# UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

## POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE ECOLOGÍA
**Ecología**

# IMPACTO DE LA URBANIZACIÓN SOBRE LIBÉLULAS Y CABALLITOS DEL DIABLO (ODONATA)

# TESIS

QUE PARA OPTAR POR EL GRADO DE:

**DOCTORA EN CIENCIAS**

PRESENTA:

**CATALINA MARÍA SUÁREZ TOVAR**

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**FACULTAD DE CIENCIAS, UNAM, CDMX**

**MÉXICO, CD. MX. NOVIEMBRE, 2023.**

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**COORDINACIÓN GENERAL DE ESTUDIOS DE POSGRADO**
**COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS**
**ENTIDAD INSTITUTO DE ECOLOGÍA**
**OFICIO: CGEP/CPCB/IE/0870/2023**
**ASUNTO: Oficio de Jurado**

**M. en C. Ivonne Ramírez Wence**
**Directora General de Administración Escolar, UNAM**
**Presente**

Me permito informar a usted, que el Comité Académico, del **Posgrado en Ciencias Biológicas**, en su reunión ordinaria celebrada el **28 de agosto de 2023**, aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **SUÁREZ TOVAR CATALINA MARÍA** con número de cuenta **517491438,** con la tesis titulada**: "IMPACTO DE LA URBANIZACIÓN SOBRE LIBÉLULAS Y CABALLITOS DEL DIABLO (ODONATA)",** realizada bajo la dirección del **DR. ALEJANDRO CÓRDOBA AGUILAR**, quedando integrado de la siguiente manera**:**

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| Presidente: | DRA. ELLEN ANDRESEN |
| Vocal: | DR. RODOLFO NOVELO GUTIÉRREZ |
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| Vocal: | DRA. EK DEL VAL DE GORTARI |
| Secretario: | DR. JORGE ERNESTO SCHONDUBE FRIEDEWOLD |

Sin otro particular, me es grato enviarle un cordial saludo.

**ATENTAMENTE**
**"POR MI RAZA HABLARÁ EL ESPÍRITU"**
Ciudad Universitaria, Cd. Mx., a 25 de octubre de 2023

**COORDINADOR DEL PROGRAMA**

**DR. ADOLFO GERARDO NAVARRO SIGÜENZA**

c. c. p. Expediente del alumno

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*El anciano pintor Wang-Fo y su discípulo Ling erraban a lo largo de los caminos del reino de Han. Avanzaban lentamente ya que Wang-Fo se detenía en la noche para contemplar los astros y en el día para mirar a las libélulas.*

Marguerite Yourcenar en “¿Cómo se salvó Wang-Fô?”

# Contenido

# PRESENTACIÓN

Los cambios en los entornos naturales derivados del establecimiento de las ciudades pueden generar diferentes tipos de respuestas en los grupos biológicos que allí habitan. Existen grupos biológicos extremadamente sensibles a las nuevas condiciones derivadas de la urbanización, mientras que otros han resultado ser muy resistentes a estas nuevas condiciones.

En este contexto, y considerando que las libélulas y caballitos del diablo (Insecta: Odonata) son un grupo que se encuentra tanto en ecosistemas urbanos como en ecosistemas no urbanos, la intención de este trabajo fue responder dos preguntas:

1. ¿Cómo responden las comunidades de odonatos ante las presiones ejercidas por la urbanización en el Centro de México?

2. ¿Qué características permiten que las especies que permanecen en las ciudades se adapten a estos nuevos entornos?

En el capítulo 1 se aborda la primera pregunta en un gradiente de urbanización en el estado de Morelos, ubicado en el centro de México. En el capítulo 2 se compara la condición fisiológica (medida por medio de reservas energéticas y la masa corporal) en individuos de dos especies (*Hetaerina americana* y *H. vulnerata*) que fueron encontradas en sitios con diferentes niveles de urbanización dentro del mismo gradiente definido para resolver la primera pregunta. En el capítulo 3 se evalúan las conductas de especies que se encuentran en un gradiente de urbanización en Belém, la segunda ciudad más poblada de la Amazonía brasileña. Posteriormente, en el capítulo 4, se hace una revisión bibliográfica de los diferentes estudios realizados hasta la fecha sobre la influencia de la urbanización en odonatos, con el fin de identificar los caracteres que permiten a las especies resistir la urbanización. De esta forma, los capítulos 2, 3 y 4 responden la segunda pregunta al identificar rasgos fisiológicos, morfológicos y conductuales que han permitido a las especies de libélulas y caballitos del diablo sobrevivir y permanecer en las ciudades. Además, se presenta una introducción y una discusión generales que abarcan lo encontrado en cada uno de los capítulos y proponen futuras direcciones para este tipo de estudios.

Finalmente, se incluyen dos apéndices. El apéndice 1 es una revisión que se realizó con el fin de entender la función de la coloración en los odonatos, tras detectar que este fue un rasgo importante para sobrevivir en entornos urbanos. En el apéndice 2 se presenta una revisión que se realizó con fines divulgativos sobre cómo los diferentes grupos de insectos se han adaptado a la vida en las ciudades.

# RESUMEN

Como cualquier otro ecosistema, la ciudad puede presentar condiciones adversas para algunas especies, pero favorables para otras. Los cambios en la estructura física, así como cambios asociados a factores sociales y económicos inherentes al desarrollo de las ciudades, pueden afectar de diferentes maneras a las comunidades biológicas y a los individuos de las especies que enfrentan la urbanización. En el presente trabajo se evaluó cómo un gradiente de urbanización (definido mediante un índice de integridad de hábitat) afecta a las comunidades de libélulas (Odonata: Anisoptera) y caballitos del diablo (Odonata: Zygoptera) en el centro de México. Además, se estudiaron cambios a nivel individual en aspectos como la condición energética y la conducta a lo largo de gradientes de urbanización en México y Brasil, y se identificaron algunos rasgos que pudieran estar favoreciendo la permanencia de ciertas especies en entornos urbanos. A nivel de comunidades, se encontró que la riqueza y abundancia de caballitos del diablo disminuyeron a medida que aumentó la urbanización, mientras que no se detectaron cambios ni en la riqueza ni en la abundancia de libélulas. Tampoco se encontró una relación de la condición energética con el gradiente de urbanización, es decir, las reservas energéticas en individuos que habitan sitios más urbanizados fueron similares a las de los individuos que habitan sitios menos urbanizados. A nivel conductual, se encontró que, dentro de las diferentes conductas observadas, solo hubo diferencias en la conducta de forrajeo: los individuos fueron más eficientes en la captura de presas en los lugares más urbanizados. Finalmente, se encontró que, a nivel mundial, de las 6,400 especies de odonatos descritas hasta el momento, 88 especies han sido registradas como tolerantes a la urbanización, mientras que 87 se han identificado como sensibles a los entornos urbanos. En cuanto a las características que favorecen la vida en las ciudades, se

identificó que especies con tamaños pequeños, un mayor grado de dimorfismo sexual y coloraciones amarillas y rojas tienden a tolerar mejor las ciudades.

# ABSTRACT

Like any other ecosystem, the city can present adverse conditions for some species, but favorable ones for others. Changes in the physical structure, as well as changes associated with social and economic factors inherent to the development of cities, can affect biological communities and individuals of species facing urbanization in different ways. In this work, we evaluated how an urbanization gradient (defined by means of a habitat integrity index) affects the communities of dragonflies (Odonata: Anisoptera) and damselflies (Odonata: Zygoptera) in central Mexico. In addition, changes at the individual level in aspects such as energy condition and behavior along urbanization gradients in Mexico and Brazil were studied, and some traits that could be favoring the permanence of certain species in urban environments were identified. At the community level, damselfly richness and abundance were found to decline as urbanization increased, while neither dragonfly richness nor abundance changed. Regarding the energy condition, no relationship was found with the urbanization gradient, that is, the energy reserves in individuals who inhabit more urbanized sites were similar to those of individuals who inhabit less urbanized sites. At the behavioral level, it was found that, within the different behaviors observed, there were only differences in foraging behavior. In this regard, individuals were more efficient in capturing prey in more urbanized locations. Finally, it was found that, worldwide, of the 6,400 species of odonates described so far, 88 species have been recorded as tolerant to urbanization, while 87 species have been identified as sensitive to urban environments. Regarding the traits that favor life in cities, it was identified that species with small sizes, a greater degree of sexual dimorphism and yellow to red colorations tend to tolerate cities better.

# INTRODUCCIÓN GENERAL

## La ciudad entendida como una amenaza a la biodiversidad

La extensa e intensa actividad humana desde tiempos prehistóricos ha generado cambios ecológicos sin precedentes en la historia del planeta a un ritmo acelerado (Kareiva *et al*. 2007). Desde el cambio de la vida nómada a la vida sedentaria, el impacto del ser humano sobre los ecosistemas naturales ha aumentado considerablemente. Este impacto ha pasado del ritmo de los agricultores y ganaderos que comenzaron a usar los recursos de su entorno más inmediato, al ritmo de la rueda y las máquinas creadas en la Revolución Industrial que no sólo permitieron la explotación de recursos en lugares cada vez más lejanos, sino que aumentaron las tasas de uso de estos recursos, que hoy en día ya no alcanzan a regenerarse para suplir las necesidades de poblaciones humanas cuyos tamaños se incrementan de manera sostenida. La Revolución Industrial, en conjunto con el desarrollo de las vacunas, generaron también un aumento en la esperanza de vida del ser humano e incentivaron la concentración de los seres humanos en centros de desarrollo: las ciudades (Hirschman y Mogford 2009).

Desde entonces, la urbanización ha sido considerada como una de las más grandes transformaciones sociales, pero también como la mayor amenaza a la biodiversidad a escala mundial (Beninde *et al*. 2015). La urbanización puede definirse como el reemplazo final de todos los elementos naturales como el suelo, el sistema hidrológico, la vegetación y la fauna, por elementos artificiales, como carreteras, redes de alcantarillado, alumbrado artificial y construcciones con fines de asentamiento y desarrollo económico (Dansereau 1957; Güneralp and Seto 2013). Las ciudades se distinguen de otros asentamientos humanos por su mayor tamaño, densidad poblacional, la presencia de infraestructura especializada y una mayor actividad económica e industrial (Grimm *et al*. 2008). Por otra parte, algunos autores han considerado a la ciudad como un "ecosistema domesticado", ya que ha sido modificado por la especie humana para su bienestar en busca de una productividad mejorada, un comercio conveniente y protección contra depredadores o fenómenos naturales (Kareiva *et al*. 2007).

Actualmente, cerca de 3% de la superficie del planeta presenta algún grado de urbanización (Alberti *et al*. 2017), y más de la mitad de la población humana vive en ciudades (United Nations 2014). Las regiones más urbanizadas incluyen América del Norte, América Latina y Europa, con 82%, 80% y 73% de la población viviendo en áreas urbanas, respectivamente; mientras que África y Asia siguen siendo en su mayoría rurales, con 40% y 48% de sus respectivas poblaciones viviendo en áreas urbanas (United Nations 2014). Según el tipo de desarrollo que presenten, las ciudades pueden clasificarse en cuatro categorías: 1) de bajo crecimiento; 2) de alto crecimiento con un desarrollo rápido y fragmentado; 3) de crecimiento expansivo, con gran dispersión y bajas densidades poblacionales; 4) de crecimiento frenético, con tasas extraordinarias de conversión de uso de suelo y con altas densidades de población (Schneider y Woodcock 2008). Cada tipo de crecimiento tiene un impacto diferente sobre los ecosistemas y afecta en mayor o menor medida a cada uno de los grupos biológicos presentes en el territorio de cada ciudad.

## La ciudad entendida como un ecosistema

La ecología urbana se define como el estudio de la estructura, la dinámica y los procesos en los sistemas ecológicos urbanos; esta disciplina surgió en 1920 y reconoce ecosistemas urbanos específicos como parte del sistema biogeoquímico, económico y demográfico humano global (Pickett y Cadenasso 2012). La mayoría de los estudios realizados desde la perspectiva de la ecología urbana han utilizado índices de urbanización que incluyen variables como el porcentaje de superficie impermeable (p. ej., pavimento o cemento), los contaminantes presentes en el agua o el aire, y la cantidad y calidad de zonas verdes, así como la conectividad entre ellas (Di Mauro *et al*. 2007; Tüzün *et al*. 2015; Shahtahmassebi *et al*. 2016). Estas variables pueden ser medidas a diferentes escalas espaciales, y de esta forma pueden brindar diferente tipo de información respecto a las comunidades biológicas. A escala local, las variables pueden indicar la idoneidad del hábitat (en términos de supervivencia de los individuos de las diferentes especies), mientras que a escala de paisaje pueden dar información sobre la permeabilidad del paisaje circundante para la dispersión de las especies (Beninde *et al*. 2015).

Más allá de los cambios en la estructura física, existen factores sociales y económicos inherentes al desarrollo de las ciudades que también afectan a las comunidades biológicas citadinas, tales como la edad, el tamaño, la densidad de población humana, el tráfico (vehicular y peatonal) y las actividades económicas o industriales típicas de cada ciudad (Pickett y Cadenasso 2012). Adicionalmente, las ciudades pueden estar compuestas por parches de hábitats heterogéneos, lo que dificulta la definición de gradientes continuos entre lo urbano y lo rural para la evaluación de cambios en la biodiversidad (McDonnell y Pickett 1990; Güneralp y Seto 2013).

Como cualquier otro ecosistema, la ciudad puede presentar condiciones adversas para algunas especies, pero favorables para otras (Szulkin 2020). En las ciudades, se modifican los parámetros estructurales y ambientales, como la temperatura, el ciclo hidrológico y los niveles de contaminación (lumínica, sonora y/o química), y aumentan aspectos como la fragmentación de los hábitats y la incidencia de especies invasoras (Kareiva *et al*. 2007;

Alberti *et al*. 2017; Johnson y Munshi-South 2017). Bajo estas nuevas condiciones ambientales, las especies que habitaban un sitio antes de ser urbanizado pueden: 1) persistir en el lugar transformado gracias a preadaptaciones, respuestas plásticas o procesos de adaptación al nuevo entorno (Johnson y Munshi-South 2017; Isaksson y Bonier 2020); 2) desplazarse en busca de hábitats que se ajusten mejor a sus requerimientos particulares (Prescott y Eason 2018) o 3) extinguirse (Fattorini, 2011; Benson et al., 2019). El mecanismo mediante el cual cada especie responda a la urbanización puede generar cambios detectables a diferentes niveles de organización biológica: comunidad, población o individuo.

Dentro de las ciudades, las especies se reorganizan en comunidades novedosas, diferenciándose de las comunidades originales (Grimm *et al*. 2008). Esto se ha registrado para plantas (Cao y Natuhara 2020), vertebrados (Chace y Walsh 2006; Devictor *et al*. 2007) y artrópodos (McIntyre *et al*. 2001; Kietzka *et al*. 2018; Chatelain *et al*. 2023) en diferentes partes del mundo. En términos generales, dentro de las ciudades son favorecidas especies de animales oportunistas (en dieta y hábitat), con ciclos de vida cortos, multivoltinos, con alta capacidad de dispersión, resistentes a la contaminación, con sistemas respiratorios altamente eficientes en ambientes hipóxicos y con la capacidad de cambiar rápidamente sus rasgos fisiológicos y/o conductuales (Ball-Damerow *et al*. 2014; Tchakonté *et al*. 2015). Adicionalmente, y debido a que la huella urbana se extiende mucho más allá de los límites políticos, la urbanización también puede reducir la diversidad de especies nativas a escala regional y global (Grimm *et al*. 2008).

A nivel poblacional, algunos estudios en aves, mamíferos e insectos han encontrado cambios en la estructura genética entre poblaciones que habitan ambientes urbanos y no urbanos, siendo menos variables las poblaciones urbanas (Slabbekoorn y Peet 2003;

MacDougall-Shackleton *et al*. 2011; Dalla-Bona *et al*. 2012; Harris *et al*. 2013). Por otro lado, a nivel individual se ha visto que diversos rasgos morfológicos, fisiológicos o conductuales de organismos urbanos presentan diferencias frente a organismos de la misma especie que habitan zonas no urbanizadas (Shochat *et al*. 2006; Langerhans y Kern 2020; Resende *et al*. 2021). Por ejemplo, la condición fisiológica de los individuos reflejada en rasgos como el tamaño corporal o el presupuesto energético (Salomão *et al*. 2020), así como la conducta de los individuos (Elango *et al*. 2021) son rasgos indicadores de cómo les va a los individuos en entornos urbanos**.**

## Agua y odonatos como parte del ecosistema urbano

Las ciudades se han establecido históricamente alrededor del agua, un recurso fundamental para la producción de alimentos, el transporte, el comercio e incluso la recreación de la especie humana (Kummu *et al*. 2011). No es coincidencia entonces, que encontremos cuerpos de agua dentro y alrededor de los centros urbanos. Sin embargo, el aumento de la demanda de agua para las actividades humanas afecta su calidad y disponibilidad, y comienza a representar una amenaza para la biodiversidad acuática (Martins *et al*. 2021).

La urbanización modifica sustancialmente las condiciones geomorfológicas, hidrológicas y biogeoquímicas de los ecosistemas de agua dulce (Langerhans y Kern 2020). Las descargas de aguas residuales causan alteraciones importantes relacionadas con las grandes cantidades de materia orgánica, nutrientes y contaminantes que ingresan a los arroyos (Paul y Meyer 2001; Walteros y Ramírez 2020). Por lo tanto, los arroyos están sujetos a la presencia de toxinas, aumentos de temperatura, sedimentación y contaminantes orgánicos, así como a la sustitución de la vegetación ribereña nativa por vegetación introducida y concreto (Tchakonté *et al*. 2015). Todas estas alteraciones pueden actuar de forma aislada o en sinergia sobre las diferentes formas de vida presentes en los ecosistemas acuáticos urbanos. En insectos se ha registrado, por ejemplo, la reducción en la riqueza taxonómica y en la abundancia de taxones más sensibles como Ephemeroptera, Plecoptera y Trichoptera, y el aumento de la abundancia de taxones tolerantes, como los dípteros de la familia Chironomidae (Langerhans y Kern 2020).

Los ecosistemas urbanos albergan una diversidad relativamente alta de insectos del orden Odonata (Monteiro Júnior *et al*. 2015; Luke *et al*. 2017). Los odonatos son depredadores voraces y pasan la mayor parte de su ciclo de vida como larvas acuáticas, por lo que son un componente importante de la comunidad de macroinvertebrados bentónicos (Corbet 1999; Perron y Pick 2020). Su ciclo de vida bifásico vincula los sistemas acuáticos y terrestres a través de cascadas tróficas (Knight *et al*. 2005; May 2019). Por ejemplo, Popova *et al*. (2017) registraron que una gran parte de la productividad acuática se exporta al paisaje terrestre circundante a través de la emergencia de odonatos. Tras realizar el seguimiento a 18 especies durante 31 años, estos autores encontraron que la emergencia de estos insectos moviliza entre 0.8 y 4.9 g de biomasa, entre 0.11 y 0.70 g de carbono orgánico (cerca del valor más alto de la estimación global para todos los insectos), y entre 1.92 y 11.76 mg de ácidos grasos altamente insaturados, que se sabe que son esenciales para muchos animales terrestres, especialmente para las aves. Este aporte resulta muy importante para los ecosistemas terrestres si se considera que los odonatos son buenos voladores y, por lo tanto, pueden contribuir significativamente a la movilización de la productividad acuática.

Los odonatos requieren de ciertas condiciones fisicoquímicas del agua para la supervivencia de sus huevos y larvas, así como de la presencia de vegetación, tanto acuática como terrestre, para propiciar la cópula y oviposición (Corbet 1999). A pesar de la generalidad de los hábitos mencionados a nivel de orden, los Anisoptera y los Zygoptera, que son los subórdenes que se encuentran en América, presentan marcadas diferencias en el tamaño corporal, tamaño y forma de las alas, estrategias de termorregulación, tipo de oviposición, capacidad de dispersión y preferencias de hábitat (Corbet 1999; Dutra y De Marco 2015). Mientras que las especies de Anisoptera (libélulas) prefieren áreas abiertas y soleadas, las especies de Zygoptera (caballitos del diablo) prefieren áreas cerradas, con sombra y con mayor heterogeneidad ambiental, y tienen, en promedio, densidades poblacionales más altas que los primeros (Samways y Steytler 1996; Corbet 1999; Luke *et al*. 2017). Estas diferencias morfológicas y ecológicas podrían generar una respuesta diferente de estos grupos ante presiones relacionadas con la urbanización.

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# CAPÍTULO I.

## Resilient dragons: Exploring Odonata communities in an urbanization gradient (Artículo requisito)

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Original Articles

### Resilient dragons: Exploring Odonata communities in an urbanization gradient

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ABSTRACT

Cities function as ecological systems composed of a geosphere, a biosphere and an anthroposphere, interacting with each other and generating various selection pressures on urban organisms. Odonates (damselflies and dragonflies) are frequent inhabitants of urban areas, showing no clear or unique responses to urbanization. Thus, we defined an urbanization gradient using a habitat integrity index (HII) calculated for 19 sites in central Mexico, and investigated: a) changes in species richness and abundance along the urbanization gradient; and, b) the relationship between presence of waste of anthropic origin, chemical conditions of water, macrophyte cover, and odonate species richness, abundance and community composition. We analyzed the data for the whole odonate community, as well as for dragonfly and damselfly communities separately in each site. We found higher damselfly species richness and abundance in sites with low urbanization than in sites with high urbanization, and no differences in dragonfly communities along the gradient. We found a positive relationship between dragonfly species richness and abundance and waste percentage and macrophyte cover, and a negative relationship with dissolved solids in water. Our results indicated that odonate communities were fairly tolerant to urbanization and dragonflies were less affected than damselflies. However, we suggest that during design and restructuring of cities, the care and conservation of water bodies and all the life forms that inhabit there, be considered.

#### 1. Introduction

The construction and exponential expansion of cities in recent decades has caused the destruction of the natural habitats of a large number of life forms (Grimm et al., 2008; Fenoglio et al., 2021). However, the places where cities have been established around the world must begin to be considered as a new type of ecosystem composed of a geosphere, a biosphere and an anthroposphere, which interact with each other and modify these places by pressures generated between these components (Endlicher et al., 2007). Consequently, like any other ecosystem, the city may present hostile conditions for some species but favorable for others (Szulkin et al., 2020). Modification of structural and environmental parameters, as well as the homogenization of microclimates and niches, generate strong selective pressures on the species present in such urban places (Alberti et al., 2017; Magura et al., 2021). Species favored by the modifications of urban environments are usually habitat generalists, opportunistic, resistant to pollution, and with a rapid and plastic capacity to change in terms of physiological and behavioral traits (Tchakonté et al., 2015).

The establishment of cities has historically been linked to the presence of water sources like rivers, ponds or streams (Kummu et al., 2011). Although these freshwater systems represent only 1% of the Earth`s surface, they support 6% of all known insect species (Samways et al., 2020). As a result, the modification of these systems by urbanization represents a pivotal threat to aquatic insects (Ball-Damerow et al., 2014; Suhonen et al., 2014). Consequently, there is a worldwide effort to embrace urban aquatic insects in the agenda of biodiversity protection (e.g. Valente-Neto et al., 2022).

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Odonata is small order of aquatic insects conformed by two main suborders: Zygoptera (damselflies) and Anisoptera (dragonflies) (May 2019). Odonates are predators that, as larvae, are part of the benthic macroinvertebrate freshwater community and, as adults, are terrestrial but remain close to the water bodies (Corbet 1999; Perron and Pick 2020). This biphasic life cycle links aquatic and terrestrial systems through trophic cascades, which grants them a key functional, regulating role in freshwater ecosystems (Knight et al., 2005; May 2019). As eggs and larvae, they require a wide range of physical, chemical and structural aquatic conditions for survival and development (related to temperature, salinity, pH and dissolved solids), while adults require aquatic and terrestrial vegetation for reproductive activities (Corbet 1999). Despite these apparently general ecological habits, dragonflies and damselflies have specific and different needs in terms of thermoregulation, oviposition resources, dispersal to new areas, and habitat selection (Corbet 1999; Juen et al., 2014; Dutra and De Marco 2015). For example, while dragonfly species prefer sunny-open areas, damselflies favor shady closed-vegetation areas with high environmental heterogeneity (Samways and Steytler 1996; Luke et al., 2017). At the community level, several studies have shown that odonates respond rapidly to urbanization after facing local stressors through changes in composition and structure (Chovanec and Waringer 2001; Ball-Damerow et al., 2014; Monteiro-Júnior et al., 2015). For example, odonate communities in urbanized environments tend to have similar species richness but different composition and be more homogeneous than those found in non-urban sites, as a result of the expansion of habitat generalist species and the decrease of specialist species (Ball-Damerow et al., 2014; Kietzka et al., 2018; Rocha-Ortega et al., 2018).

The exponential and disorderly growth of cities in central Mexico (Bezaury-Creel et al., 2017; García-Sánchez and Güereca 2019), with the consequent alteration of water bodies (Walteros and Ramírez 2020) have likely modified aquatic insect communities such as odonates. According to this, one would expect that habitat changes generated by urbanization will affect each odonate suborder differently due to their physiological and ecological variation indicated above. Therefore, in this study we evaluated changes in the whole odonate community, as well as separately in dragonfly and damselfly communities, along an urbanization gradient in central Mexico. We used a habitat integrity index (HII) to summarize in a single value several variables of our study sites that indicate the level of urbanization. We also evaluated variables that can affect odonate communities such as the amount of waste and dissolved solids and the presence of macrophytes in the water bodies around the study sites.

We expected that dragonflies, that prefer open sites, have generalist habits and a wide dispersal capacity, would be more abundant in urbanized sites, than damselflies. Additionally, members of both suborders are commonly attracted to man-made surfaces that mimic water bodies and act as ecological traps (Wildermuth 1993; Harabiš and Dolný 2012). Thus, we expected that sites with deceptive surfaces, such as plastic and metal trash elements, would attract a greater number of individuals due to their resemblance to water bodies suitable for reproduction behavior and laying eggs (Wildermuth 1993; Ensaldo-Cárdenas et al., 2021). Physical and chemical conditions of water and macrophyte community structure can also influence odonate development and reproduction (Janssens et al., 2014; Brito et al., 2021). Thus, we expected changes in the species richness and abundance associated to the different water quality conditions and amount of macrophytes found along our urbanization gradient.

## 2. Materials and methods

### 2.1. Sampling sites

We selected 19 sites characterized by the presence of lotic systems in the state of Morelos, Mexico. During the last 70 years, human population on Morelos has grown over six times and currently, 82% of the total population (1,971,520 inhabitants) is concentrated in the urban area of Cuernavaca and surrounding cities (INEGI 2020). The concentration of most of the population in urban areas has generated a great transformation of the natural ecosystems, in industrialized, touristic, and residential areas with high levels of pollution caused by the inadequate discharge of sewage and uncontrolled use of natural resources.

Our study sites were located around and within the three most populated municipalities in the state: Cuernavaca, Jiutepec and Cuautla. The altitudinal range of these sites falls between 1200 and 1655 m.a.s.l. All sites share a warm/semi-warm climate and deciduous forest native vegetation. Study sites were separated by a minimum distance of 1 km and a maximum of 36 km (Fig. 1).

At each study site we registered the geographical coordinates, elevation, and water and air temperature. We conducted two visits at each site, in December 2019 and in November-December 2020. During each visit, all metrics were taken in three 20-m transects defined in each site (corresponding to the transects where we conducted the biological sampling, as explained below). Additionally, we measured habitat variables to describe three components of the environment that specifically affect odonates: 1) a green component, referring to the dominant vegetation type, and including both macrophytes, and the vegetation adjacent to the lotic system, 2) a blue component evaluating the physical and chemical properties of the water and the solid waste present in it, and 3) a gray component, assessing urban constructions and infrastructure, and indicators of human activity.

*Green component.* We determined the dominant vegetation stratum at each study site using the Canfield line-intercept method (Canfield 1941). We considered three vegetation strata: herbaceous (0.3–1.5 m height), shrubby (1.5–5.0 m), or arboreal (>5 m) following Rangel and Velásquez (1997). In each transect we recorded the length occupied by each plant stratum every 2 m. Then, we summed the cover of each plant stratum in the three transects, divided by the 60 m length sampled (transect length occupied by each stratum / total length sampled), and multiplied by 100 to obtain the percentage of each plant stratum for each study site. Additionally, we registered macrophytes using a 1-m$^2$ PVC square frame with 100 internal 10 × 10 cm squares. We placed the square randomly at three points in the water body and counted how many of the squares contained emerging, submerged, and/or floating macrophytes.

*Blue component.* We measured water temperature, pH, percentage of dissolved solids, and percentage of dissolved oxygen with a Hanna HI9829 multiparametric probe. We measured the mean maximum width of the water body with a 50 m flexometer and the mean maximum depth with a rope marked every 5 cm and tied to a plummet that was thrown to the bottom of the water bodies. We registered channel type (concrete walls, natural, or mixed), the presence or absence of sewage discharges and the amount of anthropic waste in the water using the same PVC square used to quantified macrophytes. We placed the square randomly at three points in the water body and counted how many of the internal squares contained anthropic waste.

*Gray component.* We recorded the constructions and urban infrastructure in and around the sampling sites: roads, shops, households, or nearby buildings. Additionally, a count was made of the number of people, cars, bicycles, and motorcycles passing through each sampling site. For this, 3-min replications of observations were made at 10:00, 12:00 and 14:00 (UTC-6).

The measurements in each of the sites were made on the same day of the biological sampling, before starting the registration and collection of specimens. Each sampling site was visited for a full day from 9:00 to 16:00 h (UTC-6) each of the sampling years.

### 2.2. Habitat integrity index (HII) calculation

The HII (modified from Petersen, 1992; Monteiro-Júnior et al., 2014), was calculated to measure the degree of disturbance of aquatic habitats, considering biophysical attributes of each site (green and blue

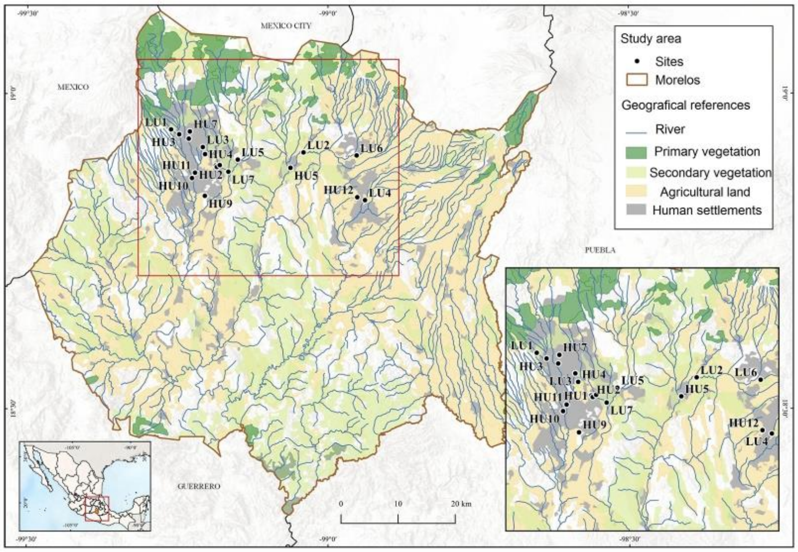

**Fig. 1.** Location of sampling sites in the State of Morelos, Mexico.

components) and the impact of anthropogenic activities (gray component) for each sampling site. We included two variables from the green component, five from the blue component, and three from the gray component. Each of these variables had three to five alternatives, with scores that increase with habitat integrity (Table 1). To weigh (*p*) the different *i* variables equally, the scores for each variable (*ao*) were divided by its maximum (*am*) possible score ($p_i = ao / am$). The final HII score (Eq. 1) for each site was obtained from the mean value of these scores for the ten variables analyzed.

$$HII = \frac{\sum_{i=1}^{n} p_i}{n} \tag{1}$$

Our HII generates values that go from zero to one, where values close to zero correspond to sites with high urbanization, and values close to one correspond to sites with low urbanization. In a bad scenario, for example, a heavily channelized stream without riparian vegetation, surrounded by many houses and urban infrastructure, with high levels of human, car traffic, and anthropogenic waste and low water quality would result in the lowest score. The highest score might be given to a stream with no obvious physical disruption (Petersen, 1992). From the HII values and considering that some authors (King et al., 2011; Monteiro-Júnior et al., 2014) propose that disturbance values between 25 and 35% are sufficient to alter aquatic communities, we categorized our sites as sites with high urbanization (HU, with HII = 0–0.65) or sites with low urbanization (LU, with HII = 0.66–1.0) for some of the analyzes (Table 2).

### 2.3. Sampling of Odonata communities

During the same visits in which the environmental variables were measured we recorded the species richness and abundance for each site. We chose the period after the rainy season for sampling because activity patterns of odonate adults can be modified during the rainy season and the registration of species can be difficult (May, 1976). Additionally, sampling periods covered periods of highest Odonata diversity at our study area. We collected Odonata adults using an entomological net. We sampled on sunny days, between 10:00 and 16:00 h (UTC-6) for one day at each stream. We followed a standardized sampling protocol in which three persons conducted observations and captures 40 min in three 20 m transects located parallel to the stream bank (Prescott and Eason, 2018; de Oliveira-Junior et al., 2015).

At each site, we collected and photographed adult male and female individuals. We identified each specimen to species level using specialized keys (Westfall and May, 1996; Förster, 2001; Garrison et al., 2006). Abundances were recorded for each species by capturing individuals and marking them with a colored point on their forewing.

### 2.4. Statistical analysis

We performed a Principal Component Analysis (PCA) with the ten characteristics included in the calculation of the HII and another PCA with the other environmental variables measured in the study to verify how environmental variation occurs in the study sites (Fig. S1).

Considering that biological communities can be understood as multivariate objects, in which each species is a different variable (Borcard et al., 2018), we performed a Threshold Indicator Taxa Analysis (TITAN) to identify which species are positively or negatively associated with the HII values, and thus identify thresholds of community change in the HII value and also indicator species of the changes faced in the environmental gradient. For TITAN, we used the natural logarithm of abundance values and considered only the taxa with five or more occurrences and with five or more individuals at each site. We calculated the confidence limits of environmental change points using bootstrap permutations (n = 500). We also performed a Principal Coordinates Analysis (PCoA) to assess species composition in sites along the gradient defined with HII values. This analysis was carried out to evaluate the differentiation of communities depending on the species abundances at each sampled site. For these multivariate analyses, we used vegan (Oksanen et al., 2019) and TITAN2 (Baker et al., 2015) libraries in R sotfware.

Using entropart (Marcon and Hérault 2015) and iNEXT (Chao et al., 2014; Hsieh et al., 2020) libraries in R software (R Core Team 2018) we performed true diversity analyses based on Hill numbers (Jost 2006), diversity profiles, and range abundance curves to compare Odonata

**Table 1**
Characteristics considered for the calculation of the HII, and the scores assigned to each of the identified conditions.

| Characteristic | Condition | Score |
|---|---|---|
| 1. Dominant plant strata | Herbaceous (0.3–1.5 m) | 0 |
| | Shrubby(1.5–5.0 m) | 1 |
| | Arboreal (>5 m) | 2 |
| 2. Macrophyte coverage (%) | 0 | 0 |
| | 1–15 | 1 |
| | 16–30 | 2 |
| | 31–45 | 3 |
| | >45 | 4 |
| 3. Anthropic waste (%) | >20 | 0 |
| | 10.1–20 | 1 |
| | 5–10 | 2 |
| | 0–4.9 | 3 |
| 4. Channel structure | Width/depth ratio 25–50 | 0 |
| | Width/depth ratio 15–25 | 1 |
| | Width/depth ratio 8–15 | 2 |
| | Width/depth ratio < 7 | 3 |
| 5. pH | Basic (8.56–11) | 0 |
| | Neutral (6.55–8-55) | 1 |
| | Acid (<6.55) | 2 |
| 6. Chanel type | Concrete | 0 |
| | Mix | 1 |
| | Natural | 2 |
| 7. Sewage discharge | Direct residual discharges (from homes or industries) | 0 |
| | Occasional discharges near or into the water body (soap, pesticides, etc) | 1 |
| | No obvious discharges | 2 |
| 8.Mean of persons walking | 11–15 | 0 |
| | 6–10 | 1 |
| | 0–5 | 2 |
| 9. Mean of vehicles passing by | >30 | 0 |
| | 16–30 | 1 |
| | 11–15 | 2 |
| | 6–10 | 3 |
| | 0–5 | 4 |
| 10. Type of constructions around | Shops, schools and / or wide roads | 0 |
| | Households | 1 |
| | No construction | 2 |

communities between sites with higher HII values LU and sites with HU. Three orders of diversity were calculated: $q = 0$ (equivalent to the total number of species), $q = 1$ (equivalent to the exponential of the Shannon index, that indicates the number of common species in each community), and $q = 2$ (the inverse of the Simpson index, that denotes the number of dominant species within a community).

We performed generalized linear models (GLM) with Poisson and quasi-Poisson distribution using the HII as explanatory variable and the species richness and abundance as response variables. Given that our samplings were carry out before and during the COVID-19 pandemic lockdown (2019 and 2020) and considering changes in city dynamics during this lockdown, we also included the sampling year in the model as another explanatory variable, to detect possible changes in species richness and abundance within communities due to an expected reduced impact of human activities in cities.

Finally, we performed a multiple regression between all the habitat variables measured at our study sites, and the species richness and abundance of both suborders, as well as a Canonical correspondence analysis (CCA) to evaluate how much variability in the communities is explained by the environmental variables measured at each site. This allowed us to detect the individual variables that most affected the species richness and abundance and community composition.

All analyses were made for the whole odonate community and for both suborders separately due to the contrasting responses of each suborder to environmental changes (Corbet, 1999; Júnior et al., 2015). Graphics were made in the R software with ggplot2 (Wickham, 2016), ggvegan (Simpson, 2019) and GGally (Schloerke et al., 2018) libraries.

## 3. Results

Our study sites had air temperature values between 19 and 27 °C. The different environmental variables varied widely between the sampling sites (Table S1). The HII calculated for the sites ranged from 0.23 to 0.84.

HU sites were characterized by mostly herbaceous vegetation, by having roads, shops, schools and/or homes around, a large number of people and vehicles passing by and a large amount of anthropic waste (Fig S1). The number of vehicles passing was high (2–71 per minute). They presented direct residual discharges. The type of channel was concrete or mixed and the amount of anthropic waste in the water was much higher compared to the LU sites. LU sites presented arboreal or shrub type vegetation, did not have any construction or small houses nearby. The number of vehicles passing was low (0–2 per minute). Residual discharges were occasional or non-existent, and channels were natural or mix (Table S1).

A total of 45 species (30 genera, 7 families) were registered. The richness at the sites varied from eight to 24 species, with an average of 14 species at HU sites, and 18 species at LU sites. The abundance ranged from 193 to 775 individuals, with an average of 499 at HU sites and 561

**Table 2**
Geographical coordinates, elevation, water temperature, air temperature and HII values calculated and categories for each site.

| Site | Latitude | Longitude | elevation | Mean water temperature (°C) | Mean air temperature (°C) | HII | Classification |
|---|---|---|---|---|---|---|---|
| HU1 | 18° 53′ 11.0′′ N | 99° 11′ 11.6′′ W | 1374 | 18.4 | 24.7 | 0.60 | High urbanization |
| HU2 | 18° 53′ 12.0′′ N | 99° 11′ 44.3′′ W | 1397 | 17.1 | 22.3 | 0.39 | High urbanization |
| HU3 | 18° 56′ 09.8′′ N | 99° 14′ 50.9′′ W | 1593 | 16.0 | 19.5 | 0.42 | High urbanization |
| HU4 | 18° 54′ 16.7′′ N | 99° 12′ 15.9′′ W | 1420 | 16.6 | 22.3 | 0.38 | High urbanization |
| HU5 | 18° 52′ 58.9′′ N | 99° 03′ 44.5′′ W | 1206 | 20.9 | 23.2 | 0.27 | High urbanization |
| HU6 | 18° 53′ 14.0′′ N | 99° 10′ 47.7′′ W | 1374 | 18.4 | 23.4 | 0.23 | High urbanization |
| HU7 | 18° 56′ 25.9′′ N | 99° 13′ 46.9′′ W | 1590 | 18.5 | 21.7 | 0.49 | High urbanization |
| HU8 | 18° 55′ 45.2′′ N | 99° 13′ 53.4′′ W | 1544 | 18.9 | 21.6 | 0.64 | High urbanization |
| HU9 | 18° 50′ 18.4′′ N | 99° 12′ 16.9′′ W | 1209 | 22.2 | 27.4 | 0.43 | High urbanization |
| HU10 | 18° 51′ 59.9′′ N | 99° 13′ 34′′ W | 1277 | 17.0 | 21.9 | 0.40 | High urbanization |
| HU11 | 18° 52′ 30.5′′ N | 99° 13′ 15.8′′ W | 1322 | 18.3 | 21.1 | 0.39 | High urbanization |
| HU12 | 18° 50′ 10.9′′ N | 98° 57′ 04.8′′ W | 1338 | 19.2 | 25.6 | 0.47 | High urbanization |
| LU1 | 18° 56′ 37.8′′ N | 99° 15′ 39.3′′ W | 1655 | 13.7 | 20.8 | 0.68 | Low urbanization |
| LU2 | 18° 54′ 26.9′′ N | 99° 02′ 26.4′′ W | 1232 | 20.8 | 23.9 | 0.68 | Low urbanization |
| LU3 | 18° 54′ 57.0′′ N | 99° 12′ 29.3′′ W | 1458 | 16.6 | 22.5 | 0.73 | Low urbanization |
| LU4 | 18° 49′ 54.2′′ N | 98° 56′ 18.5′′ W | 1341 | 19.2 | 25.5 | 0.71 | Low urbanization |
| LU5 | 18° 53′ 45.4′′ N | 99° 08′ 59.9′′ W | 1387 | 15.4 | 21.9 | 0.80 | Low urbanization |
| LU6 | 18° 54′ 09.6′′ N | 98° 57′ 08.6′′ W | 1369 | 18.8 | 22.4 | 0.84 | Low urbanization |
| LU7 | 18° 52′ 36.4′′ N | 99° 09′ 56.4′′ W | 1341 | 16.0 | 22.5 | 0.78 | Low urbanization |

at LU sites. Zygoptera was the most abundant suborder with 9044 individuals belonging to 19 species, nine genera, and three families: Coenagrionidae, Lestidae, and Calopterygidae. For Anisoptera, we observed 865 individuals distributed into 26 species, 21 genera, and four families: Libellulidae, Aeschnidae, Gomphidae, and Cordulegastridae (Table S2).

The observed and estimated species richness values for the whole community did not differ much from each other. This in addition to the sample coverage values (all above 0.9) indicated that the sampling was complete for all sites (Table 3). Due to the completeness of the sampling in all sites, we carried out the true diversity analyses, and the diversity profiles using observed, not estimated, values.

A total of 35 species was recorded at HU sites and 42 at LU sites. HU sites harbored a mean of 14 species (six common and four dominant). LU sites harbored a mean of 18 species (eight common and five dominant). Evenness values calculated by dividing diversity of order 2 (dominant species) by diversity of order 0 (richness) were the same for the two types of habitat ($E = 0.30$).

Rank abundance curves allowed us to identify dominant species at each study site (Fig. 2). For HU sites, the four dominant species identified in the diversity profiles were *Argia extranea*, *Argia tarascana*, *Hetaerina vulnerata* and *Argia plana*, while for LU sites the five dominant species were *Argia anceps*, *H. vulnerata*, *A. tarascana*, *A. extranea* and *Telebasis salva*. In both habitat conditions, Odonate communities were dominated by damselflies. All the exclusive species found at HU sites belonged to the Anisoptera suborder. This was similar to what we found in LU sites, where 9 out of the 10 exclusive species were also members of the Anisoptera.

Three species were exclusive of HU environments: *Dythemis maya*, *Pseudoleon superbus* (Anisoptera: Libellulidae), and *Rhionaeschna psilus* (Anisoptera: Aeshnidae). These species had low abundances (i.e. less than ten individuals). Ten species were exclusive of LU environments: *Argia oculata* (Zygoptera: Coenagrionidae), *Aeshna williamsoniana, Anax junius, Coryphaeschna adnexa, Remartinia luteipennis* (Anisoptera: Aeshnidae) *Brachymesia furcata*, *Erythemis vesiculosa*, *Paltothemis lineatipes* (Anisoptera: Libellulidae), and *Cordulegaster diadema* (Anisoptera: Cordulegastridae). All these species also had low abundances (less than ten individuals) and most of them showed evasive flights and very conspicuous colorations.

Although the p-values derived from the TITAN analyses were not significant (Table. 4), *Apanisagrion lais, Argia tarascana, Argia anceps, Argia extranea* and *Hetaerina vulnerata* were identified as highly associated with HII values (Indvals > 60). This association is positive, that is, as HII increases (in LU sites) the abundances of species also increase, and as HII decreases (in HU sites) the abundances of these species decrease (Table. 4). This indicates that although the species are present in all or most sampled sites, their abundance is sensitive to changes in the HII related to urbanization processes and the abrupt fall in abundance occurs when HII reaches a value of 0.38.

**Table 3**

Sample coverage values observed species richness and estimated species richness for whole Odonata communities in each site. LU = low urbanization sites, HU = high urbanization sites.

| Site | Sample coverage | Observed richness | Estimatedrichness (Chao-Shen) | Estimatedrichness (Chao1) |
|---|---|---|---|---|
| HU1 | 0.99 | 17 | 19.3 | 18.5 |
| HU2 | 0.99 | 9 | 10.5 | 10.0 |
| HU3 | 0.98 | 8 | 9.4 | 10.0 |
| HU4 | 0.98 | 15 | 18.9 | 32.0 |
| HU5 | 1.00 | 24 | 24.6 | 24.0 |
| HU6 | 0.98 | 23 | 26.5 | 27.2 |
| HU7 | 1.00 | 8 | 8.6 | 8.0 |
| HU8 | 1.00 | 9 | 9.4 | 9.0 |
| HU9 | 0.99 | 15 | 15.8 | 15.5 |
| HU10 | 0.99 | 10 | 10.7 | 10.5 |
| HU11 | 0.99 | 15 | 15.8 | 15.5 |
| HU12 | 0.99 | 10 | 10.8 | 10.5 |
| LU1 | 0.99 | 13 | 14.6 | 14.0 |
| LU2 | 0.99 | 19 | 20.0 | 19.3 |
| LU3 | 1.00 | 19 | 19.4 | 19.0 |
| LU4 | 0.99 | 15 | 16.3 | 15.9 |
| LU5 | 0.99 | 24 | 25.9 | 24.7 |
| LU6 | 1.00 | 15 | 15.5 | 15.0 |
| LU7 | 0.99 | 23 | 25.6 | 30.9 |

*Argia plana, Macrothemis pseudimitans, Erythemis plebeja* and *Tramea abdominalis* showed high Indval values (also > 60) but in these cases the association of their abundance with the HII values is negative, that is at higher HII values (in LU sites), the abundances of these species decrease and vice versa (Table. 4). The abundance of these species would then be favored at low HII values (in HU sites), which allows them to be more resistant to urban environments and perhaps to other types of disturbed environments. *M. pseudimitans* and *T. abdominalis* were the only species that presented significant p values supporting the indicator power of the Indvals and the sharp response of abundances was when the HII reaches values of 0.75 and 0.38, respectively (see Table. 4).

The PCoA graphs did not show a clear differentiation between sites with lower or higher HII values neither for the whole Odonata community, Anisoptera community or Zygoptera community (Fig. 3).

Regarding the analyzes of richness and abundance, we found a positive relationship between damselflies species richness and the HII ($R^2 = 0.11$; $p = 0.04$). However, we found no significant relationship between Odonata ($R^2 = 0.04$; $p = 0.13$) or Anisoptera ($R^2 = 0.01$; $p = 0.41$) species richness and HII (Fig. 4). We found positive relationships between HII and the abundance of Odonata ($R^2 = 0.16$; $p \ll 0.0001$) and Zygoptera ($R^2 = 0.15$; $p \ll 0.0001$). However, we found no significant relationship between Anisoptera abundance and HII values ($R^2 = 0.06$; $p = 0.12$) (Fig. 4).

Our results indicated that although damselflies were affected by the physical integrity of their habitat, dragonflies did not respond in the same way, and it was equally likely to find them both in lower urbanization and higher urbanization sites.

We found no difference in the species richness recorded in the two years of sampling, neither for Odonata, Anisoptera, or Zygoptera. However, we found higher abundances ($p < 0.0001$) of Odonata, Anisoptera and Zygoptera in 2019 than in 2020.

Finally, Odonate species richness presented a positive relationship with the macrophyte coverages ($p = 0.0007$) and a negative relationship with pH values ($p = 0.025$) recorded at each site. In the case of dragonflies, in addition to these two variables, the percentage of anthropic waste presented a positive relationship ($p = 0.018$) with the species richness of this suborder, while the total dissolved solids in water presented a negative relationship ($p = 0.0002$). Damselfly richness did not show a significant relationship with any of the variables evaluated individually.

Abundances of each suborder showed a positive relationship with the percentage of anthropic waste ($p < 0.0001$) and macrophyte coverage ($p < 0.0001$), but a negative relationship with the pH ($p = 0.02$), dissolved oxygen ($p < 0.0001$) and total dissolved solids ($p < 0.0001$). Additionally, dragonfly abundance showed a positive relationship with the number of vehicles ($p = 0.0001$) registered near our sampling sites, while the abundance of Zygoptera did not show such relationship. In addition, CCA reveals that 75.8% of the variation in the community composition is associated with the set of environmental variables measured at each study site, although this last model does not present statistical significance.

## 4. Discussion

We found a higher species richness and abundance of damselflies at LU sites than at HU sites, according to our expectations. However, dragonfly species richness and abundance did not show obvious changes in response to the urbanization index used in this study. In addition, dragonfly abundances were lower than those of damselflies and the

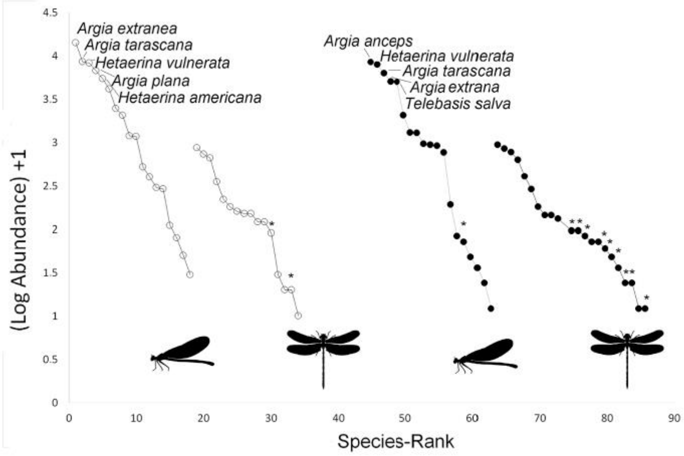

**Fig. 2.** Rank abundance curves for high urbanization (HU) sites (unfilled circles) and low urbanization (LU) sites (filled circles). Unique species of each habitat type are marked with an asterisk. From left to right, curves correspond to damselfly community at HU sites (m = -0.15), dragonfly community at HU sites (m = -0.12), damselfly community at LU sites (m = -0.16) and dragonfly community at LU sites (m = -0.08).

**Table 4**
Indvals, z-scores and change points for species included in the TITAN analysis. **env_cp** is the value of HII in which the abundance of species increases or decreases depending on whether the relationship with HII is positive or negative, **freq** indicates the number of sites where the species was collected, **grp** indicates the response type of the species 1 = negative response 2 = positive response, **IndVal** captures the strength of association between a taxon and the HII **pval** indicates if the association is significative **z_score** Indval z score. 5%, 10%, 50%, 90%, 95% change point quantiles among bootreps. **purity** proportion of maxgrp assignment that match in each permutation **reliability** proportion of Indval values that match in each permutation.

| Species | env_cp | freq | grp | IndVal | p_val | z_score | 5% | 10% | 50% | 90% | 95% | purity | reliability |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Apanisagrion lais (Brauer in Selys, 1876) | 0.38 | 19 | 2 | 90.91 | 0.24 | 0.82 | 0.27 | 0.27 | 0.38 | 0.42 | 0.71 | 0.92 | 0.12 |
| Argia tarascana Calvert, 1902 | 0.38 | 19 | 2 | 90.35 | 0.10 | 1.37 | 0.27 | 0.30 | 0.39 | 0.79 | 0.8 | 0.65 | 0.25 |
| Argia anceps Garrison, 1996 | 0.38 | 18 | 2 | 83.9 | 0.31 | 0.6 | 0.27 | 0.33 | 0.39 | 0.75 | 0.78 | 0.78 | 0.15 |
| Argia extranea (Hagen, 1861) | 0.38 | 18 | 2 | 83.38 | 0.22 | 0.66 | 0.38 | 0.38 | 0.72 | 0.8 | 0.81 | 0.23 | 0.32 |
| Hetaerina vulnerata Hagen in Selys, 1853 | 0.38 | 16 | 2 | 83.15 | 0.11 | 1.4 | 0.32 | 0.32 | 0.38 | 0.79 | 0.8 | 0.79 | 0.49 |
| Archilestes grandis (Rambur, 1842) | 0.38 | 12 | 2 | 59.59 | 0.29 | 0.64 | 0.38 | 0.38 | 0.39 | 0.69 | 0.72 | 0.68 | 0.30 |
| Libellula saturata Uhler, 1857 | 0.69 | 11 | 2 | 52.49 | 0.31 | 0.55 | 0.32 | 0.32 | 0.66 | 0.70 | 0.70 | 0.74 | 0.47 |
| Telebasis salva (Hagen, 1861) | 0.69 | 13 | 2 | 50.98 | 0.55 | −0.19 | 0.38 | 0.38 | 0.66 | 0.70 | 0.75 | 0.55 | 0.26 |
| Enallagma civile (Hagen, 1861) | 0.69 | 6 | 2 | 33.89 | 0.32 | 0.58 | 0.32 | 0.32 | 0.64 | 0.70 | 0.75 | 0.47 | 0.63 |
| Argia plana Calvert, 1902 | 0.75 | 15 | 1 | 81.88 | 0.07 | −1.5 | 0.33 | 0.42 | 0.74 | 0.79 | 0.79 | 0.88 | 0.56 |
| Macrothemis pseudimitans Calvert, 1898 | 0.75 | 12 | 1 | 75 | **0.004** | −2.39 | 0.39 | 0.423 | 0.73 | 0.75 | 0.76 | 0.88 | 0.57 |
| Erythemis plebeja (Burmeister, 1839) | 0.38 | 6 | 1 | 71.37 | 0.02 | −3.94 | 0.33 | 0.33 | 0.39 | 0.75 | 0.75 | 0.63 | 0.85 |
| Tramea abdominalis (Rambur, 1842) | 0.38 | 5 | 1 | 62.16 | **0.004** | −5.41 | 0.33 | 0.33 | 0.39 | 0.72 | 0.74 | 0.74 | 0.81 |
| Orthemis discolor (Burmeister, 1839) | 0.39 | 12 | 1 | 58.87 | 0.23 | −0.65 | 0.38 | 0.38 | 0.42 | 0.765 | 0.8 | 0.71 | 0.30 |
| Pantala flavescens (Fabricius, 1798) | 0.38 | 9 | 1 | 53.59 | 0.14 | −1.34 | 0.33 | 0.33 | 0.40 | 0.78 | 0.8 | 0.78 | 0.49 |
| Hetaerina americana (Fabricius, 1798) | 0.72 | 10 | 1 | 49.91 | 0.23 | 0.73 | 0.32 | 0.39 | 0.54 | 0.72 | 0.74 | 0.60 | 0.30 |
| Erythrodiplax basifusca (Calvert, 1895) | 0.39 | 12 | 1 | 43.94 | 0.66 | −0.51 | 0.39 | 0.39 | 0.54 | 0.755 | 0.76 | 0.48 | 0.31 |
| Enallagma novaehispaniae Calvert, 1907 | 0.68 | 9 | 1 | 41.75 | 0.42 | 0.15 | 0.32 | 0.32 | 0.44 | 0.78 | 0.8 | 0.67 | 0.40 |
| Libellula croceipennis Selys, 1868 | 0.39 | 9 | 1 | 39.34 | 0.51 | −0.02 | 0.32 | 0.32 | 0.54 | 0.73 | 0.75 | 0.58 | 0.43 |

species that were exclusive to each type of habitat were dragonflies. Overall, these results are in agreement with studies in other countries around the world such as Brazil (Carvalho et al., 2013; Monteiro-Júnior et al., 2014; Gomes Pereira et al., 2019; Oliveira-Junior and Juen 2019), Malaysia (Luke et al., 2017), Ghana (Seidu et al., 2018), United States (Prescott and Eason 2018), and India (Jere et al., 2020).

We also detected that sensible species as identified by TITAN are damselflies (*Apanisagrion lais, Argia tarascana, Argia anceps, Argia extranea* and *Hetaerina vulnerata*) while the most resilient species are mostly dragonflies (*Macrothemis pseudimitans, Erythemis plebeja* and *Tramea abdominalis). Argia plana* in turn, was identified as a resilient species, being damselfly, which leads us to think about the intraspecific processes that both dragonflies and damselflies could experience from the moment our sampling sites began to change to the urban, and that today allow us to find different species of odonates in highly disturbed places and classify them as a fairly resilient group.

It is widely acknowledged that the rates of decline in relation to anthropic disturbance for specialist species are much higher than the rates for generalist taxa (Wagner et al., 2021). For the case of odonates, the difference may be explained by the ecological traits that characterize each suborder. Damselflies contain a greater number of specialist species that prefer close-forest habitats, have endophytic oviposition habits, and more restricted dispersal compared to dragonflies (Corbet 1999; Monteiro-Júnior et al., 2014). These ecological traits make this group more sensitive to disturbances in their environment, as has been reported for other specialist animals (Merckx et al., 2018; Buchholz and Egerer 2020; Franzén et al., 2020). In contrast, open and altered sites are preferred by dragonflies which are more tolerant to disturbance (May 1978). Besides behavioral flexibility, the most common dragonfly species have short life cycles and adapt very quickly to environmental changes (Dalzochio

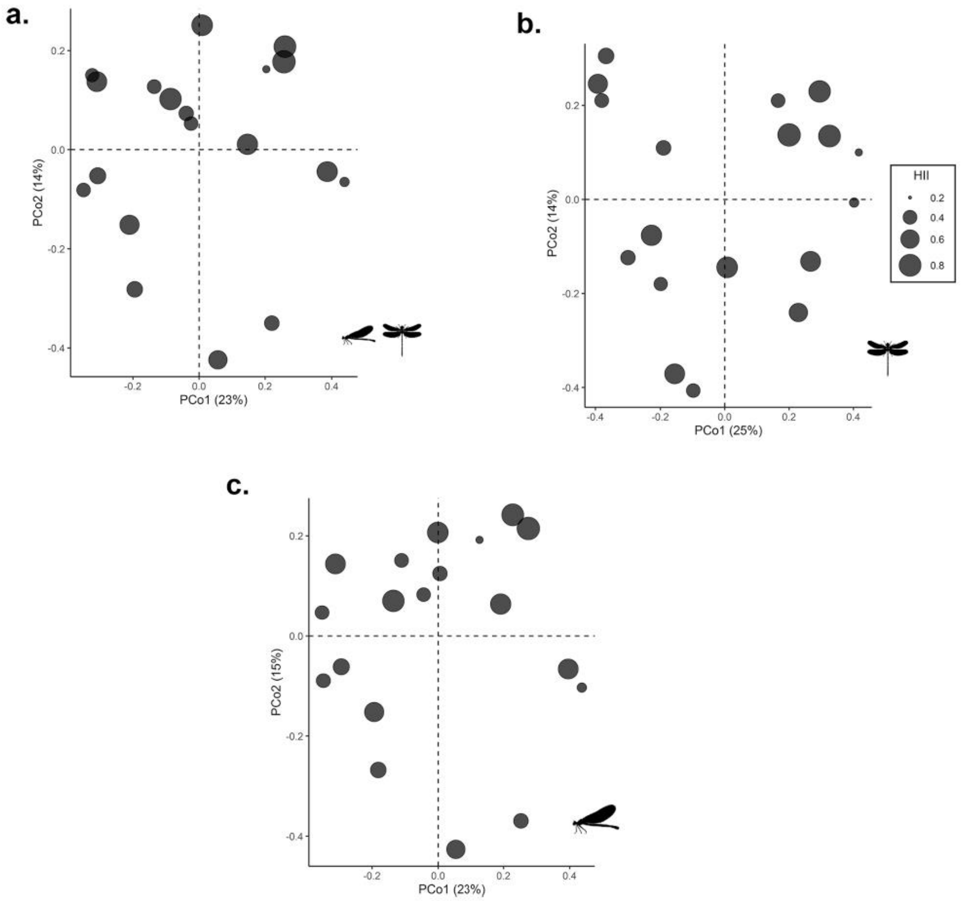

**Fig. 3.** Principal Coordinates Analysis (PCoA) of communities along HII gradient for Odonata (a) Anisoptera (b) and Zygoptera (c). Bubble sizes indicate HII value in each sampled site.

et al., 2018; Sganzerla et al., 2021). Furthermore, the high dispersal capacity of dragonflies allows them long-distance movements. So, if we consider the LU sites as possible sources of diversity and the HU sites as diversity sinks, the movement of dragonflies between these two types of habitat will be independent of the quality offered by the habitat and will rather respond to the dispersal capacity of the individuals who will be able to take advantage of what is offered by each habitat type. Actually, this can be the case for the multiple ravines present around our study sites and its surroundings. Thus, it may be simply that the dragonflies we recorded in highly disturbed sites were individuals that were able to travel long distances and visit such sites.

Dragonflies appear as a more resilient suborder than damselflies meaning that damselflies may be more vulnerable to urbanization. However, richness and abundance for the two suborders were still considerably higher in HU sites (as in the case of Willigalla and Fartmann (2012), Monteiro-Júnior et al. (2014) and Luke et al. (2017) (Fig. 4). Thus, despite suborder differences regarding the sensitivity of the species and considering the resilient nature of this group of insects, odonates have gained the reputation of being "invincible insects" as Japanese call them (Simaika and Samways 2008). Although some species are indeed threatened by the changes that characterize the Anthropocene, most odonate species do fairly well in water bodies with some degree of deterioration. This does not mean that there are no other negative consequences of living in poor quality area. For example, our study was not conducted at the individual level, so we do not know how the physiological condition for odonates is affected when individuals inhabit deteriorated sites. In relation to this, in a study site not far from ours, male and female adults of *Hetaerina americana* populations ended up with a reduced lipid content and muscle mass after ca. 10 years of being exposed to wastewater outlets (Córdoba-Aguilar and Rocha-Ortega, 2019).

Our PCoA analysis did not allow us to discern distinct composition of odonate communities along the defined HII gradient (Fig. 3). This, together with the lack of statistical significance in the TITAN analysis, reveals that the differentiation of the communities is not clear in the defined gradient. But just because today we see it that way, it does not mean that it has necessarily always been that way. Perhaps the changes in the composition of the communities were evident 70 years ago when environmental changes were just beginning in the sampled places and individuals had not yet developed strategies to survive these new

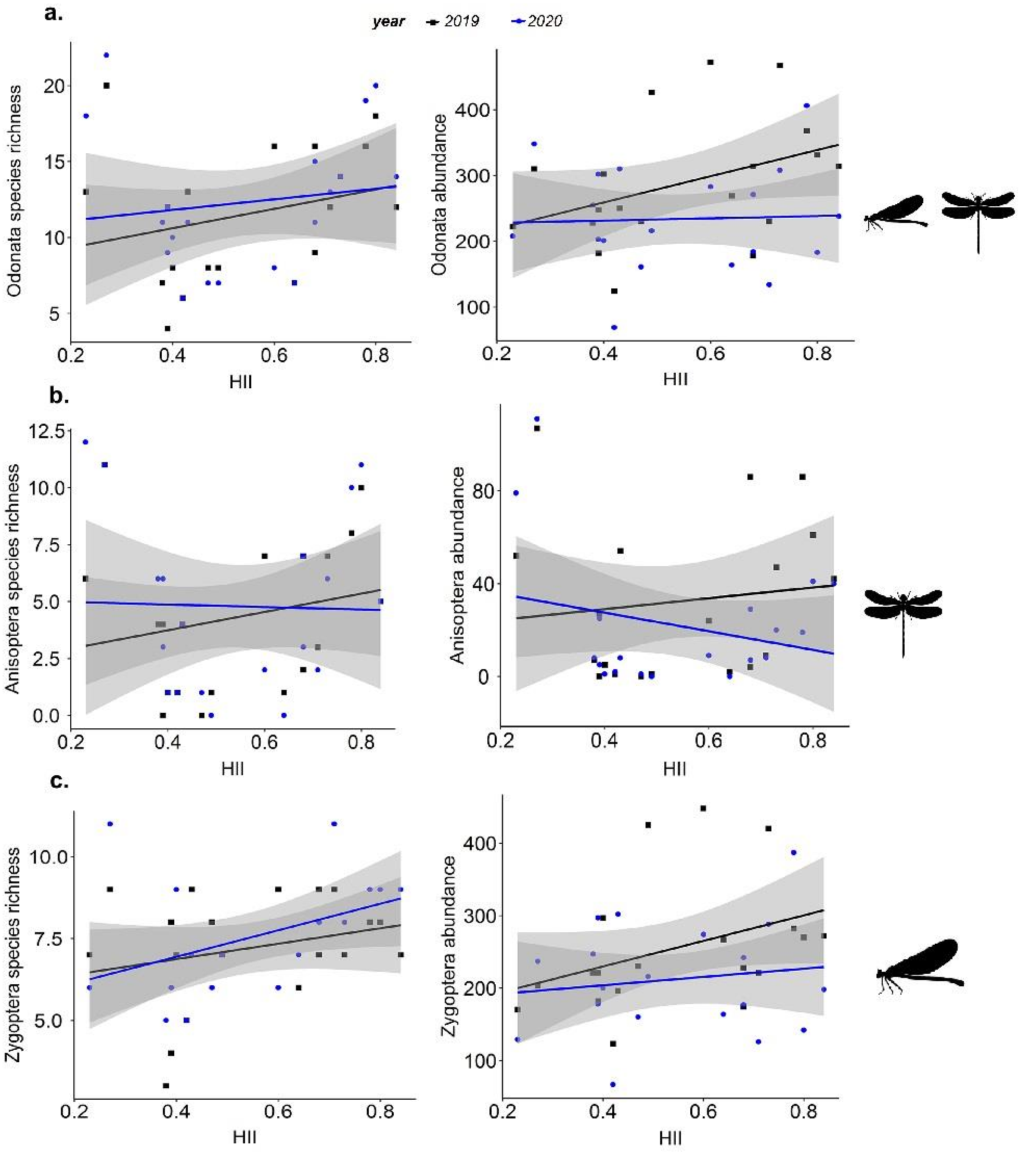

**Fig. 4.** Relationship between the HII and the richness and abundance of odonate species (a), zygopteran species (b), and anisopteran species (c). 2019 values are displayed in black, and 2020 values are displayed in blue (colors in online version). Shaded area shows 95% confidence intervals.

environments, resulting in the extinction of the most sensitive species. In this way, what we see today are the species that initially survived these environmental changes, and this may be why we are not detecting differences in the composition of the communities.

We found that for the whole odonate community, and separately in dragonfly and damselfly communities, species richness and abundances increased with macrophyte coverage. This is not surprising since aquatic and riparian vegetation is key in determining habitat selection in lotic habitats not only by these insects (Hardersen 2008; Silva et al., 2010; Carvalho et al., 2013) but also other insect taxa (like Ephemeroptera, Plecoptera, and Trichoptera) (Nessimian et al., 2008; Faria et al., 2021). Functionally, macrophytes are essential for the establishment of some odonate species, as macrophytes favor microhabitat architecture needed for perching and oviposition. Aquatic and riparian vegetation provide places for endophytic oviposition particularly for damselflies (Goertzen and Suhling 2013; Jeanmougin et al., 2014). However, excessive aquatic macrophyte mass can also reduce oxygen availability in water bodies (Boeykens et al., 2017). This may explain why the abundance of both suborders covaried negatively with dissolved oxygen values. Possibly, there is a threshold in macrophyte abundance that affects odonate viability.

We also found a positive relationship between dragonfly richness and abundance, and damselfly abundance and anthropic waste, but a negative relationship with total dissolved solids. These results may have a common explanation for both suborders. Damselflies and dragonflies are commonly attracted to man-made surfaces (i.e. glass, plastic sheets, black plastic foils, windshield cars, and bonnet cars) as these reflect polarized light which is an aquatic cue used for habitat selection (Wildermuth 1993; Van de Koken et al., 2007; Ensaldo-Cárdenas et al., 2021). Possibly, many of the artificial surfaces serve as attractors to odonates that act synergistically in urbanized areas.

About the dissolved solids, this may decompose in small foreign particles into the water with serious consequences for the development of the larvae (Monteiro-Júnior et al., 2015), which can be reflected in the decrease of abundance and species richness in the adult communities. Future studies should elucidate how the particular abiotic composition of urbanized aquatic areas impacts the performance and condition of odonate larvae and adults.

The forced lockdown due to COVID-19 pandemic generated important changes in urban environments (Srivastava et al., 2021) and biological communities (Soto et al., 2021; Ulloa et al., 2021). Although we did not design our study based on this pandemic phenomenon, our collection years coincided with the year previous (2019) and after (2020) the lockdown. Given this, we would like to discuss our results in this context. We observed an increase in species richness and abundance in the samplings carried out in 2020 compared with 2019 (Fig. 4). We found a reduction in abundance (but not in richness) between the two sampled years. We have two explanations for these results. First, possibly the production of waste from the houses near our sampling sites, increased when people stayed indoors. This waste may have reached the water bodies with a negative effect on abundance. Second, the mean annual precipitation for 2019 was higher (1691.3 mm) than for 2020 (1507.5 mm) (CONAGUA, 2021). This decrease in water availability may have implied drastic changes in biotic and abiotic variables in the second sampling year. In this way, rainfall could be related to the prey availability for larval odonates (Amundrud and Srivastava, 2016) as well as it could be involved in the dilution of water pollutants.

Odonates have become part of the urbanized fauna but, as our study shows, some species may be facing some costs and prefer to stay in more conserved places. In this sense, and in the midst of the biodiversity crisis that our world faces today, in which urbanization is one of the greatest threats, the creation of sustainable cities is essential for the conservation of some of the most threatened species (Goertzen and Suhling 2013; Fenoglio et al., 2021). In the case of odonates and other aquatic insects, designing spaces within cities with lotic and lentic water bodies connected to each other by fragments of native vegetation, and with aquatic vegetation in and around them, would benefit a greater number of species. Open habitats should be also considered for dragonfly conservation persistence (Willigalla and Fartmann 2012). Additionally, the proximity of this type of habitat to the city dwellers would facilitate awareness of the importance of proper water management and the consequences of this management on life forms that are not normally considered.

## 5. Conclusions

In the urbanization gradient defined in Central Mexico, damselflies but not dragonflies showed higher species richness and abundance at low urbanization than at high urbanization sites. Sensitive and resilient species were identified within the communities, again finding that the sensitive species are damselflies and the most resilient are mostly dragonflies. This indicates that damselflies are becoming more sensitive to environmental disturbances related to urbanization. This sensitivity can be explained by the specialist habits and low dispersal capacity of damselflies compared to dragonflies. Despite this differential sensitivity between suborders, odonates seem to be a very resilient group to the selective pressures generated by urban environments.

## Declaration of Competing Interest

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

## Data availability

Data will be made available on request.

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### *Statements and declarations*

All authors have agreed with the manuscript contents, declare no conflict of interests and approved the final version.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109134.

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## Further reading

Johnson, M.T.J., Munshi-South, J., 2017. Evolution of life in urban environments. Science 358.

# Supplementry material

## **Table S1** *Characterization of sampling sites*

| Site | Electric conductivity (µS/cm) | Total dissolved solids (ppm) | Dissolved oxygen (%) | Dominant plant strata | Macrophyte coverage (%) | Anthropic waste (%) | Mean width (m) | Mean depth (m) | pH | Chanel type | Sewage discharge | Mean of persons walking | Mean of vehicles passing by | Type of constructions around |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| HU1 | 168.7 | 84.7 | 102.0 | Herbaceus | 64.7 | 3.9 | 1.1 | 0.3 | 9.2 | Concrete | Ocasional | 3 | 2 | Households |
| HU2 | 141.3 | 70.5 | 127.8 | Herbaceus | 24.7 | 4.0 | 1.3 | 0.1 | 9.7 | Concrete | Ocasional | 10 | 17 | Households/shops |
| HU3 | 274.3 | 137.2 | 99.4 | Arboreal | 0.0 | 35.7 | 6.6 | 0.5 | 8.2 | Mix | Ocasional | 3 | 71 | Households/shops |
| HU4 | 137.2 | 68.5 | 132.5 | Herbaceus | 42.7 | 0.0 | 1.0 | 0.4 | 10.2 | Concrete | Ocasional | 7 | 53 | School/ road |
| HU5 | 1324.0 | 662.3 | 142.1 | Herbaceus | 7.7 | 7.2 | 17.8 | 0.5 | 10.5 | Mix | Direct | 15 | 8 | Households/shops |
| HU6 | 416.2 | 208.3 | 115.6 | Herbaceus | 5.3 | 14.0 | 10.2 | 0.3 | 10.0 | Mix | Direct | 3 | 20 | Households/ road |
| HU7 | 206.7 | 103.5 | 141.5 | Arboreal | 4.7 | 9.2 | 1.9 | 0.4 | 9.8 | Mix | Ocasional | 3 | 53 | Shops/road |
| HU8 | 231.7 | 117.2 | 110.3 | Arboreal | 4.0 | 1.0 | 3.0 | 0.3 | 8.3 | Mix | Ocasional | 8 | 2 | No construction |
| HU9 | 412.5 | 206.3 | 139.9 | Herbaceus | 24.7 | 4.7 | 1.1 | 0.2 | 8.1 | Concrete | Ocasional | 6 | 30 | Households/ road |
| HU10 | 397.5 | 198.7 | 134.0 | Arboreal | 0.0 | 8.7 | 9.8 | 0.5 | 9.0 | Mix | Direct | 2 | 12 | Households/ road |
| HU11 | 325.0 | 162.3 | 117.0 | Arboreal | 0.0 | 29.3 | 8.9 | 0.7 | 8.6 | Mix | Direct | 4 | 9 | Shops/road/Households |
| HU12 | 384.0 | 192.2 | 137.2 | Herbaceus | 46.7 | 4.8 | 1.3 | 0.1 | 7.9 | Concrete | Ocasional | 9 | 13 | Households/ road |
| LU1 | 105.0 | 52.3 | 140.2 | Arboreal | 0.0 | 0.0 | 2.0 | 0.4 | 9.9 | Mix | Ocasional | 5 | 0 | Households |
| LU2 | 1457.8 | 728.8 | 118.1 | Shrubby | 22.3 | 0.0 | 12.1 | 0.6 | 9.6 | Natural | No obvious | 2 | 0 | Households/shops |
| LU3 | 140.5 | 70.3 | 127.8 | Arboreal | 59.0 | 0.0 | 10.0 | 0.5 | 10.0 | Mix | No obvious | 8 | 0 | No construction |
| LU4 | 349.8 | 174.7 | 140.3 | Arboreal | 6.0 | 2.5 | 9.5 | 0.6 | 9.2 | Natural | No obvious | 1 | 0 | Households |
| LU5 | 110.6 | 55.2 | 137.1 | Arboreal | 93.3 | 0.0 | 4.0 | 0.5 | 10.5 | Mix | Ocasional | 3 | 1 | No construction |
| LU6 | 221.1 | 110.5 | 104.5 | Arboreal | 11.0 | 0.0 | 8.0 | 0.7 | 7.9 | Natural | No obvious | 8 | 1 | No construction |
| LU7 | 129.8 | 115.2 | 99.8 | Arboreal | 50.3 | 5.0 | 9.8 | 0.7 | 8.6 | Mix | No obvious | 4 | 2 | No construction |

**Table S2.** *Abundances of the species in each sampling site*

| | HU1 | HU2 | HU3 | HU4 | HU5 | HU6 | HU7 | HU8 | HU9 | HU10 | HU11 | HU12 | LU1 | LU2 | LU3 | LU4 | LU5 | LU6 | LU7 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **ANISOPTERA** | | | | | | | | | | | | | | | | | | | |
| **Aeshnidae** | | | | | | | | | | | | | | | | | | | |
| *Aeshna williamsoniana* Calvert, 1905 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 |
| *Anax junius* (Drury, 1773) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 3 | 0 | 1 |
| *Remartinia luteipennis* (Burmeister, 1839) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| *Rhionaeschna psilus* (Calvert, 1947) | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Coryphaeschna adnexa* (Hagen, 1861) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| **Cordulegastridae** | | | | | | | | | | | | | | | | | | | |
| *Cordulegaster diadema* Selys, 1868 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Gomphidae** | | | | | | | | | | | | | | | | | | | |
| *Progomphus clendoni* Calvert, 1905 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| **Libellulidae** | | | | | | | | | | | | | | | | | | | |
| *Brachymesia furcata* (Hagen, 1861) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 5 |
| *Dythemis maya* Calvert, 1906 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Dythemis nigrescens* Calvert, 1899 | 0 | 0 | 0 | 1 | 15 | 1 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 7 | 0 | 1 |
| *Erythemis plebeja* (Burmeister, 1839) | 0 | 0 | 0 | 1 | 16 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 8 | 2 |
| *Erythemis vesiculosa* (Fabricius, 1775) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| *Erythrodiplax basifusca* (Calvert, 1895) | 12 | 2 | 0 | 1 | 13 | 20 | 0 | 0 | 5 | 0 | 13 | 0 | 0 | 3 | 0 | 4 | 10 | 39 | 23 |
| *Libellula croceipennis* Selys, 1868 | 2 | 0 | 0 | 0 | 8 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 2 | 13 | 4 | 0 | 3 | 2 | 0 |
| *Libellula saturata* Uhler, 1857 | 13 | 2 | 0 | 0 | 12 | 6 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 8 | 5 | 1 | 19 | 29 | 3 |
| *Macrothemis pseudimitans* Calvert, 1898 | 2 | 1 | 0 | 3 | 6 | 2 | 0 | 0 | 14 | 6 | 6 | 0 | 3 | 18 | 21 | 11 | 0 | 0 | 0 |
| *Micrathyria aequalis* (Hagen, 1861) | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 1 |
| *Orthemis discolor* (Burmeister, 1839) | 1 | 0 | 2 | 3 | 14 | 30 | 0 | 2 | 0 | 0 | 21 | 0 | 0 | 11 | 0 | 1 | 36 | 2 | 21 |
| *Orthemis ferruginea* (Fabricius, 1775) | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 |
| *Paltothemis lineatipes* Karsch, 1890 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pantala flavescens* (Fabricius, 1798) | 1 | 0 | 1 | 3 | 4 | 5 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 9 |
| *Perithemis intensa* Kirby, 1889 | 0 | 0 | 0 | 0 | 44 | 42 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 25 | 0 | 0 | 0 | 0 | 9 |

| | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pseudoleon superbus* (Hagen, 1861) | 0 | 0 | 0 | 0 | 8 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Sympetrum illotum* (Hagen, 1861) | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 2 | 0 |
| *Tramea abdominalis* (Rambur, 1842) | 0 | 0 | 0 | 1 | 8 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 7 |
| **ZYGOPTERA** | | | | | | | | | | | | | | | | | | | |
| **Calopterygidae** | | | | | | | | | | | | | | | | | | | |
| *Hetaerina americana* (Fabricius, 1798) | 270 | 0 | 0 | 0 | 84 | 2 | 0 | 0 | 176 | 1 | 0 | 10 | 0 | 62 | 0 | 18 | 2 | 27 | 0 |
| *Hetaerina vulnerata* Hagen in Selys, 1853 | 6 | 150 | 48 | 290 | 0 | 0 | 131 | 19 | 9 | 118 | 56 | 0 | 117 | 10 | 294 | 24 | 23 | 39 | 160 |
| **Coenagrionidae** | | | | | | | | | | | | | | | | | | | |
| *Apanisagrion lais* (Brauer in Selys, 1876) | 16 | 19 | 1 | 7 | 1 | 14 | 36 | 10 | 1 | 7 | 5 | 2 | 31 | 24 | 4 | 21 | 35 | 50 | 8 |
| *Argia anceps* Garrison, 1996 | 11 | 1 | 4 | 0 | 84 | 28 | 61 | 6 | 22 | 118 | 59 | 19 | 1 | 249 | 115 | 90 | 36 | 155 | 66 |
| *Argia frequentula* Calvert, 1907 | 0 | 0 | 0 | 0 | 18 | 0 | 0 | 0 | 34 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 3 |
| *Argia extranea* (Hagen, 1861) | 302 | 212 | 32 | 17 | 28 | 88 | 191 | 85 | 36 | 107 | 121 | 195 | 93 | 0 | 45 | 66 | 29 | 42 | 151 |
| *Argia oenea* Hagen in Selys, 1865 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 47 | 0 | 17 | 0 | 0 | 0 |
| *Argia pallens* Calvert, 1902 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 8 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Argia plana* Calvert, 1902 | 0 | 35 | 0 | 149 | 5 | 1 | 129 | 199 | 38 | 18 | 10 | 90 | 34 | 2 | 5 | 4 | 0 | 0 | 36 |
| *Argia tarascana* Calvert, 1902 | 96 | 62 | 81 | 3 | 70 | 11 | 84 | 107 | 102 | 94 | 102 | 45 | 13 | 53 | 115 | 82 | 43 | 68 | 157 |
| *Argia tezpi* Calvert, 1902 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *Argia oculata* Hagen in Selys, 1865 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 |
| *Enallagma civile (Hagen, 1861)* | 3 | 0 | 0 | 0 | 11 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 66 | 11 | 2 | 0 | 0 |
| *Enallagma novaehispaniae* Calvert, 1907 | 11 | 0 | 0 | 0 | 89 | 7 | 1 | 0 | 98 | 0 | 0 | 0 | 0 | 45 | 15 | 0 | 3 | 0 | 14 |
| *Hesperagrion heterodoxum* (Selys, 1868) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| *Ischnura hastata* (Say, 1839) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 | 0 | 0 |
| *Mecistogaster ornata* Rambur, 1842 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Telebasis salva* (Hagen, 1861) | 6 | 0 | 0 | 2 | 70 | 113 | 0 | 0 | 13 | 0 | 24 | 18 | 0 | 4 | 55 | 11 | 210 | 64 | 78 |
| **Lestidae** | | | | | | | | | | | | | | | | | | | |
| *Archilestes grandis* (Rambur, 1842) | 1 | 0 | 24 | 0 | 0 | 27 | 9 | 2 | 0 | 32 | 22 | 0 | 57 | 0 | 6 | 0 | 16 | 19 | 10 |
| **TOTAL** | **755** | **484** | **193** | **483** | **658** | **430** | **642** | **433** | **560** | **503** | **451** | **391** | **362** | **585** | **770** | **364** | **510** | **552** | **774** |

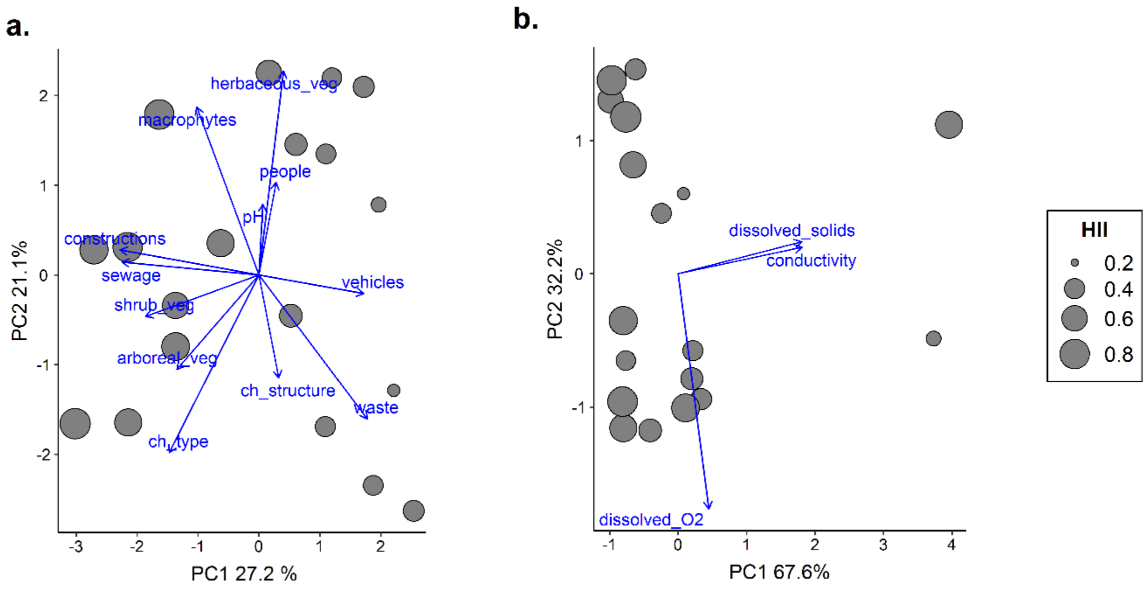

**Fig. S1** *Principal Component Analysis (PCA) with (a) the characteristics included in the calculation of the HII and (b) PCA with other environmental variables measured in the study.Bubble size represent the HII value*

# CAPÍTULO II

# Is body condition of Mexican rubyspot (Odonata:Zygoptera) associated with urbanization?

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**ORIGINAL PAPER**

## Is body condition of Mexican rubyspot (Odonata:Zygoptera) associated with urbanization?

**Catalina M. Suárez-Tovar[1,2] · Maya Rocha-Ortega[2] · Alex Córdoba-Aguilar[2]**

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**Abstract**
Urbanized areas can impose selective pressures on insects which can be identified at the individual level based on animal physiological condition. Physiological condition can be measured from variables such as body size, body mass or energetic budget of individuals. We examined whether body mass, wing spot size and energy reserves (proteins, lipids and carbohydrates) were reduced as urbanization increases, using adults of two damselflies, *Hetaerina americana* and *H. vulnerata*, in Central Mexico. We used a Habitat Integrity Index to assess the degree of urbanization in our sampled sites, considering biophysical attributes and the impact of anthropogenic activities. We did not find relation of above individual variables with urbanization degree. These results support possible resilience of rubyspot damselflies in the face of radical changes such as urbanization. Our finding echoes other results in damselflies research.

**Implications for insect conservation** Our results highlight the resilience of these damselflies species in the face of urban disturbances. Thus design cities considering not only requirements of humans is essential to promote the presence and conservation of these and other species of insects in cities.

**Graphical abstract**

**Keywords** Urban ecology · Habitat Integrity Index · Odonata · Resilience · Energy budget · *Hetaerina*

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Extended author information available on the last page of the article

## Introduction

Human concentration in urban areas and continuous modifications of native ecosystems for the construction of houses, roads, businesses, buildings and industries, have generated an irreversible impact on terrestrial and aquatic native environments worldwide (Grimm et al. 2008; Johnson and Munshi-South 2017). Even for species surviving in urban ecosystems, the modification of structural and environmental parameters as well as the alteration of the climate and microclimates, and the loss of the complexity of the available niches imply strong selective pressures (Alberti et al. 2017). These urban species can respond to new conditions at different levels: community, population or individual. Although, we have a good idea of community- (Blair & Launer 1997; Monteiro-Júnior et al. 2014; Kelly et al. 2019) and population-level effects (de Carvalho et al. 2017; da Conceição et al. 2020), we are still far from having a sound knowledge of individual-level effects of urbanization (e.g. Salomão et al. 2020).

The fact that many insect species can occur in both urban and non-urban habitats (Sattler et al. 2010), implies an opportunity to study the consequences of urbanization at the individual (i.e. morphological and/or physiological) level. For example, the physiological condition of individuals as reflected by traits such as body size or energy budget, could give an indication of how individuals do in altered environments (e.g. Salomão et al. 2020). Additionally, changes in the energy budget, can also modify behavior, resulting in the modulation or change of behavioral patterns when there is less energy available as a consequence of additional energy costs generated by new threats that take place in cities (Tynkkynen et al. 2008; Magura et al. 2021; Resende et al. 2021).

One insect genus with the ability to live in urbanized and non-urbanized areas, is that of *Hetaerina* Hagen, 1853 damselflies. Members of this taxon are also commonly known as rubyspot given the red wing spot adult males bear. *Hetaerina* species are good study subjects for answering how urbanization degree affects condition. For example, a recent study found that *H. americana* adults and larvae exposed to an increased level of wastewater inlets was related to a reduction in fat and muscle mass as well as egg hatching (Córdoba-Aguilar and Rocha-Ortega 2019). This study implied that a proxy of urbanization level negatively affected *Hetaerina* adult fitness in the long term.

One other advantage of using *Hetaerina* damselflies is that we have a good knowledge of which traits could be used as proxies of condition. In this regard, wing spot size and aggressive behavior act as honest signals of physiological condition in these damselflies (Contreras-Garduño et al. 2006; González-Santoyo et al. 2014). Within the genus *Hetaerina, H. americana* Fabricius, 1798 and *H. vulnerata* Hagen, 1853 are species widely distributed in Mexico. There, these two species can be found in sympatry, but it is more common to find them in allopatry due to their great similarity in both biology and sexual behavior (Álvarez et al. 2013). Both species are territorial species and from very early in their evolutionary history they are well adapted to open habitats (Córdoba-Aguilar and Cordero-Rivera 2005; Standring et al. 2022). Given these arguments, we provide here the results after asking whether adult *Hetaerina americana* and *H. vulnerata* show a reduced body condition with increasing urbanization in Central Mexico. We predicted that urbanization will negatively covary with the expression of body mass, wing spot size and energy reserves (proteins, lipids, and carbohydrates).

## Materials and methods

### Study area

We selected 18 lotic systems (small streams or small rivers) between 1200 and 1655 m.a.s.l. in the state of Morelos (Fig. 1) that shared similar physical conditions in terms of width and depth but that differed in urbanization levels ranging from highly modified to less modified streams with marginal vegetation that cover the stream bed. Morelos is located in Central Mexico where the concentration of most of the population in urban areas has generated a large transformation of the natural ecosystems, into industrialized, touristic and residential areas with high levels of pollution caused by the inadequate discharge of sewage and uncontrolled use of natural resources (INEGI 2020; Valladares-Cisneros et al. 2021).

At each study site, we registered the geographical coordinates, elevation, and water and air temperature. We conducted two visits at each site, in December 2019 and in November–December 2020. During each visit, we defined three 20-m transects in each site (corresponding to the transects where we conducted the biological sampling, as explained below). In each transect we measured habitat variables to describe three components of the environment that specifically affect odonates: (1) a green component, including both macrophytes and the vegetation adjacent to the lotic system, (2) a blue component, evaluating the physical and chemical properties of the water and the solid waste present in it, and (3) a gray component, assessing urban constructions and infrastructure, and indicators of human activity. How we determined such components are described below.

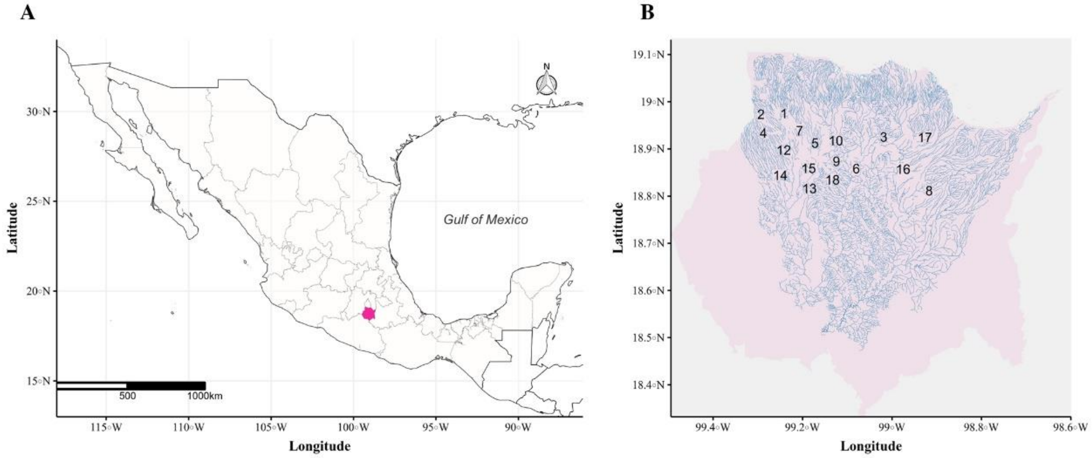

**Fig. 1** **A** Location of Morelos in México. **B** Location of the 18 sampling sites in the State of Morelos

### Green component

We determined the dominant vegetation stratum at each study site using the Canfield line-intercept method (Canfield 1941). For this, we considered three vegetation strata: herbaceous (0.3–1.5 m height), shrubby (1.5–5.0 m), or arboreal (> 5 m) following Rangel and Velásquez (1997). Then, we summed up the cover of each plant stratum in the three transects, divided by the 60 m length sampled (transect length occupied by each stratum/total length sampled), and multiplied by 100 to obtain the percentage of each plant stratum for each study site. Considering the predominant stratum of native vegetation, we calculate the state of preservation of the vegetation around each body of water. Additionally, we registered macrophytes using a 1-$m^2$ PVC square frame with 100 internal $10 \times 10$ cm squares. We placed the square randomly at three points in the water body and counted how many of the squares contained emerging, submerged, and/or floating macrophytes.

### Blue component

We measured water temperature, pH, percentage of both dissolved solids and dissolved oxygen using a Hanna HI9829 multiparametric probe. We measured the mean maximum width of the water body with a 50 m flexometer and the mean maximum depth with a rope marked every 5 cm and tied to a plummet that was thrown to the bottom of each water body. We registered channel type (concrete walls, natural, or mixed), the presence or absence of sewage discharges and the amount of anthropic waste in the water using the same method used to quantify macrophytes. We placed the square randomly at points of each transect in the water body and counted how many of the internal squares contained anthropic waste. Sewage discharges was defined as any liquid flow of at least 15 cm in width from any building into the river. We did not record the volume of these outlets nor the type of water contents. However, we observed that wastewaters included mainly laundry chemicals.

### Gray component

We recorded the constructions and urban infrastructure in and around 300 m the sampling sites: roads, shops, households, or nearby buildings. This record was made by direct observation before beginning the collection of variables and the sampling of individuals in each site. Additionally, a count was made of the number of people and vehicles (cars, bicycles motorcycles) passing through each sampling site. For this, 3-min replications of observations were made at 10:00, 12:00 and 14:00 (UTC-6).

Measurements in each site were made on the same day of biological sampling, before starting the registration and collection of specimens. Each sampling site was visited for a full day from 9:00 to 16:00 h (UTC-6) each of the sampling years.

## Habitat Integrity index (HII) calculation

The HII (modified from Petersen 1992), was calculated to assess the degree of disturbance of aquatic habitats, considering biophysical attributes of each site (green and blue components) and the impact of anthropogenic activities (gray component) for each sampling site. We included two variables from the green component, five from the blue component, and three from the gray component. Each

**Table 1** Characteristics considered for the calculation of the Habitat Integrity Index, and the scores assigned to each of the identified conditions

| Characteristic | Condition | Score |
|---|---|---|
| 1. Preservation of the riparian forest | Grass with some shrubs | 0 |
| | Grass mixed with some pioneer trees and shrubs | 1 |
| | Regenerating habitat, with a predominance of pioneer species, secondary forest, and dense undergrowth | 2 |
| | More than 90% of the vegetation constituted by native or non-pioneer trees | 3 |
| 2. Macrophyte coverage (%) | 0 | 0 |
| | 1–15 | 1 |
| | 16–30 | 2 |
| | 31–45 | 3 |
| | > 45 | 4 |
| 3. Anthropic waste (%) | > 20 | 0 |
| | 10.1–20 | 1 |
| | 5–10 | 2 |
| | 0–4.9 | 3 |
| 4. Channel structure | Width/depth ratio 25–50 | 0 |
| | Width/depth ratio 15–25 | 1 |
| | Width/depth ratio 8–15 | 2 |
| | Width/depth ratio < 7 | 3 |
| 5. pH | Basic (8.56–11) * urban streams with high levels of impermeability are associaaated with neutral to slightly alkaline pH (Tippler et al. 2018) | 0 |
| | Neutral (6.55–8-55) | 1 |
| | Acid (< 6.55) * Non-urban streams with low impermeability are associated with generally acidic pH (Tippler et al. 2018) | 2 |
| 6. Channel type | Concrete | 0 |
| | Mix | 1 |
| | Natural | 2 |
| 7. Sewage discharge | Direct residual discharges (from homes or industries) | 0 |
| | Occasional discharges near or into the water body (soap, pesticides, etc.) | 1 |
| | No obvious discharges | 2 |
| 8.Mean of persons walking | 11–15 | 0 |
| | 6–10 | 1 |
| | 0–5 | 2 |
| 9. Mean of vehicles passing by | > 30 | 0 |
| | 16–30 | 1 |
| | 11–15 | 2 |
| | 6–10 | 3 |
| | 0–5 | 4 |
| 10. Type of constructions around (within 300 m) | Shops, schools and / or wide roads | 0 |
| | Households | 1 |
| | No construction | 2 |

variable had three to five alternatives, with scores that increase with habitat integrity (Table. 1). To weigh ($p$) the different $i$ variables equally, the scores for each variable ($ao$) were divided by its maximum ($am$) possible score ($p_i = ao / am$). The final HII score (Eq. 1) for each site was obtained from the mean value of these scores for the ten variables analyzed.

$$HII = \frac{\sum_{i=1}^{n} p_i}{n} \tag{1}$$

Our HII generates values that go from zero to one, where values close to zero correspond to sites with high urbanization, and values close to one correspond to sites with low urbanization.

### Odonata collection and determination of individual variables

In each of the sampling sites, we used an entomological net, and collected at least ten adult males of *H. americana* or *H. vulnerate* (ten individuals of each species). This is due to the fact that males were more abundant compared to females in the sampled sites. In each of the sites we observed exuviae of the collected species, so we could infer that the collected adults have spent their entire life cycle in the sampled sites. Next, body mass (g), proportion of the wing spot to wing size, and the content of protein, lipid, and carbohydrate (µg/mg) of each individual were calculated. All these variables were considered as proxies of energetic condition (see Meillère et al. 2015).

To measure the size of the wing spot, each individual's right forewing was removed and photographed. We measured the area occupied by the red spot in the right forewing and the total area of the wing using Imagej 1.53e (Schneider et al. 2012). Then, we calculated the spot ratio relative to the total wing area. To minimize possible errors of measurement, each metric was determined three times to obtain a mean that was used for the analysis. Finally, the content of energy reserves was performed following the protocol of Foray et al. (2012). According to this protocol, we used the thorax which was weighed on a Velab VE-210 analytical balance, with a sensitivity of 0.1 mg and a maximum capacity of 210 g. Then, we placed the thorax in a 2 ml centrifuge tube and crushed it with 180 µL of saline phosphate buffer to a hyaline solution using a TissueLyser II bead mill (Qiagen, Valancia, CA, U.S.A.). Once the thoracic tissue was homogenized, we calculated the amount of protein present in the tissue by centrifuging at 180 g relative centrifugal force (RCF) for 5 min at 4 °C. Next, we took 2.5 µL of the supernatant in duplicate and placed it into a 96-well microplate. Finally, we added 250µL of Bradford reagent, incubated for 20 min, and read spectrophotometrically at 595 nm using an EPOCH spectrophotometer 200-900 nm (BioTek, Winooski, VT, U.S.A). To calculate the amount of protein in the tissue from the absorbance values given by the spectrophotometer, we made a calibration curve using bovine serum albumin dilution series.

For lipid and carbohydrate determination we used 180 µL of original homogenized tissue and added 20µL of Na2SO4, 5µL of PBS and 1500 µL of methanol:chloroform solution (2:1). We shook the vial for 2 min. The samples were then centrifuged twice for 15 min at 180 g RCF. After centrifugation, and for lipid quantification, we transferred 100µL of supernatant to a U-bottom plate and heated at 90 °C until complete evaporation in a water bath. After total evaporation, we placed 10µL of 98% sulfuric acid in each well and incubated for 2 min at 90 °C. We then cooled the reaction, added 190 µL vanillin reagent, incubated for 15 min and read absorbance at 525 nm with a glyceryl trioleate lipid dilution series as standard for calibration. For carbohydrate calculation, we placed 150µL of supernatant obtained after centrifugation in duplicate in a 96-well microplate until we get approximately 10µL in a water bath. After obtaining 10µl of sample, we placed 240µL of anthrone reagent in each well and incubated the plate for 15 min at room temperature. We covered the microplate and incubated it at 90 °C for 15 min in a water bath. Finally, we read the absorbance at 625 nm with a standard curve of glucose dilution series as standard for calibration.

### Statistical analysis

We used independent generalized linear mixed-effects using *lme4* (Bates et al. 2015) and *car* (Fox and Weisberg 2019) libraries in R, with the HII as an explanatory variable and body mass, proportion of the wing spot and the amount of energy content (proteins, lipids, and carbohydrates) as response variables. Additionally, the species were included in the model as a random effect to control their effect on the response variables. In order to know if any of variables used to calculate the HII affected independently response variables, we also repeated each model using each variable as an explanatory variable. We assessed the assumptions of normality and homoscedasticity in models residuals using *performance* library (Lüdecke et al. 2021) and finally we used *ggplot2* (Wickham 2016) to perform graphics. All these analyzes and graphs were performed in RStudio v. 1.1.456 (R Core Team 2018).

## Results

The HII calculated for the study sites ranged from 0.27 to 0.84 (Table. 2). The different environmental variables varied between the sampling sites (Table. S1). *H. americana* and *H. vulnerata* were abundant in the study area, but rarely occurred in sympatry: out of the 18 sampled sites, *H. americana* was present at 5 sites while *H. vulnerata* was present at 13 sites. We thus collected data for 61 individuals of *H. americana* and 143 of *H. vulnerata*. Body mass and wing spot were not related to HII ($R^2 = 0.9$, $F = 0.12$, $p = 0.76$ and $R^2 = 0.26$, $F = 0.03$, $p = 0.85$ respectively), as well as the content of protein ($R^2 = 0.29$, $F = 0.0004$, $p = 0.98$), lipid ($R^2 = 0.026$, $F = 0.07$, $p = 0.79$) and carbohydrates ($R^2 = 0.39$, $F = 0.26$, $p = 0.6$) (Fig. 2). However, when we evaluated each variable individually we found a negative relation between the amount of lipids and proteins with the pH ($F = 12.98$, $p = 0.0002$ and $F = 12.14$, $p = 0.0005$, respectively). That is, at higher (i. e.basic) values of pH the amount of lipids and proteins decreases (Fig S1).

**Table 2** Geographical coordinates, elevation and Habitat Integrity Index values calculated for each sampled site

| Site | HII | Latitude | Longitude | Elevation (masl) |
|---|---|---|---|---|
| 1 | 0.60 | 18° 53′ 11.0″ N | 99° 11′ 11.6″ W | 1374 |
| 2 | 0.39 | 18° 53′ 12.0″ N | 99° 11′ 44.3″ W | 1397 |
| 3 | 0.68 | 18° 56′ 37.8″ N | 99° 15′ 39.3″ W | 1655 |
| 4 | 0.68 | 18° 54′ 26.9″ N | 99° 02′ 26.4″ W | 1232 |
| 5 | 0.42 | 18° 56′ 09.8″ N | 99° 14′ 50.9″ W | 1593 |
| 6 | 0.38 | 18° 54′ 16.7″ N | 99° 12′ 15.9″ W | 1420 |
| 7 | 0.27 | 18° 52′ 58.9″ N | 99° 03′ 44.5″ W | 1206 |
| 8 | 0.73 | 18° 54′ 57.0″ N | 99° 12′ 29.3″ W | 1458 |
| 9 | 0.71 | 18° 49′ 54.2″ N | 98° 56′ 18.5″ W | 1341 |
| 10 | 0.80 | 18° 53′ 45.4″ N | 99° 08′ 59.9″ W | 1387 |
| 11 | 0.49 | 18° 56′ 25.9″ N | 99° 13′ 46.9″ W | 1590 |
| 12 | 0.64 | 18° 55′ 45.2″ N | 99° 13′ 53.4″ W | 1544 |
| 13 | 0.43 | 18° 50′ 18.4″ N | 99° 12′ 16.9″ W | 1209 |
| 14 | 0.40 | 18° 51′ 59.9″ N | 99° 13′ 34″ W | 1277 |
| 15 | 0.39 | 18° 52′ 30.5″ N | 99° 13′ 15.8″ W | 1322 |
| 16 | 0.47 | 18° 50′ 10.9″ N | 98° 57′ 04.8″ W | 1338 |
| 17 | 0.84 | 18° 54′ 09.6″ N | 98° 57′ 08.6″ W | 1369 |
| 18 | 0.78 | 18° 52′ 36.4″ N | 99° 09′ 56.4″ W | 1341 |

*masl* meters above sea level

## Discussion

Unlike previous works (Salomão et al. 2020; Córdoba-Aguilar and Rocha-Ortega 2019; Iserhard et al. 2019), we did not find a significant relation between insect´s body condition and urbanization measure as HII. However, and despite the values recorded in our sampling sites were neutral to basic (7.9–10.5), it is possible to appreciate a negative relationship of lipids and proteins with pH values, similar to what was found by Córdoba-Aguilar and Rocha-Ortega (2019). Basic pH values have previously been associated with urbanized environments (Tippler et al. 2018). If we consider that the lipid and protein reserves, being long-term reserves (Arrese and Soulages 2010), are stored from the larval stage, we could infer that the way in which the pH affects the larvae´s muscle construction and fat reserves generation, also affects the constitution of the adult, as previously reported Tüzün and Stoks (2018) in *Coenagrion puella* populations reared in water with different physicochemical conditions.

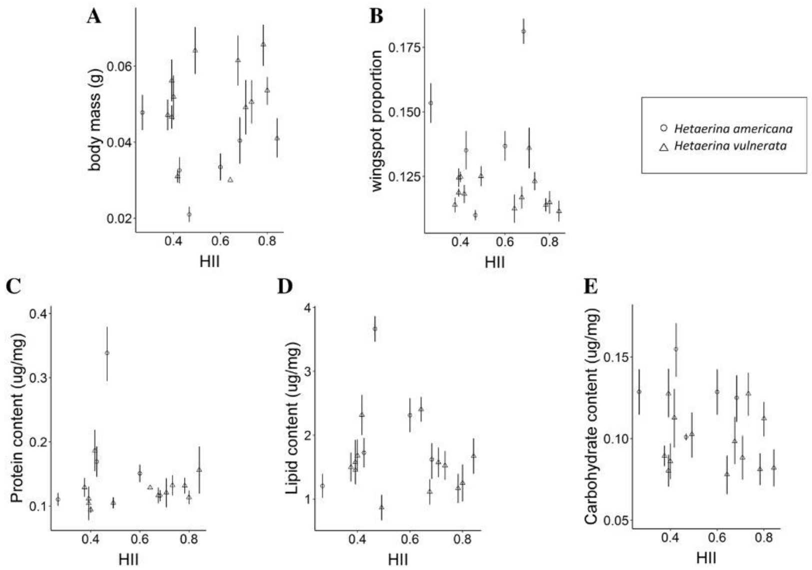

**Fig. 2** Observed data included in linear mixed-effects models for how urbanization relates to **A** Body mass. **B** Wingspot proportion, **C** Protein content, **D** Lipid content and **E** Carbohydrate content. Error bars indicate standard deviation (SD)

Although we do not have a reference point from which we can ensure that the energetic condition that we find in the individuals is good or bad, we can infer from our results that the energetic condition of the individuals, measured from different proxies, is maintained in high urbanized and less urbanized sites included in our study. These results support possible resilience of rubyspot damselflies in the face of radical changes such as urbanization. There are several possible explanations for the absence of a relation between energy condition indicators and habitat integrity related to urbanization.

First, it is important to consider that rubyspot damselflies are abundant and widely distributed species in the American continent (Garrison 1990; Standring et al. 2022). These two characteristics may be a reflection of the fact that they are highly variable species in their traits, which allows them to adapt more easily to stressful environments like cities without presenting radical changes in its morphology or energetic condition. This has been recorded in other common damselflies species (e.g. *Ischnura elegans*) that face urban environments in Europe (Goertzen and Suhling 2013; Villalobos-Jiménez and Hassall 2019). Continuing to study the responses at the individual level, not only of abundant and widely distributed species, but also of more sensitive species with restricted distribution, will allow us to clarify the scenario of changes in the individual condition of organisms that face changes in their environment derived from urbanization.

A second reason could be that animals have already responded to habitat changes. Urbanization processes in the study area began around 70 years ago (INEGI 2020) which can be enough time for current individuals to be already adapted to environmental disturbance. This considering, for example, that in previous studies *Hetaerina* species have responded (modifying aspects such as habitat use and interspecific fights frequency) after three-year observations in populations that face changes in their environment associated with the density of competing species (Anderson and Grether 2011). In this sense, the impact of urbanization on common and tolerant species (as *Hetaerina* species) could only be detected by sampling in the same place over time. This explanation is not at all surprising considering that insects respond quickly to stressors related to changes in their environment (Halsch et al. 2021).

A third possible explanation is about food resources. Although wing spot size in *Hetaerina* males is determined by the amount of resources that individuals obtain from their diet during their larval stage, energy reserves depend almost exclusively on the feeding of individuals during their adult stage (Contreras-Garduño et al. 2008; Córdoba-Aguilar and González-Tokman 2014). Our results, together with recent findings where the availability of food resources of *H. vulnerata* were assessed daily (Córdoba-Aguilar et al. 2021), indicate that despite the alteration caused by urban habitats, food resources may remain stable which could explain why individual body condition did not vary.

Finally, another explanation could be associated with the fact that individuals are modifying their behavior in urbanized places to reduce energy expenditure facing up new stressors. Some studies have recorded changes in the diversity of behaviors in the face of environmental impacts (Resende et al. 2021) and others have registered that changes in behavior patterns are the fastest response of some animals to relatively quick environmental changes (Tynkkynen et al. 2008; Magura et al. 2021). In this sense, rubyspot damselflies and other Odonata or insect species could be responding with changes in their behavior in urbanized or novel environments. Thus, further studies should be carried out to unravel a possible relation between fitness, behavior, and urbanization.

Although cities can drastically affect native ecosystems worldwide, urban areas can also be a suitable habitat for different groups of animals that can maintain viable populations and individuals with a good energetic condition (e.g. Pacheco-Muñoz et al. 2022). These animals have a set of morphological and physiological traits that allow them to survive the environmental filters imposed by cities (Iserhard et al. 2019; Villalobos-Jiménez and Hassall 2019; Salomão et al. 2020). However, it is important to highlight that not all species can survive in the face of environmental changes related to urbanization. It is enough to compare communities associated with lotic or lentic environments (e.g. Prescott and Eason 2018) to realize that there are different responses of the species depending on the initial conditions of the environments they inhabit. For this reason and being aware of the multiple species and their different requirements, we must generate cities designed not only for the human species, but for all the others that fly over the urban jungle and its surroundings.

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**Author contributions** Author contributions: CMST project design, data collection, writing original draft and analysis, MRO analysis, ACA project design, corrections of final versions, and funding acquisition. All authors commented on original draft of the manuscript. All authors read and approved the final manuscript.

## Declarations

**Competing interests** The authors declare no competing interests.

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## Supplementary material

**Table S1** *Characterization of sampling sites*

| Site | Electric conductivity (µS/cm) | Total dissolved solids (ppm) | Dissolved oxygen (%) | Dominant plant strata | Macrophyte coverage (%) | Anthropic waste (%) | Mean width (m) | Mean depth (m) | pH | Chanel type | Sewage discharge | Mean of persons walking | Mean of vehicles passing by | Type of constructions around |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 168.7 | 84.7 | 102 | Herbaceus | 64.7 | 3.9 | 1.1 | 0.3 | 9.2 | Concrete | Ocasional | 3 |  | Households |
| 2 | 141.3 | 70.5 | 127.8 | Herbaceus | 24.7 | 4 | 1.3 | 0.1 | 9.7 | Concrete | Ocasional | 10 | 17 | Households/shops |
| 3 | 105 | 52.3 | 140.2 | Arboreal | 0 | 0 | 2 | 0.4 | 9.9 | Mix | Ocasional | 5 | 0 | Households/shops |
| 4 | 1457.8 | 728.8 | 118.1 | Shrubby | 22.3 | 0 | 12.1 | 0.6 | 9.6 | Natural | No_obvious | 2 | 0 | School/ road |
| 5 | 274.3 | 137.2 | 99.4 | Arboreal | 0 | 35.7 | 6.6 | 0.5 | 8.2 | Mix | Ocasional | 3 | 71 | Households/shops |
| 6 | 137.2 | 68.5 | 132.5 | Herbaceus | 42.7 | 0 | 1 | 0.4 | 10.2 | Concrete | Ocasional | 7 | 53 | Shops/road |
| 7 | 1324 | 662.3 | 142.1 | Herbaceus | 7.7 | 7.2 | 17.8 | 0.5 | 10.5 | Mix | Direct | 15 | 8 | No construction |
| 8 | 140.5 | 70.3 | 127.8 | Arboreal | 59 | 0 | 10 | 0.5 | 10 | Mix | No_obvious | 8 | 0 | Households/ road |
| 9 | 349.8 | 174.7 | 140.3 | Arboreal | 6 | 2.5 | 9.5 | 0.6 | 9.2 | Natural | No_obvious | 1 | 0 | Households/ road |
| 10 | 110.6 | 55.2 | 137.1 | Arboreal | 93.3 | 0 | 4 | 0.5 | 10.5 | Mix | Ocasional | 3 | 1 | Shops/road/Households |
| 11 | 206.7 | 103.5 | 141.5 | Arboreal | 4.7 | 9.2 | 1.9 | 0.4 | 9.8 | Mix | Ocasional | 3 | 53 | Households/ road |
| 12 | 231.7 | 117.2 | 110.3 | Arboreal | 4 | 1 | 3 | 0.3 | 8.3 | Mix | Ocasional | 8 | 2 | Households |
| 13 | 412.5 | 206.3 | 139.9 | Herbaceus | 24.7 | 4.7 | 1.1 | 0.2 | 8.1 | Concrete | Ocasional | 6 | 30 | Households/shops |
| 14 | 397.5 | 198.7 | 134 | Arboreal | 0 | 8.7 | 9.8 | 0.5 | 9 | Mix | Direct | 2 | 12 | No construction |
| 15 | 325 | 162.3 | 117 | Arboreal | 0 | 29.3 | 8.9 | 0.7 | 8.6 | Mix | Direct | 4 | 9 | Households |
| 16 | 384 | 192.2 | 137.2 | Herbaceus | 46.7 | 4.8 | 1.3 | 0.1 | 7.9 | Concrete | Ocasional | 9 | 13 | No construction |
| 17 | 221.1 | 110.5 | 104.5 | Arboreal | 11 | 0 | 8 | 0.7 | 7.9 | Natural | No_obvious | 8 | 1 | No construction |
| 18 | 129.8 | 115.2 | 99.8 | Arboreal | 50.3 | 5 | 9.8 | 0.7 | 8.6 | Mix | No_obvious | 4 | 2 | No construction |

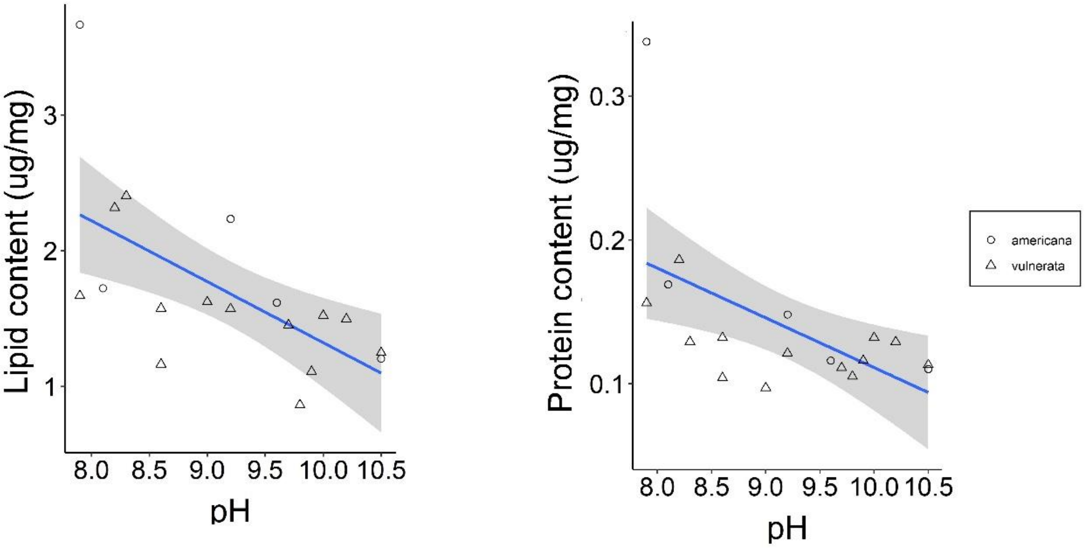

**Figure S1.** Observed data included in linear mixed-effects models for how pH relates to lipid and protein content.

# CAPÍTULO III

# The fierce hunters of the city: More effective predation of dragonflies and damselflies urbanized areas

*(Sometido a Animal Behaviour 12 mayo 2023- Aceptado:17 octubre 2023)*

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## Highlights

- Behavioral traits are adaptive tools that animals use to respond to rapid environmental changes caused by urbanization
- Odonata are a group of insects whose communities appear to be resilient to urbanization
- We evaluated whether adult odonate behaviors changed along a defined urbanization gradient in the Brazilian Amazon
- Odonates were less likely to fail during prey catching in more urbanized sites. This may be one strategy to deal with urbanized environments.

## ABSTRACT

One area of animal behavior of growing interest is the one that studies behavioral traits that favor species' survival in rapidly changing environments, such as cities. An animal group that seems to be relatively resilient to urbanization is that of odonate insects. These animals are formidable generalist predators that exhibit large behavioral flexibility. Here, we tested whether adult odonates show differences in behavioral traits associated to reproduction, foraging, and thermoregulation along an urbanization gradient. Our results indicate that individuals were more efficient at capturing prey in more urbanized places. The more effective predation inside the cities may occur as a consequence of changes in the environment, changes in the odonates behavior, or changes in prey communities whose characteristics influence the success rate of odonates during hunting.

**Keywords:** dragonflies, damselflies, behavior, urbanization, Amazon

## INTRODUCTION

Rapid environmental changes driven by urbanization impose novel and strong selective pressures on urban organisms, which must respond to these pressures on very short time scales to survive and settle (Alberti *et al*., 2017). However, a reduced group of species have traits that pre-adapt them to such novel urban conditions. In contrast, other species have to respond with shifts in traits that allow them to maintain their fitness under these new environmental conditions, as occurs with plasticity or microevolutionary processes (McDonnell and Hahs, 2015). As a consequence of this adaptive plasticity, individuals can to face modifications in their environment through morphological, genetic, physiological, and/or behavioral changes (Ghalambor *et al*., 2007; Tchakonté *et al*., 2015).

Among the plethora of traits animals are endowed with to face abrupt environmental modifications, behavioral traits are the fastest adaptive tools. This is supported by evidence from different animal groups, like birds (Estes and Mannan, 2003; Luther *et al*., 2016), mammals (Mazza *et al*., 2020; Uchida *et al*., 2020), and insects (Tynkkynen *et al*., 2008; Guillermo-Ferreira and Juen 2021, Magura *et al*., 2021). For example, in the beetle *Carabus convexus*, rural populations show two personalities, exploratory and risky, but in urban areas beetles prefer to adopt their risky personality, which is more adaptive to face the new urban conditions (Magura *et al*., 2021). Using a different example, in *Temnothorax nylanderi* ants have been recorded a higher foraging effort in urban colonies. In this case ants are more sensitive to starvation for fewer fat reserves or a higher metabolic rate inside cities due to warmer temperatures (Jacquier *et al*., 2023). From these examples we can infer that other groups of insects that inhabit urban environments may present different changes in their behavior.

Urban ecosystems support a relatively high diversity of Odonata species, dragonflies and damselflies (Monteiro-Júnior *et al*., 2014; Luke *et al*., 2017). Interestingly, there is a link between urban habitats and odonate behavior. Resende *et al*. (2021) found that territorial and reproductive behaviors in these insects are strongly linked to environmental conditions and that changes in habitat integrity can lead to a decrease in behavioral diversity. In natural areas, these authors recorded species with different types of oviposition (endophytic, exophytic, and epiphytic), while in areas modified by human activities, such as agricultural or urban landscapes, species with exophytic oviposition prevailed. Similarly, the frequency of males exhibiting territorial behaviors was lower in modified areas compared to natural areas (Resende *et al*., 2021). However, this previous study is based on the bibliographic review of behavioral traits of the species that inhabit cities, so it is necessary to carry out studies directly in the field that compare the frequencies of each of the behaviors carried out by individuals in urban areas

To explore odonate behavioral flexibility in urban environments, we conducted a study evaluating the reproductive, foraging, or thermoregulatory behaviors of adults of different Odonata species in conserved and urbanized sites. We predicted that, given the resilient nature of odonates, urban communities of dragonflies and damselflies would show differences in the frequency of behaviors performed, compared to communities in conserved areas. In this way, we would expect that behaviors that have a direct link with reproduction (i.e., mating behavior) and/or survival (i.e., foraging and thermoregulation), are carried out more efficiently in urban environments, to better cope with the challenges posed by urbanization.

## MATERIALS AND METHODS

### Study area

The region where the study was conducted has a dense vegetation cover, which can reach a canopy of more than 30 meters in height in areas not altered by anthropic action. We thus chose ten lotic systems separated from each other by a minimum distance of 2.7 km and between 3 and 25 m a.s.l. in the metropolitan region of Belem, in the Brazilian state of Pará. These systems are distributed across several municipalities, including Belem, Ananindeua, Benevides, Benfica and Castanhal, covering an area of 1827.7 $km^2$ (Fig. 1). We selected streams of up to second order that shared similar physical conditions in terms of width and depth but that differed in urbanization levels ranging from highly modified to less modified streams with marginal vegetation that covers the stream bed.

Belem is the second largest city in the Brazilian Amazon, with a population of approximately 2.5 million inhabitants. It is characterized by a humid environment and it is surrounded and crossed by rivers and stream. The concentration of most of the population in the metropolitan region of Belem has transformed the natural ecosystems into industrialized, touristic, and residential areas, with high pollution levels due to inadequate sewage discharge and uncontrolled exploitation of natural resources (Brito *et al*., 2021). For each study site, we recorded the geographical coordinates, elevation, and water temperature. In September 2022, during the dry season, we defined two 20-m transects in each of the ten study sites.

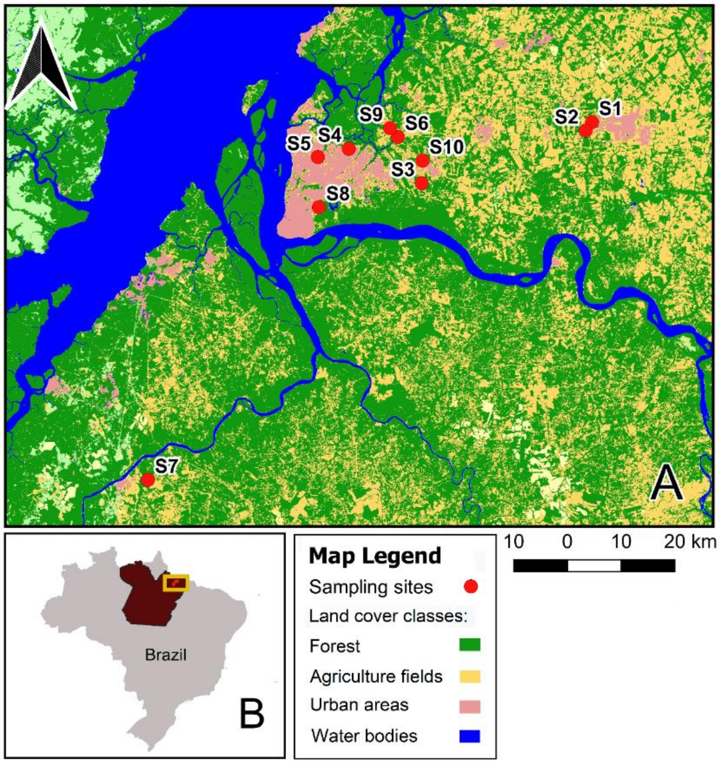

**Figure 1.** *A. Distribution of sampling sites in the metropolitan region of Belem, Pará, Brazil. B. Location of Pará state within Brazil.*

## Habitat Integrity index (HII)

We measured different habitat variables along each transect to calculate the habitat integrity index (HII hereafter) of each sampling site (modified from Petersen, 1992). The HII was used to assess the degree of disturbance of the sampling sites, considering the biophysical attributes and the impact of anthropogenic activities. The following characteristics were assessed: (i) stream access, (ii) width of the riparian forest; (iii) preservation of riparian forest; (iv) riparian forest condition within 10-m of the stream, (v) water retention mechanisms, (vi) channel structure, (vii) water flow in the channel, (viii) canopy cover, (ix) human physical occupation, (x) disposal of domestic and industrial effluents, (xi) building density within 100 m, and (xii) presence of dumped trash. How we determined these components is described below (Table 1).

Each variable had three to five conditions, with scores that increased with habitat integrity (Table 1). To weigh ($p$) the different $i$ variables equally, the scores for each variable ($ao$) were divided by its maximum ($am$) possible score ($p_i = ao / am$). The final HII score (Eq. 1) for each site was obtained from the mean value of these scores for the twelve variables analyzed.

$$HII = \frac{\sum_{i=1}^{n} p_i}{n} \quad \text{(Equation 1)}$$

The HII generates values from zero to one. Values close to zero correspond to sites with high urbanization, and values close to one correspond to sites with low urbanization.

**Table 1.** *Characteristics considered for the calculation of the habitat integrity index (HII), and the scores assigned to each of the identified conditions*

| **Variable** | **Condition** | **score** |
|---|---|---|
| I. Access to the stream | Paved road | 0 |
| | Unpaved road | 1 |
| | Track | 2 |
| | Path | 3 |
| II. Width of the riparian forest | No woody riparian vegetation | 0 |
| | No riparian forest, but some shrubs | 1 |
| | Well-defined riparian forest, 1–5 m in width | 2 |
| | Well-defined riparian forest, 5–30 m in width | 3 |
| | Well-defined riparian forest, more than 30 m in width | 4 |
| | Riparian vegetation contiguous with the surrounding forest | 5 |
| III. Preservation of the riparian forest | Frequent forest gaps with some regrowth | 0 |
| | Gaps at intervals of 25 m to 50 m | 1 |
| | Gaps at intervals of more than 50 m | 2 |
| | Riparian forest intact | 3 |
| IV. Riparian Forest condition within 10-m of the stream | Grass with some shrubs | 0 |
| | Grass mixed with some pioneer trees and shrubs | 1 |
| | Regenerating habitat, with a predominance of pioneer species, secondary forest, and dense undergrowth | 2 |
| | Pioneer species mixed with mature trees | 3 |
| | More than 90% of the vegetation constituted by native or non-pioneer trees | 4 |
| V. Water retention mechanisms | Retention by five or more of the following: plastic, metal, glass, rubber, building materials, organic matter | 0 |
| | Retention by three or more of the following: plastic, metal, glass, rubber, building materials,organic matter | 1 |
| | Retention by one or more of the following: plastic, metal, glass, rubber, building materials, organic atter | 2 |
| | Retention by leaves and trunks with no urban refuse | 3 |
| VI. Channel structure | Width/depth ratio > 50 | 0 |
| | Width/depth ratio 25–50 | 1 |
| | Width/depth ratio 15–25 | 2 |
| | Width/depth ratio 8–15 | 3 |
| | Width/depth ratio < 7 | 4 |
| VII. Water flow in the channel | Little water in the channel, many pools | 0 |
| | 25–50% of available channel filled with water (50–75% exposed) | 1 |
| | 50–75% of available channel filled with water (25–50% exposed) | 2 |
| | >75% of available channel filled with water (<25 exposed) | 3 |

| | | |
|---|---|---|
| | Water covering the bases of both banks | 4 |
| VIII. Canopy cover | Open – 0% to 10% | 0 |
| | Partly open – 11% to 40% | 1 |
| | Intermediate – 41% to 60% | 2 |
| | Partly closed – 61% to 90% | 3 |
| | Closed – 91% to 100% | 4 |
| IX. Human physical occupation | Urban or industrial development on the stream bank | 0 |
| | Urban or industrial development at a distance of more than 15 m from the edge of the stream | 1 |
| | Urban or industrial development at a distance of more than 25 m from the edge of the stream | 2 |
| | Urban or industrial development at a distance of more than 50 m from the edge of the stream | 3 |
| | No urban or industrial development | 4 |
| X. Domestic or industrial effluents | Domestic or industrial effluents discharged directly into the stream | 0 |
| | Urban development without adequate public sanitation, with waste being discharged near or into the stream | 1 |
| | Urban or industrial development connected to public sanitation network and treatment stations | 2 |
| | No buildings or effluent discharge | 3 |
| XI. Building density (within 100 m) | More than 100 buildings | 0 |
| | Between 51 and 100 buildings | 1 |
| | Between 11 and 50 buildings | 2 |
| | Between 1 and 10 buildings | 3 |
| | No buildings | 4 |
| XII. Dumped trash (inside or outside of the stream) | Five or more of the following: plastic, metal, glass, rubber, building materials, organic matter | 0 |
| | At least three of the following: plastic, metal, glass, rubber, building materials, organic matter | 1 |
| | At least one of the following: plastic, metal, glass, rubber, building materials, organic matter (principally leaves and woody material with sediments) | 2 |
| | Organic waste only | 3 |
| | No evidence | 4 |

## Odonata observations and determination of behavioral variables

We observed adult Odonata males and females along the defined gradient. After identifying the species and for behavioral observations, we followed the focal animal temporal sampling technique (*sensu* Altmann 1974). Observations were conducted from 10:00 to 13:00 hours. During each observation session, we divided the time into periods of 10 min per individual, recording the frequency of activities of each individual when leaving the perch. After the ten-minute observation, each observed individual was marked with a point of color on its wings to avoid recording the same individual twice, and then a different individual was observed. Two observers were present at each sampling site, classifying the observed behaviors into the following categories:

Failed foraging**:** when the individual pursued one prey but failed to catch it

Foraging**:** when the individual caught a prey

Mating behavior: when copulation, tandem, oviposition and/or pursuit of females occurred

Thermoregulation**:** when individuals assumed the obelisk position or made rapid movements of wings under the sun rays

Grooming**:** when the individual cleaned its head with its legs

Territory delimitation**:** when the individual flew around the same area several times

Territory defense**:** wing displays or direct confrontations with individuals approaching its territory

Inactivity: when individuals were on their perch without performing any of the activities or movements mentioned above

The relative frequency of each of the behaviors was calculated for each individual.

**Statistical Analysis**

To identify the predominant environmental variables in more or less urbanized sites, we performed a Principal Component Analysis (PCA) with the environmental variables measured to evaluate the environmental variation between study sites. The environmental variables were previously standardized (scale x to zero mean and unit variance) to have the same weight in the analyses. We used a correlation matrix and applied the Broken Sticks criterion to select the number of axes to include in the ordination analysis. Additionally, we used the HII values as bubble variables to create the ordering graph.

Because we have several species and their shared evolutionary history can influence the results obtained, we calculate the phylogenetic signal of the recorded behaviors. For this, we used the phylogenetic tree proposed by Waller and Svensson (2017), which we cropped with the *match.phylo.data* function in R to include only the observed species (Kembel *et al*., 2010). For any observed species that was not present in the original tree, we substituted it with the closest congeneric species from the original tree (Beaulieu *et al*., 2012; Li *et al*., 2019). The resulting phylogenetic tree (Fig. 2) was used to calculate the *K* statistic of the phylogenetic signal and its associated *p*-value based on the variance of phylogenetically independent contrasts with 999 replications (Blomberg *et al*., 2003; Kembel *et al*., 2010) for each behavioral category. The *K* statistic falls within the interval 0 to ∞. A value of 1 indicates that evolution follows a Brownian model, while *K* values greater than 1 indicate that species are more similar than expected under a Brownian model (i.e., high phylogenetic signal). Conversely, when *K* approaches 0, there is no phylogenetic signal, meaning that closely related species are as different as distantly related species (Blomberg *et al*., 2003).

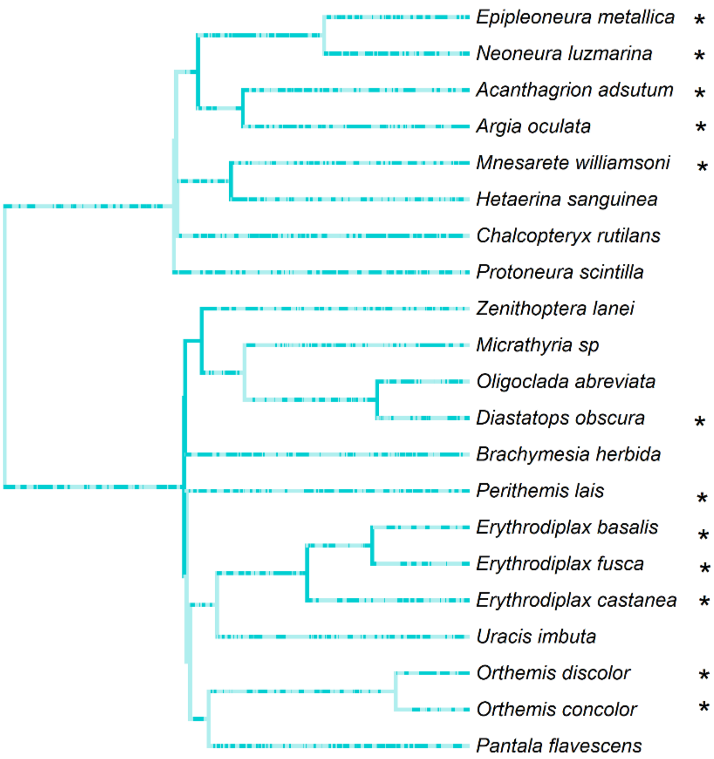

**Figure 2.** *Phylogenetic tree assembled from the phylogeny hypothesis of Waller and Svenson (2017), including species observed in our study. Asterisks indicate species observed at more than two sampling sites.*

Since we found no significant phylogenetic signal for any behavior (Table 2), we constructed our models without phylogenetic control. Specifically, we used generalized linear mixed-effects models with family *gaussian* and link *logit*, with the HII as explanatory variable and the relative frequency of each behavior as response variables. The species were included in the models as a random effect. We assessed the assumptions of normality and homoscedasticity of the models. However, the reproductive behavior and grooming models did not meet the assumptions of homocedasticity. Therefore, we employed a beta distribution with logit link, constructing these models using the *glmmTMB* function. Only species observed at more than two sites (12 species) were included in these analyses.

**Table 2.** *Phylogenetical signal for the different behavioral categories included in this study.*

| Behaviour category | K | PIC.variance.obs | PIC.variance.rnd.mean | PIC.variance.P | PIC.variance.Z |
|---|---|---|---|---|---|
| Mating behavior | 0.50 | 5.18E-05 | 7.96E-05 | 0.17 | -0.95 |
| Failed foraging | 0.24 | 8.62E-05 | 6.30E-05 | 0.89 | 1.25 |
| Foraging | 0.36 | 2.14E-05 | 2.34E-05 | 0.42 | -0.31 |
| Grooming | 0.32 | 3.15E-06 | 3.11E-06 | 0.58 | 0.05 |
| Inactivity | 0.37 | 3.38E-04 | 3.69E-04 | 0.44 | -0.28 |
| Termoregulation | 0.55 | 3.12E-05 | 4.96E-05 | 0.15 | -0.95 |
| Territory defense | 0.28 | 1.26E-04 | 1.06E-04 | 0.74 | 0.71 |
| Territory delimitation | 0.50 | 1.29E-04 | 1.93E-04 | 0.13 | -1.07 |

All analyses were performed in the R computing environment (R Development Core Team 2018) version 4.2.2 using the *vegan* (Oksanen *et al*., 2022), *tidyverse* (Wickham *et al*., 2019), *picante* (Kembel *et al*., 2010), *lme4* (Bates *et al*., 2015), *performance* (Lüdecke *et al*., 2021), *ggplot2* (Wickham, 2016), *GGally* (Schloerke *et al*., 2021), and *car* (Fox and Weisberg, 2019) packages.

## RESULTS

Our study sites had water temperatures that ranged between 26.3 and 30.1 ◦C (mean=27.8 ± 1.22). The HII values ranged from 0.17 to 0.79 (mean=0.39 ± 0.20) (Table 3), indicating that we were able to capture a gradient of habitat integrity in our study. Principal components analysis (PCA) showed that the first two axes accounted for 59.67 % of the total variation of the data. Longitude, latitude, and elevation were the variables that most strongly determined the first axis, with the first two related negatively and the last one positively with this axis. The depth and width of the streams contributed the most to the formation of the second axis, being both positively related to the axis. Conserved sites with higher HII values, were characterized by a denser canopy cover and macrophyte cover (Fig. 3, Table 4).

**Table 3.** *Geographical coordinates, elevation, water temperature, depth, width, canopy cover, macrophyte cover and HII values calculated for each site.*

| Site | Latitude | Longitude | Elevation | Mean water temperature (°C) | Depth (m) | Width (m) | Canopy cover (%) | Macrophyte cover (%) | HII |
|---|---|---|---|---|---|---|---|---|---|
| 1 | -1.282711 | -47.979952 | 14 | 26.65 | 0.45 | 6.3 | 59.5 | 0 | 0.608 |
| 2 | -1.297045 | -47.990693 | 14 | 26.3 | 0.34 | 7.9 | 44.5 | 25 | 0.346 |
| 3 | -1.385057 | -48.264777 | 10 | 28.3 | 0.305 | 4.45 | 60 | 7.5 | 0.533 |
| 4 | -1.327582 | -48.386946 | 18 | 27.3 | 0.265 | 1.6 | 17.5 | 65 | 0.218 |
| 5 | -1.341328 | -48.438631 | 14 | 28.85 | 0.19 | 1.4 | 38.5 | 0 | 0.228 |
| 6 | -1.307663 | -48.304744 | 4 | 26.3 | 0.66 | 4.99 | 40.5 | 70 | 0.438 |
| 7 | -1.88183 | -48.722986 | 25 | 27.7 | 0.4 | 2.1 | 0 | 0 | 0.174 |
| 8 | -1.425407 | -48.436614 | 23 | 30.1 | 1.09 | 6 | 65 | 20 | 0.793 |
| 9 | -1.292955 | -48.317737 | 3 | 28.15 | 1.2 | 7 | 9.5 | 30 | 0.224 |
| 10 | -1.347938 | -48.262962 | 19 | 28.55 | 0.8 | 8.05 | 10 | 0 | 0.322 |

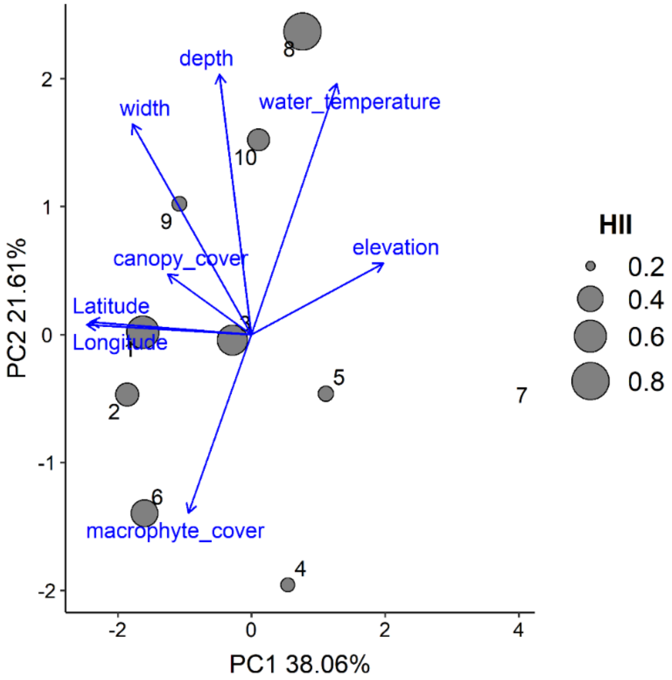

**Figure 3.** *Principal Component Analysis (PCA) results showing the environmental variables measured in the study. Bubble size represents the HII value.*

**Table 4.** *Environmental variables and their correlations with the first two axes of Principal Component Analysis (PCA)*

| | PC1 | PC2 | PC3 | PC4 |
|---|---|---|---|---|
| **Latitude** | -0.500 | 0.027 | 0.010 | -0.298 |
| **Longitude** | -0.511 | 0.021 | 0.311 | 0.235 |
| **Elevation** | 0.409 | 0.153 | 0.306 | 0.157 |
| **water_temperature** | 0.265 | 0.540 | 0.005 | -0.496 |
| **Depth** | -0.099 | 0.560 | -0.525 | -0.026 |
| **Width** | -0.370 | 0.453 | -0.057 | 0.447 |
| **canopy_cover** | -0.259 | 0.130 | 0.520 | -0.525 |
| **macrophyte_cover** | -0.195 | -0.384 | -0.510 | -0.332 |
| **Eigenvalues** | 3.045 | 1.729 | 1.382 | 0.919 |
| **Broken-stick** | 2.718 | 1.718 | 1.218 | 0.885 |
| **% explanation** | **38.060** | **21.610** | 17.57 | 11.49 |

We observed 21 species in the ten study sites (13 Anisoptera and 8 Zygoptera) (Table 5). The *K-values* for all recorded behaviors were less than 1 and were not significantly different from zero, indicating a low phylogenetic signal. Mating behavior showed a K-value = 0.50 (p=0.17), failed foraging K-value = 0.24 (p= 0.89), foraging K-value = 0.35 (p= 0.42), grooming K-value = 0.32 (p=0.58), inactivity K-value = 0.36 (p= 0.44), thermoregulation K-value = 0.55 (p=0.15), territory defense K-value = 0.28 (p= 0.74) and territory delimitation K-value = 0.49 (p=0.13).

**Table 5.** *Odonata species observed in each of the study sites.*

| | **S1** | **S2** | **S3** | **S4** | **S5** | **S6** | **S7** | **S8** | **S9** | **S10** |
|---|---|---|---|---|---|---|---|---|---|---|
| **ANISOPTERA** | | | | | | | | | | |
| *Brachymesia herbida* | | | | | | | X | | | |
| *Diastatops obscura* | | X | X | | | | | X | | X |
| *Erythrodiplax basalis* | | X | | | X | | | | X | X |
| *Erythrodiplax castanea* | | X | X | X | X | X | | | | |
| *Erythrodiplax fusca* | | X | X | X | | X | | | X | X |
| *Micrathyria sp.* | | | | X | | | | X | X | |
| *Oligoclada abbreviata* | X | | | | | | | | | X |
| *Orthemis concolor* | | | | X | X | | | X | X | |
| *Orthemis discolor* | | | | X | X | | X | X | X | X |
| *Pantala flavescens* | | | | | | | X | | | |
| *Perithemis lais* | X | | | X | | | X | X | | X |
| *Uracis imbuta* | | | | | | | | X | | |
| *Zenithoptera lanei* | | | | | | X | | | | |
| **ZYGOPTERA** | | | | | | | | | | |
| *Acanthagrion adustum* | | | | | | X | | X | X | X |
| *Argia oculata* | X | X | X | X | X | X | | X | | |
| *Chalcopteryx rutilans* | X | | | | | | | | | |
| *Epipleoneura metallica* | | X | X | X | | | | | | X |
| *Hetaerina sanguinea* | | | X | X | | | | | X | |
| *Mnesarete williamsoni* | X | | X | | | X | | | | |
| *Neoneura luzmarina* | | X | X | | | | | | | X |
| *Protoneura scintilla* | | | | | | | | | | X |
| **Total species observed per site** | **5** | **7** | **8** | **9** | **5** | **6** | **4** | **8** | **7** | **10** |

We found a positive relationship between relative frequencies of failed foraging and HII ($R^2$=0.46, *p*<0.01). In other words, in more urbanized sites, the frequency of failed foraging decreased (Fig. 4 A.).

We found no significant relationship between HII and the relative frequencies of foraging ($R^2$=0.002, *p*=0.96), grooming ($R^2$=0.3, *p*= 0.65), inactivity ($R^2$=0.024, *p*= 0.44), mating behavior ($R^2$=0.88, *p*=0.44), thermoregulation ($R^2$=0.004, *p*=0.96), territory delimitation ($R^2$= 0.092, *p*= 0.13) and territory defense ($R^2$= 0.037, p= 0.40) (Fig 4. B-H).

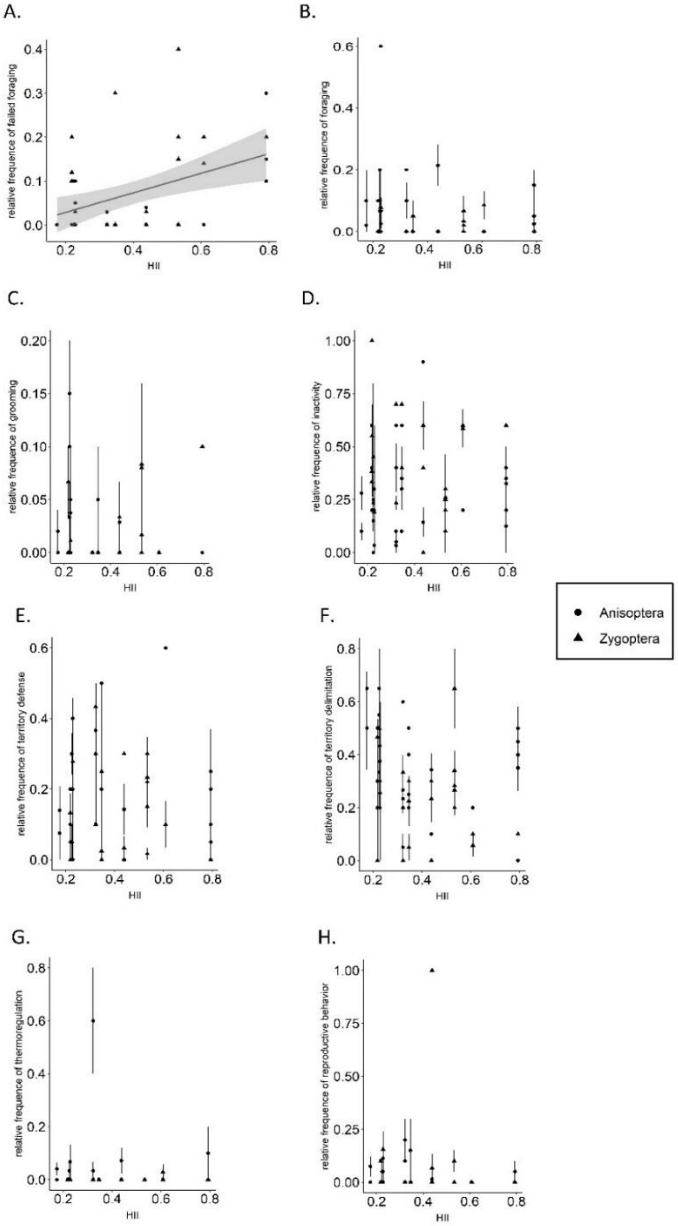

**Figure 4.** *Relationship between the Habitat Integrity Index (HII) and relative frequency of (A) failed foraging, (B) foraging, (C) grooming, (D) inactivity, (E) territory defense (F) territory delimitation, (G) thermoregulation and (H) mating behavior. Shaded area shows 95% confidence intervals and error bars indicate standard deviation (std).*

## DISCUSSION

Within the registered behaviors, failed foraging was the only behavior with a significant difference along the Habitat Integrity Index (HII) gradient. Our results indicate that dragonflies and damselflies were less likely to fail during prey catching in sites with low HII values (= more urbanized), a result that echoes those found in other insect orders (Jacquier et al., 2023) and also damselfly larvae (Tüzün et al., 2015). However, contrary to what we expected, we did not find differences in reproductive behaviors or territoriality along the urbanization gradient. Given this, one may wonder why it was only failed foraging what correlated with urbanization but not the other behaviors especially given that odonates have shown flexibility in such behaviors (i.e. the ability to learn among female morph to mate by ischnuran males; Fincke, 2004). Further research is needed here, especially in relation to mechanisms and constrains behind of adapting to rapidly changing environments (Lowry et al., 2013).

The lower frequency in which Odonata fail to catch prey in more urbanized sites (i.e. the more effective predation inside the cities) may be due to any of the following factors or a sum of all of them: 1) environmental changes, 2) changes in predator behaviour or 3) changes in prey communities. About environmental changes we know that in more urbanized environments the complexity of vegetation structure and environmental heterogeneity tends to be reduced (Threlfall et al., 2016). This implies that inside cities the vegetation is less complex in architecture so that odonate flights could be more direct and effective to catch preys. Furthermore, the difference in vegetation structure also generates changes in the intensity of light received by the odonates, which has been identified as a factor involved in the frequency of foraging (Shelly, 1982) and in the success rate during prey capture in odonates (Combes et al., 2012).

Odonates are generalist and very efficient predators: they capture any flying prey as long as this fits their mandible size (Corbet, 1999) with a success rate of close to 90% (Olberg et al., 2000; Combes et al., 2013; Gonzalez-Bellido et al., 2013). Several studies confirm that their nervous system is completely coordinated with their visual system, their muscles and their wings, so the motor response when intercepting prey is highly precise (Olberg et al., 2007; Olberg, 2012). Although the strategy to catch preys is a very stable behavior in this group, small and accurate changes that allow maintaining precision and reducing energy expenditure during foraging, could be favorable for odonates in highly modified environments such as cities. These behavioral adjustments imply the ability to learn that has been shown to occur at both the adult and larval stage when female damselflies learn whether to submerge during oviposition or not (Helebrandová et al., 2019) or damselfly larvae can learn the odour of predators (Wisenden et al., 1997).

On the other hand, our results could be a reflection of what is happening not with predator behaviors but with prey communities, as has been reported in other groups of predators (e.g. raptor birds) that must modify their hunting strategies due to changes in the communities of their prey inside urban areas (Møller, 2012). Different studies carried out in Odonata have reported that its capture success depend on the type of prey, its size and its population density (Combes et al., 2012; Combes et al., 2013). Although prey availability is abundant in urban ecosystems, prey diversity tends to decline, with urban streams often dominated by mosquitoes from the Chironomidae and Culicidae families (Kelly et al., 2019). This type of prey dominant in cities may present more uniform flight patterns and smaller body sizes, compared to prey communities in more urbanized places, both variables that facilitate the interception of these prey by odonates (Combes et al., 2013). Another factor that may be involved in capture success is prey density. Combes et al. (2012) found that the flies pursued by dragonflies when prey density is low fly more erratically while preys have more consistent flights patterns when prey density is high. It is known that in cities, mosquitos' densities can be much higher than in less urbanized places (Wilke et al., 2019). In this way, more consistent flight patterns under mosquitos' higher population densities would allow greater efficiency on the part of the odonates when catch them inside cities.

In odonates, as in any other animal, gain in mass associated with predation is inherently linked to fitness and survival (Marden, 1989; Anholt, 1991). Inquire into the different variables involved in the capture success and energy efficiency of odonates during their foraging behavior, considering dynamics not only of the predator but of the preys communities, will allow us to understand in a more comprehensive way what mechanisms are allowing odonates to survive within urban environments and to get on the list of winners after human disturbance. For example, the fact that some preys are highly abundant in urbanized areas (e.g., mosquitoes), that odonates do not compete inside cities for food apparently, and that these can increase their activity without apparent costs (e.g. attracting visual predators), would grant these predators to become part of the cities' biodiversity. These facts make it easier to consider these invertebrate predators as part of the protected fauna and enrich conservation programs in urban areas.

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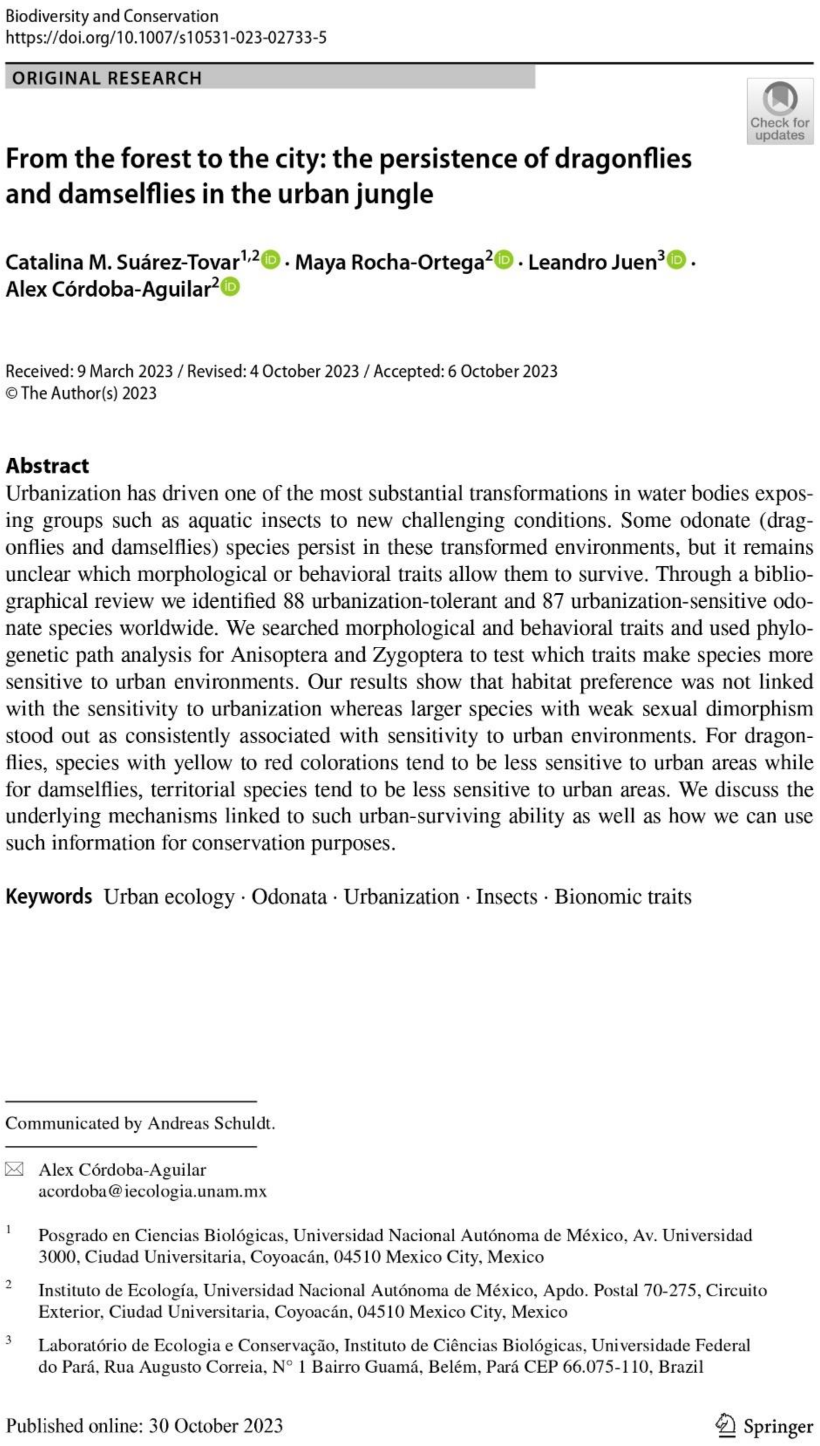
# CAPÍTULO IV

# From the forest to the city: the persistence of the dragonflies and damselflies in the urban jungle



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ORIGINAL RESEARCH

## From the forest to the city: the persistence of dragonflies and damselflies in the urban jungle

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### Abstract

Urbanization has driven one of the most substantial transformations in water bodies exposing groups such as aquatic insects to new challenging conditions. Some odonate (dragonflies and damselflies) species persist in these transformed environments, but it remains unclear which morphological or behavioral traits allow them to survive. Through a bibliographical review we identified 88 urbanization-tolerant and 87 urbanization-sensitive odonate species worldwide. We searched morphological and behavioral traits and used phylogenetic path analysis for Anisoptera and Zygoptera to test which traits make species more sensitive to urban environments. Our results show that habitat preference was not linked with the sensitivity to urbanization whereas larger species with weak sexual dimorphism stood out as consistently associated with sensitivity to urban environments. For dragonflies, species with yellow to red colorations tend to be less sensitive to urban areas while for damselflies, territorial species tend to be less sensitive to urban areas. We discuss the underlying mechanisms linked to such urban-surviving ability as well as how we can use such information for conservation purposes.

**Keywords** Urban ecology · Odonata · Urbanization · Insects · Bionomic traits

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## Introduction

The establishment of large cities in a relatively short time has promoted some of the largest and fastest environmental impacts (Johnson and Munshi-South 2017). Cities refer to the built infrastructure and land use change associated with increasing human population density (Schmitt and Burghardt 2021). The massive growth of urbanization has driven one of the most substantial transformations in water bodies among other habitats for multiple reasons (Goertzen and Suhling 2019; Johansson et al. 2019; Meland et al. 2019). In general, urban streams are subjected to toxins, temperature change, siltation, organic pollutants, and the replacement of riparian vegetation for concrete, which limits rainfall infiltration, modifying flow regimes and increasing runoff and flooding risk (Bogan et al. 2020; Walteros and Ramírez 2020).

The impact of urbanization on different biological groups vary depending on factors related to each city or particular taxa characteristics. With respect to cities, their geographical location, type of original biome, age of establishment, size, human population density and type of economic activities in each one, can generate different selective pressures on organisms (Szulkin 2020). For example, in temperate zones, the effect of urbanization is the opposite to that of dessert biomes. While in temperate zones, urbanization leads to increases in temperature and generates the urban heat island effect, in dessert areas, cities may be cooler than their natural surroundings (during the day) (Imhoff et al. 2010).

Species can respond to the selective pressures of urbanization at a population or individual level (Harris et al. 2013; Salomão et al. 2020). The evolution of environmental tolerance depends greatly on certain aspects of population structure such as the mating system or dispersal strategy, and is a function of both the between-individual variance in environmental optima and the within-individual breadth of adaptation (Lynch and Gabriel 1987). At the individual level, urban alterations exert strong direct and indirect selection on morphological (e.g. body size and body shape) and behavioral traits (e.g. mating behavior and habitat selection) of aquatic macroinvertebrates (Langerhans and Kern 2020; Resende et al. 2021). Thus, it is important to highlight that species respond differently to the same type of disturbance (Le Gall et al. 2018).Therefore, revealing how each species or group of species responds and what are the traits that allow them to survive in urban environments is essential to be able to understand what are the factors that affect each biological group and what is the best way to preserve the biodiversity that inhabits the city.

Despite all negative impacts that cities impose on aquatic ecosystems, urbanization can also lead to the creation of novel anthropogenic water bodies, such as canals, stormwater runoff basins, and recreational ponds in urban parks (Davies et al. 2008; Simaika et al. 2016; Ngiam et al. 2017). Not surprisingly, these novel habitats have become important reservoirs of biodiversity and, consequently, provide key ecosystem services such as cooling from urban heat, water filtration of pollutants, carbon sequestration, materials for construction and food sources (Ngiam et al. 2017; Bogan et al. 2020; Walteros and Ramírez 2020). Due to the availability of different types of aquatic environments (natural vs artificial; lotic vs lentic) in and around cities, some groups of habitat and feeding generalist aquatic organisms, such as Hemiptera, Diptera or Odonata, could find suitable habitats in cities to survive and reproduce in this new ecosystems (Vermonden et al. 2009; Monteiro-Júnior et al. 2014; Luke et al. 2017).

Odonata (Anisoptera [or dragonflies], Zygoptera [or damselflies], and Anisozygoptera), are typically labelled as forest animals (Cordero-Rivera 2006). However, this tendency to inhabit forests seems to be an ancestral condition: families such as Aeschnidae, Libellulidae, and Coenagrionidae, have basal genera (e. g. *Nannophlebia*, *Boyeria* and *Erythromma*) that appear to be forest-dwellers while derived genera (eg. *Anax*, *Pantala* and *Ischnura*) occur mostly in open habitats. This indicates that in odonates, life in open habitats (like farms or cities), is a recent adaptation (Paulson 2006). Although some studies have detected high richness and abundance of Odonata in forests (Rith-Najarian 1998; von Ellenrieder 2000), open and drastically transformed ecosystems such as cities show surprisingly high diversity (Jeanmougin et al. 2014; Luke et al. 2017). A great diversity of species have been recorded in remnants of lakes or wetlands located within cities around the world (Craves and O'Brien 2013; Goertzen and Suhling 2015). These species, mostly belonging to the families Coenagrionidae and Libellulidae, are capable of rapidly colonizing new or restored environments and can maintain viable populations in relatively small habitat remnants.

In Odonata, body size (Rocha-Ortega et al. 2020), body coloration (Sanmartín-Villar et al. 2017; Leveau 2021), the degree of color sexual dimorphism (Tüzün et al. 2017), territorial or reproductive behaviors and habitat selection (Resende et al. 2021) bear an important role when dealing with challenges imposed by human-modified habitats. Open areas would be filtering species on the basis of their body size, resulting in the loss of larger odonate species (Rocha-Ortega et al. 2020). Likewise, habitat modification could determine fitness alterations in species with a fixed coloration-based strategies, due to the spectrum change of the background (Sanmartín-Villar et al. 2017). Finally, warm adapted and more habitat generalist species deal fairly well with conditions of a modified environment (Ferreras-Romero et al. 2009; Resende et al. 2021).

In order to understand how some traits enable dragonfly or damselfly species to inhabit cities, we have reviewed analytically the different studies on the impact of urbanization on Odonata communities worldwide. Although there are already some reviews on this subject (see: Willigalla and Fartmann 2012; Villalobos-Jiménez et al. 2016, and Deacon and Samways 2021), these have not identified which odonate species are tolerating urban environments and what morphological or behavioral traits are linked to such tolerance. We expect that the species that we identify as sensitive to urban environments have larger sizes, compared to species from environments less altered by human, since small body sizes will facilitate heat exchange between the insect and its environment (Sanborn 2005) avoiding the possible warming generated by heat islands in cities. Regarding coloration, polymorphic species with duller colorations are expected to dominate urban environments (Leveau 2021). Finally, we expect that species that are more sensitive to urbanization tend to exhibit more territorial-based behaviors and live in lotic or phytotelmata environments with greater canopy cover (Resende et al. 2021; Goertzen and Suhling 2019; Rocha-Ortega et al. 2020).

## Methods

The data were compiled from a searching in Web of Science and Scopus databases focusing on the studies published between 1992 and 2022. The search criteria were "(urban* OR cit*) AND (Odonata OR dragonfl * OR damselfl *)". These terms were searched in titles, abstracts, or key words. In addition to this general literature search, we examined the two journals that specialize in this order: *Odonatologica* and *International Journal of Odonatology*. The survey was conducted in August 2022. The selection process of scientific papers was performed in four steps: (1) identification: We searched for scientific papers in WoS and Scopus using the aforementioned keywords; (2) first screening: We then read abstracts to select scientific articles that evaluated the impact of urban infrastructure on Odonata Communities. In this step, we also removed duplicated papers; (3) second screening: we read in full all selected papers from the previous step to extract the necessary data to answer the questions of our study; and (4) selection of papers for the scientometric analyses.

Of the almost 400 articles returned by the search, after reading the title and the abstract, and checking the keywords, we removed 330 papers from our dataset as they did not meet the requirements established in our study (first screening). Thus, we ended up with 70 articles that evaluated the impact of urban infrastructure on Odonata communities and changes in odonata communities in an urbanization gradient. For each manuscript we seek to collect the following information: (1) authors and year of publication; (2) city and country where the study was conducted, (3) geographical scope; (4) taxonomic scope; (5) habitat type (lotic or lentic); (6) the species richness registered (7) life cycle phase included in the study and (8) the type of impact that was found (on the abundance of individuals, change in richness or species composition) (Supplementary material 1).

Additionally, we identified species sensitive and tolerant to urbanization based on the results of the reviewed articles and linked some of the species' adaptations to urbanization. For the latter, we searched some morphological (body size, body color, strength of sexual dimorphism, polymorphisms by sex) and behavioral (territorial behavior, flight mode, type of mate guarding, and habitat preference) traits for identified species (Supplementary material 2). We collected this information from databases such as Odonata phenotypic database (Waller et al. 2019) and Encyclopedia of life (2022), and, when necessary, we looked for the information of each species individually. We used the non-information coding (NI) in cases where information for some of the traits were not found for each species.

## Phylogenetic data

A phylogeny for all species in our database was obtained by using the informatics tool Phylomatic (Webb and Donoghue 2005) (Fig. 1). Phylomatic uses the Odonata mega-tree (Waller and Svensson 2017) as a backbone onto which species are added based on their taxonomy. For families missing in Waller and Svensson, (2017), we took into account the fossil dating dates proposed by Suvorov et al. (2022), while nodes with no estimated dates were estimated by *bladj* algorithm in Phylocom (Webb et al. 2008).

## Analysis

To test how traits influence the ability of odonates to live in urban environments, we used phylogenetic path analysis (Hardenberg and Gonzalez-Voyer 2013). This analysis allows comparing causal hypotheses of the relationship among traits disentangling direct from indirect effects, while correcting for the non-independence of trait data due to common ancestry. Additionally, this approach deals with multicollinearity better than multivariate linear models, because partition the variance in the response among fewer predictors (Gonzalez-Voyer and von Hardenberg 2014).

In order to include the variables in the path analysis, we encoded each character as indicated in Supplementary material 3, assigning higher values to traits that might make species more sensitive to urbanization. We combine some of the variables to include them in the models. Habitat type and habitat openness together were considered as "Habitat preference", strength of sexual dimorphism and polymorphisms by sex was considered as "Sexual

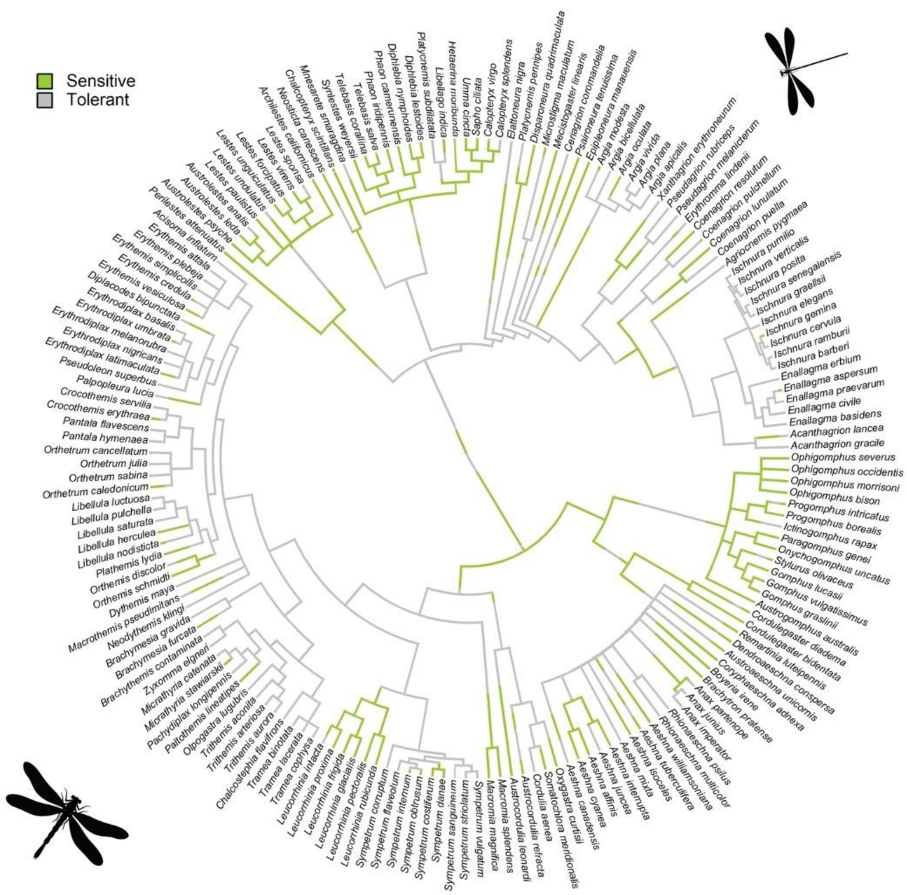

**Fig. 1** Phylogenetic tree assembled from the phylogeny hypothesis of Waller and Svensson (2017) with Odonata species identified as tolerant (gray) or sensitive (green) to urbanization

Dimorphism" and type of mate guarding, flight mode and territorial behavior was considered as "Territoriality". Then, we identified a taxon-specific model representing the relationships between body length, body colors, sexual dimorphism, territoriality, habitat preference and sensitivity to urbanization. In these models, we only considered significant paths, and we ensured that all conditional independencies (i.e., non-significant relationships between non-linked variables) were met (Gonzalez-Voyer and von Hardenberg 2014). To define the trait-only model for each suborder, we tested specific directional relationships based on a priori knowledge and expectations derived from published information. Phylogenetic path analysis models were built and tested in RStudio v. 1.1.456 (R Core Team 2018) using '*phylopath*' package (van der Bijl 2018).

## Results

A total of 70 papers related with the effect of urbanization on Odonata were considered (see Supplementary material 1): 21 were carried out in Europe, 20 in North America, 10 in Asia, 8 in Africa, 8 in South America, 2 in Oceania and 1 in Central America (Fig. 2). Thirty were carried out in lentic environments, 25 in lotic environments and 15 in lotic and lentic environments; 41 were performed using adults, 3 using adults and exuviae, 12 using adults and larvae, 1 using exuviae, 12 using larvae and 1 using larvae and exuviae (Supplementary material 1).

We identified 88 urbanization-tolerant species (Table 1) and 87 urbanization-sensitive species (Table 2, Fig. 1). The most common families reported as tolerant to urbanization were Aeshnidae, Libellulidae and Coenagrionidae (see Table 1), whilst the most common families reported as sensitive to urbanization were Lestidae, Calopterygidae, Gomphidae, as well as some specialist aeshnids and libellulids (see Table 2).

The phylogenetic path analyses indicated that some traits influenced the use urban areas for dragonflies and damselflies species (Fig. 3). The model obtained for Anisoptera explained 41.7% of variation (Table 3), while the model obtained for Zygoptera explained 44.8% of variation (Table 4). For both suborders, habitat preference was not linked to the sensitivity to urbanization, whereas larger species with weak sexual dimorphism stood out as consistently associated with sensitivity to urban environments (Fig. 3).

Furthermore, it was found that different traits indirectly influence the species' sensitivity to urban areas in each suborder. For dragonflies, body size is negatively related to body color, in turn, body color is positively related to the strength of sexual dimorphism and negatively to sensitivity to urbanization (Fig. 3). That is, although there is no direct relationship between body color and sensitivity to urbanization; smaller, yellow–red colourful, monomorphic species tend to be less sensitive to urban areas. Finally, for dragonflies, the territoriality of the species was not related to urbanization sensitivity.

For damselflies, territoriality is positively related to the strength of sexual dimorphism which is negatively related to sensitivity to urbanization (Fig. 3). Thus, with higher territoriality is greater sexual dimorphism and the species are less sensitive to

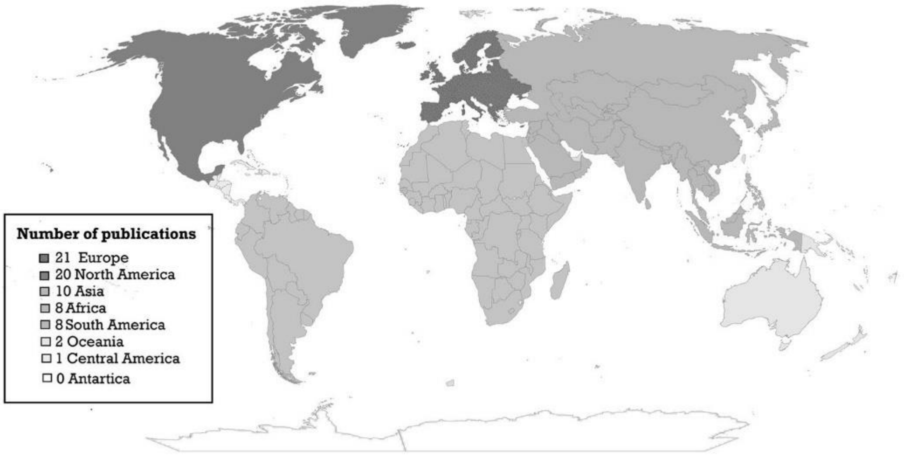

**Fig. 2** Number of works on the effect of urbanization in Odonata carried out in each continent

**Table 1** Odonata species tolerant to urbanization

| Species | Distribution | References |
|---|---|---|
| Anisoptera | | |
| Aeshnidae | | |
| *Aeshna canadensis* 1908 | North America | Perron and Pick (2020a) |
| *Aeshna cyanea* 1764 | Africa, Asia, Europe | Vilenica et al. (2020) |
| *Aeshna mixta* 1805 | Asia, Europe | Ferreras-Romero et al. (2009) |
| *Aeshna juncea* 1758 | Asia, Europe, North America | Villalobos-Jiménez et al. (2017), Bobrek (2020) |
| *Anax imperator* 1815 | Africa, Asia | Goertzen and Suhling, (2019), Perron and Pick, (2020a), Bobrek (2020) |
| *Anax junius* 1773 | Asia, Europe, North America | Perron and Pick (2020a), Perron and Pick (2020b), Ball-Damerow et al. (2014) |
| *Anax partenope* 1839 | Africa, Asia, Europe | Ferreras-Romero et al. (2009) |
| *Rhionaeschna multicolor* 1861 | North America | Benchalel et al. (2018) |
| *Rhionaeschna psilus* 1947 | North America, South America | Suárez-Tovar et al. (2022) |
| Libellulidae | | |
| *Acisoma inflatum* | Africa | Tippler et al. (2018) |
| *Brachymesia gravida* | North America | Husband and McIntyre (2021) |
| *Brachythemis contaminata* | Asia | Jere et al. (2020), Chen et al. (2020) |
| *Chalcostephia flavifrons* | Africa | Tippler et al. (2018) |
| *Crocothemis servilia* | Asia, North America | Jere et al. (2020) |
| *Diplacodes bipunctata* | Africa, Asia, Australia | Tippler et al. (2018) |
| *Dythemis maya* | North America, South America | Suárez-Tovar et al. (2022) |
| *Erythemis attala* | North America, South America | Sganzerla et al. (2021) |
| *Erythemis plebeja* | North America, South America | Suárez-Tovar et al. (2022) |
| *Erythemis simplicollis* | North America, South America | Perron and Pick (2020a) |
| *Erythrodiplax basalis* | South America | Monteiro Júnior et al. (2015) |
| *Erythrodiplax melanorubra* | South America | Sganzerla et al. (2021) |
| *Erythrodiplax nigricans* | South America | Sganzerla et al. (2021) |

**Table 1** (continued)

| Species | Distribution | References |
|---|---|---|
| *Leucorrhinia intacta* | North America | Perron and Pick (2020b) |
| *Libellula luctuosa* | North America | Perron and Pick (2020b) |
| *Libellula pulchella* | North America | Perron and Pick (2020b) |
| *Libellula saturata* | North America | Benchalel et al. (2018) |
| *Macrothemis pseudimitans* | North America, South America | Suárez-Tovar et al. (2022) |
| *Micrathyria catenata* | South America | Sganzerla et al. (2021) |
| *Neodythemis klingi* | Africa | Tippler et al. (2018), Seidu et al. (2018) |
| *Olpogastra lugubris* | Africa | Tippler et al. (2018), Seidu et al. (2018) |
| *Orthemis discolor* | North America, South America | Sganzerla et al. (2021) |
| *Orthetrum cancellatum* | Africa, Asia, Europe | Ferreras-Romero et al. (2009), Bobrek (2020), Buczyński et al. (2020) |
| *Orthetrum julia* | Africa | Tippler et al. (2018), Seidu et al. (2018) |
| *Orthetrum sabina* | Africa, Asia, Australia | Jere et al. (2020) |
| *Pantala flavescens* | Africa, Asia, Australia, Europe, North America, South America | Seidu et al.(2018), Ball-Damerow et al. (2014) |
| *Pantala hymenaea* | North America, South America | Benchalel et al. (2018), Ball-Damerow et al. (2014) |
| *Pachydiplax longipennis* | Europe, North America, South America | Benchalel et al. (2018) |
| *Palpopleura lucia* | Africa | Tippler et al. (2018) |
| *Plathemis lydia* | North America | Perron and Pick (2020a), Perron and Pick (2020b) |
| *Pseudoleon superbus* | Central America, North America | Suárez-Tovar et al. (2022) |
| *Sympetrum corruptum* | North America | Benchalel et al. (2018) |
| *Sympetrum flaveolum* | Asia, Europe | Buczyński et al. (2020) |
| *Sympetrum sanguineum* | Asia, Europe | Bobrek (2020), Buczyński et al. (2020) |
| *Sympetrum striolatum* | Africa, Asia, Europe | Goertzen and Suhling (2019), Buczyński et al. (2020) |
| *Sympetrum vulgatum* | Asia, Europe | Buczyński et al. (2020) |
| *Tramea binotata* | South America | Sganzerla et al. (2021) |
| *Tramea lacerata* | North America | Benchalel et al. (2018), Ball-Damerow et al. (2014) |

**Table 1** (continued)

| Species | Distribution | References |
|---|---|---|
| *Trithemis aconita* | Africa | Tippler et al. (2018) |
| *Trithemis arteriosa* | Africa, Asia, Europe | Tippler et al. (2018) |
| *Zyxomma elgneri* | Australia | Tippler et al. (2018) |
| Corduliidae | | |
| *Cordulia aenea* | Asia, Europe | Buczyński et al. (2020) |
| *Hemicordulia sp.* | Africa, Australia | Tippler et al. (2018) |
| Gomphidae | | |
| *Ictinogomphus rapax* | Asia | Jere et al. (2020) |
| Zygoptera | | |
| Coenagrionidae | | |
| *Acanthagrion gracile* | South America | Sganzerla et al. (2021) |
| *Acanthagrion lancea* | South America | Sganzerla et al. (2021) |
| *Agriocnemis pygmaea* | Asia, Australia | Chen et al. (2020) |
| *Argia apicalis* | North America | Husband and McIntyre (2021) |
| *Argia bicellulata* | South America | Monteiro Júnior et al. (2015) |
| *Argia plana* | North America | Suárez-Tovar et al. (2022) |
| *Argia vivida* | North America | Benchalel et al. (2018) |
| *Ceriagrion coromandelia* | Asia | Jere et al. (2020) |
| *Coenagrion puella* | Asia, Europe | Buczyński et al. (2020), Bobrek (2020), Husband and McIntyre (2021), Goertzen and Suhling (2019) |
| *Enallagma basidens* | North America | Husband and McIntyre (2021) |
| *Enallagma civile* | North America, South America | Perron and Pick (2020b), Benchalel et al. (2018) |
| *Enallagma erbium* | North America | Perron and Pick (2020b) |
| *Enallagma praevarum* | North America | Benchalel et al. (2018) |
| *Erythromma lindenii* | Africa, Europe | Ferreras-Romero et al. (2009) |
| *Ischnura barberi* | North America | Husband and McIntyre (2021) |

**Table 1** (continued)

| Species | Distribution | References |
|---|---|---|
| *Ischnura cervula* | North America | Benchalel et al. (2018) |
| *Ischnura elegans* | Asia, Europe | Goertzen and Suhling (2019), Bobrek (2020), Buczyński et al. (2020) |
| *Ischnura graellsii* | Africa, Europe | Ferreras-Romero et al. (2009), Husband and McIntyre (2021) |
| *Ischnura posita* | North America | Husband and McIntyre (2021) |
| *Ischnura pumilio* | Africa, Asia, Europe | Buczyński et al. (2020) |
| *Ischnura ramburii* | North America, South America | Husband and McIntyre (2021) |
| *Ischnura senegalensis* | Africa, Asia | Jere et al. (2020), Chen et al. (2020) |
| *Ischnura verticalis* | North America | Perron and Pick (2020b) |
| *Pseudagrion melanicterum* | Africa | Seidu et al. (2018) |
| *Pseudagrion rubriceps* | Asia | Jere et al. (2020) |
| *Xanthagrion erythroneurum* | Australia | Tippler et al. (2018) |
| *Telebasis salva* | North America, South America | Husband and McIntyre (2021) |
| Lestidae | | |
| *Lestes sponsa* | Asia, Europe | Buczyński et al. (2020) |
| *Lestes undulatus* | South America | Sganzerla et al. (2021) |
| *Austrolestes analis* | Australia | Tippler et al. (2018) |
| Platycnemididae | | |
| *Platycnemis pennipes* | Asia, Europe | Villalobos-Jiménez et al. (2017), Buczyński et al. (2020) |
| *Platycnemis subdilatata* | Africa | Husband and McIntyre (2021) |
| Protoneuridae | | |
| *Elattoneura nigra* | Africa | Seidu et al. (2018) |
| Calopterygidae | | |
| *Calopteryx splendens* | Asia, Europe | Vilenica et al. (2020), Buczyński et al. (2020) |
| *Calopteryx virgo* | Asia, Europe | Buczyński et al. (2020) |
| *Mnesarete smaragdina* | South America | Pereira-Moura et al. (2021) |

**Table 2** Odonata species sensitive to urban stressors

| Species | Distribution | References |
|---|---|---|
| Anisoptera | | |
| Aeshnidae | | |
| *Aeshna affinis* | Africa, Asia, Europe | Bobrek (2020) |
| *Aeshna interrupta* | North America | Ball-Damerow et al. (2014) |
| *Aeshna isoceles* | Africa, Asia Europe | Bobrek (2020) |
| *Aeshna tuberculifera* | North America | Perron and Pick (2020b) |
| *Aeshna williamsoniana* | Central America, North America | Suárez-Tovar et al. (2022) |
| *Boyeria irene* | Africa, Europe | Ferreras-Romero et al. (2009) |
| *Brachytron pratense* | Asia, Europe | Bobrek (2020) |
| *Coryphaeschna adnexa* | North America, South America | Suárez-Tovar et al. (2022) |
| *Remartinia luteipennis* | North America, South America | Suárez-Tovar et al. (2022) |
| Austrocorduliidae | | |
| *Austrocordulia leonardi* | Australia | Tippler et al. (2018) |
| *Austrocordulia refracta* | Australia | Tippler et al. (2018) |
| Brachytronidae | | |
| *Dendroaeschna conspersa* | Australia | Tippler et al. (2018) |
| Cordulegastridae | | |
| *Cordulegaster bidentata* | Africa, Europe | Dolný et al. (2021) |
| *Cordulegaster diadema* | North America | Suárez-Tovar et al. (2022) |
| Gomphidae | | |
| *Austrogomphus australis* | Australia | Tippler et al. (2018) |
| *Gomphus graslinii* | Europe | Ferreras-Romero et al. (2009) |
| *Gomphus lucasii* | Africa | Benchalel et al. (2018) |
| *Gomphus vulgatissimus* | Europe | Vilenica et al. (2020) |
| *Ophigomphus bison* | North America | Ball-Damerow et al. (2014) |

**Table 2** (continued)

| Species | Distribution | References |
|---|---|---|
| *Ophigomphus morrisoni* | North America | Ball-Damerow et al. (2014) |
| *Ophigomphus occidentis* | North America | Ball-Damerow et al. (2014) |
| *Ophigomphus severus* | North America | Ball-Damerow et al. (2014) |
| *Onychogomphus uncatus* | Africa, Europe | Ferreras-Romero et al. (2009) |
| *Paragomphus genei* | Africa, Europe | Benchalel et al. (2018) |
| *Progomphus borealis* | North America | Ball-Damerow et al. (2014) |
| *Progomphus intricatus* | South America | Sganzerla et al. (2021) |
| *Stylurus olivaceus* | North America | Ball-Damerow et al. (2014) |
| Corduliidae | | |
| *Cordulia sp.* | Asia, Europe, North America | Perron and Pick (2020a) |
| *Dorocordulia sp.* | North America | Perron and Pick (2020a) |
| *Oxygastra curtisii* | Europe | Ferreras-Romero et al. (2009) |
| *Somatochlora meridionalis* | Europe | Vilenica et al. (2020) |
| Libellulidae | | |
| *Brachymesia furcata* | North America, South America | Sganzerla et al. (2021), Suárez-Tovar et al. (2022) |
| *Crocothemis erythraea* | Africa, Asia, Australia, Europe | Bobrek (2020) |
| *Erythemis credula* | South America | Sganzerla et al. (2021) |
| *Erythemis vesiculosa* | North America, South America | Suárez-Tovar et al. (2022) |
| *Erythrodiplax latimaculata* | South America | Sganzerla et al. (2021) |
| *Erythrodiplax umbrata* | North America, South America | Sganzerla et al. (2021) |
| *Ladona sp.* | North America, Europe | Perron and Pick (2020a) |
| *Leucorrhinia frigida* | North America | Perron and Pick (2020b) |
| *Leucorrhinia glacialis* | North America | Ball-Damerow et al. (2014) |
| *Leucorrhinia pectoralis* | Europe | Bobrek (2020) |
| *Leucorrhinia proxima* | North America | Perron and Pick (2020b) |

**Table 2** (continued)

| Species | Distribution | References |
|---|---|---|
| *Leucorrhinia rubicunda* | Asia, Europe | Bobrek (2020) |
| *Libellula herculea* | North America, South America | Sganzerla et al. (2021) |
| *Libellula nodisticta* | North America | Ball-Damerow et al. (2014) |
| *Micrathyria stawiarskii* | South America | Sganzerla et al. (2021) |
| *Orthemis schmidti* | South America | Sganzerla et al. (2021) |
| *Orthetrum caledonicum* | Australia | Tippler et al. (2018) |
| *Paltothemis lineatipes* | North America, South America | Suárez-Tovar et al. (2022) |
| *Sympetrum costiferum* | North America | Ball-Damerow et al. (2014) |
| *Sympetrum danae* | Asia, Europe, North America | Ball-Damerow et al. (2014) |
| *Sympetrum internum* | North America | Perron and Pick (2020b) |
| *Sympetrum obtrusum* | North America | Ball-Damerow et al. (2014) |
| *Tramea cophysa* | South America | Sganzerla et al. (2021) |
| *Trithemis aurora* | Asia | Jere et al. (2020) |
| Macromiidae | | |
| *Macromia magnifica* | Central America, North America | Ball-Damerow et al. (2014) |
| *Macromia splendens* | Europe | Ferreras-Romero et al. (2009) |
| Telephlebiidae | | |
| *Austroaeschna unicornis* | Australia | Tippler et al. (2018) |
| Zygoptera | | |
| Chlorocyphidae | | |
| *Libellago indica* | Asia | Jere et al. (2020) |
| Calopterygidae | | |
| *Hetaerina moribunda* | South America | Monteiro Júnior et al. (2015) |
| *Phaon camerunensis* | Africa | Seidu et al. (2018) |
| *Phaon iridipennis* | Africa | Seidu et al. (2018) |

**Table 2** (continued)

| Species | Distribution | References |
|---|---|---|
| *Sapho ciliata* | Africa | Seidu et al. (2018) |
| *Umma cincta* | Africa | Seidu et al. (2018) |
| Coenagrionidae | | |
| *Argia modesta* | South America | Villalobos-Jiménez et al. (2017) |
| *Argia oculata* | Central America, North America, South America | Suárez-Tovar et al. (2022) |
| *Coenagrion lunulatum* | Asia, Europe | Buczyński et al. (2020) |
| *Coenagrion pulchellum* | Asia, Europe | Bobrek (2020) |
| *Coenagrion resolutum* | North America | Ball-Damerow et al. (2014) |
| *Enallagma aspersum* | North America | Perron and Pick (2020b) |
| *Ischnura gemina* | North America | Ball-Damerow et al. (2014) |
| *Mecistogaster linearis* | South America | Monteiro Júnior et al. (2015) |
| *Microstigma maculatum* | South America | Monteiro Júnior et al. (2015) |
| *Telebasis corallina* | South America | Sganzerla et al. (2021) |
| Isostictidae | | |
| *Neosticta canescens* | Australia | Tippler et al. (2018) |
| Lestidae | | |
| *Archilestes californicus* | North America, South America | Ball-Damerow et al. (2014) |
| *Austrolestes leda* | Australia | Tippler et al. (2018) |
| *Austrolestes psyche* | Australia | Tippler et al. (2018) |
| *Lestes forcipatus* | North America | Perron and Pick (2020b) |
| *Lestes paulistus* | South America | Sganzerla et al. (2021) |
| *Lestes unguiculatus* | North America | Ball-Damerow et al. (2014) |
| *Lestes virens* | Africa, Asia, Europe | Bobrek (2020) |
| Lestoideidae | | |
| *Diphlebia lestoides* | Australia | Tippler et al. (2018) |

**Table 2** (continued)

| Species | Distribution | References |
|---|---|---|
| *Diphlebia nymphoides* | Australia | Tippler et al. (2018) |
| Perilestidae | | |
| *Perilestes attenuatus* | South America | Monteiro Júnior et al. (2015) |
| Protoneuridae | | |
| *Epipleoneura manauensis* | South America | Monteiro Júnior et al. (2015) |
| *Disparoneura quadrimaculata* | Asia | Jere et al. (2020) |
| *Psaironeura tenuissima* | South America | Monteiro Júnior et al. (2015), Pereira-Moura et al. (2021) |
| Synlestidae | | |
| *Synlestes weyersii* | Australia | Tippler et al. (2018) |
| Polythoridae | | |
| *Chalcopteryx scintillans* | South America | Monteiro Júnior et al. (2015) |

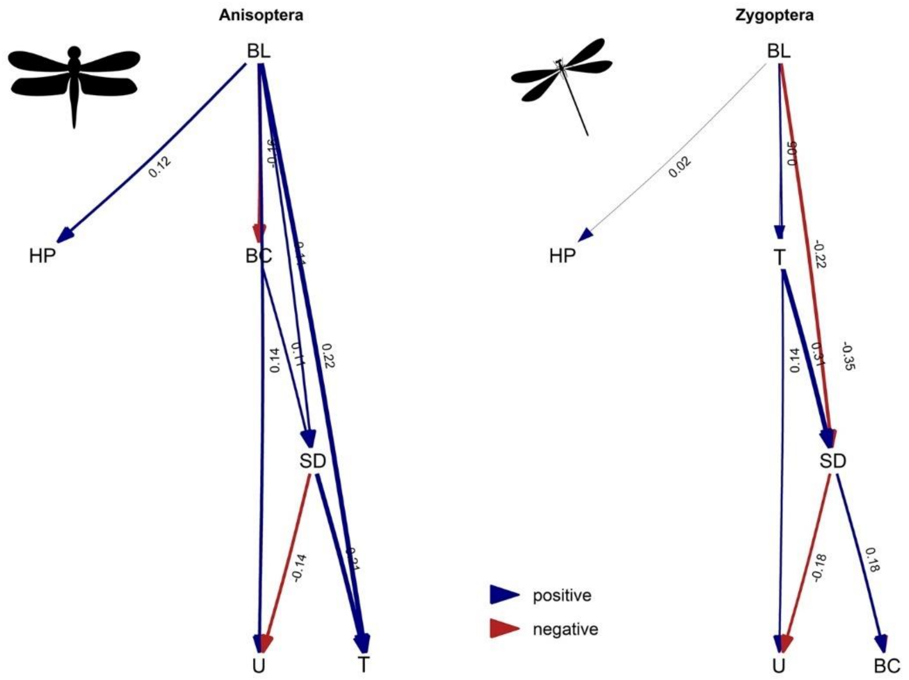

**Fig. 3** Average causal models obtained for relationship between species traits and sensitivity to urbanization. Blue indicates positive relationships, red indicate negative relationships. Values represent standardized path coefficients reported in Tables 3 and 4. *BL* body length, *HP* habitat preference, *BC* body colors, *SD* color sexual dimorphism, *T* territoriality, *U* sensitivity to urbanization

**Table 3** Standardized path coefficients (Coeff.) with standard errors (SE) between significant explanatory variables of Anisoptera species estimated through phylogenetic path analysis. Coefficients indicate whether significant relationships between variables have a positive or negative trend

| | Coeff. | SE |
|---|---|---|
| Body length-body color | −0.162 | 0.096 |
| Body length-habitat preference | 0.125 | 0.127 |
| Body length-sexual dimorphism | 0.111 | 0.126 |
| Body length-territoriality | 0.218 | 0.125 |
| Body color-sexual dimorphism | 0.113 | 0.096 |
| Sexual dimorphisms-territoriality | 0.211 | 0.089 |
| Body length-urbanization | 0.140 | 0.117 |
| Sexual dimorphisms-urbanization | −0.140 | 0.092 |

urbanization. Nevertheless, the relationship between territoriality and sexual dimorphism is indirect to the sensitivity to urbanization. Finally, for damselflies, body color was not related to urbanization sensitivity.

**Table 4** Standardized path coefficients (Coeff.) with standard errors (SE) between significant explanatory variables of Zygoptera species estimated through phylogenetic path analysis. Coefficients indicate whether significant relationships between variables have a positive or negative trend

| | Coeff. | SE |
|---|---|---|
| Body length-body color | −0.354 | 0.127 |
| Body length-habitat preference | 0.016 | 0.140 |
| Body length-sexual dimorphism | −0.223 | 0.118 |
| Body length-territoriality | 0.055 | 0.140 |
| Body color-sexual dimorphism | 0.180 | 0.087 |
| Sexual dimorphism-territoriality | 0.312 | 0.118 |
| Body length-urbanization | 0.136 | 0.129 |
| Sexual dimorphisms-urbanization | −0.180 | 0.120 |

## Discussion

We found that some traits prompt species to persist in urban environments. According to our expectations, in the studied odonate species, sensitivity to urbanization is linked to morphology. Sensitive species having both a larger sizes and weaker sexual dimorphism, compared to the more tolerant species. This result coincides with previous studies on Odonata (Brito et al. 2021; Rocha-Ortega et al. 2020) and other insects (Shahabuddin and Ponte 2005; Theodorou et al. 2021), where species with larger individuals are the most vulnerable ones in the face of environmental disturbance. Likewise, species with weak sexual dimorphism were identified as more sensitive to urbanization. This is also consistent with previous studies where changes in the environment (e.g. loss of vegetation) could determine fitness costs in monomorphic species, due to the spectrum change of the background (Sanmartín-Villar et al. 2017).

Moreover, contrary to our expectations, we found that for dragonflies, duller colorations were indirectly associated with sensitivity to urbanization, while yellow and red colors were more associated with tolerance to urban areas. In damselflies, no relationship was found between body color and sensitivity to urbanization. In this latter suborder, we found an indirect relationship between territoriality and sensitivity to urbanization, with less territorial species being more sensitive to urbanization. In dragonflies, no such relationship was found for these last variables. Finally, we did not find any association between habitat preference and sensitivity to urbanization.

Why would larger species be more vulnerable in urbanized environments? Possibly, smaller species can quickly recolonized empty source and sink patches inside cities, whereas that building up a large body requires long developmental periods, more food and, consequently, there are more risks associated to such demands (Suhonen et al. 2014, 2022). Other explanation is that having a greater dispersal capacity, larger species search habitats with better conditions around cities, implying a reduced chance to be recorded within urbanized areas (e.g. Prescott and Eason 2018). Regarding sexual color dimorphism, previous studies in Lepidoptera (Franzén et al. 2020) and Odonata (Sanmartín-Villar et al. 2017) have reported that dimorphic or polymorphic species may have an advantage in urban environments with visual heterogeneity created by light pollution and non-native plants. The presence of more than one color morph in the species could facilitate their adaptation to the city, considering the changing environment in which they will have to hide from potential prey or predators.

Different types of stressors influence different species inside an order (e.g. Luke et al. 2017; Seidu et al. 2018; Huikkonen et al. 2019; Jere et al. 2020). In relation to this, we found that the traits identified in species that are tolerant to urbanization are different for dragonflies and damselflies. In dragonflies, urban species tend to have red and yellow colors. The open habitats that occur in cities could promote these reddish colors in dragonflies. As for the mechanism of color production, ommochromes are responsible for red and yellow coloration, and have been associated to antioxidant production (McGraw 2005), and UV ray protection (Needham 1974; Cooper 2010). For example, in *Megalagrion calliphya* a higher frequency of males and females with red coloration was found in environments with higher solar radiation due to the fact that both sexes acquire coloration to protect themselves from solar rays (Cooper 2010). Although this is reported in a damselfly species, the mechanism that may be behind our finding for dragonflies may have a similar basis to that which explains the maintenance of the red color in places with high solar radiation. In this way, the red and yellow dragonflies are more likely to endure the higher incidence of solar radiation typical of cities, through the antioxidant and protective function of the cuticle-embedded ommochromes.

Contrary to what we expected, urban damselflies tend to present more territorial behaviors compared to their counterparts in conserved sites. In Odonata, the selection and defense of a territory is determined by the presence of optimal sites for reproduction and ovipositing (Kohli et al. 2020). Our results could indicate that the territorial behaviors in damselflies become more important within cities, where there may be fewer available sites for couples to copulate or for females to oviposit, therefore those few available sites are defended more intensively. Results similar to this have been reported for birds, which defend their territories more vigorously in cities than their rural counterpart (Davies and Sewall 2016).

Although the results obtained in this study allow us to have a first approximation of which traits allow Odonata species to adapt to cities, it is important to consider that the lack of information for some of the evaluated traits is a limitation of our study. In addition, we include information for 175 species of the nearly 6400 Odonata species described so far, and we included traits for adults and not for larvae of the different species. Therefore, continuing to generate information about the response of these species to urbanization is essential to confirm the trends we detected.

There is also a limitation in terms of the regions of the world that have been most studied in this topic. Within the papers we reviewed, most studies were carried out in Europe and North America which are places with a large history of urbanization, yet they are less diverse than the tropical region. This finding implies a bias in our results, since we were not able to control for differences in urbanization times, size, or geographic location of cities. For instance, due to physiological adaptations responding to its evolutionary history, species in subtropical and temperate zones might have stronger responses to urban heat islands than species in tropical zones (Langerhans and Kern 2020). In damselflies species, it has been reported that forests can become even more important at lower latitudes so that species could be more sensitive to urbanization there, compared to high latitude species (Paulson 2006). To correct such bias, we suggest that the impact of urbanization on dragonfly and damselfly diversity be assessed with greater emphasis on species-rich areas such as Asia, Africa, and South America.

Given that urbanization is a phenomenon that grows by leaps and bounds every day, we must understand their ecological implications immediately. It is important to know odonate responses since they are an important link in aquatic food webs (Knight et al. 2005) and export a large part of aquatic productivity to terrestrial environments (Popova et al. 2017), both very important functions for the functioning of ecosystems. To know the dynamics of these aquatic insects in cities (transformed environments with little possibility of returning to their initial state) allow us to predict future distribution trends and consequently design appropriate conservation strategies focused on this group and applicable to other groups of aquatic insects. In this regard, management of urban freshwater habitats should account not only the aesthetic part but ecological needs to benefit people and biodiversity, two fundamental components within cities (Ngiam et al. 2017; Goertzen and Suhling 2019; Huikkonen et al. 2019). Additionally, we should be able to recognize biodiversity hotspots where future anthropic activities should be avoided, and to continue building the necessary theory to propose the most suitable conservation plans for our beloved odonates: creatures of the forest and the city!

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**Author contributions** All authors contributed to the study conception and design. The search for articles and literature review were performed by CMS-T. Analyses were performed by MR-O. The first draft of the manuscript was written by CMS-T and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

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# Supplementary material

## **Table 1.** *Reviewed papers*

| Authors | Paper Title | Country | City | Geographical scope | Taxonomic scope | Habitat type | species richness registered | Life cycle phase | Level of detected changes |
|---|---|---|---|---|---|---|---|---|---|
| **(Steytler and Samways, 1995)** | Biotope selection by adult male dragonflies (Odonata) at an artificial lake created for insect conservation in South Africa | South Africa | Pietermaritzburg | Local | Odonata | lentic | 26 | adults | species richness |
| **(Samways and Steytler, 1996)** | Dragonfly (Odonata) distribution patterns in urban and forest landscapes, and recommendations for riparian management | South Africa | Pietermaritzburg | local | Odonata | lotic | 26 | adults | species richness and abundance |
| **(Solimini *et al*., 1997)** | Life history and species composition of the damselfly assemblage along the urban tract of a river in central Italy | Italy | Rome | local | Odonata_Coenagrionidae | lotic | 6 | larvae | species richness, species composition and life history patterns |
| **(Azrina *et al*., 2006)** | Anthropogenic impacts on the distribution and biodiversity of benthic macroinvertebrates and water quality of the Langat River, Peninsular Malaysia | Malaysia | Langat river_Selangor | local | Macrobenthic invertebrates | lotic | 5 | larvae | species richness, diversity and eveness |
| **(Bried and Ervin, 2006)** | Abundance patterns of dragonflies along a wetland buffer | USA | Mississippi | local | Anisoptera | lentic | 7 | adults | abundance |
| **(Oppel, 2006)** | Comparison of two Odonata communities from a natural and a modified rainforest in Papua New Guinea | Papua New Guinea | Herowana | local | Odonata | lotic and lentic | 78 | adults | species richness and species composition |
| **(Ferreras-Romero *et al*., 2009)** | Implications of anthropogenic disturbance factors on the Odonata assemblage in a Mediterranean fluvial system | Spain | Andalusia | local | Odonata | lotic | 36 | adults and larvae | species richness, species composition |

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|---|---|---|---|---|---|---|---|---|---|
| **(Lubertazzi and Ginsberg, 2010)** | Emerging dragonfly diversity at small Rhode Island (U.S.A.) wetlands along an urbanization gradient | USA | Rhode Island | local | Odonata | lentic | 20 | exuviae | species richness and evenness |
| **(Silva *et al*., 2010)** | Adult odonate abundance and community assemblage measures as indicators of stream ecological integrity: A case study | Brazil | Viçosa | local | Odonata | lotic | 28 | adults | species richness and species composition |
| **(Craves and O'Brien, 2013)** | The Odonata of Wayne County, MI: Inspiration for Renewed Monitoring of Urban Areas | USA | Wayne County | local | Odonata | lotic and lentic | 90 | adults and larvae | species richness |
| **(Goertzen and Suhling, 2013)** | Promoting dragonfly diversity in cities: major determinants and implications for urban pond design | Germany | Dortmund | local | Odonata | lentic | 30 | adults and larvae | species richness, abundance and assemblage structure |
| **(Jomoc *et al*., 2013)** | Species richness of Odonata in selected wetland areas of Cagayan de Oro and Bukidnon, Philippines | Philippines | Manolo Fortich, Sumilao, Impasug-ong, Damulog, Bugo and Tablon | regional | Odonata | lentic | 38 | adults | species richness |
| **(Ball-Damerow *et al*., 2014b)** | Local and regional factors influencing assemblages of dragonflies and damselflies (Odonata) in California and Nevada | USA | California and Nevada | regional | Odonata | lotic and lentic | 83 | adults | species richness |
| **(Ball-Damerow *et al*., 2014a)** | Changes in occurrence, richness, and biological traits of dragonflies and damselflies (Odonata) in California and Nevada over the past century | USA | California and Nevada | local | Odonata | lotic and lentic | 69 | adults | species richness, occurrence, similarity |
| **(Jeanmougin *et al*., 2014)** | Fine-scale urbanization affects Odonata species diversity in ponds of a megacity (Paris, France) | Francia | Paris | local | Odonata | lentic | 17 | adults and exuviae | species composition |
| **(Monteiro-Júnior *et al*., 2014)** | Effects of urbanization on stream habitats and associated adult dragonfly and damselfly communities in central Brazilian Amazonia | Brazil | Manaus | local | Odonata | lotic | 60 | adults | species composition |

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|---|---|---|---|---|---|---|---|---|---|
| **(Goertzen and Suhling, 2015)** | Central European cities maintain substantial dragonfly species richness - a chance for biodiversity conservation? | Austria, the Czech Republic, Germany, and Switzerland | Central Europe cities (from the Netherlands to Poland) | regional | Odonata | lotic and lentic | 81 | adults and larvae | species richness, frequence of ocurrence |
| **(Monteiro Júnior *et al*., 2015)** | Analysis of urban impacts on aquatic habitats in the central Amazon basin: Adult odonates as bioindicators of environmental quality | Brazil | Manaus | local | Odonata | lotic | 60 | adults | species richness |
| **(Docile *et al*., 2016)** | Macroinvertebrate diversity loss in urban streams from tropical forests | Brazil | Teresópolis | regional | Macroinvertebrates | lotic | 5 | larvae | species richness, species composition, and abundance |
| **(Foglini, 2016)** | Odonata next-door: An updated check-list of two parks in the Northern Milan outskirt (Lombardy, Italy) | Italy | Milan | regional | Odonata | lentic | 27 | adults | species richness |
| **(Koparde, 2016)** | Damsels in distress-seasons, habitat structure and water pollution changes damselfly diversity and assemblage in urban wetlands | India | Pune | local | Odonata | lentic | 44 | adults | species richness |
| **(Nayak and Roy, 2016)** | An observation on the Odonata fauna of the Asansol-Durgapur Industrial Area, Burdwan, West Bengal, India | India | Burdwan District | local | Odonata | lotic | 57 | adults | species richness, occurrence and distribution pattern |
| **(Cuevas-Yáñez *et al*., 2017)** | Large-scale human environmental intervention is related to a richness reduction in Mexican odonates | Mexico | Mexico | national | Odonata | lotic and lentic | 275 | adults | species richness |
| **(Luke *et al*., 2017)** | The impacts of habitat disturbance on adult and larval dragonflies (Odonata) in rainforest streams in Sabah, Malaysian Borneo | Malaysia | Sabah | local | Odonata | lotic | 49 | adults and larvae | species richness, community composition |
| **(Ngiam *et al*., 2017)** | A balancing act in urban social-ecology: human appreciation, ponds and dragonflies | England | London | local | Odonata | lentic | 15 | adults | species richness |
| **(Ramos *et al*., 2017)** | Odonata Diversity and Synanthropy in Urban Areas: A Case Study in | Argentina | Avellaneda | local | Odonata | lotic | 20 | adults | species richness, beta diversity |

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|---|---|---|---|---|---|---|---|---|---|
| | Avellaneda City, Buenos Aires, Argentina | | | | | | | | |
| **(Tüzün *et al*., 2017)** | Sexual selection reinforces a higher flight endurance in urban damselflies | Belgium | Flanders | local | Odonata | lentic | 1 | adults | phenotypic traits |
| **(Villalobos-Jiménez *et al*., 2017)** | Environmental noise reduces predation rate in an aquatic invertebrate | England | Liverpool | experimental | Odonata | lentic _ laboratory | 1 | larvae | impacts on trophic interactions |
| **(Benchalel *et al*., 2018)** | Odonata of Wadi Bouarroug (northeastern Algeria) and environmental determinants of their distribution | Algeria | El Kala_Wadi Bouarroug | local | Odonata | lotic | 19 | adults | species richness |
| **(Holtmann *et al*., 2018)** | Stormwater ponds promote dragonfly (Odonata) species richness and density in urban areas | Germany | Münster | local | Odonata | lentic | 26 | adults and exuvia | species richness, species composition, and abundance |
| **(Kietzka *et al*., 2018)** | Comparative effects of urban and agricultural land transformation on Odonata assemblages in a biodiversity hotspot | South Africa | Western Cape Province | local | Odonata | lotic | 37 | adults | species richness and species composition |
| **(Prescott and Eason, 2018)** | Lentic and lotic odonate communities and the factors that influence them in urban versus rural landscapes | USA | Louisville | local | Odonata | lotic and lentic | 50 | adults | species richness and species composition |
| **(Seidu *et al*., 2018)** | Odonata assemblages along an anthropogenic disturbance gradient in Ghana's Eastern Region | Ghana | Akim | local | Odonata | lotic | 51 | adults | species richness and species composition |
| **(Sellam-Bouattoura *et al*., 2018)** | Odonata of the Mazafran hydrosystem: Distribution and community structure | Algeria | Koléa | local | Odonata | lotic | 15 | adults | species richness and abundance |
| **(Tippler *et al*., 2018)** | Are Odonata nymph adversely affected by impaired water quality in urban streams | Australia | Sydney | local | Macroinvertebrates | lotic | 33 | larvae | species richness and species composition |

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|---|---|---|---|---|---|---|---|---|---|
| **(Chien *et al.*, 2019)** | Appropriate management practices help enhance odonate species richness of small ponds in peri-urban landscapes | Taiwan | Taoyuan | regional | Odonata | lentic | 21 | adults | species richness and abundance |
| **(Córdoba-Aguilar and Rocha-Ortega, 2019)** | Damselfly (Odonata: Calopterygidae) population decline in an urbanizing watershed | Mexico | Tehuixtla | local | Odonata | lotic | 1 | adults and larvae | abundance, duration of adults exposed directly to sunlight, lipid content, muscle mass, and egg survival |
| **(Goertzen and Suhling, 2019)** | Urbanization versus other land use: Diverging effects on dragonfly communities in Germany | Germany | Germany cities | national | Odonata | lotic and lentic | 72 | adults and larvae | species richness, species composition |
| **(Hjalmarson and Patten, 2019)** | Win–win urban ecology: near-home fishing promotes diversity of Odonata | USA | Norman, Cleveland County | local | Odonata | lotic and lentic | 63 | adults | species richness and abundance |
| **(Holtmann *et al.*, 2019)** | Odonate assemblages of urban stormwater ponds: the conservation value depends on pond type | Germany | Münster | local | Odonata | lentic | 21 | adults and exuvia | species richness and exuviae density |
| **(Huikkonen *et al.*, 2019)** | Heterogenic aquatic vegetation promotes abundance and species richness of Odonata (Insecta) in constructed agricultural wetlands | Finland | Central Finland | local | Odonata | lentic | 17 | larvae and exuviae | species richness and abundance |
| **(Johansson *et al.*, 2019)** | Environmental variables drive differences in the beta diversity of dragonfly assemblages among urban stormwater ponds | Sweden | Upsala | local | Odonata | lentic | 31 | adults | beta diversity |
| **(Mangahas *et al.*, 2019)** | Chronic Exposure to High Concentrations of Road Salt Decreases the Immune Response of Dragonfly Larvae | Canada | Ontario | local | Odonata | lentic | 1 | larvae | immune response |
| **(Meland *et al.*, 2019)** | Road related pollutants induced DNA damage in dragonfly nymphs (Odonata, | Noruega | Oslo | local | Odonata | lentic | 1 | larvae | DNA damage |

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| | Anisoptera) living in highway sedimentation ponds | | | | | | | | |
| **(Rocha-Ortega *et al*., 2019)** | Spatial and temporal effects of land use change as potential drivers of odonate community composition but not species richness | México | México | national | Odonata | lotic and lentic | 254 | adults | species richness, body size and individual species' response |
| **(Villalobos-Jiménez and Hassall, 2019)** | Wing shape patterns among urban, suburban, and rural populations of Ischnura elegans (Odonata: Coenagrionidae) | England | Leeds and Bradford | local | Odonata | lentic | 1 | adults | phenotypic patterns of flight |
| **(Bogan *et al*., 2020)** | If you build it, they will come: Rapid colonization by dragonflies in a new effluent-dependent river reach | USA | Tucson_Santa Curz river | local | Odonata | lotic | 50 | adults | species richness, species composition, and colonization patterns |
| **(Blanckenberg *et al*., 2020)** | Protected and un-protected urban wetlands have similar aquatic macroinvertebrate communities: A case study from the Cape Flats Sand Fynbos region of southern Africa | South Africa | Cape Town | local | Macroinvertebrates | lentic | 3 | larvae | species richness, diversity and community structure |
| **(Bobrek, 2020)** | High biodiversity in a City Centre: Odonatofauna in an abandoned limestone quarry | Poland | Kraków | local | Odonata | lentic | 37 | adults | species richness and abundance |
| **(Buczyński *et al*., 2020)** | Dragonflies (Odonata) of the city of Lublin (Eastern Poland) | Poland | Lublin | local | Odonata | lotic and lentic | 54 | adults and larvae | diversity and abundance |
| **(Chen *et al*., 2020)** | Influences of Physical Vegetation Management on Odonata Abundance in Urbanized Ecosystem: a Case Study in Northern Taiwan | Taiwan | New Taipei | local | Odonata | lentic | 19 | adults and larvae | species richness and abundance |
| **(Jere *et al*., 2020)** | Assessing the response of odonates (dragonflies and damselflies) to a tropical urbanization gradient | India | Pune | local | Odonata | lotic | 15 | adults | species richness |

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|---|---|---|---|---|---|---|---|---|---|
| **(Perron and Pick, 2020b)** | Water quality effects on dragonfly and damselfly nymph communities: A comparison of urban and natural ponds | Canada | Otawa | regional | Odonata | lentic | 22 | larvae | species richness and abundance |
| **(Perron and Pick, 2020a)** | Stormwater ponds as habitat for Odonata in urban areas: the importance of obligate wetland plant species | Canada | Ottawaand Gatineau | local | Odonata | lentic | 52 | adults | species richness and abundance |
| **(Sharma and Kumar, 2020)** | Odonata diversity in and around Vadodara, Gujarat, India | India | Vadodara | local | Odonata | lotic and lentic | 38 | adults | species richness |
| **(Vilenica *et al.*, 2020)** | Odonata assemblages in anthropogenically impacted lotic habitats | Croatia | Pannonian lowland ecoregion | local | Odonata | lotic | 19 | larvae | species richness and species composition |
| **(Worthen and Chamlee, 2020)** | Determinants of adult odonate community structure at several spatial scales: effects of habitat type and landscape context | USA | Pickens and Greenville | regional | Odonata | lotic and lentic | 45 | adults | species richness, abundance and community structure |
| **(Husband and McIntyre, 2021)** | Urban areas create refugia for odonates in a semi-arid region | USA | Brownfield, Levelland, Lubbock, Muleshoe, and Plainview | regional | Odonata | lentic | 33 | adults | species richness |
| **(Pereira-Moura *et al*., 2021)** | Environmental integrity as a modeler of the composition of the Odonata community | Brazil | Santarém | local | Odonata | lotic | 35 | adults | species richness, abundance and community composition |
| **(Dolný *et al*., 2021)** | Effects of Landscape Patterns and Their Changes to Species Richness, Species Composition, and the Conservation Value of Odonates (Insecta) | Czech Republic | Czech Republic | national | Odonata | lotic and lentic | 68 | adults | species richness |
| **(Perron *et al*., 2021)** | Plants, water quality and land cover as drivers of Odonata assemblages in urban ponds | Canada | Ottawa and Gatineau | regional | Odonata | lentic | 56 | adults and larvae | species richness and species composition |
| **(Sganzerla *et al*., 2021)** | Effects of urbanization on the fauna of odonata on the coast of southern Brazil | Brazil | municipalities of Rio Grande do Sul | regional | Odonata | lentic | 38 | adults | species richness, abundance and community structure |

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|---|---|---|---|---|---|---|---|---|---|
| **(Strungaru *et al*., 2021)** | Response of aquatic macroinvertebrates communities to multiple anthropogenic stressors in a lowland tributary river | Romania | Iasi | local | Macroinvertebrates | lotic | 4 | larvae | species richness and species composition |
| **(Worthen *et al*., 2021)** | Downstream changes in odonate (Insecta: Odonata) communities along a suburban to urban gradient: Untangling natural and anthropogenic effects | USA | Greenville | local | Odonata | lotic | 42 | adults and larvae | species richness and abundance |
| **(Getnet, *et al*., 2022)** | Macroinvertebrate community structure and diversity in relation to environmental factors in wetlands of the lower Gilgel Abay River catchment, Ethiopia | Ethiopia | Amhara | local | Macroinvertebrates | lentic | 5 | larvae | family richness |
| **(Guadalquiver *et al*., 2022)** | Odonatofauna in the freshwater system of Kibalabag, Malaybalay City, Bukidnon, Philippines | Philippines | Malaybalay | local | Odonata | lotic and lentic | 25 | adults | species richness and species composition |
| **(Lozano *et al*., 2022)** | Recovery of local dragonfly diversity following restoration of an artificial lake in an urban area near Buenos Aires | Argentina | Avellaneda | local | Odonata | lentic | 31 | adults | species richness |
| **(Maldonado-Benítez *et al*., 2022)** | Effects of urbanization on Odonata assemblages in tropical island streams in San Juan, Puerto Rico | Puerto Rico | San Juan | local | Odonata | lotic | 14 | adults | species richness, abundance and community structure |
| **(Suárez-Tovar *et al*., 2022)** | Resilient dragons: Exploring Odonata communities in an urbanization gradient | Mexico | Cuernavaca | local | Odonata | lotic | 45 | adults | species richness, abundance and species composition |
| **(Zhang *et al*., 2022)** | Chronic Road Salt Exposure Across Life Stages and The Interactive Effects of Warming and Salinity in a Semiaquatic Insect | Canada | Ontario | experimental | Odonata | lentic _ laboratory | 1 | adults and larvae | life history transitions and carry-over effects |

**Supplementary Table S2** *Traits of each species recorded in the literature.*

| Species | Urban propensity | Body length | Body colors | Body colors type | Sexual Dimorphism | Polymorphisms by sex | Mate guarding | Flight Mode | Territoriality | Habitat openness | Habitat preference |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aeshna_affinis* | Sensitive | 71.5 | blue_green_yellow_brown | pigment | strong | NI | contact | flier | NI | semi | lentic |
| *Aeshna_interrupta* | Sensitive | 66.5 | blue_yellow_brown | pigment | strong | females | NI | flier | T | closed | lentic |
| *Aeshna_isoceles* | Sensitive | 67 | yellow_orange_green | pigment | weak | weak | none | percher | T | NI | lentic_and_lotic |
| *Aeshna_tuberculifera* | Sensitive | 75.5 | brown_green_blue | pigment | weak | females | none | flier | NI | closed | lentic |
| *Aeshna_williamsoniana* | Sensitive | 71 | brown_green_black_blue | pigment | weak | monomorphic | NI | NI | NI | closed | lotic |
| *Archilestes_californicus* | Sensitive | 51 | brown_blue_white | pigment_pruinescence_structural | strong | NI | contact | percher | T | closed_open | lentic_and_lotic |
| *Argia_modesta* | Sensitive | 35 | blue_black | pigment | strong | NI | contact | percher | NI | NI | lotic |
| *Argia_oculata* | Sensitive | 37 | black_blue_purple | pigment | strong | females | contact | percher | NI | closed_open | lotic |
| *Austroaeschna_unicornis* | Sensitive | 67.5 | brown_yellow_blue | pigment | weak | NI | NI | NI | NI | NI | lotic |
| *Austrocordulia_leonardi* | Sensitive | 65 | brown_yellow_green | pigment | strong | NI | NI | NI | NI | NI | lotic |
| *Austrocordulia_refracta* | Sensitive | 50 | brown_yellow_black | pigment | weak | NI | NI | NI | NI | NI | lotic |
| *Austrogomphus_australis* | Sensitive | 45 | yellow_black | pigment | weak | NI | NI | NI | NI | NI | lentic_and_lotic |
| *Austrolestes_leda* | Sensitive | 37.5 | blue_black_brown | pigment | strong | NI | NI | NI | NI | NI | lentic |
| *Austrolestes_psyche* | Sensitive | 32 | black_blue_black | pigment | weak | NI | NI | NI | NI | NI | lentic |
| *Boyeria_irene* | Sensitive | 67 | brown_green | pigment | weak | females | contact | flier | NI | closed | lentic_and_lotic |
| *Brachymesia_furcata* | Sensitive | 43.5 | red_brown | pigment | strong | females | noncontact | percher_flier | T | open | lentic |
| *Brachytron_pratense* | Sensitive | 58.5 | blue_green_brown | pigment | strong | NI | NI | flier | NI | closed | lentic |
| *Chalcopteryx_scintillans* | Sensitive | 26.6 | black_yellow | pigment | weak | monomorphic | noncontact | NI | T | closed | lotic |
| *Coenagrion_lunulatum* | Sensitive | 32 | blue_black_green | pigment | strong | NI | contact | percher | NI | closed | lentic |
| *Coenagrion_pulchellum* | Sensitive | 38.25 | blue_black | pigment | weak | NI | contact | percher | NT | semi | lentic |
| *Coenagrion_resolutum* | Sensitive | 30 | blue_black_green | pigment | strong | NI | contact | percher | NI | semi | lentic |
| *Cordulegaster_bidentata* | Sensitive | 73.5 | brown_yellow_green | pigment | weak | NI | none | percher | NI | closed_open | lotic |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cordulegaster_diadema* | Sensitive | 81 | yellow_black | pigment | medium | monomorphic | none | percher_flier | NT | closed_open | lotic |
| *Coryphaeschna_adnexa* | Sensitive | 67.75 | green_brown_blue | pigment | weak | monomorphic | none | flier | T | closed | lentic_and_lotic |
| *Crocothemis_erythraea* | Sensitive | 39 | red | pigment | strong | females | noncontact | percher | T | semi | lentic_and_lotic |
| *Dendroaeschna_conspersa* | Sensitive | 40 | brown_blue_green | pigment | weak | NI | NI | NI | NI | NI | lotic |
| *Diphlebia_lestoides* | Sensitive | 28 | blue_black | pigment | weak | NI | NI | NI | NI | NI | lotic |
| *Diphlebia_nymphoides* | Sensitive | 33.7 | blue_black | pigment | strong | NI | NI | NI | NI | NI | lotic |
| *Disparoneura_quadrimaculata* | Sensitive | 35.34 | brown_red_black | pigment | strong | monomorphic | NI | percher | NI | NI | lotic |
| *Enallagma_aspersum* | Sensitive | 30.5 | blue_black | pigment | weak | monomorphic | noncontact | percher | NI | semi | lentic |
| *Epipleoneura_manauensis* | Sensitive | 26.5 | green_black_brown | pigment | weak | NI | NI | NI | NI | NI | lotic |
| *Erythemis_credula* | Sensitive | 34 | black_brown_purple | pigment_pruinescence | strong | monomorphic | NI | percher_flier | NI | NI | lentic |
| *Erythemis_vesiculosa* | Sensitive | 60.25 | green_brown | pigment | weak | monomorphic | NI | percher_flier | T | closed | lentic_and_lotic |
| *Erythrodiplax_latimaculata* | Sensitive | 48.62 | black_brown | pigment_pruinescence | weak | NI | NI | percher | NI | NI | lentic |
| *Erythrodiplax_umbrata* | Sensitive | 45.25 | brown_yellow | pigment | strong | females | noncontact | percher_flier | T | closed_open | lentic_and_lotic |
| *Gomphus_graslinii* | Sensitive | 49 | yellow_black | pigment | strong | NI | none | percher | NT | semi | lotic |
| *Gomphus_lucasii* | Sensitive | 46.5 | green_black | pigment | weak | NI | NI | percher | NT | closed | lotic |
| *Gomphus_vulgatissimus* | Sensitive | 47.5 | yellow_black | pigment | strong | NI | NI | percher | T | semi | lotic |
| *Hetaerina_moribunda* | Sensitive | 45.7 | black_brown_green | pigment | weak | NI | NI | NI | NI | NI | lentic_and_lotic |
| *Ischnura_gemina* | Sensitive | 25.5 | black_green_blue | pigment | strong | females | noncontact | percher | NT | open | lotic |
| *Lestes_forcipatus* | Sensitive | 37.5 | black_blue_yellow | structural_pruinescence | weak | monomorphic | contact | percher | NI | semi | lentic |
| *Lestes_paulistus* | Sensitive | 45.5 | blue_green_brown | pigment_structural | weak | monomorphic | NI | NI | NI | NI | lentic |
| *Lestes_unguiculatus* | Sensitive | 37.5 | blue_green_brown | pigment_pruinescence_structural | strong | males | contact | percher | NT | open | lentic |
| *Lestes_virens* | Sensitive | 36 | green_blue_brown | pigment_pruinescence_structural | weak | monomoprhic | contact | percher | NT | closed_open | lentic |
| *Leucorrhinia_frigida* | Sensitive | 30 | black_white | pigment_pruinescence | strong | females | noncontact | percher | T | open | lentic |
| *Leucorrhinia_glacialis* | Sensitive | 33.5 | black_red_white | pigment | strong | females | NI | percher | NI | closed | lentic |
| *Leucorrhinia_pectoralis* | Sensitive | 35.5 | black_red_brown | pigment | strong | NI | contact | flier | T | semi | lentic |
| *Leucorrhinia_proxima* | Sensitive | 34.5 | black_red_white_brown | pigment_pruinescence | strong | NI | NI | percher | T | closed | lentic |
| *Leucorrhinia_rubicunda* | Sensitive | 34.75 | red_black | pigment_pruinescence | strong | NI | contact | percher | T | closed_open | lentic |
| *Libellago_indica* | Sensitive | 24.5 | yellow_black | pigment | strong | NI | NI | NI | NI | NI | lotic |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| *Libellula_herculea* | Sensitive | 57.25 | red_white_brown | pigment_pruinescence | strong | monomorphic | noncontact | percher | T | closed | lotic |
| *Libellula_nodisticta* | Sensitive | 49 | brown_yellow_blue | pigment_pruinescence | strong | monomorphic | contact | percher | T | open | lentic_and_lotic |
| *Macromia_magnifica* | Sensitive | 64.25 | brown_yellow | pigment_structural | weak | monomorphic | NI | NI | NI | closed | lentic_and_lotic |
| *Macromia_splendens* | Sensitive | 72.5 | yellow_green_brown | pigment_structural | strong | NI | none | flier | T | closed_open | lotic |
| *Mecistogaster_linearis* | Sensitive | 80.5 | black_green | pigment | medium | females | NI | NI | NI | closed | phytotelmata |
| *Micrathyria_stawiarskii* | Sensitive | 32 | black_white_blue | pigment_pruinescence_structural | weak | NI | NI | percher | NI | NI | lentic |
| *Microstigma_maculatum* | Sensitive | 120 | black_brown | pigment | weak | NI | NI | NI | NI | NI | phytotelmata |
| *Neosticta_canescens* | Sensitive | 25 | black_white_green_blue | pigment_pruinescence | weak | NI | NI | NI | NI | NI | lotic |
| *Onychogomphus_uncatus* | Sensitive | 51.5 | yellow_black | pigment | weak | NI | NI | percher | NI | closed | lotic |
| *Ophigomphus_bison* | Sensitive | 41.75 | yellow_black_green | pigment | medium | monomorphic | NI | percher | NI | closed | lotic |
| *Ophigomphus_morrisoni* | Sensitive | 52.5 | yellow_black_green | pigment | weak | monomorphic | NI | percher_flier | NI | open | lentic_and_lotic |
| *Ophigomphus_occidentis* | Sensitive | 41.75 | yellow_black_green | pigment | weak | monomorphic | NI | percher | NI | semi | lentic_and_lotic |
| *Ophigomphus_severus* | Sensitive | 75.5 | yellow_green_black_brown | pigment | weak | monomorphic | NI | percher | NI | closed_open | lentic_and_lotic |
| *Orthemis_schmidti* | Sensitive | 52 | red_brown_pink | pigment | strong | NI | NI | percher | NI | semi | lentic |
| *Orthetrum_caledonicum* | Sensitive | 45 | brown_blue | pruinescence | strong | NI | NI | NI | NI | NI | lentic_and_lotic |
| *Oxygastra_curtisii* | Sensitive | 50.5 | brown_yellow_green | pigment_structural | medium | NI | none | flier | T | semi | lentic_and_lotic |
| *Paltothemis_lineatipes* | Sensitive | 50.5 | red_black_brown | pigment | weak | monomorphic | noncontact | percher_flier | T | semi | lotic |
| *Paragomphus_genei* | Sensitive | 41 | green_black_brown | pigment | medium | NI | NI | percher | NI | open | lentic_and_lotic |
| *Perilestes_attenuatus* | Sensitive | 53.1 | black_green_blue | pigment_structural | weak | monomorphic | NI | NI | NI | NI | lotic |
| *Phaon_camerunensis* | Sensitive | 68.1 | green_brown | pigment_structural | medium | NI | NI | NI | NI | closed | lotic |
| *Phaon_iridipennis* | Sensitive | 70 | green_brown | pigment_structural | medium | NI | NI | percher | NT | closed | lotic |
| *Progomphus_borealis* | Sensitive | 51 | black_white | pigment | weak | NI | NI | percher | NI | open | lentic_and_lotic |
| *Progomphus_intricatus* | Sensitive | 47.48 | green_brown_blue | pigment | medium | NI | NI | NI | NI | NI | lentic |
| *Psaironeura_tenuissima* | Sensitive | 32 | red_black_green | pigment_structural | strong | monomorphic | NI | NI | NI | closed | lotic |
| *Remartinia_luteipennis* | Sensitive | 78 | black_green_blue | pigment | weak | monomorphic | none | flier | NI | closed_open | lentic_and_lotic |
| *Sapho_ciliata* | Sensitive | 58.7 | green_blue | pigment | strong | NI | NI | NI | NI | open | lotic |
| *Somatochlora_meridionalis* | Sensitive | 56 | green | structural | weak | NI | none | flier | T | closed_open | lotic |
| *Stylurus_olivaceus* | Sensitive | 58 | yellow_green_black_brown | pigment | weak | monomorphic | NI | percher_flier | NI | closed | lotic |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sympetrum_costiferum* | Sensitive | 34 | red_black_brown | pigment | strong | females | contact | percher_flier | NI | NI | lentic |
| *Sympetrum_danae* | Sensitive | 31.5 | yellow_black | pigment_structural | strong | males | contact | percher | NT | semi | lentic_and_lotic |
| *Sympetrum_internum* | Sensitive | 33.5 | red_black | pigment | strong | females | contact | percher | T | semi | ephemeral |
| *Sympetrum_obtrusum* | Sensitive | 35 | red_black_white_brown | pigment | strong | females | noncontact | percher | NI | closed | lentic |
| *Synlestes_weyersii* | Sensitive | 57.1 | yellow_black_green_blue | pigment_structural | medium | NI | NI | percher | NI | NI | lotic |
| *Telebasis_corallina* | Sensitive | 31.180 | red_black_orange_green_yellow | pigment | strong | monomorphic | NI | NI | NT | NI | lentic |
| *Tramea_cophysa* | Sensitive | 46.5 | yellow_green_black_brown | pigment_structural | strong | NI | NI | percher_flier | NI | open | lentic |
| *Trithemis_aurora* | Sensitive | 37.5 | red_black_pink | pigment_pruinescence | strong | monomorphic | NI | percher | NI | NI | lentic_and_lotic |
| *Umma_cincta* | Sensitive | 54.6 | green_bue | pigment | weak | NI | NI | NI | NI | NI | lotic |
| *Acanthagrion_gracile* | Tolerant | 29.3 | blue_black | pigment | weak | monomorphic | contact | NI | NT | semi | lentic_and_lotic |
| *Acanthagrion_lancea* | Tolerant | 32.13 | blue_black_green | pigment | weak | NI | contact | percher | NI | NI | lentic |
| *Acisoma_inflatum* | Tolerant | 24 | black_white_yellow_brown | pigment | weak | NI | NI | NI | NI | NI | lentic_and_lotic |
| *Aeshna_canadensis* | Tolerant | 71 | blue_brown | pigment | strong | NI | contact | percher_flier | T | NI | lentic |
| *Aeshna_cyanea* | Tolerant | 71.5 | brown_yellow_blue | pigment | strong | NI | none | flier | T | closed | lentic |
| *Aeshna_juncea* | Tolerant | 75.5 | brown_green_blue | pigment | strong | females | none | flier | T | closed_open | lentic |
| *Aeshna_mixta* | Tolerant | 42.5 | blue_brown_green | pigment | strong | NI | contact | flier | NI | semi | lentic_and_lotic |
| *Agriocnemis_pygmaea* | Tolerant | 22 | orange_yellow_black_green | pigment | strong | females | NI | flier | T | NI | lentic |
| *Anax_imperator* | Tolerant | 76.5 | blue_black_green | pigment | strong | monomorphic | none | flier | NI | closed | lentic |
| *Anax_junius* | Tolerant | 74 | blue_green_brown_black | pigment | strong | females | contact | flier | NI | semi | lentic_and_lotic |
| *Anax_partenope* | Tolerant | 68.5 | yellow_black_green_blue | pigment | strong | monomorphic | contact | flier | NI | semi | lentic_and_lotic |
| *Argia_apicalis* | Tolerant | 36.5 | blue_black_gray | pigment | strong | females | contact | percher | T | closed_open | lentic_and_lotic |
| *Argia_bicellulata* | Tolerant | 23.4 | blue_black_purple | pigment | strong | NI | NI | percher | NI | NI | lentic |
| *Argia_plana* | Tolerant | 36.5 | blue_black_purple | pigment | strong | females | contact | percher | NT | closed_open | lotic |
| *Argia_vivida* | Tolerant | 29.75 | blue_black_purple | pigment | strong | females | NI | percher | T | semi | lentic_and_lotic |
| *Austrolestes_analis* | Tolerant | 38 | black_brown_blue | pigment | strong | NI | NI | NI | NI | NI | lentic |
| *Brachymesia_gravida* | Tolerant | 52 | orange_brown_black | pigment_pruinescence | strong | monomorphic | noncontact | percher_flier | T | open | lentic |
| *Brachythemis_contaminata* | Tolerant | 33 | orange_red_black | pigment | strong | monomorphic | NI | percher_flier | T | open | lentic |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| *Calopteryx_splendens* | Tolerant | 46.5 | green | structural | strong | females | noncontact | percher | T | semi | lotic |
| *Calopteryx_virgo* | Tolerant | 47 | blue | structural | strong | NI | NI | percher | T | closed | lotic |
| *Ceriagrion_coromandelia* | Tolerant | 36 | yellow_orange_green | pigment | strong | monomorphic | NI | flier | T | NI | lotic |
| *Chalcostephia_flavifrons* | Tolerant | 44.25 | blue_yellow | structural_pruinescence | strong | monomorphic | NI | percher | NI | closed | lentic |
| *Coenagrion_puella* | Tolerant | 34 | blue_black | pigment | strong | females | contact | percher | NT | semi | lentic_and_lotic |
| *Cordulia_aenea* | Tolerant | 51 | brown_green_yellow | pigment_structural | weak | NI | none | flier | T | closed | lentic |
| *Crocothemis_servilia* | Tolerant | 35.5 | red_brown | pigment | strong | monomorphic | noncontact | percher | T | open | lentic_and_lotic |
| *Diplacodes_bipunctata* | Tolerant | 30.5 | red_brown_yellow | pigment | strong | monomorphic | NI | flier | NI | NI | lentic_and_lotic |
| *Dythemis_maya* | Tolerant | 44 | red | pigment | strong | monomorphic | noncontact | percher_flier | T | NI | lotic |
| *Elattoneura_nigra* | Tolerant | 31.9 | black_blue | pigment | weak | NI | NI | NI | NI | semi | lotic |
| *Enallagma_basidens* | Tolerant | 24.5 | blue_black | pigment | strong | monomorphic | contact | percher | NI | semi | lentic_and_lotic |
| *Enallagma_civile* | Tolerant | 33.5 | blue_black | pigment | strong | females | noncontact | percher | T | semi | lentic_and_lotic |
| *Enallagma_erbium* | Tolerant | 29.5 | blue_black | pigment | strong | females | noncontact | percher | NT | semi | lentic |
| *Enallagma_praevarum* | Tolerant | 45.25 | blue_black | pigment | strong | females | none | percher | NT | semi | lentic_and_lotic |
| *Erythemis_attala* | Tolerant | 43 | black_brown_yellow | pigment | strong | monomorphic | NI | percher | T | semi | lentic_and_lotic |
| *Erythemis_plebeja* | Tolerant | 44.5 | black_brown | pigment | strong | monomorphic | noncontact | percher | T | open | lentic_and_lotic |
| *Erythemis_simplicollis* | Tolerant | 41 | brown_blue_green | pruinescence | strong | monomorphic | noncontact | percher | T | closed_open | lentic_and_lotic |
| *Erythrodiplax_basalis* | Tolerant | 26 | yellow_black_blue | pigment_pruinescence | medium | monomorphic | NI | NI | NI | NI | lotic |
| *Erythrodiplax_melanorubra* | Tolerant | 36 | orange_brown_blue | pigment_pruinescence | strong | NI | NI | percher | NI | NI | lentic_and_lotic |
| *Erythrodiplax_nigricans* | Tolerant | 34 | yellow_black_brown | pigment | weak | NI | NI | NI | NI | NI | lentic |
| *Erythromma_lindenii* | Tolerant | 43.5 | blue_black | pigment | strong | NI | NI | percher | NI | semi | lentic_and_lotic |
| *Ictinogomphus_rapax* | Tolerant | 57 | yellow_black_brown | pigment | weak | monomorphic | NI | percher_flier | T | semi | lentic_and_lotic |
| *Ischnura_barberi* | Tolerant | 31.5 | blue_orange_brown | pigment | strong | females | none | percher | NT | semi | lentic |
| *Ischnura_cervula* | Tolerant | 27.5 | black_blue | pigment | strong | females | none | percher | NI | semi | lentic |
| *Ischnura_elegans* | Tolerant | 32.25 | black_blue_green | pigment | weak | females | none | percher | NT | open | lentic |
| *Ischnura_graellsii* | Tolerant | 29 | black_blue_brown | pigment_structural | strong | females | none | percher | NT | semi | lentic_and_lotic |
| *Ischnura_posita* | Tolerant | 25 | black_green | pigment_pruinescence | strong | monomorphic | none | percher | NT | closed | lentic_and_lotic |

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|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ischnura_pumilio* | Tolerant | 29 | black_green | pigment | strong | females | none | percher | NT | open | lentic |
| *Ischnura_ramburii* | Tolerant | 31.5 | orange_black_green_blue | pigment | strong | females | none | percher | NT | closed_open | lentic |
| *Ischnura_senegalensis* | Tolerant | 29 | yellow_black_green_blue | pigment | strong | females | none | percher | NT | semi | lentic_and_lotic |
| *Ischnura_verticalis* | Tolerant | 26.5 | black_green_blue | pigment | strong | females | none | percher | NT | semi | lentic_and_lotic |
| *Lestes_sponsa* | Tolerant | 37 | green_brown_blue | pigment_pruinescence | weak | monomorphic | contact | percher | NT | semi | lentic |
| *Lestes_undulatus* | Tolerant | 41.2 | blue_green_brown | pigment_structural | weak | NI | contact | NI | NI | NI | lentic |
| *Leucorrhinia_intacta* | Tolerant | 31 | yellow_black | pigment | weak | females | noncontact | percher | T | open | lentic |
| *Libellula_luctuosa* | Tolerant | 46 | white_brown | pigment_pruinescence | strong | females | noncontact | percher_flier | T | closed_open | lentic_and_lotic |
| *Libellula_pulchella* | Tolerant | 54.5 | brown_yellow_green | pigment_pruinescence | strong | monomorphic | noncontact | percher_flier | T | open | lentic_and_lotic |
| *Libellula_saturata* | Tolerant | 55 | orange_brown | pigment | strong | females | noncontact | percher | T | NI | lentic_and_lotic |
| *Macrothemis_pseudimitans* | Tolerant | 39 | white_green_black_brown_blue | pigment_pruinescence_structural | weak | monomorphic | noncontact | flier | T | closed_open | lotic |
| *Micrathyria_catenata* | Tolerant | 33.5 | black_yellow_brown_blue | pigment_pruinescence | strong | monomorphic | NI | percher_flier | T | semi | lentic_and_lotic |
| *Mnesarete_smaragdina* | Tolerant | 35.2 | green | structural | medium | monomorphic | NI | NI | NI | NI | lotic |
| *Neodythemis_klingi* | Tolerant | 28.8 | brown:yellow_black | pigment | weak | NI | NI | percher | NI | closed | lotic |
| *Olpogastra_lugubris* | Tolerant | 57.5 | brown_yellow_black | pigment | medium | NI | noncontac | percher | NI | semi | lotic |
| *Orthemis_discolor* | Tolerant | 50.5 | red_pink_brown | pigment_pruinescence | strong | monomorphic | noncontact | percher_flier | T | semi | lentic_and_lotic |
| *Orthetrum_cancellatum* | Tolerant | 47 | brown_blue_yellow | pigment_pruinescence | strong | NI | noncontact | percher | T | open | lentic_and_lotic |
| *Orthetrum_julia* | Tolerant | 47 | black_blue_yellow | pigment_pruinescence | weak | females | NI | percher | NI | closed | lotic |
| *Orthetrum_sabina* | Tolerant | 46.5 | yellow_black_white_green | pigment | weak | monomorphic | noncontact | percher_flier | NI | open | lentic_and_lotic |
| *Pachydiplax_longipennis* | Tolerant | 35.5 | yellow_green_brown_blue | pigment_pruinescence_structural | strong | females | noncontact | percher | T | semi | lentic_and_lotic |
| *Palpopleura_lucia* | Tolerant | 29 | black_blue_yellow | pigment_pruinescence | strong | NI | NI | percher | NI | semi | lotic |
| *Pantala_flavescens* | Tolerant | 50.5 | yellow_orange_brown | pigment | weak | monomorphic | noncontac | percher_flier | NT | closed_open | lentic_and_lotic |
| *Pantala_hymenaea* | Tolerant | 47.5 | yellow_brown_red | pigment | medium | monomorphic | noncontact | percher_flier | T | open | lentic_and_lotic |
| *Plathemis_lydia* | Tolerant | 45 | white_brown | pigment_pruinescence | strong | monomorphic | noncontact | percher | T | open | lentic_and_lotic |
| *Platycnemis_pennipes* | Tolerant | 36 | blue_black | pigment | strong | NI | contact | percher | NT | semi | lentic_and_lotic |
| *Platycnemis_subdilatata* | Tolerant | 34.5 | black_blue | pigment | strong | NI | contact | percher | NI | semi | lotic |
| *Pseudagrion_melanicterum* | Tolerant | 39.2 | black_white_green | pigment | weak | NI | NI | NI | NI | closed | lotic |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pseudagrion_rubriceps* | Tolerant | 35.75 | black_orange_green_yellow_blue | pigment_structural | strong | monomorphic | NI | percher | NI | semi | lentic_and_lotic |
| *Pseudoleon_superbus* | Tolerant | 41.5 | black_brown | pigment | weak | monomorphic | NI | NI | NI | open | lentic_and_lotic |
| *Rhionaeschna_multicolor* | Tolerant | 67 | black_brown_blue | pigment | strong | females | NI | flier | NI | semi | lentic_and_lotic |
| *Rhionaeschna_psilus* | Tolerant | 60 | green_brown_blue | pigment | weak | monomorphic | NI | percher | NI | closed_open | lentic_and_lotic |
| *Sympetrum_corruptum* | Tolerant | 40.5 | red_yellow_brown | pigment | strong | monomorphic | contact | percher | NT | open | lentic_and_lotic |
| *Sympetrum_flaveolum* | Tolerant | 34.5 | red_black_brown | pigment | medium | NI | contact | percher | NI | semi | lentic |
| *Sympetrum_sanguineum* | Tolerant | 36.5 | red_black | pigment | strong | NI | contact | percher | NT | closed_open | lentic |
| *Sympetrum_striolatum* | Tolerant | 39.5 | red_black_orange | pigment | weak | NI | noncontact | percher | NI | open | lentic |
| *Sympetrum_vulgatum* | Tolerant | 37.5 | red_orange | pigment | strong | NI | contact | percher | NI | semi | lentic |
| *Telebasis_salva* | Tolerant | 26.5 | red_yellow_black_orange | pigment | strong | monomorphic | contact | percher | NI | closed_open | lentic_and_lotic |
| *Tramea_binotata* | Tolerant | 42 | black_gray_blue | pigment_pruinescence | strong | monomorphic | NI | flier | NI | semi | lentic |
| *Tramea_lacerata* | Tolerant | 53 | yellow_black | pigment | medium | monomorphic | noncontact | flier | T | NI | lentic |
| *Trithemis_aconita* | Tolerant | 37 | black_blue | pigment_pruinescence | weak | NI | NI | percher | NI | closed | lotic |
| *Trithemis_arteriosa* | Tolerant | 38 | red_brown | pigment | strong | NI | NI | NI | NI | NI | lentic_and_lotic |
| *Xanthagrion_erythroneurum* | Tolerant | 40 | red_black_orange_blue | pigment | strong | NI | NI | NI | NI | NI | lotic |
| *Zyxomma_elgneri* | Tolerant | 45 | green_black_brown | pigment | weak | NI | NI | NI | NI | NI | lentic_and_lotic |

***Table S3** Coding of characters used for path analysis*

| | | |
|---|---|---|
| **SENSITIVITY TO URBANIZATION** | Tolerant | 1 |
| | Sensitive | 2 |
| **BODY COLORS** | Black (sometimes with white spots) | 1 |
| | Brown-back | 2 |
| | Blue-green | 3 |
| | Yellow-orange | 4 |
| | Red | 5 |
| **STRENGTH SEXUAL DIMORPHISM** | Weak | 1 |
| | Medium | 2 |
| | Strong | 3 |
| **POLYMORPHISMS BY SEX** | Females or males | 1 |
| | Monomorphic | 2 |
| **TYPE OF MATE GUARDING** | None | 1 |
| | Non_contact | 2 |
| | Contact | 3 |
| **FLIGHT MODE** | Percher_flier | 1 |
| | Flier | 2 |
| | Percher | 3 |
| **TERRITORIAL BEHAVIOR** | Non-Territorial | 1 |
| | Territorial | 2 |
| **HABITAT OPENNESS** | Closed-open | 1 |
| | Open | 2 |
| | Semi | 3 |
| | Closed | 4 |
| **TYPE OF HABITAT** | Lentic_and_lotic | 1 |
| | Lentic | 2 |
| | Lotic | 3 |
| | Phytotelmata | 4 |

**HABITAT PREFERENCE:** To run the path analysis models, the combination between Type of habitat and Habitat openness was considered as "Habitat preference".

**SEXUAL DIMORPHISM:** To run the path analysis models, the combination between strength sexual dimorphism and polymorphism by sex was considered as "Sexual Dimorphism".

**TERRITORIALITY:** To run the path analysis models, the combination between type of mate guarding, flight mode and territorial behavior was considered as "Territoriality".

# DISCUSIÓN GENERAL

Los odonatos están respondiendo de forma diferencial a la urbanización, dependiendo del suborden al que pertenecen. Los hallazgos del capítulo 1 indican que la riqueza y abundancia de Zygoptera (caballitos del diablo) disminuyeron a medida que aumentó la urbanización en el gradiente definido en el Centro de México, mientras que no se detectaron cambios ni en la riqueza ni en la abundancia de Anisoptera (libélulas). De esta forma, los resultados obtenidos en este trabajo se suman a la evidencia que afirma que Zygoptera es el suborden más sensible ante los cambios en su entorno (Monteiro-Júnior *et al*. 2014; Prescott y Eason 2018; Seidu *et al*. 2018; Jere *et al*. 2020). Es ampliamente reconocido que las tasas de disminución poblacional en relación con la perturbación antrópica para las especies especialistas son mucho más altas que estas tasas para los taxones generalistas (Wagner *et al*. 2021). El suborden Zygoptera contiene una mayor cantidad de especies especialistas que prefieren hábitats con vegetación conservada, presentan hábitos de oviposición endofíticos y tienen una dispersión más restringida en comparación con las especies del suborden Anisoptera (Corbet 1999; Monteiro-Júnior *et al*. 2014). Por el contrario, las especies de Anisoptera en su mayoría, presentan hábitos generalistas, tienen una mayor tolerancia térmica, prefieren los sitios abiertos y tienen una mayor capacidad de dispersión (May 1978), lo cual puede facilitar la vida de estas especies dentro de las ciudades.

A partir de los resultados de este primer capítulo y después de interpretar los resultados obtenidos en las comunidades de cada suborden, es importante resaltar que incluso los sitios con mayor influencia de la urbanización albergaron una gran cantidad de especies de odonatos, lo cual resalta la resiliencia de estos insectos. No obstante, para sobrevivir a un ambiente altamente modificado como las ciudades, los individuos requieren de ciertas características que les permitan tolerar las nuevas condiciones en su entorno. En este sentido, en los capítulos 2, 3 y 4 se evaluaron rasgos fisiológicos, conductuales y morfológicos en individuos pertenecientes a especies que habitan ciudades en diferentes partes del mundo, con el fin de detectar cuáles de estos rasgos podrían estar involucrados con la adaptación al entorno urbano.

A nivel fisiológico y a diferencia de trabajos previos realizados en varios grupos de insectos (Salomão *et al*. 2020; Córdoba-Aguilar y Rocha-Ortega, 2019; Iserhard *et al*., 2019), en el presente trabajo no se encontró una relación entre el gradiente de urbanización y las reservas energéticas o tamaño de la mancha alar (caracteres indicadores de la condición fisiológica de los individuos) de las dos especies del género *Hetaerina* evaluadas. Es decir, los individuos que habitan la ciudad tienen una cantidad de lípidos, carbohidratos y proteínas, así como una proporción de la mancha alar, similar a los individuos que viven en zonas menos urbanizadas. Esta falta de relación puede deberse a que el filtro selectivo afectó individuos de generaciones anteriores, ya que los procesos de urbanización comenzaron en la zona de estudio hace alrededor de 70 años (INEGI, 2020). Los individuos que observamos actualmente ya estarían entonces adaptados a este ambiente urbano, por lo que no presentan costos energéticos que se reflejen actualmente en los caracteres evaluados. Otra opción puede ser que la cantidad de comida en sitios urbanizados sea suficiente para suplir los requerimientos energéticos de los individuos, independientemente de condiciones no tan favorables en el ambiente urbano. Y finalmente, una tercera opción está relacionada con que los individuos estén ajustando sus conductas para reducir el gasto energético en lugares urbanizados y de esta forma su presupuesto energético será similar al de zonas menos urbanizadas. Esto último puede ser posible debido a que los cambios de conducta son la respuesta más rápida de algunos animales ante cambios ambientales relativamente rápidos como las ciudades (Tynkkynen *et al*. 2008; Magura *et al*. 2021).

Respecto a los cambios conductuales observados en odonatos a lo largo del gradiente de urbanización definido, esta vez en el Amazonas Brasilero, se encontró que los individuos fueron más eficientes en la captura de presas en los lugares más urbanizados. Este resultado puede explicarse por el tipo de presas disponibles en zonas urbanas. Si bien la disponibilidad de presas (p. ej., mosquitos) puede ser abundante en los ecosistemas urbanos, su diversidad tiende a disminuir y los arroyos urbanos suelen estar dominados por mosquitos de las familias Chironomidae y Culicidae (Kelly *et al*. 2019). Por lo tanto, los odonatos que viven en áreas urbanizadas pueden especializarse mejor en un solo tipo de presa, lo que lleva a una mayor eficiencia al atrapar su alimento. Otro factor que podría afectar la precisión al atrapar las presas puede ser que, en entornos más urbanizados, la complejidad de la estructura de la vegetación y la heterogeneidad ambiental tienden a reducirse (Threlfall *et al*. 2016). Esto implica que dentro de las ciudades la vegetación es menos compleja en arquitectura y de esta forma los vuelos de los odonatos a la hora de perseguir a sus presas pueden ser más directos y efectivos.

Finalmente, en la revisión bibliográfica se encontró que a nivel mundial 88 especies han sido registradas como tolerantes, mientras que 87 han sido registradas como sensibles a la urbanización. En cuanto a los caracteres que permiten que estas especies permanezcan dentro de las ciudades se detectó que las especies urbanas de Anisoptera y Zygoptera presentan tamaños más pequeños y un dimorfismo sexual más débil respecto a las especies de sitios no urbanizados. Posiblemente, construir un cuerpo grande requiere largos períodos de desarrollo, más alimento y, en consecuencia, más riesgos (Suhonen *et al*. 2022), por lo que en ambientes impredecibles como las ciudades resulta ventajoso tener un tamaño pequeño. Respecto al nivel de dimorfismo sexual, puede ser que las ciudades estén favoreciendo especies con mayor tendencia a ser dimórficas debido a que ser monomórfico puede acarrear más desventajas en entornos altamente cambiantes, debido a que un único morfo en entornos variables puede aumentar el riesgo de depredación o detección en momentos que sería preferible pasar desapercibidos (p. ej. Sanmartín-Villar *et al*. 2017).

A nivel de suborden también se encontraron diferentes caracteres involucrados en la sensibilidad a la urbanización. En Anisoptera, además del tamaño, las especies con colores amarillos o rojos fueron más frecuentes en las zonas urbanas, mientras que en Zygoptera las especies menos territoriales fueron más sensibles a la urbanización. Los hábitats abiertos típicos de las ciudades podrían promover colores rojizos en anisópteros debido a que los omocromos, responsables de la coloración roja y amarilla, se han asociado previamente con la producción de antioxidantes (McGraw 2005) y con protección contra los rayos UV (Needham 1974; Cooper 2010), que tendrían más incidencia en los individuos de zonas urbanas. Por otra parte, los resultados obtenidos para caballitos del diablo, podrían estar indicando que los comportamientos territoriales cobran mayor importancia dentro de las ciudades, donde hay pocos sitios disponibles para que las hembras ovipositen, por lo que esos pocos sitios disponibles deben ser defendidos con más ímpetu como ha sido reportado en otros grupos taxonómicos (Davies y Sewall 2016).

Hasta este punto y con los resultados obtenidos se descifraron algunos de los aspectos que favorecen la vida de los odonatos adultos en las ciudades. Sin embargo, hace falta incluir rasgos de las larvas que podrían estar favoreciendo la vida de este grupo de insectos en las ciudades. Asimismo, queda pendiente explorar un enfoque poblacional donde se pueda detectar si el mecanismo detrás de la supervivencia de estos insectos en las ciudades tiene que ver con adaptaciones, exaptaciones o plasticidad fenotípica. Además, detectar genes y proteínas clave detrás de estos procesos de adaptación a lo urbano, así como las variables particulares que más afecten a este grupo dentro de las ciudades (p. ej., pH y temperatura, entre otros factores) será clave para entender la dinámica de estos insectos en los entornos urbanos.

Tradicionalmente, las ciudades han sido percibidas como una amenaza a la biodiversidad y han sido consideradas por muchos autores como "desiertos biológicos" (Güneralp y Seto 2013). Sin embargo, diferentes estudios han evidenciado la gran diversidad que albergan las ciudades (Bertone *et al*. 2016). Los resultados de este trabajo evidencian, por ejemplo, que los odonatos son parte fundamental de la fauna urbana y que pueden permanecer en las ciudades con una condición fisiológica similar a la que mantienen en lugares más conservados. Ante este escenario y siendo conscientes de las múltiples especies que habitan las ciudades y sus diferentes requerimientos, debemos generar ciudades pensadas no solo para la especie humana, sino para todas las demás especies que sobrevuelan y caminan en la jungla urbana.

Las ciudades juegan un papel importante en la conservación de la biodiversidad global, particularmente a través de la planificación y gestión de los espacios verdes y azules urbanos (Aronson *et al*. 2017; Fenoglio *et al*. 2021). Abandonar la percepción de la ciudad como un disturbio y considerarla un ecosistema, en donde los hábitats muy modificados por el uso humano puedan rediseñarse, organizarse espacialmente y gestionarse para maximizar la biodiversidad, facilitará que asumamos la responsabilidad de conservarla al mismo tiempo que proporciona beneficios económicos y servicios ecosistémicos (Grimm *et al*. 2008). En este contexto y considerando el caso particular de los odonatos y otros insectos acuáticos, diseñar espacios dentro de las ciudades con cuerpos de agua lóticos y lénticos conectados entre sí por fragmentos de vegetación nativa, y con vegetación acuática dentro y alrededor de ellos, beneficiaría a un mayor número de especies. Además, la presencia de este tipo de hábitats en la ciudad facilitaría la sensibilización de los habitantes sobre la importancia de una adecuada gestión del agua y las consecuencias de esta gestión sobre formas de vida que normalmente no son consideradas. De esta forma los resultados de este tipo de estudios no se quedarán solamente en la generación de nuevos conocimientos, sino que propiciarán una comunicación bidireccional entre investigadores, ciudadanos y tomadores de decisiones durante el diseño de ciudades sostenibles (Pickett y Cadenasso 2012).

Kareiva *et al*. (2007) proponen que la ciudad puede entenderse como un ecosistema domesticado considerando que es modificado por el ser humano para obtener beneficios en términos de productividad, comercio, protección y salud. Recientemente se atribuyó la importancia de las áreas naturales dentro de las ciudades para la salud mental (Clark *et al*. 2014) y se han reportado beneficios para la salud humana a través de la regulación del sistema inmunológico por contacto con la microbiota en espacios verdes (Rook 2013). Reconciliarnos con las ciudades y como especie humana sentirnos parte de este ecosistema nos permitirá seguirlas domesticando, pero no en el sentido de sacar utilidad de ellas, sino de crear lazos, como el zorro enseñó al Principito (Saint-Exupéry 2004). A partir de esto, podremos diseñar ciudades que sean concebidas por cada habitante como un lugar único en el mundo, necesitar de ellas tanto como ellas necesiten de sus habitantes, y de esta forma habitarlas y modificarlas con la dosis adecuada de cuidado que permita que todas las formas de vida que la ocupan puedan sobrevivir y convivir.

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# APÉNDICE 1. Revisión sobre la función de la coloración en odonatos

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REVIEW

## Dragon colors: the nature and function of Odonata (dragonfly and damselfly) coloration

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## Abstract

Adult odonates (dragonflies and damselflies) exhibit a great diversity of colors which vary remarkably between species, between individuals within species, and throughout the individual's lifetime in some species. Here, we provide a summary of what is known about color recognition, and production of color including pigmentary absorption, structural reflectance, and fluorescence, in odonates. We also review the current understanding of the function of color in adult odonates, such as in signals during mate choice, in species recognition, and in predator avoidance, as well as in physiological adaptations to abiotic conditions. Finally, we provide some directions for future research: eye and pterostigma color, coloration at different life stages, UV color, phylogenetic analysis of color evolution, color and hot climate patterns, and standardization of color recordings. Given how easily they can be marked and tracked, odonates are exemplary animals for field and laboratory research. Therefore, unraveling the physiology, evolution, and ecology of odonate color can provide significant advances, in general, to understand insect color.

## Introduction

Like the striking plumage of birds or the kaleidoscopic wings of butterflies, dragonflies and damselflies show a dazzling array of colors. Research on this order of insects serves as a conceptual framework for a number of questions about color variation, production, and function. Here, we present a summary of what is known about color production and function in adult odonates, such as its ecological importance, starting with the definition of odonate color and a description of color variation between and within species. We explain the mechanics behind the production of different types of coloration, including pigmentary absorption, structural coloration, and fluorescence. We also cover the adaptive role of color as a visual signal to members of the same or different species and as protection. We finally highlight valuable future research directions, including the need for additional biochemical, ecological, and phylogenetic analyses of odonate color.

## Odonate color vision

Consideration of color naturally begins with an examination of vision. Among metazoans, odonates have some of the largest eyes relative to body size, which are equipped with ca. 30 000 ommatidia each (the largest number among living insects; Sherk, 1978). Dragonflies and damselflies have some of the most advanced insect visual systems, with the ability to perceive light from almost all directions and resolve fine details in their field of view (Chauhan et al., 2014; Corbet, 1999; Land & Nilsson, 2002). Each ommatidia exhibits its own lens overlaying a crystalline cone, which is immediately above the photoreceptive cells. The ommatidia located on the dorsal surface of the eye are sensitive at between 300 and 500 nm wavelengths, which allows the animal to see objects clearly against the bright background of the sky (Bybee et al., 2012; Labhart & Nilsson, 1995). The ventral eye is sensitive to a wider range of wavelengths (~300 and ~700 nm), facilitating the detection of conspecifics against different visual backgrounds (Futahashi et al., 2015; Lancer et al., 2020). The acute zones of the eye contain larger ommatidia that permit the entrance of more photons per unit, reducing diffraction among the lenses of the ommatidia and permitting the formation of a clearer image with better color perception (Bybee et al., 2012).

Specific types of odonate opsin genes produce light sensors (i.e., photosensitive intramembranous proteins) that are sensitive to different wavelengths. Bybee et al. (2012) and Chauhan et al. (2014) provided some insights on the evolution and distribution of opsins among odonates. More recently, Futahashi et al. (2015) have identified from 15 to 33 opsin genes in odonate eyes, several of which exhibit multiple copies for color detection, including long wavelength (i.e., red, yellow, and green), short wavelength (i.e., violet and blue) and even ultraviolet-sensitive opsins. These opsins are expressed differently in larvae and adults, and in ventral and dorsal regions of the eyes (Futahashi et al., 2015). The expression variation along ontogeny is related to the versatility of morphological and ecological adaptations of these insects in the aquatic and terrestrial environments they inhabit, which implies that opsin genes may have evolved according to the habitat and/or behavior of each species (Futahashi, 2017). Finally, odonates also exhibit optimized ommatidia in their eyes that enable them to detect light polarization (Lancer et al., 2020).

## Adult color variation

### Body color

A few days after emerging as terrestrial adults from aquatic larvae, odonates exhibit a plethora of body colors (Supporting Information Figure S1). Before this stage, teneral imagos are pale, but this period does not last more than 10% of the adult life span (Corbet, 1999). The range of larval and adult odonate colors includes the entire visual spectrum (some examples shown in Supporting Information Figure S1) as well as UV reflectance range (~300 – 400 nm). Colors can be based on: (i) pigments (such as in Supporting Information Figure S1c); (ii) micro- and nanostructures on the cuticle (i.e., structural coloration) that may result in iridescent or metallic visual effects (such as in Supporting Information Figure S1j); (iii) bright blue or whitish pruinosity derived from wax crystals; and to a lesser extent, (iv) fluorescence (e.g., Futahashi, 2020; Guillermo-Ferreira et al., 2014).

### Wing color

Most odonates have hyaline or somewhat translucent wings, yet some species have small or large wing patches formed by pigment deposition, nanostructures, and/or epicuticular wax. Examples of some types of wing color variation are shown in Supporting Information Figure S2. Coloration can be found at the base, middle, or distal part of wings, and some species even have coloration throughout the entire wing. The coloration patterns can also vary from irregular or round patches on the wing to brown or black bands that span the wing from the costal vein to the posterior edge of the wing. Furthermore, colors such as red, brown, or black may overlap at the base of the wings.

### Sexual dimorphism and color polymorphisms

Color variation within a species may result in sexual dimorphism (Cooper et al., 2016; Futahashi, 2017; Grether & Grey, 1996) with usually brighter and more conspicuous males, when sexual maturity is achieved (Corbet, 1999; Futahashi, 2016).

Hereditary color polymorphism is defined as the coexistence of at least two discrete morphs in adults of one or both sexes within a single population of a species (Huxley, 1955). Some odonate species express such color polymorphism in adults of both sexes (Futahashi, 2017), although it is usually restricted to only one sex (Fincke et al., 2005; Svensson et al., 2005; Van Gossum & Mattern, 2008). In odonates, such sex-limited color polymorphism is primarily found in females and is particularly common within the family Coenagrionidae (Andrés et al., 2002; Fincke et al., 2005; Sirot et al., 2003). Though less common, there are also cases of male-limited polymorphism in odonates (e.g., *Mnais andersoni*, *Mnais costalis*, *Paraphlebia quinta*) (Hooper et al., 1999; Romo-Beltrán et al., 2009). Diversity of color traits in polymorphic species is usually associated with certain behaviors in individuals (e.g., territoriality), which do not change when the color of an individual is modified experimentally (Rivas-Torres et al., 2019), but such modification can elicit different responses from conspecifics (Beatty et al., 2015).

### Ontogenetic color change

Adults of some species can exhibit developmental color transitions during sexual maturation. In the dragonfly *Erythemis simplicicollis*, temperature and food quality determine the development of coloration in adult individuals (McVey, 1985). Upon reaching nuptial coloration, the mature odonate male is physiologically prepared to compete for mates. This nuptial coloration may be of the pruinescent type (see color production section), which allows the clear differentiation between males and females. As competition for mates lessens with age, the conspicuous nuptial coloration can be lost, and duller colors may indicate physiological aging (McVey, 1985).

Additional examples of color changes during maturation can be seen in *Crocothemis* and some species of *Sympetrum*, in which males turn from yellow to red during maturation, while females remain yellow throughout their lives (Futahashi et al., 2012). In species of *Hetaerina*, immature males present a pale coloration on their bodies and a light brown spot at the base of the wings. As they reach maturity, the body darkens and three black stripes become clear on the thorax, while the brown spot takes on an intense red color (Córdoba-Aguilar, 1993). Males of *Mnesarete pudica* (Zygoptera: Calopterygidae) exhibit a dark wing coloration when young, resembling female wing color, which matures into a vivid red wing color when sexual maturity is reached, and their territorial and sexual behaviors are more expressed (Guillermo-Ferreira et al., 2014).

Several coenagrionid damselflies species show ontogenetic color change being the case of *Ischnura elegans* one of the best known. In this species, color changes in adults depend on physiological processes (e.g., spermatogenesis or oogenesis), waste neutralization, and reduction in water content throughout adult life (Hinnekint, 1987).

### Physiological color change

Some species show reversible, temperature-dependent changes in coloration (Prum et al., 2004; Veron et al., 1974), or rapid short-term changes during mating or oviposition (May, 1976). The mechanism known for this color change is a vertical migration of the ommochrome spheres located in the epidermis below the cuticle (Okude & Futahashi, 2021). For instance, the abdomen of several light-blue colored species becomes darker blue/gray, while bright red dragonflies turned dull orange-brown or red-brown when continuously exposed to lower temperatures (4–10°C) (May, 1998; Okude & Futahashi, 2021). Prum et al. (2004) found that *Anax junius* has a blackish coloration at low temperatures and turns to blue at higher temperatures. There is evidence for convergent evolution of this mechanism in many odonate clades (Prum et al., 2004; Veron et al., 1974).

## How do odonates produce color?

Odonates present three of four mechanisms of producing colors recorded in animals: pigmentary absorption, structural reflectance, and fluorescence (Futahashi, 2016). Bioluminescence, the fourth type of color production in animals (Kemp et al., 2012), has not been reported for odonates. Usually, coloration is generated by pigments deposited on the cuticular layers (i.e., epi, endo, or mesocuticle), epidermal cells, or both (Okude & Futahashi, 2021). However, some species also present metallic or iridescent coloration produced by cuticular multilayers, light-scattering nanospheres (that can vary in shape and size), and wax crystals (Futahashi et al., 2019; Gorb et al., 2000; Guillermo-Ferreira, Bispo, et al., 2015; Guillermo-Ferreira, Gorb, et al., 2015; Guillermo-Ferreira et al., 2019; Xu & Fincke, 2015). In addition to influencing color, wax crystals on wings have self-cleaning and hydrophobic properties (Futahashi et al., 2019; Hasan et al., 2012), which is crucial for insects that are in frequent contact with water during oviposition or territory defense displays, as is the case with odonates. Moreover, epicuticular wax is known to reflect UV radiation (Guillermo-Ferreira et al., 2019), which is deleterious to cells, and even helps the animal to avoid being caught on spider webs (Gorb, 2019).

### Pigments

Animal coloration can be caused by the presence of biochemical compounds in surface layers that selectively absorb part of the light spectrum (Poulton, 1890). In odonates, such compounds include pigments like melanin, ommochromes, and pteridines (Okude & Futahashi, 2021). Okude and Futahashi (2021) provided evidence that the reddish-brown and/or dark-colored granules in the proximal epidermal layer of *Ischnura senegalensis* contain ommochrome pigments. Moreover, ommochrome (arranged in pigment granules) and pteridine-containing nanospheres are localized in pigment granules within cells, respectively, in proximal and distal epidermal cells, while melanins can be deposited directly on cuticular layers.

In odonates, melanin is involved in the hardening and darkening of the exocuticle. Insect [eu]melanin (a pigment derived from L-tyrosine amino acid) (Solano, 2014) is an insoluble and resistant pigment (different from pheomelanin), which is responsible for the black and/or brown colors in the body parts of several odonates (Okude & Futahashi, 2021). [Eu]melanin-based pigments (red, orange, ochre, black, and brown colors) are generally fixed even after the individual's death, such that they are considered permanent, though they can be bleached by continuous exposure to light, ommochromes (red, brown, blue, and yellow colors) and pteridines (yellow and blue colors) usually disappear when the insect dies (Henze et al., 2019; Hooper et al., 1999; Tillyard, 1917).

### Structural coloration

Structural coloration is generated by optically functional surfaces or surface layer architectures and nanostructures that selectively reflect part of the light spectrum (Kemp et al., 2012; Poulton, 1890). For example, blue integumentary structural colors of Odonata are produced by spherical nanostructures within living epidermal cells that lie below the cuticle (Henze et al., 2019; Prum et al., 2004). Structural coloration in odonates is usually derived from an optical crystal formed by alternated melanized and non-melanized cuticle layers with different refractive indexes, which result in thin-film interference and an iridescent optical effect. This structure is very common in body, wings, and even in the eyes and frons of both males and females odonates.

The color produced may vary depending on the viewing angle and the refraction of the light that hits these surfaces (Guillermo-Ferreira et al., 2019; Tillyard, 1917). This iridescent optical feature may be used by dragonflies and damselflies for intraspecific communication during territorial fights and courtship (Guillermo-Ferreira, Bispo, et al., 2015; Guillermo-Ferreira, Gorb, et al., 2015; Vukusic et al., 2004). Moreover, non-iridescent blue color can also be attained by micro- and nanostructures, attributed to coherent light scattering from the quasi-ordered nanostructures within pigment cells (Prum et al., 2004).

Differences in the multilayered ultrastructure of the cuticle may produce many different hues (i.e., pure colors) on surfaces that can present bright patterns due to the arrangement of wax crystals with different sizes and shapes, folds, and cuticle layers with different optical properties (Mason, 1926; Vukusic et al., 2004; Wellenreuther et al., 2014). It is interesting to consider why structural coloration is so conspicuous and how color may change over the lifetime of an individual (e.g., brown wings in immature to dark-blue wings in mature males of *Calopteryx japonica*, Stavenga et al., 2012). These differences in coloration occur because of the multilayer structure and the high concentration of melanin in wing veins of mature males, a mix of pigmentary and structural coloration (Appel et al., 2015; Stavenga et al., 2012). In this regard, it is important to highlight that although there is a clear difference between pigment-mediated coloration and structural coloration, thin-film interference and pigment nanospheres creating iridescence and other visual effects in odonate body and wings involve a combination of the two mechanisms (pigments and structures). Indeed, even the bright pruinosity of several dragonflies requires a dark background (the basal integumental layer and epicuticle) to properly express their contrasting colors.

The hind wings of *Pseudolestes mirabilis* contain reflective patterns that vary between the dorsal and ventral parts of the wing. Such variation is the result of a combination of small amounts of melanin in the wing membrane which provides its coppery color, and the structural arrangement of a set of wax fibers secreted by the transverse veins of the wing. These fibers accumulate in each of the wing cells as the male matures to form what has often been referred to as "scales" (Orr et al., 2017).

Metallic colors can be produced by arrangement of cuticular pigment granules or the presence of pigmented (dark) and non-pigmented (pale) layers of the exocuticle (Guillermo-Ferreira, Bispo, et al., 2015; Guillermo-Ferreira, Gorb, et al., 2015; Tillyard, 1917). In pigmentary and non-pigmentary granules (e.g., nanospheres associated with Rayleigh effect [the predominantly elastic light scattering or other electromagnetic radiation by particles much smaller than the wavelength of the radiation] and other visual effects), while part of the light spectrum is absorbed, other wavelengths are reflected, generating a scattering effect.

Pruinescence is formed from the epicuticular wax nanostructures, such as filaments and plate-like crystals that cover the wings and/or the body (Gorb, 1995; Guillermo-Ferreira et al., 2019). The chemical composition of the odonates' wax pruinescence may vary according to the body part they are found on. For instance, Futahashi et al. (2019) unveiled a previously uncharacterized long-chain methyl ketone production mechanism that determines the physical properties, chemical composition, and molecular mechanisms of the wax-producing structures found in the abdomen of some libellulids. Ivanova et al. (2013), on the contrary, identified the chemicals that constitute the epicuticular wax of dragonfly wings which are known to be predominantly fatty acids (hexadecanoic acid and octadecanoic acid). Wax filaments and crystals are of mesodermal origin and product of gonad maturation, which is why pruinescence is an indicator of maturity (Futahashi et al., 2019; Tillyard, 1917). This coloration is distinguished by its gradual expression, beginning just after larval emergence or, in some cases, several days or months after emergence (e.g., *Sympetrum*). In females particularly, pruinescence may only appear after egg posture in older females (Tillyard, 1917). Wax nanostructures play an important role in color formation of pruinescence and represent a functional aspect in odonate communication, camouflage, and, probably, photoprotection/thermoregulation (Guillermo-Ferreira, Bispo, et al., 2015; Guillermo-Ferreira, Gorb, et al., 2015; Cezário et al. *in press*).

Pigments and nanostructures are the underlying mechanisms of the diverse array of conspicuous coloration patterns in odonates (Contreras-Garduño et al., 2006; Córdoba-Aguilar, 2002; Guillermo-Ferreira et al., 2014; Guillermo-Ferreira, Bispo, et al., 2015; Guillermo-Ferreira, Gorb, et al., 2015; Hassall, 2014; Prum et al., 2004), which might act simultaneously and interactively in most cases (Guillermo-Ferreira, Bispo, et al., 2015; Guillermo-Ferreira, Gorb, et al., 2015; Hilton, 1986; Prum et al., 2004). Such color patterns are present on the cuticle of the body, wings, and thoracic and abdominal setae and appear to reflect UV light in both sexes, creating a reflective halo around the body (Harris et al., 2011).

## UV reflectance and fluorescence

Hilton (1986) recorded two different response patterns to UV light in some Odonata species: UV-absorbing and UV-reflecting wing patterns. Calopterygids as well as aeshnids, libellulids, and gomphids have UV-absorbing wing patterns, probably due to wing pigments involved in yellow, orange, or brown wing patches. Meanwhile, calopterygids, coenagrionids, aeshnids, and libellulids species with pruinosity show UV-reflecting patterns (Futahashi, 2020; Harris et al., 2011; Hilton, 1986). Pruinescence and some iridescent effects are known to reflect UV light in several odonate groups, mainly Libellulidae and Calopterygoidea (Futahashi, 2020; Futahashi et al., 2019; Hilton, 1986; Robertson, 1984).

The reflectance of UV light appears to be important in at least one odonate species for species, sex, and age recognition (Guillermo-Ferreira et al., 2014). *Mnesarete pudica* damselflies exhibit UV-reflective wings which allow specific, sexual and age recognition. The experimental reduction in the UV reflection from the pigmented wings of both males and females of *M. pudica* caused reduced intraspecific interactions (i.e., territorial or sexual interactions) between conspecifics (Guillermo-Ferreira et al., 2014). Whether such function applies to other species awaits to be investigated.

Fluorescence, which should not be confused with UV reflectance, occurs when there are biochemical compounds that selectively absorb part of the light spectrum in specific wavelengths, and reemits the energy in a different region of the spectrum (e.g., pigments that absorb in the UV region and reemit light in long wavelengths) (Kemp et al., 2012). When coupled with UV reflection and pigmentary colors, fluorescence may increase the output of the visual signal in odonates (Guillermo-Ferreira et al., 2014). In *M. pudica*, the red-pigmented male wings emit red fluorescent signals when exposed to near-ultraviolet light (405 nm) (Guillermo-Ferreira et al., 2014). The wings of *Hetaerina americana*, and probably several other calopterygids, also emit fluorescent signals in the visible spectra (with highest intensity between 615 and 725 nm) when excited at 561 nm (see González-Santoyo et al., 2021).

We now know that most color signals arise from the interaction between diverse suites of pigments and reflecting (structural) mechanisms (Futahashi et al., 2019; Henze et al., 2019; Kemp et al., 2012). Thus, structural coloration and pigmentation could have evolved in parallel (Guillermo-Ferreira et al., 2019). Many pigments also have high refractive indices and nanostructured arrays of pigment granules and are often involved in structural color production, blurring the line between pigmentary and structural coloration even further (Henze et al., 2019; Prum et al., 2004). In addition, the interaction with the environment can also modify some of the mechanisms of color production. Some species of *Enallagma* do not develop their usual coloration when raised in the laboratory or greenhouse, but instead are melanized. This effect could be due to different levels of UV radiation experienced in captivity and in the field (Barnard et al., 2015). It will be useful to consider such plastic responses of color development and expression, particularly with respect to environmental and climate change effects on odonates.

## Future directions

To highlight future directions on the nature, function, and evolution of Odonata color patterns research, in this section we identify research gaps and particularly highlight the need for integrative studies. We begin by noting understudied color variation in addition to the body and wing color addressed in this review.

### Eye and pterostigma color

In addition to body and wing color, eyes can also show color patterns that are well defined and differ between males and females (Supporting Information Figure S3). For example, males of the fiery-eyed dancer, *Argia oenea* Hagen in Selys, have dark red eyes (Supporting Information Figure S3c), while females have brown eyes. Two explanations for this eye color dimorphism are as follows: a) sex differences in habitat use that lead to light-dependent adaptations, and b) aspects of sexual selection in which competition for mates leads to different eye colors in the two sexes. Meanwhile, the dorsal region of *Sympetrum*'s eyes exhibits a yellow-orange screening pigment (Labhart & Nilsson, 1995). The particular color patterns of the odonates' eyes may be due to ommochromes and pteridines pigments (Langer, 1975). Moreover, the screening pigments of *Sympetrum* dorsal eyes absorb blue and UV wavelengths but transmit and scatter yellow wavelengths, which allow optimized photoreconversion of the visual pigment (Labhart & Nilsson, 1995) and enhance the overall sensitivity of the visual system (Stavenga, 1992). Eye color is an important but neglected indicator of several aspects of animals' visual and behavioral ecology which deserves better comprehension, especially in colorful and visually oriented animals such as Odonata.

The color of the wing pterostigma merits further research as well. Most coenagrionids present dark or dark-brown pterostigma, though several *Leptagrion* and ischnurid species exhibit blue pterostigma (Machado, 2012). Pterostigma coloration may be visible by heterospecifics and conspecifics only when the odonate hold their wings spread or during flight as this morphological feature only appear on the upper wing surface (Machado, 2012). Thus, it may indicate a role in courtship or territorial interactions, but there are no published studies addressing this topic (Machado, 2012).

### Coloration throughout life cycle

Odonate eggs vary in color yet we know little about the reasons for this. In other insects, egg color plays an important role in thermoregulation, development time, and water retention (Farnesi et al., 2017), which may also be the case for odonates, particularly those in colder waters at high elevations and latitudes.

Odonate larvae are predators and their cryptic coloration, which includes patches of melanin in their integument, allows them to go unnoticed by their prey (Corbet, 1999). The intensity of the melanic coloration depends on the time that the larva passes in a determined habitat before ecdysis, and it can also be determined by the presence of predators (Moore & Martin, 2018). Possibly, a similar type of plasticity during metamorphosis could determine the formation of the "hylochromes" and "heliochromes" categories among adults proposed by Tillyard (1917). The larvae of some species, however, are characterized by brown or dark-colored morphs, each of which being genetically determined and independent of the habitat where the individual emerged (Yong et al., 2013).

Over the course of their molts, larval coloration can be a dynamic character. For example, larvae that hide among aquatic plants, such as those from the genus *Aeschna*, can modify their coloration to blend in with the vegetation (Corbet, 1999). In the family Coenagrionidae, the ability to change color substantially throughout larval molts has been recorded when larvae move to a habitat very different from where they hatched (Corbet, 1962).

### UV color

The mechanisms behind the UV color patterns expressed by odonates and the way these patterns relate to intra- and interspecific communication are not well understood. Some authors (e.g., Futahashi et al., 2019; Harris et al., 2011) propose that these UV reflectance patterns could be an honest signal of fitness in odonates, but this has not been tested.

### Evolutionary analysis

Although color and coloration patterns are used as high-resolution phylogenetic characters in various invertebrate taxa, they are sometimes difficult characters to quantify due to their high variability and plasticity. While phylogenetic reconstructions of color exist for some genera (Cooper et al., 2016; Sánchez-Guillén et al., 2020; Sanchez-Herrera et al., 2015), it would be valuable to consider such phylogenetic signals of coloration on a larger taxonomic scale within Odonata. Overall, how color and color patterns evolve and relate to other biological traits remains an unexplored field.

Such phylogenetic reconstructions would be more informative with information from extinct species, which may now be possible using recent technological advances. For example, recent studies deduced the presence of melanin granules by analyzing deposits of benzothiazole in the integument of dinosaur fossils (Brown et al., 2017; Vinther et al., 2016).

### Hot climate patterns

Given increasing global temperatures and urbanization, we predict a modification in odonate color in response to these changes (see also Moore et al., 2019). We may expect to see such changes, especially in melanin-based color polymorphism, which plays a role in photoprotection against UV radiation and is associated with resilience to increasing global temperature (Roulin, 2014). Additionally, changes in land use and abrupt replacements of green environments by gray environments in cities will have consequences in temperature changes and habitat destruction. These changes will impose a strong selective force on animals living near or within cities, which among other traits, can modify coloration (Leveau, 2021).

### Standardizing color measurements

In order to address the outstanding questions in odonate color research that we list above, we think that is important to define and standardize the form of collection and preservation of specimens for the evaluation of coloration in odonates. By doing so, we may increase our comparable data and address broader questions across taxa. To this end, we compiled some methods for color preservation (see Supporting Information Table S1), based on oral tradition among odonatologists and from our experience during specimen collection.

## Conclusions

Adult dragonflies and damselflies display an enormous palette of color and color patterns that can be produced in different ways and perceived differently by prey and predators depending on their visual systems. Odonata color can vary depending on their age, condition, the environment they inhabit, and their population dynamics. A formal understanding of the mechanisms (i.e., biochemical and physiological), historical processes (i.e., evolutionary), and ecological functions behind such colors may help illuminate and celebrate such diversity in nature.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1**. Diversity of coloration in the body of adult odonates. (a) *Sympetrum illotum*, (b) *Argia oenea*, (c) *Argia oenea*, (d) *Pantala flavescens*, (e) *Megalagrion calliphya*, (f) *Megalagrion blackburnii*, (g) *Anax junius*, (h) *Megalagrion nigrohamatum*, (i) *Megalagrion calliphya*, (j) *Calopteryx aequabilis*, (k) *Ischnura ramburii*, (l) *Dythemis* sp, (m) *Archilestes grandis*, (n) *Argia* sp (o) *Megalagrion adytum*, and (p) *Calopteryx maculata*. Photos: Catalina María Suárez-Tovar and Idelle A. Cooper

**Figure S2**. Diversity of coloration in the wings of adult odonates. (a) *Calopteryx aequabilis*, (b) *Calopteryx maculata*, (c) *Calopteryx maculata*, (d) *Calopteryx aequabilis*, (e) *Perithemis intense*, (f) *Hetaerina americana*, (g) *Plathemis lydia*, (h) *Mecistogaster ornata*, and (i) *Tramea onusta*. Photos: Catalina María Suárez-Tovar and Idelle A. Cooper

**Figure S3**. Diversity of coloration in the eyes of adult odonates. (a) *Megalagrion hawaiiense,* (b) *Megalagrion nifrohamatum,* (c) *Argia oenea,* and (d) *Ischnura ramburii*. Photos: Catalina María Suárez-Tovar and Idelle A. Cooper.

**Table S1**. How to preserve odonate coloration?

*Figure S1. Diversity of coloration in the body of adult odonates. (a) Sympetrum illotum, (b) Argia oenea, (c) Argia oenea, (d) Pantala flavescens, (e) Megalagrion calliphya, (f) Megalagrion blackburnii, (g) Anax junius, (h) Megalagrion nigrohamatum, (i) Megalagrion calliphya, (j) Calopteryx aequabilis, (k) Ischnura ramburii, (l) Dythemis sp, (m) Archilestes grandis, (n) Argia sp (o) Megalagrion adytum, and (p) Calopteryx maculata. Photos: Catalina María Suárez-Tovar and Idelle A. Cooper*

*Figure S2. Diversity of coloration in the wings of adult odonates. (a) Calopteryx aequabilis, (b) Calopteryx maculata, (c) Calopteryx maculata, (d) Calopteryx aequabilis, (e) Perithemis intense, (f) Hetaerina americana, (g) Plathemis lydia, (h) Mecistogaster ornata, and (i) Tramea onusta. Photos: Catalina María Suárez-Tovar and Idelle A. Cooper*

*Figure S3. Diversity of coloration in the eyes of adult odonates. (a) Megalagrion hawaiiense, (b) Megalagrion nifrohamatum, (c) Argia oenea, and (d) Ischnura ramburii. Photos: Catalina Mar_ıa Su_arez-Tovar and Idelle A. Cooper.*

*Supplementary material Table 1. How to preserve odonate coloration?*

Studying coloration in odonates is challenging because color information is usually lost in preserved specimens (Hilton, 1986). We present some tips so that when specimens are collected, their coloration patterns can be preserved as well as possible.

To conserve patterns of coloration in larvae, collect them alive in a container with water and some of the vegetation from the collection site. Then, submerge them in hot (not boiling) water to preserve the color patterns and prevent the disintegration of internal tissues, and then store them in 70% ethanol (Abbott, 2010).

To preserve the colors of adult specimens, collect them in glass or plastic vials. Cellophane bags usually employed for the collection of these insects could contaminate samples that need to be analyzed in Scanning Electron Microscopy (SEM) or Transmission Electron Microscopy (TEM).

Scan the live specimen in 1200 dpi or macrophotography and if possible, build a colorimetric map of the live specimen with an optical spectrometer.

When wings are colorful, remove the wings and keep them in a collection in glass or plastic containers. Kill the specimen in absolute ethanol or glutaraldehyde and keep them refrigeraded under -5C.

# APÉNDICE 2. ¿Cómo los insectos han soportado la vida en la ciudad? (Artículo de divulgación)

**BOLETÍN** de la SCME

Fotografía: Catalina María Suárez-Tovar

## Urbanitas de seis patas: ¿cómo algunos insectos han soportado la vida en la ciudad?

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### Resumen

Las ciudades representan uno de los mayores desafíos ecológicos de origen antropogénico para muchos organismos, incluyendo a los insectos: los animales más abundantes y diversos del planeta. El impacto de las ciudades sobre la biodiversidad de insectos puede variar según las particularidades de cada ciudad y de cada grupo de insectos, lo que hace que su estudio sea un desafío importante. En esta contribución, hacemos una revisión de los principales efectos que las ciudades tienen sobre los insectos e identificamos los rasgos que favorecen su adaptabilidad a estos entornos. Así mismo, mencionamos algunas formas en que las ciudades pueden ser más amigables para este grupo biológico.

### Palabras clave

adaptación, entomología urbana, especies ganadoras, urbanización

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El crecimiento exponencial de las poblaciones humanas y el aumento en la esperanza de vida promedio de nuestra especie ha elevado drásticamente el número de humanos que conviven en un mismo tiempo y espacio. Esto ha resultado en un uso desbordado de los recursos naturales y en un manejo del espacio bastante

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desequilibrado; cerca de 60 % de la población humana habita en ciudades, pero éstas se concentran en tan solo 3 % del planeta (Liu *et al*. 2014), por ende, los ecosistemas sobre los que se han establecido los centros urbanos han experimentado fuertes cambios en su estructura y en la biodiversidad que allí habita.

Una ciudad se define como una modificación en el uso del suelo con finalidades de asentamiento y desarrollo económico. Se distingue de otros asentamientos humanos por su mayor tamaño, densidad poblacional, la presencia de infraestructura especializada (p. ej., sistemas de transporte) y una mayor actividad económica e industrial (Grimm *et al*. 2008). Por las consecuencias ambientales de su establecimiento, las ciudades han sido estudiadas como un disturbio ecológico. Sin embargo, según Rykiel (1985), los disturbios ecológicos son "*eventos que modifican el estado inicial de un ecosistema y tienen una frecuencia y una intensidad, que determinan el tiempo en el que el sistema modificado vuelve a su estado inicial o a un estado parecido al inicial*".

Entendidos entonces como el resultado de continuas modificaciones, y lejos de volver a su estado inicial, los lugares donde se han establecido las ciudades deberían considerarse como un nuevo tipo de ecosistema con características geológicas, biológicas y antropogénicas que interactúan y se modifican por presiones generadas entre sí (Endlicher *et al*. 2007). Al igual que otros ecosistemas, las ciudades pueden presentar condiciones adversas para algunas especies, pero favorables para otras. Sin embargo, características de los entornos urbanos, como la reducción de la cobertura vegetal, la presencia de superficies impermeables, las altas emisiones de carbono, los altos niveles de contaminación (lumínica, sonora y ambiental) y las temperaturas elevadas generan fuertes presiones selectivas sobre las especies urbanas (Miles *et al*. 2019).

Los insectos (grupo caracterizado por la presencia de seis patas, alas y antenas) representan cerca de 90 % del total de especies animales descritas. Son el grupo animal más diverso en el planeta y están presentes en todos los niveles de la cadena alimenticia. Por su alta diversidad, abundancia y facilidad de colecta, los insectos se han convertido en un excelente modelo para estudiar cómo la urbanización afecta la biodiversidad. El estudio de los insectos en contextos urbanos inició a finales de la década de 1970 y ha crecido exponencialmente en los últimos 20 años, principalmente en mariposas, escarabajos, grillos, libélulas, caballitos del diablo, abejas y otros grupos de polinizadores.

Los estudios realizados hasta la fecha para evaluar el efecto de la urbanización sobre los insectos han utilizado diferentes indicadores del grado de urbanización como el porcentaje de superficie impermeable (p. ej. pavimento o cemento), los contaminantes presentes en el agua o el aire y el área ocupada por zonas verdes. Sin embargo, más allá de los cambios en la estructura física, existen factores sociales y económicos inherentes al desarrollo de las ciudades que también afectan a las comunidades biológicas citadinas, tales como la edad, el tamaño, la densidad de población humana, la cantidad de tráfico y las actividades económicas de cada ciudad. En consecuencia, la urbanización es una variable compleja y contexto-dependiente que debe ser definida muy cuidadosamente.

La mayoría de los estudios sobre insectos en zonas urbanas se han enfocado en detectar cambios en su riqueza y abundancia a medida que aumenta el grado de urbanización. Otros se han centrado en detectar cambios en la morfología, fisiología o conducta de los individuos, y un menor número han evaluado cómo es que los cambios en la estructura física interfieren en el intercambio de señales acústicas, o cuál es el efecto de los contaminantes volátiles de origen humano (pinturas, disolventes, productos de limpieza) sobre la comunicación olfativa (Jürgens y Bischoff 2017). A pesar de que la urbanización ha sido identificada como uno de los principales impulsores de la pérdida de insectos a nivel mundial (Fenoglio *et al*. 2021), diversos estudios han demostrado que las respuestas de los insectos pueden ser contradictorias: mientras que algunas especies se benefician con la urbanización otras se ven perjudicadas.

La mayoría de los estudios coinciden en que los insectos “ganadores” en los entornos urbanos son aquellos con hábitos oportunistas tanto en alimentación como en selección de hábitat, de tamaño pequeño, colores que protegen de la radiación solar, con mayor tolerancia térmica, ciclos de vida cortos, multivoltinos (es decir, especies con múltiples eventos reproductivos al año) y alta capacidad de dispersión (Figura 1). Dentro de los grupos de insectos con al menos una de estas características destacan algunas especies de cucarachas, hormigas, mosquitos, libélulas y abejas melíferas. Estas especies también son altamente resistentes a la contaminación, poseen sistemas respiratorios eficientes en ambientes con poco oxígeno y presentan conductas más arriesgadas en comparación con sus contrapartes rurales (Tchakonté *et al*. 2015). Cabe señalar que aún no se ha determinado si estas características son el resultado de plasticidad fenotípica (capacidad que tienen los organismos para cambiar su apariencia y conducta a partir de la misma información genética) o de adaptaciones ante las nuevas condiciones del ambiente.

**Figura 1.** Rasgos que permiten la supervivencia y establecimiento de insectos en centros urbanos. Elaboración propia

Por otra parte, diversos estresores urbanos pueden afectar de diferente forma a los insectos de una misma especie según su etapa de desarrollo (larva, pupa, adulto) y sexo (machos, hembras). Además, se pueden ver afectadas las interacciones depredador-presa no solamente entre diferentes grupos de insectos, sino también las que involucran otros grupos animales, como mamíferos o aves. En cuanto a las interacciones de herviboría, también se presentan cambios. Por ejemplo, las tasas de herbivoría por insectos con movilidad reducida son mayores en zonas urbanas ya que estos insectos tienen que satisfacer sus demandas de agua con una cantidad menor de plantas disponibles, y por lo tanto comen más de unas pocas.

Hasta la fecha, hay evidencia de que las ciudades generan cambios en los insectos, tanto a nivel de comunidad como individual, pero dichos cambios dependen en gran medida de las particularidades de cada ciudad. Si bien es cierto que muchas ciudades destruyen gran cantidad de hábitats naturales durante su establecimiento, también pueden generar nuevos espacios donde antes no había hábitat disponible para ciertas especies. Por ejemplo, la construcción de lagos o estanques con diferentes propósitos (ornamentación, recreación o drenaje) pueden favorecer a algunos grupos de insectos acuáticos siempre y cuando se les dé el manejo adecuado para que cumplan con los requerimientos que cada grupo de insectos necesita para sobrevivir y mantener poblaciones estables en estos lugares. Lo anterior puede implicar diversos aspectos clave como garantizar la calidad de agua, libre de contaminantes químicos o metales pesados. Además, es importante mantener niveles adecuados de temperatura y oxígeno disuelto en el agua y proporcionar una amplia disponibilidad de sitios de refugio, alimento y reproducción para los insectos acuáticos (p. ej. presencia de vegetación riparia, plantas flotantes o algas).

No es la construcción de ciudades *per se* lo que está amenazando a las poblaciones naturales de insectos, sino el tipo de ciudades que estamos diseñando y la cantidad de hábitats que mantenemos dentro de éstas. Si consideramos las ciudades como desiertos biológicos, con habitantes únicamente de la especie humana, estaremos excluyendo cada vez más formas de vida diferentes a la nuestra. Por el contrario, si reconocemos las múltiples formas de vida que nos acompañan, podremos diseñar ciudades que consideren los requerimientos de la diversa biota que puede habitar la ciudad. Así, para tener ciudades con mayor diversidad de insectos, en su diseño se debe incluir una alta variedad de especies vegetales, techos y muros verdes, jardines para polinizadores y "hoteles" para abejas o avispas, así como gestiones adecuadas para minimizar la contaminación del agua y promover la apreciación de las funciones que cumplen los insectos a través de la educación ambiental.

Los desafíos que imponen los entornos urbanos son únicos en la historia evolutiva de las especies debido a la rapidez con la que estos se presentan. Los insectos que han soportado la vida en las ciudades lo han logrado porque presentan un conjunto de rasgos morfológicos, fisiológicos y conductuales que les han permitido mantenerse a pesar de estos nuevos desafíos. Sin embargo, es esencial realizar estudios que nos permitan entender el contexto ecológico y evolutivo de las especies de insectos que sobreviven en las ciudades, así como las bases genéticas de los rasgos que las favorecen con el fin de ampliar nuestra comprensión de por qué algunas especies soportan las condiciones urbanas y otras no. Con esta información, tendremos un escenario más completo y entenderemos qué aspectos particulares dentro del diseño de ciudades deben ser modificados para reducir el impacto sobre nuestros vecinos de seis patas.

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