cold and temperate climates or *C. mirifica* with a preference for tropical

climates. However, precipitation tends to be the most important variable to explain species dispersion.

As previously suggested by Contreras-Ramos (1998) and Álvarez (2012), there is a pattern of geographical ranges for the species of Megaloptera in this zone, specifically our results suggested that almost all species are present in the neotropical south of the country. Then, within the nearctic-neotropical transition zone, near to the Balsas depression and the volcanic belt the geographic range of the species diverge. For example, regarding the genus *Corydalus*, three species *C. peruvianus*, *C. magnus*, and *C. luteus* remain in the centre, east, and south-east. Their geographic range is highly similar and share almost the same hydro-ecoregions, especially *C. peruvianus* and *C. magnus*, which prefer semi-cold climates. However, *C. magnus* had a more restricted range due to its preference for temperate climates. These three species range from the neotropical region to the centre of the transition zone and disperse within the Sierra Madre Oriental, being *C. luteus* and *C. peruvianus* the ones that reach the Gulf of Mexico. Interestingly, these three species have an origin in Central and South America (Contreras-Ramos 1998; 2011). Conversely, two species *C. texanus* and *C. bidenticulatus* remain in the south, centre, and west. They do not share all the same hydro-ecoregions, in this case, *C. texanus* is the most widespread species in the country and therefore in the transition zone. Particularly, this species disperses over the neotropical south-west and centre-west, but also over the centre of the transition zone surrounding the Sierra Madre Occidental. *Corydalus bidenticulatus* remains in the neotropical west and the centre of the transition zone. Regarding the genus *Chlorinia*, only *C. mexicana* disperses across the neotropical south and east into the transition zone following the Sierra Madre

Oriental and through the centre of the transition zone. The rest of species remain in the neotropical south. Finally, regarding the *Platyneuromus* genus, *P. soror* which is the most widespread species of the genus, share almost the same pattern and hydro-ecoregions with *C. magnus*. Indeed, it is common to find this species sharing the same habitat and be collected in the same regions (see Álvarez et al., 2019).

In addition, there are two endemisms of Megaloptera in Mexico that can be explained by our analysis, i.e., *C. bidenticulatus* and *C. pallida*. Our results showed a relation with the nearctic-neotropical transition zone and their origin might be caused by the transition zone. We hypothesise that an ancestral species in both *C. luteus*, *C. magnus*, *C. bidenticulatus* group (Contreras-Ramos, 1998; 2011) and *C. mirifica*, *C. gloriosoi*, *C. pallida*, *C. mexicana* group (Penny and Flint, 1982) dispersed through the area known as the Tehuantepec isthmus (hydro-ecoregions: Coatzacoalcos (172), Papaloapan (171), Sierra Madre del Sur (170), and Chiapas-Fonseca (201)), then reaching the Balsas depression. It is there at the Balsas depression where a speciation event might occur as an effect of the orogeny that gave rise to the Sierras Madre around the mid-Tertiary (as suggested by Contreras-Ramos 1998). Then the new species dispersed, i.e., *C. bidenticulatus* to the north and south-east and *C. pallida* to the south and east, both following the neotropical Pacific coast and the Balsas depression.

Unfortunately, we were unable to produce model distributions for the representative of Chauliodinae and Sialidae. The species that were not included in modelling may have no relation with the nearctic-neotropical transition zone. For example, *P. honduranus* and *P. reflexus* have

been collected in the north section of Chiapas, their geographic range is associated mostly to Central America, and thus, this species may never reach the transition zone. *Ilyobius mexicana*, has been collected in Chiapas and Veracruz, it is possible that this species has a geographic range similar to that of *C. mirifica* (figure 1). Finally, *Neohermes filicornis*, has been collected in Sonora and Baja California, in the northwest of Mexico, its geographic range is mostly associated to the west of the United States of America.

Overall, it is possible that, while precipitation is most important, the current geographic range of these species could be affected due to the degree of habitat conservation (pollution and fragmentation) and the continuum of the total ecosystem (Estrada and Coates-Estrada 1996; Cayuela et al. 2006; Arriaga-Weiss et al. 2008). Thus, the geographic range of Corydalinae species could be minor than model prediction. It has been shown that in landscapes that are less homogeneous, mountainous formations are not extremely modified by human activities, in fact, some conservational approaches have been successful, focusing on this type of landscape features (DeClerck et al. 2010). These rugged landscapes naturally provide zones where species can inhabit with lower perturbation compared to other types of regions. This could explain the tendencies in the geographic ranges of Megaloptera fauna within the nearctic-neotropical transition zone. The Sierra Madre Occidental, the Sierra Madre Oriental, the volcanic belt, the Sierra Madre del Sur and their sub-divisional lower formations, provide a continuous of aquatic habitats that megalopterans may inhabit (Álvarez 2012). Then specific climate types might constraint the distribution of the species for lower (near sea level) or higher altitudes.

Here we provide the first approach to understand biogeographic distribution of the Megaloptera from the nearctic-neotropical transition zone. However, more efforts are needed to achieve biogeographical modelling of Megaloptera fauna. Field sampled data and large-scale approaches such as continental scale will allow a better understanding of the biogeographic patterns and evolution of this insect order. Nonetheless, our results are in agreement with biogeographical hypothesis for new world Megaloptera proposed by Contreras-Ramos (1998) and Penny (1993), and the results provided by Jiang et al. (2021), which showed that the biogeographical patterns in North America are the result of two main events, first, Sialidae, Corydalinae, and Chauliodinae originated previous to the breakup of Pangea (late Jurassic ~160-145 Ma). Chauliodinae and Sialidae dispersed through Laurentia and West Gondwana and then dispersed across the area until the new continent was formed, with subsequent events of vicariance. Conversely, Corydalinae and especially the *Corydalis* lineage dispersed from Asia via Europe and Africa to South America as a result of the second Eurogondwanan connection (Late Cretaceous ~100-90 Ma) (Oliveira et al. 2010; Jiang et al. 2021). Then they disperse first through South America then to Central and North of America, with subsequent events of vicariance, which for North America was the rise and formation of the nearctic-neotropical transition zone.

Acknowledgments

The authors want to thank Manolo Tierno de Figueroa and Lorelí Carranza for their helpful comments on an earlier version of the manuscript. Also, the authors want to highlight the remarkable work of Atilano Contreras Ramos creating the free database of Mexican Megaloptera records of CONABIO.

Disclosure statement

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as constituting a conflict of interest.

ORCID

Hugo Alejandro Álvarez <https://orcid.org/0000-0001-6576-9425>

References

- Abell, R., et al. (2008), ‘Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation’, *Bioscience* 58, 5.
- Álvarez, H.A. (2012), ‘New records of Mexican dobsonflies of the genus *Corydalus* Latreille (Megaloptera: Corydalidae). *Entomotropica* 27, 77-81.
- Álvarez, H.A. (2014). ‘Contributions to the knowledge of dobsonflies of Puebla State, Mexico (Megaloptera: Corydalidae: *Corydalus*)’, *Entomotropica* 29, 125-127.
- Álvarez, H.A., García-Chávez, J.H., and Cebada-Ruiz, J.A. (2017a), ‘Do Social Environments Affect the Use of Exaggerated Traits in the Dobsonfly *Corydalus bidenticulatus*?’, *Entomological Science*, 20, 168–176.
- Álvarez, H.A., Carrillo-Ruiz, H., and Cebada-Ruiz, J.A. (2017b), ‘Estudio del sistema reproductivo de *Corydalus bidenticulatus* Contreras-Ramos (Megaloptera: Corydalidae)’, *Entomología Mexicana*, 4, 698–702.

Álvarez, H.A., Tierno de Figueroa J.M., and Cebada-Ruiz, J.A. (2019), ‘The expression of aggression in the dobsonflies *Corydalus magnus* Contreras-Ramos, 1998 and *Platyneuromus soror* (Hagen, 1861) (Megaloptera: Corydalidae)’, *Aquatic Insects*, 40, 137-145.

Anderson, N.H. (2009), ‘Megaloptera (Alderflies, Fishflies, Hellgrammites, Dobsonflies)’, in Encyclopedia of Insects. (2nd ed.), eds. V.H. Resh and R.T. Carde, Burlington, MA: Academic Press, pp. 620–623.

Arriaga-Weiss, S.L., Calmé, S., Kampichler, C., (2008), ‘Bird communities in rainforest fragments: guild responses to habitat variables in Tabasco, Mexico’, *Biodiversity and Conservation*, 17, 173-190.

Cayuela, L., Benayas, J.M.R., Echeverría, C., (2006), ‘Clearance and fragmentation of tropical montane forests in the Highlands of Chiapas, Mexico’ (1975–2000). *Forest Ecology and Management*, 226, 208-218.

Contreras-Ramos, A., (1998), ‘*Systematics of the dobsonfly genus Corydalus Latreille (Megaloptera: Corydalidae)*’, Thomas Say Monographs, Entomological Society of America. Lanham, MD.

Contreras Ramos, A., (2000), ‘Megaloptera (Insecta: Neuropterida) de México’, Universidad Nacional Autónoma de México. Instituto de Biología. Bases de datos SNIB2010-CONABIO, proyecto No. K022. México.

Contreras-Ramos, A., (2011), ‘Phylogenetic review of dobsonflies of the subfamily Corydalinae and the genus *Corydalus* Latreille (Megaloptera: Corydalidae)’, *Zootaxa*, 2862, 1-38.

Contreras-Ramos, A., Rosas, M., (2014), ‘Biodiversidad de Megaloptera y Raphidioptera en México’, *Revista Mexicana de Biodiversidad*, 85.

- Cover, M.R., Bogan, M.T., (2015), ‘Minor Insect Orders’, in Thorp and Covich’s Freshwater Invertebrates. Ecology and General Biology. (4th ed.), eds. J.H. Thorp and D.C. Rogers, London, UK: Academic Press, pp. 1059–1072.
- Cover, M.R., Resh, V.H., (2008), ‘Global biodiversity of dobsonflies, fishflies and alderflies (Megaloptera; Insecta) and spongillafly, nevrothids, and osmylids (Neuroptera; Insecta) in freshwater’, *Hydrobiologia*, 595, 409-417.
- Cuervo-Robayo, A. P., Ureta, C., Gómez-Albores, M. A., Meneses-Mosquera, A. K., Téllez-Valdés, O., Martínez-Meyer, E., (2020), ‘One hundred years of climate change in Mexico’, *Plos one*, 15, e0209808.
- DeClerck, F.A., et al., (2010), ‘Biodiversity conservation in human-modified landscapes of Mesoamerica: Past, present and future’, *Biological Conservation*, 143, 2301-2313.
- Elliott, J.M., (1996), ‘British freshwater Megaloptera and Neuroptera. A Key with Ecological Notes’, Ambleside. Cumbria, UK: Freshwater Biological Association, Scientific Publication No. 54.
- Espinosa, D., et al., (2008), ‘El conocimiento biogeográfico de las especies y su regionalización natura’. In: CONABIO, editor. Capital Natural de México. México, D.F. pp. 33–65.
- Estrada, A., Coates-Estrada, R., (1996), ‘Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico’, *International Journal of Primatology*, 17, 759-783.
- Hayashi, F., (1999), ‘Rapid Evacuation of Spermatophore Contents and Male Post-mating Behaviour in Alderflies’, *Entomological Science*, 2, 49–56.

- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., (2005), ‘Very high resolution interpolated climate surfaces for global land areas’, *International Journal of Climatology*, 25, 1965-1978.
- Jiang, Y., et al., (2021), ‘Similar pattern, different paths: tracing the biogeographical history of Megaloptera (Insecta: Neuropterida) using mitochondrial phylogenomics’, *Cladistics*, 1-18.
- Maki, A.W., Stewart, K.W., Silvey, J.K.G., (1973), ‘The effects of Dibrom on respiratory activity of the stonefly, *Hydroperla crosbyi*, hellgrammite, *Corydalis cornutus* and the golden shiner, *Notemigonus crysoleucas*’, *Transactions of the American Fisheries Society*, 102, 806-815.
- Nair, G.A., Morse, J.C., Marshall, S.A., (2015), ‘Aquatic insects and their societal benefits and risks’, *Journal of Entomology and Zoolgy Studies*, 3, 171-177.
- Oliveira, F.B., Molina, E.C., Marroig, G., (2010), ‘Paleogeography of the South Atlantic: a route for primates and rodents into the New-World? South American primates’, Springer, New York, NY, pp. 55–68.
- Olson, D.M., et al., (2001), ‘Terrestrial ecoregions of the World: a new map of life on earth’, *BioScience*, 51, 933.
- Penny, N.D., (1993), ‘The phylogenetic position of *Chloroniella peringueyi* (Megaloptera: Corydalidae) and its zoogeographic significance’, *Entomological News*, 104, 17–30.
- Penny, N.D., Flint, O.S., Jr., (1982), A revision of the genus *Chloronia* (Neuroptera: Corydalidae)’, *Smithsonian Contributions to Zoology*, 348, 1–27.
- Phillips, S.J., Dudík, M., Schapire, R.E., (2004), A maximum entropy approach to species distribution modeling’ In: *Proceedings of the 21st International Conference on Machine Learning*, ACM Press, New York, pp. 655–662.

Phillips, S.J., Anderson, R.P., Schapire, R.E., (2006), ‘Maximum entropy modeling of species geographic distributions’, *Ecological Modelling*, 190, 231-259.

Stange, L.A., (1990), ‘The alderflies of Florida (Megaloptera: Sialidae)’, *Entomology Circular*, (Gainesville) 329.

Tarter, D.C., Bailey, J.E., Whitman, M.J., (2010), ‘New Distribution Records and Seasonal Emergence Pattern of *Corydalus cornutus* (Linnaeus) (Megaloptera: Corydalidae) in West Virginia, U.S.A’, *Entomological News*, 121, 342-347.

Table 1. Climate types and their general characteristics, annual average temperature (AAT), temperature of the coldest month (TCM), temperature of the hottest month (THM), rainfall (Rf), precipitation of the driest month (PDM), temperature/precipitation index (T/PI), winter rainfall rate (WRR). Rainfall periods: summer rainfall (SR), winter rainfall (WR), all year rainfall (AY).

Acronym	Climate type	AAT	TCM	THM	Rf	PDM	T/PI	WRR
SaSw	Semi-arid semi-warm	> 18°C	< 18°C	> 22°C	SR	Na	Na	5% - 10.2 %
SaW	Semi-arid warm	> 22°C	> 18°C	Na	SR	Na	Na	5% - 10.2 %
ScStL	Semi-cold subtropical with long fresh summer	5°C - 12°C	-3°C - 18°C	< 22°C	SR	< 40 mm	Na	5% - 10.2 %
SwSt1	Semi-warm subtropical	> 18°C	< 18°C	> 22°C	SR	< 40 mm	> 55	5% - 10.2 %
SwSt2	Semi-warm subtropical	> 18°C	< 18°C	> 22°C	SR	< 40 mm	43.2 - 55	5% - 10.2 %
SwSt3	Semi-warm subtropical	> 18°C	< 18°C	> 22°C	SR	< 40 mm	< 43.2	5% - 10.2 %
SwTr1	Semi-warm tropical	> 18°C	< 18°C	> 22°C	SR	> 40 mm	Na	> 10.2%
SwTr2	Semi-warm tropical	> 18°C	< 18°C	> 22°C	SR	> 40 mm	Na	5% - 10.2 %
SwTr3	Semi-warm tropical	> 18°C	< 18°C	> 22°C	SR - WR	> 40 mm	Na	< 18%
TeSt1	Temperate subtropical	12°C - 18°C	-3°C - 18°C	< 22°C	SR	< 40 mm	> 55	5% - 10.2 %
TeSt2	Temperate subtropical	12°C - 18°C	-3°C - 18°C	< 22°C	SR	< 40 mm	43.2 - 55	5% - 10.2 %
TeTr	Temperate tropical	12°C - 18°C	-3°C - 18°C	< 22°C	AY	> 40 mm	Na	> 18%
WSt1	Warm subtropical	> 22°C	> 18°C	Na	SR	< 60 mm	43.2 - 55.3	5% - 10.2 %
WSt2	Warm subtropical	> 22°C	> 18°C	Na	SR	0 - 60 mm	> 55.3	5% - 10.2 %
WSt3	Warm subtropical	> 22°C	> 18°C	Na	SR	0 - 60 mm	< 43.2	5% - 10.2 %
WTr1	Warm tropical	> 22°C	> 18°C	Na	SR - WR	> 40 mm	Na	> 18%
WTr2	Warm tropical	> 22°C	> 18°C	Na	SR	< 60 mm	Na	5% - 10.2 %
WTr3	Warm tropical	> 22°C	> 18°C	Na	SR	< 60 mm	Na	5% - 10.2 %

Table 2. Climates (acronyms) with higher incidences on the niche models for each species.

Megaloptera species	Climates
<i>Chloronia mexicana</i>	SwTr3, SwSt2, WSt2, SwSt1, WSt1, SwSt3
<i>Chloronia mirifica</i>	SwTr3, SwTr2, WTr1, TeTr, WTr2
<i>Chloronia pallida</i>	SwSt2, WSt1, SwSt1, SwSt3, WSt3
<i>Corydalus bidenticulatus</i>	SwSt2, SwSt1, WSt1, SwSt3, SaW
<i>Corydalus luteus</i>	SwSt2, SwSt1, SwSt3, TeSt2, SwTr3, SwTr2, TeSt1
<i>Corydalus magnus</i>	ScSt, SwSt1, TeSt1, TeSt2, SwSt2
<i>Corydalus peruvianus</i>	ScSt, SwSt2, SwTr3, SwSt1, WSt2
<i>Corydalus texanus</i>	SwSt2, SwSt1, TeSt2, SwSt3, SaSw
<i>Platyneuromus soror</i>	SwSt1, ScSt, TeSt1, SwSt2, SwTt2

Table 3. Freshwater ecoregions present in the Nearctic-Neotropical transition zone (Mexico).

ID	Zone	Type	Name
134	Nearctic	Xeric freshwaters and endorheic (closed) basins	Rio Conchos
135	Nearctic	Temperate floodplain rivers and wetlands	Lower Rio Grande - Bravo
136	Nearctic	Xeric freshwaters and endorheic (closed) basins	Cuatro Cienegas
137	Nearctic	Xeric freshwaters and endorheic (closed) basins	Rio Salado
138	Nearctic	Xeric freshwaters and endorheic (closed) basins	Rio San Juan (Mexico)
159	Nearctic	Xeric freshwaters and endorheic (closed) basins	Southern California Coastal - Baja California
160	Nearctic	Xeric freshwaters and endorheic (closed) basins	Sonora
161	Nearctic	Xeric freshwaters and endorheic (closed) basins	Guzman - Samalayuca
162	Nearctic	Tropical and subtropical coastal rivers	Sinaloa
163	Nearctic	Xeric freshwaters and endorheic (closed) basins	Mayran - Viesca
164	Neotropic	Tropical and subtropical coastal rivers	Rio Santiago
165	Nearctic	Xeric freshwaters and endorheic (closed) basins	Lerma - Chapala
166	Nearctic	Xeric freshwaters and endorheic (closed) basins	Llanos El Salado
167	Neotropic	Tropical and subtropical coastal rivers	Panuco
168	Neotropic	Tropical and subtropical coastal rivers	Ameca - Manantlan
169	Neotropic	Tropical and subtropical coastal rivers	Rio Balsas
170	Neotropic	Tropical and subtropical coastal rivers	Sierra Madre del Sur
171	Neotropic	Tropical and subtropical coastal rivers	Papaloapan
172	Neotropic	Tropical and subtropical coastal rivers	Coatzacoalcos
173	Neotropic	Tropical and subtropical coastal rivers	Grijalva - Usumacinta
174	Neotropic	Tropical and subtropical upland rivers	Upper Usumacinta
175	Neotropic	Tropical and subtropical coastal rivers	Yucatan
201	Neotropic	Tropical and subtropical coastal rivers	Chiapas - Fonseca
202	Neotropic	Tropical and subtropical coastal rivers	Quintana Roo - Motagua

Figure 1. Neartic-Neotropical transition zone maps. Biogeographic ecoregions separating the neartic, neotropical, and the transition zone (a), and freshwater ecoregions in the area (b).

Potential geographic distribution of *Chloronia*, *Corydalus*, and *Platyneuromus* species resulted from modelling.