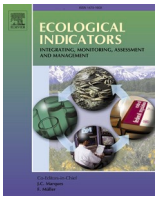
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Congruency between adult male dragonflies and their larvae in river systems is relative to spatial grain

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ABSTRACT

Dragonflies are globally renowned bioindicators, with larvae, exuviae and/or adult life stages used in freshwater quality assessments. However, little is known about the extent to which conspecific adults and larvae occur within close proximity of each other, or how they comparably respond to biotic and abiotic factors. Firstly, we test the extent to which adult male dragonflies are congruent with their larvae at three independent sample unit scales (small 10 m × 3 m, medium 90 m × 3 m, and large 450 m × 3 m) along four rivers, along with a subset of 40 randomly selected small scale sites (small 40) to test for a possible effect of sampling design on the outcomes of the spatial scale analyses. Secondly, we test the extent to which adult males and larvae share similar responses to environmental variables. At medium and large spatial scales, larvae and adults were strongly congruent for abundance, species richness, and Dragonfly Biotic Index (DBI) scores. Despite this, at the small spatial scale, only 15% of observations matched (contained adults and conspecific larvae). This increased to 46% at the medium scale, and 60% at the large scale, neither of which were significantly different from the number of mismatches. Dragonfly species composition differed between larval and adult assemblages at the small, small 40, and medium scales but did not differ at the large scale. Water temperature was the only variable that generally elicited similar responses in both life stages, at all spatial scales. Exuviae here were so under-represented that they provided no extra information. Assessments, where medium or large spatial scales are suitable for sampling, such as measuring the state of a river, can utilize either life stage. However, for comprehensive biodiversity surveys, both larvae and adults should be sampled.

1. Introduction

Freshwater insects, by occupying a wide range of micro-habitats and being variously sensitive to environmental change, are valuable for conservation prioritization and management (Brito et al., 2018), and indication of system change over time (Shafie et al., 2017; Morrison et al., 2018). Some studies suggest they are low-cost and easy to sample, and their small body sizes, global abundance, and short life cycles add to their value as indicators (Agouridis et al., 2015). Alternatively, aquatic plants and organisms such as diatoms, fish, frogs, and crabs are also valued as indicators (Sanders et al., 1998; Araújo et al., 2000; Jansen and Healey, 2003; Clayton and Edwards, 2006; Holmes and Taylor, 2015). However, physical and chemical analyses are often favoured over invertebrate sampling. Although these can be more precise and useful when environmental factors inhibit insect sampling, they are generally more expensive (requiring specialized machinery and trained personnel) and can only reflect water conditions at the time of sampling, whereas with aquatic insect sampling, it is possible to detect changes that have occurred over a longer period (Stein et al., 2008). Despite the advantages of aquatic invertebrate sampling, the taxonomic challenge inhibits use of some taxonomic groups in assessments (Allan and Flecker, 1993). However, others, such as the Odonata (dragonflies and damselflies, here referred to as 'dragonflies'), are taxonomically well known, and globally recognised for their indicator potential (Renner et al., 2016; Lesch and Bouwman, 2018).

The amphibiotic life cycle of dragonflies involves a realm shift from water to air when maturing from a young to adult stage. The aquatic larval stage is often long, lasting many weeks and even years, in some species. At the final moult, larvae leave their aquatic habitats and metamorphose into the aerial, adult phase, leaving behind the larval skin (exuvia). Young adults disperse away from water bodies, and once sexually mature and in their reproductive phase, return to aquatic habitats that have suitable conditions for successful development of their offspring (Corbet, 1999; Stoks and Córdoba-Aguilar, 2012).

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Many adult male dragonflies are territorial, defending their selected habitats from other conspecifics and occasionally heterospecifics (Kemp, 2018). In principle then, both the adult male and conspecific larva should occur at the same general site (Patten et al., 2015). Although both the larval and adult stages are used in freshwater assessments, the most suitable stage is dependent on various factors: the specific research or management questions being asked, geographic conditions of the area being surveyed, time of year, and degree of knowledge of the dragonfly species in the area.

Larvae would ideally be sampled for questions related to in-water characteristics, such as nutrient concentrations, because they are more sensitive to conditions in their surrounding habitat than the aerial adults (Raebel et al., 2012). Adult dragonflies would be the obvious life stage choice for research on riparian vegetation for example (Samways and Sharratt, 2010). However, this is not to say that the life stages are not interchangeable for these different scenarios. Globally, records of dragonflies typically favour the adult over the larval stage (Kalkman et al., 2018). For example, out of 1 410 055 records from five European countries (Belgium, France, Netherlands, Slovenia, and the United Kingdom), 85% to 98% are adults and 0.06% to 15% are larvae (Raebel et al., 2010). Compared to the larvae, adults are conspicuous (particularly the colourful males) and more appealing to people, as well as being relatively easy to sample and identify to species level (Clausnitzer et al., 2017). However, in cooler climates, they can be comprehensively surveyed only during the warmer months, when the adult stage is on the wing, and when conditions are sunny and windless (McCauley et al., 2018). Owing to their high mobility, adults easily disperse to areas where they do not necessarily reproduce. These areas may act as stepping-stone or temporary habitats, favoured for food resources rather than as breeding habitats (Simaika et al., 2016; Maynou et al., 2017). Therefore, use of adults in assessments has been criticized, as it may lead to unreliable overestimates of reproductive populations (Hardersen, 2008; Raebel et al., 2010).

Bried et al. (2015) found that repeat observations of adults at $\geq$4 site visits, tenerals on $\geq$2 surveys, and recording >20 adult individuals on at least 1 survey were reliable indicators of species residency and provided stronger evidence than oviposition or mating observations. The exuvia is a sure sign of life cycle completion in an area (Ott et al., 2007; Raebel et al., 2010). However, exuviae are difficult to find, and do not last for long after emergence, especially in areas with adverse weather conditions (Lubertazzi and Ginsberg, 2009).

In contrast to the adult stage, the larval stage is long, inhabiting aquatic systems for months or even years. During this stage, the larvae have relatively limited dispersal abilities and their presence is not weather dependent, so sampling can take place under most conditions and also when adult sampling is difficult (e.g. rocky terrain or overgrown vegetation) (Corbet, 1999). Compared to adult surveys, larvae do not need to be sampled as often during the season and sampling time is shorter (Raebel et al., 2010). However, larval sampling is usually lethal and the netting techniques used are destructive to both dragonflies and the local environment and require greater effort compared to visually surveying adults. Furthermore, conditions such as fast-flowing water, very wide or deep waterbodies, and the presence of dangerous animals like crocodiles and harmful diseases such as bilharzia can inhibit aquatic sampling (Samways, 2008; Bird et al., 2019). Larvae are not reliable indicators of life cycle completion as a large number (~50–95%) of larvae do not emerge. The probability of detecting them is usually lower than for adults, due to their cryptic nature and species-specific microhabitat requirements (Niba and Samways, 2006; Bried et al., 2012, 2015). Additionally, in parts of the world, the larvae of many species are not described, and there is insufficient knowledge of their habitat preferences, which is crucial for finding them (Samways, 1992). Even for described species, larval identification may be difficult, time-consuming, and requires a high level of expertise, especially in species-rich areas. The season of sampling is also important because accurate identification usually requires individuals to be in their final instar. These challenges may result in under-representation of the actual assemblage when only using larvae (Simaika and Samways, 2009a, 2011; Briggs et al., 2019a).

Despite these various challenges, both life stages are used as indicators of water quality. In South Africa, the Dragonfly Biotic Index (DBI) uses presence of dragonfly adults, supplemented by larvae and exuviae when available, as a measure of ecological integrity based on the total complement of species present in a defined area (Simaika and Samways, 2009a, 2012; Samways and Simaika, 2016). As it operates at the species level, it is a highly sensitive index (Simaika and Samways, 2009a), and functions favourably in comparison with many other freshwater assessment indices (Rosset et al., 2013). The DBI has been used to measure habitat recovery, select sites for conservation action, and assess stream restoration after the removal of invasive alien trees species (Samways and Taylor, 2004; Simaika and Samways, 2011, 2012; Harabiš and Dolný, 2012).

In studies on congruency of life stages, it is possible that some did not account for detectability differences when sampling the different stages (Hawking and New, 1999, 2002; D'Amico et al., 2004; Raebel et al., 2010; Giugliano et al., 2012; Bried et al., 2015). Regardless of life stage, it is important to consider the appropriate spatial scale to use for any general assessments using indicators (Boulton, 1999), yet little is known about the optimal scale to use for dragonfly larvae in freshwater assessments. For the highly mobile adults, Samways and Simaika (2016) recommend sampling sites be 100 m in length for use of the DBI. However, whether the relationships between dragonfly larvae and adults are scale dependent is unknown.

Here, we aim to determine the extent to which conspecific larvae and adults are congruent with each other at three spatial scales, while recognizing that dragonfly species and their life stages are variously mobile. Therefore, by testing congruence between the larvae and adults at three spatial scales, we can then better select for the appropriate scale to use in future assessments. Then we determine whether larvae and adult assemblages are driven by the same environmental variables at these same three spatial scales. Due to territoriality in many adult male dragonflies, coupled with selection pressure to choose the best-suited conditions to ensure the survival of their progeny, we expect to find larvae and adults of the same species in the same local area, and driven by the same environmental variables, despite new colonists and temporary visitors present.

2. Materials and methods

2.1. Study area and sites

The Cape Floristic Region (CFR) is a biodiversity hotspot, rich in endemic plant species and aquatic invertebrates (Wishart and Day, 2002). The mosaic structure of CFR rivers creates a range of diverse habitats to colonize (Meek et al., 2013). The mountainous rivers are also a major centre of endemism for dragonfly species (Simaika and Samways, 2009b). The heterogeneous nature of these rivers, coupled with the high habitat specificity of the many endemic dragonfly species, make it a suitable geographical area to determine whether there are links between habitats (and environmental factors) of conspecific dragonfly larvae and adults.

Study sites were along four rivers in the CFR (the Eerste (34°00′28.19′S; 19°00′6.46′E), Lourens (34°00′56.90′S; 18°58′42.54′E), Molenaars (33°42′00′S; 19°13′60′E), and Palmiet (34°03′24.95′S; 19°00′48.52′E) Rivers). All rivers had untransformed sections of natural fynbos vegetation, as well as sections of cultivated land, planted with vineyards and orchards. Untransformed sites of the Eerste, Lourens, and Molenaars Rivers were in the upper river reaches, whereas agricultural sites were downstream (middle reaches). However, in the case of the Palmiet River, the untransformed sites were in the lower reaches, and agricultural sites in the upper reaches. The choice of a range of variously disturbed habitats was to 'stretch' the responses of the two life stages

under conditions from transformed to fully historic.

A total of 360 sampling units (SUs) were randomly selected using QGIS 2.14.3 (QGIS Development Team, 2014) and groundtruthed for accessibility. The SUs were equally spread among the four rivers, and within each river, were evenly divided between natural and agricultural land use (45 natural and 45 agricultural per river). Each SU comprised a 10 m × 3 m area of water, starting from the edge of the river, and each SU was at least 50 m from the next. Using these SUs alone or by combining them with adjacent SUs, always with those closest to each other, three site sizes representing different spatial scales were used: small (10 m × 3 m = 1 SU = 1 small site, 360 replicates), medium (90 m × 3 m = 9 SUs = 1 medium site, 40 replicates), and large (450 m × 3 m = 45 SUs = 1 large site, 8 replicates). Large sampling sites consisted of the continuous stretches of either the natural or the agricultural reaches of each of the four rivers, creating eight large sites in total. A fourth dataset, small 40, was included and comprised 40 small scale sites that were randomly selected using the R 3.5.2 function *sample* (R Core Team, 2018). This was equal to the number of sites used at the medium scale (40 sites). This nested design was included to test for the effect of sample size in the spatial scale analyses. Sampling took place twice per SU, once during spring/early summer, and once in late summer/autumn, to account for both larvae and adult seasonal differences.

2.2. Sampling of adults, exuviae, and larvae

On warm, cloudless days, two observers recorded each species and the abundance of mature male dragonflies present at each site. Observations were conducted for 30 min/site, using close-focus binoculars, between 10:00 and 15:00. In South Africa, according to Samways and Simaika (2016) a 100 m site should be surveyed for 30 min and be visited a minimum of two times. Here, although we visited the sites only twice, accuracy was increased by surveying each 10 m site for 30 min and by using two people to record the species present. Voucher specimens and individuals that were difficult to identify in the field were collected for later identification according to Samways and Simaika (2016). The species *Trithemis dorsalis* and *T. furva* are indistinguishable in the field, and were recorded as one taxon ('TD'). Exuviae were searched for along the same transects used for adults for 30 min/site.

Larvae were sampled along the same transects used for adult observations. River substrate was disturbed by foot, and a 30 cm × 30 cm, 1 000 μm mesh net was used to simultaneously collect the suspended samples. To account for habitat differences between species, all microhabitats present at each SU were sampled for flow rates, vegetation, and substrate. Each SU was sampled for 3 min, after which, larvae were separated from debris on a tray and preserved in 90% ethanol. Individuals close to or in their final instar were identified to species, mainly according to Suhling et al. (2014). Specimens that were too small to accurately identify were excluded from the dataset.

2.3. Environmental variables

At each site, 15 environmental variables were recorded. These included the categorical variables of river catchment (Eerste, Lourens, Palmiet, or Molenaars Rivers) and land use (natural, agricultural). Percentage shade was visually estimated, and river depth at each site was determined with a tape measure. A handheld GPS recorded site positions. A multi-parameter water quality meter (Model: YSI 556 Multi Probe System; Make: YSI Fondriest Environmental) was used to measure water parameters (temperature, dissolved oxygen, conductivity, and pH) at each site. For river edges and beds combined, two observers visually estimated percentages of rocks and sand. For vegetation data, average vegetation height, percentage cover of alien vegetation and of indigenous vegetation, as well as the percentage cover of *Prionium serratum* (palmiet reed) and aquatic macrophytes were recorded as separate variables, as they have a strong influence on dragonflies in the area (Samways and Sharratt, 2010). We assigned values to the categories of land use into binary classifications. To account for multicollinearity between environmental variables, the variance inflation factor (VIF) was calculated, with function *vif* from the package *car* (Fox et al., 2012) at each scale for each variable in the global model. Thereafter, the explanatory variable with the highest VIF was removed and repeated until all VIFs were <5. Multicollinearity was detected for conductivity at the medium scale, and was excluded from all analyses of the medium-scale data. Agricultural land use and alien vegetation cover positively correlated with water temperature and were excluded from further analyses. Water temperature negatively correlated with indigenous vegetation cover and the latter was removed.

2.4. Data analyses for congruence among larvae and adults

All analyses were conducted at the three spatial scales. Three datasets were used for analyses, and included larvae, adults, and 'adjusted' adults. The adjusted adult dataset excluded the six species (*Zosteraeschna minuscula*, *Chlorolestes umbratus*, *Ceriagrion glabrum*, *Tramea limbata*, *Pantala flavescens*, and *Elattoneura glauca*) that were only observed as adults, and not sampled as larvae. This was done to discount non-resident species.

To determine whether sampling effort was sufficient, the non-parametric species estimators ICE, Chao2, and second-order Jackknife were calculated in R 3.5.2 (R Core Team, 2018) using the *fossil* package (Vavrek, 2011). For insect assemblages where a large number of rare species are present, as is often the case in the CFR, non-parametric species estimators are recommended (Hortal et al., 2006). Rarefied species accumulation curves were constructed for the larvae, exuviae, and adult dragonflies in R (R Core Team, 2018) using the *vegan* package (Oksanen et al., 2015). There were such poor returns from the exuviae sampling that this stage was not included in any further analyses.

Analyses were run using three assemblage measures: abundance, species richness, and Dragonfly Biotic Index scores (DBI). DBI scores were obtained from Samways and Simaika (2016). Thereafter, the average score per site was calculated by dividing the sum of all the species' DBI scores at a site by the number of species observed at that site.

Spearman rank correlations in R (R Core Team, 2018) tested the degree of association between larvae vs. adults, and larvae vs. adjusted adults for abundance, species richness, and DBI scores. The function *manyglm* in the *mvabund* package (Wang et al., 2012) was used to determine the best-fit distribution for the data, which best fitted a negative binomial distribution. Thereafter, generalised linear models (GLMs) with multivariate extensions were run with abundance data to determine whether larvae and adult dragonfly assemblages differed in composition. To determine whether larvae and adults of the same species occurred at the same sites, exact tests of goodness-of-fit were performed with the *binom.test* function in the native *stats* package in R (R Core Team, 2018). The hypothesis tested was that there would be significantly different proportions of matches and mismatches between the larvae and adults of a species, against the null hypothesis that there would be no differences, assuming an equal likelihood of both. The constituents of the function are the number of successes/matches (number of matches between the same species of larvae and adult), number of trials: number of matches + number of mismatches (sites where only the larvae or the adult of a species was found), and the hypothesized probability of success (here 0.5). Here, the exact test was selected over a chi-squared or G-test, as it is applicable to sample sizes of <1 000 or when at least one of the expected values is small (<5) (Wickham and Chang, 2008).

2.5. Data analyses for comparative environmental drivers

Model selection and averaging, using the *MuMIn* package in R (Barton, 2018), determined which environmental variables influenced variation in abundance, species richness, and DBI scores for larvae,

adults, and adjusted adults (Burnham and Anderson, 2002). Abundance data at the small, small 40, and medium scales as well as species richness at the small scale best fitted Poisson distribution, and all other data were normally distributed. Eleven variables were included in the final model sets, which included: percentage shade cover, river depth, water temperature, conductivity (not at the medium scale), dissolved oxygen and pH, percentage cover of sand and rock (including the river edges and river bed), average vegetation height, and percentage cover of palmiet reed and aquatic macrophytes. A nested random variable comprising river and site was included in all models. All variables were standardized to allow for direct comparisons. The *dredge* function was used to rank the models of all possible combinations of variables, including the intercept-only model. Second-order Akaike's information criterion (AICc) was used as the selection criterion, and only models with ΔAICc values of <2 were included in the subset of best models (Burnham and Anderson, 2002). The values of the parameters were estimated by full model averaging of the best model subset using the *model.avg* function. A variable was considered to have a significant effect if the confidence interval did not include zero.

The *mvabund* package (Wang et al., 2012) in R (R Core Team, 2018) was used to identify the most important environmental variables influencing the assemblage structure of the larvae, adults, and adjusted adults. An additional group was included in the multivariate analyses, which comprised sites where both the larvae and adult of a species was present (here named 'combined'). The function *manyglm* determined the best-fit distributions for the datasets. Thereafter, GLMs with multivariate extensions were run with abundance data on the four groups using the 11 selected variables, that were divided into three groups. These

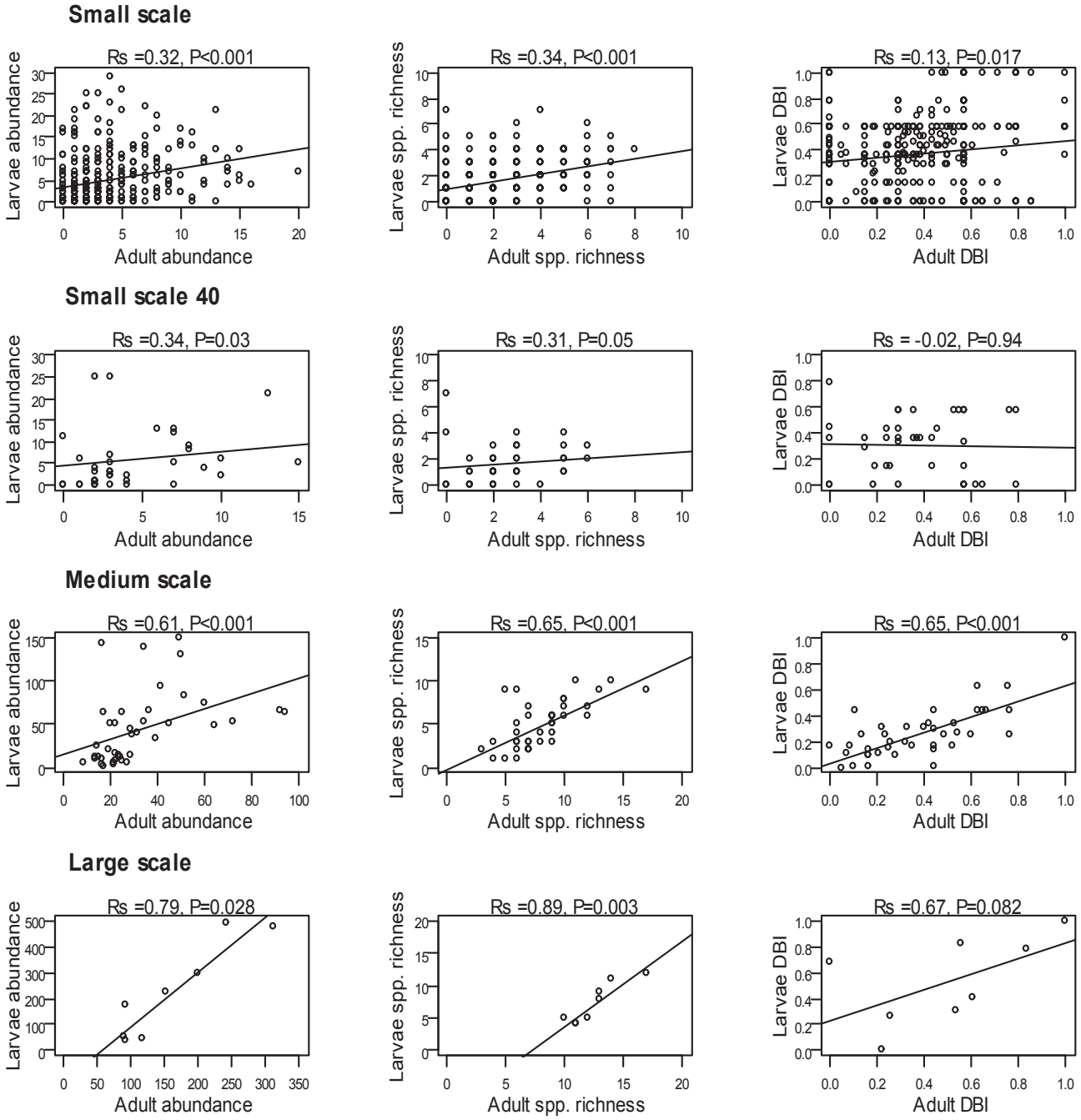


Fig. 1. Scatterplots showing the results of Spearman rank correlations for larvae vs. adults for dragonfly abundance, species richness, and Dragonfly Biotic Index scores. Bolded numbers signify significance. R_s = Spearman's Rank Correlation Coefficient, DBI = Dragonfly Biotic Index.

Table 1
Exact tests of proportions between matches vs. mismatches. POS = probability of success (the number of matches between larvae and adults of the same species (successes)/ the number of trials (matches + mismatches)). Bold numbers signify significance.

Species	Small scale		Medium scale		Large scale	
	p-value	POS	p-value	POS	p-value	POS
Overall	**< 0.001**	0.13	0.130	0.46	0.059	0.60
Anax imperator	**< 0.001**	0.09	0.424	0.40	1.000	0.50
Allocnemis leucosticta	**< 0.001**	0.00	**0.003**	0.08	0.625	0.25
Anax speratus	**< 0.001**	0.00	**0.001**	0.11	0.688	0.33
Chlorolestes conspicuus	0.250	0.00	0.250	0.00	1.000	1.00
Crocothemis erythraea	**< 0.001**	0.00	**0.008**	0.00	0.125	0.00
Ceriagrion glabrum	**0.029**	0.27	0.625	0.75	1.000	1.00
Ceratogomphus pictus	0.500	0.00	0.500	0.00	1.000	0.00
Crocothemis sanguinolenta	**< 0.001**	0.00	**0.002**	0.00	0.375	0.20
Chlorolestes umbratus	**0.021**	0.10	0.375	0.20	1.000	1.00
Elattoneura frenulata	0.063	0.00	0.125	0.00	0.250	0.00
Elattoneura glauca	0.125	0.00	0.250	0.00	0.250	0.00
Orthetrum julia capicola	**< 0.001**	0.11	0.875	0.48	0.727	0.63
Pantala flavescens	**< 0.001**	0.09	0.375	0.80	1.000	1.00
Paragomphus cognatus	**< 0.001**	0.10	0.108	0.68	0.219	0.83
Pseudagrion draconis	**< 0.001**	0.13	1.000	0.48	0.289	0.75
Pseudagrion furcigerum	**< 0.001**	0.18	0.524	0.41	1.000	0.50
Platycypha fitzsimonsi	1.000	0.00	1.000	0.00	1.000	0.00
Pseudagrion kersteni	**< 0.001**	0.13	0.405	0.39	1.000	0.57
Pinheyschna subpupillata	**< 0.001**	0.27	**< 0.001**	0.95	**0.008**	1.00
Syncordulia gracilis	1.000	0.00	1.000	0.00	1.000	0.00
Trithemis arteriosa	**< 0.001**	0.19	0.834	0.46	0.688	0.67
Trithemis dorsalis/furva	**< 0.001**	0.04	**0.004**	0.25	0.727	0.38
Tramea limbata	0.250	0.00	0.250	0.00	1.000	1.00
Zosteraeschna minuscula	0.125	0.14	0.375	0.20	1.000	1.00
Zygonyx natalensis	**< 0.001**	0.14	0.791	0.57	0.625	0.75

were best-fitted with a negative binomial distribution, which assumes a quadratic mean–variance. This model-based approach, tests multiple effects at the assemblage level, by fitting a separate GLM to each species, using the given explanatory variables. This method accounts for between-species correlations, and uses resampling-based hypothesis testing to determine which environmental variables are associated with the abundances (Wang et al., 2012).

3. Results

3.1. Results for congruence among larvae and adults

A total of 1 795 larvae (19 species) and 1 268 adult (25 species) dragonfly individuals were sampled. All rarefaction curves neared asymptote, which indicates that sampling effort was sufficient (Appendix A). This was further supported by species estimates for larvae (ICE = 19.37, Chao2 = 19.17, and second-order Jackknife = 18) and adults (ICE = 27.42, Chao2 = 30, and second-order Jackknife = 27) nearing observed species richness.

Only 118 exuviae of just five species were recorded, which is too low a number and species richness to be included for statistical analyses, and far from the recorded number of larvae or adult species. This was despite sufficient sampling according to the rarefaction curve (Appendix A). No exuviae at all were recorded along the agricultural sections of the Palmiet River, the natural section of the Eerste River, or the entire Molenaars River.

At the small scale, there were positive but weak correlations between larvae and adults, as well as between larvae and adjusted adults for abundance, species richness, and DBI scores; all were significant (Fig. 1). Positive but weak correlations also occurred at the small 40 scale for abundance and species richness, which were significant. However, correlations for DBI scores were negative, weak, and not significant (Fig. 1). Correlations for all three assemblage measures strengthened as spatial scale increased for larvae vs. adults, and larvae vs. adjusted adults, with the strongest correlations at the largest scale (Fig. 1). Despite the high R_s values at the large spatial scale, the P-values for DBI scores were not significant at the 5% level, where sample sizes were small (Fig. 1). The correlations between adults and larvae closely resembled those between the adjusted adults and larvae, therefore only graphs of the adults and larvae were plotted (Fig. 1). For the adjusted adults and larvae, Spearman's Rank Correlation Coefficients and P-values were: small scale (abundance: Rs = 0.33, P = < 0.001; species richness: Rs = 0.34, P = < 0.001; DBI: Rs = 0.11, P = 0.046), small 40 scale (abundance: Rs = 0.33, P = 0.04; species richness: Rs = 0.31, P = 0.05; Rs = -0.06, P = 0.72), medium scale (abundance: Rs = 0.62, P < 0.001; species richness: Rs = 0.70, P < 0.001; DBI: Rs = 0.62, P < 0.001), and large scale (abundance: Rs = 0.78, P = 0.023; species richness: Rs = 0.90, P = 0.003; DBI: Rs = 0.67, P = 0.069). Dragonfly species composition differed between larvae and adult assemblages at the small (LRT = 351; P = 0.001), small 40 (LRT = 60.92; P = 0.001), and medium scales (LRT = 134.1; P = 0.002), but did not differ at the large scale (LRT = 38.42; P = 0.141).

Exact tests analysed the proportions of matches vs. mismatches, and at the small scale, there were 179 matches (proportion: 0.15) vs. 1 024 mismatches (proportion: 0.85), with a significant difference in the distribution skewed towards the higher proportion of mismatches (Table 1; Appendix B), meaning that the observed proportions differed from the expected proportions (0.5:0.5). Seventeen of the species had significantly different proportions of matches vs. mismatches, skewed towards the mismatches (Table 1; Appendix B). Eight species (*Chlorolestes conspicuus* (CC), *Elattoneura frenulata* (EF), *E. glauca* (EG), *Ceratogomphus pictus* (CP), *Syncordulia gracilis* (SG), *Pantala flavescens* (PFL), *Tramea limbata* (TL), and *Zosteraeschna minuscula* (ZM)) did not have significantly different proportions of matches vs. mismatches, although the proportions of mismatches were always higher (Table 1; Appendix B). Of these eight species, half (EG, PFL, TL, and ZM) were only observed as adults, and never sampled as larvae. At the medium scale, 157 matches (proportion: 0.46) vs. 186 mismatches (proportion: 0.54) were observed, and did not differ significantly (Table 1; Appendix B). For the species individually, *Allocnemis leucosticta* (AL), *Anax speratus* (AS), *Crocothemis erythraea* (CE), *C. sanguinolenta* (CS), *Pinheyschna subpupillata* (PS), and *Trithemis dorsalis/furva* (TD) had significantly

different proportions of matches vs. mismatches (Table 1; Appendix B). All of the abovementioned species, except for *P. subpupillata* (PS), had significantly greater proportions of mismatches. At the large scale, 55 matches (proportion: 0.60) vs. 36 mismatches (proportion: 0.40) were recorded (Appendix B). Although skewed towards the proportion of matches, this was not significant (Table 1). *P. subpupillata* (PS) was the only species with a significant difference between proportions of matches vs. mismatches, skewed towards matches (Appendix B). Although not always significant, as scale increased, a greater proportion of matches occurred. At the small scale, there were no species with higher proportions of matches than mismatches, this increased to five species at the medium scale, while reaching 12 species at the large scale (Appendix B). As scale increased, so did the probability of success for all the species (Table 1).

3.2. Comparative environmental drivers

At the small scale, two of the 11 environmental variables, water temperature and palmiet reed cover, significantly positively influenced abundances of larvae, adults, and the adjusted adults (Appendix D). Differences between the stages were that larval abundance was influenced positively by pH, adult abundance positively by river depth, and adult and adjusted adult abundances positively by both sand and aquatic macrophyte cover (Appendix D). For species richness, only water temperature significantly and positively influenced larvae, adult, and adjusted adults at the small scale (Appendix D). Regarding differences between the life stages, adult and adjusted adult species richness were positively influenced by sand, palmiet reed, and aquatic macrophyte cover (Appendix D). The DBI scores for larvae and adults were significantly and negatively influenced by water temperature (Appendix D). Regarding differences between the life stages, at the small scale, larval DBI scores were negatively influenced by pH, adults were negatively influenced by conductivity, and adjusted adult DBI scores negatively influenced by rock cover (Appendix D).

At the small scale of 40 random sites, dissolved oxygen significantly positively influenced abundances of larvae, adults, and the adjusted adults (Appendix D). Percentage rock and river depth positively influenced adult and adjusted adult abundances. Differences between the stages were that larval abundance was positively influenced by pH and water temperature and adult abundance was positively influenced by aquatic macrophyte and sand cover (Appendix D). For species richness, only water temperature significantly and positively influenced larvae (Appendix D). Adult and adjusted adult species richness were positively influenced by rock cover, dissolved oxygen, and river depth (Appendix D). The DBI scores for larvae and adults were significantly and negatively influenced by water temperature (Appendix D). Adult DBI scores were negatively influenced by conductivity and shade cover (Appendix D).

At the medium scale, dissolved oxygen was the only variable that significantly and positively influenced the abundances of larvae, adults, and the adjusted adults (Appendix D). Larval abundance was positively affected by water temperature and pH, and negatively by vegetation height. Adult and adjusted adult abundances were positively influenced by sand and palmiet cover and negatively by percentage cover of rocks (Appendix D). Species richness of larvae and adults were positively influenced by water temperature and species richness of larvae and adjusted adults were negatively affected by pH (Appendix D). Regarding differences, larval species richness was negatively affected by average vegetation height and shade cover. Adult species richness was negatively influenced by rock cover, and adjusted adult species richness by pH and positively influenced by dissolved oxygen (Appendix D). The DBI scores of larvae and adjusted adults were negatively influenced by rock cover (Appendix D). In terms of differences between the stages, larvae DBI scores were positively affected by shade cover and adult DBI scores were negatively influenced by water temperature (Appendix D).

At the large scale, larvae abundance was significantly positively influenced by water temperature (Appendix D). Adult and adjusted adult species richness were positively affected by palmiet cover and

Table 2
Assemblage analyses using multivariate generalised linear modelling of the effects of environmental variables on dragonfly larvae, adults, adjusted adults, and combined. Bold numbers signify significance.

Variables	Small scale				Medium scale			
	Deviation test statistic				Deviation test statistic			
	Larvae	Adults	Adj. adults	Combined	Larvae	Adults	Adj. adults	Combined
% Shade	**84.56** ***	**70.12** ***	**68.09** ***	**100.5****	**78.3** ***	**76.92** **	**67.69** **	**92.86****
Depth	**76.87** ***	**93.61** ***	**127** ***	**106.1****	**69.26** ***	**59.64** *	**53.57** **	**69.27****
Water temperature	**234.50** ***	**258.8** ***	**315.1** ***	**390.1****	**103.6** ***	**148.5** ***	**134.4** ***	**167.1****
Conductivity	**38.79** **	18.62	18.2	**38.3****	/	/	/	/
Dissolved oxygen	**78.34** ***	**72.23** ***	**96.18** ***	**102.4****	**46.49** *	**71.46** **	**62.47** **	**65.45****
pH	**131.70** ***	**68.54** ***	**63.77** **	**158.4****	**56.75** **	35.01	29.51	**54.32***
% Sand	**30.34** *	**77.99** ***	**117.6** ***	**62.1****	**39.52** *	**54.41** *	**44.22** *	43.24
% Rock	**104.90** ***	**112.9** ***	**108.1** ***	**170.1****	**66.83** **	**90.49** **	**72.36** **	**88.17****
Avge veg height	**81.79** ***	**48.44** **	**49.03** **	**80.85****	**77.9** ***	**74.78** **	**65.61** **	**85.53****
Prionium serratum	**83.75** ***	**103.6** ***	**149.9** ***	**141.7****	**60.95** **	**78.11** **	**72.1** **	**81.36****
Aquatic macrophytes	28.42	**97.46** ***	**110.5** ***	**65.33****	28.31	**58.93** *	**48.07** **	**44.79***
	Large scale				Small scale (40)			
Variables	**Deviation test statistic**				**Deviation test statistic**			
	Larvae	Adults	Adj. adults	Combined	Larvae	Adults	Adj. adults	Combined
% Shade	**84.77** *	**122.5** **	**108.6** **	**112.2****	12.05	15.01	13.31	11.68
Depth	45.38	64.13	52.24	53.92	4.80	**29.31***	23.01	12.57
Water temperature	**69.62***	**87.55***	**67.36** *	**77.02***	15.74	20.58	19.74	**30.84***
Conductivity	33.1	34.23	32.42	33.66	10.54	7.429	7.241	12.22
Dissolved oxygen	51.97	69.96	56.16	56.03	7.33	**30.7***	**28.96***	19.51
pH	27.77	28.92	20.77	26.42	25.61	16.18	13.83	**30.44***
% Sand	33.33	36.07	27.27	40.56	/	/	/	/
% Rock	46.27	**83.31** *	**64.18** *	60.81	12.77	**37.42***	26.72	26.94
Avge veg height	55.57	72.13	59.09	61.07	/	/	/	/
Prionium serratum	57.17	69.7	62.86	62.73	20.18	23.95	19.83	15.36
Aquatic macrophytes	43.44	50.95	42.04	45	6.97	**33.26****	**32.15****	**30.09***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

negatively by shade cover, and dissolved oxygen positively influenced adjusted adult species richness (Appendix D). No variables influenced DBI scores at the large scale.

Of the 11 selected variables, species composition of the larvae, adults, adjusted adults, and combined group shared nine variables at the small scale (shade cover, river depth, water temperature, dissolved oxygen, pH, sand cover, rock cover, average vegetation height, and palmiet reed cover), seven variables at the medium scale (shade cover, river depth, water temperature, dissolved oxygen, sand cover, rock cover, average vegetation height, and palmiet reed cover), two variables at the large scale (water temperature and shade cover), and no variables were shared between them at the 40 sites small scale (Table 2). Water temperature and shade cover were the only variables that significantly influenced species composition of all the groups at the small, medium, and large spatial scales (Table 2). For small and medium scales, water temperature had the greatest influence on species composition of all the groups (Table 2). At the large scale, shade, followed by water temperature, had the greatest influence on species composition of the four groups (Table 2). There were no other significant variables influencing larvae and the combined group at the large scale, and rock cover was the only other variable influencing the species composition of adults and adjusted adults at the large scale (Table 2). At the 40 sites small scale, species composition of adults, adjusted adults, and the combined group were influenced by aquatic macrophyte cover (Table 2).

4. Discussion

4.1. Degree of congruence among larvae and adults

Larval and adult dragonfly assemblages varied in degree of congruency for abundance, species richness, and DBI scores according to spatial scale. At the large scale (here 450 m × 3 m), congruence was high, and although significant at the 5% level for abundance and richness, it was not significant for the DBI. There was moderately high congruence at the medium scale (90 m × 3 m). At the small spatial scale (10 m × 3 m), congruence between the two life stages was poor. Nevertheless, the relationship between larvae and adults was always positive for abundance, species richness, and DBI scores. The weak congruence at the small scale is important in the case of the DBI, which is highly sensitive in freshwater assessments as it pertains to particular species. Exclusion of a single species at a site can have a large effect on site score value, especially with high-scoring, threatened, habitat specialist, narrow-range endemic species. Six species were present as adults but not as larvae. Of these, *Zosteraeschna minuscula* and *Chlorolestes umbratus* both have high DBI scores, and their absence in larval samples would greatly alter site scores (Samways and Simaika, 2016). The absence of some larvae species may be due to not sampling the specific niches they inhabit, which is especially true for some narrow range, specialist species, whose habitat preferences we lack knowledge for (Bried et al., 2012).

At all four spatial scales, species presence, whether as larva or adult, did not lead to a significantly greater chance of the converse life stage occurring at the same site. However, the proportion of matches (i.e. level of congruence) increased with spatial scale, despite differences in comparative sampling efficiency of the two life stages (Hawking and New, 1999; Samways and Simaika, 2016). This was emphasized by extreme specialised requirements of some species, such as *Trithemis dorsalis/furva* and *Platycypha fitzimonsi*, which were more strongly represented as adults than larvae, whereas others, like *Zygonyx natalensis* and *Paragomphus cognatus*, were present mostly as larvae. Some species were only observed as adults and not as larvae, including *Tramea limbata* and *Pantala flavescens*. The larvae of both these species mostly develop in temporary waters and are associated with habitats like rice fields, small ponds, and temporary pools (Sherratt and Harvey, 1989; Johansson and Suhling, 2004; Kandibane et al., 2005). It would also be expected that with greater sampling effort there would be a higher chance of both stages being found. In addition to comparative sampling efficiency, these differences are also related to behavioural differences in habitat requirements, territory guarding or perching, egg-laying habits, whether individuals are natal residents or non-natal immigrants, the degree to which adults use rivers for mate finding, foraging, and ovipositing, as well as adults leaving the natal site to forage (Bried et al., 2016; Luke et al., 2017). For example, some gomphid species forage over the wide landscape and only visit rivers to mate and oviposit (Orr, 2006), as seen here for *Ceratogomphus pictus*. Furthermore, some of the recorded adult individuals were possibly only feeding or touring in sub-optimal breeding sites, whereas presence of larvae is usually a sign of residency, due to their limited dispersal abilities (Valente-Neto et al., 2016). Adult dispersal and oviposition aim to select suitable habitats to optimize the fitness of their offspring (Buskirk and Sherman, 1985). Despite this, larval mortality is high, for example Benke and Benke (1975) found that 80% or more of last instar larvae die before emergence, making larval presence not an indication of life cycle completion. Alternatively, adult males may have been driven away by competition, and females not choosing to mate with males holding sub-optimal territories, resulting in few or no larvae at certain sites.

4.2. Presence of exuviae

Only 118 exuviae from five species were sampled here and the rarefaction curve quickly reached asymptote, which means for the collection method used here, increased sampling effort would not have increased the number of species observed. Bried et al. (2012) concluded that lower species detection probability for exuviae would typically result in species richness observations that are biased low. It is not entirely clear why exuviae are so scarce in the CFR because in many other parts of the world (such as Europe) they are sampled far more readily (Raebel et al., 2010). Perhaps this is due to a combination of factors in the CFR, such as fluctuating water levels, strong water flows, scavenger activity, and our lack of knowledge of their behaviour for selecting cryptic locations at the time of adult emergence.

4.3. Comparative response of larvae vs. Adults to environmental variables

Despite species differences at sites, water temperature was the most influential variable, particularly at the small (both with all 360 sites and with just 40 sites) and medium scales for both larvae and adults. Abundance and species richness positively correlated with water temperature (which positively correlated with agricultural land use and alien vegetation cover). Warmer water temperatures are associated with higher productivity and promote faster egg development (Pritchard and Leggott, 1987), as well as faster growth of larvae (Suhling et al., 2015). Net thermal radiation is a key determinant of water temperature (Karr and Schlosser, 1978). Adult dragonflies, especially those that thermoregulate exogenously, are sensitive to the thermal landscape, and select suitable microhabitats accordingly (May, 1978).

The great differences in microhabitats experienced along CFR rivers cause in-water conditions in the lower reaches to vary from those of the mountainous upper reaches. Lower reaches characteristically have warmer water temperatures from lower elevations, wider, and less turbulent sections (Dallas and Day, 2007). These sections are often largely transformed, and agricultural development is likely to increase water temperature, due to reduced riparian shade and lower elevation, important drivers of dragonfly assemblages (Samways and Sharratt, 2010; Piggott et al., 2012), and here at all three spatial scales.

At the small and medium scales, for both larvae and adults, there was higher abundance and species richness at warmer water temperatures, which translates to the agriculturally transformed sites. This may be due to increased area to colonize rather than simply the degree of transformation. Species sensitive to disturbance and temperature can be absent at transformed sites, and replaced by habitat generalists (De Marco Júnior et al., 2015), including at CFR rivers (Kietzka et al., 2018).

Furthermore, larvae and adult DBI scores negatively correlated with water temperature/land transformation at the small and medium scales. The DBI is a measure of habitat quality, with the lower scores in the transformed areas, resulting from local loss of sensitive, habitat specialists such as *P. fitzimonsi* and *C. conspicuus*.

While small and medium scale analyses identified the important environmental drivers of both larvae and adult assemblages, this was not the case at the large scale, strongly suggesting that spatial scales of the order of 450 m × 3 m should not be used when identifying important environmental drivers.

Other than water temperature, adult assemblages were influenced mostly by vegetation-related and substrate-related characteristics. The indigenous palmiet reed plays an important functional role in CFR river systems (Kietzka et al., 2017), and was key driver here of assemblage composition, abundance, and species richness of adult dragonflies, particularly at the small and medium scales. It is favoured as a perching site, and is particularly important for some endemic species such as *P. furcigerum* (Samways and Sharratt, 2010). Other aquatic vegetation was also important for adults as both perching, but more importantly, as suitable oviposition sites (Clausnitzer et al., 2009; Luke et al., 2017; Briggs et al., 2019b). Differences between the life stages may indicate that habitat selection is based on the microhabitat features that are more important for that specific life stage, such as optimal foraging locations (Jooste et al., 2020), than on sites suitable for their offspring. Additionally, after larvae have hatched, they may disperse to nearby areas with the most favourable conditions.

5. Conclusion

Level of congruency between larvae vs. adult dragonflies for river assessment varied according to spatial scale. This means that choosing either larvae or adults, or both, in assessments depends on the question being asked, and then selecting the appropriate spatial scale to address that question. Dragonfly larvae and adults were locally congruent for abundance, species richness, and DBI scores, which increased with spatial scale. Furthermore, both life stages were driven by water temperature at all spatial scales, which positively correlated with agricultural land use and alien vegetation cover. This emphasizes that use of either life stage is just as effective for assessing land transformation, and even restoration. In short, for coarse ecological questions, where sampling at larger scales is appropriate, either the larvae or adults can be used. Furthermore, choice of life stage would then be dependent on factors like sampling season, favoured sampling method, river accessibility, and degree of expertise in identifying the different life stages. However, at small scales, larvae and adult species differed here in site occurrences and in their environmental drivers. Therefore, for complete taxonomic assessments, or for fine scale ecological questions, it is important to survey both life stages. It is also essential to ensure that all microhabitats are sampled, both within the water, and for some adults, also away from it.

Authors' contributions

All authors, Gabriella Kietzka, James Pryke, René Gaigher, and Michael Samways contributed to the study conception and design. Data collection and the first draft of the manuscript was by Gabriella Kietzka. All authors commented and contributed on previous versions of the manuscript. All authors read, edited and approved the final manuscript.

Declaration of Competing Interest

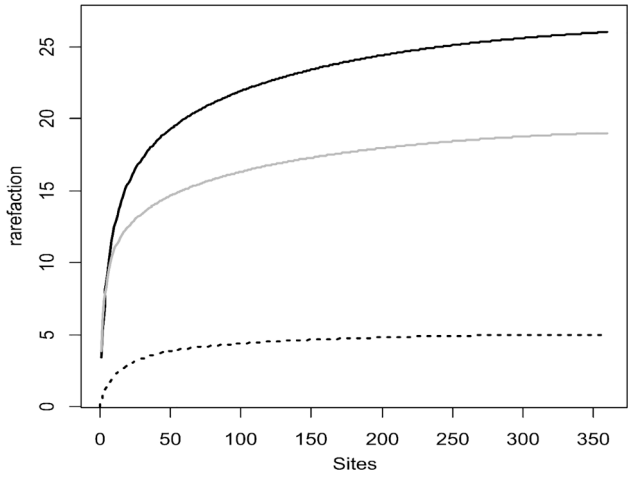
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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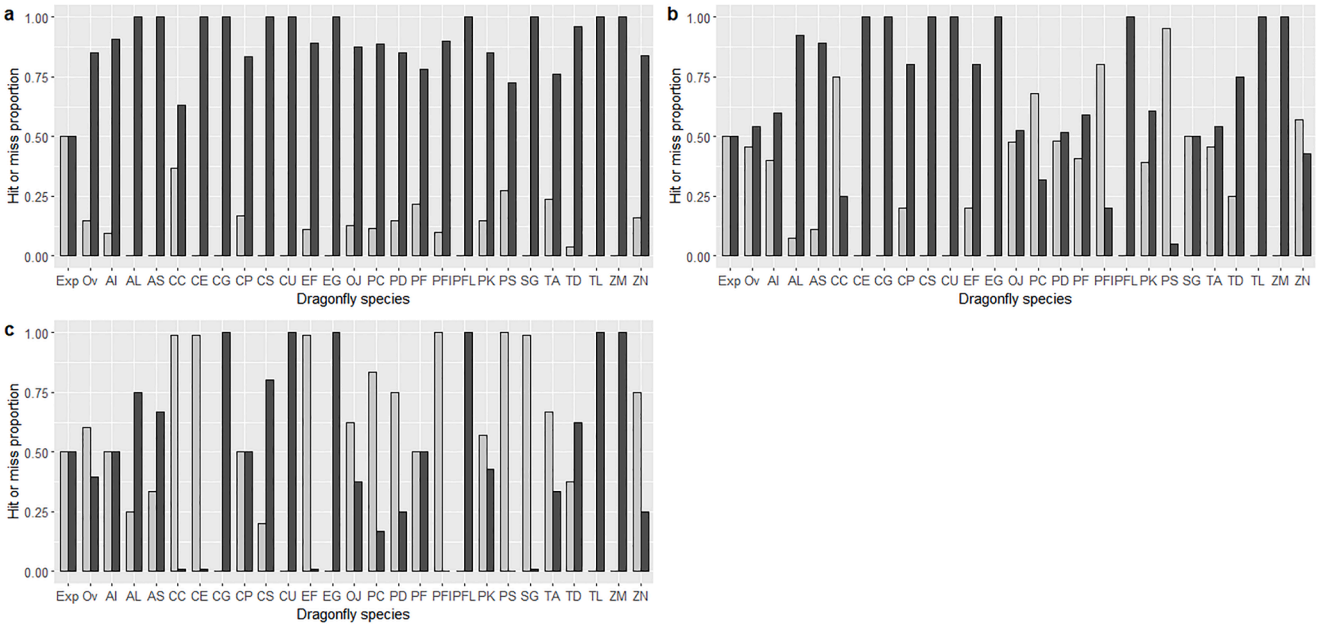
Appendix A

Rarefied species accumulation curves for dragonflies. Solid black line = adults, solid grey line = larvae, and dashed black line = exuviae.



Appendix B

Proportions of matches (grey) and mismatches (black) for overall dragonflies, and each species separately at the a) small scale, b) medium scale, and c) large scale. Exp = expected, Ov = overall. See Appendix C for species names.



Appendix C

Species names and codes.

Scientific name	Species code
Suborder ZYGOPTERA	
Family CHLOROCYPHIDAE	
Platycypha fitzsimonsi (Pinhey 1950)	Pfi
Family SYNLESTIDAE	
Chlorolestes conspicuus (Hage in Selys 1862)	CC
Chlorolestes umbratus (Selys 1862)	CU
Family PROTONURIDAE	
Elattoneura glauca (Selys 1862)	EG
Elattoneura frenulata (Hage in Selys 1862)	EF
Family PLATYCNEMIDIDAE	
Allocnemis leucosticta (Selys 1863)	AL
Family COENAGRIONIDAE	
Ceriagrion glabrum (Burmeister 1839)	CG
Pseudagrion draconis (Barnard 1937)	PD
Pseudagrion furcigerum (Rambur 1842)	PF
Pseudagrion kersteni (Gersaecker 1869)	PK
Suborder ANISOPTERA	
Family AESHNIDAE	
Zosteraeschna minuscula (McLachlan 1896)	ZM
Pinheyschna subpupillata (McLachlan 1896)	PS
Anax imperator (Rambur 1842)	AI
Anax speratus (Hagen 1867)	AS
Family GOMPHIDAE	
Ceratogomphus pictus (Selys 1854)	CP
Paragomphus cognatus (Rambur 1842)	PC
Family CORDULIIDAE	
Syncordulia gracilis (Burmeister 1839)	SG
Family LIBELLULIDAE	
Orthetrum julia capicola (Kimmins 1957)	OJ
Crocothemis erythraea (Brullé 1832)	CE
Crocothemis sanguinolenta (Burmeister 1839)	CS
Trithemis arteriosa (Burmeister 1839)	TA
Trithemis dorsalis/furva (Rambur 1842/Karsch 1899)	TD
Zygonyx natalensis (Martin 1900)	ZN
Pantala flavescens (Fabricius 1798)	Pfl
Tramea limbata (Desjardins 1832)	TL

Appendix D

Model-averaged estimates (conditional averaged) of explanatory variables on abundance, species richness and DBI scores of the groups at a) small scale, b) medium scale, c) large scale, and d) small scale of 40 sites. Wat temp = water temperature, Conduct = conductivity, dix oxy = dissolved oxygen, Veg height = average vegetation height, Aq macro = aquatic macrophytes.

a) Small	% Shade	Depth	Wat temp	Conduct	Dis oxy	pH	% Sand	% Rock	Veg height	P. serratum	Aq macro
Larvae abd											
Est(SE)	0.09(0.06)	0.06(0.05)	0.27(0.1)	0.06(0.04)	0.03(0.06)	0.3(0.09)	−0.05(0.05)	−0.07(0.06)	−0.13(0.07)	0.14(0.06)	0.04(0.05)
CI 95%	−0.08;0.16	−0.06;0.09	0.08;0.45	−0.05;0.13	−0.02;0.02	0.13;0.47	−0.05;0.04	−0.11;0.07	−0.26;0.06	0.03;0.25	−0.03;0.04
RI	0.49	0.26	1	0.64	0.02	1	0.1	0.28	0.78	1	0.08
No. models	14	8	29	19	1	29	4	9	22	29	3
Adult abd											
Est(SE)	0.08(0.05)	0.08(0.04)	0.21(0.05)		0.08(0.04)		0.14(0.04)	−0.04(0.05)	−0.07(0.05)	0.17(0.04)	0.11(0.04)
CI 95%	−0.05;0.16	−0.01;0.16	0.1;0.32		−0.05;0.15		0.06;0.22	−0.06;0.04	−0.11;0.06	0.09;0.26	0.03;0.18
RI	0.68	0.95	1		0.66		1	0.21	0.34	1	1
No. models	9	12	13		8		13	4	4	13	13
Adj adult abd											
Est(SE)	0.09(0.05)	0.08(0.04)	0.23(0.06)	−0.06(0.05)	0.08(0.05)		0.15(0.04)	−0.05(0.05)	−0.07(0.05)	0.18(0.04)	0.11(0.04)
CI 95%	−0.04;0.18	−0.03;0.15	0.12;0.34	−0.1;0.06	−0.05;0.15		0.07;0.23	−0.05;0.04	−0.11;0.06	0.1;0.27	0.03;0.19
RI	0.82	0.78	1	0.4	0.62		1	0.13	0.31	1	1
No. models	19	16	23	9	13		23	4	7	23	23
Larvae spp rich											
Est(SE)		0.06(0.04)	0.37(0.06)			0(0.07)			−0.05(0.06)	0.05(0.04)	0.03(0.04)
CI 95%		−0.04;0.13	0.24;0.49			−0.04;0.04			−0.08;0.06	−0.05;0.08	−0.03;0.04
RI		0.66	1			0.09			0.19	0.29	0.13
No. models		11	17			2			4	5	3
Adult spp rich											
Est(SE)	0.06(0.04)	0.05(0.03)	0.18(0.05)	−0.03(0.04)	0.06(0.04)	−0.02(0.04)	0.09(0.03)		−0.04(0.05)	0.11(0.03)	0.09(0.03)
CI 95%	−0.05;0.11	−0.04;0.1	0.09;0.28	−0.05;0.03	−0.05;0.11	−0.02;0.02	0.03;0.16		−0.05;0.04	0.05;0.18	0.02;0.15
RI	0.49	0.52	1	0.2	0.53	0.03	1		0.15	1	1
No. models	10	10	20	5	10	1	20		4	20	20
Adj adult spp rich											
Est(SE)	0.07(0.04)	0.05(0.03)	0.19(0.05)	−0.03(0.04)	0.06(0.04)	−0.02(0.04)	0.1(0.03)	−0.03(0.04)	−0.03(0.05)	0.12(0.04)	0.08(0.03)
CI 95%	−0.05;0.13	−0.04;0.08	0.09;0.29	−0.04;0.03	−0.05;0.13	−0.02;0.01	0.04;0.16	−0.03;0.02	−0.05;0.04	0.05;0.19	0.02;0.15
RI	0.62	0.36	1	0.18	0.64	0.03	1	0.06	0.15	1	1
No. models	15	9	25	5	16	1	25	2	5	25	25
Larvae DBI											
Est(SE)	0.44(0.23)	0.21(0.27)	−1.1(0.3)	23.3(22.76)	0.2(0.25)	−0.83(0.27)	0.38(0.32)	−0.4(0.28)	−1.08(0.79)		
CI 95%	−0.09;0.89	−0.2;0.25	−1.69;-0.51	−13.38;15.89	−0.21;0.28	−1.37;-0.29	−0.34;0.51	−0.68;0.36	−2.27;0.93		
RI	0.91	0.12	1	0.05	0.16	1	0.22	0.4	0.62		
No. models	17	3	19	1	4	19	4	7	11		
Adult DBI											
Est(SE)			−0.63(0.24)	−30.26(13.43)	−0.27(0.25)	0.39(0.3)	−1.99(1.65)	−0.52(0.32)			
CI 95%			−0.97;0.42	−52.54;18.41	−0.38;0.26	−0.3;0.41	−5.23;1.25	−1.15;0.1			
RI			0.44	0.56	0.22	0.14	1	1			
No. models			3	2	1	1	5	5			
Adj adult DBI											
Est(SE)	−0.1(0.21)	0.17(0.2)	−0.38(0.25)	−10.91(10.31)	−0.14(0.21)	0.21(0.46)	−0.37(0.32)	−0.71(0.33)	−0.34(0.76)	0.3(0.22)	−0.28(0.72)
CI 95%	−0.11;0.1	−0.17;0.23	−0.77;0.3	−14.67;10.29	−0.19;0.15	−0.16;0.17	−0.59;0.37	−1.35;-0.07	−0.4;0.36	−0.27;0.45	−0.37;0.34
RI	0.05	0.16	0.61	0.2	0.12	0.03	0.29	1	0.05	0.29	0.05
No. models	2	5	17	5	4	1	7	26	2	8	2

(*continued on next page*)

(*continued*)

b) Medium	% Shade	Depth	Wat temp	Conduct	Dis oxy	pH	% Sand	% Rock	Veg height	P. serratum	Aq macro
b) Medium	% Shade	Depth	Wat temp	Conduct	Dis oxy	pH	% Sand	% Rock	Veg height	P. serratum	Aq macro
Larvae abd											
Est(SE)			**0.54(0.11)**		**0.25(0.11)**	**0.38(0.15)**		−0.29(0.15)	**−0.34(0.13)**	0.18(0.12)	
CI 95%			**−0.27;0.38**		**−0.1;0.48**	**−0.02;0.7**		−0.52;0.21	**−0.61;-0.08**	−0.15;0.26	
RI			**0.1**		**0.77**	**0.9**		0.53	**1**	0.3	
No. models			**1**		**4**	**5**		3	**6**	2	
Adult abd											
Est(SE)		−0.09(0.07)	−0.21(0.14)		**0.13(0.06)**	0.11(0.07)	**0.26(0.06)**	**−0.27(0.09)**		**0.2(0.07)**	
CI 95%		−0.08;0.06	−0.21;0.15		**−0.09;0.21**	−0.07;0.1	**0.14;0.38**	**−0.44;-0.1**		**0.06;0.34**	
RI		0.1	0.15		**0.5**	0.13	**1**	**1**		**1**	
No. models		1	1		**3**	1	**6**	**6**		**6**	
Adj adult abd											
Est(SE)					**0.16(0.06)**	0.11(0.07)	**0.27(0.06)**	**−0.24(0.09)**		**0.24(0.06)**	
CI 95%					**0.03;0.28**	−0.09;0.16	**0.15;0.39**	**−0.44;0.07**		**0.11;0.36**	
RI					**1**	0.31	**1**	**0.77**		**1**	
No. models					**3**	1	**3**	**2**		**3**	
Larvae spp rich											
Est(SE)	**−0.22(0.11)**		**0.24(0.09)**			**−0.34(0.11)**		−0.21(0.12)	**−0.25(0.11)**	0.13(0.08)	0.07(0.07)
CI 95%	**−0.44;0.07**		**−0.13;0.17**			**−0.6;0.11**		−0.22;0.15	**−0.32;0.18**	−0.1;0.15	−0.05;0.06
RI	**0.82**		**0.09**			**0.72**		0.17	**0.28**	0.21	0.08
No. models	**7**		**1**			**6**		2	**3**	2	1
Adult spp rich											
Est(SE)	−0.13(0.07)	0.09(0.06)	**0.18(0.07)**		0.11(0.06)		0.08(0.06)	**−0.18(0.07)**	−0.11(0.07)	0.1(0.06)	
CI 95%	−0.24;0.09	−0.05;0.06	**−0.1;0.3**		−0.08;0.12		−0.05;0.07	**−0.3;0.1**	−0.16;0.1	−0.07;0.1	
RI	0.55	0.08	**0.56**		0.18		0.12	**0.56**	0.3	0.16	
No. models	6	1	**4**		2		1	**4**	3	2	
Adj adult spp rich											
Est(SE)	−0.13(0.08)				**0.14(0.06)**	**−0.18(0.08)**				0.08(0.07)	0.06(0.06)
CI 95%	−0.19;0.11				**−0.09;0.13**	**−0.35;0.04**				−0.07;0.1	−0.05;0.07
RI	0.34				**0.15**	**0.85**				0.18	0.14
No. models	2				**1**	**4**				1	1
Larvae DBI											
Est(SE)	**0.67(0.23)**		−0.23(0.24)		−0.26(0.23)			**−0.82(0.27)**		−0.21(0.24)	
CI 95%	**0.19;1.14**		−0.31;0.23		−0.36;0.25			**−1.37;-0.27**		−0.29;0.22	
RI	**1**		0.17		0.22			**1**		0.17	
No. models	**4**		1		1			**4**		1	
Adult DBI											
Est(SE)		0.31(0.25)	**−0.71(0.34)**		0.28(0.32)	−0.41(0.3)		−0.35(0.28)		0.43(0.26)	
CI 95%		−0.21;0.27	**−1.36;0.35**		−0.16;0.19	−0.3;0.24		−0.45;0.31		−0.36;0.67	
RI		0.09	**0.72**		0.04	0.07		0.21		0.37	
No. models		2	**11**		1	1		4		6	
Adj adult DBI											
Est(SE)	0.35(0.22)		−0.59(0.33)				−0.55(0.34)	**−0.65(0.3)**		0.5(0.29)	−1.41(0.91)
CI 95%	−0.21;0.27		−1.19;0.33				−0.61;0.41	**−1.1;0.44**		−0.37;0.56	−2.64;1.19
RI	0.09		0.72				0.19	**0.5**		0.19	0.51
No. models	1		6				2	**4**		2	4

c) Large	% Shade	Depth	Wat temp	Conduct	Dis oxy	pH	% Sand	% Rock	Veg height	P. serratum	Aq macro
Larvae abd											
Est(SE)			**123.1(37.96)**	122.27(51.06)	100.47(60)	−7.48(74.96)				84.63(68.85)	
CI 95%			**−71.2;216.09**	−80.32;244.6	−101.12;168.52	−65.37;63.94				−88.54;119.62	
RI			**0.59**	0.67	0.34	0.1				0.18	
No. models			**1**	2	2	1				1	
Adult abd											

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c) Large	% Shade	Depth	Wat temp	Conduct	Dis oxy	pH	% Sand	% Rock	Veg height	P. serratum	Aq macro
Est(SE)			50.94(24.66)	46.01(27.9)	49.45(26.94)					54.5(26.76)	
CI 95%			−44.74;80.98	−47.57;84.38	−45.23;104.57					−48.39;96.7	
RI			0.36	0.4	0.6					0.44	
No. models			1	1	1					1	
Adj adult abd											
Est(SE)			51(24.2)	48.71(25.41)	51.51(25.34)	2.67(33.16)				52.99(26.42)	
CI 95%			−43.87;76.75	−44.46;78.01	−45.13;95.3	−29.59;30.15				−47.59;87.98	
RI			0.32	0.34	0.49	0.1				0.38	
No. models			1	2	2	1				1	
Larvae spp rich											
Est(SE)			2.08(0.82)		2.3(0.9)					2.24(0.94)	
CI 95%			−1.3;1.8		−1.68;2.65					−1.55;2.26	
RI			0.12		0.21					0.158	
No. models			1		1					1	
Adult spp rich											
Est(SE)	**−1.96(0.41)**			122.27(51.06)	100.47(60)	−7.48(74.96)				**1.85(0.54)**	
CI 95%	**−3.37;0.65**			−80.32;244.6	−101.12;168.52	−65.37;63.94				**−1.3;2.35**	
RI	**0.69**			0.67	0.34	0.1				**0.284**	
No. models	**1**			2	2	1				**1**	
Adj adult spp rich											
Est(SE)	**−1.78(0.43)**				**1.77(0.51)**					**1.86(0.46)**	
CI 95%	**−2.88;1.01**				**−1.24;2.32**					**−1.22;2.71**	
RI	**0.52**				**0.31**					**0.4**	
No. models	**1**				**1**					**1**	

d) Small (40)	% Shade	Depth	Wat temp	Conduct	Dis oxy	pH	% Sand	% Rock	Veg height	P. serratum	Aq macro
Larvae abd											
Est(SE)		−0.25(0.13)	**0.59(0.26)**	0.15(0.11)	**0.44(0.18)**	**0.52(0.21)**	0.18(0.15)	−0.29(0.16)	−0.2(0.17)	−0.3(0.16)	
CI 95%		−0.12;0.1	**−0.28;1.11**	−0.1;0.12	**0.07;0.82**	**−0.27;0.93**	−0.08;0.09	−0.35;0.22	−0.18;0.14	−0.5;0.23	
RI		0.04	**0.7**	0.09	**1**	**0.63**	0.04	0.24	0.1	0.44	
No. models		1	**13**	2	**19**	**12**	1	5	3	9	
Adult abd											
Est(SE)		**0.34(0.09)**			**0.41(0.1)**	0.18(0.11)	**0.13(0.01)**	**0.28(0.11)**			**0.17(0.08)**
CI 95%		**0.17;0.52**			**0.22;0.61**	−0.15;0.25	**−0.07;0.1**	**−0.1;0.51**			**−0.1;0.14**
RI		**1**			**1**	0.28	**0.11**	**0.75**			**0.11**
No. models		**6**			**6**	2	**1**	**4**			**1**
Adj adult abd											
Est(SE)		**0.38(0.07)**		−0.12(0.12)	**0.43(0.1)**	0.13(0.09)		**0.26(0.1)**			
CI 95%		**0.23;0.53**		−0.16;0.12	**0.23;0.62**	−0.12;0.19		**0.05;0.47**			
RI		**1**		0.2	**1**	0.27		**1**			
No. models		**3**		1	**3**	1		**3**			
Larvae spp rich											
Est(SE)			**0.39(0.16)**		0.15(0.14)				−0.16(0.15)	−0.11(0.14)	
CI 95%			**0.05;0.72**		−0.13;0.18				−0.21;0.15	−0.15;0.12	
RI			**1**		0.16				0.18	0.14	
No. models			**5**		1				1	1	
Adult spp rich											
Est(SE)		**0.23(0.09)**			**0.31(0.11)**			**0.25(0.12)**			
CI 95%		**0.04;0.42**			**0.09;0.52**			**−0.11;0.48**			
RI		**1**			**1**			**0.74**			
No. models		**3**			**3**			**2**			
Adj adult spp rich											
Est(SE)		**0.25(0.1)**	0.13(0.12)		**0.31(0.11)**			**0.29(0.12)**			
CI 95%		**0.05;0.45**	−0.11;0.15		**0.09;0.53**			**−0.07;0.55**			
RI		**1**	0.15		**1**			**0.83**			

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d) Small (40)	% Shade	Depth	Wat temp	Conduct	Dis oxy	pH	% Sand	% Rock	Veg height	P. serratum	Aq macro
No. models		**4**	1		**4**			**3**			
Larvae DBI											
Est(SE)			**−1.26(0.56)**		0.71(0.61)	0.47(0.52)	−0.89(1.05)	−0.93(0.53)		0.81(0.45)	
CI 95%			**−2.43;0.11**		−0.62;0.87	−0.34;0.4	−1.18;0.91	−1.77;0.67		−0.58;1.51	
RI			**0.92**		0.18	0.07	0.15	0.59		0.58	
No. models			**8**		2	1	2	5		5	
Adult DBI											
Est(SE)	**−2.14(0.99)**	1.25(0.63)	**−2.79(1.12)**	**−185.95(87.38)**	−0.9(0.59)					1(0.53)	−15.36(879.88)
CI 95%	**−4.15;-0.13**	−0.86;2.22	**−5.21;0.18**	**−140;103.56**	−1.66;0.78					−0.53;0.69	−615.34;611.72
RI	**1**	0.55	**0.9**	**0.1**	0.49					0.08	0.12
No. models	**8**	4	**7**	**1**	4					1	1
Adj adult DBI											
Est(SE)	−0.9(0.72)		−1.2(0.7)	0.96(2.13)		−0.71(0.47)			−0.68(0.52)	0.74(0.5)	0.64(0.45)
CI 95%	−1.09;0.76		−2.15;0.93	−2.08;2.57		−0.88;0.57			−0.33;0.29	−0.65;1.35	−0.58;1.05
RI	0.18		0.51	0.25		0.22			0.03	0.48	0.37
No. models	5		13	6		5			1	13	10

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