

# Artificial ponds increase local dragonfly diversity in a global biodiversity hotspot

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**Abstract** Human demands have led to an increased number of artificial ponds for irrigation of crops year-round. Certain insect species have established in these ponds, including dragonflies (Insecta: Odonata). There has been discussion around the value of artificial ponds for encouraging dragonfly diversity, with little work in biodiversity hotspots rich in rare and endemic species. We focus here on the Cape Floristic Region (CFR) global biodiversity hotspot, which has many endemic dragonfly species but has few natural ponds. Yet it has many artificial ponds mostly used for irrigation on local farms. This leads to an interesting question: to what extent do these artificial ponds provide habitats for dragonflies in this biologically rich, agriculturally fragmented landscape? To answer this, we recorded dragonfly species richness and abundances from 17 artificial ponds and 13 natural stream deposition pools as reference, in an area of the CFR where there are no local, natural, perennial ponds. Thirteen environmental and physical variables were recorded at the ponds and pools. We found that although ponds attracted no rare or threatened dragonfly species, they increased the area of occupancy and population sizes of many generalist species. These came from nearby natural deposition pools or from unknown sources elsewhere in the region, so providing refuges which otherwise would not be there. Interestingly, some CFR endemic species were also recorded at our artificial

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ponds. Overall dragonfly assemblages and those of true dragonflies (Anisoptera) and damselflies (Zygoptera) differed between artificial ponds and deposition pools, suggesting that artificial ponds are to some extent a novel ecosystem. Habitat type, elevation and temperature were significant drivers in structuring overall species assemblages. For the Anisoptera, riparian vegetation and level of landscape connectivity was important, while temperature was not. In contrast, Zygoptera species were most affected by river catchment, habitat type and temperature. In sum, these artificial ponds are stepping stone habitats across an increasingly fragmented landscape. Managing these ponds with perennial water, constant water levels, and maximum complexity and heterogeneity of habitats in terms of vegetation will conserve a wide range of generalists and some specialists.

**Keywords** Artificial reservoir · Pond · Pool · Aquatic conservation · Richness · Diversity · Odonata · Dragonfly Biotic Index · Cape Floristic Region · South Africa

## Introduction

A pond is an extent of water, smaller than a lake, and usually artificially made. Ponds can contribute greatly to regional diversity in many parts of the world (Williams et al. 2003; Indermuhle et al. 2004; Kadoya et al. 2004; Briers and Biggs 2005; Hinden et al. 2005; Oertli et al. 2005a; Jocqué et al. 2006; Suhling et al. 2006; Davies et al. 2008; Harabiš and Dolný 2012; Raebel et al. 2012a, b; De Marco et al. 2014; Kietzka et al. 2014). Yet we still need to find ways of best assessing the value of ponds in any particular area, as well as developing approaches for establishing networks of ponds to enable metapopulations of the pond species to function optimally (Biggs et al. 2005; Oertli et al. 2005b). When we do this, we also need to consider the quality and value of the adjacent terrestrial habitats as well as the ponds themselves (Declerck et al. 2006). For undertaking assessments we need bioindicators that express the value of the focal ponds for maintaining biodiversity. In this regard, dragonflies (Odonata: Anisoptera and Zygoptera) offer a good general umbrella (Sahlén and Ekestubbe 2001) as well as being a useful subset for assessing freshwater condition and that of the adjacent vegetation (Smith et al. 2006; Simaika and Samways 2008; Clark and Samways 1996; Samways and Sharratt 2010). Dragonflies have also been used in pond assessment (Osborn and Samways 1996; Rosset et al. 2013; De Marco et al. 2014) and for changes in ponds over time (Moore 1997), as well as for optimal pond design (Samways et al. 1996).

Artificial ponds are an integral feature of an agricultural landscape (Raebel et al. 2012a), especially in relatively dry southern Africa, where they contribute to raising the overall level of abundance and area of occupancy of dragonfly species in the area (Samways 1989a). Interestingly, in arid Namibia, farm ponds, water holes and spring pools host only generalist species, with these ponds and pools increasing the dragonfly gamma diversity of the region (Suhling et al. 2006).

A freshwater assessment index (the Dragonfly Biotic Index) was developed for assessing running water in South Africa (Simaika and Samways 2009) and recently has been extended for use in still waters (Samways and Simaika 2016). Despite this regional progress, there has been little research done on dragonfly assemblages of artificial ponds in the Cape Floristic Region (CFR) biodiversity hotspot (Mittermeier et al. 2004), well known for its rich biota and high level of endemic species of many taxa (Rouget et al. 2003; Rebelo and Siegfried 1992; Bond and Goldblatt 1984; Wishart and Day 2002; Day and Day 2009), including dragonflies (Grant and Samways 2007, 2011). Besides being an area of outstanding

biological diversity, the CFR is also largely lacking low elevation natural ponds and lakes, especially in its core of the Hottentots-Holland Mountains. Yet it has many artificial ponds used at the farm level for irrigation of crops. This leads us to an intriguing question: what species of dragonflies are using these ponds, and from where are they coming?

Apinda-Legnouo et al. (2013) showed that rare aquatic beetles and bugs use artificial ponds in the CFR, which emphasises the value of artificial ponds for conservation of certain rare and threatened species in this hotspot. However, it is not known whether these artificial ponds are of conservation value for the local dragonflies, and in particular, the rare and threatened species. In response to this information gap, our aim here is to investigate artificial ponds for dragonfly species to determine their value as conservation ecosystems. The key objectives are to (a) confirm and quantify the assumptions which relate to which specific dragonfly and damselfly species increase their area of occupancy by inhabiting artificial ponds, and whether some of these species are locally present in natural deposition pools of rivers in the immediate area; (b) assess dragonfly species richness and composition so as to attach a conservation value to specific pond types; (c) determine the environmental variables shaping dragonfly assemblages; and (d) determine whether the dragonfly and damselfly diversity in our study area compares to that of the aquatic bug and beetle diversity. We hypothesize that ponds do not have such an important conservation role for dragonflies as they do for aquatic bugs and beetles, as dragonflies are generally more mobile, and as adults, occupy larger areas and may be less specialist. Furthermore, we hypothesize that lentic species are habitat generalists, with a wide spectrum of tolerance and low sensitivity, and are generally wide dispersers.

## Methods

### Study area

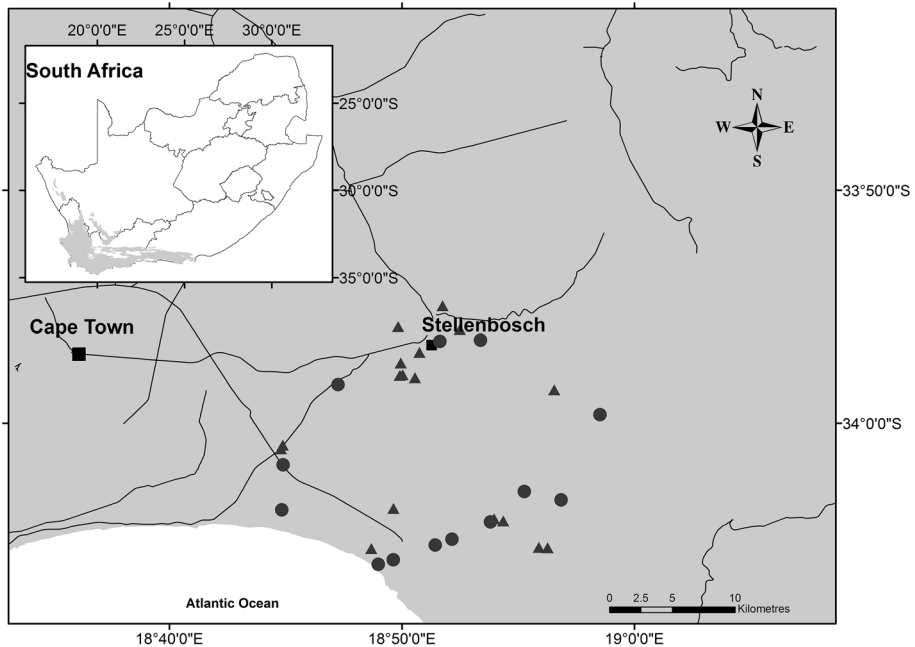
Our study was conducted around Stellenbosch in the Western Cape, South Africa (Fig. 1; see electronic supplementary material for description of sites) in the heart of the CFR biodiversity hotspot, the Hottentots-Holland Mountains. Our focal area spanned two different water catchments fed by the small Eerste and Lourens Rivers, and covered a combined area of 450 km<sup>2</sup>. The ponds selected were mostly those used by Apinda-Legnouo et al. (2013) who selected the sites along a gradient of permanency and flow regime. However, since that study was done, some of the ponds have been degraded or have become inaccessible. In these instances, new ponds were selected in the same vicinity.

All ponds were close to one of the two small rivers with their many deposition pools. Slow flowing and still reaches in rivers and ponds have similar characteristics (Juen et al. 2007). As well as our study focusing on 17 artificial ponds, it also included seven deposition pools in the Lourens River and six pools in the Eerste River. The ponds or pools were about 1.5 km apart in the Lourens River and 3.5 km apart in the Eerste River.

Our ponds obtain their water directly from the river, from run-off or from other tributaries in their respective catchment. Most of the ponds were created to supply the agricultural sector with water during the summer months when rainfall is low.

### Biotic sampling

Dragonflies were recorded over three seasons (spring, summer and autumn) to encompass the main peaks of flight activity in the area (Samways and Grant 2006). So sampling was from end of November 2014 to end January 2015, and again from March to April 2015



**Fig. 1** Map showing the different study sites situated in the CFR, South Africa. On the lowest image, the *black triangles* indicate the location of the artificial ponds (A1–A17) whilst the *black circles* indicate the location of the natural deposition pools (N18–30). See electronic supplementary material for description of sites

using 2-week sampling intervals. In total, there were 90 sampling sessions during which all ponds and pools were visited.

Both male and female adult dragonflies were sampled over 45 min at each pond or pool (Bried et al. 2012, 2015). A standardised time unit was chosen in place of a set transect distance because of variation between sites (Simaika and Samways 2011; Harms et al. 2014). In order to prevent duplication of counts, individuals were carefully observed to estimate their approximate territory. All individuals were identified and recorded using a pair of close-focus binoculars. The two species *Trithemis dorsalis* and *Trithemis furva* are indistinguishable in the field and so are recorded here as one taxon.

Dragonfly individuals were observed within a radius of 8 m from the centre of the river sites. At the pond sites, the method was adapted by counting individuals that were within a radius of 8 m from the water's edge. Sampling was only conducted on days which were windless and fine between 9:00 and 16:00.

### Dragonfly Biotic Index (DBI)

Use of dragonflies as biological indicators has increased in recent years, as they have several advantages, including being easy to identify in the field to species (Kutcher and Bried 2014), sensitive to changes in ecological conditions such as water quality and habitat structure (Kinvig and Samways 2000; Simaika and Samways 2011), taxonomically well-known and occupy a variety of different habitats throughout their life cycle (Harms et al. 2014) and cover a large range of spatial distributions making them an excellent candidate taxon for assessment (Simaika and Samways 2009).

Dragonfly assemblages respond to various environmental variables which help to explain ecological patterns in the landscape. The DBI is used for monitoring the species response to differences in habitat or change over time. Each species has a specific DBI value composed of three sub-indices (Simaika and Samways 2008; Samways and Simaika 2016): (a) a specific species geographic distribution, (b) the threat status of the species which is based on the IUCN categories and criteria (IUCN Standards and Petitions Subcommittee 2016), and (c) the species overall sensitivity to habitat disturbance. Each of these sub-indices has a value which ranges between 0 and 3. The sum of the values for three sub-indices is regarded as the DBI score for a particular species and can range between 0 and 9. Low scores indicate dragonfly species which are widespread, common and able tolerate high human disturbance. In contrast, high DBI values are indicative of threatened, sensitive and range restricted species.

A change in species assemblages, and thus DBI site values, can indicate the decline or improvement in habitat quality. Furthermore, it is possible to rate a specific study site as one of conservation significance using these values. To accomplish this, a standardised DBI is calculated for each site. For each site, it is calculated by summing the DBI values of all the species occurring at a particular site and dividing it by the number of species present at the site. These values can then be compared to determine the conservation significance of a site. Here, the DBI/Site values were used to compare the relative value of artificial ponds to natural deposition pools.

## Environmental variables

At each site, 13 variables were recorded. These variables included, sampling season (spring, summer, autumn), river catchment (Lourens River, Eerste River), habitat type (natural pool, artificial pond), elevation, and distance to river. Permanency, pond/pool area, riparian vegetation and flow regime were categorized as in Apinda-Legnouo et al. (2013) (see electronic supplementary material for site characteristics). For permanence, ponds and pools were categorized as: (1) temporary i.e. loses its water by late summer, (2) a pool which becomes slightly stagnant in summer, (3) one where the water level drops >20 cm, (4) water level fluctuates by <20 cm, and, (5) river deposition pools. Riparian vegetation was categorised into: (1)  $50 < X < 60$  % cover, (2)  $60 < X < 75$  % cover, (3)  $X > 75$  % cover. Finally, connectedness was categorized into: (1) strong connection, where there was a two-way direct connection, (2) moderately strong connection, where there was a single direct connection from the river to the pond, (3) moderately weak connection, where there was a direct connection from a pond to a river, and (4) weak connection, where there was no direct connection. Dissolved oxygen, conductivity, temperature and pH were recorded with a handheld multiprobe (Model: YSI 556 Multi Probe System; Make: YSI Environmental) at a depth of 0.3 m.

## Data analyses

Chao2 and Jackknife estimators were used to determine whether there was adequate sampling using EstimateS (Cowell 2006). We plotted and examined species accumulation curves for the full dataset, natural deposition pools only, and artificial ponds only. Hortal et al. (2006) suggest that non-parametric species richness estimators work best for estimating insect species richness. For datasets that contain small sample sizes, Chao2 and Jackknife estimators are most suitable to eliminate any bias that may occur (Cowell and Coddington 1994).

The software package PRIMER V6 (Primer-E. 2008; Clarke and Warwick 2001) was used for species assemblage-based analyses. Species abundance data and the associated site environmental data were prepared for subsequent analysis. Species abundance data were square-root transformed, and a Bray-Curtis similarity index was calculated to assess the similarity between ponds/pools. Clarke and Warwick (2001) recommend a square-root transformation of abundance data to down-weight the contributions of particularly abundant species in assemblages. Bray-Curtis similarity is recommended for ecological studies, as this is not affected by absences and gives more weight to abundance when comparing species.

Prior to their use in analysis, we visualized the environmental variables using a correlation matrix. Non-normally distributed variables were log-transformed. All variables were then normalized to allow comparison at the same scale. A correlation matrix was generated, and strongly correlated values identified. Strongly collinear (matrix value  $>0.95$ ) variables were then removed from further analysis. Similarity based on Euclidean distances was performed on the treated abiotic data. In order to identify variables that best explain assemblage pattern, we used a Bio-Env analysis, which selects environmental variables, or species best explaining assemblage pattern, by maximizing a rank correlation between their respective resemblance matrices (Clarke and Warwick 2001). The Bio-Env analysis calculates the correlation coefficient ( $\rho$ ) for every possible combination of predictor variables until it identifies the ‘best’ fit (i.e. the combination of predictor variables whose distance matrix yields the highest correlation).

Analyses were done using SPSS 13 (SPSS Inc. 2004) to test for significant differences in species richness, abundance, and DBIs between habitats types. Skewness and kurtosis tests revealed that the data are both skewed and kurtotic. Therefore, a Mann–Whitney U test was employed.

## Results

### Species richness, abundance and DBI

A total of 1905 individuals were sampled, representing 28 nominal species (i.e. with *Trithemis furva* and *T. dorsalis* counted as one), of which 10 were Zygoptera and 18 were Anisoptera (Table 1). Species richness estimators indicated that the sampling was adequate overall (Observed species richness (OSR): 28; Estimated species richness (ESR):  $23.48 \pm 1.41$ ; Chao2:  $26.43 \pm 3.41$ ; Jackknife2:  $29.18 \pm 4.24$ ) in natural habitats (OSR: 22; ESR:  $17.85 \pm 0.93$ ; Chao2:  $20.41 \pm 3.04$ ; Jackknife2:  $22.36 \pm 3.81$ ) and artificial habitats (OSR: 22; ESR:  $18.15 \pm 1.35$ ; Chao2:  $20.47 \pm 2.85$ ; Jackknife2:  $22.77 \pm 3.70$ ).

Of the national total of 162 odonate species, 22 (13.6 %) were recorded at both ponds and natural deposition pools (Fig. 2). Of these 22, six (27.3 %) were endemic to the CFR (four species and *Orthetrum julia capicola* as an evolutionarily significant unit (ESU)) and one was a near national endemic (*Zosteraeschna minuscula*). At the natural deposition pools, three endemic species were recorded: *Chlorolestes conspicuus*, *Pseudagrion furcigerum*, and *Z. minuscula*, and three endemic species/ESUs were shared between both artificial ponds and natural deposition pools: *Pseudagrion draconis*, *Elatoneura frenulata* and *O. j. capicola*. No CFR or South African endemic species were found solely at artificial ponds. None of the species are Red Listed as Threatened (IUCN 2015, 2016).

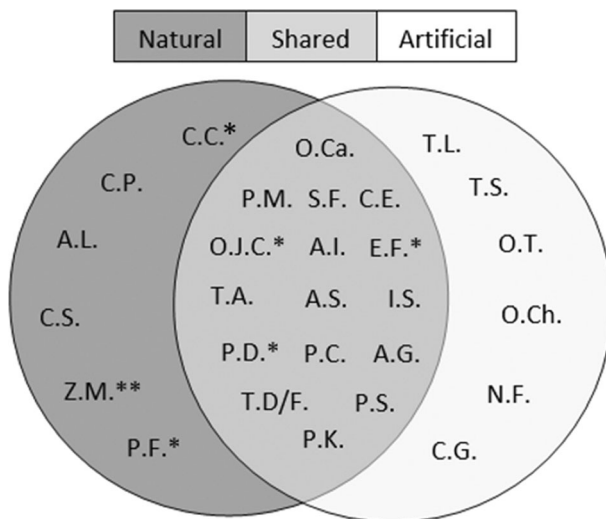
A ranked percentage species presence curve (Fig. 3) illustrates dragonfly species presences across the ponds and pools. The best represented species were the Anisoptera species: the CFR endemic ESU *O. j. capicola*, as well as *Anax imperator*, *Crocothemis*

**Table 1** Odonata species/evolutionarily significant units that we recorded across all the sites

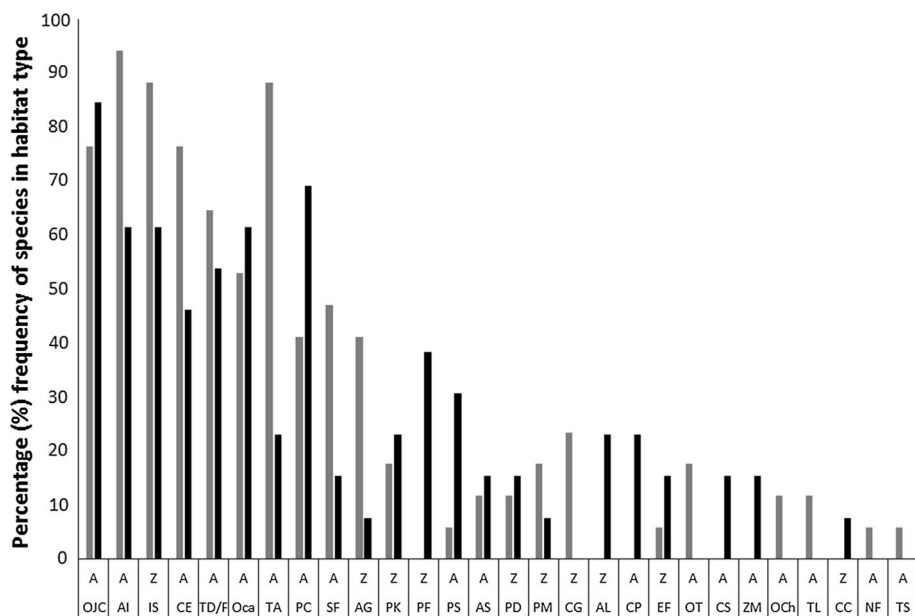
Scientific name	Common name	Abbreviation	Distribution	DBI score
Suborder Anisoptera	Dragonflies			
Family Aeshnidae	Hawkers			
<i>A. imperator</i>	Blue Emperor	AI	SA	1
<i>Anax speratus</i>	Orange Emperor	AS	SA	2
<i>Pinheyschna subpupillata</i>	Stream Hawker	PS	SA endemic	4
<i>Z. minuscula</i>	Friendly Hawker	ZM	SA near endemic	5
Family Gomphidae	Clubtails			
<i>Ceratogomphus pictus</i>	Common Thorntail	CP	SA	2
<i>P. cognatus</i>	Boulder Hooktail	PC	SA	1
Family Libellulidae	Skimmers			
<i>C. erythraea</i>	Broad Scarlet	CE	SA	0
<i>Crocothemis sanguinolenta</i>	Little Scarlet	C	SA	3
<i>N. farinosa</i>	Black-tailed Skimmer	NF	SA	1
<i>O. caffrum</i>	Two-striped Skimmer	OCa	SA	3
<i>O. chrysostigma</i>	Epaulet Skimmer	OCh	SA	2
<i>O. j. capicola</i>	Julia Skimmer	OJC	CFR endemic	3
<i>Orthetrum trinacria</i>	Long Skimmer	OT	SA	1
<i>Sympetrum fonscolombii</i>	Nomad	SF	SA	0
<i>T. limbata</i>	Voyaging Glider	TL	SA	0
<i>T. arteriosa</i>	Red-veined Dropwing	TA	SA	0
<i>Trithemis dorsalis</i> <sup>a</sup>	Round-hook Dropwing	TD/F	SA	0
<i>Trithemis furva</i> <sup>a</sup>	Navy Dropwing	TD/F	SA	0
<i>Trithemis stictica</i>	Jaunty Dropwing	TS	SA	1
Suborder Zygoptera	Damselflies			
Family Coenagrionidae	Pond Damsels			
<i>A. glaucum</i>	Swamp Bluet	AG	SA	1
<i>C. glabrum</i>	Common Citril	CG	SA	0
<i>I. senegalensis</i>	Marsh Bluetail	IS	SA	0
<i>P. draconis</i>	Mountain Sprite	PD	SA endemic	4
<i>P. furcigerum</i>	Palmiet Sprite	PF	CFR endemic	7
<i>Pseudagrion kersteni</i>	Kersten's Sprite	PK	SA	1
<i>Pseudagrion massaicum</i>	Masai Sprite	PM	SA	1
Family Platycnemididae	Featherlegs			
<i>A. leucosticta</i>	Goldtail	AL	SA	5
<i>E. frenulata</i>	Sooty Threadtail	EF	CFR	5
Family Synlestidae	Malachites			
<i>C. conspicuus</i>	Conspicuous Malachite	CC	CFR	7

It also includes the geographic distribution, as well as the DBI score per species. The distribution key is: SA [=occurs throughout South Africa—including the Cape Floristic Region (CFR)], and CFR [=indicates only within the Cape Floristic Region]

<sup>a</sup> *T. dorsalis* and *T. furva* data are combined and referred to as *Trithemis dorsalis/furva* (TD/F)



**Fig. 2** Venn diagram of species at natural deposition pools, artificial ponds or shared between the two habitat types. Natural deposition pools and artificial ponds host six unique species each and share 16 species. Abbreviations are of species names, and described in Table 1. The Western Cape endemic species are denoted with a *single asterisk* (\*) and South African endemic/near endemic species with a *double asterisk* (\*\*) are also indicated in the diagram



**Fig. 3** Ranked percent (%) presence of species at natural (*black bars*) and artificial (*grey bars*) ponds. A Anisoptera, Z Zygoptera. Abbreviations are of species names, and described in Table 1



*erythraea*, *T. dorsalis/furva*, *Orthetrum caffrum*, *Trithemis arteriosa* and *Paragomphus cognatus*. The Zygoptera species *Ischnura senegalensis* was the best represented damselfly, with the second most represented damselfly being *Africallagma glaucum*. With the exception of *O. j. capicola*, these species had very low DBI scores (Table 1). At the lower end of the ranked percentage presence curve, species such as *P. draconis*, *Allocnemis leucosticta*, *E. frenulata*, *C. sanguinolenta*, *Z. minuscula* and *C. conspicuus* were species with fairly high DBI scores.

Analysis of variance on the differences in overall dragonfly species richness and abundances showed that both were significantly higher in artificial ponds (51 sites, mean richness =  $5.00 \pm 1.82$ ; mean abundance =  $25.06 \pm 17.61$ ) than in natural pools (39 sites, mean richness =  $3.77 \pm 2.08$ ; mean abundance =  $16.08 \pm 15.73$  (Mann–Whitney U test result for species richness:  $U = 672.0$ ,  $p < 0.008$ , and abundance:  $U = 645$ ,  $p < 0.004$ )). However, mean DBI/Site values of the species found at natural pools (mean =  $1.97 \pm 1.12$ ) were significantly higher than in artificial ponds (mean =  $0.95 \pm 0.44$  (DBI/Site:  $U = 406.0$ ,  $p < 0.0001$ )), indicating that the more sensitive taxa were at the natural pools.

### Drivers of assemblage patterns and species richness

Variables with significant effects on overall dragonfly assemblages were habitat type, elevation and temperature ( $\rho = 0.342$ ,  $P = 0.01$ ). For Anisoptera, habitat type and elevation were also important, as well as riparian vegetation and connectivity ( $\rho = 0.26$ ,  $P = 0.01$ ). Catchment, habitat type and temperature explained Zygoptera assemblage patterns best ( $\rho = 0.274$ ,  $P = 0.01$ ).

## Discussion

### Role of artificial ponds

The CFR has few remaining natural ponds, but today has many artificial ponds throughout, as well as natural soaks, streams, and small rivers with deposition pools. Suhling et al. (2006) found that artificial ponds increase the gamma diversity in nearby Namibia, while Williams et al. (2004) showed that United Kingdom ponds contribute to conservation by providing additional habitats, so increasing local species' population sizes. In the CFR, we found equal species richness in both ponds and natural deposition pools, although they did not have the same species composition. In short, there was partial spill over from natural deposition pools to artificial ponds, but not completely. As with Suhling et al. (2006), we found that generalist species (i.e. with low DBI, e.g. *C. erythraea*) in particular, increase their area of occupancy, and hence population sizes, by using artificial ponds. This means that ponds can contribute to regional conservation of generalist species (Ruggiero et al. 2008). The overall lower DBI/Site values at our artificial ponds emphasises this, and is also supported by similar findings in a different ecoregion in South Africa (Samways 1989a; Samways and Steytler 1996). This support of species by these CFR ponds is substantial, with Ruggiero et al. (2008) recording half the number of local species being supported by ponds in France. Although rare species may galvanize conservation action (Carchini et al. 2003; Hart et al. 2014), conservation of the total assemblage is also important as some may become rare in the future. Our small array of ponds attracted >13 % of the national species total, as well as three CFR endemic species/ESUs.

We found here, as elsewhere in South Africa (Samways 1989a), that the vagile Anisoptera species made use of additional pond habitats to a greater extent than did the more sedentary Zygoptera species, with more Anisoptera species actively searching for new sites (Samways and Niba 2010). This may also explain why ‘river catchment’ here was a significant variable driving Zygoptera species, which have more limited dispersal abilities.

### Why are some species found only at ponds?

Six species were present only at the artificial ponds, which raises the question from where did they come? It is possible that these individuals have dispersed from other local populations (Conrad et al. 1999), but as natural water bodies are so scarce in this part of the CFR, presumably they must have established over time from sections of rivers not sampled here (e.g. in the case of *Orthetrum chrysostigma*) or from nearby marshes or small streams (e.g. *Nesciothemis farinosa*, and *Ceriagrion glabrum* which were recorded in natural wooded streams several kilometres away), or are tourists (as is probably the case with *Tramea limbata*). Whatever the case, these artificial ponds are important stepping stones across the landscape. Most species are probably residents in the pools (see Valente-Neto et al. 2016), based on details in Samways (2008) and Suhling and Martens (2007), but confirming this would require further studies (sensu Angelibert and Giani 2003; McCauley 2006), including those with larvae and exuviae data (Raebel et al. 2012a, b).

Conrad et al. (1999) suggest that the habitat between ponds is as important as the ponds themselves. Dispersal is regarded as an adaptation to overcome extinction, and to ensure the long-term existence and persistence of dragonfly species, it is crucial to link habitat patches for a stable population in an unstable and fragmented environment (Harabiš and Dolný 2012). Thus, both natural and artificial water features may act as complementary stepping stones for functional connectivity.

When species establishment occurs in ponds, it can lead to high species richness (Williams et al. 2004), but we did not find this, with similar richness in artificial ponds and natural pools. However, additional sampling may have produced more species records, as suggested by the Jackknife estimate, especially if even more ponds were included, by virtue of area effect. We did though, find higher abundances of many species in ponds than in natural deposition pools. Kadoya et al. (2004) suggest that higher abundances could be the result of older ponds being more established and thus being able to support a large variety of micro-habitats which are able to host more abundant populations. Although age of the pond was not a specific point of our study, most had already been determined at 20–60 years old (Apinda-Legnouo et al. 2013), suggesting that many populations could be well-established. Riparian vegetation is indirectly an indication of pond age and may be a cue enabling females to identify suitable oviposition sites (Kadoya et al. 2004; Osborn and Samways 1996).

### Significant drivers of dragonfly species assemblages

We found that habitat type (natural or artificial), elevation, and temperature were the most important drivers for the overall odonate assemblage. But for Anisoptera alone, in addition to habitat type and elevation, riparian vegetation and connectivity, but not temperature, were also important. For Zygoptera, river catchment, habitat type and temperature best explained assemblage patterns.

The most influential driver of the overall dragonfly assemblage was habitat type. Even though natural pools and artificial ponds share similar physical characteristics (Juen et al.

2007), their assemblages can be different, being composed of highly vagile and generalist species that are able to exploit these habitats. The natural deposition pools here provided greater habitat heterogeneity, resulting in a more complex assemblage structure than ponds, as found elsewhere (Clark and Samways 1996).

Elevation (as a proxy for climate) is a significant driver of many invertebrate assemblages, especially across the ancient, weathered African landscape, which has had no glaciations for tens of millions of years (Pryke and Samways 2009). Although several studies have attempted to unify hypotheses on the importance of elevation for various insect groups (e.g. McCoy 1990; Axmacher et al. 2004), there is still little consensus. For South African dragonflies, as elevation increases, species richness decreases, over the range 0–390 m asl (Niba and Samways 2006). Over the range 0–3000 m asl, there is a distinct decrease in species richness at the very high elevations, but this is not a steady decrease, with points of constant species richness at some of the mid-elevation bands (Samways 1989b).

Dragonflies have various responses to tree canopy cover around the world, from a proportionately large number of species with a preference for shade in the tropics (Samways 2003; De Marco et al. 2015) to a largely shade adverse assemblage in South Africa, where shade reduces water temperature (Smith et al. 2006; Samways and Sharratt 2010). However, although shade can be important, trees also are important for particular organic input for certain species (Valente-Neto et al. 2016). Furthermore, Anisoptera can decrease with shade in South Africa (Clark and Samways 1996), with similar results from Brazil where the more sunlit waterways favour Anisoptera and the shady habitats favour Zygoptera (De Marco et al. 2015). There are also other important habitat characteristics, such as availability of sufficient quality riparian vegetation for Anisoptera species (Schindler et al. 2003; Osborn and Samways 1996).

We also found that connectivity across the landscape was significant for Anisoptera assemblages, and despite their strong dispersal ability, the more isolated a pond, the lower the likelihood of successful colonisation. Only opportunistic, strong flying species crossed the transformed landscape, suggesting that the structure of the landscape with respect to the location of the source sites (i.e. natural deposition pools) can influence dragonfly assemblage structure (McCauley 2006). Different river catchments greatly affected our Zygoptera assemblages, related in part to habitat complexity, heterogeneity, level and type of disturbance, as well as lesser mobility in this sub-order (Stewart and Samways 1998; Schindler et al. 2003; Scher and Thiery 2005; McCauley 2006).

We found that seasonality was not a major driver for these pond species as it is elsewhere (Bella Della et al. 2005) or for the running water species in the same area (Samways and Grant 2006). As might be expected, given the similar ranges in pH across our ponds and pools, it did not significantly shape any of our assemblages, nor did it affect species richness. Conductivity can shape some Zygoptera assemblages (Gomez-Anaya et al. 2011), with elevated conductivity in transformed landscapes leading to a decline in pond species richness (Hinden et al. 2005; Rychla et al. 2011). Yet we found here that pond water conductivity did not play a major role, which was also the case for beetles and bugs at many of the same ponds (Apinda-Legnouo et al. 2013).

Higher nutrient load and lower dissolved oxygen is a feature of less permanent ponds (Apinda-Legnouo et al. 2013), and can have an impact on dragonflies (Schindler et al. 2003), but we did not find this here. Most of our ponds did not reach fatal critical conditions (Harabiš and Dolný 2012), but they did experience intermediate disturbance which resulted in high species richness as in some South African rivers (Stewart and Samways 1998).

## Implications for conservation

Natural deposition pools are a natural source habitat for many species, including dragonflies, especially during drought when ponds dry out. So these pools need to be conserved as they provide refuges for many endemic species, and especially through removal of invasive alien plants which are a great threat to many of the local species (Samways et al. 2005). Although these CFR ponds supported largely the generalist species, they nevertheless did also provide additional habitat for a few CFR endemic species/ESUs. This means that artificial ponds can improve the chances of survival of many species by increasing overall local population sizes, including those of some localised endemics, while also increasing regional gamma diversity, as Suhling et al. (2006) found in Namibia.

The value of ponds for conservation depends on whether management focuses on maximising dragonfly species richness or opting for taxonomic uniqueness. The reason for our ponds' existence is economic, as they are used for water storage mainly for irrigation, and they were not designed for conservation. Nevertheless, there are some clear pointers for conservation, including increasing habitat complexity and heterogeneity within ponds, which goes hand in hand with maintaining constant water levels, which has been identified as important in the design of conservation ponds (Samways et al. 1996).

There appear to be several other requirements for successful dragonfly conservation in these CFR ponds. Water permanency is important, with its secondary feature of maintaining water levels as constant as possible to maintain the vegetated margins intact (Bella Della et al. 2005). This is especially important for the CFR endemic species where any opportunity to increase their population size will contribute to their long-term survival. In turn, establishing a wide range of indigenous riparian vegetation along the pond verges would provide increased habitat heterogeneity, as well as adding the a pond's aesthetic value. For example, the CFR endemic *E. frenulata* requires tall grass between bushes. It is important that there is not too much shade which has an adverse effect on most dragonflies in the region (Samways et al. 2011), and this would include removal of invasive alien trees. In addition, there should be increased pond quality by limiting livestock access to ponds and avoiding agricultural runoff (containing fertilisers and pesticides). All activities should also be monitored over time for pond quality assurance.

We show here that these dragonfly assemblages are governed more by landscape scale (e.g. elevation, connectivity) variables than point or local variables (e.g. pH, conductivity). Therefore, management decisions should be approached from a landscape perspective, yet with an awareness of letting natural processes taking their course (D'Amico et al. 2004). Many of our ponds host many species, as well as much regional dragonfly diversity, and also many other taxa, and with further improvement could possibly support even more species. Finally, these ponds improve functional connectivity across the landscape, which is likely to extend to other taxa besides beetles, bugs (Apinda-legnouo et al. 2013) and dragonflies.

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