



MAJOR REVIEW

Biases of Odonata in Habitats Directive: Trends, trend drivers, and conservation status of European threatened Odonata

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Abstract. 1. Dragonflies and damselflies, within the order of Odonata, are important ecological indicators with widely recognised conservation value. They are generally better researched and protected than other invertebrates, yet, they have received limited protection from the European Union (EU)'s Habitats Directive, which serves as the major legislative tool for species conservation in Europe.

2. We reviewed the conservation status and trends, legal protection status, and knowledge gaps of Odonates within the EU. Among the 22 threatened and 27 endemic species in EU, respectively 19 and 11 of them are not protected by the Directive. Out of the 35 species which are threatened and/or listed on the Annexes, 61.5% of them are declining.

3. Nevertheless, threatened non-Annex species are more likely to have a decreasing population trend than Annex species. There are also 26% of threatened non-Annex species with unknown trends. Inaccuracies in evaluating Odonata trends are also revealed due to the lack of standardised methodology and incomplete surveys.

4. Moreover, most conservation research focuses on climate change's effects on range shift, therefore knowledge gaps exist in understating how water and habitat qualities, the most important Odonate trend drivers, shape Odonata conservation status.

5. There is an urgent need to revise the legal protection status of Odonata in Europe, for instance by revising the EU Habitats Directive Annexes to include threatened damselflies and dragonflies.

6. There is also an urgent need for systematic, standardised, and regular survey to be able to investigate trends and drivers of change to identify priority conservation actions.

Key words. Conservation priority, damselflies, dragonflies, endangered species, environmental policy, European Union, Habitats Directive, Odonata, Red List.

Introduction

Dragonflies and damselflies (order Odonata) are important ecological indicators and provide irreplaceable ecological functions. Their value as ecological indicators stems from their sensitivity to environmental stressors (Harabis & Dolny, 2010) and their relative identification ease (Kalkman *et al.*, 2010). They are ecologically important because they help structure many freshwater ecosystems as predators in both larval (Thorpe & Cothran, 1984)

and adult (McPeck, 1998) stages, particularly in fishless wetlands as the top predators (Batzer & Wissinger, 1996; McPeck, 1998). They are also essential food resources for fish and amphibians (Caldwell *et al.*, 1980). As they inhabit diversified aquatic and terrestrial environments (Clausnitzer *et al.*, 2009), they are frequently studied to evaluate environmental changes in many freshwater (Kalkman *et al.*, 2010) and urban habitats (Villalobos-Jimenez *et al.*, 2016). Their distribution and biodiversity are therefore relatively well studied compared to other invertebrates (Sahlén *et al.*, 2004; Kalkman *et al.*, 2010). Odonates' ecological importance and their aesthetic appearance make them popular with both scientists and the public. Along with butterflies, Odonata are among the few insect taxa with comprehensive conservation plans and assessments in Europe (Clausnitzer *et al.*, 2009).

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In Europe¹, 135 species have been described, including 14 endemic species (Kalkman *et al.*, 2010). Nevertheless, the fragmented natural landscape and intense human activities, such as pollution, river canalisation, agricultural intensification, and deforestation, have significantly reduced the European Odonata biodiversity in the mid-20th century (Kalkman *et al.*, 2008, 2010). Currently, 22 Odonata species are considered threatened with extinction within the EU by the International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species, with 3 critically endangered (CR), 5 endangered (EN), and 14 vulnerable (VU) (Kalkman *et al.*, 2010).

The EU Habitats Directive, adopted in 1992, sets out the major goals and mandatory national actions to protect prioritised endangered and endemic European species, including Odonates (European Commission, 2016). Nevertheless, the distribution of species listed in the appendices of the Habitats Directive are geographically biased towards the Central and Western European countries and therefore often ignores the more threatened Odonates in Southern and Eastern Europe (Cardoso, 2012). Furthermore, threatened Odonates' biodiversity trends are still unclear in many European countries (van Strien *et al.*, 2013a, 2013b).

European conservation legislation has been criticised for not adequately protecting European threatened species (Cardoso, 2012; Hochkirch *et al.*, 2013a; Kalkman *et al.*, 2018). Despite the clear mismatch between conservation needs and conservation priorities within EU legislation, it is controversial whether the Habitats Directive should be revised in the planned 2020 Reporting (European Commission, 2017). Supporters argue that it is wasting time, money, and personnel to exclude the most threatened species (Cardoso, 2012) as Habitats Directive is the most effective mechanism to ensure conservation success (Hochkirch *et al.*, 2013b). Opponents argue that any amendments on the species listed on the Annexes (hereafter Annex species) would need to be agreed upon by the European Commission which may incur complex political negotiations and risks of weakening the complete Directive. Revising the Habitats Directive now may be counterproductive and divert resources from established conservation management (Maes *et al.*, 2013).

This review evaluates the current mismatches in Odonates' conservation and trend knowledge gaps. In the first part, the mismatch between conservation policy and needs is discussed by comparing IUCN extinction risk assessment and EU's priority species and evaluates whether revisions on the Habitats Directive are needed. In the second part, European threatened and Annex Odonates' known trends are summarised to identify the current unknowns and gaps in conservation research. In the third part, solutions to reduce mismatches by bridging the conservation reality and needs are recommended.

Materials and methods

A systematic review on prior work regarding European threatened and Annex Odonata trends was conducted. Through a

¹This review discusses Europe as European Union 27 (2007–2013) (EU) ("The History of the European Union"; Europa, 2018) due to the availability of data and the ease of applying the broader EU policies.

systemic search on the Web of Science database on 31 October 2017 using standardised terms (drangonfl* OR damselfl* OR odonata*) AND (trend* OR status OR population OR extinction OR distribution OR range OR increas* OR decreas* OR stabl*) in post-2000 papers' abstract, 2139 papers were retrieved, and 194 papers related to European Odonata trend, status, and conservation were identified. Twenty-eight papers (14.4%) were related to threatened and Annex Odonates' distribution. There were also another 28 papers related to the European Odonata trend, including 11 (39.3%) which mentioned threatened and Annex species' trends.

Supplemented with the trend data (2007–2012) from the 2013 Habitats Directive Reporting and the 2010 IUCN European Assessment of Odonata Red List (Kalkman *et al.*, 2010), these primary literature data are summarised to provide the drivers of change and trends in population and distribution of threatened and Annex Odonata. To understand the conservation value of the Habitats Directive, the trends of abundance and range of Annex species are compared against non-Annex species. To further understand the origins of mismatches and unknown gaps between different sources, broader literature about EU Habitats Directive and detailed methodology of Habitats Directive Reporting were consulted. These literatures were eventually summarised to provide suggestions for future conservation efforts and amendments in the Habitats Directive.

Results and discussion

Biases in legislative conservation status of threatened Odonata

Current European Legislation. Species in Annex II of the EU Habitats Directive should have core areas of their habitat protected under the Natura 2000 Network and the sites managed in accordance with the ecological requirements of the species. This is crucial for small and fragmented threatened populations (Kalkman *et al.*, 2010). Species in the Annex IV must be strictly protected throughout their range. There are respectively two and five species exclusively (Fig. 1).

Mismatch between annex and threatened species. The strongest criticism to the Habitats Directive is on its geographical bias. Southern Europe has the highest endemism (Sahlén *et al.*, 2004; Cardoso, 2012), highest diversity (Cardoso, 2012), and most threatened species (Sahlén *et al.*, 2004; Kalkman *et al.*, 2010) of Odonata, yet most Annex species are Central and Northern European species (Sahlén *et al.*, 2004; Cardoso, 2012). The geographical bias in the Habitats Directive may result in geographical hotspots of species extinction (Cardoso, 2012). An imbalance in conservation resources across countries may also undermine the effectiveness of regional conservation implementation and cross-countries cooperation (Schmeller *et al.*, 2008).

Only 3 out of 22 species of globally threatened Odonates occurring in the EU are included in the Annexes of the Habitats Directive, the remaining 19, including 3 Critically Endangered and 6 Endangered species do not enjoy a legal protection status according to EU law (Table 1). In terms of endemism, out of the 14 EU27 endemic species (Kalkman *et al.*, 2010), only three

Table 1. The number and percentage of European Odonata species listed on the two annexes of the habitats directive (II and IV) in each IUCN Red List category (European Commission, 2016).

	II, IV	II	IV	Not listed	Total
Odonata species listed as threatened on the IUCN Red List					
Critically endangered				3 (100%)	3
Endangered				6 (100%)	6
Vulnerable			3 (23%)	10 (77%)	13
Odonata species listed as not threatened on the IUCN Red List					
Near threat	4 (45%)	2 (22%)	3 (33%)		9
Least concern	2 (50%)		2 (50%)		4

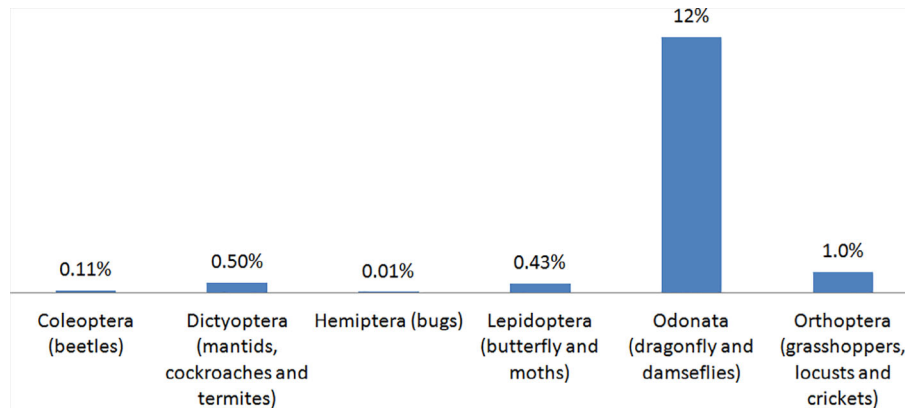


Fig. 1. A comparison of the percentages of species included in the Annexes of the Habitats Directive across different invertebrate taxonomic groups (European Commission, 2016). The percentage is calculated from the total number of European species as predicted by Fauna Europaea (Fauna Europea, 2016).

are included in the Annexes (*Gomphus graslinii*, *Cordulegaster trinacriae*, and *Macromia splendens*), and only one is listed by the IUCN Red List as globally threatened (*M. splendens*). The under-representation of threatened species is contrary to the intended goal of the Habitats Directive to focus European conservation efforts to prevent biodiversity declines, especially of species of community importance (European Commission, 2016).

These mismatches are historical legacies of the Bern Convention (1979). As the Habitats Directive’s drafting was conceptualised from the Bern Convention (European Commission, 1992), it is biased towards the then-declining Western European Odonates (Kalkman *et al.*, 2010). Since then, many of these then-declining species have shown strong recovery following the habitat restoration in Central and Western Europe (Kalkman *et al.*, 2010), yet the Habitats Directive is not regularly updated with these population changes (Hochkirch *et al.*, 2013a). As a result, there have been debates on whether the Annexes should be revised, and the following section discusses the validity of these arguments.

Distribution discrepancy between annex and threatened species. Opponents to a revision on the Habitats Directive suggest that by protecting previously threatened Annex species, their threatened habitats and all EU threatened species will also be protected (Kalkman *et al.*, 2010; Maes *et al.*, 2013). Nevertheless, this assumption lacks empirical evidence. Firstly, these

habitats often do not represent currently threatened habitats. Annex species’ past decline was driven by watercourses mismanagement and water pollution in Western and Central Europe (Hassall *et al.*, 2010; Kalkman *et al.*, 2010), yet the water quality of these regions has improved greatly since the 21st century (Kalkman *et al.*, 2018), as suggested by several longitudinal Odonata studies (Swaegers *et al.*, 2013; Powney *et al.*, 2015; Termaat *et al.*, 2015; van Strien *et al.*, 2016). Nevertheless, in Southern Europe, water resource over-exploitation, diffuse pollution, and watercourse degradation are still serious issues (Moss, 2008; Barrios *et al.*, 2014). While previously threatened habitats in Western and Central Europe are no longer the most threatened, severely threatened habitats in Southern Europe remain largely unprotected from over-exploitation and pollution.

Secondly, the ranges of Annex and threatened species seldom overlap due to the geographical bias of the Habitats Directive. While Annex species cluster in the Western, Central, and North-eastern Europe, most of the threatened species have the core of their range in Southern Europe. Only 3 out of the 22² threatened species have a significant proportion of their range covered by the Habitats Directive (Kalkman *et al.*, 2018). Furthermore, most of the threatened species have small ranges, therefore these ranges generally have little overlap with non-threatened ones (Kalkman *et al.*, 2018), invalidating the assumption of surrogacy in protection between Annex and non-Annex

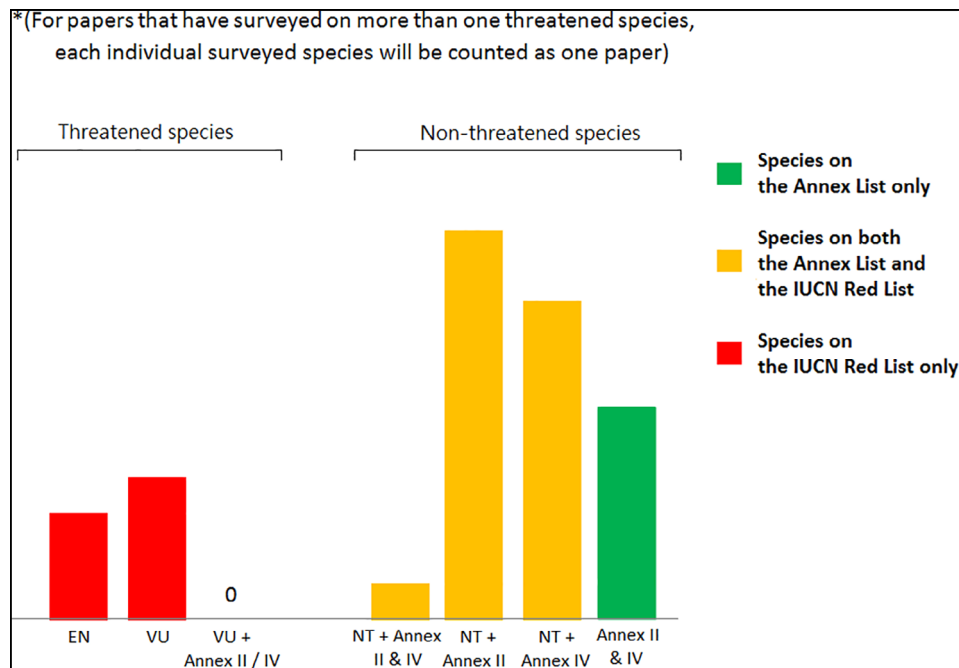


Fig. 2. Number of peer-reviewed papers investigating the diversity drivers of threatened and non-threatened European Odonata species. These species are further categorised according to their IUCN Red List Categories and whether they are listed on the Annexes.

threatened species. As a result, most threatened Odonata do not benefit from the Habitats Directive neither directly nor indirectly (Fig. 1).

Research focus on annex species. Proponents who support revising the Habitats Directive believe that monitoring and conservation action resources are misallocated to less-threatened species (Hochkirch *et al.*, 2013a). Our literature review shows that Annex species indeed dominate conservation research. Among the 28 peer-reviewed papers investigating threatened and Annex Odonates' diversity drivers, covering 34 populations, almost 80% papers discuss non-threatened Annex species (shown on the right in Fig. 2). There is 1 paper discussing near threatened (NT) species on both Annexes (Boda *et al.*, 2015b), 11 for NT species on Annex II (Watts *et al.*, 2004, 2005, 2006; Rouquette & Thompson, 2005, 2007; Jaeschke *et al.*, 2013; Allen & Thompson, 2014; Harabis & Dolny, 2015; Lorenzo-Carballa *et al.*, 2015; Tichanek & Tropek, 2016), 9 for NT species on Annex IV (Keller *et al.*, 2009, 2010; Bolliger *et al.*, 2011; Jaeschke *et al.*, 2012, 2013; Suhonen *et al.*, 2013; Goertzen & Suhling, 2015; Andersen *et al.*, 2016), and 6 for least concern species which are on both Annexes (Hacet & Aktac, 2008; Mauersberger, 2010; Harabis & Dolny, 2012; Jaeschke *et al.*, 2013; Goertzen & Suhling, 2015). Meanwhile, only 20% papers discuss threatened species (shown on the left in Fig. 2). There are three papers discussing endangered species (Leipelt, 2005; Mueller, 2008; Matushkina *et al.*, 2016) and four for vulnerable species (Hacet, 2009; Dolny *et al.*, 2013, 2014; De Knijf *et al.*, 2016). There are no papers discussing species which are both threatened and on the Annexes. The above analysis suggests that

policy priorities but not the threat level of a species shape research priorities for Odonate species. Therefore, there are often knowledge gaps about the trends and trend drivers of non-priority species, which we further elaborate on below.

Inadequacy in current knowledge of Odonata trend

Trends and trend drivers. Understanding trends and trend drivers is important to design and evaluate conservation policies. The IUCN Red List provides estimated trends and threats for each European Odonata species (Kalkman *et al.*, 2010). Specifically for the Annex species, the Habitats Directive requires all countries to report their conservation status and trends every 6 years with supporting data including population size (European Environment Agency, 2015), though in practice this data is rarely available for Odonates (European Commission, 2017). Data from the literature provide supplementary knowledge about their population status and trends, especially trends in range extent and trend drivers. Threatened and Annex Odonates' current known trends and present major trend drivers are summarised in Supporting Information Table S1.

Known Odonata trends. The trend evaluations from the IUCN Red List assessments, Habitats Directive Reporting, and primary literature usually agree with each other (Supplementary Table 1). Through extensive community-scale and national-scale surveys, they provide complementary data particularly for VU and Annex species. In particular, all Annex species have well-known

population and trends and range shifts, except there is no range shift data for *Coenagrion hylas* and *Cordulegaster heros*. With regards to threatened species, most of them have known trends (77.3%), with 15 decreasing, 2 stable, and none increasing. Meanwhile, about a quarter of all threatened species (27.3%) had known geographic range changes. They are both expanding northwards and southwards, with an overall increase in areas of suitable habitats. Nevertheless, there are several local extinction records.

Out of the 35 threatened and Annex species, most threatened and Annex species (61.5%) have a decreasing trend. Nevertheless, Annex species are more likely to have an increasing or stable trend than non-Annex species (Fig. 3), which stresses the need to consider a revision of the Annexes to shift conservation attention towards threatened non-Annex species. There is only one increasing species, *Gomphus flavipes*, which is listed on Annex IV. Nevertheless, by comparing the VU category, within the same threatened category Annex species still outperform non-Annex species. Among VU species, only 10% non-Annex species have a stable trend, while 33.3% Annex-species are stable. Therefore, Annex species are better conserved both within and across the threatened categories in the IUCN Red List.

Most threatened and Annex Odonata species (62.5%) are shifting northwards. There is no significant difference between the direction of range shift among Annex and non-Annex species. Nevertheless, among the 8 non-threatened Annex species with data on change in range size, 7 of them have an increasing range. In comparison, only 2 non-Annex threatened species have expanded their range albeit one of them has at the same time a decreasing population (*Sympetrum depressiusculum*).

To summarise, it appears that Annex species are both in a better conservation status and better monitored. The Habitats Directive appears to be an effective conservation tool for listed species, but not for other Odonates which appear disproportionately threatened and less well monitored and known.

Known Odonata trend drivers. IUCN and primary literature identify five major drivers for the trends of Odonata species. They include water management (including dam construction,

river regulation, etc.), water pollution (including urban, domestic and industrial pollution, etc.), habitat alternation (including forest destruction, habitat restoration, and destruction due to urbanisation and tourism), climate change (including changing temperature, increased droughts, habitat alternation due to climate change, etc.), and agriculture (including wetland conversion to farmland, agriculture pollution, fish aquaculture, livestock tramping, etc.).

Water and habitat qualities are the two most important trend drivers of threatened and Annex species (Fig. 4). This agrees with the empirical evidence of the correlation between population changes and water and habitat conditions. In the mid-20th century, European Odonata declined significantly due to worsening water (Hassall *et al.*, 2010; Kalkman *et al.*, 2010) and habitat quality (Suhonen *et al.*, 2010) under economic intensification. Currently, due to improved management of waterways and wetlands (Hickling *et al.*, 2005; Kalkman *et al.*, 2008, 2010; Powney *et al.*, 2015; van Strien *et al.*, 2016) and improved habitat quality (De Knijf *et al.*, 2001; Swaegers *et al.*, 2013), most Odonata that are both non-threatened and non-Annex species are recovering. The IUCN Red List assessments also conclude similarly that water quality is important both European threatened and non-threatened Odonata diversity (Kalkman *et al.*, 2010).

Climate change is the third most important trend driver after water and habitat quality. This is due to the fact that Odonates are sensitive to water conditions (Harabis & Dolny, 2010). Therefore, extreme rainfall (Fleener & Sahlen, 2008), increased flooding (Powney *et al.*, 2015), and droughts (Kalkman *et al.*, 2010) can significantly reduce species abundance. Odonata's origin in the Carboniferous, a geological period dominated tropical climate, also results in their sensitivity to environmental warming (Pritchard & Leggott, 1987). As a result, Odonates response drastically towards changes in the climate.

Range shift of Odonates are particularly prevalent because they have high dispersal abilities and generalised niches. Odonates shift polewards faster than other taxa under climate change (Hickling *et al.*, 2006), with a mean 74 km northward shift from 1960 to 1995 in UK (Hickling *et al.*, 2005), and similar northward shifts across Europe such as Scotland (Fitt & Lancaster,

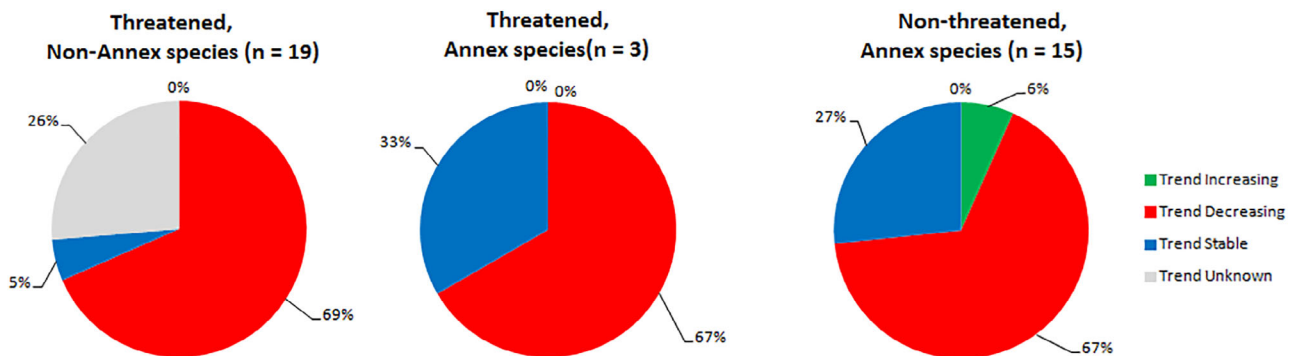


Fig. 3. The comparison of the percentage of different trends for European Odonata species which are threatened but not on the Annexes of the Habitats Directive (left), threatened and on the Annexes (centre), and non-threatened but on the Annexes (right). Their trends were evaluated by IUCN (Kalkman *et al.*, 2010), yet the evidence is tenuous as many trends of threatened, non-Annex species are unknown.

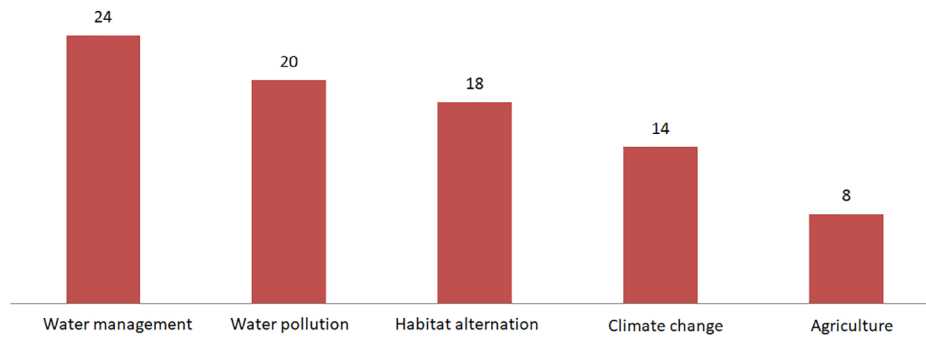


Fig. 4. The frequency of trend drivers identified as the major trend drivers for each European threatened and Annex Odonata species. Major trend drivers are identified from the evaluation by IUCN (IUCN, 2017a) and different primary literature sources listed in Supporting Information Table S1.

2017), Germany (Ott, 2010), Belgium (De Knijf *et al.*, 2001), and the Netherlands (van Strien *et al.*, 2016). In particular, Southern species are generally more responsive to climate change under the severe habitat loss and degradation in Southern Europe (Swaevers *et al.*, 2013; Powney *et al.*, 2015). Supporting Information Table S1 suggests that these range shifts have significantly altered the distribution of threatened and Annex Odonates in Europe, potentially undermining protected areas' effectiveness in conserving Annex II species as their legally protected habitats are shifting under climate change.

Knowledge gaps for the conservation of threatened and annex Odonates

Unknown Odonata trends. There is a lack of trend data for threatened Odonata species. For all CR and most EN species (85.7% of all European EN Odonates), there is no peer-reviewed primary literature data on their trends of abundance and range shift (Supporting Information Table S1). A significant proportion of non-Annex threatened species' trends (26%) also have unknown trends in the IUCN Red List assessments (Fig. 3). Even for Annex species which generally have more data, two out of three VU Annex species do not have population abundance data in the Habitats Directive Reporting. *Coenagrion hylas*, the only VU species with abundant data, is better surveyed and understood because it has only 14 fixed reproducing sites in Austria (IUCN, 2017a), suggesting the lack of comprehensive surveying for widespread species.

Furthermore, the available trend knowledge is geographically biased. The Habitats Directive Reporting lacks participation from Greece (European Environment Agency, 2015) which has the highest Annex Odonata diversity, including *Lindenia tetraphylla*, *C. heros*, and *Ophiogomphus cecilia* which are on both Annexes and *Coenagrion ornatum* on Annex II (Kalkman *et al.*, 2018). Furthermore, excluding France (van Strien *et al.*, 2013b), Belgium (De Knijf *et al.*, 2001), the Netherlands (Collins & McIntyre, 2015), UK, and Ireland (Hickling *et al.*, 2005; Powney *et al.*, 2015), most countries do not have detailed Odonata population distribution maps (van Strien *et al.*, 2010). As a result, the most accurate trends are usually from Western

European countries with comparatively lower threatened Odonata diversity (Kalkman *et al.*, 2018). The mismatch between national Odonata diversity and the countries' trend knowledge can potentially limit the effective uses of conservation resources in countries with the highest national Odonata diversity.

There are also several mismatches between the evidence provided by the Habitats Directive Reporting (2013), primary literature and the IUCN Red List assessments (2010). Many species have contrasting evidence for different trends, mostly stable and decreasing trends. In particular, four of them have evidence for both increasing and decreasing trends, including *S. depressiusculum*, *C. mercuriale*, *C. ornatum*, and *G. graslinii*. This may be explained by the fact that these species' ranges have shifted in the recent decades under climate change (Supporting Information Table S1); furthermore, it is possible that they have different trends in northern and southern ranges (Hickling *et al.*, 2005; Grewe *et al.*, 2013; Powney *et al.*, 2015). For example, *C. mercuriale*'s range shifted 22 km northwards from 1960 to 1995 (Hickling *et al.*, 2005) and 2.55 km southwards from 1988 to 2006 (Grewe *et al.*, 2013). It is likely that insufficient monitoring efforts, especially in Southern Europe, might bring biases and inaccuracies in the estimation of population trends and range extent.

Across taxonomic groups, evaluating an accurate trend is difficult. Insects are especially hard to survey because of their typical larger range and smaller size (Clausnitzer *et al.*, 2009). As a result, most changes in trend are often non-genuine caused by increasing sampling efforts and knowledge (European Environment Agency, 2015). For Odonates, trend evaluation is usually based on expert opinion, population projection from a monitored small population, and whole species' complete surveys (Maes *et al.*, 2013; European Commission, 2017). For threatened species with limited knowledge on their distribution and habitats, these methods may further yield biased results. Expert opinions rely significantly on the current understanding of the species, and may be significantly biased due to previous insufficient sampling (IUCN, 2017b), limited sampling in urbanised ecological communities (Villalobos-Jimenez *et al.*, 2016), and remote mountain regions (Sahlén *et al.*, 2004). Population projection may be unrepresentative of the whole population of the species (Maes *et al.*, 2013), as these monitored populations are often inhabiting in long-term research sites which have better

environmental quality (Brereton *et al.*, 2011). Furthermore, as Odonata range extends across countries, and different countries vary significantly in their conservation effectiveness (Kalkman *et al.*, 2010), regional trends cannot represent a comprehensive Odonata trend. Complete surveys can give the best trend evaluation, yet its implementation is undermined by the unknown population distribution in many countries (van Strien *et al.*, 2010). Moreover, there are currently no standardised monitoring and trend evaluation methods for Odonata, resulting in inaccurate multi-national trends (van Strien *et al.*, 2010) which discourage comparison and trend verification between countries.

In particular, Annex species despite having more data on their trends, accuracy is still an issue as Habitats Directive Reporting relies significantly on the less accurate expert opinion and population projection (Fig. 5). The trends of larger populations, which are usually more stable (European Environment Agency, 2015), are mostly evaluated using population projection (78.3%). Only 6.33% evaluations are complete surveys, and mostly on very small (size < 100) populations (60%) (European Commission, 2017). Complete surveys on smaller populations are more feasible yet comparatively much less informative (van Strien *et al.*, 2013a). As a result, the validity and accuracy of Habitats Directive Reporting are debatable.

The lack of accurate surveying in major large populations has undermined the previous Reporting's accuracy. Comparing to the last 2007 Reporting, the 2013 Habitats Directive Reporting is more accurate, as suggested by that fact that 70.3% of trend changes between the two Reports are non-genuine changes due to corrections of previous inaccuracies with better data and evaluation methods (Fig. 6). This is especially important for major population evaluation as they have increasingly adopted more accurate methods (European Commission, 2017). Still, this suggests the current lack of representative data and complete surveys will indeed lead to inaccuracies in trend evaluation. The above analysis reflects that not only are there many known gaps in the trends of threatened and Annex species, the lack of knowledge towards Odonata ecologies, inaccuracies of and the lack of standardisation in evaluation methods across countries also result in unknown gaps in Odonata trends.

Unknown Odonata trend drivers. There is a mismatch between dominant Odonata research field areas and the most important Odonata trend drivers. For both threatened (Fig. 4) and non-threatened (Kalkman *et al.*, 2010) species, the most important trend drivers are water and habitat qualities. Nevertheless, most previous studies have focused on climate change impacts on Odonata distribution (57.1%) instead of the impacts of water and habitat management projects. Climate change studies are particularly popular among meta-scale national or European trend analyses (73.3%) (Fig. 7), which are comparatively more resource-intensive and informative than community-based and species-based analyses (van Strien *et al.*, 2010). Furthermore, although water quality is the most important Odonata trend driver (Fig. 4), it is even less studied (17.9%) than habitat management (25.0%) (Fig. 7). Even within habitat management studies, there is also a lack of meta-scale research, which are generally considered as crucial as they provide important quantitative data for comparison and projection (Stewart, 2010), particularly in the heterogeneous European landscape

context (Kalkman *et al.*, 2010). There is also a lack of species-level research, which is highly informative for Odonates as they often have vastly different responses to different environmental modification (Villalobos-Jimenez *et al.*, 2016). The effectiveness of the mandatory natural habitat management for Annex II species is also constrained by the lack of species-level research (Cardoso, 2012). Therefore, current research fails to address the comprehensive cross-national picture and the urgent threats of Odonata decline (Kalkman *et al.*, 2010).

Furthermore, there is a misrepresentation of the impacts of climate change on Odonata trends. Most studies focus on the effects of increasing temperature on Odonata range shift (Powney *et al.*, 2015), yet the most important impacts of climate change on Odonata is increasing drought (Kalkman *et al.*, 2010). Nevertheless, out of the 16 papers studying climate change as a trend driver, only three investigate climate change impacts through freshwater distribution, including water habitat types, changes in droughts, and flooding (Hof *et al.*, 2012; Grewe *et al.*, 2013; Powney *et al.*, 2015). As a result, Odonata research is dominated by studying range shift caused by temperature changes but not the other important trend indicators including population abundance, hindering the reflection of urgent conservation threats (Collins & McIntyre, 2015). This limits the comprehensive representation necessary in biodiversity change monitoring.

While there is a significant lack of understanding of the interaction between Odonata trends and water and quality management, there are also unsettled controversies in the intensely studied climate change effects. Literature from the 2000s usually suggests a northward and expansive range shift in species from Western and Central European countries, including UK and Ireland (Hickling *et al.*, 2005, 2006; Hassall *et al.*, 2010), Germany (Ott, 2010), and Belgium (Hof *et al.*, 2012). Nevertheless, recent literature suggests such northward shift is not observed across many other species, especially for species from Northern Europe (Hof *et al.*, 2012; Grewe *et al.*, 2013). These studies often make a distinction between lentic Odonates, which inhabit standing waters such as lakes, and lotic Odonates, which inhabit running waters such as streams. Lentic Odonates have higher dispersal abilities than lotic Odonates as their habitats are less stable and predictable (Hof *et al.*, 2006). Therefore, several studies have suggested that lentic Odonates can track climate change faster, experiencing larger northward range shift (Grewe *et al.*, 2013) and larger range size change (Hof *et al.*, 2012). Nevertheless, several other studies suggest that lotic Odonates are more responsive to climate change because they are more sensitive towards the changes in water quality (Powney *et al.*, 2015) which opens up and closes down range space for them in Western and Eastern Europe, respectively (Vaughan & Ormerod, 2012). These studies argue that habitat availability matters more than dispersal ability for Odonata migration (Powney *et al.*, 2015). The unsettled debate reflects that climate change as a trend driver is highly synergistic, relying significantly on Odonata phenology and the other environmental factors. As a result, these studies will also be significantly benefited by more comprehensive studies on broader environmental factors including the currently limited studies on water and habitat.

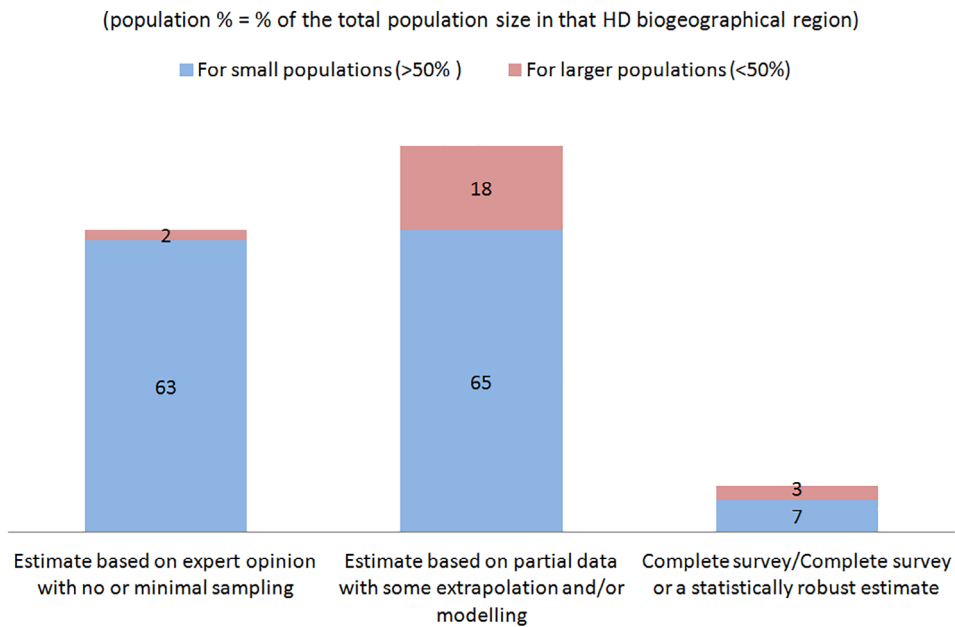


Fig. 5. The frequency of use of different methods to evaluate the population trends of Annex Odonata species in the 2013 Habitats Directive Reporting (European Commission, 2017), including expert opinion (left), population projection (centre), and complete survey (right). Populations are divided according to their relative population size in that HD biogeographical region, with those exceeding 50% as large populations.

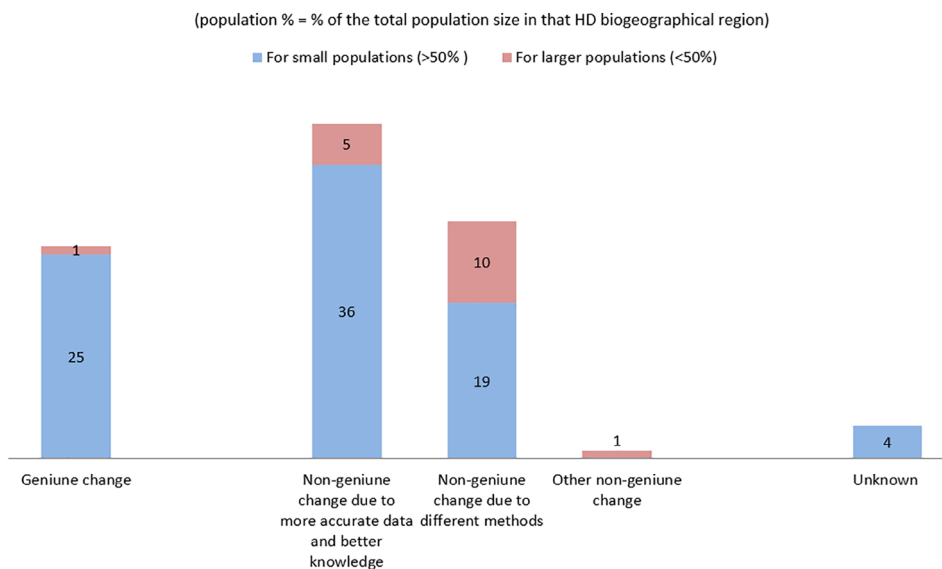


Fig. 6. The frequency of the reasons for trend changes for Annex Odonata species from 2007 to the 2013 Habitats Directive Reporting (European Commission, 2017), including genuine change (left), non-genuine change (centre), and unknown reasons (right). Populations are divided according to their relative population size in that HD biogeographical region, with those exceeding 50% as large populations.

The future of Odonata conservation in Europe

Based on the above-mentioned mismatches, we make a list of recommendations for the Habitats Directive revision and for future scientific research direction.

Revision on the annexes of the habitats directive. There is increasing evidence to suggest that the 2020 Habitats Directive revision is urgently needed (Cardoso, 2012; Hochkirch *et al.*, 2013a; Kalkman *et al.*, 2018). World-leading odonatologists have shifted their previous stance of keeping the Annex

(For papers that have investigated on more than one driver,
each driver will be counted as one paper here)

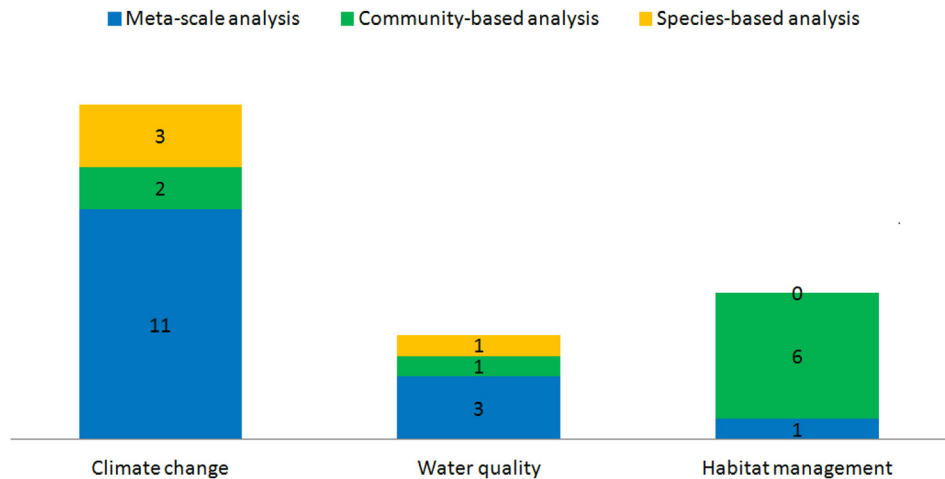


Fig. 7. The frequency of the number of papers investigating European Odonata trend drivers, including climate change (left), water quality (centre), and habitat management (right). Each paper is further divided according to their scale of research, in either nation/Europe (meta-scale), community, or specific species.

untouched (Kalkman *et al.*, 2010) to their current opinion that the Habitats Directive has failed to protect threatened Odonates because of its several biases (Kalkman *et al.*, 2018). Replacing non-threatened Annex species will unlikely desert the already-established conservation success as many of them now have stable or increasing population and range trend. Nevertheless, as current Annex species still act as integral indicators of habitat quality especially in Western and Central Europe (Kalkman *et al.*, 2018), threatened species should be added onto the Annexes without excluding species currently in the Annexes, at least until new indications are established and unified across different countries.

It is controversial whether to include CR species with extremely high extinction probability as it might be more costly and risky than acting on a larger number of less threatened species. This form of conservation triage is a result of the constraints posed by limited conservation resources. Nevertheless, to achieve the Aichi Biodiversity Target 12 in the Convention on Biological Diversity of halting the extinction of known threatened species, conservation effort should not be restricted exclusively to species with brighter outlooks. Furthermore, considering that all EN and 77% VU Odonata species (Table 1) are not on the Annexes, there is a significant room for including more EN and VU species on the Annexes, particularly on the habitat-protecting Annex II (Cardoso, 2012). Moreover, listing these threatened species on the Annexes may possibly be the only incentive for protecting their habitat. This is because countries with high diversity of endemic or threatened Odonates, including Greece, Italy, Portugal, Spain, France, and Bulgaria (Kalkman *et al.*, 2018), have already exceeded the Aichi Biodiversity Target 11 of having 17% terrestrial protected area coverage (World Bank, 2018). Local conservation resources are also almost fully occupied with implementing Habitats Directive (Hochkirch *et al.*, 2013b),

leaving Habitats Directive the most effective conservation mechanism. As a result, to balance between evidence-based conservation policies, national conservation context, and resource practicality, there is a need to include most CR, EN, and VU Odonata on Annex II. Decisions should be based on the up-to-date distributions and trends of the threatened Odonates and discussed on an open panel with biodiversity scientists, odonatologists, and EU and national representatives.

Revision on trend evaluation methodology. Significant knowledge gaps in the trends of threatened Odonates have been identified. All CR, EN, and VU species should have regular updates on their national-scale population trends as part of an amended Habitats Directive or a cross-country monitoring system (Hochkirch *et al.*, 2013a), preferably evaluated by complete surveys which are more accurate and also more feasible in these threatened populations as they are often smaller (van Strien *et al.*, 2013a). In particular, the trends of *S. depressiusculum*, *C. mercuriale*, *C. ornatum*, and *G. grasilinii* should also be updated due to the disagreement between the IUCN Red List assessments and the evidence from the Habitats Directive Reporting and primary literature. It has also been suggested that the threatened *Aeshna viridis* is locally extinct in Sweden due to alien species invasion but with no solid evidence (Flenner & Sahlén, 2008), calling for further research needs.

In European-scale trend evaluation, to reduce biases caused by inaccurate data and evaluation methods, surveying methods should be standardised across countries (van Strien *et al.*, 2010, 2013b, 2010, 2013b). Furthermore, Odonata distribution databases should be developed in more countries (van Strien *et al.*, 2010; Collins & McIntyre, 2015), especially in countries with more endemic and threatened species (Kalkman *et al.*, 2018) including Portugal, Italy, Spain, and particularly Greece

to facilitate updating its Habitats Directive Reporting (European Commission, 2017).

Revision on the direction of trend driver research. Conservation research should focus more on the effects of habitat and water management on Odonata trends, with a balance between qualitative and quantitative data from community-scale and meta-scale analyses, respectively. These studies will be facilitated by the currently rich data on the correlation between Odonata population abundance and water pollution (Van Dijk *et al.*, 2013; Rosset *et al.*, 2014; Golfieri *et al.*, 2016; Al Jawaheri & Sahlen, 2017), water management (Schmidt, 2004; Carchini *et al.*, 2005; Menetrey *et al.*, 2005; Belmar *et al.*, 2013; Jeanmougin *et al.*, 2014; Harabis & Dolny, 2015; Boda *et al.*, 2015a; Thornhill *et al.*, 2017), and habitat management (Wildermuth, 2008; Raebel *et al.*, 2012; Isaac *et al.*, 2014; Maynou *et al.*, 2017). These data can facilitate transforming the occurrence data in different contexts into longer-term population trends using standardised protocols such as Bayesian occupancy modelling (van Strien *et al.*, 2013a; Isaac *et al.*, 2014; Powney *et al.*, 2015).

Conservation research should enhance the attention to understanding the role and mechanisms of water and habitat management projects in driving Odonata trend changes as they are the two most important trend drivers. Although climate change research is indeed highly valuable in long-term conservation programmes (Kalkman *et al.*, 2010), it is also less indicative for regional conservation efforts such as EU Habitats Directive as climate change cannot be addressed by regional efforts alone. It is therefore important to balance research on both the shorter-term and finer-scale habitat and water alternations and the long-term and larger-scale climate threats.

Climate change research should increase studying the impacts of freshwater distribution, and also broader synergistic drivers of Odonates changes in population size and distribution at different scales (Suhling & Suhling, 2013). Firstly, studies on species-level synergistic drivers can investigate different shift rates resulting from differential habitat requirements and biotic interactions between southern and northern range limits (Hickling *et al.*, 2005), the interaction between climate change responses and phenology changes including advanced life cycle (Richter *et al.*, 2005; Hassall *et al.*, 2007; Feehan *et al.*, 2009) and extended growing seasons (Flenner & Sahlen, 2008; Suhling & Suhling, 2013), especially by moving out from modelling to field studies (Richter *et al.*, 2005; Soendergerath *et al.*, 2012). Secondly, while there is a lack of community-level research for Odonates, community-level synergies have been observed across different invertebrate taxonomic groups. These include enhanced invasion (Walther *et al.*, 2009) and altered biotic interactions coupled with altered phenology (Both *et al.*, 2009; Pearson *et al.*, 2014), and morphology (Suhling & Suhling, 2013). Lastly, abiotic level synergies should be investigated as modelling studies have demonstrated the importance of abiotic components in Odonata ecology but with no empirical support. For example, European landscape can influence the establishment rate after range shift due to climate change (Hassall & Thompson, 2010), depending on the species' traits (Angert *et al.*, 2011) and dispersal rate (Ward & Mill, 2007; Fitt &

Lancaster, 2017). The complicated climate change synergies on Odonata trend require more research besides analysing the effects of purely increasing temperature.

From science to policy. With a better understanding of trends and trend drivers of threatened Odonata, their status can be better represented in possible revisions of European Environmental Legislation. While negotiating the details of Habitats Directive inevitably involves untangling political controversies (Moss, 2008) such as differential national responsibilities (Schmeller *et al.*, 2008), scientific knowledge can be better incorporated with political considerations into the Directives through transparent amendment criteria and regular biodiversity updates in all EU countries (Cardoso, 2012).

Ultimately, there is a need to better define the objectives and fundamental values of the Habitats Directive. As conservation resources are not unlimited, practicality is crucial and resource allocation compromises are unavoidable. Should globally threatened species, such as *M. splendens* (VU for both global and Europe), be allocated more resources than species which are only threatened in Europe, such as *Cordulegaster insignis* (LC for global and EN for Europe)? Should more resources be allocated to less-threatened species than species which will have no suitable future habitats under climate change projection? Answering these questions involve fundamental ethical dialogues between the European Commission, government representatives, conservationists, odonatologists, and even the wider public. While these questions are unlikely to be completely settled due to conflicting values, a definitive clarification on the Habitats Directive's fundamental goals is crucial for future effective implementation and coordination between different European countries.

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Data availability statement

The data that support the findings of this study are openly available in European Red List of Dragonflies at <http://doi.org/10.2779/84650>, and the trend data (2007 - 2012) from the 2013 European Union Habitats Directive Reporting which is available in the public domain: https://ec.europa.eu/environment/nature/knowledge/rep_habitats/index_en.htm.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supplementary Table 1 A summary of European threatened and Annex Odonates' trends and major trend drivers. Species are grouped under their respective IUCN Red List Categories, and marked with an asterisk * if it is endemic, in the scale of EU27. Trends are evaluated by IUCN (Kalkman *et al.*, 2010), 2013 Habitats Directive Reporting of major populations (European Commission, 2017), and primary literature. Major populations refer to populations with <50% size of the total population in that biogeographical region. Trend drivers are a summary of IUCN findings (IUCN, 2017a) and primary literature (1: Dolny *et al.*, 2013; Domeneghetti *et al.*, 2015; 2: Rouquette & Thompson, 2005; Lorenzo-Carballea *et al.*, 2015; 3: Harabis & Dolny, 2015; 4: Koch *et al.*, 2014; 5: Flenner & Sahlen, 2008; 6: Harabis & Dolny, 2012). If there several trend drivers, the most important three are considered as major trend drivers.

References

- Al Jawaheri, R. & Sahlen, G. (2017) Negative impact of lake liming programmes on the species richness of dragonflies (Odonata): a study from southern Sweden. *Hydrobiologia*, **788**, 99–113.
- Allen, K.A. & Thompson, D.J. (2014) Population size and survival estimates for the rare damselflies, *Coenagrion mercuriale* and *Ischnura pumilio*. *Insect Conservation and Diversity*, **7**, 241–251.
- Andersen, E., Nilsson, B. & Sahlen, G. (2016) Survival possibilities of the dragonfly *Aeshna viridis* (Insecta, Odonata) in southern Sweden predicted from dispersal possibilities. *Journal of Insect Conservation*, **20**, 179–188.
- Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J. J. & Chuncuo, A.J. (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, **14**, 677–689.
- Barrios, V., Carrizosa, S., Darwall, W.R.T., Freyhof, J., Numa, C. & Smith, K. (2014) *Freshwater Key Biodiversity Areas in the Mediterranean Basin Hotspot: Informing Species Conservation and Development Planning in Freshwater Ecosystems*. IUCN, Cambridge, UK.
- Batzer, D. & Wissinger, S. (1996) Ecology of insect communities in non-tidal wetlands. *Annual review of entomology*, **41**, 75–100.
- Belmar, O., Velasco, J., Gutierrez-Canovas, C., Mellado-Diaz, A., Millan, A. & Wood, P.J. (2013) The influence of natural flow regimes on macroinvertebrate assemblages in a semi-arid Mediterranean basin. *Ecohydrology*, **6**, 363–379.
- Boda, R., Bereczki, C., Ortmann-Ajkai, A., Mauchart, P., Pernecker, B. & Csabai, Z. (2015a) Emergence behaviour of the red listed Balkan Goldenring (*Cordulegaster heros* Theischinger, 1979) in Hungarian upstreams: vegetation structure affects the last steps of the larvae. *Journal of Insect Conservation*, **19**, 547–557.
- Boda, R., Bereczki, C., Pernecker, B., Mauchart, P. & Csabai, Z. (2015b) Life history and multiscale habitat preferences of the red-listed Balkan Goldenring, *Cordulegaster heros* Theischinger, 1979 (Insecta, Odonata), in South-Hungarian headwaters: does the species have mesohabitat-mediated microdistribution? *Hydrobiologia*, **760**, 121–132.
- Bolliger, J., Keller, D. & Holderegger, R. (2011) When landscape variables do not explain migration rates: an example from an endangered dragonfly, *Leucorrhinia caudalis* (Odonata: Libellulidae). *European Journal of Entomology*, **108**, 327–330.
- Both, C., Van Asch, M., Bijlsma, R.G., Van Den Burg, A.B. & Visser, M.E. (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology*, **78**, 73–83.
- Brereton, T., Roy, D.B., Middlebrook, I., Botham, M. & Warren, M. (2011) The development of butterfly indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation*, **15**, 139–151.
- Caldwell, J.P., Thorp, J.H. & Jervey, T.O. (1980) Predator-prey relationships among larval dragonflies, salamanders, and frogs. *Oecologia*, **46**, 285–289.
- Carchini, G., Solimini, A.G. & Ruggiero, A. (2005) Habitat characteristics and odonate diversity in mountain ponds of central Italy. *Aquatic Conservation-Marine and Freshwater Ecosystems*, **15**, 573–581.
- Cardoso, P. (2012) Habitats Directive species lists: urgent need of revision. *Insect Conservation and Diversity*, **5**, 169–174.
- Clausnitzer, V., Kalkman, V.J., Ram, M., Collen, B., Baillie, J.E.M., Bedjanic, M., Darwall, W.R.T., Dijkstra, K.D.B., Dow, R., Hawking, J., Karube, H., Malikova, E., Paulson, D., Schütte, K., Suhling, F., Villanueva, R.J., von Ellenrieder, N. & Wilson, K. (2009) Odonata enter the biodiversity crisis debate: the first global assessment of an insect group. *Biological Conservation*, **142**, 1864–1869.
- Collins, S.D. & McIntyre, N.E. (2015) Modeling the distribution of odonates: a review. *Freshwater Science*, **34**, 1144–1158.
- De Knijf, G., Anselin, A. & Goffart, P. (2001) Trends in dragonfly occurrence in Belgium (Odonata). Proceedings 13th International Colloquium European Invertebrate Survey, Leiden.
- De Knijf, G., Sparrow, D.J., Dimitriou, A.C., Kent, R., Kent, H., Siedle, K., Lewis, J. & Crossley, L. (2016) Distribution, ecology and status of a threatened species *Ischnura intermedia* (Insecta: Odonata), new for Europe. *International Journal of Odonatology*, **19**, 257–274.
- Dolny, A., Harabis, F. & Mizicova, H. (2014) Home range, movement, and distribution patterns of the threatened dragonfly *Sympetrum depressiusculum* (Odonata: Libellulidae): a thousand times greater territory to protect? *PLoS One*, **9**.
- Dolny, A., Mizicova, H. & Harabis, F. (2013) Natal philopatry in four European species of dragonflies (Odonata: Sympetrinae) and possible implications for conservation management. *Journal of Insect Conservation*, **17**, 821–829.
- Domeneghetti, D., Mondini, S. & Carchini, G. (2015) Odonata species richness in the Castelporziano presidential estate, present and past. *Rendiconti Lincei-Scienze Fisiche e Naturali*, **26**, S367–S377.
- Europa. (2018) *The History of the European Union* [WWW Document]. European Union. <https://europa.eu/european-union/about-eu/history_en>. Accessed on March, 2018.
- European Commission. (1992) *Guidance document on the strict protection of animal species of Community interest under the Habitats Directive 92/43/EEC* [WWW Document]. European Commission. <http://ec.europa.eu/environment/nature/conservation/species/guidance/pdf/guidance_en.pdf>. Accessed on March, 2018.
- European Commission. (2016) *The Habitats Directive* [WWW Document]. <http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm>. Accessed on March, 2018.
- European Commission. (2017) *Habitats Directive reporting* [WWW Document]. European Commission. <http://ec.europa.eu/environment/nature/knowledge/rep_habitats/index_en.htm>. Accessed on March, 2018.
- European Environment Agency. (2015) *State of nature in EU*.
- Fauna Europea. (2016) *Fauna Europea* [WWW Document]. <<https://fauna-eu.org/>>. Accessed on March, 2018.
- Feehan, J., Harley, M. & van Minnen, J. (2009) Climate change in Europe. 1. Impact on terrestrial ecosystems and biodiversity. A review (Reprinted). *Agronomy for Sustainable Development*, **29**, 409–421.
- Fitt, R.N.L. & Lancaster, L.T. (2017) Range shifting species reduce phylogenetic diversity in high latitude communities via competition. *Journal of Animal Ecology*, **86**, 543–555.
- Flenner, I. & Sahlen, G. (2008) Dragonfly community re-organisation in boreal forest lakes: rapid species turnover driven by climate change? *Insect Conservation and Diversity*, **1**, 169–179.

- Goertzen, D. & Suhling, F. (2015) Central European cities maintain substantial dragonfly species richness - a chance for biodiversity conservation? *Insect Conservation and Diversity*, **8**, 238–246.
- Golfieri, B., Hardersen, S., Maiolini, B. & Surian, N. (2016) Odonates as indicators of the ecological integrity of the river corridor: development and application of the Odonate River Index (ORI) in northern Italy. *Ecological Indicators*, **61**, 234–247.
- Grewe, Y., Hof, C., Dehling, D.M., Brandl, R. & Braendle, M. (2013) Recent range shifts of European dragonflies provide support for an inverse relationship between habitat predictability and dispersal. *Global Ecology and Biogeography*, **22**, 403–409.
- Hacet, N. (2009) The easternmost record of *Somatochlora borisi* Marinov, 2001 from Turkish Thrace, with a zoogeographic assessment on the distribution of the species (Odonata: Corduliidae). *Journal of the Entomological Research Society*, **11**, 51–56.
- Hacet, N. & Aktac, N. (2008) Two new records of Odonata (Gomphidae) for Turkey, *Gomphus flavipes* (Charpentier, 1825) and *Ophiogomphus cecilia* (Geoffroy in Fourcroy, 1785), with distributional notes on *G. flavipes* and *G. ubadschii* Schmidt, 1953. *Entomological News*, **119**, 81–89.
- Harabis, F. & Dolny, A. (2010) Ecological factors determining the density-distribution of Central European dragonflies (Odonata). *European Journal of Entomology*, **107**, 571–577.
- Harabis, F. & Dolny, A. (2012) Human altered ecosystems: suitable habitats as well as ecological traps for dragonflies (Odonata): the matter of scale. *Journal of Insect Conservation*, **16**, 121–130.
- Harabis, F. & Dolny, A. (2015) Necessity for the conservation of drainage systems as last refugia for threatened damselfly species, *Coenagrion ornatum*. *Insect Conservation and Diversity*, **8**, 143–151.
- Hassall, C. & Thompson, D.J. (2010) Accounting for recorder effort in the detection of range shifts from historical data. *Methods in Ecology and Evolution*, **1**, 343–350.
- Hassall, C., Thompson, D.J., French, G.C. & Harvey, I.F. (2007) Historical changes in the phenology of British Odonata are related to climate. *Global Change Biology*, **13**, 933–941.
- Hassall, C., Thompson, D.J. & Harvey, I.F. (2010) The impact of climate-induced distributional changes on the validity of biological water quality metrics. *Environmental Monitoring and Assessment*, **160**, 451–456.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.
- Hickling, R., Roy, D.B., Hill, J.K. & Thomas, C.D. (2005) A northward shift of range margins in British Odonata. *Global Change Biology*, **11**, 502–506.
- Hochkirch, A., Schmitt, T., Beninde, J., Hiery, M., Kinitz, T., Kirschey, J., Matenaar, D., Rohde, K., Stofen, A., Wagner, N., Zink, A., Lötters, S., Veith, M. & Proelss, A. (2013a) Europe needs a new vision for a Natura 2020 network. *Conservation Letters*, **6**, 462–467.
- Hochkirch, A., Schmitt, T., Beninde, J., Hiery, M., Kinitz, T., Kirschey, J., Matenaar, D., Rohde, K., Stofen, A., Wagner, N., Zink, A., Lötters, S., Veith, M. & Proelss, A. (2013b) How much biodiversity does Natura 2000 cover? *Conservation Letters*, **6**, 470–471.
- Hof, C., Brandl, M. & Brandl, R. (2006) Lentic odonates have larger and more northern ranges than lotic species. *Journal of Biogeography*, **33**, 63–70.
- Hof, C., Brändle, M., Dehling, D.M., Munguía, M., Brandl, R., Araújo, M.B. & Rahbek, C. (2012) Habitat stability affects dispersal and the ability to track climate change. *Biology Letters*, **8**, 639–643.
- Isaac, N., Van Strien, A., August, T., De Zeeuw, M. & Roy, D. (2014) Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, **5**, 1052–1060.
- IUCN. (2017a) *The IUCN Red List of Threatened Species*. Version 2017-3. [WWW Document].
- IUCN. (2017b) *The IUCN Red List of Threatened Species: Summary Statistics* [WWW Document]. IUCN. <<http://www.iucnredlist.org/about/summary-statistics>>. Accessed on March, 2018.
- Jaeschke, A., Bittner, T., Jentsch, A., Reineking, B., Schlumprecht, H. & Beierkuhnlein, C. (2012) Biotic interactions in the face of climate change: a comparison of three modelling approaches. *PLoS One*, **7**, e51472.
- Jaeschke, A., Bittner, T., Reineking, B. & Beierkuhnlein, C. (2013) Can they keep up with climate change? - integrating specific dispersal abilities of protected Odonata in species distribution modelling. *Insect Conservation and Diversity*, **6**, 93–103.
- Jeanmougin, M., Leprieur, F., Lois, G. & Clergeau, P. (2014) Fine-scale urbanization affects Odonata species diversity in ponds of a megacity (Paris, France). *Acta Oecologica-International Journal of Ecology*, **59**, 26–34.
- Kalkman, V.J., Boudot, J.-P., Bernard, R., Conze, K.-J., De Knijf, G., Dyatlova, E., Ferreira, S., Jović, M., Ott, J., Riservato, E. & Sahlén, G. (2010) *European Red List of Dragonflies*. Luxembourg.
- Kalkman, V.J., Boudot, J.-P., Bernard, R., De Knijf, G., Suhling, F. & Termaat, T. (2018) Diversity and conservation of European dragonflies and damselflies (Odonata). *Hydrobiologia*, **811**, 269–282.
- Kalkman, V.J., Clausnitzer, V., Dijkstra, K.D.B., Orr, A.G., Paulson, D. R. & Van Tol, J. (2008) Global diversity of dragonflies (Odonata) in freshwater. *Hydrobiologia*, **595**, 351–363.
- Keller, D., Brodbeck, S., Floess, I., Vonwil, G. & Holderegger, R. (2010) Ecological and genetic measurements of dispersal in a threatened dragonfly. *Biological Conservation*, **143**, 2658–2663.
- Keller, D., Brodbeck, S. & Holderegger, R. (2009) Characterization of microsatellite loci in *Leucorrhinia caudalis*, a rare dragonfly endangered throughout Europe. *Conservation Genetics Resources*, **1**, 179–181.
- Koch, K., Wagner, C. & Sahlén, G. (2014) Farmland versus forest: comparing changes in Odonata species composition in western and eastern Sweden. *Insect Conservation and Diversity*, **7**, 22–31.
- Leipelt, K.G. (2005) Behavioural differences in response to current: implications for the longitudinal distribution of stream odonates. *Archiv Fur Hydrobiologie*, **163**, 81–100.
- Lorenzo-Carballa, M.O., Ferreira, S., Sims, A.M., Thompson, D.J., Watts, P.C., Cher, Y., Damoy, V., Evrard, A., Gelez, W. & Vanappelghem, C. (2015) Impact of landscape on spatial genetic structure and diversity of *Coenagrion mercuriale* (Zygoptera: Coenagrionidae) in northern France. *Freshwater Science*, **34**, 1065–1078.
- Maes, D., Collins, S., Munguira, M.L., Šašić, M., Settele, J., van Swaay, C., Verovnik, R., Warren, M., Wiemers, M. & Wynhoff, I. (2013) Not the right time to amend the annexes of the European Habitats Directive. *Conservation Letters*, **6**, 468–469.
- Matushkina, N., Larnbret, P. & Gorb, S. (2016) Keeping the golden mean: plant stiffness and anatomy as proximal factors driving endophytic oviposition site selection in a dragonfly. *Zoology*, **119**, 474–480.
- Mauersberger, R. (2010) *Leucorrhinia pectoralis* can coexist with fish (Odonata: Libellulidae). *International Journal of Odonatology*, **13**, 193–204.
- Maynou, X., Martin, R. & Aranda, D. (2017) The role of small secondary biotopes in a highly fragmented landscape as habitat and connectivity providers for dragonflies (Insecta: Odonata). *Journal of Insect Conservation*, **21**, 517–530.
- McPeck, M.A. (1998) The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecological Monographs*, **68**, 1–23.

- Menetrey, N., Sager, L., Oertli, B. & Lachavanne, J.B. (2005) Looking for metrics to assess the trophic state of ponds. Macroinvertebrates and amphibians. *Aquatic Conservation-Marine and Freshwater Ecosystems*, **15**, 653–664.
- Moss, B. (2008) The Water Framework Directive: total environment or political compromise? *Science of the Total Environment*, **400**, 32–41.
- Mueller, O. (2008) Larval habitats and life history of the Crete Island endemic *Boyeria cretensis* (Odonata: Aeshnidae). *International Journal of Odonatology*, **11**, 195–207.
- Ott, J. (2010) Dragonflies and climatic change - recent trends in Germany and Europe. *BioRisk*, **5**, 253–286.
- Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J., Horning, N., Fordham, D.A., Raxworthy, C.J., Ryu, H. Y., McNees, J. & Akçakaya, H.R. (2014) Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, **4**, 217–221.
- Powney, G.D., Cham, S.S.A., Smallshire, D. & Isaac, N.J.B. (2015) Trait correlates of distribution trends in the Odonata of Britain and Ireland. *PeerJ*, **3**, e1410.
- Pritchard, G. & Leggett, M. (1987) Temperature, incubation rates and origins of dragonflies. *Advances in Odonatology*, **3**, 121–126.
- Raebel, E.M., Merckx, T., Feber, R.E., Riordan, P., Thompson, D.J. & Macdonald, D.W. (2012) Multi-scale effects of farmland management on dragonfly and damselfly assemblages of farmland ponds. *Agriculture Ecosystems & Environment*, **161**, 80–87.
- Richter, O., Soendergerath, D., Suhling, F. & Braune, E. (2005) Impact of climate change on population dynamics and temporal patterns of benthic assemblages of rivers. *International Congress on Modelling and Simulation* (ed. by A. Zenger and R. Argent), pp. 531–537. The University of Western Australia, Nedlands, Australia.
- Rosset, V., Angelibert, S., Arthaud, F., Bornette, G., Robin, J., Wezel, A., Vallod, D. & Oertli, B. (2014) Is eutrophication really a major impairment for small waterbody biodiversity? *Journal of Applied Ecology*, **51**, 415–425.
- Rouquette, J.R. & Thompson, D.J. (2005) Habitat associations of the endangered damselfly, *Coenagrion mercuriale*, in a water meadow ditch system in southern England. *Biological Conservation*, **123**, 225–235.
- Rouquette, J.R. & Thompson, D.J. (2007) Patterns of movement and dispersal in an endangered damselfly and the consequences for its management. *Journal of Applied Ecology*, **44**, 692–701.
- Sahlén, G., Bernard, R., Rivera, A.C., Ketelaar, R. & Suhling, F. (2004) Critical species of Odonata in Europe. *International Journal of Odonatology*, **7**, 385–398.
- Schmeller, D.S., Gruber, B., Budrys, E., Framsted, E., Lengyel, S. & Henle, K. (2008) National responsibilities in European species conservation: a methodological review. *Conservation Biology*, **22**, 593–601.
- Schmidt, E.G. (2004) The influence of a dam on the Odonata fauna in a lowland stream in NW-Germany. *Entomologia Generalis*, **27**, 87–104.
- Soendergerath, D., Rummland, J. & Suhling, F. (2012) Large spatial scale effects of rising temperatures: modelling a dragonfly's life cycle and range throughout Europe. *Insect Conservation and Diversity*, **5**, 461–469.
- Stewart, G. (2010) Meta-analysis in applied ecology. *Biology Letters*, **6**, 78–81.
- Suhling, I. & Suhling, F. (2013) Thermal adaptation affects interactions between a range-expanding and a native odonate species. *Freshwater Biology*, **58**, 705–714.
- Suhonen, J., Hilli-Lukkarinen, M., Korkeamaki, E., Kuitunen, M., Kullas, J., Penttinen, J. & Salmela, J. (2010) Local extinction of dragonfly and damselfly populations in low- and high-quality habitat patches. *Conservation Biology*, **24**, 1148–1153.
- Suhonen, J., Suutari, E., Kaunisto, K.M. & Krams, I. (2013) Patch area of macrophyte *Stratiotes aloides* as a critical resource for declining dragonfly *Aeshna viridis*. *Journal of Insect Conservation*, **17**, 393–398.
- Swaegers, J., Mergeay, J., Therry, L., Larmuseau, M.H.D., Bonte, D. & Stoks, R. (2013) Rapid range expansion increases genetic differentiation while causing limited reduction in genetic diversity in a damselfly. *Heredity*, **111**, 422–429.
- Termaat, T., van Grunsven, R.H.A., Plate, C.L. & van Strien, A.J. (2015) Strong recovery of dragonflies in recent decades in the Netherlands. *Freshwater Science*, **34**, 1094–1104.
- Thornhill, I., Batty, L., Death, R.G., Friberg, N.R. & Ledger, M.E. (2017) Local and landscape scale determinants of macroinvertebrate assemblages and their conservation value in ponds across an urban land-use gradient. *Biodiversity and Conservation*, **26**, 1065–1086.
- Thorp, J.H. & Cothran, M.L. (1984) Regulation of freshwater community structure at multiple intensities of dragonfly predation. *Ecology*, **65**, 1546–1555.
- Tichanek, F. & Tropek, R. (2016) The endangered damselfly *Coenagrion ornatum* in post-mining streams: population size, habitat requirements and restoration. *Journal of Insect Conservation*, **20**, 701–710.
- Van Dijk, T.C., Van Staalduinen, M.A. & der Sluijs, J.P. (2013) Macroinvertebrate decline in surface water polluted with imidacloprid. *PLoS One*, **8**.
- van Strien, A.J., Meyling, A.W.G., Herder, J.E., Hollander, H., Kalkman, V.J., Poot, M.J.M., Turnhout, S., van der Hoorn, B., van Strien-van Liempt, W.T.F.H., van Swaay, C.A.M., van Turnhout, C. A.M., Verweij, R.J.T. & Oerlemans, N.J. (2016) Modest recovery of biodiversity in a western European country: the living planet index for the Netherlands. *Biological Conservation*, **200**, 44–50.
- van Strien, A.J., Termaat, T., Groenendijk, D., Mensing, V. & Kery, M. (2010) Site-occupancy models may offer new opportunities for dragonfly monitoring based on daily species lists. *Basic and Applied Ecology*, **11**, 495–503.
- van Strien, A.J., Termaat, T., Kalkman, V., Prins, M., De Knijf, G., Gourmand, A.-L., Houard, X., Nelson, B., Plate, C., Prentice, S., Regan, E., Smallshire, D., Vanappelghem, C. & Vanreusel, W. (2013b) Occupancy modelling as a new approach to assess supranational trends using opportunistic data: a pilot study for the damselfly *Calopteryx splendens*. *Biodiversity and Conservation*, **22**, 673–686.
- van Strien, A.J., van Swaay, C.A.M. & Termaat, T. (2013a) Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *Journal of Applied Ecology*, **50**, 1450–1458.
- Vaughan, I.P. & Ormerod, S.J. (2012) Large-scale, long-term trends in British river macroinvertebrates. *Global Change Biology*, **18**, 2184–2194.
- Villalobos-Jimenez, G., Dunn, A.M. & Hassall, C. (2016) Dragonflies and damselflies (Odonata) in urban ecosystems: a review. *European Journal of Entomology*, **113**, 217–232.
- Walther, G.R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarošík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland, K. & Settele, J. (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution*, **24**, 686–693.
- Ward, L. & Mill, P. (2007) Long range movements by individuals as a vehicle for range expansion in *Calopteryx splendens* (Odonata: Zygoptera). *European Journal of Entomology*, **104**, 195–198.

- Watts, P.C., Kemp, S.J., Saccheri, I.J. & Thompson, D.J. (2005) Conservation implications of genetic variation between spatially and temporally distinct colonies of the endangered damselfly *Coenagrion mercuriale*. *Ecological Entomology*, **30**, 541–547.
- Watts, P.C., Rouquette, J.R., Saccheri, J., Kemp, S.J. & Thompson, D.J. (2004) Molecular and ecological evidence for small-scale isolation by distance in an endangered damselfly, *Coenagrion mercuriale*. *Molecular Ecology*, **13**, 2931–2945.
- Watts, P.C., Saccheri, I.J., Kemp, S.J. & Thompson, D.J. (2006) Population structure and the impact of regional and local habitat isolation upon levels of genetic diversity of the endangered damselfly *Coenagrion mercuriale* (Odonata: Zygoptera). *Freshwater Biology*, **51**, 193–205.
- Wildermuth, H. (2008) Habitat requirements of *Orthetrum coerulescens* and management of a secondary habitat in a highly man-modified landscape (Odonata: Libellulidae). *International Journal of Odonatology*, **11**, 261–276.
- World Bank. (2018) *Terrestrial Protected Areas (% of Total Land Area)* [WWW Document]. <<https://data.worldbank.org/indicator/ER.LND.PTLD.ZS>>. Accessed on March, 2018.

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