

Short communication

Sensitivity of biodiversity indices to life history stage, habitat type and landscape in Odonata community

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ABSTRACT

Assessing biodiversity and prioritizing the conservation of sites requires a robust methodology that minimizes the estimation errors of biodiversity indices and thus maximizes management efficiency. In aquatic insects, while there is still a debate about the use of different life history stages to increase the reliability of the biodiversity estimates, little is known about the effect of habitat and landscape characteristics. Here, odonates are used to assess the sensitivity of important biodiversity indices to the use of different life history stages (adult, oviposition, exuvia, and larva) and the influence of habitat type (lotic vs. lentic) and freshwater landscape complexity (proximity to a diversity of wetlands). Unlike exuvia and larvae, the use of adults gave inaccurate estimates of species richness, Relative Taxonomic Distinctness (RTD), Conservation Priority Index (CPI), but was quite reliable for Dragonfly Biotic Index (DBI). Interestingly, recording the mating state (oviposition) of the adult improved the accuracy of RTD and CPI by ≈ 40 and 60%, respectively. The estimation bias was higher in lotic than in lentic habitat and it increased with the freshwater landscape complexity. Our study shows that applying a multi-life stage approach in biodiversity indices reveals site connectivity at the landscape level.

1. Introduction

Site-oriented conservation is a valuable management tool for conservationists to face the increasing extinction rate of species (Mittermeier et al., 2011; Myers et al., 2000; Strayer and Dudgeon, 2010). Based on criteria such as the species richness, scarcity, endemism, conservation status, conservationists attribute a biodiversity value that reflects the conservation priority of sites (Abellán et al., 2005; Simaika and Samways, 2009a, 2009b). Although this conservation approach can be straightforward in some taxa, it is quite challenging in others because of the difficulty to determine the true presence of species (Fielding and Bell, 1997; Wilson et al., 2005) and the implication of landscape configuration in the local and regional (meta-)population dynamics (Morrison et al., 2012). The latter is of a particular importance because it affects the local biodiversity estimates (Dennis et al., 2006; Dennis and Shreeve, 2003) and influences conservation and management decisions by highlighting areas that are highly connected, requiring regional rather than site-oriented conservation (Ferraro and Pattanayak, 2006).

Species with a complex life cycle such as odonates (dragonflies and damselflies) occupy different ecosystems – an aquatic larval stage and a terrestrial adult stage (Stoks and Córdoba-Aguilar, 2012). Adults can actively disperse from one habitat to another; however, the larval stage

is generally sedentary, remaining in the reproductive sites. Whether the assessment of the diversity of such insects should be based on adults or larvae has been debated for the past few decades (Bried et al., 2012; Hardersen, 2008; Raebel et al., 2010). The sampling of adults is thought to overestimate the actual reproductive population (Hardersen, 2008; Raebel et al., 2010), because individuals can fly to habitats where they do not reproduce. Nonetheless, adults are still commonly used in estimating species occurrence and distribution range because, compared to larvae and exuviae, they are charismatic and appealing to people (Cordero-Rivera and Stoks, 2008), readily detectable (Bried et al., 2012), and easier to identify (Dijkstra and Lewington, 2006). As an example, the majority of the records compiled in the world's largest database of odonates concern adults (Kalkman et al., 2018), namely UK (BDS, <https://www.british-dragonflies.org.uk>), Switzerland (CSCF, <http://www.cscf.ch/>), the Netherlands (EIS, <https://www.eis-nederland.nl/>), Sweden (Artportalen, <https://www.artportalen.se/>), Africa (GBIF: <https://www.gbif.org/dataset/929d10ff-6f80-4ab3-a422-509c6721d402>) and US (Odonata Central: <https://www.odonatacentral.org/>). Therefore, it is valuable to identify which supplementary information could be collected during adult sampling to reduce the uncertainty of the successful reproduction and distribution range (Elith and Leathwick, 2009; Lobo et al., 2010). For instance, recording mating state such as oviposition not only does not require extra

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sampling efforts, but also likely gives better estimate of habitat suitability than single adults (Córdoba-Aguilar, 2008; Raitanen et al., 2013). Here I assess whether it increases the reliability of the occurrence of species.

Several freshwater systems such as the riverine systems have a complex hydrological, geomorphological and ecological structure where a mosaic of patches and habitats are linked by various processes promoting the coexistence of complex communities (Malmqvist, 2002). These ecosystems support diverse macroinvertebrate communities that are linked by passive dispersal such as larval drifting, flooding, and vector species (Bilton et al., 2001) and more frequently by active adult dispersal (Bohonak and Jenkins, 2003). Hence, lotic species living in rivers and streams and lentic species inhabiting lakes and ponds can meet in the same area, resulting in high local biodiversity (Ward et al., 1999). Such complex hydrological systems, therefore, represent a good system to test how adults reflect the actual occurrence of species and how landscape complexity affects species richness (Heino, 2009).

Spatial configuration at the landscape scale is a key component in the conservation of freshwater ecosystems (Domisch et al., 2015; Harms et al., 2014). The major reason is that communities of freshwater organisms such as odonates are interconnected such that different populations of the same species form a metapopulation (Yamanaka et al., 2009) and different communities of the same landscape form a meta-community (McCauley et al., 2008). A better understanding of the role of the ecological processes that maintain populations and species in the long-term is essential for better management of biodiversity (Linke et al., 2011). Therefore, understanding how species richness and composition at the site-scale are influenced by ecological processes at the regional scale will move conservation forward towards the development of a landscape perspective of site-specific conservation.

Here, a dataset was compiled on the distribution of odonates including different life history stages (adult, oviposition, larva, and exuvia) in the Seybouse watershed (Northeast Algeria) which hosts a diverse Odonata fauna (Khelifa et al., 2016), including some locally and globally endangered species (Mellal et al., 2018; Zebba et al., 2014). The main purpose of the present study is to determine how the effect of habitat type (lentic or lotic), landscape heterogeneity (complexity of freshwater ecosystem), and life history stage affects species richness (SR) and biodiversity indices. Given the higher dispersal propensity of lentic species with respect to lotic species (Hof et al., 2006), I hypothesize that lentic species are more likely to be observed in lotic habitats. Considering the overall positive effect of landscape heterogeneity on species diversity and community composition (Grainger and Gilbert, 2016), I hypothesize that complex freshwater landscapes influence SR and biodiversity indices of sites. Finally, I hypothesize that the use of different life history stages yields different estimates of SR and biodiversity indices (D'amico et al., 2004); adults (single) being the least reliable (Raebel et al., 2010).

2. Methods

2.1. Odonata dataset

Data were gathered in the Seybouse watershed (Northeast Algeria) during 2009–2018 by people who have a background in odonatology. Data were compiled from sites that have been visited for 6–10 years and where adults, larvae, and exuviae were sampled at least 10 times a year. In total, there were 49 sites, of which 36 were lotic (river, stream, channel, and ditch) and 13 were lentic (ponds) (Fig. S1, Table S1), and 40 species (23 Anisoptera and 17 Zygoptera; recorded as adults), belonging to 7 families and 21 genera (Table S2, Supplementary information).

The sampling of adults lasted usually 0.5–1 h in the morning and early afternoon (10:00–15:00) where observers actively search for individuals in the banks of the water body and in nearby terrestrial habitat using transects of 100 m. Adults were captured with a hand net and identified by eye. For exuviae, the bank vegetation, stones, and other substrates were searched thoroughly for 1 h throughout the emergence season of odonates (April–August). Exuviae were put in a box and identified in the laboratory (Heidemann and Seidenbusch, 2002; Seidenbusch, 2010). For larvae, monthly sampling was undertaken (at least 8 months/year) with a rectangular net within ten-meters stretch for one hour, and then brought to the laboratory for identification. Rare species were brought back to their original site after identification.

2.2. Ecological indices

Four life-cycle-stages were used in this study to assess species richness: (1) 'Single adults' were recorded when a single male or a single non-ovipositing female were observed; (2) 'oviposition' was recorded when an ovipositing single female or pair was detected; (3) 'larva' when a larva from any instar was collected; and (4) 'exuvia' when at least one exuvia was recorded. Sampling different life history stages decreases the probability of non-detection of species (false negative). The 'true reproduction' was also determined based on all life stages of the life cycle (Fig. S2). Although exuvia and larva were shown to be good indicators of the true reproduction (Ott, 2007; Raebel et al., 2010), they might disperse passively (e.g. flood) and appear in areas where oviposition did not take place. To compare the sensitivity of SR and biotic indices to life-cycle-stage, the estimates based on each life-cycle stage was compared with those based on the true reproduction.

DBI (Dragonfly Biotic Index) is a popular ecological metric that involves three components, namely the geographic distribution of the species, the conservation status of the species based on the classification of the IUCN and the sensitivity of the species to habitat degradation and disturbance (Simaika and Samways, 2009a) (Table 1). Each component ranges from 0 to 3, and the DBI of a certain site is the sum of the three

Table 1
Scoring of the components of the Dragonfly Biotic Index (DBI) (modified from Simaika and Samways, 2009a).

Score	Distribution	Threat	Sensitivity
0	Very widespread	LC	Apparently not sensitive to habitat disturbance; may thrive in natural and/or artificial waterbodies
1	Localized across a wide area in North Africa, and localized or common in Algeria in general	NT	Low sensitivity to habitat disturbance such as bank degradation; may occur commonly in natural and/or artificial waterbodies
2	Quite localized in North Africa, relatively rare in Algeria and the Seybouse watershed	VU	Medium sensitivity to habitat disturbance; may recolonize areas where it went extinct
3	Patchy geographic range and rare in the region and the Seybouse watershed	EN, CR	Extremely sensitive to habitat change from alien plants; low tendency to recolonize areas where it went extinct

The DBI of a species is the sum of the scores related to the distribution, threat, and sensitivity of the species (Simaika and Samways, 2009a). The threat is based on the IUCN Redlist of North Africa (Boudot et al., 2009). The DBI thus ranges from 0 to 9. A species like *Calopteryx exul* which has a patchy and restricted global geographic distribution (endemic), listed as endangered in the IUCN red list, and is very sensitive to habitat degradation will have a DBI of 9. A species like *Ischnura graellsii* which has the opposite features of the latter species (large distribution, very abundant and not sensitive to habitat disturbance) will have a DBI of 0. The abbreviation used for the second component is the IUCN acronyms for the different ranks of conservation status of the species.

components. Thus, the standard DBI of a species ranges from 0 to 9. To obtain a site-specific DBI, the sum of the standard DBIs of all species is divided by the species richness of the site. Therefore, as for standard DBI, site DBI ranges from 0 (low conservation priority) to 9 (high conservation priority).

RTD (Relative Taxonomic Distinctness) is a biodiversity measure of the taxonomic distance of a community (Freitag and Van Jaarsveld, 1997; White et al., 2014). This equation was used to calculate it: $RTD = 1/\sqrt{N_{family} \times N_{genus} \times N_{species}}$ (where N is the number). It characterizes whether a community consists of closely related species (less diverse) or distantly related species (more diverse). It is adequate with checklists based on presence/absence data, and it has been widely used in the assessment of macroinvertebrate communities (Ellingsen et al., 2005; Heino et al., 2007).

CPI (Conservation Priority Index) was derived from the Tunisian Stream Odonatological Index (TSOI) (Korbaa et al., 2018) and it combines in the same equation both the taxonomic distance of the community and its conservation priority.

$$CPI = (N_F + N_G)/2 \times (3E + R + \Sigma RTD + \Sigma RLC)/N.$$

N_F and N_G are the number of families and genera, respectively; E is the number of endemic species, R is the number of remaining species (total – endemic species), RTD is the accumulated relative taxonomic distinctness, and RLC is the sum of scores assigned to regionally threatened species.

2.3. Statistical analyses

All statistical analyses were computed using the R 3.4.0 software (R Development Core Team, 2019). I analyzed whether biodiversity indices are affected by habitat type (lotic and lentic) and wetland diversity (this includes the number of different types of wetlands within the radius of 2 km from the site) (Fig. S3). The model including the interaction of the two main effects was compared to the additive model using AIC (Akaike information criterion). SR (counts of species) was analyzed with a Poisson regression, and overdispersion was checked with the *dispersiontest* function from the AER package (Kleiber and Zeileis, 2017) and found non-significant ($P = 0.71$). DBI (+0.1, log-transformed), RTD (log-transformed), and CPI were modeled with multiple linear regressions using the two main effects habitat type (lotic and lentic) and the number of nearby wetlands. To reveal how adult-based estimation of SR is influenced by the life-history stage and the landscape, a Poisson model regressing the difference in the SR between the pairs of life-history stages against habitat type and the number of nearby wetlands was carried out. To conduct a pair-wise comparison of the stage-based estimations of SR, DBI, RTD, and CPI, log-transformation was first carried out, then reduced major axis regressions were carried out using the R-package *lmodel2* (Legendre, 2018) to test for the departure from the slope of identity (slope = 1). Additionally, linear models were used to reveal a potential correlation between CPI, RTD, and DBI.

3. Results

3.1. Integrating individual stage in species richness

The true SR was higher in lentic habitat than in lotic habitat (Fig. 1, $P < 0.0001$) with an average \pm SD of 9.18 ± 3.99 in lentic habitat and 5.52 ± 2.55 in lotic habitat. The SR increased with the number of nearby wetlands (Table S3a). All pairwise comparison of SR between the adult state and the four other states (oviposition, larva, exuvia, and true) showed significant departure from the slope of identity (1:1), whereas all others pairwise comparisons showed a slope that is close to identity (Fig. 2). When comparing the SR of the different life-history stages, the average difference in SR was 1.57 ± 2.47 between adults and ovipositing adults, 2.08 ± 2.48 between adult and exuvia, and 2.30 ± 2.83 between adult and larva. There was a positive relationship

between the number of nearby wetlands and the difference in SR of the pairs adults-ovipositing adult (GLM: $z = 4.31$, $P < 0.0001$), adult-exuvia (GLM: $z = 4.50$, $P < 0.0001$), adult-larva (GLM: $z = 5.07$, $P < 0.0001$) and adult-true (GLM: $z = 5.07$, $P < 0.0001$) (Table S4, Fig. S4). There was a significant effect of habitat type and the interaction between the number of wetlands and the habitat type for the adult-exuvia, adult-larva, adult-true pairs (Table S4), showing that the overestimation of the Odonata fauna is higher in lotic habitat, and that the slope of the increase in the overestimation was slightly steeper for the lentic habitat. In isolated sites (no nearby site within 2 km), the difference in the SR overestimation with adults was 38.8% higher in lotic habitat, but this difference declined to 25.8% in sites within complex wetland network.

3.2. Biodiversity indices

Based on the true diversity, linear models were used to test for the effect of the number of nearby wetlands and habitat type on CPI, RTD, and DBI (Table S3b-d). The number of nearby wetlands was positively correlated with CPI ($P = 0.04$), negatively correlated with RTD ($P < 0.001$), but not correlated with DBI ($P = 0.77$) (Table S3b-d). There was no significant difference in CPI and DBI between lotic and lentic habitats, but RTD was greater in lotic habitat (Fig. 1, Table S3b-d).

SR was negatively correlated with RTD ($P < 0.0001$, $R^2 = 0.82$), positively correlated with CPI ($P = 0.0001$, $R^2 = 0.26$), but not related with DBI ($P = 0.58$, $R^2 = 0.006$) (Fig. S5). RTD was not significantly correlated with DBI ($P = 0.09$, $R^2 = 0.05$). However, CPI was positively correlated with DBI ($P < 0.0001$, $R^2 = 0.34$) and negatively correlated with RTD ($P < 0.0001$, $R^2 = 0.34$) (Fig. S5).

3.3. Integrating individual stage in biodiversity indices

All pairwise comparison of DBI among the five stages showed no significant difference, revealing that the use of adults, oviposition, exuviae or larvae gave relatively similar estimates (Fig. 2, S6). As the RTD declines when there are more taxonomically distant species, I found a general pattern of underestimation when using adults more than oviposition, exuvia, and larva (Fig. 2, S7). RTD was underestimated by 22.2% when using adults and by 13.4% when using oviposition (equivalent to 39.6% of uncertainty amelioration). Exuvia and larvae gave a very close estimate of the true RTD.

CPI calculated based on adults was significantly greater than those estimated based on oviposition, exuvia, and larva (Fig. 2, S8). On average, the true CPI was overestimated by 17.5% when using adults (linear mixed-effects model [LME]: $P = 0.0003$) and only 6.8% when using oviposition (LME: $P = 0.0008$) (equivalent to 61.1% of uncertainty amelioration). CPI calculated based on exuvia (LME: $P = 0.12$) and larva (LME: $P = 0.69$) were not significantly different from that estimated with the true diversity. Comparison of CPI among exuvia and larva showed no significant difference (Fig. 2).

4. Discussion

4.1. Habitat type effect

SR was higher in lentic habitat than in lotic habitat, RTD was significantly higher in lotic habitats, and the DBI and CPI were not significantly different in the two habitat types. The greater RTD in lotic habitat is due to the fact that the number of families in the lotic environment was higher (Clarke and Warwick, 2001) – Libellulidae, Aeshnidae, Coenagrionidae, and Lestidae are present in both habitat types, whereas Gomphidae, Calopterygidae, and Platycnemididae are exclusively lotic. The DBI was slightly but not significantly higher in lotic habitat, and this is because there were more threatened and endemic species inhabiting rivers. In the Seybouse watershed, lotic species

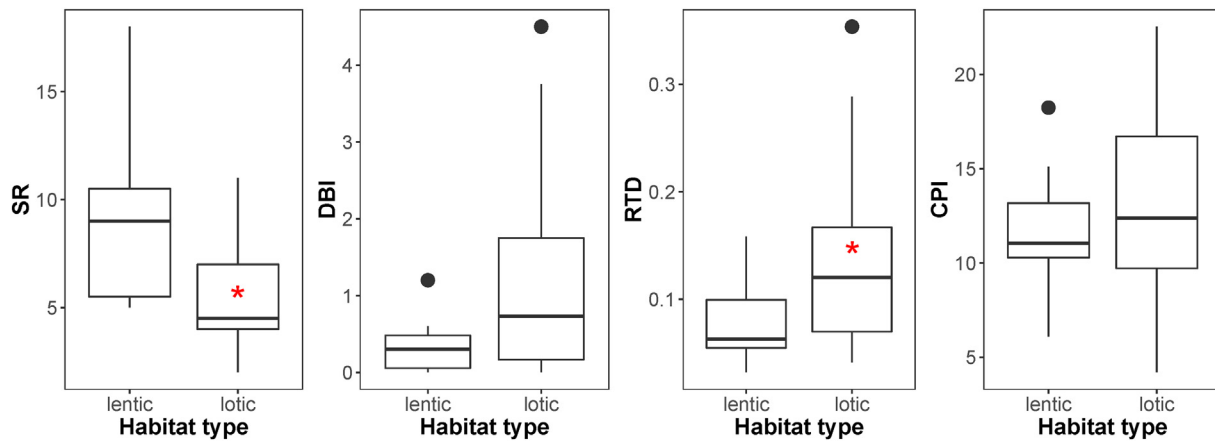


Fig. 1. Boxplot showing species richness (SR), Dragonfly Biotic Index (DBI), Relative Taxonomic Distinctiveness (RTD) and Conservation Priority Index (CPI) of odonates community in lentic and lotic habtiat of the Seybouse watershed (based on true reproduction). Red asteriks show significance (Table S3). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(*Calopteryx exul*, *Platycnemis subdilatata*, and *Gomphus lucasii*) belonging to Gomphidae, Calopterygidae, and Platycnemididae are either endemic, threatened and/or sensitive to environmental disturbance (Khelifa and Mellal, 2017; Mellal et al., 2018). Studies at the global scale have shown that odonates of lotic habitat are more at risk than those of lentic habitat (Clausnitzer et al., 2009). CPI, however, was relatively similar in lotic and lentic habitats, which might be explained by the combination of higher species richness with lower taxonomic relatedness and conservation priority in lentic habitat and lower species richness with higher taxonomic relatedness, endemism and conservation priority in lotic habitat, which evened out the scores.

Importantly, SR based on adults was quite similar to that estimated with larvae and exuviae in lentic habitat, but adults overestimated the

real SR in lotic habitats. This discrepancy in the biodiversity indices between lentic and lotic habitat most likely comes from the fundamental ecological difference (notably in dispersal and terrestrial niche breath) between the communities of the two habitats (Dijkstra et al., 2014). Lentic species are more likely to disperse and thus to occupy larger niche breadth than lotic species (Rosset et al., 2017). Therefore, the study supports the hypothesis that habitat type might determine, to some extent, the reliability of adults in depicting the true biodiversity and conservation priority of aquatic insects. However, Raebel et al. (2010) found that adults had low reliability in assessing dragonfly communities of farmland ponds in a British catchment. This suggests that there are other factors such as landscape features that might contribute to adult-based estimation bias of biodiversity.

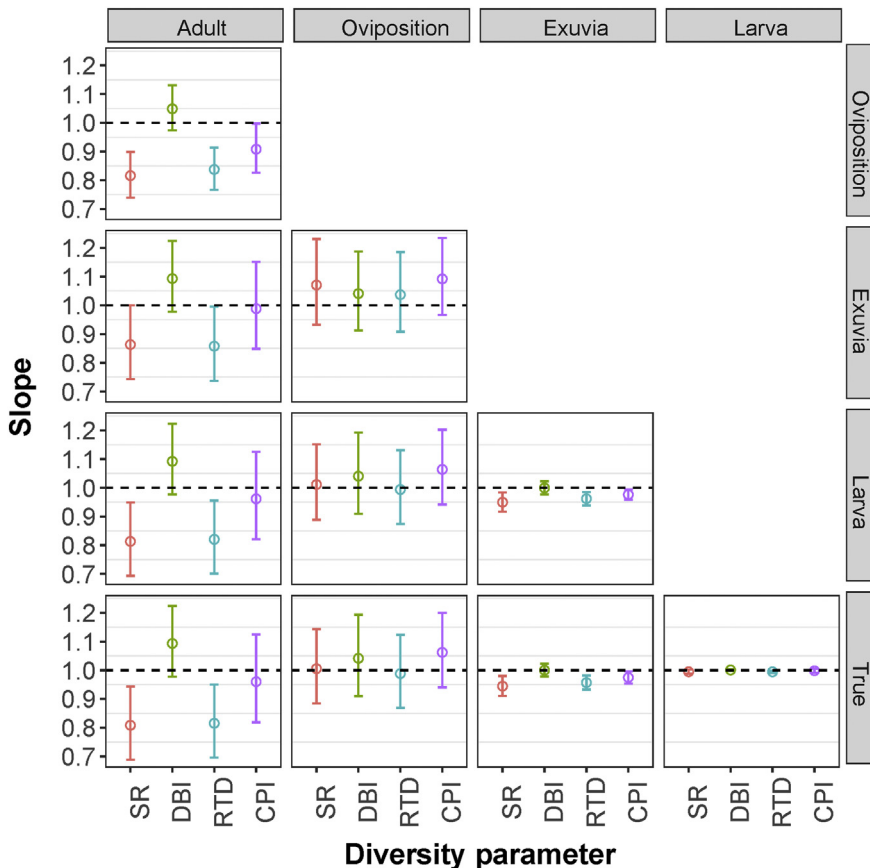


Fig. 2. The slope (based on major reduced axis regression) of the relationship between five measures of species richness (SR), Dragonfly Biotic Index (DBI + 0.1), Relative Taxonomic Distinctiveness (RTD), and Conservation Priority Index (CPI) of odonates based on different life history stages. All parameters were log-transformed. The analysis is based on 49 sites. Error bars are 95% confidence intervals. The scatterplots used to estimate the slopes are presented in (Fig. S4, 6–8).

4.2. Landscape perspective

This study highlights the importance of the regional habitat heterogeneity and connectivity in freshwater ecosystems (Grainger and Gilbert, 2016; Leibold et al., 2004). First, the results show that regional habitat heterogeneity tended to be positively correlated with increased adult immigration, which has been reported in other studies (Benard and McCauley, 2008; McCauley, 2006). Dispersal is a major force that determines the diversity of species inhabiting spatially structured environments such as freshwater ecosystems, mixing different communities, and increasing compositional similarity (Brown et al., 2011; Howeth and Leibold, 2010). Therefore, it is important to integrate the spatial scale in biodiversity indices to understand the ecological processes structuring biological communities (Patrick and Swan, 2011) and the maintenance of biodiversity in freshwater habitats (Legendre et al., 2005). The second important point that the study shows is the asymmetry in the directionality of species dispersal between lotic and lentic habitat where lentic species were more likely to frequent lotic habitat than the other way around. This is concordant with Hardersen (2008) who found that exuvia sampling in streams represented 45% of the adult sampling, suggesting that there is a phenomenon called ‘ecological traps’ where species are attracted to habitats by proximate factors while the overall environmental conditions are not suitable for larval development (Schlaepfer et al., 2002). This was probably due to (1) differences in the cues driving site selection between lotic (mainly water flow) and lentic species (other habitat features such as bank vegetation) (Butler, 2008; Hofmann and Mason, 2005), (2) the higher dispersal tendencies of lentic species (Grewe et al., 2013), and (3) the larger number of habitat generalists in lentic species. Thus, it is reasonable to suggest that the reliability of adults to estimate the true diversity is dependent on the type of habitat (lotic or lentic) which dictates community composition and the proximity to other types of habitats which shapes dispersal and connectivity.

4.3. Life stage effect

The sensitivity of three popular ecological indices (DBI, RTD, and CPI) over using different life history stages showed an interesting pattern. DBI was not sensitive to life history stage, even though the SR of adults was higher than that of the other life stages. This reflects some ecological and behavioral characteristics of the non-reproductive species. DBI takes into account the species distribution, sensitivity, and conservation status, but it scores zero for the cosmopolitan species (Simaika and Samways, 2009b). Given that the surplus of species recorded as adults often consists of dispersers, cosmopolitan and abundant species (Clausnitzer et al., 2009; Simaika et al., 2016) which theoretically are good dispersers (Lester et al., 2007) with a large niche breadth (Slatyer et al., 2013), DBI estimated with adults does not show significant deviation from the real DBI. However, if the non-reproductive species were rare and/or endemic, the DBI would not provide accurate estimates of the true reproductive community.

RTD which calculates the taxonomic distance of species (Clarke and Warwick, 2001) and CPI which takes into account taxonomic richness, endemism, relative taxonomic distinctiveness, and regional conservation status (Korbaa et al., 2018) showed sensitivity to using a particular life stage. The use of adults underestimated RTD by 22.2% and overestimated CPI by 17.5%. These deviations come from the fact that the non-reproductive species belong to a different genus and/or family than the reproductive species. For instance, several species of Libellulidae which generally do not successfully reproduce in rivers and streams are commonly recorded as adults and thus counted in the RTD and CPI calculation. Nonetheless, both RTD and CPI estimates were improved when using the oviposition state of the adult. By considering only species that oviposit as the successful reproducers, the deviation from true estimates declined by 13.4% and 6.8% in RTD and CPI, respectively. Although not all eggs that a species oviposit will lead to the

emergence of adults, odonate females are usually meticulous during oviposition site selection (Rudolf and Rödel, 2005) because they lay eggs where subsequent larval development and adult emergence is most likely (Buskirk and Sherman, 1985). However, the assumption here is that oviposition is carried out in the typical preferred sites for species and not in unusual habitats, which is sometimes the case (Corbet, 1999).

4.4. Conservation implications and recommendations

The current study shows that the key components of conservation priority is not only the SR, but also taxonomic distinctiveness, endemism and vulnerability to habitat degradation. Habitat type and regional habitat heterogeneity shape the immigration probability and thus contribute to the estimation bias of dragonfly biodiversity using adults. This has important conservation implications because it emphasizes the role of dispersal in connecting different ecological communities (metacommunity), indicates a larger gamma diversity at the landscape level (Sayer, 2014), and highlights the potential vulnerability of site-priority conservation for the long-term maintenance of diversity (Economo, 2011). Since there is a lack of knowledge of the role of movement to non-breeding habitats (e.g. refuges, feeding areas, or a stop-over of a dispersal phase) on the regional population dynamics of species and communities (May, 2013; Sheldon et al., 2010), it is risky not to prioritize the conservation of sites where SR is overestimated based on adults. It is thus reasonable to recommend a large buffer zone while prioritizing habitat units for protection which allows nearby habitats to be protected, larger-scale biological and ecological processes to be maintained, and higher biodiversity to be conserved (Roe and Georges, 2007). Further experimental applied studies should test whether this site protection strategy has regional conservation and management values (Grainger and Gilbert, 2016). Moreover, it is necessary to develop long-term conservation monitoring that account for yearly fluctuations in species occurrences at the site-level which could be caused by habitat degradation or change in the magnitude of biotic interaction (Torben et al., 2010). Regarding the choice of conservation priority indices, the study recommends the DBI especially when the species that are detected only as adults are widespread and not of conservation concern. Most importantly, the results highly recommend recording oviposition life stage instead of adults alone because it improves the reliability of the biodiversity indices, and thus can be a relatively good proxy (when oviposition is conducted in preferred habitats) for larvae and exuviae which require more efforts to sample and identify. Given the rapid decline of insects worldwide and the urgency for conservation actions (Sánchez-Bayo and Wyckhuys, 2019), improving our estimates of the distribution range and biodiversity in natural habitats is an essential step towards better management and conservation of biodiversity.

Declaration of Competing Interest

No conflict of interest to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.06.010>.

References

- Abellán, P., Sánchez-Fernández, D., Velasco, J., Millán, A., 2005. Conservation of freshwater biodiversity: a comparison of different area selection methods. *Biodivers. Conserv.* 14, 3457–3474.
- Benard, M.F., McCauley, S.J., 2008. Integrating across life-history stages: consequences of natal habitat effects on dispersal. *Am. Nat.* 171, 553–567.
- Bilton, D.T., Freeland, J.R., Okamura, B., 2001. Dispersal in freshwater invertebrates. *Annu. Rev. Ecol. Syst.* 32, 159–181.
- Bohonak, A.J., Jenkins, D.G., 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecol. Lett.* 6, 783–796.
- Boudot, J.-P., Kalkman, V.J., Amorin, A., Bogdanović, T., Rivera, A.C., Degabriele, G., Dommangeat, J.-L., Ferreira, S., Garrigós, B., Jović, M., 2009. Atlas of the Odonata of the Mediterranean and North Africa. 9. Libellula, pp. 1–256.
- Bried, J.T., D'Amico, F., Samways, M.J., 2012. A critique of the dragonfly delusion hypothesis: why sampling exuviae does not avoid bias. *Insect Conservation and Diversity* 5, 398–402.
- Brown, B.L., Swan, C.M., Auerbach, D.A., Campbell Grant, E.H., Hitt, N.P., Maloney, K.O., Patrick, C., 2011. Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. *J. N. Am. Benthol. Soc.* 30, 310–327.
- Buskirk, R.E., Sherman, K.J., 1985. The influence of larval ecology on oviposition and mating strategies in dragonflies. *Fla. Entomol.* 39–51.
- Butler, R.G., 2008. The significance of littoral and shoreline habitat integrity to the conservation of lacustrine damselflies (Odonata). *J. Insect Conserv.* 12, 23–36.
- Clarke, K., Warwick, R., 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar. Ecol. Prog. Ser.* 216, 265–278.
- Clausnitzer, V., Kalkman, V.J., Ram, M., Collen, B., Baillie, J.E., Bedjanich, M., Darwall, W.R., Dijkstra, K.-D.B., Dow, R., Hawking, J., 2009. Odonata enter the biodiversity crisis debate: the first global assessment of an insect group. *Biol. Conserv.* 142, 1864–1869.
- Corbet, P., 1999. *Dragonflies: Behaviour and Ecology of Odonata*. Harley Books, Colchester.
- Cordero-Rivera, A., Stoks, R., 2008. Mark-recapture studies and demography. In: Córdoba-Aguilar, A. (Ed.), *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research*. Oxford University Press, Oxford, pp. 7–20.
- Córdoba-Aguilar, A., 2008. Introduction. In: Córdoba-Aguilar, A. (Ed.), *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research*. Oxford University Press, Oxford, pp. 1–3.
- D'Amico, F., Darblade, S., Avignon, S., Blanc-Manel, S., Ormerod, S.J., 2004. Odonates as indicators of shallow lake restoration by liming: comparing adult and larval responses. *Restor. Ecol.* 12, 439–446.
- Dennis, R.L., Shreeve, T.G., 2003. Gains and losses of French butterflies: tests of predictions, under-recording and regional extinction from data in a new atlas. *Biol. Conserv.* 110, 131–139.
- Dennis, R., Shreeve, T., Isaac, N., Roy, D., Hardy, P., Fox, R., Asher, J., 2006. The effects of visual apparency on bias in butterfly recording and monitoring. *Biol. Conserv.* 128, 486–492.
- Dijkstra, K.-D.B., Lewington, R., 2006. *Field Guide to the Dragonflies of Britain and Europe: Including Western Turkey and North-Western Africa*. British Wildlife Publishing Dorset.
- Dijkstra, K.-D.B., Monaghan, M.T., Pauls, S.U., 2014. Freshwater biodiversity and aquatic insect diversification. *Annu. Rev. Entomol.* 59, 143–163.
- Domisch, S., Jähnig, S.C., Simaika, J.P., Kuemmerlen, M., Stoll, S., 2015. Application of species distribution models in stream ecosystems: the challenges of spatial and temporal scale, environmental predictors and species occurrence data. *Fundamental and Applied Limnology/Archiv für Hydrobiologie* 186, 45–61.
- Economu, E.P., 2011. Biodiversity conservation in metacommunity networks: linking pattern and persistence. *Am. Nat.* 177, E167–E180.
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Syst.* 40, 677–697.
- Ellingsen, K., Clarke, K., Somerfield, P., Warwick, R., 2005. Taxonomic distinctness as a measure of diversity applied over a large scale: the benthos of the Norwegian continental shelf. *J. Anim. Ecol.* 74, 1069–1079.
- Ferraro, P.J., Pattanayak, S.K., 2006. Money for nothing? A call for empirical evaluation of biodiversity conservation investments. *PLoS Biol.* 4, e105.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49.
- Freitag, S., Van Jaarsveld, A., 1997. Relative occupancy, endemism, taxonomic distinctiveness and vulnerability: prioritizing regional conservation actions. *Biodivers. Conserv.* 6, 211–232.
- Grainger, T.N., Gilbert, B., 2016. Dispersal and diversity in experimental metacommunities: linking theory and practice. *Oikos* 125, 1213–1223.
- Grewe, Y., Hof, C., Dehling, D.M., Brandl, R., Brändle, M., 2013. Recent range shifts of European dragonflies provide support for an inverse relationship between habitat predictability and dispersal. *Glob. Ecol. Biogeogr.* 22, 403–409.
- Hardersen, S., 2008. Dragonfly (Odonata) communities at three lotic sites with different hydrological characteristics. *Italian Journal of Zoology* 75, 271–283.
- Harms, T.M., Kinkead, K.E., Dinsmore, S.J., 2014. Evaluating the effects of landscape configuration on site occupancy and movement dynamics of odonates in Iowa. *J. Insect Conserv.* 18, 307–315.
- Heidemann, H., Seidenbusch, R., 2002. Larves et exuvies des libellules de France et d'Allemagne (suff de Corse). *Société française d'odonatologie*.
- Heino, J., 2009. Biodiversity of aquatic insects: spatial gradients and environmental correlates of assemblage-level measures at large scales. *Fr. Rev.* 2, 1–29.
- Heino, J., Mykrä, H., Hämäläinen, H., Aroviita, J., Muotka, T., 2007. Responses of taxonomic distinctness and species diversity indices to anthropogenic impacts and natural environmental gradients in stream macroinvertebrates. *Freshw. Biol.* 52, 1846–1861.
- Hof, C., Brändle, M., Brandl, R., 2006. Lentic odonates have larger and more northern ranges than lotic species. *J. Biogeogr.* 33, 63–70.
- Hofmann, T.A., Mason, C.F., 2005. Habitat characteristics and the distribution of Odonata in a lowland river catchment in eastern England. *Hydrobiologia* 539, 137–147.
- Howeth, J.G., Leibold, M.A., 2010. Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. *Ecology* 91, 2727–2741.
- 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.
- Khelifa, R., Mellal, M.K., 2017. Host-plant-based restoration as a potential tool to improve conservation status of odonate specialists. *Insect Conservation and Diversity* 10 (2), 151–160.
- Khelifa, R., Zebba, R., Amari, H., Mellal, M.K., Mahdjoub, H., Kahalerras, A., 2016. A hotspot for threatened Mediterranean odonates in the Seybouse River (Northeast Algeria): are IUCN population sizes drastically underestimated? *International Journal of Odonatology* 19, 1–11.
- Kleiber, C., Zeileis, A., 2017. *Package 'AER': Applied Econometrics with R*. Springer-Verlag, New York R package version 1.2.4. <https://CRAN.R-project.org/package=AER>.
- Korbaa, M., Ferreras-Romero, M., Ruiz-García, A., Boumaiza, M., 2018. TSOI – a new index based on Odonata populations to assess the conservation relevance of watercourses in Tunisia. *Odonatologica* 47, 43–72.
- Legendre, P., 2018. *lmodel2: Model II Regression*, In R package version 1.7-3. <https://CRAN.R-project.org/package=lmodel2>.
- Legendre, P., Borcard, D., Peres-Neto, P.R., 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol. Monogr.* 75, 435–450.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613.
- Lester, S.E., Ruttenberg, B.I., Gaines, S.D., Kinlan, B.P., 2007. The relationship between dispersal ability and geographic range size. *Ecol. Lett.* 10, 745–758.
- Linke, S., Turak, E., Nel, J., 2011. Freshwater conservation planning: the case for systematic approaches. *Freshw. Biol.* 56, 6–20.
- Lobo, J.M., Jiménez-Valverde, A., Hortal, J., 2010. The uncertain nature of absences and their importance in species distribution modelling. *Ecography* 33, 103–114.
- Malmqvist, B., 2002. Aquatic invertebrates in riverine landscapes. *Freshw. Biol.* 47, 679–694.
- May, M.L., 2013. A critical overview of progress in studies of migration of dragonflies (Odonata: Anisoptera), with emphasis on North America. *J. Insect Conserv.* 17, 1–15.
- McCauley, S.J., 2006. The effects of dispersal and recruitment limitation on community structure of odonates in artificial ponds. *Ecography* 29, 585–595.
- McCauley, S.J., Davis, C.J., Relyea, R.A., Yurewicz, K.L., Skelly, D.K., Werner, E.E., 2008. Metacommunity patterns in larval odonates. *Oecologia* 158, 329–342.
- Mellal, M.K., Bensouilah, M., Houhamd, M., Khelifa, R., 2018. Reproductive habitat provisioning promotes survival and reproduction of the endangered endemic damselfly *Calopteryx exul*. *J. Insect Conserv.* 22, 563–570.
- Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M., Gascon, C., 2011. Global biodiversity conservation: the critical role of hotspots. In: *Biodiversity Hotspots*. Springer, pp. 3–22.
- Morrison, M.L., Marcot, B., Mannan, W., 2012. *Wildlife-Habitat Relationships: Concepts and Applications*. Island Press.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853.
- Ott, J., 2007. *Artenschutzprogramm für die Gekielte Smaragdlibelle (Oxygastra curtisii, Insecta, Odonata) in Deutschland: das Beispiel der Population an der Our*. Pensoft Publishers, Sofia.
- Patrick, C.J., Swan, C.M., 2011. Reconstructing the assembly of a stream-insect metacommunity. *J. N. Am. Benthol. Soc.* 30, 259–272.
- R Development Core Team, 2019. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raebel, E.M., Merckx, T., Riordan, P., Macdonald, D.W., Thompson, D.J., 2010. The dragonfly delusion: why it is essential to sample exuviae to avoid biased surveys. *J. Insect Conserv.* 14, 523–533.
- Raitanen, J., Forsman, J.T., Kivelä, S.M., Mäenpää, M.I., Välimäki, P., 2013. Attraction to conspecific eggs may guide oviposition site selection in a solitary insect. *Behav. Ecol.* 25, 110–116.
- Roe, J.H., Georges, A., 2007. Heterogeneous wetland complexes, buffer zones, and travel corridors: landscape management for freshwater reptiles. *Biol. Conserv.* 135, 67–76.
- Rosset, V., Ruhl, A., Bogan, M.T., Datry, T., 2017. Do lentic and lotic communities respond similarly to drying? *Ecosphere* 8, e01809.
- Rudolf, V.H., Rödel, M.-O., 2005. Oviposition site selection in a complex and variable environment: the role of habitat quality and conspecific cues. *Oecologia* 142, 316–325.
- Sánchez-Bayo, F., Wyckhuys, K.A., 2019. Worldwide decline of the entomofauna: a review of its drivers. *Biol. Conserv.* 232, 8–27.
- Sayer, C.D., 2014. Conservation of aquatic landscapes: ponds, lakes, and rivers as integrated systems. *Wiley Interdiscip. Rev. Water* 1, 573–585.
- Schlaepfer, M.A., Runge, M.C., Sherman, P.W., 2002. Ecological and evolutionary traps. *Trends Ecol. Evol.* 17, 474–480.
- Seidenbusch, R., 2010. Key to the Western Palaearctic Exuviae of Odonata., *Sulzbach-Rosenberg, Deutschland*.
- Sheldon, F., Bunn, S.E., Hughes, J.M., Arthington, A.H., Balcombe, S.R., Fellows, C.S.,

2010. Ecological roles and threats to aquatic refugia in arid landscapes: dryland river waterholes. *Mar. Freshw. Res.* 61, 885–895.
- Simaika, J.P., Samways, M.J., 2009a. An easy-to-use index of ecological integrity for prioritizing freshwater sites and for assessing habitat quality. *Biodivers. Conserv.* 18, 1171–1185.
- Simaika, J.P., Samways, M.J., 2009b. Reserve selection using Red Listed taxa in three global biodiversity hotspots: dragonflies in South Africa. *Biol. Conserv.* 142, 638–651.
- Simaika, J.P., Samways, M.J., Frenzel, P.P., 2016. Artificial ponds increase local dragonfly diversity in a global biodiversity hotspot. *Biodivers. Conserv.* 25, 1921–1935.
- Slatyer, R.A., Hirst, M., Sexton, J.P., 2013. Niche breadth predicts geographical range size: a general ecological pattern. *Ecol. Lett.* 16, 1104–1114.
- Stoks, R., Córdoba-Aguilar, A., 2012. Evolutionary ecology of Odonata: a complex life cycle perspective. *Annu. Rev. Entomol.* 57, 249–265.
- Strayer, D.L., Dudgeon, D., 2010. Freshwater biodiversity conservation: recent progress and future challenges. *J. N. Am. Benthol. Soc.* 29, 344–358.
- Torben, W., Göran, S., Frank, S., 2010. Does one community shape the other? Dragonflies and fish in Swedish lakes. *Insect Conservation and Diversity* 3, 124–133.
- Ward, J., Tockner, K., Schiemer, F., 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *River Res. Appl.* 15, 125–139.
- White, E., Hunt, P., Schlesinger, M., Corser, J., De Maynadier, P., 2014. A Conservation Status Assessment of Odonata for the Northeastern United States. New York Natural Heritage Program, Albany.
- Wilson, K.A., Westphal, M.I., Possingham, H.P., Elith, J., 2005. Sensitivity of conservation planning to different approaches to using predicted species distribution data. *Biol. Conserv.* 122, 99–112.
- Yamanaka, T., Tanaka, K., Hamasaki, K., Nakatani, Y., Iwasaki, N., Sprague, D.S., Bjørnstad, O.N., 2009. Evaluating the relative importance of patch quality and connectivity in a damselfly metapopulation from a one-season survey. *Oikos* 118, 67–76.
- Zehs, R., Khelifa, R., Kahalerras, A., 2014. Emergence pattern, microhabitat choice, and population structure of the Maghribian endemic *Gomphus lucasii* Selys, 1849 (Odonata: Gomphidae) in northeastern Algeria. *Aquat. Insects* 36, 245–255.