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REVIEW

Dragonflies and damselflies (Odonata) in urban ecosystems: A review

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Abstract. The expansion of urban areas is one of the most significant anthropogenic impacts on the natural landscape. Due to their sensitivity to stressors in both aquatic and terrestrial habitats, dragonflies and damselflies (the Odonata) may provide insights into the effects of urbanisation on biodiversity. However, while knowledge about the impacts of urbanisation on odonates is growing, there has not been a comprehensive review of this body of literature until now. This is the first systematic literature review conducted to evaluate both the quantity and topics of research conducted on odonates in urban ecosystems. From this research, 79 peer-reviewed papers were identified, the vast majority (89.87%) of which related to studies of changing patterns of biodiversity in urban odonate communities. From the papers regarding biodiversity changes, 31 were performed in an urban-rural gradient and 21 of these reported lower diversity towards built up city cores. Twelve of the cases of biodiversity loss were directly related to the concentrations of pollutants in the water. Other studies found higher concentrations of pollutants in odonates from built-up catchments and suggested that odonates such as *Aeshna juncea* and *Platycnemis pennipes* may be candidate indicators for particular contaminants. We conclude by identifying current research needs, which include the need for more studies regarding behavioural ecology and life-history traits in response to urbanisation, and a need to investigate the mechanisms behind diversity trends beyond pollution.

INTRODUCTION

Urbanisation is one of the main drivers of ecosystem change. The expansion of urban areas is a main cause of many environmental stressors: (i) removal of native vegetation leading to degradation and fragmentation of the natural landscape, (ii) modification of hydrological systems through water extraction for human use, (iii) increase of local minimum temperature creating a "heat island" effect, and (iv) accumulation of pollutants to a point at which the environment cannot fully process and degrade them, causing eutrophication and affecting biogeochemical cycles (Grimm et al., 2008; McDonald, 2008). Moreover, the estimated percentage of the world population living in urban areas now exceeds 50% (Grimm et al., 2008) and almost 60% will be living in urban areas by the year 2030 (Seto et al., 2012; Güneralp & Seto, 2013). Given the range of impacts and rapid growth of urban development, it is essential that we understand in depth the implications for natural systems both in and around cities. Dragonflies and damselflies (the Odonata) have been suggested as barometers for environmental change due to their sensitivity to other anthropogenic stressors such as climate change (Hassall, 2015) and variation in habitat quality (Clark & Samways, 1996). However, the impacts of urbanisation on odonates remain poorly understood. In this review, we will investigate current research on the impacts of urbanisation using odonates as a model group. First, we will present a brief overview on the impacts of urbanisation on terrestrial and freshwater ecosystems, then we conduct a systematic literature review regarding odonates in urban environments and outline the plausible effects on odonates, followed by the use of odonates as bioindicators, the conservation value of urban wetlands for odonates, a summary of evolutionary strategies for species to cope with urban stressors, and finally we conclude by identifying research needs.

THE EFFECTS OF URBAN STRESSORS ON TERRESTRIAL AND FRESHWATER ECOSYSTEMS

The wide range of impacts associated with urbanisation indicates that it exerts a considerable effect on terrestrial biodiversity. Most studies show that species richness and evenness is reduced in highly urbanised regions, depending on the taxonomic group observed, degree of urbanisation, and spatial scale of analysis (McKinney, 2002, 2008). For example, butterflies (Ruszczyk, 1987; Ruszczyk & De Araujo, 1992; Blair & Launer, 1997) and ground arthropods (McIntyre et al., 2001) show this tendency. The general pattern of biodiversity decrease in cities is probably due to the fact that over 80% of land in city cores is covered by buildings and pavements, with the remaining area used for lawns, trees, and shrubs (Blair & Launer, 1997), thus fragmenting the landscape and homogenising vegetation composition (Blair & Launer, 1997; Faeth et al., 2011; Faeth et al., 2012; McKinney, 2002). However, plant biodiversity peaks at intermediate levels of urbanisation, perhaps due to the high numbers of species associated with suburban gardens (McKinney, 2008).

Urban freshwaters have not been explored as much as terrestrial urban ecosystems, despite the high degree of vulnerability that freshwaters exhibit to the pressures of urbanisation (Paul & Meyer, 2001; Dudgeon et al., 2006). Urban streams, for example, are usually modified to carry out storm water into natural streams, washing away industrial and human wastes, as well as road runoff (Forman, 2014). Streams are subjected to toxins, temperature change, siltation, organic pollutants, and the replacement of riparian vegetation and substrate for rocks or concrete and, consequently, insects, molluscs, crustaceans, and annelids tend to have decreased species richness and abundance (Paul & Meyer, 2001; Forman, 2008, 2014; Vaughan & Ormerod, 2012). The presence of organic pollution has been associated with increased abundance of chironomids and oligochaetes, making them the dominant members of urban stream communities (Campbell, 1978; Seager & Abrahams, 1990; Paul & Meyer, 2001).

Ponds are very frequent in parks and gardens for aesthetic purposes and to improve human well-being (Forman, 2014; Hassall, 2014), and are greatly influenced by a variety of factors such as the land use of the surroundings, the runoff to the pond, subsurface groundwater flow, and shoreline conditions (Forman, 2014). Parks and gardens are heavily managed and fertilisers are commonly used, and due to their limited capacity for the processing of pollutants and nutrients, ponds often suffer from eutrophication with an accompanying decline in biodiversity (Forman, 2014). However, the relative isolation of urban ponds generates a substantial degree of habitat heterogeneity. Each pond possesses its own physical, chemical, and hydrological features, facilitating the presence of a range of species of specialised habitat requirements, hence increasing the differentiation among these ecosystems and the landscape diversity (β and γ diversity, respectively) (De Meester et al., 2005). They also work as "stepping stones", thus facilitating landscape connectivity and potentially acting as metapopulations (De Meester et al., 2005; Hassall, 2014).

The biodiversity of odonates in urban areas is expected to be different from their rural counterparts, as is the case for other taxa. However, as already discussed, urbanisation is a complex process that encompasses a wide range of selective pressures, and each of them is expected to have a different impact on odonates according to the species and the life stages. Sensitive odonate species may be severely affected by stressors such as contaminants from sewage input, but generalist species are expected to tolerate these conditions, leading to decreased species richness. Moreover, generalist species may exploit the resources available due to decreased interspecific competition, resulting in high abundance of tolerant species. This variation in sensitivity to a range of urban stressors means that odonate communities have the potential to act as barometers of environmental change in urban areas, as has been demonstrated successfully in South Africa for habitat quality (Clark & Samways, 1996) and as has been suggested for climate change (Hassall, 2015). In this review we outline the stressors associated with urban environments that have the potential to affect odonates considerably across their life cycle.

DRAGONFLIES AND DAMSELFLIES AS A MODEL SYSTEM

Dragonflies and damselflies (the Odonata) are highly suitable model organisms for the study of urban ecosystems because (a) they are sensitive to different stressors, such as pollutants (Ferreras-Romero et al., 2009) and temperature changes (Hassall & Thompson, 2008), therefore can be a powerful tool to assess the general conditions of the city environment; (b) they are aquatic as larvae and terrestrial as adults, hence can be used as bioindicators in both aquatic and terrestrial habitats (Oertli, 2008); (c) they have an important role as predators, hence have a wide range of interactions with different organisms in both aquatic and terrestrial ecosystems (Knight et al., 2005); (d) they are ideal for studying movement through the landscape, as their adult stage exhibits a high dispersal ability and are very conspicuous (Conrad et al., 1999), and (e) their biodiversity, ecology and evolutionary biology is well-documented, providing a robust foundation for drawing general conclusions (Córdoba-Aguilar, 2008).

LITERATURE REVIEW

We conducted a literature review of the prior work regarding urbanisation and odonates, in order to evaluate the potential of odonates as a model system for studying urbanisation. During January–April 2014, we used standardised search terms with three online databases: Web of Science, Scopus and ScienceDirect. The words "urban" and "Odonata OR dragonfl* OR damselfl*" were searched in title, keywords and abstract (except in Web of Science, where the search was in Topic). Only peer-reviewed papers including odonates in an urban environment were selected, reviews were excluded. According to the nature of the study, each paper was classified into one, two or three of the following categories: diversity (variables considered here were taxa richness, abundance, probability of occurrence for creating habitat suitability models, diversity indices such as Shannon-Wiener, etc.), toxicology (such as physicochemical features of the water bodies and heavy metal concentration), behavioural ecology (dispersal, trophic dynamics), and life-history traits (reproduction, life growth). We went on to examine the references from the papers found in the standardised search and also added those to the analysis where appropriate.

The search returned a total of 79 papers, most of which (65.82%) were published after 2004 (see Fig. 1, and Table S1 for a complete list of papers with categories). We were also interested in analysing geographical patterns in re-

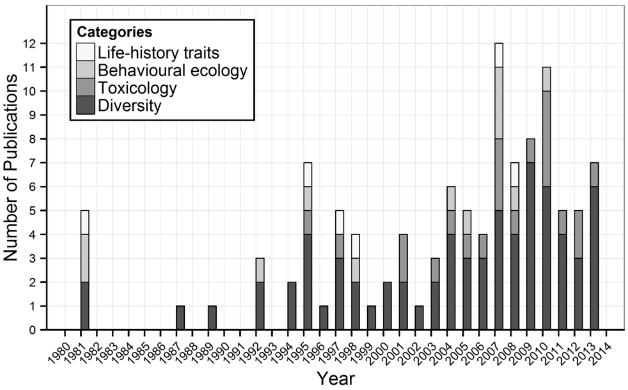

Fig. 1. Urban odonate peer-reviewed publications found by year and category.

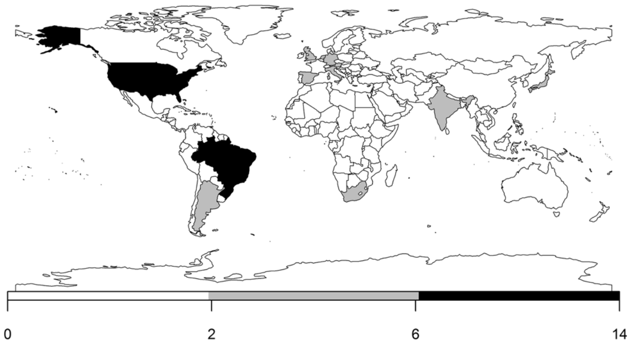

Fig. 2. Map of urban odonate peer-reviewed publications found per country.

search regarding odonates in urban ecosystems and found most studies were conducted in United States and Brazil, though plenty were from Austria, South Africa, Germany, Japan, and others (see Fig. 2).

Of the 79 papers found, 71 (89.87%) investigated patterns in biodiversity, of which 31 were executed in an urban-rural gradient or compared diversity in streams before and after the water flow reached an urbanised area. Of the studies regarding biodiversity in an urban-rural gradient, 21 reported less diversity in cities, and 12 cases of diversity loss were related to pollutant concentration in the water (see Table 1). Below, we discuss the general trend within these papers and give example studies to illustrate those trends; a comprehensive list of studies and summaries of findings can be found in the Supplementary Information (Table S1).

The effects of urban stressors on odonates

Our results suggest that increasing urbanisation seems to affect odonate diversity negatively, on the whole, as has been shown in other groups (McKinney, 2008). However, urbanisation is a multi-faceted problem and the studies reviewed herein offer some perspectives on which aspects of urbanisation are having the greatest impacts on Odonata across their life cycle and how this may reflect the biodiversity loss in cities (see Fig. 3). It is worth mentioning that the stressors listed may not only have a considerable impact in a given stage of their life cycle, but the effects can also be transferred to other stages via carry-over effects (e.g. maternal effects from adult to larva, or persistence of impacts between life history stages from larva to adult), except when a decoupling mechanism interferes (for a detailed review see Stoks & Córdoba-Aguilar, 2012).

Table 1. Urban odonate peer-reviewed papers found related to diversity.

	No urban-rural gradient	Less diversity	More diversity	No change
Urban odonate diversity publications	38	21	3	7
Diversity related to increased pollutants	4	12	—	1

Fragmentation

Fragmented landscapes with little vegetation cover and few water bodies may not provide sufficient corridors to facilitate dispersal, thus limiting odonate connectivity within cities (Chovanec et al., 2000; Watts et al., 2004; Sato et al., 2008). Urban landscapes were found to function as barriers for *Paracercion calamorum*, *Ischnura senegalensis*, and *I. asiatica* in Japan when the genetic differentiation among populations was analysed (Sato et al., 2008), showing that the effect of fragmentation in urban areas is consistent within at least three zygopteran species. These results are also consistent between methods of dispersal analysis: Watts et al. (2004) provide evidence from genetic techniques and a mark-release-recapture study that urban areas cause a strong negative effect in the dispersal of *Coenagrion mercuriale* in UK. Although we did not find any studies using odonates linking habitat selection and urban landscapes, fragmentation may also affect habitat selection negatively by constraining access to optimal sites, as has been shown in a study using two model species representing territorial animals (van Langevelde, 2015).

Vegetation removal and/or modification

Increased vegetation cover and biodiversity of plants was associated with increased odonate richness and overall evenness in Austria (Chovanec et al., 2002), Germany

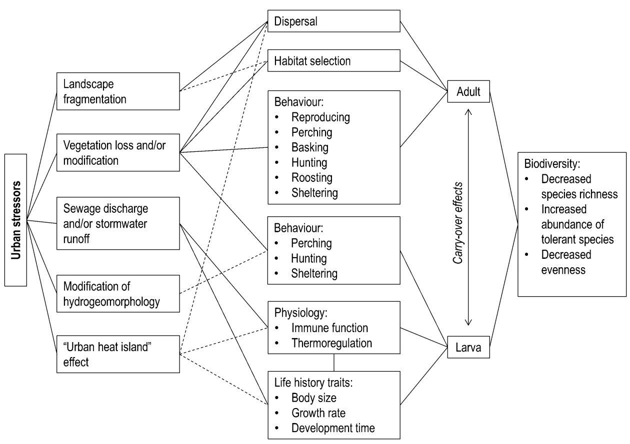

Fig. 3. Summary of drivers of odonate biodiversity in cities due to heavy management. Dashed lines represent hypothetical effects, since no studies were found to investigate the association between the specified stressor and the corresponding trait(s) on odonates.

Table 2. Bioindicators of urbanisation.

Indicator taxon	Response to urbanisation	Urban stressor	Reference
Aeshna spp.	Tolerant	Urban land use	Brazner et al. (2007)
Gomphidae	Sensitive	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009); Malherbe et al. (2010)
Ischnura graellsii (Rambur, 1842)	Tolerant	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009)
Anax parthenope (Selys, 1839)	Tolerant	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009)
Aeshna mixta Latreille, 1805	Tolerant	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009)
Orthetrum cancellatum (Linnaeus, 1758)	Tolerant	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009)
Libellulidae	Tolerant	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009)
Aeshna juncea (Linnaeus, 1758)	Tolerant	Manganese, lead and nickel	Girgin et al. (2010)
Platycnemis pennipes (Pallas, 1771)	Tolerant	Cadmium, boron, iron and total hardness	Girgin et al. (2010)
Erythrodiplax fusca (Rambur, 1842)	Tolerant	Urban development (deforestation)	Monteiro et al. (2013)
Argia sp.	Tolerant	Urban development (deforestation)	Monteiro et al. (2013)
Argia modesta Selys, 1865	Sensitive	Urban development (water pollution)	Silva et al. (2010)
Ischnura elegans (Vander Linden, 1820)	Tolerant	Urban development (water pollution)	Solimini et al. (1997)
Erythromma (= *Cercion*) *lindenii* (Selys, 1840)	Tolerant	Urban development (water pollution)	Solimini et al. (1997)

(Goertzen & Suhling, 2013), France (Jeanmougin et al., 2014), and South Africa (Samways & Steytler, 1996; Pryke & Samways, 2009), among others. For example, Goertzen & Suhling (2013) studied odonate diversity patterns in ponds across an urban-rural gradient using a multivariate approach and found that vegetation was not only one of the major drivers of alpha diversity, but also trampling vegetation had a significant negative effect. Other studies have reported similar results, but suggested percentage cover of submerged macrophytes was the main component of vegetation affecting odonate diversity (Jeanmougin et al., 2014). Additionally, indigenous plant species have also been highlighted as a key factor shaping odonate communities in urban wetlands, and leaving a strip of indigenous riparian vegetation of at least 20 m between the stream edge and commercial plantations seems to facilitate the presence of sensitive odonate species such as *Chlorolestes tessellatus* in South Africa (Samways & Steytler, 1996).

The strong management of vegetation in terrestrial ecosystems in cities has a considerable impact on the adult phase of odonates (Silva et al., 2010) because vegetation is one of the main cues used for habitat selection and it influences a vast range of behaviours such as basking, foraging, roosting, sheltering, among others (Buchwald, 1992). Removal or modification of aquatic vegetation from urban freshwater habitats also might have a considerable effect on the behaviour of odonates not only on the adult phase, but throughout their life cycle. Adults use aquatic vegetation as an oviposition substrate (Buchwald, 1992), often by inserting eggs into submerged plant stems (Corbet, 1999). Once the eggs hatch, the larvae use the submerged plant stems for perching, hiding from predators, and for sit-and-wait ambush hunting (Buchwald, 1992). During emergence, the larva climbs upwards out of the water along vertical plant stems and proceeds to full metamorphosis once it leaves the water. The composition of plant communities may also exclude some specialist species that rely on particular plants, such as *Aeshna viridis* that only oviposits on *Stratiotes aloides* (Dijkstra, 2006). However, it is worth mentioning that sensitivity to aquatic vegetation loss may vary across odonates, since not all species require aquatic vegetation for oviposition.

Sewage discharge and stormwater runoff

Sewage is formed primarily of domestic, commercial, and industrial waste. Wastewater is collected through the sewage system and treated before releasing into freshwater. However, sewer overflows are not uncommon, and some countries lack these facilities or treat wastewater only partially (Rosa & Clasen, 2010) and in many occasions, treatment is not enough to remove all the contaminants (Paul & Meyer, 2001).

Several studies found in our literature search examined the effects of sewage input or "urban pollutants" in general rather than particular contaminants. In these cases, diversity was negatively related to sewage input (Solimini et al., 1997; Henriques-de-Oliveira et al., 2007), although most of the papers from the search were focused on aquatic macroinvertebrates and the overall group of odonates as bioindicators rather than particular species. Urban pollution was associated with increased abundance and dominance of Libellulidae and other taxa (see Table 2), but decreased abundance of Gomphidae (Ferreras-Romero et al., 2009) and overall evenness (Henriques-de-Oliveira et al., 2007). However, it is worth mentioning that even though there are many tolerant species within Libellulidae and sensitive species in Gomphidae (Ferreras-Romero et al., 2009), the sensitivity or tolerance of a stressor depends on the particular species rather than a larger taxon, therefore caution must be taken when considering libellulids or gomphids as bioindicators.

Wastewater contains a wide variety of contaminants ranging from metals, organic and inorganic fertilisers and pesticides to polychlorinated biphenyls (PCBs) and polycyclic aromatic hydrocarbons (PAHs) (Paul & Meyer, 2001), forming a cocktail of pollutants which may affect odonate larvae – and other aquatic macroinvertebrates – in a number of ways. First, high contents of organic matter and fertilisers cause eutrophication, leading to algal and bacterial blooms and decreasing levels of dissolved oxygen in water (Forman, 2008). Second, organic and inorganic contaminants from both sewage discharge and stormwater runoff may be toxic for some species. For example, pesticide has been shown to increase mortality in odonate larvae and in sublethal concentrations, it also increases fluctuating asymmetry (e.g. Chang et al., 2007). A study looking at the life history of *Coenagrion puella* under pesticide stress suggested that the sensitivity of life-history traits depends on the type of pesticide and the exposure time, being increased development time the only life-history trait which showed consistency across pesticide treatments in the long-term exposure experiment (atrazine, carbaryl and endosulfan in this case) (Campero et al., 2007). On the other hand, exposure of *Ischnura elegans* larvae to a pesticide (chlorpyrifos) decreased immune function significantly, and adult heat stress caused a stronger decrease in immune function, indicating that temperature and pesticide stress interact across metamorphosis (Janssens et al., 2014). Moreover, urban populations of *C. puella* larvae showed increased activity levels when exposed to chlorpyrifos at 20° and 24°C while showing decreased food intake under pesticide stress at 24°C, compared to rural populations which showed decreased activity and food intake in all treatments (Tüzün et al., 2015). These results suggest that urban larvae populations are locally adapted to higher contaminant levels (Tüzün et al., 2015). These studies are particularly useful when analysing the impacts of urbanisation due to their multiple-stressor approach, which highlight the effect of interactions between urban stressors and contribute to a more integral understanding of urban ecosystems.

Certain contaminants such as PCBs and heavy metals may bioaccumulate in tissues. There are 209 different types of PCBs, and the mid-chlorinated congeners (e.g. PCB-153 and PCB-138) have been found in high concentrations among chironomids and dragonflies in an urban riparian ecosystem in Beijing (Yu et al., 2013). Similar results have been found with other organic persistent pollutants such as polybrominated diphenyl ethers (PBDEs) and hexachlorobenzene (HCB) in *I. elegans* larvae in several ponds across Flanders, Belgium (Van Praet et al., 2012). Heavy metals may come from both sewage input and road runoff, and they also tend to accumulate in the exoskeleton of odonate larvae (Meyer et al., 1986). Although lead and copper can cause deformities in other insects, e.g. *Chironomus mentum* (de Bisthoven et al., 1998), *Aeshna juncea* showed tolerance of high concentrations of manganese and nickel, while *Platycnemis pennipes* showed a sensitivity to cadmium, boron, and iron (Girgin et al., 2010), providing evidence of their use as suitable candidates for biomonitoring programmes.

ODONATES AS BIOINDICATORS IN URBAN ENVIRONMENTS

Aquatic biomonitoring programmes are aimed at evaluating water quality and identify water pollution in an early stage before it leads to decreased environmental health and ultimately affects human health and the security of public water supplies, which is particularly important in cities (Jones et al., 2010). Odonates have been used extensively as a bioindicator group of habitat quality (Clark & Samways, 1996; Sahlén & Ekestubbe, 2001; Foote & Rice Hornung, 2005; Subramanian et al., 2008; Clausnitzer et al., 2009; Dolný et al., 2011) and are one of the taxa included in the Biological Monitoring Working Party (BMWP) score system (Biological Monitoring Working Party, 1978). The BMWP score system has been used as a biological classification system for river pollution surveys in UK since 1980 (Paisley et al., 2014). The revised BMWP system includes Calopterygidae, Platycnemididae, Coenagrionidae, Cordulegastridae, Aeshnidae and Libellulidae (see Paisley et al., 2014 for the scores of each group). However, some species from these groups seem to be tolerant to urban stressors, such as *Ischnura elegans*, *I. graellsii*, *Erythrodiplax fusca*, among others (see Table 2). The presence of tolerant taxa in this system, as well as the absence of sensitive taxa such as *Gomphus vulgatissimus* (Brooks, 2004), might result in a misleading BMWP score. For instance, if in a given freshwater habitat there are abundant odonates, but 50% of the abundance includes tolerant species such as *I. elegans,* the result would be a high BMWP score which might not indicate water quality appropriately. Conversely, if there were abundant *G. vulgatissimus*, the BMWP score would be low, although the water quality in fact might be high. In order to reduce error using the current BMWP score system, we suggest that this system include sensitive species such as *G. vulgatissimus* and reduce the value of tolerant taxa. It has also been suggested that BMWP scores relying on Odonata might be influenced by shifting distributions under climate change (Hassall et al., 2010).

ECOLOGICAL TRAPS IN CITIES

Several studies have demonstrated that ecological traps can arise for dragonflies within urban areas, reducing the fitness of urban populations (e.g. Horváth et al., 2007). The term "ecological trap" refers to situations in which unsuitable sites unable to sustain a population are preferred over the suitable sites or the unsuitable habitats mimic the cues that species use for selecting ideal habitats, leading species to choose unsuitable habitats over the optimal sites for roosting, feeding, and mostly reproducing (Donovan & Thompson, 2001; Schlaepfer et al., 2002; Robertson & Hutto, 2006). Ecological traps are often induced by anthropogenic modifications of the environment (Schlaepfer et al., 2002), hence urban locations could be used as model sites for studying ecological traps (Hale et al., 2015). Alongside anthropogenically-modified water bodies that might be sub-optimal for odonates (Hale et al., 2015), human activity also produces a range of surfaces that reflect polarised light to an equal or greater extent than water (Horváth et al., 1998). Since odonates (and other semi-aquatic insects) use polarised light as a cue for oviposition site selection, such surfaces represent important ecological traps. For example, it was found in Brazil that the reflectance of cars imitates the reflectance pattern of ponds, encouraging the presence of *Pantala flavescens* in parking areas and even causing them to oviposit on the cars' surfaces, representing an important energy loss (Van de Koken et al., 2007). This behaviour has not only been observed in response to cars (Watson, 1992; Gunther, 2003; Wildermuth & Horváth, 2005; Blaho et al., 2014), but also to black plastic foil (Wildermuth, 1998), crude oil ponds (Horváth et al., 1998) and grave stones (Horváth et al., 2007). According to Kokko & Sutherland (2001), this behaviour could produce an Allee effect in low population densities. In high densities where there is increased competition, most individuals would compete for the preferred but unsuitable habitats, whereas the losing rivals would settle in the less preferred, high-quality habitat. However, in low population densities, the lack of competition will allow most individuals to make poor decisions on choosing proper habitats, therefore decreasing population density even more and eventually leading to extinction (Kokko & Sutherland, 2001; Schlaepfer et al., 2002).

THE CONSERVATION VALUE OF URBAN WATER BODIES FOR ODONATES

Although most studies showed a decrease in biodiversity as a result of urbanisation, there is evidence suggesting that urbanisation per se is not necessarily negative, but rather the negative impacts on biodiversity arise from highly intensive management associated with urban environments. Urban sites with a variety of vegetation composition, along with a proper management to minimise water pollution, were found to host more diverse communities of dragonflies and damselflies than those with limited vegetation diversity and increased water pollution (Colding et al., 2009; Goertzen & Suhling, 2013). For example, urban drainage systems in The Netherlands with low nutrient content and rich vegetation have been shown to have comparable macroinvertebrate diversity to rural drainage systems (Vermonden et al., 2009). In the Austrian Danube River floodplain system located within the city limits of Vienna, a water enhancement programme was implemented (which consisted of restructuring the embankments of an artificial island by creating shallow water areas, gravel banks, small permanent backwaters and temporary waters) and showed increased vegetation, odonate diversity and connectivity in the landscape in a long-term monitoring programme (e.g. Chovanec et al., 2000, 2002). A study conducted in South Africa compared odonate diversity (and other invertebrate taxa) in natural and recovering forests and fynbos to alien pine plantations and botanical gardens rich in indigenous plants, and surprisingly the botanical gardens presented the highest species richness and abundance, especially compared with alien pine plantations (Pryke & Samways, 2009), providing evidence that botanical gardens represent a major refuge for invertebrate species. Parks in South Africa have shown high odonate diversity, whereas alien plantation forests where *Eucalyptus* sp. was the most abundant had the lowest odonate richness (Samways & Steytler, 1996). From a social perspective, increased biodiversity of odonates in urban green areas such as botanical gardens and parks is also important because they help attract tourists and increase awareness of the role of wetlands (Lemelin, 2007).

Additionally, urban ecosystems offer a vast diversity of pond types, ranging from ornamental ponds to drainage systems, each of these being subjected to different management plans (Hassall, 2014). This heterogeneity of pond types provides different hydrological and ecological conditions which may promote a higher β and γ- diversity of odonates, not only generalist species (Goertzen & Suhling, 2013). Likewise, ponds are abundant mostly in suburban areas in Central Europe (Willigalla & Fartmann, 2012), perhaps due to garden ponds. Garden ponds are also common in UK, between 2.5 and 3.5 million garden ponds are estimated in UK (Davies et al., 2009), providing abundant aquatic habitats which facilitate connectivity and promote metapopulations (Hassall, 2014).

In spite of generalist species being abundant in cities, there are some specialist species that can also find refuge in urban habitats. For example, the threatened damselfly *Coenagrion ornatum* has been reported to inhabit drainage systems (Harabiš & Dolný, 2015), and golf courses in Sweden have demonstrated to serve as a refuge for endangered species e.g. *Leucorrhinia pectoralis*, a dragonfly considered "near threatened" in the Appendix II of the Bern Convention (Colding et al., 2009).

An interesting case is presented by *Ischnura gemina*. This species is endemic to the San Francisco Bay area, USA, which is highly urbanised. Even though *I. gemina* has been able to survive despite the stressors in the region (Garrison & Hafernik, 1981a, b), populations are decreasing and now it is threatened by urban development, in spite of repatriation efforts (Hannon & Hafernik, 2007). This species is currently under protection, which is predicted to benefit the species under climate change scenarios as well (Sánchez-Guillén et al., 2014). This situation represents an important case study in urban invertebrate conservation not only for conservation biologists, but also for the regional authorities and urban planners with whom conservationist must work, since *I. gemina* and other odonates, as previously discussed, are helpful indicators of habitat quality and can work as "umbrella species" (Bried et al., 2007; Clausnitzer et al., 2009). This is particularly important in cities because by meeting the conditions required for odonates to survive, other species' requirements will be met as well (Bried et al., 2007), thus saving time and effort in developing biodiverse, sustainable cities. They also work as "flagship species" for wetlands due to their attractiveness (Lemelin, 2007), which may help attract visitors to urban green areas.

ADAPTING TO URBANISATION

As we have mentioned throughout this review, some odonate species may be more tolerant of urban stressors. In order to unravel the specific traits driving the success of species in urban ecosystems, some studies have examined the role of the life history of odonates in light of the stressors caused by urbanisation. For example, a study in Italy observed the life history patterns of *Erythromma lindenii* and *Ischnura elegans* along an urban tract of a river and suggested the key factors to allow these species to cope with organic pollution is a longer reproductive period, absence of diapause, and tolerance of low oxygen concentration (Solimini et al., 1997). Studies performed in Japan demonstrated that the life cycle of *Sympetrum striolatum imitoides* was synchronised with the use of swimming pools; this species laid eggs in autumn, the larvae hatched in mid-winter and most adults emerged before the pools were drained and cleaned (Matsura et al., 1995; Matsura et al., 1998). However, the mechanisms underlying the life history of these species in both studies are uncertain, i.e. whether the species possessed pre-adaptations to urban habitats or exhibit plastic responses that allow them to persist despite urban stressors.

However, the Odonata represent one group within which common garden rearing experiments using multiple stressors have yielded considerable insights (Stoks et al., 2015). These studies allow the partitioning of genetic and environmental factors to investigate the relative contributions of plasticity and adaptation, and have suggested that local adaptation to temperature (Dinh Van et al., 2014; Arambourou & Stoks, 2015) and pesticide stress (Tüzün et al., 2015) is common in odonates. Hence, studying phenotypic variation in urban environments represents a great opportunity for researchers in ecology and evolution to observe the complex, underlying processes of how species adapt to new circumstances through the use of urban habitat patch networks as "natural experiments".

RESEARCH NEEDED

While general patterns of diversity are well described and some of the mechanisms underlying those patterns have been quantified, a number of important areas of research are under-represented in the current literature. Below, we outline some of these key areas:

Trophic interactions

We found very few studies regarding trophic interactions of odonates in cities, in spite of being considered key predators in both aquatic and terrestrial ecosystems (Knight et al., 2005). Some studies using turtles (Martins et al., 2010) and bats (Srinivasulu & Srinivasulu, 2005; Kalcounis-Rueppell et al., 2007) encountered odonates as prey, in both urban and non-urban habitats. However, there is little information regarding how their role as predators changes in urban ecosystems. Possible intraguild predation has been suggested, but not observed in detail (Agüero-Pelegrín & Ferreras-Romero, 1994; Sacha, 2011). Other than that, it is commonly known that they feed on chironomids (Matsura et al., 1998). Thus, there is no comprehensive knowledge regarding the diet of dragonflies and damselflies in cities. Given the fact that aquatic macroinvertebrate communities (i.e. prey) differ in cities from their rural counterparts (Azrina et al., 2006), there might be a significant impact on the energy flow in both aquatic and terrestrial habitats from urban environments (Knight et al., 2005) and the potential role for control of disease vectors in densely populated areas (Saha et al., 2012). Moreover, given the fact that odonate larvae tend to bioaccumulate contaminants such as heavy metals and PCBs that come from human activities, odonate larvae can transfer the contaminants to other organisms via trophic interactions, either in aquatic or terrestrial ecosystems, that is, in the absence of a decoupling mechanism preventing the transfer of contaminants from larvae to adults (Yu et al., 2013).

Behaviour

Research on behaviour in relation to urban odonate populations has focused on dispersal and the selection of oviposition sites, but a much wider suite of behavioural traits would be expected to vary across urban-rural gradients. Considering, for example, the different stressors from urban areas (reviewed above), it is common to find tolerant species in cities (i.e. urban adapters and exploiters; McKinney, 2002) such as *I. elegans* (Solimini et al., 1997). Urban adapters and exploiters among invertebrates would be predicted to exhibit syndromes involving multiple behavioural responses such as increased boldness, that is, being willing to take more risks (Lowry et al., 2013) like those exhibited by vertebrates (e.g. song sparrows, Evans et al., 2010). Only one study to our knowledge has investigated the behavioural response of odonates to urban stressors, and found that exploration behaviour, activity, and food intake of *C. puella* larvae were affected by pesticide stress except for boldness, although urban populations in general showed increased activity rate compared to rural populations (Tüzün et al., 2015). Therefore, there is a current lack of studies regarding behavioural syndromes in odonates and other invertebrates in response to other urban stressors along urban-rural gradients and the ecological and evolutionary consequences of those syndromes. Further studies regarding odonate behavioural ecology could also provide important insights into how odonates and other animals interact with urban ecosystems and test for a generalisation of urban evolutionary pressures across taxa.

Urban thermal ecology

Furthermore, we must consider that temperature increases in urban environments, creating a regional climate change effect called "Urban Heat Island" (UHI, Grimm et al., 2008). This temperature increase is most noticeable during the night (Karl et al., 1988), and operates both in terrestrial areas where pavements and rooftops absorb and radiate heat to increase the ambient air temperature, and in aquatic systems where heated runoff that passes over hot concrete and asphalt enters water bodies (Jones et al., 2012). Temperature is a major driver of odonate phenology (Hassall et al., 2007), polymorph frequency (Gosden et al., 2011), and body size (Hassall, 2013; Hassall et al., 2014). Additionally, temperature has a great impact on many physiological processes, such as metabolism, respiration, muscular activity, immunology, development, reproduction, and – naturally – thermoregulation (i.e. pigmentation, basking, wing-whirring) (Hassall & Thompson, 2008; Neven, 2000). Therefore, there may be phenological, morphological and physiological shifts in odonates caused by the urban heat island effect, as well as interactions between these shifts. However, the effect of the UHI might not necessarily be negative. Most odonates are likely to tolerate such warm conditions due to their tropical evolutionary origin (Pritchard & Leggott, 1987), although thermal stress can be lethal if the temperatures exceed upper tolerance thresholds. In fact, the UHI may facilitate dispersal of odonates, as has been found in scale insects (Meineke et al., 2013) and mosquitoes (Araujo et al., 2015). It has been suggested that cities in temperate regions may benefit from the increased temperature, particularly during winter, although the UHI can also increase thermal and drought stress in tropical, subtropical and desert cities (Shochat et al., 2006). The UHI also has a great impact on freshwater habitats. However, there is no research regarding these topics, hence we can only speculate at this point.

Modified hydrogeomorphology of freshwaters

Rivers and ponds are frequently subjected to human alterations mostly by increasing imperviousness, which increases temperature, decreases infiltration of water and increases stormwater runoff drastically (for a detailed review see Paul & Meyer, 2001). Sediment is also coarser in urban water bodies as a result of alteration of sediment supply and velocities, and also tends to accumulate high metal contents such as lead, zinc, and cadmium (Paul & Meyer, 2001). The lack of natural substrate may interfere with microhabitat use, habitat selection, and a variety of behaviours (e.g. sheltering, hunting). However, to our knowledge no studies have yet been carried out on the importance of flow regimes and sediment change to odonates within urban rivers and ponds.

Urban genomics

As mentioned previously, the intraspecific variation throughout an urban gradient may be driven via phenotypic plasticity or genetic adaptation. Other than studies looking at dispersal (Watts et al., 2004; Sato et al., 2008), there are no investigations to our knowledge that link genetics to the phenotypic variation in urban odonate populations. Thus, the underlying mechanisms that drive phenotypic variation of odonates in cities are not well-documented. While one study has looked at population differentiation across an urban landscape (Sato et al., 2008), there could be far greater insights through a combination of gene-flow models, cost surfaces, and corridor analyses to use odonate movement as an indicator of large-scale habitat connectivity in cities. Modern advances in transcriptomics and metabolomics also offer opportunities to explore the stressors experienced by urban populations through the differential expression of genes (e.g. Chapman et al., 2009).

CONCLUSION

To summarise, this review illustrates that odonate diversity is generally lower in built-up city cores than in surrounding areas. However, with suitable management and design, urban areas could increase diversity and landscape connectivity, which has various promising implications for ecology, evolutionary biology, conservation biology and urban planning. While patterns in diversity are well-documented, there has been a lack of research into the behavioural, genetic, and life history processes that might act as mechanisms to drive those diversity patterns. The literature reviewed here provides a strong case for the use of odonates as a model taxon in both the lab and field for the study of a wide range of phenomena related to urbanisation. In order to achieve an integrated understanding of urban ecosystems, we encourage further research, specifically using odonates due to their versatility as bioindicators in both aquatic and terrestrial habitats.

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Table S1. Summary of publications considered in the analysis and the categories in which they were included.

Reference	Studied group	Location	Habitat type	Variables	Categories	Results summary
Agüero-Pelegrín & Ferreras-Romero (1994)	Odonates	Spain	Urban pond	Taxa richness, abundance, exuviae dry weight, sex ratio	Diversity	*Anax imperator, Crocothemis erythraea, Sympetrum fonscolombii* and *Trithemis annulata* were found. *T. annulata* was the most abundant and male exuviae were heavier. There were slightly more males than females.
Alvarez & Pardo (2007)	Aquatic macroinvertebrates	Spain	Temporary streams	Taxa richness, abundance, community assemblage, flow permanence, riparian land use	Diversity	Taxa richness was higher in undisturbed riparian land use in all aquatic invertebrates including odonates; Abundance was related to flow permanence, independent from land use.
Azrina et al. (2006)	Aquatic macroinvertebrates	Malaysia	River	Physicochemical features upstream (undisturbed) and downstream (highly urbanised) sites, taxa richness and abundance, BMWP scores	Diversity Toxicology	In all aquatic invertebrates including odonates, upstream pollution indices were significantly lower than downstream, where urban pollution was discharged. Diversity measurements were also correlated with pollution indices.
Bracken & Lewis (2004)	Odonates	Canada	Highly urbanised Conservation area	Taxa richness	Diversity	Fifty species of odonates encountered, which represents 47.2% of the county richness.
Brandt & Buchwald (2011)	Odonates	Germany	Ponds	Taxa richness and abundance	Diversity	A total of 28 species of odonates was recorded, 21 of them were native from the area.
Brazner et al. (2007)	Birds, fish, amphibians, aquatic macroinvertebrates, wetland vegetation, and diatoms	USA	Coastal wetlands	Human disturbance factors (agriculture, urban development, contaminants), non-stressor variables (vegetation, watershed), taxa richness	Diversity Toxicology	Non-stressor variables were a better predictor of diversity than human disturbance factors; fish (*Ambloplites rupestris*) and *Aeshna* spp. were the strongest indicators of urban development.
Burton (1995)	Plants and animals	United Kingdom	Woodland and parkland (now golf-course)	Taxa richness	Diversity	A total of 210 species of higher plants; 24 species of mammals, reptiles and amphibians; 82 species of birds; 101 species of lepidopterans, and some more records of other insect orders, including odonates.
Chovanec (1994)	Amphibians and odonates	Austria	Artificial urban pond	Taxa richness and abundance	Diversity	Richness was considerably high; all amphibians found were included in the Red List of Endangered Species and the odonate species were native from the area.
Chovanec & Raab (1997)	Odonates	Austria	Canals and urban pond	Taxa richness and abundance	Diversity	Overall odonate diversity had increased since the implementation of the canal system and creation of artificial pond.
Chovanec et al. (2000)	Plants, odonates, amphibians, reptiles, waterfowl	Austria	River-floodplain systems	Taxa richness, abundance, community assemblage	Diversity	Shallow sites without direct connection to the main river (Danube) were rich in odonates, amphibians, and riparian vegetation. The new presence of *Ischnura pumilio* demonstrates the connectivity facilitated by the new landscape.
Chovanec et al. (2002)	Odonates, amphibians and fish	Austria	River-floodplain systems	Taxa richness, abundance, community assemblage	Diversity	Ponds were inhabited mostly by amphibians and odonates, whereas fish richness was related to connectivity. New floodplain system facilitated migration paths for amphibians and dragonflies, but no suitable breeding sites were found.
Cleto Filho & Walker (2001)	Aquatic macroinvertebrates	Brazil	Streams	Water quality measurements, taxa richness, diversity and similarity indices	Diversity Toxicology	Water quality was lower in streams with urban input, which negatively affected overall diversity, including odonates.
Colding et al. (2009)	Amphibians and odonates	Sweden	Golf-course and off-course ponds	Taxa richness in golf courses and off-course ponds, diversity and similarity indices	Diversity	Species composition was not significantly different between ponds. *Leucorrhinia pectoralis,* an endangered species, was found exclusively in golf course ponds.
Craves & O'Brien (2013)	Odonates	USA	Lotic and lentic aterbodies	Taxa richness and abundance	Diversity	Ninety species of odonates encountered within a highly-urbanised county.
Dombrovskiy & Kharchenko (2005)	Aquatic macroinvertebrates	Ukraine	Urban lake	Taxa richness, abundance, diversity and saprobic indices	Diversity Toxicology	Both diversity and saprobic indices were inversely related. Zygopterans were the dominant predators.
Edokpayi et al. (2004)	Aquatic macroinvertebrates	Nigeria	Lagoon	Water quality measurements, taxa richness and diversity index	Diversity Toxicology	Low diversity in all sampling sites, elevated pollution rates. BOD and TDB content were significantly different among sites. No anisopterans were found.
Ferreras-Romero et al. (2009)	Odonates	Spain	River	Physicochemical features, ecological quality and land use upstream (undisturbed) and downstream (highly urbanised) sites, taxa richness, abundance, IBMWP scores	Diversity Toxicology	Species composition was negatively related to physicochemical values and modification of land use. Communities in sites less affected by human impact were dominated by semivoltine anisopterans.
Fischer et al. (2000)	Aquatic insects	Argentina	Urban rain pools	Meteorological parameters, taxa richness and abundance along seasons	Diversity	The highest richness of adults was recorded during the warmer months; immatures were out of phase. Most ponds accounted less than 25% of the recorded taxa. Only two odonate taxa recorded.

Table S1 (continued).

Reference	Studied group	Location	Habitat type	Variables	Categories	Results summary
Fontanarrosa et al. (2004)	Aquatic insects	Argentina	Temporary, urban pools and permanent, rural lagoons	Taxa richness and diversity index	Diversity	Odonate richness was higher where floating vegetation was found. Taxa richness in temporary pools was not significantly different from permanent ponds, but overall diversity was lower. Only four odonate taxa recorded.
Funk et al. (2009)	Aquatic molluscs, dragonflies and fish	Austria	River-floodplain systems	Taxa richness, abundance, and species composition was assessed before and after a water enhancement scheme	Diversity	Molluscs and dragonflies were positively affected; fish showed no change. Dragonflies had increased taxa richness and abundance, but no significant change in species composition.
Funk et al. (2013)	Reptiles, amphibians, fish, snails and odonates	Austria	River-floodplain systems	Probability of occurrence with connected and isolated conditions	Diversity	Most of the species selected had a higher probability of being found in connected conditions. Odonate species included in the model were *Leucorrhinia pectoralis* and *Ophiogomphus cecilia.*
Garrison & Hafernik (1981b)	*Ischnura gemina*	USA	Urban park creek	Population dynamics	Diversity Behavioural ecology Life-history traits	Dispersal was mostly local, but potential for larger dispersal was detected. Constant population size, short life span, quick maturation rate, slightly more males than females; one satellite population found.
Garrison & Hafernik (1981a)	*Ischnura gemina*	USA	Urban park creek	Geographic range	Diversity Behavioural ecology	Range is limited to small urban area, may have adapted to disturbance. Andromorphic female was described.
Girgin et al. (2010)	Aquatic insects	Turkey	Streams	Heavy metal concentration related to taxa richness, abundance and diversity index	Diversity Toxicology	*Aeshna juncea* was a good bioindicator for Mn, Pb, and Ni; *Platycnemis pennipes* for Cd, B, Fe, and total hardness.
Goertzen & Suhling (2013)	Odonates	Germany	Ponds	Habitat variables (human disturbance, vegetation, substrate types, percentage of detritum, mud, etc.) related to taxa richness, abundance, diversity indices	Diversity	Vegetation increased taxa richness and evenness, but decreased dominance. Human disturbance was not a significant factor.
Hannon & Hafernik (2007)	*Ischnura gemina*	USA	Urban park creek	Population size, survivorship, longevity, oviposition, and dispersal	Diversity Behavioural ecology Life-history traits	Reintroduction of the endangered damselfly was successful only one year. Reintroduced males moved longer distances than the ones recorded in 1979 and 1983, before their local extinction. No oviposition observed at the end of the year.
Henriques-de-Oliveira et al. (2007)	Aquatic macroinvertebrates associated to *Typha domingensis*	Brazil	Lagoon	Taxa richness, abundance, community assemblage, diversity and similarity indices in sites with urban sewage input	Diversity Toxicology	Richness increased in site with less sewage input, but evenness decreased; trichopterans and ephemeropterans were characteristic of these sites. Abundance was positively related to sewage input; chironomids and oligochaetes were present in such sites. *Micrathyria* spp. and *Miathyria* sp. were found exclusively in the site with less sewage input.
Jara et al. (2013)	Predatory aquatic insects	Argentina	Pools	Relation of richness and abundance with hydroperiod of the ponds, physical features, vegetation and presence of fish	Diversity	Taxa richness peaked in early summer in ponds surrounded by forest. Presence of fish did not alter taxa richness significantly. The most frequent odonate species were *Rhionaeschna variegata* and *Cyanallagma interruptum*
Kalcounis-Rueppell et al. (2007)	Insectivorous bats and insects	USA	Urban stream system	Taxa richness, abundance, community structure (insects and bats) and foraging behaviour (bats) related to wastewater treatment plant effluent	Diversity Behavioural ecology	Dipterans, coleopterans, and lepidopterans were more abundant upstream; odonates were more abundant downstream. Wastewater effluent affected bat community structure, but not their foraging behaviour.
Karouna-Renier & Sparling (2001)	Aquatic macroinvertebrates	USA	Stormwater ponds	Metal concentrations in invertebrates, sediments, and water in relation to watershed land use	Toxicology	Zn and Cu concentrations in odonates were significantly higher in watersheds with commercial development. All concentrations were below lethal for fish diet. No differences in sediments and water concentration.
Kulkarni & Subramanian (2013)	Odonates	India	River	Taxa richness, relative abundance, diversity and similarity indices, and community assemblage along different land use types	Diversity	Community assemblage was significantly different among land use types and season, presenting high diversity and abundance in urbanised regions during the post monsoon season.
Kury & Christ (2010)	Odonates	Switzerland	Lotic and lentic waterbodies	Taxa richness and abundance	Diversity	A total of 42 species encountered, including two endangered (*Gomphus pulchellus* and *Gomphus simillimus*).
Lenders et al. (2001)	Higher plants, odonates, butterflies, fish, amphibians, reptiles, birds and mammals	The Netherlands	River floodplains	Taxa richness, diversity, protection status using BIO-SAFE method	Diversity	The BIO-SAFE biodiversity assessment method was developed based on several species of rivers and their floodplains, including 14 species of odonates. This method was tested in different ecotopes from urban floodplains, and showed that ecotope saturation (TES) and the actual ecotope importance (ATEI) scores must be taken into account to gain insight in the value of ecotopes for endangered species.
Lubertazzi & Ginsberg (2010)	Odonates	USA	Ponds	Community assemblage, taxa richness, and diversity indices along an urban-to-rural gradient	Diversity	Richness and evenness did not differ significantly between urban and rural sites; many species were more commonly found in urban sites with fish.
Lunde & Resh (2012)	Aquatic macroinvertebrates	USA	Ponds	Physicochemical features, habitat variables (vegetation composition, substrate, urbanisation percentage), taxa richness and abundance	Diversity Toxicology	The Index of Biotic Integrity (IBI) was developed using percent Ephemeroptera, Odonata, and Trichoptera (EOT); EOT richness; percent Tanypodinae/Chironomidae; Oligochaeta richness; percent Coleoptera; and predator richness. This method was negatively related to percentage of urbanisation and showed no significant bias with environmental gradients.
Mahato & Kennedy (2008a)	Aquatic macroinvertebrates	USA	Streams	Physicochemical features, taxa richness and abundance	Diversity Toxicology	Abundance was significantly higher in the urban stream, no differences in richness. Two odonate taxa found.
Mahato & Kennedy (2008b)	*Erpetogomphus designatus*	USA	Ponds	Survival, head width, total width, wing pad length and wet weight	Life-history traits	No survival in three sites (all of them in summer, two in spring). Growth rate was significantly higher in one of the urbanised sites.
Majumder et al. (2013)	Aquatic insects	India	Lakes	Taxa richness, abundance, diversity indices	Diversity	Hemipterans and odonates had the highest taxa richness.
Malherbe et al. (2010)	Aquatic macroinvertebrates	South Africa	River and tributaries	Physicochemical features, taxa richness, abundance, and community assemblages	Diversity Toxicology	Community assemblage in the main stem and its tributaries was significantly different due to abundance of chironomids and oligochaetes and low water quality. The polluted river had decreased sensitive taxa such as Atyidae, Naucoridae, Gomphidae and Leptoceridae.

Table S1 (continued).

Reference	Studied group	Location	Habitat type	Variables	Categories	Results summary
Martins et al. (2010)	*Phrynops geoffroanus* (Chelidae) and its prey	Brazil	River	Composition of stomach contents	Behavioural ecology	*Chironomus* sp. was the most frequent and abundant prey; odonate larvae, molluscs, fish and plants were present as well.
Matsura et al. (1998)	Odonates	Japan	Swimming pools	Taxa richness, abundance, life-history traits	Diversity Behavioural ecology Life-history traits	A total of 11 species were found, *Sympetrum striolatum imitoides* was abundant in all pools, since chironomids (their prey) are very abundant. Females lay their eggs directly on water and eggs hatch before other dragonfly species, which also increases their abundance.
Matsura et al. (1995)	Odonates	Japan	Swimming pools	Taxa richness and abundance, survival, predation	Diversity Life-history traits	*Sympetrum striolatum imitoides* was the most abundant in all pools, which fed on chironomid larvae. They emerge in May-June and deposit eggs directly on water in October, coinciding with non-use period of the pools. Male established their territory for 1–18 days.
Monteiro et al. (2013)	Odonates	Brazil	Streams	Taxa richness, abundance and community assemblage with and without riparian vegetation	Diversity	A total of 32 species were found. *Erythrodiplax basifusca* and *Argia* sp. were associated with deforested streams, hence could potentially be used as bioindicators for deforestation from creation of new roads.
Moreno et al. (2009)	Aquatic macroinvertebrates	Brazil	River and tributaries	Taxa richness, abundance, and community assemblage using BEAST method	Diversity	Community assemblage allowed site classification in four categories: natural, altered, highly altered and degraded. Sites in the degraded category were near urban sites. Calopterygidae and Gomphidae represented non-impacted sites.
Mostert (1998)	Odonates	The Netherlands	Waterbodies in meadows, arable land, nature reserves, recreational areas and urban areas	Taxa richness, population density, water turbidity	Diversity	Taxa richness and density were negatively related to turbidity and positively related to riparian vegetation. Natural areas were the most diverse. However, richness was higher in urban sites than in agricultural areas.
Murdoch (1989)	Odonates	United Kingdom	Lotic and lentic waterbodies	Taxa richness	Diversity	A total of 11 species were found, five of them were probably breeding.
Neiss et al. (2008)	*Microstigma maculatum*	Brazil	Pond	Not defined	Diversity	The larval description of the species was made.
Nelson (2011)	Aquatic macroinvertebrates	USA	Drainage	Taxa richness, abundance, community assemblage, hydrology features (velocity, depth, width) and water quality measurements before and after a treatment plant	Diversity Toxicology	Wastewater input increased flow and abundance, but decreased conductivity and taxa richness. Tributary communities, which were associated with high conductivity, were taxa-rich compared with other groups and tended to contain odonates and a variety of dipteran and beetle taxa.
Nummelin et al. (2007)	Predatory aquatic insects	Finland	Ponds	Heavy metal concentration in dragonflies, antlions, waterstriders and ants, both polluted and control sites	Toxicology	All demonstrated to be good indicators for heavy metal pollution, although ants were the least effective. Waterstriders displayed high levels of Fe and Mn; antlions and odonates for Fe and Cd; antlions and ants for Pb and Mn.
Osada & Tabata (1992)	Odonates and aquatic plants	Japan	Pond	Taxa richness and abundance, succession (hydrophytes) and dispersal (odonates)	Diversity Behavioural ecology	Odonate richness increased after improvement of the pond, aquatic plants established there as well. Five distribution patterns were described.
Poulton et al. (2003)	Aquatic macroinvertebrates	USA	River	Water quality metrics, taxa richness and diversity indices	Diversity Toxicology	One third of the taxa collected belonged to the sensitive EPOT insect orders (Ephemeroptera, Plecoptera, Odonata, and Trichoptera). However, Trichoptera abundance decreased downstream, next to a large city, whereas Oligochaeta relative abundance increased. Water quality metrics were particularly low downstream as well.
Principe & Corigliano (2006)	Aquatic macroinvertebrates	Argentina	River	Biomass, taxa richness, and diversity indices in rural and urban sites	Diversity	Marginal fauna was more diverse than in benthos and drift. Rural sites had higher biomass and abundance, yet urban sites showed higher richness. Odonates were mostly representative of marginal fauna, both in urban and rural sites, except for *Aeshna* sp., which was only found in urban sites.
Pryke & Samways (2009)	Plants and invertebrates	South Africa	Natural and recovering forests (riverine and non-riverine), natural and recovering fynbos, botanical gardens and alien pine plantations	Taxa richness and abundance, species accumulation curves, non-parametric estimators of richness, community assemblage	Diversity	Pines had low taxa richness and abundance. Gardens provided refugees in urban areas for invertebrate diversity. Odonates and lepidopterans were more commonly found in fynbos and botanical gardens.
Pujol-Luz (1987)	Odonates	Brazil	Urban water cisterns	Taxa richness and abundance	Diversity	Twenty species of odonates were found, mostly during the month of November.
Rivera Rondón et al. (2010)	Algae, zooplankton and aquatic macroinvertebrates	Colombia	River-floodplain systems	Physicochemical features, community assemblage, taxa richness, abundance, and diversity indices	Diversity Toxicology	Most systems showed low levels of pH, nutrients and ions. Dominant algae were Bacillariophyceae and Zygnemaphyceae; coleopterans, odonates and ephemeropterans were the most abundant in all communities, and were more diverse in substrates rich in leaf litter.
Rizzoni et al. (1995)	Aquatic macroinvertebrates and *Vicia faba*	Italy	River	Community assemblage, diversity indices, taxa richness, biomass and micronucleus frequency	Diversity Toxicology	Micronucleus frequency increased towards the city centre, as well as invertebrate biomass, but diversity decreased. Only two odonate taxa were reported.
Sacha (2011)	Odonates	Slovakia	Garden pond	Taxa richness, abundance, and population size	Diversity	Three species were found at first, *Aeshna cyanea* was the most abundant. After a year, the other species were outcompeted or eliminated by predation. Abundance grew up to 1 individual per litre.
Saito & Owada (2005)	Odonates	Japan	Garden pond	Taxa richness and abundance	Diversity	A total of 18 species were enlisted, including the rare damselfly *Ceriagrion nipponicum*.
Samraoui et al. (1992)	Plants, odonates and birds	Algeria	Lake	Taxa richness and vegetation composition	Diversity	A description of the vegetation composition and structure was made, as well as an inventory of 45 bird species and 23 odonates.

Table S1 (continued).

Reference	Studied group	Location	Habitat type	Variables	Categories	Results summary
Samways & Steytler (1996)	Odonates	South Africa	A river through plantation forests, residential areas, parklands, and industrial areas	Environmental data, taxa richness and abundance, species accumulation curves, non-parametric estimators of richness, community assemblage	Diversity	Industrial areas were the second lowest taxa richness, but had the highest abundance in anisopterans. Parks, on the other hand, were the highest in zygopteran richness and abundance.
Sato et al. (2008)	Zygoptera	Japan	Rice paddies, natural and man-made ponds	Genetic variability	Diversity Behavioural ecology	No significant differences in genetic diversity in urban and rural populations. However, genetic differentiation was significantly higher in urban populations, meaning that dispersal is limited.
Scolozzi & Geneletti (2011)	*Muscardinus avellanarius, Sitta europaea, Erinacaeus europaeus, Lanius collurio, Rana synklepton esculenta,* and *Calopteryx virgo*	Italy	Valley	Probability of occurrence according to their breeding, survival, dispersal, habitat unsuitability and hostility	Diversity	Habitat suitability models were used for mapping the impact of urban land use.
Silva et al. (2010)	Odonates	Brazil	River	Physicochemical features, ecological quality, taxa richness and abundance up- and downstream	Diversity Toxicology	*Argia modesta* was abundant upstream; taxa richness and abundance were affected by seasonality and lack of riparian vegetation.
Sinclair et al. (2012)	Invertebrates	Canada	River	Methylmercury concentration in sediment, water and invertebrates	Toxicology	MeHg concentration in sediment, water and invertebrates was higher in the newest (urban) wetlands. Odonates were significantly greater in wetlands equal to or less than 2 years old. Odonate MeHg concentrations from new and old wetland were not significantly different.
Smith & Lamp (2008)	Aquatic insects	USA	Streams	Community assemblage, taxa richness, abundance, diversity and similarity indices in urban and rural watersheds	Diversity	Taxa richness and diversity were lower in urban sites. However, urban sites had high similarity in both headwater and main-stem communities, unlike rural sites. The unique headwater taxa in urban headwater streams belonged only to Odonata (*Ischnura* spp. and *Calopteryx maculata*) and Diptera (*Aedes* and *Odontomyia*).
Solimini et al. (1997)	Zygoptera	Italy	River	Water quality metrics, community assemblage and life-history traits	Diversity Toxicology Life-history traits	Damselfly assemblage was mostly formed by generalist species found in lentic habitats. *Ischnura elegans* and *Erythromma* (= *Cercion*) *lindenii* were the most abundant in highly polluted wetlands, presenting a longer reproductive period, absence of diapause, and tolerance of low oxygen concentration.
Srinivasulu & Srinivasulu (2005)	Bats and their prey	India	Forest caves and urban sites	Composition of faecal pellets	Behavioural ecology	All studied samples contained mostly insects and spiders, including odonates. Forest bats presented opportunistic feeding behaviour, while urban ones were selective with their prey.
Steytler & Samways (1995)	Odonates	South Africa	Artificial park pond	Biotope preference, taxa richness	Diversity Behavioural ecology	Stenotopic species were highly sensitive to changes in sunlight, water flow and vegetation structure. Yet, taxa richness increased over 100% after the creation of the pond.
Suh & Samways (2005)	Odonates	South Africa	Stream in an urban reservoir	Taxa richness, community assemblage, habitat variables (shade, vegetation structure and composition, substrate, etc.)	Diversity	Taxa richness doubled after implementation of the reservoir. The most important factors determining species assemblage were vegetation structure and composition, percentage shade, submerged vegetation, water flow and amount of open water.
Suhling et al. (2009)	Odonates	Germany	Lotic and lentic waterbodies	Species richness, abundance and population trends	Diversity	A total of 51 species were found. *Sympetrum pedemontanum, Coenagrion pulchellum, Ischnura pumilio* and *Sympetrum danae* had declined, although species like *Sympecma fusca, Gomphus vulgatissimus, Ophiogomphus cecilia, Orthetrum brunneum* and *Orthetrum coerulescens* had increased in a period of almost 30 years.
Uboni et al. (2006)	*Cordulegaster heros*	Italy	Stream	Not defined	Diversity	A population of *Cordulegaster heros* was found in an urban stream, where it co-occurs with *Cordulegaster bidentata* and *Calopteryx virgo*.
Van de Koken et al. (2007)	*Pantala flavescens*	Brazil	Parking areas	Eggs laid, occurrence frequency, amount of cars in the parking area, light/dark car ratio	Behavioural ecology	*P. flavescens* occurrence was positively related to the amount of cars found in the parking area. There was also a preference towards light coloured cars. Oviposition was recorded on the hood surfaces, which represents an energy loss for the females.
van Laar (1999)	*Calopteryx splendens*	The Netherlands	Streams	Population density	Diversity	*C. splendens* had disappeared around 1970 due to pollution and deforestation. After mitigation measures, the species recolonised the area, including urban sites.
Watts et al. (2004)	*Coenagrion mercuriale*	United Kingdom	River	Genetic variability	Diversity Behavioural ecology	Genetic differentiation was significant throughout sampling area, thus species is mostly sedentary. Urban areas made a barrier effect and limited their dispersal.
Willigalla & Fartmann (2012)	Odonates	Central Europe	Cities	Taxa richness and city area	Diversity	Taxa richness is positively related to city size, but decreases towards city centres.
Willigalla & Fartmann (2009)	Odonates	Germany	Rain-storage ponds	Taxa richness, abundance, community assemblage and similarity index	Diversity	A total of 32 species were recorded. Richness increased in suburban ponds and was positively related to pond size. Similarity index was negatively related to distance between ponds.
Willigalla et al. (2003)	Odonates	Germany	Rain-storage ponds	Taxa richness	Diversity	A total of 27 species were recorded. Exposure to sunlight and vegetation structure defined odonate diversity.
Wilson (1997)	Odonates	China	Streams	Taxa richness and abundance	Diversity	Two sites were particularly rich in Gomphidae and Macromiidae species.
Yu et al. (2013)	Zooplankton and aquatic macroinvertebrates	China	River	Polychlorinated biphenyl (PCB) concentration in invertebrates	Toxicology	Zooplankton presented the highest PCB levels, followed by soil-dwelling invertebrates. Chironomids and odonates had high concentrations of mid-chlorinated congeners (PCB-153 and PCB-138).