Abiotic and biotic drivers of African aquatic insect distribution

by

Charl Deacon

Dissertation presented for the degree of

Doctor of Philosophy (Entomology)

at

Stellenbosch University

Department of Conservation Ecology and Entomology, Faculty of AgriSciences

Supervisors:

Prof. Michael J. Samways and Prof. James S. Pryke

March 2020

Declaration

By submitting this dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: March 2020

Summary

Freshwater habitats are disproportionately rich in biodiversity, and are among the most threatened, yet poorly protected ecosystems. Aquatic insects make up much of the total freshwater fauna and contribute greatly to ecosystem functioning. At the broad-scale, aquatic insect distribution is driven by combinations of traits, as well as regional climate gradients and historical landscape context. Locally, both aquatic insect species richness and diversity are driven by various aspects related to vegetation and to physiochemical environments. Effective conservation requires thorough understanding of species distribution patterns at various spatial scales. My overall aim here is to combine broad-scale, theoretical biogeography, and local-scale empirical ecology to investigate drivers of aquatic insect distribution across Africa.

Species are often binarily classified as ‘widespread generalists’ or ‘narrow-range specialists’ based on their ecological traits. Results in Chapter 2 show that ecological and biological traits are highly interactive among dragonflies, and inferring geographical range size based on ecological preference and/or biotope specialization alone should be approached with caution. Biological traits related to phenology and mobility were also strong drivers of dragonfly range size, indicating that conservation efforts should include multiple species across all habitat types.

Regional climates show considerable variation across latitudinal and longitudinal gradients, and determine areas of high species richness and diversity. In Chapter 3, I show strong latitudinal and longitudinal gradients for South-African dragonfly species richness and endemism. Dragonfly assemblage-turnover boundaries coincided with significant geographical features and/or areas where contemporary climate changed from one condition to another. However, these dragonfly assemblage turnover-boundaries were gradual rather than discrete throughout South Africa.

At the local scale, natural and artificial ponds contribute greatly to overall biodiversity, especially when they are of high quality and occur in networks across the landscape. I show that ponds characterized by high heterogeneity support diverse aquatic insect assemblages (Chapters 4 and 5). Chapter 4 showed artificial reservoirs, occurring alongside natural ponds in ecological networks, to expand the area of occupancy for most widespread dragonflies, aquatic beetles and true bugs. Some species with specific habitat requirements were confined to natural ponds, suggesting the significance of natural ponds for conserving the full range of insects.

Dragonflies, aquatic beetles and true bugs occupy low-quality artificial reservoirs at low abundance to survive the adverse effects of drought (Chapter 5). However, many insects exclusively occupied natural ponds, emphasizing the overall importance of naturalness, and suggests that there is merit in improving artificial reservoirs. This would most likely be by having macrophytes and vegetated banks similar to those of natural ponds.

Investigating aquatic insect distribution patterns is important for conservation, and here, I demonstrate the value of dragonflies as model organisms for investigating the drivers of broad-scale distribution patterns. Studying other taxa is also appropriate, as I have demonstrated at the local scale, but not always possible due to limited distribution knowledge. I recommend broad-scale investigations of other complementary taxa to determine their added value for elucidating the drivers of overall insect distribution patterns, and so address our current shortfalls to improve insect conservation.

Opsomming

Varswaterhabitatte is besonders biodivers, en val onder die mees bedreigde, onder-beskermde ekosisteme. Varswaterinsekte vorm ‘n groot deel van alle varswaterdiere, en het hoë waarde vir ekosisteem-werking. Breë-skaalse waterinsekverspreiding word aangedryf deur kombinasies van eienskappe, sowel as streeksklimaat en historiese landskap-konteks. Oor plaaslike skale word beide waterinsek spesierykheid en diversiteit aangedryf deur verskeie aspekte van plantegroei, en chemiese omgewings. Effektiewe bewaring vereis goeie begrip van spesieverspreidingspatrone oor verskeie ruimtelike skale. My algehele doel is om breë-skaalse, teoretiese bio-geografie, en fyn-skaalse empiriese ekologie te kombineer, om sodoende die dryfkragte van waterinsekverspreiding oor Afrika te ondersoek.

Spesies word dikwels op ‘n binêre wyse geklassifiseer as ‘wyd-verspreide generaliste’ of ‘streeksgebonde spesialiste’, gebaseer op hul ekologiese eienskappe. Bevindinge in Hoofstuk 2 toon dat ekologiese en biologiese eienskappe onder naaldekokers hoogs interaktief is. Afleidings van geografiese verspreiding, gebaseer op ekologiese voorkeur en/of biotoop spesialisme, hoort versigtig benader te word. Biologiese eienskappe verwant aan fenologie en beweeglikheid was ook beduidende dryfkragte van geografiese verspreiding onder naaldekokers, wat aandui dat bewaringspogings verskeie spesies vanaf alle habitat moet betrek.

Streeksklimaat verskil aansienlik oor breedte- en lengtegradiënte, en bepaal waar areas van hoë spesierykheid en diversiteit voorkom. Ek bewys in Hoofstuk 3 dat sterk breedte- en lengtegradiënte vir Suid-Afrikaanse naaldekoker spesierykheid en inheemsheid bestaan. Naaldekoker gemeenskapsomsetgrense stem ooreen met beduidende geografiese strukture en/of areas waar kontemporêre klimaat verander tussen streke. Hierdie naaldekoker gemeenskapsomsetgrense is egter geleidelik eerder as diskreet oor Suid-Afrika.

Natuurlike en kunsmatige damme dra by tot algehele biodiversiteit oor die plaaslike skaal, veral wanneer dié damme van hoë kwaliteit is, en aangetref word in netwerke wat strek oor die landskap. My bevindinge bewys dat damme wat gekenmerk word deur hoë variasie diverse waterinsek-gemeenskappe ondersteun (Hoofstukke 4 en 5). Bevindinge in Hoofstuk 4 bewys dat kunsmatige damme, tesame met natuurlike damme in ekologiese netwerke, die besettingsarea van meeste wyd-verspreide naaldekokers, waterkewers en ware watergoggas

vergroot. Sommige spesies met spesifieke habitatvereistes was beperk tot natuurlike damme, wat aandui dat natuurlike damme belangrik is vir die bewaring van die volle spektrum van waterinsekte.

Naaldekokers, waterkewers en ware watergoggas beset lae-gehalte kunsmatige damme in lae hoeveelhede, om die ongunstige toestande van droogte te oorleef (Hoofstuk 5). Heelwat waterinsekte word egter slegs in en rondom natuurlike damme aangetref, wat beklemtoon dat die natuurlikheid van damme belangrik is. Hierdie bevindinge dui aan dat daar meriete is om kunsmatige damme te verbeter, waarskynlik deur om plantegroei wat soortgelyk aan dié van natuurlike damme is, te stimuleer.

Om ondersoek in te stel op waterinsek-verspreidingspatrone is belangrik vir natuurbewaring, en hier bewys ek dat naaldekokers waardevol is om die drywers van breë-skaalse verspreidingspatrone aan te dui. Om ander insek-groepe te ondersoek is hoogs gepas, soos hier aangedui vir plaaslike studies, alhoewel dit nie altyd moontlik is nie, as gevolg van beperkte kennis met betrekking tot hul verspreidingspatrone. Ek beveel breë-skaalse studies aan vir ander ooreenstemmende insek-groepe, om te bevestig wat hul bydraende waarde is om die dryfkragte van algehele insekverspreiding te verklaar. Sodoende kan ons huidige tekortkominge aanspreek om insekbewaring te verbeter.

Acknowledgements

I wish to express my sincere gratitude and appreciation to the following persons and organizations, in no specific order:

My parents, Andrew and Girty Deacon, and my brother, Jacques Deacon, thank you for your love and support during my entire university career.

Prof. Michael Samways, Prof. James Pryke and Dr René Gaigher, thank you for your friendship, support and guidance throughout the years. I was truly very fortunate to be part of a fantastic research team.

Marlene Isaacks, Monean Jacobs, Colleen Louw and Riaan Keown, thank you for your help with finances and field trip arrangements.

Aileen van der Mescht, Julia van Schalkwyk, Gabi Kietzka, Michelle Eckert, Jurie Theron, and Timia Sanchez-Alcocer, thank you for your help in the field and around the department.

Robyn Symons, Louis Jonk, Wessel du Toit, Llelani Coetzer, Craig Swanepoel, Nicol Pirow and Wildene le Roux, thank you so much for your support throughout the last few years.

A heartfelt thank you to Mondi Group for financial support.

Mondi Group, Vergelegen Wine Estate, Meerlust Wine Estate, Lourensford Wine Estate and Elgin Valley Wine Estate, thank you for granting access to some of your ponds and reservoirs.

The list of individual Nature Reserves and National Parks is too long to mention, but I would like to thank everyone involved with CapeNature, Ezemvelo KZN Wildlife, SANParks, Northern Cape Department of Environment and Nature Conservation, and Eastern Cape Parks and Tourism Agency for accommodating my field work.

I dedicate my thesis to the absolute best parents and brother in the entire world, and my best friend, Zippo. I miss you, buddy.

Table of Contents

List of Figures

List of Tables

Chapter 1 Introduction

1.1 The significance of freshwater habitats

Freshwater habitats cover about 1% of the world's surface, and are disproportionally rich in biodiversity compared to terrestrial habitats, containing nearly 10% of all described species (Dijkstra et al. 2014). Freshwater ecosystems are among the most threatened and poorly protected ecosystems on the planet, as delineation of protected areas is mostly focused on terrestrial habitats (Heino 2009). Yet, freshwater ecosystems experience greater biodiversity loss compared to any other terrestrial ecosystems (Sala et al. 2000; Moilanen et al. 2007). Adding to the vulnerability of freshwater ecosystems, is that freshwater is a necessary resource for life and collectively provides a range of goods and services, including material goods (e.g. clean water and food) and recreational services (e.g. fishing, boating and overall spiritual well-being) (Revenga et al. 2005; Doi et al. 2013). Due to our reliance on water, urban settlements are concentrated close to freshwater bodies (Strayer 2006), and with the ever-expanding human population globally, freshwater resources are increasingly exploited through abstraction, diversion, and contamination (Dudgeon et al. 2006).

Based on the assumption that high aquatic diversity is associated with larger waterbodies, several past investigations have focused mainly on lotic habitats (Davies et al. 2008). There is no doubt that large rivers and streams contribute substantially to local and regional biodiversity (Williams et al. 2004; Gehrke 2005; Brasil et al. 2018), through their inter-basin variation in habitat conditions and dynamic flow regimes (Wan et al. 2015; Domisch et al. 2017). The threats to lotic habitats are well recognized, and include pollution input (Lorenz et al. 2017), loss of riparian vegetation (Dallas and Day 2007), invasion of alien plants (Bennett et al. 2001) and reduction of infiltration capacity through substrate compaction and substrate covering (Trombulak and Frissell 2000; Alberti et al. 2007). Lentic habitats, both natural and artificial, are common and widespread across the world (Downing et al. 2006), and have recently received increasing research attention (Oertli et al. 2009). Their overall small sizes, abundance and immense heterogeneity have led to a significant contribution to regional biodiversity, comparable to that of the most biodiverse rivers (Williams et al. 2004). Some of the main threats to lentic habitats include trampling and grazing (Carchini et al. 2005), infilling and removal due to urbanization (Ball-Damerow et al. 2014; Hill et al. 2017a), and accumulation of pollutants (Biggs et al. 2005). Lentic habitats are not only important from a biodiversity perspective, but are also valued for their contribution to socio-economic stability and agricultural productivity (Oertli et al. 2009).

1.2 The significance of insects

Insects make up much of total fauna and are one of the most diverse groups globally, with well over 1 million species described, yet an immense number of species remain undiscovered (Stork et al. 2015; Foottit and Adler 2017). Due to the rich evolutionary history of insects (Labandeira 2018), they possess a wide variety of traits that enable them to thrive in a range of habitats (Poff et al. 2006). Insects live in close association with their physical and chemical environment and are highly sensitive to changes to their surroundings (Webster and Cardé 2017). Being one of the most abundant groups, insects make a substantial contribution to ecosystem function through the provision of valuable ecosystem services, such as food web stabilization (Griffiths et al. 2015), pollination (Hoehn et al. 2008), nutrient cycling (Jouquet et al. 2011), and biocontrol (Frank et al. 2008). As a result, insects are of major conservation concern and a range of synergistic threats to their overall diversity have been identified (Gerlach et al. 2012). These include habitat loss due to urbanization and agriculture, local and regional establishment of alien invasive species and global climate change, all driving functional and habitat homogenization (Gossner et al. 2016).

Aquatic insects, defined as those that spend at least one life stage below the water surface, occupy a wide range of aquatic habitats and collectively make up 6% of all known insect species (Dijkstra et al. 2014; Harrison et al. 2016). Aquatic insects contribute greatly to freshwater ecosystem functioning, and aside from being important food sources for a range of aquatic vertebrates, they fulfill many roles as primary consumers, detritivores and predators, and provide several other ecosystem services related to water filtration and control of pest species populations (Green et al. 2015; Macadam and Stockhan 2015). Most rely on aquatic environments during their immature stages, and terrestrial environments during their highly mobile adult stages, making them particularly vulnerable to environmental change. Anthropogenic activities exert immense direct pressure on freshwater insects (Darwall et al. 2012), some of which include poor water management (Haxton and Findlay 2008), pollution from various sources (Biggs et al. 2005; Lorenz et al. 2017), and disruption of river courses through reservoir construction (Bredenhand and Samways 2009; Krajenbrink et al. 2019). There are also several indirect pressure forces (i.e. those that are associated with their terrestrial surroundings), such as vegetation removal, soil erosion, and urbanization (Revenga et al.

2005). Aside from anthropogenic activity, global climate change contributes greatly to overall changes in aquatic insect population sizes (Dudgeon et al. 2006), and the symphony of anthropogenic activities and climate change places about 33% of all aquatic insects at risk of extinction (Sánchez-Bayo and Wyckhuys 2019).

1.3 Biological traits, climate and historical context as broad-scale drivers of aquatic insect distribution

Insects possess several biological attributes, or traits, which enable their overall success in a variety of aquatic habitats (Arribas et al. 2012). ‘Traits’ is the broad term referring to various aspects of ecology, life history, morphology, and biological interaction, all of which are interactive and important driving forces of species’ adaptive capacity, and ultimately, range sizes (Gaston 2003; Rundle et al. 2007; Diniz-Filho et al. 2010). In the aquatic realm, lentic and lotic habitats are very different in terms of geological permanence and overall ecological stability (Arribas et al. 2012), and the relationships between ecological preference and range size have received much attention (e.g. Ribera et al. 2003; Hof et al. 2006, Marten et al. 2006). Since most lentic habitats are short-lived in comparison to lotic habitats, there is strong evidence for lentic insects being more mobile, and having wider ranges farther away from the equator, as was found for European and North American dragonflies (Hof et al. 2006), and European water beetles (Ribera and Vogler 2000). Life history traits, or those associated with phenology and lifespan, can be expected to interact directly with ecological traits, and collectively contribute to colonization capacity of insects (Ribera 2008). For example, insects with shorter generation times may be able to outlive and persist in seasonal aquatic habitats, and reproductive stages can reach new habitats to complete their life cycles (Suhling 2001).

Dispersal ability has been the topic of studies investigating the underlying biological mechanisms of aquatic insect distribution ranges. However, there is an overall lack of information on dispersal tendencies and capabilities for most aquatic insects (Rundle et al. 2007). Yet, their ability to move between habitats in response to changing environmental conditions has a profound effect on their distribution ranges, and movement between habitats may be facilitated by either passive (e.g. on wind currents) or active means (e.g. directed flight movement) (Bilton et al. 2001). Most large aquatic insects disperse actively during their adult stages, and morphological traits, specifically those related to body size and wing size, have been used as surrogate measures for dispersal ability (e.g. Guitiérrez and Menéndez 1997;

Wakeling and Ellington 1997; Malmqvist 2000; Schilder and Marden 2004). Many of these studies have concluded that body size, wing size, and wing muscle mass play important roles in determining insect dispersal ability, and ultimately, their range sizes.

How climate affects the broad-scale distribution patterns of insects, especially in the aquatic realm, has received considerably less research attention compared to plants and terrestrial taxa (Diniz-Filho et al. 2010; Heino 2011), challenging the evaluation of abiotic driving forces behind diversity patterns. However, for some aquatic insects, latitudinal and elevation variation in temperature and rainfall are significant factors determining regional species richness and diversity (Heino 2001, 2009; Pearson and Boyero 2009). These findings show contemporary regional climates to be strong driving forces of aquatic insect distribution and migration patterns, through associations with hydrology (Bêche and Statzner 2009) and availability of breeding habitat (Pedgley et al. 1995). Historical context, especially with regards to past glaciations, may also have affected geographical gradients (Heino 2011). This is related to varying rates of speciation and dispersal, which is assumed to be higher in tropical regions with more opportunities for speciation, leading to higher species richness closer to the equator (Mittelbach et al. 2007). Areas that experienced long periods of relatively stable climatic conditions, and are characterized by variable topographic gradients, are also expected to have higher levels of species endemism, driven by prolonged geographical isolation (Griffiths 2010). It has also been suggested that other historical factors, including changes in sea level and periods of floods and drought, may have had an influence on species distribution patterns (Matthews 1998). Yet, the effects of historical factors on aquatic insect distribution patterns are poorly investigated, predominantly due to the lack of taxonomic information for most insect taxa.

1.4 Local factors influencing richness and diversity, and aquatic insects as indicators

Aquatic insects depend on various aspects related to their local habitats (Paavola et al. 2000; Diniz-Filho et al. 2010), and vegetation cover and composition plays a key role in determining local aquatic insect diversity and assemblage composition. Most aquatic insects are associated with marginal, submerged and riparian vegetation of ponds (Fairchild et al. 2003; Pryke et al. 2015; Briggs et al. 2019) and rivers (Karaouzas and Gritzalis 2006; Samways and Sharratt 2010). Although vegetation cover overall promotes aquatic insect diversity, especially in urban settings (Goertzen and Suhling 2013), vegetation structure plays an equally important role in determining the local distribution of species (Smith et al. 2007; Briggs et al. 2019). Invasion by alien plant species has a profound effect on local aquatic insect communities, as these aliens can spread quickly and replace native vegetation assemblages (Strayer et al. 2003). This homogenizing effect, along with increasing shade cover beyond the natural threshold, reduces riparian vegetation complexity, and eliminates perching and breeding microhabitats for many aquatic insects. However, the impoverishing effects of alien vegetation are reversible, and several insects show remarkable recovery after alien tree removal (Magoba and Samways 2010; Samways and Sharratt 2010).

Aside from vegetation characteristics, aquatic insects are also sensitive to chemical properties of their habitats, as it relates to water quality (Kietzka et al. 2016; Hill et al. 2017b). Water chemistry gradients can determine local insect diversity directly, e.g. by influencing their activity, development, and physiology (Thorp and Rogers 2014), as well as indirectly, e.g. by determining presence or absence of competitors and/or predators (Lytle 2015). Responses to vegetation cover and in-water chemical gradients are highly variable among freshwater taxa (Mlambo et al. 2011; da Rocha et al. 2016; Briggs et al. 2019), indicating that locally diverse insect assemblages require a wide variety of resources and environmental conditions, both being important determinants of habitat heterogeneity (Palmer et al. 2010; Hill et al. 2015).

Due to their overall high local abundance, short life-cycles, high ecological sensitivity, and varying responses to change in their surroundings (Baker and Sharp 1998; Masese and Raburu 2017), aquatic insects have widely been used as environmental and ecological indicators to ascertain freshwater quality (Bulánková 1997; Bonada et al. 2006). Aquatic insects can also be useful as biodiversity indicators, and some may be representative of other co-occurring taxa (Englund et al. 2007). Dragonflies and damselflies (Odonata, hereafter collectively referred to as 'dragonflies') are one of few insect groups that are well-known at the species-level and are widely used as indicators of freshwater ecosystems at local scale (Clark and Samways 1996). Adult dragonflies are particularly sensitive to changes in vegetation characteristics (Samways and Taylor 2004; Samways and Sharratt 2010), water flow dynamics and habitat permanency (Clark and Samways 1996), and water chemistry (Kietzka et al. 2016). They also respond to several anthropogenic impacts, including habitat transformation (Samways and Steytler 1996), the spread of alien invasive plants (Samways and Taylor 2004), water pollution, and road construction (Soluk et al. 2011). Their overall ability to move between habitats in response to deteriorating environmental conditions emphasizes their use as indicators of ecological integrity of lentic and lotic systems. These species-level responses to local environmental change led to the development of the Dragonfly Biotic Index (DBI) in South Africa, which has been used successfully to identify areas of conservation concern (Simaika and Samways 2012) and to monitor habitat recovery following alien tree removal (Samways and Sharratt 2010).

Although not as well-known at species-level compared to dragonflies, aquatic beetles (Coleoptera) and true bugs (Hemiptera) have received increasing attention as complementary indicators of freshwater quality (Englund et al. 2007; da Rocha et al. 2010; Guareschi et al. 2012; Apinda-Legnouo et al. 2014). In the case of both taxa, they are common occupants of a wide variety of aquatic habitats (Reavell 2003; Turner 2007b, Romero et al. 2017), and are variably sensitive to vegetation structure, water quality components, disturbance levels and flow regimes, at least at the family-level. Aside from being food items to many other freshwater taxa, beetles and bugs serve several ecological roles as predators, scavengers, and algae feeders (Lytle 2015; Yee and Kehl 2015). Due to their overall high adaptive capacity, some beetle families (e.g. Dytiscidae, Gyrinidae and Hydrophilidae) and some bug families (e.g. Notonectidae and Veliidae) have been identified as early colonizers of most aquatic habitats, and are useful for detecting local changes in ecological integrity (da Rocha et al. 2010). These taxa are important components of indices such as the Walley-Hawkes-Paisley-Trigg Index (WHPT) used in the United Kingdom (Paisley et al. 2014), and the South African Scoring System (SASS), used as a rapid assessment tool for lotic ecosystems across southern Africa (Chutter 1995; Dickens and Graham 2002). Beetles and bugs, along with other macroinvertebrates, have been used successfully to determine ecological reserves and flow requirements of single rivers (O’ Keeffe and Dickens 2000), have been used in several river impact assessments (Dickens and Graham 1998), and also have high value for assessing lentic habitat integrity (Apinda-Legnouo et al. 2014; Romero et al. 2017; Briggs et al. 2019).

1.5 Biodiversity hotspots in South Africa

The Maputaland-Pondoland-Albany (MPA) biodiversity hotspot is the region encompassing the east coast of southern Africa, and is recognized as an important area of plant endemism, supporting more than 1 900 endemic species (Steenkamp et al. 2004). The MPA biodiversity hotspot is naturally subject to El Niño-Southern Oscillation (ENSO) events, leading to periodic drought and flooding events (Wessels et al. 2007). High human population density has led to the region becoming increasingly impacted by anthropogenic activities (Bailey et al. 2015), mostly through urbanization and land cover transformation as a result of plantation-forestry (Smith et al. 2008). However, instigation of Ecological Networks (ENs; networks of conservation corridors) in the MPA biodiversity hotspot is a design and management procedure specifically aimed at mitigating the harsh effects of plantation-forestry on biodiversity, through conserving structural and functional complexity of whole ecosystems (Samways et al. 2010). Using the EN approach, about one-third of the landscape remains unplanted, making up a network of inter-connected corridors and patches containing natural grassland, natural forest, streams, ponds, and wetlands (Samways and Pryke 2016). These ENs can be as effective as adjacent protected areas in conserving biodiversity (Joubert and Samways 2014; Pryke et al. 2015), and have been shown to be effective for conserving several terrestrial taxa (Bazelet and Samways 2011; Yekwayo et al. 2016; Gaigher et al. 2019; Joubert-van der Merwe et al. 2019), as well as some aquatic taxa (Pryke et al. 2015; Kietzka et al. 2015; Briggs et al. 2019).

The Greater Cape Floristic Region (GCFR) biodiversity hotspot is the smallest floral kingdom in the world, restricted to the southern tip of Africa (Day and Day 2009). Regardless of the small geographical area the GCFR covers, the region is renowned for its astounding plant diversity, supporting more than 9 000 plant species, with more than 70% endemic to the region (Goldblatt and Manning 1999). The combination between the rich geological history and characteristic topographical variability of the region provides a unique and contrasting environment for various localized fauna, and the degree of endemism and diversity for aquatic invertebrates is comparable to that of terrestrial plants (Wishart and Day 2002; Samways 2006; Turner 2007a). In addition to geology and topography, variability and seasonality of rainfall driven by ENSO events (van der Niet and Johnson 2009) and the effects of fire (Linder 2005) set the stage for high species diversification throughout the region. For aquatic insects, the most notable examples include dragonfly genera such as *Syncordulia* and *Chlorolestes* (Samways and Simaika 2016), aquatic beetle genera such as *Coelhydrus* and *Capelatus* (Toledo and Turner 2004; Bilton et al. 2015), and some aquatic true bug genera such as *Notonecta* (Griffiths et al. 2015), all confined to the south-western Cape.

1.6 Challenges to effective conservation of insects and other invertebrates

Regardless of their high diversity and the important ecosystem functions that insects provide, most species (along with other invertebrate species) have greatly been neglected in conservation efforts globally (Cardoso et al. 2012). To emphasize, merely 70 invertebrate species have been reported as extinct over the last 600 years (Dunn 2005), greatly under representative of the projected number of invertebrate species believed to exist on the planet. Of particular concern is that all other species have gone extinct before their discovery and formal description, known as Linnean extinctions (Triantis et al. 2010). Cardoso et al. (2011) identified three societal dilemmas which face parties and practitioners when determining the relevance of insect conservation. Firstly, the general public is unaware of the important roles that insects play in ecosystem functioning, with the exception of some butterflies and bees (the public dilemma). Consequently, the importance of insects for ecosystem functioning is often disregarded, challenging public participation in conservation efforts and in slowing current extinction rates (Martín-López et al. 2007; Ladle and Jepson 2008). Secondly, stakeholders and policymakers are mostly unaware of the conservation issues that face insects, with a strong focus on vertebrate species (the political dilemma). While focusing on vertebrate species as umbrellas for conservation is valid in some cases (Simberloff 1998), the effectivity of this approach is often misconstrued (Martín et al. 2010). Thirdly, basic information on insects and their environments is lacking (the scientific dilemma). Most modern scientists focus on other biological fields, leaving little monetary incentive to advance exploration, taxonomy, and biological and ecological studies (Cotterill and Foissner 2010).

Complementing these societal dilemmas, Cardoso et al. (2011) and Hortal et al. (2015) identified additional shortfalls of modern global science. Among these are the lack of information on the distribution of species (Wallacean shortfall), the lack of information on the functional traits of species (Raunkiæran shortfall), the limited information available on the biological interactions among species (Eltonian shortfall), and the lack of knowledge of the sensitivity of species to environmental change (Hutchinsonian shortfall). The situation is similar across Africa, and effective conservation of freshwater habitats and their inhabitants is specifically challenging as most aquatic species are not well-known in terms of their distributions, biological attributes, biological interactions and their responses to habitat transformation.

1.7 Thesis aim and outline

The African continent is characterized by a unique combination of topographic settings and some of the world’s most variable arid and tropical climates, giving rise to a wide variety of lentic and lotic habitats across the continent (Dudgeon et al. 2011). It is now recognized that

African freshwater resources are no longer free from anthropogenic impact, and rapidly expanding human populations in developing countries place substantial pressure on freshwater resources, as is the case elsewhere (Darwall et al. 2011). Effective conservation requires a holistic understanding of biodiversity patterns at various spatial scales, as some factors operate at different, or multiple scales (Hui et al. 2010; Kriticos and Leriche 2010). To address the shortfalls identified by Cardoso et al. (2011) and Hortal et al. (2015), my overall aim was to combine broad-scale, theoretical biogeography and local-scale, empirical ecology to investigate the fundamental drivers of aquatic insect distribution across Africa (Figure 1.1).

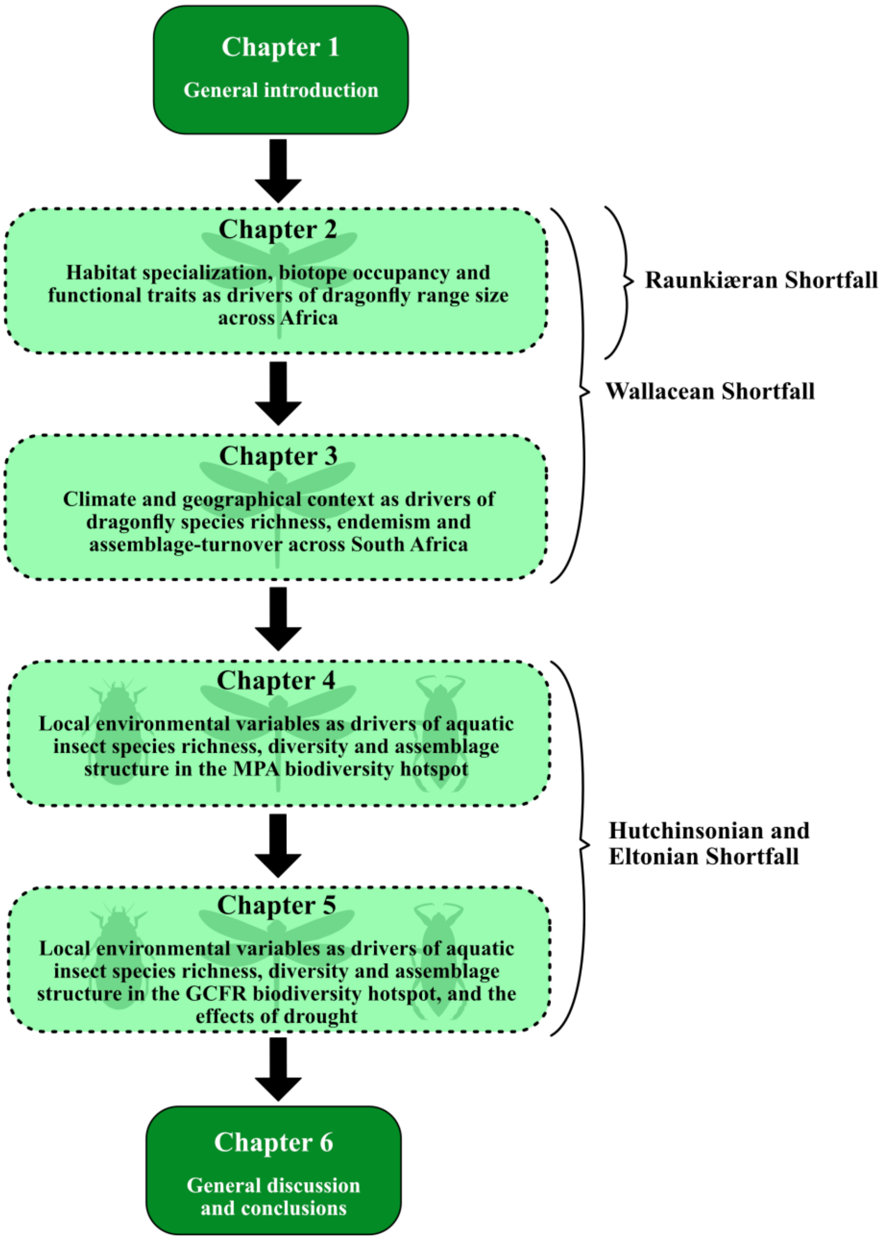


Figure 1.1 Schematic chapter outline.

In chapter 2, I set out to address the Raunkiæran and Wallacean shortfalls by investigating the overall importance of functional traits as drivers of aquatic insect distribution at a continental scale. The hard classification of species as ‘widespread habitat generalists’ or ‘narrow-range habitat specialists’ based only on habitat specialization may not be truly representative of geographic ranges in all cases, as several other functional traits contribute to species’ range sizes (Rundle et al. 2007; Büchi and Vuilleumier 2014). Dragonflies occurring in South Africa are well-known in terms of their biological traits and continental distributions at the species-level, partly attributed to the development of the DBI (Simaika and Samways 2016). This makes dragonflies an ideal group to use as model organisms. My first hypothesis in chapter 2 is that traits related to habitat preference, habitat specialization, life history, and mobility are interactive and carry equal weight in driving species range size. I also hypothesize that ecological sensitivity is complementary to traits driving the range size of individual species.

In South Africa, regional climate is subject to pronounced effects of oceanic current systems, and climate is highly variable throughout the country as a result (Diester-Haass et al. 2012). In chapter 3, I focus on the Raunkiæran shortfall specifically, and investigate the role of contemporary climate and topography in driving dragonfly species richness and local endemism at the national scale. As dragonflies are well-known at sub-regional scale (Simaika and Samways 2016), I also investigate the relevance of contemporary climate, topography and geographical context as predictors of assemblage-turnover boundaries using South African dragonflies as model organisms. In chapter 3, I hypothesize that areas with high species richness are located where average rainfall and temperature is high, and that areas with high levels of endemism are determined by the combination of variable climate and topography. I further hypothesize that assemblage-turnover boundaries are well-defined and coincident with climate gradients and significant topographical features.

To address the Eltonian and Hutchinsonian shortfalls, I investigate the effects of a set of environmental variables on the local distribution of lentic insects in two biodiversity hotspots in South Africa. The country is classified as semi-arid, which has led to a high density of artificial reservoirs, especially in agricultural areas (Bernstein 2013; Apinda-Legnouo et al. 2014). In chapter 4, I use a complement of lentic taxa, i.e. dragonflies, aquatic beetles, and aquatic true bugs, to determine the ecological value of artificial reservoirs compared to natural ponds in conservation corridors in the MPA biodiversity hotspot, and investigate whether artificial reservoirs can expand their local area of occupancy. Conservation corridors benefit several terrestrial taxa (e.g. Yekwayo et al. 2016; Gaigher et al. 2019) and some aquatic taxa (e.g. Pryke et al. 2015), and I hypothesize that artificial reservoirs which resemble natural ponds in terms of physical structure and water quality components benefit widespread species, but have little ecological value for endemic species.

Finally, the GCFR biodiversity hotspot experienced one of the most severe hydrological droughts in recent years (Botai et al. 2018), and in chapter 5, I use the same complement of lentic taxa (i.e. dragonflies and aquatic beetles and bugs) to determine whether artificial reservoirs act as refuge habitats for pond insects during extreme hydrological drought. Extended periods of drought place substantial ecological pressure on freshwater communities (Collinson et al. 1995), and I hypothesize that aquatic insects predominantly found in natural ponds occupy artificial habitats during stress periods as a survival strategy against adverse ecological conditions, in spite of ecological difference between the two pond types. I also hypothesize that artificial reservoirs are unattractive habitats to endemic species, placing them at higher risk during stress periods.

Individual chapters mentioned above are intended for peer-reviewed publication and some repetition among chapters was unavoidable. Chapter titles and major objectives are as follows:

Chapter 2: **Widespread habitat generalists vs. narrow-range habitat specialists: a valid division or not?**

Under review with Journal of Biogeography

1. Determine whether habitat preference and/or biotope occupancy (i.e. habitat specialization) can be used to explain latitude, longitude, and elevation range size of dragonflies across Africa.
2. Determine the overall importance and significance of other functional traits, related to mobility and life history.
3. Investigate whether findings correlate with existing measures of ecological sensitivity.

Chapter 3: **Drivers of regional dragonfly species richness and assemblage turnover at the southern tip of Africa**

Recently submitted to Biological Conservation

1. Determine the climatic and spatial factors driving regional trends in overall dragonfly species richness, local endemism, and assemblage-turnover.
2. Identify assemblage-turnover boundaries across the coastal and interior regions of South Africa.
3. Provide recommendations for conservation of local freshwater insects.

Chapter 4: **Artificial reservoirs complement natural ponds to improve pondscape resilience in conservation corridors in a biodiversity hotspot**

Published as: Deacon, C., Samways, M.J. and Pryke, J.S. 2018. Artificial ponds complement natural ponds to improve pondscape resilience in conservation corridors in a biodiversity hotspot. PLoS One 13(9): e0204148. DOI: 10.1371/journal.pone.0204148.

1. Identify the physical and environmental variables driving dragonfly, water beetle, and water bug species richness, abundance, diversity, and composition in the MPA biodiversity hotspot.
2. Determine the ecological value of artificial reservoirs vs. natural ponds for maintaining population sizes and expanding the local area of occupancy for dragonflies, beetles and bugs in conservation corridors.

Chapter 5: **Aquatic insects decline in abundance and occupy low-quality artificial habitats to survive hydrological droughts**

Published as: Deacon, C., Samways, M.J. and Pryke, J.S. 2019. Aquatic insects decline in abundance and occupy low quality artificial habitats to survive hydrological droughts. Freshwater Biology 64: 1643-1654. DOI: 10.1111/fwb.13360.

1. Calculate the percentage change in average precipitation between the sampling period (i.e. the dry period) and the last consistently wet decade.

2. Identify the environmental variables driving aquatic insect species richness and composition.
3. Identify environmental differences between natural ponds and artificial reservoirs.
4. Determine whether artificial reservoirs can act as suitable habitats for the focal taxa during drought.
5. Compare results with other, pre-drought studies on the focal insect taxa in the same study area.

Chapter 6: **General conclusions**

1.7 References

Apinda-Legnouo, E.A., Samways, M.J. and Simaika, J.P. 2014. Value of artificial ponds for aquatic beetle and bug conservation in the Cape Floristic Region biodiversity hotspot. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24: 522-535.

Alberti, M., Booth, D., Hill, K., Coburn, B., Avolio, C., Coe, S. and Spirandelli, D. 2007. The impact of urban patterns on aquatic ecosystems: An empirical analysis in Puget lowland sub-basins. *Landscape and Urban Planning*, 80: 345-361.

Arribas, P., Valasco, J., Abellán, P., Sánchez-Fernández, D., Andújar, C., Calosi, P., … Bilton, D.T. 2012. Dispersal ability rather than ecological tolerance drives differences in range size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). *Journal of Biogeography*, 39: 984-994.

Bêche, L.A. and Statzner, B. 2009. Richness gradients of stream invertebrates across the USA: taxonomy- and trait-based approaches. *Biodiversity and Conservation*, 18: 3909-3930.

Bailey, K.M., McCleery, R.A., Binford, M.W. and Zweig, C. 2015. Land-cover change within and around protected areas in a biodiversity hotspot. *Journal of Land Use Science*, 11: 154-176.

Ball-Damerow, J.E., M'Gonigle, L.K. and Resh, V.H. 2014. Local and regional factors influencing assemblages of dragonflies and damselflies (Odonata) in California and Nevada. *Journal of Insect Conservation*, 18: 1027-1036.

Baker, S.C. and Sharp Jr, H.F. 1998. Evaluation of the recovery of a polluted urban stream using the Ephemeroptera-Plecoptera-Trichoptera index. *Journal of Freshwater Ecology*, 13: 229-234.

Bazelet C.S. and Samways M.J. 2011. Relative importance of management vs. design for implementation of large-scale ecological networks. *Landscape Ecology*, 26: 341-353.

Bennett, E.M., Carpenter, S.R., and Caraco, N.F. 2001. Human impact on erodable phosphorus and eutrophication: A global perspective increasing accumulation of phosphorus in soil threatens rivers, lakes, and coastal oceans with eutrophication. *BioScience*, 51: 227-234.

Bernstein, H. 2013. Commercial Agriculture in South Africa since 1994: 'Natural, Simply Capitalism'. *Journal of Agrarian Change*, 13: 23-46.

Biggs, J., Williams, P., Whitfield, M., Nicolet, P. and Weatherby, A. 2005. 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15: 693-714.

Bilton, D.T., Freeland, J.R. and Okamura, B. 2001. Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics*, 32: 159-181.

Bilton, D.T., Toussaint, E.F., Turner, C.R. and Balke, M. 2015. *Capelatus prykei* gen. et sp. n. (Coleoptera: Dytiscidae: Copelatinae) - a phylogenetically isolated diving beetle from the Western Cape of South Africa. *Systematic Entomology*, 40: 520-531.

Bonada, N., Prat, N., Resh, V.H. and Statzner, B. 2006. Developments in aquatic insect biomonitoring: A comparative analysis of recent approaches. *Annual Review of Entomology*, 51: 495-523.

Botai, C.M., Botai, J.O. and Adeola, A.M. 2018. Spatial distribution of temporal precipitation contrasts in South Africa. *South African Journal of Science*, 114: 1-9.

Brasil, L.S., Oliveira-Júnior, J.M., Calvão, L.B., Carvalho, F.G., Monteiro-Júnior, C.S., Dias-Silva, K. and Juen, L. 2018. Spatial, biogeographic and environmental predictors of diversity in Amazonian Zygoptera. *Insect Conservation and Diversity*, 11: 174-184.

Bredenhand, E. and Samways, M.J. 2009. Impact of a dam on benthic macroinvertebrates in a small river in a biodiversity hotspot: Cape Floristic Region, South Africa. *Journal of Insect Conservation*, 13: 297-307.

Briggs, A., Pryke, J.S., Samways, M.J. and Conlong, D.E. 2019. Macrophytes promote aquatic insect conservation in artificial ponds. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29: 1190-1201.

Bulánková, E. 1997. Dragonflies: Odonata as bio-indicators of environmental quality. *Biologia*, 52: 177-180.

Büchi, L. and Vuilleumier, S. 2014. Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. *The American Naturalist*, 183: 612-624.

Carchini, G., Solimini, A.G. and Ruggiero, A. 2005. Habitat characteristics and odonate diversity in mountain ponds of central Italy. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15: 573-581.

Cardoso, P., Erwin, T.L., Borges, P.A.V. and New, T.R. 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, 144: 2647-2655.

Cardoso, P., Borges, P.A., Triantis, K.A., Ferrández, M.A. and Martín, J.L. 2012. The underrepresentation and misrepresentation of invertebrates in the IUCN Red List. *Biological Conservation*, 149: 147-148.

Cotterill, F.P.D. and Foissner, W. 2010. A pervasive denigration of natural history misconstrues how biodiversity inventories and taxonomy underpin scientific knowledge. *Biodiversity and Conservation*, 19: 291-303.

Chutter, F.M. 1995. The role of aquatic organisms in for sustainable utilisation. *Water Science and Technology*, 32: 283-291.

Clark, T.E. and Samways, M.J. 1996. Dragonflies (Odonata) as indicators of biotope quality in the Kruger National Park, South Africa. *Journal of Applied Ecology*, 33: 1001-1012.

Collinson, N.H., Biggs, J., Corfild, A., Hodson, M.J., Walker, D., Whitfield, M. and Williams, P.J. 1995. Temporary and permanent ponds: An assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. *Biological Conservation*, 74: 125-134.

da Rocha, J.R.M., De Almeida, J.R., Lins, G.A. and Durval, A. 2010. Insects as indicators of environmental changing and pollution: a review of appropriate species and their monitoring. *Holos Environment*, 10: 250-262.

da Rocha, F.C., de Andrade, E.M., Lopes, F.B., de Paula Filho, F.J., Costa Filho, J.H. and da Silva, M.D. 2016. Physical-chemical determinant properties of biological communities in continental semi-arid waters. *Environmental Monitoring and Assessment*, 188: 1-15.

Dallas, H.F. and Day, J.A. 2007. Natural variation in macroinvertebrate assemblages and the development of a biological banding system for interpreting bioassessment data – A preliminary evaluation using data from upland sites in the south–western Cape, South Africa. *Hydrobiologia*, 575: 231-244.

Darwall, W., Seddon, M., Clausnitzer, V. and Cumberlidge, N. 2012. Freshwater invertebrate life. In: Collen, B., Böhm, M., Kemp, R. and Baillie, J.E.M. (eds.). *Spineless: Status and Trends of the World's Invertebrates.* Zoological Society of London, London, UK. pp. 26-33.

Davies, B., Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Sear, D., … Maund, S. 2008. Comparative biodiversity of aquatic habitats in the European agricultural landscape. *Agriculture, Ecosystems and Environment*, 125: 1-8.

Dickens, C.W.S. and Graham, P.M. 1998. Biomonitoring for effective management of wastewater discharges and the health of the river environment. *Aquatic Ecosystem Health and Management*, 1: 199-217.

Dickens, C.W.S. and Graham, P.M. 2002. The South African scoring system (SASS) version 5 rapid bioassessment method for rivers. *African Journal of Aquatic Science*, 27: 1-10.

Diester-Haass, L., Meyers, P.A. and Vidal, L. 2002. The late Miocene onset of high productivity in the Benguela current upwelling system as part of a global pattern. *Marine Geology*, 180: 87-103.

Dijkstra, K.-D.B., Monaghan, M.T. and Pauls, S.U. 2014. Freshwater biodiversity and insect diversification. *Annual Review of Entomology*, 59: 143-163.

Diniz-Filho, J.A.F., De Marco, P. and Hawkins, B.A. 2010. Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity*, 3: 172-179.

Doi, H., Katano, I., Negishi, J. N., Sanada, S. and Kayaba, Y. 2013. Effects of biodiversity, habitat structure, and water quality on recreational use of rivers. *Ecosphere*, 4: 1-11.

Domisch, S., Portmann, F.T., Kuemmerlen, M., O'Hara, R.B., Johnson, R.K., Davy-Bowker, J., … Haase, P. 2017. Using streamflow observations to estimate the impact of hydrological regimes and anthropogenic water use on European stream macroinvertebrate occurrences. *Ecohydrology*, 10: e1895.

Downing, J.A., Prairie, Y.T., Cole, J.J., Duarte, C.M., Tranvik, L.J., Striegl, R.G., … Middelburg, J.J. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnology and Oceanography*, 51: 2388-2397.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., ... Sullivan, C.A. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews*, 81: 163-182.

Dudgeon, D., Pauly, D., Lévêque, C., Rebelo, L.-M. and McCartney, M.P. 2011. Background. In: Darwall, W.R.T., Smith, K.G., Allen, D.J., Holland, R.A., Harrison , I.J. and Brooks. E.G.E. (eds.), *The Diversity of Life in African Freshwaters: Under Water, Under Threat. An analysis of the status and distribution of freshwater species throughout mainland Africa*. IUCN, Cambridge, UK and Gland, Switzerland. pp. 126-177.

Dunn, R.R. 2005. Modern insect extinctions, the neglected majority. *Conservation Biology*, 19: 1030-1036.

Englund, R.A., Wright, M.G. and Polhemus, D.A. 2007. Aquatic insect taxa as indicators of aquatic species richness, habitat disturbance, and invasive species impacts in Hawaiian streams. *Bishop Museum Bulletin in Cultural and Environmental Studies*, 3: 207-232.

Fairchild, G.W., Cruz, J., Faulds, A.M., Short, A.E.Z. and Matta, J.F. 2003. Microhabitat and landscape influences on aquatic beetle assemblages in a cluster of temporary and permanent ponds. *Journal of the North American Benthological Society*, 22: 224-240.

Foottit, R.G. and Adler, P.H. 2017. *Insect Biodiversity: Science and Society*. Wiley-Blackwell, Oxford, UK.

Frank, S.D., Shrewsbury, P.M. and Esiekpe, O. 2008. Spatial and temporal variation in natural enemy assemblages on Maryland native plant species. *Environmental Entomology*, 37: 478-486.

Gaigher, R., Pryke, J.S. and Samways, M. J. 2019. Divergent fire management leads to multiple beneficial outcomes for butterfly conservation in a production mosaic. *Journal of Applied Ecology*, https://doi.org/10.1111/1365-2664.13357.

Gaston, K.J. 2003. *The Structure and Dynamics of Geographic Ranges*. Oxford University Press Inc., New York, USA.

Gehrke, P.C. 2005. Sustainable futures for Australia’s tropical rivers: introduction to current research and information needs. *Marine and Freshwater Research*, 56: 5-7.

Goertzen, D. and Suhling, F. 2013. Promoting dragonfly diversity in cities: major determinants and implications for urban pond design. *Journal of Insect Conservation*, 17: 399-409.

Gossner, M.M., Lewinsohn, T.M., Kahl, T., Grassein, F., Boch, S., Prati, D., … Arndt, H. 2016. Land-use intensification causes multitrophic homogenization of grassland communities. *Nature,* 540: 266-269.

Green, P.A., Vörösmarty, C.J., Harrison, I., Farrell, T., Sáenz, L. and Fekete, B.M. 2015. Freshwater ecosystem services supporting humans: Pivoting from water crisis to water solutions. *Global Environmental Change*, 34: 108-118.

Griffiths, D. 2010. Pattern and process in the distribution of North American freshwater fish. *Biological Journal of the Linnean Society*, 100: 46-61.

Griffiths, C., Day, J. and Picker, M. 2015. *Freshwater Life: A Field Guide to the Plants and Animals of Southern Africa*. Struik Nature, Cape Town, South Africa.

Griffiths, H.M., Bardgett, R.D., Louzada, J. and Barlow, J. 2016. The value of trophic interactions for ecosystem function: dung beetle communities influence seed burial and seedling recruitment in tropical forests. *Proceedings of the Royal Society B: Biological Sciences*, http://dx.doi.org/10.1098/rspb.2016.1634.

Guareschi, S., Gutiérrez-Cánovas, C., Picazo, F., Sánchez-Fernández, D., Abellán, P., Velasco, J. and Millán, A. 2012. Aquatic macroinvertebrate biodiversity: patterns and surrogates in mountainous Spanish national parks. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22: 598-615.

Guitiérrez, D. and Menéndez, R. 1997. Patterns in the distribution, abundance and body size of carabid beetles (Coleoptera: Caraboidea) in relation to dispersal ability. *Journal of Biogeography*, 24: 903-914.

Harrison, I.J., Green, P.A., Farrell, T.A., Juffe–Bignoli, D., Sáenz, L. and Vörösmarty, C.J. 2016. Protected areas and freshwater provisioning: a global assessment of freshwater provision, threats and management strategies to support human water security. Aquatic Conservation: *Marine and Freshwater Ecosystems*, 26: 103-120.

Haxton, T.J. and Findlay, C.S. 2008. Meta-analysis of the impacts of water management on aquatic communities. *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 437-447.

Heino, J. 2001. Regional gradient analysis of freshwater biota: do similar biogeographic patterns exist among multiple taxonomic groups? *Journal of Biogeography*, 28: 69-76.

Heino, J. 2011. A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology*, 56: 1703-1722.

Hill, M.J., Mathers, K.L. and Wood, P.J. 2015. The aquatic macroinvertebrate biodiversity of urban ponds in a medium sized European town (Loughborough, UK). *Hydrobiologia*, 760: 225-238.

Hill, M.J., Ryves, D.B., White, J.C. and Wood, P.J. 2017a. Macroinvertebrate diversity in urban and rural ponds: implications for freshwater biodiversity conservation. *Biological Conservation*, 201: 50-59.

Hill, M.J., Heino, J., Thornhill, I., Ryves, D.B. and Wood, P.J. 2017b. Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. *Oikos*, doi: 10.1111/oik.04266.

Hoehn, P., Tscharntke, T., Tylianakis, J.M. and Steffan-Dewenter, I. 2008. Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B: Biological Sciences*, 275: 2283-2291.

Hof, C., Brändle, M. and Brandl, R. 2006. Lentic odonates have larger and more northern ranges than lotic species. *Journal of Biogeography*, 33: 63-70.

Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. and Ladle, R.J. 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology*, 46: 523-549.

Hui, C., Veldtman, R. and McGeoch, M.A. 2010. Measures, perceptions and scaling patterns of aggregated species distributions. *Ecography*, 33: 95-102.

Joubert, L. and Samways, M. J. 2014. Equivalence of grasslands in an ecological network and a World Heritage Site. *Biodiversity and Conservation*, 23: 2415-2426.

Joubert-van der Merwe, L., Pryke, J.S. and Samways, M.J. 2019. Well-managed grassland heterogeneity promotes butterfly conservation in a corridor network. *Journal of Environmental Management*, *238*: 382-395.

Jouquet, P., Traore, S., Choosai, C., Hartmann, C. and Bignell, D. 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. *European Journal of Soil Biology*, 47: 215-222.

Karaouzas, I. and Gritzalis, K.C. 2006. Local and regional factors determining aquatic and semi-aquatic bug (Heteroptera) assemblages in rivers and streams of Greece. *Hydrobiologia*, 573: 199-212.

Kietzka G.J., Pryke J.S. and Samways M.J. 2015. Landscape ecological networks are successful in supporting a diverse dragonfly assemblage. *Insect Conservation and Diversity*, 8: 229-237.

Kietzka G.J., Pryke J.S. and Samways M.J. 2016. Aerial adult dragonflies are highly sensitive to in-water conditions across an ancient landscape. *Diversity and Distributions*, 23: 14-26.

Krajenbrink, H.J., Acreman, M., Dunbar, M.J., Hannah, D.M., Laizé, C.L.R. and Wood, P.J. 2019. Macroinvertebrate community responses to river impoundment at multiple spatial scales. *Science of The Total Environment*, 650: 2648-2656.

Kriticos, D.J. and Leriche, A. 2010. The effects of climate data precision on fitting and projecting species niche models. *Ecography*, 33: 115-127.

Labandeira, C.C. 2018. The fossil history of insect diversity. In: Foottit, R.G. and Adler, P.H. (eds). *Insect Biodiversity: Science and Society*. Wiley-Blackwell, Oxford, UK. pp. 723-788.

Ladle, R.J. and Jepson, P. 2008. Toward a biocultural theory of avoided extinction. *Conservation Letters*, 1: 111-118.

Linder, H.P. 2005. Evolution of diversity: the Cape flora. *Trends in Plant Science*, 10: 536-541.

Lorenz, S., Rasmussen, J.J., Süß, A., Kalettka, T., Golla, B., Horney, P., … Schäfer, R.B. 2017. Specifics and challenges of assessing exposure and effects of pesticides in small water bodies. *Hydrobiologia*, 793: 213-224.

Lytle, D.A. 2015. Chapter 37: Order Hemiptera. In: Thorp, J. H. and Rogers, D. C. (eds.). *Thorp and Covich's Freshwater Invertebrates: Ecology and General Biology*. Elsevier, Amsterdam, The Netherlands. pp. 1953-1979.

Macadam, C.R. and Stockan, J.A. 2015. More than just fish food: ecosystem services provided by freshwater insects. *Ecological Entomology*, 40: 113-123.

Magoba, R.N. and Samways, M.J. 2010. Recovery of benthic macroinvertebrate and adult dragonfly assemblages in response to large scale removal of riparian invasive alien trees. *Journal of Insect Conservation*, 14: 627-636.

Malmqvist, B. 2000. How does wing length relate to distribution patterns of stoneflies (Plecoptera) and mayflies (Ephemeroptera)? *Biological Conservation*, 93: 271-276.

Marten, A., Brändle, M. and Brandl, R. 2006. Habitat type predicts genetic population differentiation in freshwater invertebrates. *Molecular Ecology*, 15: 2643-2651.

Martin, J.L., Cardoso, P., Arechavaleta, M., Borges, P.A.V., Faria, B.F., Abreu, C, … Mendonça, E. 2010. Using taxonomically unbiased criteria to prioritize resource allocation for oceanic island species conservation. *Biodiversity and Conservation*, 19: 1659-1682.

Martín-López, B., Montes, C. and Benayas, J. 2007. The non-economic motives behind the willingness to pay for biodiversity conservation. *Biological Conservation*, 139; 67-82.

Masese, F.O. and Raburu, P.O. 2017. Improving the performance of the EPT Index to accommodate multiple stressors in Afrotropical streams. *African Journal of Aquatic Science*, 42: 219-233.

Matthews, W.J. 1998. *Patterns in Freshwater Fish Ecology*. Chapman and Hall, New York.

Mittelbach, G.G., Schemske D.W., Cornell H.V., Allen A.P., Brown J.M., Bush M.B., … Turelli, M. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, 10: 315-331.

Mlambo, M.C., Bird, M.S., Reed, C.C. and Day, J.A. 2011. Diversity patterns of temporary wetland macroinvertebrate assemblages in the south-western Cape, South Africa. *African Journal of Aquatic Science*, 36: 299-308.

Moilanen, A., Leathwick, J. and Elith, J. 2008. A method for spatial freshwater conservation prioritization. *Freshwater Biology*, 53: 577-592.

O’Keeffe, J.H. and Dickens, C.W.S. 2000. Aquatic Invertebrates, In: King, J. M., Tharme, R. E. and de Villiers, M. S. (eds.). *Environmental flow assessments for rivers: Manual for the Building Block Methodology*, Report No. TT 131/00, Water Research Commission, Pretoria, South Africa. pp. 231-244.

Oertli, B., Céréghino, R., Hull, A. and Miracle, R. 2009. Pond conservation: from science to practice. *Hydrobiologia*, 634: 1-9.

Paavola, R., Muotka, T. and Tikkanen, P. 2000. Macro-invertebrate community structure and species diversity inhumic streams of Finnish Lapland. *Verhandlungen derInternationalen Vereinigung für Theoretische und Angewandte Limnologie*, 27: 2550-2555.

Paisley, M.F., Trigg, D.J. and Walley, W.J. 2014. Revision of the biological monitoring working party (BMWP) score system: derivation of present- only and abundance-related scores from field data. *River Research and Applications*, 30: 887-904.

Palmer, M.A., Menninger, H.L. and Bernhardt, E. 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? *Freshwater Biology*, 55: 205-222.

Pearson, R.G. and Boyero, L. 2009. Gradients in regional diversity of freshwater taxa. *Journal of the North American Benthological Society*, 28: 504-514.

Pedgley, D.E., Reynolds, D.R. and Tatchell, G.M. 1995. Long-range insect migration in relation to climate and weather: Africa and Europe. In: Drake, V.A. and Gatehouse, A.G. (eds.). *Insect migration: tracking resources through space and time*. Cambridge University Press, Cambridge, UK. pp. 3-29.

Poff, N.L., Olden, J.D., Vieira, N.K., Finn, D.S., Simmons, M.P. and Kondratieff, B.C. 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, 25: 730-755.

Pryke, J.S., Samways, M.J. and De Saedeleer, K. 2015. An ecological network is as good as a major protected area for conserving dragonflies. *Biological Conservation*, 191: 537-545.

Reavell, P. 2003. Hemiptera. In de Moor, I., Day, J. and de Moor, F. (eds.). *Guides to the Freshwater invertebrates of Southern Africa: Insecta II Hemiptera, Megaloptera, Neuroptera, Trichoptera and Lepidoptera*. Water Research Commission, Pretoria, South Africa. pp. 16-71.

Revenga, C., Campbell, I., Abell, R., De Villiers, P. and Bryer, M. 2005. Prospects for monitoring freshwater ecosystems towards the 2010 Targets. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360: 397-413.

Ribera, I. and Vogler, A.P. 2000. Habitat type as a determinant of species range sizes: the example of lotic-lentic differences in aquatic Coleoptera. *Biological Journal of the Linnean Society*, 71: 33-52.

Ribera, I., Foster, G.N. and Vogler, A.P. 2003. Does habitat use explain large scale species richness patterns of aquatic beetles in Europe? *Ecography*, 26: 145-152.

Romero, K.C., Del Río, J.P., Villarreal, K.C., Anillo, J.C.C., Zarate, Z.P., Gutierrez, L.C., ... Valencia, J.W.A. 2017. Lentic water quality characterization using macroinvertebrates as bioindicators: An adapted BMWP index. *Ecological Indicators*, 72: 53-66.

Rundle, S.D., Bilton, D.T. and Foggo, A. 2007. Chapter 10. By wind, wings or water: body size, dispersal and range size in aquatic invertebrates. In Hildrew, A.G., Raffaelli, D.G. and Edmonds-Brown, R. (eds). *Body size: The Structure and Function of Aquatic Ecosystems*. Cambridge University Press, Cambridge, UK. pp. 186-209.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, R., Bloomfield, J., Dirzo, J., … Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science*, 287: 1770-1774.

Samways, M.J. 2006. National Red List of South African Odonata. *Odonatologica*, 35: 341-368.

Samways, M.J. and Pryke J.S. 2016. Large-scale ecological networks do work in an ecologically complex biodiversity hotspot. *Ambio*, 45: 161-172.

Samways, M.J. and Sharratt, N.J. 2010. Recovery of endemic dragonflies after removal of invasive alien trees. *Conservation Biology*, 24: 267-277.

Samways, M.J. and Steytler, N.S. 1996. Dragonfly (Odonata) distribution patterns in urban and forest landscapes, and recommendations for riparian management. *Biological Conservation*, 78: 279-288.

Samways, M.J. and Taylor, S. 2004. Impacts of invasive alien plants on Red-Listed South African dragonflies (Odonata): Working for Water. *South African Journal of Science*, 100: 78.

Samways, M.J., Bazelet C.S. and Pryke J.S. 2010. Provision of ecosystem services by large scale corridors and ecological networks. *Biodiversity and Conservation*, 19: 2949-2962.

Sánchez–Bayo, F., and Wyckhuys, K.A. 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, 232: 8-27.

Schilder, R.J. and Marden, J.H. 2004. A hierarchical analysis of the scaling of force and power production by dragonfly flight motors. *Journal of Experimental Biology*, 207: 767-776.

Simaika, J.P. and Samways, M.J. 2012. Using dragonflies to monitor and prioritize lotic systems: A South African perspective. *Organisms Diversity and Evolution*, 12: 251-259.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation*, 83: 247-257.

Smith, J., Samways, M.J. and Taylor, S. 2007. Assessing riparian quality using two complementary sets of bioindicators. *Biodiversity and Conservation*, 16: 2695-2713.

Smith, R.J., Easton, J., Nhancale, B.A., Armstrong, A.J., Culverwell, J., Dlamini, S.D. and Leader-Williams, N. 2008. Designing a transfrontier conservation landscape for the Maputaland centre of endemism using biodiversity, economic and threat data. *Biological Conservation*, 141: 2127-2138.

Soluk, D.A., Zercher D.S. and Worthington, A.M. 2011. Influence of roadways on patterns of mortality and flight behavior of adult dragonflies near wetland areas. *Biological Conservation*, 144: 1638-1643.

Steenkamp, Y., Van Wyk, B., Victor, J., Hoare, D., Smith, G., Dold, T. and Cowling, R. 2004. Maputaland-Pondoland-Albany. *Hotspots Revisited: Earth's Biologically Richest and most Endangered Terrestrial Ecoregions.* CEMEX, Mexico City, Mexico. pp. 218-229.

Stork, N.E., McBroom, J., Gely, C. and Hamilton, A.J. 2015. New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proceedings of the National Academy of Sciences of the USA*, 112: 7519-7523.

Strayer, D. 2006. Challenges for freshwater invertebrate conservation. *Journal of the North American Benthological Society*, 25: 271-287.

Strayer, D.L., Lutz, C., Malcom, H.M., Munger, K. and Shaw, W.H. 2003. Invertebrate communities associated with a native (*Vallisneria americana*) and an alien (*Trapa natans*) macrophyte in a large river. *Freshwater Biology*, 48: 1938-1949.

Suhling, F. 2001. Intraguild predation, activity patterns, growth and longitudinal distribution in running water odonate larvae. *Archiv für Hydrobiologie*, 151: 1-15.

Thorp, J.H. and Rogers, D.C. (Eds.). 2014. *Thorp and Covich's Freshwater Invertebrates: Ecology and General Biology*. Elsevier.

Toledo, M. and Turner, C.R. 2004. *Andex insignis* Sharp 1882 from the Northern Cape region of South Africa. *Latissimus*, 18: 34-38.

Triantis, K.A., Borges, P.A.V., Ladle, R.J., Hortal, J., Cardoso, P., Caspar, C, … Whittaker, R.J. 2010. Extinction debt on oceanic islands. *Ecography*, 33: 285-294.

Trombulak, S.C. and Frissell, C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, 14: 18-30.

Turner, C. 2007a. Water beetles associated with reservoirs on Table Mountain, Cape Town: implications for conservation. *Journal of Insect Conservation*, 11: 75-83.

Turner, C. 2007b. Chapter 23. Bioinventory methodology for water beetles: a practical introduction. In Stals, R. and de Moor, I.J. (eds.). *Guides to the freshwater Invertebrates of Southern Africa: Vol. 10 Aquatic Coleoptera*. Water Research Commission, Pretoria, South Africa. pp. 193-204.

van der Niet, T. and Johnson, S.D. 2009. Patterns of plant speciation in the Cape Floristic Region. *Molecular Phylogenetics and Evolution*, 51: 85-93.

Wakeling, J.M. and Ellington, C.P. 1997. Dragonfly flight III. Lift and power requirements. *Journal of Experimental Biology*, 200: 583-600.

Wan, Y., Xu, L., Hu, J., Xu, C., Wan, A., An, S. and Chen, Y. 2015. The role of environmental and spatial processes in structuring stream macroinvertebrates communities in a large river basin. *Clean Soil Air Water*, 43: 1633-1639.

Webster, B. and Cardé, R.T. 2017. Use of habitat odour by host-seeking insects. *Biological Reviews*, 92: 1241-1249.

Wessels, K.J., Prince, S.D., Malherbe, J. Small, J., Frost, P.E. and Van Zyl, D. 2007. Can human-induced land degradation be distinguished from the effects of rainfall variability? A case study in South Africa. *Journal of Arid Environments*, 68: 271-297.

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P. and Sear, D. 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation*, 115: 329-341.

Yee, D.A. and Kehl, S. 2015. Chapter 39: Order Coleoptera. In Thorp, J.H. and Rogers, D.C. (eds.). *Thorp and Covich's Freshwater Invertebrates: Ecology and General Biology*. Elsevier, Amsterdam, The Netherlands. pp. 2056-2154.

Yekwayo, I., Pryke, J.S., Roets, F. and Samways, M.J. 2016. Surrounding vegetation matters for arthropods of small, natural patches of indigenous forest. *Insect Conservation and Diversity*, 9: 224-235.

Chapter 2 Widespread habitat generalists vs. narrow-range habitat specialists: a valid division or not?

*Under review with Journal of Biogeography

Abstract

In insect ecology, species are often binarily assigned to ‘widespread habitat generalists’ vs. ‘narrow-range habitat specialists’, implying that widely-distributed species are adapted to many biotopes over a large area, while narrowly-distributed species are adapted to a few selected biotopes in a small area. For conservation, this often translates into any one species being either a ‘less threatened generalist’ or a ‘threatened specialist’. We investigate here whether biotope occupancy and/or habitat preference can describe latitude, longitude and elevation range size, and determine the significance of other functional traits. We hypothesize that functional traits related to mobility and life history are equally important for determining species’ geographical range size. Species distribution data were obtained from the Odonata Database of Africa. Adult and larval biotope occupancy, as well as adult functional trait information, were captured from published sources. We then classified each focal species as lotic, lentic, or lotic/lentic, based on larval biotope occupancy. Using generalised linear modelling, we determined the significance of biotope occupancy by each of the two life stages, habitat preference, and other functional traits, in driving range size. We then tested for significant relationships between each driver of range size, and an existing measure of ecological sensitivity. We found significant relationships between number of adult biotopes occupied, as well as overall habitat preference, and species range size. Other functional traits, related to life history and adult morphology, also significantly influenced distribution ranges. Furthermore, we found that ecological sensitivity measures can be useful for understanding biogeographical patterns. Binary classifications of ‘widespread habitat generalists’ vs. ‘narrow-range habitat specialists’ is largely valid. Although when based solely on habitat occupancy, hard categorization must be treated with caution, as additional functional traits related to phenology and mobility are important determinants of species range size.

Keywords: dragonflies, damselflies, macro-ecology, freshwater, distribution, range size, habitat, Africa

2.1 Introduction

Differences in species' niche-size result from evolutionary trade-offs between their ability to use a spectrum of resources and their ability to use each one effectively (McArthur 1972). When native habitats become unsuitable, species respond to change by moving to suitable habitat, or having acclimatory or evolutionary responses over several generations (Durant et al. 2007). A 'habitat generalist' is defined as a species with multiple interactions with its surroundings, and is not specifically adapted to particular environmental conditions or habitat types (Devictor et al. 2010; Büchi and Vuilleumier 2014). The 'jack-of-all-trades is a master of none' hypothesis (Levins 1962) suggests that generalists can perform many activities, but they often perform these activities poorly, resulting in their highly opportunistic nature (Wilson and Yoshimura 1994). Consequently, habitat generalists are often highly efficient at obtaining resources from various sources and occupy many ecological niches, including human-disturbed ecosystems, and/or ecosystems experiencing high ecological pressure from climatic variation such as arid and semi-arid environments (Smart et al. 2006). This suggests that most generalists have wide geographical ranges over multiple biomes (Julliard et al. 2006).

In turn, a 'habitat specialist' is defined as a species with few interactions with its surroundings, and is well adapted to its specific habitat (Wilson and Yoshimura 1994; Büchi and Vuilleumier 2014). As most specialists occupy narrower niche space compared to their generalist counterparts, they are expected to have narrow and fragmented geographical ranges (Futuyma and Moreno 1988; Brouat et al. 2004). However, specialisation is often regarded as an evolutionary dead end, as it implies certain morphological and physiological characteristics that are highly modified (Rensch 1959). Whether specialisation is biologically irreversible remains poorly investigated, and requires that sister taxa together with their specialised and generalised ancestors are compared on the genetic level (Futuyma and Moreno 1988).

A first premise for classifying species into 'widespread habitat generalists' or 'narrow-range habitat specialists' is that a definition of 'habitat' is required. It has been defined in various ways (Dennis 2010), with a workable definition being that of Haslett (2007) as 'the sum of the abiotic and biotic factors essential to the life and reproduction of the species within its natural geographic range'. This is not to be confused with 'biotope' (which we also use here), defined as the 'the specific physical features and structures (e.g. plants, rocks, water features) that make up habitats'.

Meaningful interpretation of ‘widespread habitat generalist’ vs. ‘narrow-range habitat specialist’ is challenging as to how specialisation relates to species’ range size (Julliard et al. 2006; Verberk et al. 2018; Poisot et al. 2015). Furthermore, there are several other factors that influence species’ spatial distribution, including life history traits (Rundle et al. 2007), dispersal efficiency (Rundle et al. 2007; Büchi and Vuilleumier 2014), and biogeographical constraints (Hof et al. 2006). These additional drivers may vary with disturbance levels, presence/absence of competitors, predators and pathogens, climatic variation, and differences in requirements between different life cycle stages (Dall and Cuthill 1997; Büchi and Vuilleumier 2014), suggesting that ordering species along a generalist/specialist gradient is more practical. Doing so should include quantification of specialisation among multiple biotopes and habitat classes, in combination with ecological traits, such as diet and ecological resilience, responses to competition from con- and inter-specifics, and dispersal ability to track favourable conditions (Sol et al. 2009).

Insects, being diverse, relatively easy to sample and highly responsive to change in their surrounding environments, are often good models for testing macro-ecological hypotheses. Dragonflies and damselflies (hereafter collectively referred to as ‘dragonflies’) have a long history of adaptation to many lotic (flowing water) and lentic (still water) habitats (Kalkman et al. 2008), and are generalist apex predators of various other invertebrate groups as both aquatic larvae and terrestrial adults (Simaika and Samways 2009a). They are also highly mobile as adults, easy to identify on the wing, and all species are variably sensitive to ecological conditions, making them excellent model organisms (Samways and Simaika 2016), particularly for biogeographical studies (Hassall 2015).

Drivers of species’ geographical ranges have been investigated previously (e.g. Calosi et al. 2010; Buckley and Roughgarden 2005). In turn, insect species are often categorised as either ‘widespread habitat generalists’ or ‘narrow-range habitat specialists’ based on habitat occupancy, which may not be truly representative of other factors that contribute to variation in range size. Here, we challenge this binary assertion, and aim to 1) determine whether habitat preference and/or biotope occupancy can be used to explain latitude, longitude and elevation range size of dragonflies across Africa, 2) determine the overall importance and significance of other functional traits, related to mobility and life history, and 3) investigate whether our findings correlate with existing measures of ecological sensitivity. We hypothesise that species which occupy both lentic and lotic habitats, or lentic-lotic transition habitats, have the widest geographical ranges, and that species which interact with multiple biotopes have relatively wider ranges compared to species that interact with few biotopes. We expect traits related to mobility and life history to correlate with habitat preference and biotope occupancy as drivers of range sizes, and expect our findings to support existing measures of ecological sensitivity.

2.2 Data and methods

2.2.1 Geographical and functional trait data acquisition

We extracted northern and southern latitude range boundaries, western and eastern longitude range boundaries, and minimum and maximum elevation across Africa for each species recently confirmed from South Africa (154 species, comprising 62 genera and ~82 000 point records; see Appendix S2.1 in supporting information), from the Odonata Database of Africa (ODA; Clausnitzer et al. 2012). We then calculated the latitude, longitude and elevation range size (maximum latitude, longitude, elevation – minimum latitude, longitude, elevation) for each model species (refer to Appendix S2.2 for full species list). We considered using the area of occupancy for each model species, yet due to wide areas throughout Africa that remain unexplored, this measure was inaccurate for most species and produced unreliable results. We selected the species occurring in South Africa as our focal taxon set, as they are the most well-known in terms of their taxonomy, habitat preferences, and functional traits (Dijkstra 2003).

For the adult stage of each dragonfly species, we categorised and quantified their biotope preferences based on taxonomic descriptions and published field guides from across Africa. These categories included ‘lotic habitats’ (flowing water), ‘lentic habitats’ (still water), ‘lentic/lotic habitats’ (transition aquatic habitats), ‘riparian and edge characteristics’ (i.e. terrestrial microhabitats), and ‘features associated with open water’ (57 biotope categories in total; See Appendix S2.3). For larval stages, we categorised and quantified their biotope preferences in a similar way to that of the adults, using all available taxonomic descriptions (from 1957-present), but excluded the ‘shallow river or stream’ and ‘deep river or stream’ categories, as larvae rarely occur below a depth of 1.2 m (Samways et al. 1996). We replaced ‘riparian and edge characteristics’ with ‘margin characteristics’ (i.e. aquatic microhabitats along the margins of water bodies), and ‘features associated with open water’ with ‘substratum’ (50 biotope categories in total; see Appendix S2.4). Following these classifications, we determined which species predominantly prefer lotic, lentic or lotic/lentic habitats based on their larval biotopes, as adults often occupy both lentic and lotic habitats.

To determine the start, end, and duration of the adult life stage, we extracted recording dates for each model species from the ODA. For start of adult life stage, flight season starting mid-September to mid-October was ‘Early spring’, flight season starting mid-October to mid-November was ‘Late spring’, flight season starting mid-November to mid-December was ‘Early summer’ and flight season starting late December to mid-February was ‘Late summer’. For end of adult life stage, flight season ending late January to late February was ‘Late summer’, flight season ending early March to mid-April was ‘Early autumn’, flight season ending late April to mid-May was ‘Late autumn’ and flight season ending late May to mid-June was ‘Early winter’. For each dragonfly species, duration of adult life stage was summarised, as well as whether a particular species was previously recorded as an overwintering adult, extracted from Samways and Simaika (2016), van Huyssteen and Samways (2009) and van Schalkwyk et al. (2014). Average hind-wing length, average adult body length and adult flight mode (darter, hawker, percher, glider, etc.) were extracted from Samways and Simaika (2016) and the average hind-wing length to body-length ratio was calculated (values ranging between 0 and 1, hereafter referred to as ‘wing-to-body ratio’). To avoid ambiguity of our results, only ecological sensitivity (one of the three sub-indices from the Dragonfly Biotic Index (DBI); scores 0-3) was extracted from Samways and Simaika (2016), since the full score out of nine already contains some information regarding the distribution of the dragonfly species studied here.

2.2.2 Statistical analyses

The latitude, longitude and elevation range data were non-normally distributed according to Shapiro-Wilks tests. We used generalised linear modelling (GLM) with Gamma distributions and Log-link functions to test the significant effects of number of biotopes occupied by larvae and adults, overall habitat preference, and a set of additional functional traits, on latitude, longitude and elevation range sizes respectively.

We used model selection to determine the functional traits that were most descriptive of latitude, longitude and elevation range size. Eleven variables were included in the model set used for final selection: number of adult biotopes occupied, number of larval biotopes occupied, habitat preference (lentic vs. lotic vs. lentic/lotic), start of adult life stage, end of adult life stage, duration of adult life stage, overwintering as adults, adult temperament/behaviour, average hind wing size, average adult body size and wing-to-body ratio. We then built GLMs for each response variable with all possible combinations of independent variables. None of the models were overdispersed (Pearson's Test for overdispersion), and we used the second-order Akaike's information criterion (AIC_C) values to rank candidate models and ΔAIC_C to determine if more than one model was important, using the *dredge* function in the *MuMIn* package for R (Barton 2019; R Development Core Team 2016).

Subsequently, three independent GLMs containing the set of variables with the lowest AIC_C values were constructed in R (R Development Core Team, 2016) for latitude, longitude and elevation range size to determine their overall significance, using the *lme4* package (Bates, Maechler et al. 2014). In addition, we performed generalised linear modelling for each significant variable for latitude, longitude and elevation range size, against ecological sensitivity derived from the DBI. In the case of all significant categorical variables, Tukey post-hoc tests were used to determine the pairwise differences for categories within each categorical variable, using the *multcomp* package in R (Hothorn et al. 2008).

2.3 Results

Of the 11 variables tested, five were important for latitude, longitude and elevation range sizes of dragonflies across Africa. These were: number of biotopes occupied by adults, habitat preference, end of adult life stage, wing-to-body ratio, and adult overwintering. Number of biotopes occupied by larvae, start of adult life stage, duration of adult life stage, adult flight mode, average hind-wing length, and average adult body length were not important descriptors of distribution range size.

The best models identified by model selection for latitude and longitude range size included number of biotopes occupied by adults, late summer as the end of adult life stage, wing-to-body ratio, lotic habitat preference for latitude range size, and lentic habitat preference for longitude range size. Lentic/lotic habitat preference, early autumn, late autumn, and early winter as end of adult life stage, and adult overwintering had no strong effects on predicting latitude and longitude range size. The best model for elevation range size included number of biotopes occupied by adults, late summer as end of adult life stage, and adult overwintering. Habitat preference, early autumn, late autumn and early winter as the end of adult life stage, and wing-to-body ratio were not significant in determining elevation range. Subsets of the best models for each model scenario ($\Delta AIC_C \leq 2$) are given in Table 2.1.

Table 2.1 Model ranking and selection estimates for functional traits explaining variation in latitude, longitude and elevation range size of dragonflies across Africa.

Model	Df	AICc	ΔAICc	Weight
Latitude range				
A_Biot + E_Seas + Habitat + WBR	**6**	**1369.87**	**0**	**0.1**
A_Biot + E_Seas + Habitat + WBR + OW	7	1370.58	0.71	0.07
A_Biot + E_Seas + Habitat + WBR + M_Acti	7	1370.76	0.89	0.06
A_Biot + E_Seas + Habitat + WBR + WL	7	1370.96	1.09	0.06
A_Biot + E_Seas + Habitat + WBR + BL	7	1371.01	1.15	0.06
A_Biot + E_Seas + Habitat + WBR + OW + WL	8	1371.40	1.53	0.05
A_Biot + E_Seas + Habitat + BL + WL	7	1371.44	1.57	0.05
A_Biot + E_Seas + Habitat + WBR + OW + BL	8	1371.45	1.58	0.04
A_Biot + E_Seas + Habitat + WBR + M_Acti + WL	8	1371.63	1.76	0.04
A_Biot + E_Seas + Habitat + WBR + M_Acti + BL	8	1371.68	1.81	0.04
Longitude range				
A_Biot + E_Seas + Habitat + WBR	**6**	**1381.14**	**0**	**0.14**
Elevation range				
A_Biot + OW + E_Seas	**5**	**2497.99**	**0**	**0.19**
A_Biot + M_Acti + E_Seas	5	2499.22	1.22	0.1
A_Biot + OW + E_Seas + WBR	6	2499.35	1.36	0.1
A_Biot + E_Seas	4	2499.58	1.59	0.09
A_Biot + M_Acti	4	2499.71	1.71	0.08
A_Biot + OW + E_Seas + WL	6	2499.87	1.88	0.08

Models with ΔAICc < 2 are shown. Best models highlighted in bold text. A_Biot: number of biotopes occupied by adults; E_Seas: end of adult life stage; Habitat: habitat preference based on larval biotope occupancy; M_Acti: duration of adult life stage; OW: overwintering as adults; WL: average hind-wing length; BL: average body length; WBR: wing-to-body ratio.

Latitude range size differed significantly between species with different habitat preferences ($F = 15.78$, $p < 0.001$). Lotic species had significantly narrower latitude ranges than lentic and lentic/lotic species, and lentic species had slightly narrower ranges than lentic/lotic species, although not significantly (Figure 2.1a, see Appendix S2.5). End season of adult life stage had a further significant effect on latitude range ($F = 9.08$, $p < 0.001$). Species with adult life stages ending late summer had significantly narrower latitude ranges than those with adult stage ending early autumn, late autumn and early winter. Species with adult life stages ending early autumn had narrower latitude ranges than those ending in late autumn and early winter, and species with adult life stages ending in late autumn had narrower latitude ranges than those ending early winter, though none of these differences were significant (Figure 2.1b). Species occupying comparatively more adult biotopes ($t = 7.53$, $p < 0.01$) and with higher wing-to-body ratios ($t = 22.92$, $p < 0.001$) had significantly wider latitude ranges (Figure 2.1c and d).

Longitude range size differed significantly between species with different habitat preferences ($F = 15.41$, $p < 0.001$). Lotic species had significantly narrower longitude ranges than lentic species, and lentic species had significantly wider longitude ranges than lentic/lotic species. Lotic species had narrower longitude ranges compared to lentic/lotic species, but not significantly (Figure 2.1e, see Appendix S2.5). As with latitude range size, end season of adult life stage had a significant effect on longitude range ($F = 8.37$, $p < 0.001$), and species with adult life stages ending late summer had significantly narrower latitude ranges than those ending with adult stage ending early autumn, late autumn and early winter. Species with adult life stages ending early autumn had narrower latitude ranges than those ending late autumn and early winter, and species with adult life stages ending late autumn had narrower latitude ranges than those ending early winter, yet not significantly (Figure 2.1f). Species occupying more adult biotopes had significantly wider longitude ranges ($t = 2.55$, $p < 0.05$; Figure 2.1g), and species with higher wing-to-body ratios had significantly wider longitude ranges ($t = 3.95$, $p < 0.001$; Figure 2.1h).

For elevation, adult overwintering species had wider elevation ranges than those that do not overwinter as adults, although this difference was only marginally significant ($t = 1.76$, $p = 0.08$; Figure 2.1i). Season in which adult life stages ended had a significant effect on range size ($F = 7.14$, $p < 0.001$). Species with adult life stages ending late summer had significantly narrower ranges compared to those with adult life stage ending late autumn. There was no significant difference in elevation range between adult life stages ending early autumn, late autumn and early winter (Figure 2.1j, see Appendix S2.5). Elevation range was also significantly higher for species that occupied more adult biotopes ($t = 3.63$, $p < 0.001$; Figure 2.1k).

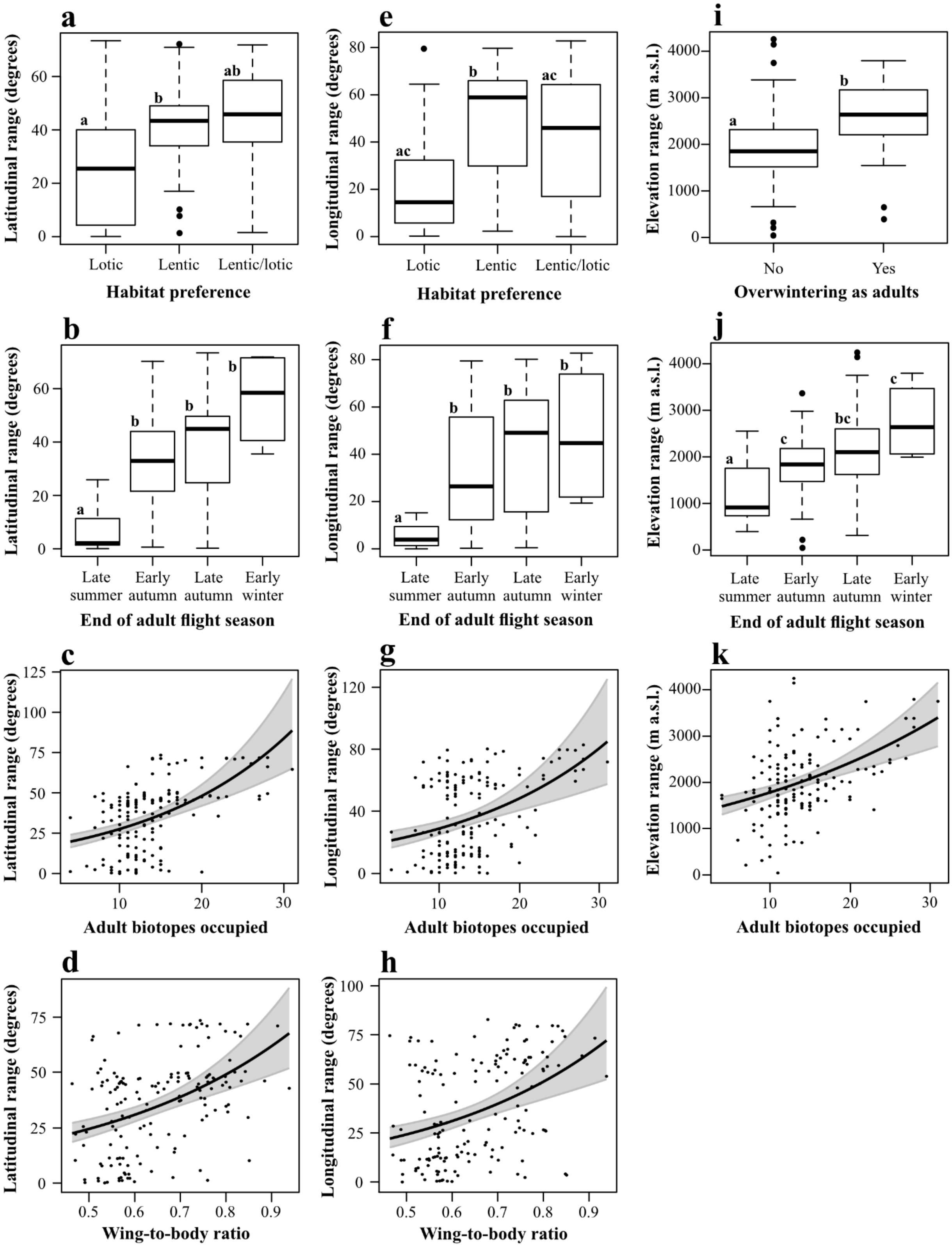


Figure 2.1 Functional traits driving dragonfly latitude (a-d), longitude (e-f) and elevation ranges (i-k) across Africa. For categorical variables, different letters indicate significantly different medians. For continuous variables, shaded areas indicate 95% confidence intervals.

Ecological sensitivity scores decreased with an increase in number of adult biotopes occupied ($z = -4.80$, $p < 0.001$; Figure 2.2a) and wing-to-body ratio ($z = -1.99$, $p < 0.05$; Figure 2.2b). Lotic species were significantly more sensitive to environmental change than lentic/lotic species ($z = 3.31$, $p < 0.01$; Figure 2.2c), and there was no significant difference in ecological sensitivity between lentic and lotic species, and lentic and lentic/lotic species. Adult overwintering species had significantly lower ecological sensitivity compared to those species that did not overwinter as adults ($z = -2.71$, $p < 0.01$; Figure 2.2d). There was no significant difference in ecological sensitivity between species with adult stages ending in different seasons.

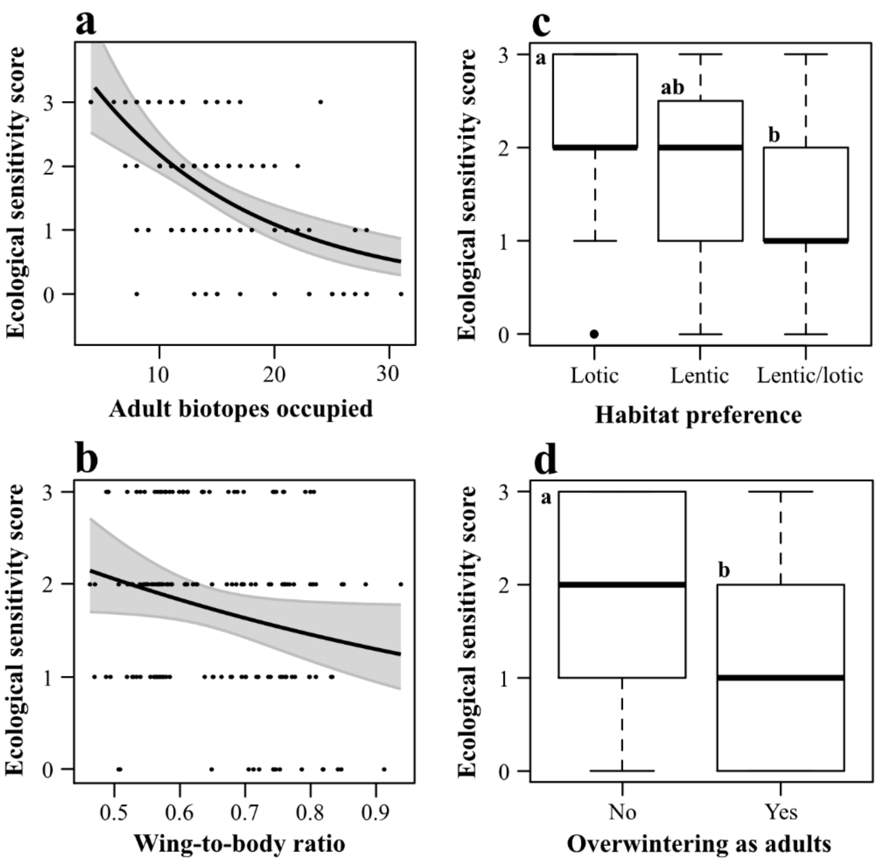


Figure 2.2 Relationships between ecological sensitivity derived from the DBI, and significant traits driving dragonfly latitude, longitude and elevation ranges across Africa. For continuous variables, shaded areas indicate 95% confidence intervals. For categorical variables, different letters indicate significantly different medians.

2.4 Discussion

Overall habitat preference and number of biotopes occupied by adults were significant in determining species range sizes. However, several species did not conform to the general pattern. Furthermore, in addition to habitat preference and biotope occupancy, there were other functional traits related to life history and morphology that were significant in determining dragonfly ranges at a continental scale. These predictive factors varied in importance, yet ending season of adult life stage, ability to overwinter as adults, and wing-to-body ratios (as a proxy for dispersal ability of a particular species) were the most significant in determining distribution ranges overall. Season of adult emergence, duration of adult life stage (as a proxy for adult life span) and adult behaviour related to phylogenetic pedigree were of lesser importance. Finally, ecological sensitivity, as calculated by the DBI, correlated significantly with habitat preference, number of biotopes occupied, and functional traits related to phenology and mobility.

2.4.1 Significance of habitat and biotope specificity

Habitat specificity among freshwater species relates to flow regimes vis-à-vis water chemistry, restricting them to either lentic or lotic habitats (Foster and Eyre 1992; Larson 1997; Ribera and Vogler 2000). Yet many dragonflies occupy both lentic and lotic habitats, or occupy lentic-lotic transition habitats. This ability to occupy multiple broad habitat types should have strong effects on their geographical distribution (Ribera and Vogler 2000; Hof et al. 2006). Here, lentic and lentic/lotic dragonflies had the widest latitude ranges, and lentic species had the widest longitude ranges, as was found for aquatic beetles across the Iberian Peninsula (Ribera and Vogler 2000) and dragonflies across Europe and North America (Hof et al. 2006). To compensate for habitat instability (Dobson and Frid 1998; Ribera et al. 2001), lentic species colonise new habitats faster than lotic species, and as a result, have comparatively wider latitude and longitude ranges (Ribera and Vogler 2000; Hof et al. 2006). For example, *Sympetrum fonscolombii* is a common and widespread lentic species throughout Africa, and one of the first species to arrive at many different types of lentic water bodies. Yet many lentic species (e.g. *Orthetrum rubens*, *Africallagma sapphirinum* and *Urothemis luciana*) are isolated by geographic features and/or climatic barriers, resulting in their comparatively narrow ranges. On the other hand, not all lotic species have narrow ranges, and some savanna species (e.g. *Zygonyx torridus*, *Brachythemis lacustris* and *Pseudagrion sublacteum*) have wide ranges over west-east river courses. The dragonflies investigated here had similar elevation ranges across all broad habitat types, suggesting that different elevations did not exclude particular habitat types.

We regarded 'biotopes' as the small, specific physical features that make up broad habitat types, and quantified generalisation/specialisation as the number of occupied biotopes. Ordering species along a generalist/specialist gradient is more robust when dealing with a high number of rare and localised species (Julliard et al. 2006), as with African dragonflies overall (Samways 2004; Samways and Simaika 2016). As expected, species with multiple interactions with their surroundings had wider latitude, longitude and elevation ranges than species with few such interactions (Gaston and Spicer 2001; Calosi et al. 2008). These widespread generalists included *Ceriagrion glabrum*, *Anax imperator*, *Ischnura senegalensis*, *Pantala flavescens* and *O. julia*, all opportunistic and common residents of many widely-distributed freshwater bodies and biotopes. In contrast, *Ceratogomphus triceraticus*, *Syncordulia gracilis, P. newtoni* and *O. rubens*, all rare narrow-range South African endemics, are restricted to specific biotopes, and have much narrower latitude, longitude and elevation ranges as their preferred biotopes. However, several species did not conform to this general pattern. These included *Bradinopyga cornuta* (highly adapted to life in and around rock pools), *B. lacustris* (residents of tree- and bush-lined meandering rivers in hot regions) and *Lestes pallidus* (restricted to shallow pans in open savanna), all showing high fidelity for their occupied biotopes (Samways and Simaika 2016). Yet they have wide latitude and longitude ranges, with their favoured biotopes being widespread but spottily distributed. Similarly, for elevation range size, some species (e.g. *Agriocnemis exilis*, *P. spernatum*, *P. kersteni* and *Z. torridus*) occupy few biotopes as adults, but occupy them across a wide elevation range, as their preferred microhabitats are common at various elevations and functionally similar. In contrast, some biotope generalists (e.g. *Proischnura polychromatica* and *Chlorolestes umbratus*) have narrow latitude ranges and are local endemics, likely resulting from geographical isolation by extensive mountain ranges (Hof et al. 2006), and habitat stability (Hamilton and May 1977). Some other species (e.g. *Tetrathemis polleni* and *O. trinacria*) occupy many biotopes, but across narrow elevation ranges, due to their preferred biotopes (e.g. marshes, swamps and forest pools) only occurring in lowland tropical/subtropical settings.

We expected that the number of larval biotopes occupied would be as important as the number of adult biotopes occupied for determining range size, since larval biotopes are the specific features which each dragonfly species needs to complete its life cycle (*sensu* Dennis et al.

2006). Yet, larval biotope occupancy was not significant for any of the range-size metrics investigated here. Perhaps larval biotope occupancy was a less significant factor because, firstly, most past dragonfly research has been on adult stages, and general ecology and taxonomy of larvae are poorly understood at the species level, leading to potential inconclusive interpretation (Simaika and Samways 2009b; Bried and Samways 2015). Indeed, the ODA focuses mostly on adult dragonflies, being easier to sample and identify, bringing into question whether adult data entries can reliably translate to larval distribution. Secondly, we noted that larval biotope occupancy was related within families, challenging species-level-interpretation. Thirdly, the 'mother knows best' principle (Valladares and Lawton 1991) might be involved, where reproducing females oviposit in suitable habitats and drive range size (Simaika and Samways 2009b), and larvae survive as they escape interspecific competition from co-occurring dragonfly species (Suhling 2001).

2.4.2 Significance of other functional traits

Phenological events have strong limiting effects on insect population sizes, interactions with prey populations, and distribution ranges (Nakano and Murakami 2001; van Schalkwyk et al. 2014). Adult dragonfly emergence in response to changes in environmental conditions is also a survival strategy to avoid water shortage, especially in Mediterranean-type and subtropical environments where flow regimes are unpredictable (Samways 2003). However, we found that adult life stage duration and emergence season had no significant effect on distribution ranges, yet adult dragonflies that died in late summer had the narrowest latitude, longitude and elevation ranges. Dragonflies are tropical of origin (Corbet 1999), yet some are adapted to survive cold climates (van Huyssteen and Samways 2009; Denlinger and Lee 2010). Those here that died by late summer (e.g. *S. legator*, *S. gracilis* and *P. polychromatica*) likely cannot survive lower temperatures coming about in later months, and have little opportunity to move across latitude, longitude and elevation gradients.

Overwintering adults could theoretically have more generations/year, traverse the landscape as pre-reproductive adults during sub-optimal climatic conditions in search of favourable breeding sites, and ultimately breed when surface water becomes available (Corbet 1999; van Huyssteen and Samways 2009). We were unable to investigate the effects of voltinism on range size, as this information is lacking for most species investigated here. Yet, we found that overwintering adults had marginally wider elevation ranges, indicating that their resilience to cold allows them to occupy habitats across wide elevation gradients, and they likely migrate across elevation gradients according to favourability of seasonal habitats. However, this is not the case for all adult overwintering dragonflies, and some (e.g. *Aciagrion dondoense* and *Spesbona angusta*) have much narrower elevation ranges than others with this trait. This is presumably linked to the unavailability of favourable habitats and/or biotopes across elevation gradients.

Functional traits affecting dispersal ability are highly variable along the generalist/specialist gradient (Bilton et al. 2001; Jocque et al. 2010), and are fundamental in evolutionary persistence and biogeography (Rundle et al. 2007a). Freshwater taxa need to disperse to persist in their generally isolated aquatic habitats (Moss 1998), and consequently, many are able to travel long distances to avoid adverse environmental conditions and establish in favourable habitats (Rundle et al. 2007b). Here, we found that dragonflies with high wing-to-body ratios (e.g. *Rhyothemis semihyalina*, *Trithemis annulata* and *U. assignata*) had wider latitude and longitude ranges than those with low wing-to-body ratios (e.g. *Ecchlorolestes nylephtha, A. falcifera* and *P. polychromatica*). This is consistent with findings on mayflies (Ephemeroptera) and stoneflies (Plecoptera) in Sweden (Malmqvist 2000), with an overall positive correlation between wing-to-body ratio and range size.

Unsurprisingly, most species with relatively high wing-to-body ratios here were anisopterans, and those with low wing-to-body ratios were zygopterans. Anisopterans are adapted for rapid flight in open spaces, while most zygopterans are reluctant fliers and adapted for manoeuvring in localised spaces (Wakeling and Ellington 1997), leading to significant differences in their range sizes. Yet, wing-to-body ratios were variable, with several species (e.g. *A. exilis*, *I. senegalensis* and *C. glabrum*) having low wing-to-body ratios and wide latitude and longitude ranges, and vice-versa (e.g. *Hemicordulia africana* and *U. luciana*). In cases where wing-to-body ratios are weak predictors of range size, other factors, e.g. interspecific competition (Travis and Dytham 1999; Vogler and Ribera 2003), restrictive biogeographic settings (Hof et al. 2006), and ecological resilience (Malmqvist 2000) may be at play.

We found that wing-to-body ratio had no strong effects on elevation range size, suggesting that dispersal ability does not influence performance of dragonflies across elevation gradients. As with Swedish mayflies and stoneflies (Malmqvist 2000) and North American dragonflies (Rundle et al. 2007b), our results support body size as a weak predictor of range size. Yet the interaction between wing and body sizes is an important predictor of how well insects move across the landscape and maintain their distribution ranges (Rundle et al. 2007a). We expected adult flight mode to account for some variation in range size between species, but we found that this was not a clear case.

2.4.3 Other considerations related to drivers of range size

The sensitivity sub-index from the DBI reflects how well species survive in transformed habitats, and indicates which species require natural conditions to sustain their populations at any given habitat (Samways and Simaika 2016). Our results aligned well with the sensitivity sub-index of the DBI. Dragonflies that occupied the least biotopes, had lowest wing-to-body ratios, and did not overwinter as adults, had highest ecological sensitivity, and most had narrow latitude, longitude and elevation ranges. Furthermore, dragonflies occupying lentic/lotic transition habitats, and/or both lentic and lotic habitats had lower ecological sensitivity compared to lotic species. We did not include DBI sensitivity measures as part of our main analysis, as this sub-index comprises other ecological measures (e.g. habitat preference and resilience to disturbance) which is often difficult to quantify across wide geographic areas, and this measure of sensitivity gives priority to range-restricted and red-listed species (Simaika and Samways 2009b). Nevertheless, we aimed to demonstrate that such measures of ecological sensitivity are versatile and can further inform range sizes of organisms, while providing information on which species are most likely negatively affected by habitat disturbance.

2.5 Conclusion

Drivers of range size identified here align well with findings on dragonflies, and other aquatic insects, across various other geographical areas. Overall habitat preference and biotope occupancy/specialisation can at least in part explain general trends in range size variation for dragonflies across Africa, supporting classical description of habitat generalists being more widespread than habitat specialists. However, our results emphasise that such strict classifications and assumptions should be treated with caution, as there are several other traits (e.g. phenology, morphological traits related to dispersal, and sensitivity to ecological disturbance) that are equally important and interactive with habitat preference and biotope occupancy/specialisation. Subsequently, these traits should be considered along with habitat occupancy and biotope specialisation when determining the drivers of species distribution ranges. Here, we demonstrate that there is great variation in functional traits within taxonomic groups, emphasising the need for more species-level investigations to improve our understanding of the biological drivers of range size variation, and to facilitate effective large-scale conservation.

2.6 References

Barton, K. 2019. MuMIn: Multi-model inference. R package version 1.42.1. Retrieved from https://CRAN.R-project.org/package=MuMIn.

Bates, D., Maechler, M., Bolker, B. and Walker, S. 2014. lme4: Linear mixed-effects models using S4 classes. R package version 1.1-7. Retrieved from https://CRAN.R-project.org/package=lme4.

Bilton, D.T., Freeland, J.R. and Okamura, B. 2001. Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics,* 32: 159-181.

Bried, J.T. and Samways, M.J. 2015. A review of odonatology in freshwater applied ecology and conservation science. *Applied Odonatology,* 34: 1023-1031.

Brouat, C., Chevallier, H., Meusnier, S., Noblecourt, T. and Rasplus, J.-Y. 2004. Specialization and habitat: spatial and environmental effects on abundance and genetic diversity of forest generalist and specialist *Carabus* species. *Molecular Ecology,* 13: 1815-1826.

Büchi, L. and Vuilleumier, S. 2014. Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. *The American Naturalist*, 183: 612-624.

Buckley, L.B. and Roughgarden, J. 2005. Lizard habitat partitioning on islands: the interaction of local and landscape scales. *Journal of Biogeography*, 32: 2113-2121.

Calosi, P., Bilton, D.T. and Spicer, J.I. 2008. Thermal tolerance, acclimatory capacity and vulnerability to global climate change. *Biology Letters,* 4: 99-102.

Calosi, P., Bilton, D.T., Spicer, J.I., Votier, S.C. and Atfield, A. 2010. What determines a species' geographic range? Thermal biology and latitudinal range size relationships in European diving beetles (Coleoptera: Dytiscidae). *Journal of Animal Ecology*, 79: 194-204.

Clausnitzer, V., Dijkstra, K.-D.B., Koch, R., Boudot, J.-P., Darwall, W.R.T., Kipping, J., … Suhling, F. 2012. Focus on African freshwaters: hotspots of dragonfly diversity and conservation concern. *Frontiers in Ecology and the Environment*, 10: 129-134.

Corbet, P.S. 1999. *Dragonflies: Behaviour and ecology of Odonata*. Harley Books, Colchester, UK.

Dall, S.R.X. and Cuthill, I.C. 1997. The information costs of generalism. *Oikos*, 80: 197-202.

Denlinger, D.L. and Lee, R.E. 2010. *Low Temperature Biology of Insects*. Cambridge University Press, Cambridge, UK.

Dennis, R.L.H. 2010. *A Resource-based Habitat View for Conservation of Butterflies in the British Landscape*. Wiley-Blackwell, Wallingford, Oxon, UK.

Dennis, R.L.H., Shreeve, T.G. and van Dyck, H. 2006. Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodiversity and Conservation*, 15: 1943-1966.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villeger, S. and Mouquet, N. 2010. Defining and measuring ecological specialization. *Journal of Applied Ecology*, 47: 15-25.

Dijkstra, K.-D.B. 2003. A review of the taxonomy of African Odonata: finding ways to better identification and biogeographic insight. *Cimbebasia*, 18: 191-206.

Dobson, M. and Frid, C. 1998. *Ecology of Aquatic Systems*. Longman, Harlow, UK.

Durant, J.M. Hjermann, D.O. Ottersen, G. and Stenseth, N.C. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33: 271-283.

Fontaine, C., Thébault, E. and Dajoz, I. 2009. Are insect pollinators more generalist than insect herbivores? *Proceedings of the Royal Society B: Biological Sciences,* 276: 3027-3033.

Foster, G.N. and Eyre, M.D. 1992. *Classification and ranking of water beetle communities*. Nature Conservation No. 1, Joint Nature Conservation Committee, Peterborough, UK.

Futuyma, D. J. and Moreno, G. (1988). The evolution of ecological specialisation. *Annual Review of Ecology and Systematics*, 19, 207-233.

Gaston, K.J. and Spicer, J.I. 2001. The relationship between range size and niche breadth: a test using five species of *Gammarus* (Amphipoda). *Global Ecology and Biogeography,* 10: 179-188.

Hamilton, W.D. and May, R.M. 1977. Dispersal in stable habitats. *Nature,* 269: 578-581.

Haslett, J.R. 2007. *European strategy for the Conservation of Invertebrates*. Nature and the Environment No. 145. Council of Europe Publishing ,Strasbourg Cedex. France.

Hassall, C. 2015. Odonata as candidate macroecological barometers for global climate change, *Freshwater Science,* 34: 1040-1049.

Hof, C., Brändle, M. and Brandl, R. 2006. Lentic odonates have larger and more northern ranges than lotic species. *Journal of Biogeography*, 33: 63-70.

Hothorn, T., Bretz, F. and Westfall, P. 2008. Simultaneous inference in general parametric models. *Biometrical Journal*, 50: 346-363.

Jocque, M., Field, R., Brendonck, L. and De Meester, L. 2010. Climatic control of dispersal-ecological specialization trade-offs: A metacommunity process at the heart of the latitudinal diversity gradient? *Global Ecology and Biogeography*, 19: 244-252.

Julliard, R., Clavel, J., Devictor, V., Jiguet, F. and Couvet, D. 2006. Spatial segregation of specialists and generalists in bird communities. *Ecology Letters,* 9: 1237-1244.

Kalkman, V.J., Clausnitzer, V., Dijkstra, K.-D.B., Orr, A.G., Paulson, D.R. and van Tol, J. 2008. Global diversity of dragonflies (Odonata) in freshwater. *Hydrobiologia,* 595: 351-363.

Kneitel, J.M. 2018. Occupancy and environmental responses of habitat specialists and generalists depend on dispersal traits. *Ecosphere,* 9: e02143.

Larson, D.J. 1997. Habitat and community patterns of tropical Australian Hydradephagan water beetles (Coleoptera: Dytiscidae, Gyrinidae, Noteridae). *Australian Journal of Entomology,* 36: 269-285.

Levins, R. 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *The American Naturalist,* 96: 361-373.

Malmqvist, B. 2000. How does wing length relate to distribution patterns of stoneflies (Plecoptera) and mayflies (Ephemeroptera)? *Biological Conservation,* 93: 271-276.

McArthur, R.H. 1972. *Geographic Ecology*. Harper and Row, New York, USA.

Moss, B. 1998. *Ecology of Fresh Waters, Man and Medium, Past to Future*. Blackwell, Oxford, UK.

Nakano, S. and Murakami, M. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America,* 98: 166-170.

Poisot, T., Kéfi, S., Morand, S., Stanko, M., Marquet, P.A. and Hochberg, M.E. 2015. A continuum of specialists and generalists in empirical communities. *PLoS ONE,* 10: e0114674.

R Development Core Team. 2016. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/.

Rensch, B. 1959. *Evolution Above the Species Level*. Columbia University Press, New York, USA.

Ribera, I. and Vogler, A.P. 2000. Habitat type as a determinant of species range sizes: the example of lotic-lentic differences in aquatic Coleoptera. *Biological Journal of the Linnaean Society*, 71: 33-52.

Ribera, I., Barraclough, T.G. and Vogler, A.P. 2001. The effect of habitat type on speciation rates and range movements in aquatic beetles: inferences from species-level phylogenies. *Molecular Ecology,* 10: 721-735.

Rundle, S.D., Bilton, D.T. and Foggo, A. 2007a. Chapter 10. By wind, wings or water: body size, dispersal and range size in aquatic invertebrates. In: Hildrew, A.G., Raffaelli, D.G. and Edmonds-Brown, R. (eds). *Body size: The Structure and Function of Aquatic Ecosystems*. Cambridge University Press, Cambridge, UK. pp. 186-209.

Rundle, S.D., Bilton, D.T., Abbott, J.C. and Foggo, A. 2007b. Range size in North American *Enallagma* damselflies correlates with wing size. *Freshwater Biology,* 52: 471-477.

Samways, M.J. 2003. Conservation of an endemic odonate fauna in the Seychelles archipelago. *Odonatologica,* 32: 177-182.

Samways, M.J. 2004. Critical species of Odonata in southern Africa. *International Journal of Odonatology,* 7: 255-262.

Samways, M.J. and Simaika, J.P. 2016. *Manual of Freshwater Assessment for South Africa: Dragonfly Biotic Index*. Suricata 2. South African National Biodiversity Institute. Pretoria, South Africa.

Samways, M.J., Osborn, R. and van Heerden I. 1996. Distribution of benthic invertebrates at different depths in a shallow reservoir in the KwaZulu-Natal Midlands. *Koedoe,* 39: 69-76.

Simaika, J.P. and Samways, M.J. 2009a. Reserve selection using Red Listed taxa in three global biodiversity hotspots: Dragonflies in South Africa. *Biological Conservation,* 142: 638-651.

Simaika, J.P. and Samways, M.J. 2009b. An easy-to-use index of ecological integrity for prioritizing freshwater sites and for assessing habitat quality. *Biodiversity and Conservation,* 18: 1171-1185.

Smart, S.M., Thompson, K., Marrs, R.H., Le Duc, M.G., Maskell, L.C. and Firbank, L.G. 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. *Proceedings of the Royal Society B: Biological Sciences,* 273: 2659-2665.

Sol, D., Timmermans, S. and Levebvre, L. 2002. Behavioural flexibility and invasion success in birds. *Animal Behaviour,* 63: 495-502.

Suhling, F. 2001. Intraguild predation, activity patterns, growth and longitudinal distribution in running water odonate larvae. *Archiv für Hydrobiologie,* 2001: 1-15.

Travis, J.M. and Dytham, C. 1999. Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 266: 723-728.

Valladares, G. and Lawton, J.H. 1991. Host-plant selection in the Holly Leaf-miner: Does mother know best? *Journal of Animal Ecology,* 60: 227-240.

van Huyssteen, P., and Samways, M.J. 2009. Overwintering dragonflies in an African savanna (Anisoptera: Gomphidae, Libellulidae). *Odonatologica,* 38: 167-172.

van Schalkwyk, J., Samways, M.J. and Pryke, J.S. 2014. Winter survival by adult dragonflies in the Cape Floristic Region. *International Journal of Odonatology,* 17: 17-30.

Verberk, W.C., Siepel, H. and Esselink, H. 2008. Life-history strategies in freshwater macroinvertebrates. *Freshwater Biology*, 53: 1722-1738.

Vogler, A.P. and Ribera, I. 2003. Evolutionary analysis of species richness patterns in aquatic beetles: why macroecology needs a historical perspective. In: Blackburn, T.M. and Gaston, K.J. (eds). *Macroecology: Causes and Consequences*. Blackwell Science, Oxford, UK. pp 17-30.

Wakeling, J.M. and Ellington, C.P. 1997. Dragonfly flight III. Lift and power requirements. *Journal of Experimental Biology*, 200: 583-600.

Wilson, D.S. and Yoshimura, J. 1994. On the coexistence of specialists and generalists. *The American Naturalist*, 144: 692-707.

Chapter 3 Drivers of regional dragonfly species richness and assemblage-turnover at the southern tip of Africa

*Recently submitted to Biological Conservation

Abstract

Freshwater insect species distributions are poorly understood in southern Africa, yet knowing where species occur is essential for effective conservation planning. Regional climatic variation is subject to strong effects of oceanic current systems, which in turn, determine regional species occupancy. We hypothesize that oceanic currents, along with regional climates and topography, have been, and still are, important drivers of aquatic insect species richness, endemism, and assemblage composition, and expect strong assemblage-turnover boundaries to be concurrent with long-existing topographical features. We used generalized linear modelling, generalized dissimilarity modelling, and dragonflies as model organisms to determine the drivers of species richness metrics and assemblage-turnover rates, and to investigate the extent to which there are assemblage-turnover boundaries across South Africa. We found that regional latitudinal and longitudinal gradients were significant for species richness, levels of local endemism, and assemblage composition. In turn, these were related to seasonal rainfall, seasonal solar radiation, underlying geology, and topography, all of which are significant drivers of overall distribution patterns. We also found significant variation in assemblages between different sub-regions, and turnover boundaries were concurrent with topographical features and/or areas where there are significant spatial changes in sub-regional climate. However, assemblage turnover boundaries were only gradual and not sharp throughout the region, related to overall high dragonfly dispersal ability and gradual climatic changes between sub-regional climates. Modern-day regional climate and topography only partially explained dragonfly distribution, and we conclude that local factors and past geological events both contribute to current dragonfly distribution patterns. We recommend conservation efforts to be focused on areas with high species richness and endemism levels, but importantly also in areas with high assemblage-turnover rates to ensure protection of as many species as possible. We also propose further searches in areas with high endemism and high assemblage-turnover for possible discovery of unknown species, and further searches in under-represented areas to overall improve distribution data for known species.

Keywords: Odonata, aquatic insect conservation, distribution, macro-ecology, turnover boundaries, South Africa

3.1 Introduction

Species geographical distribution is not random, with significant variation in distribution patterns between taxa and geographical areas (Heiser and Schmitt 2010). Consequently, investigating species distribution patterns is not only fundamental to biogeography, but also useful for conservation planning (Basset et al. 2011). Large-scale changes in species richness and diversity across latitude and elevation gradients are well-documented for terrestrial and marine taxa in the northern hemisphere (Heino 2001), with most showing an increase in species richness towards the equator (Ribera et al. 2003). Furthermore, high species diversity is associated with high habitat heterogeneity and low elevations at regional scales (Ricklefs and Lovette 1999). In contrast, biogeographical patterns among freshwater taxa have received much less attention (Willig et al. 2003; Hillebrand 2004), with broad-scale patterns generally weaker than for terrestrial taxa (Pearson and Boyero 2009), seemingly related to poor connectivity between freshwater habitats (Hillebrand 2004).

To investigate overall changes in species richness and diversity in isolation from assemblage-turnover (i.e. the interaction between local and regional assemblages) provides limited information regarding complex local assemblage structuring (Lennon et al. 2001), which is strongly driven by regional species pools (Ricklefs and Schluter 1993). Assemblage-turnover boundaries, or areas of high β-diversity, are significant indicators of where species assemblages change between local sites and/or wider regions (Moir et al. 2009), and provide important information regarding the underlying drivers which structure biological assemblages (Pires et al. 2018). At the regional scale, factors that influence dispersal of organisms (e.g. topography, significant geographical features, and connectedness between populations) can be greater than climatic drivers in determining assemblage structures (Henriques-Silva et al. 2013), especially for taxa with low mobility.

A major challenge is defining whether and where assemblage-turnover boundaries occur, as they often follow climate gradients, and are gradual over wide geographic areas. In the context of South Africa, climatic conditions are highly variable throughout the country, and along the east coast, climate is driven by the warm, southwards-flowing Agulhas oceanic current system (Diester-Haass et al. 2002), while the northeast coastal region is characterized by a strong East African component. With increasing latitude southwards, the gradual change in climatic conditions from tropical-type climate to Mediterranean-type climate drives a gradual decrease in tropical species richness, at least for frogs (Poynton 1961, 1969). An inverse trend is expected for the southern Mediterranean-type species, which decrease in richness with decreasing latitude northwards. In contrast, the climate along the west coast of the region is driven by the northwards-flowing, cold Benguela oceanic current system, resulting in strong aridification effects and a general decrease in species richness with decreasing latitude northwards (Diekmann et al. 2003). These biotic and abiotic gradients are expected to lead to gradual changes in species assemblage composition along the coastal regions in southern Africa.

Climatic conditions are also highly variable across the interior of South Africa, with assemblage-turnover boundaries proposed, at least in the south-eastern region, for flies (Stuckenberg and Kirk-Spriggs 2009), cicadas (Price et al. 2007) and fleas (van der Mescht et al. 2015). This area broadly coincides with the meeting place of five South African biomes (fynbos, succulent Karoo, Nama-Karoo, grassland, and savanna) (Mucina and Rutherford 2006), and coincides with the division between the western and eastern sides of the Cape Fold Mountains. The western side is characterized by rolling hills combined with flat country, in contrast to the highly variable topographical gradients of the eastern side (Willows-Munro and Matthee 2011). Furthermore, the eastern side is affected by rearrangement of atmospheric current systems, creating an individualistic and contrasting abiotic environment (Chase and Meadows 2007). This is likely not the only turnover boundary occurring in interior South Africa, and other regions of interest include the transition between the Cape Fold Mountains and the Karoo, and the transition between Karoo and the central, high-elevation grasslands.

Despite the global abundance and ecological importance of insects, their distribution patterns, and underlying drivers, have received much less attention than those for vertebrates (Diniz-Filho et al. 2010), in part related to lack of information regarding their taxonomy and geographical ranges. However, dragonflies and damselflies (Odonata; hereafter collectively referred to as ‘dragonflies’) are taxonomically well known, especially in South Africa, and their distribution is well established (Samways and Simaika 2016). Most dragonflies as adults are strong dispersers, common occupants of many freshwater habitats (Grönroos et al. 2013), and variably sensitive to environmental conditions (De Marco et al. 2015). Species richness, diversity and assemblage structure are determined by local factors, such as water physiochemical factors, vegetation cover and connectivity to nearby habitats (Harrington et al. 2016), as well as regional factors, such as landscape heterogeneity and climate (Kalkman et al. 2008). These species-level responses to various aspects of environmental heterogeneity make dragonflies excellent model organisms for detecting broad-scale biogeographical patterns.

Using dragonflies as model organisms, our overall aim here is to investigate broad-scale biogeographical patterns across South Africa, with three objectives: 1) determine the climatic and spatial factors driving regional trends in overall dragonfly species richness, local endemism, and assemblage turnover, 2) identify assemblage-turnover boundaries across the coastal and interior regions of the country, and 3) provide recommendations for conservation of local freshwater insects. We hypothesize that climatic factors related to rainfall and temperature, and spatial factors related to topography and connectedness carry equal weight in determining species richness and assemblage patterns. We further anticipate assemblage-turnover boundaries to be easily defined and concurrent with significant topographical features.

3.2 Materials and methods

3.2.1 Biological data

Dragonfly distribution points for South Africa were extracted from the Odonata Database of Africa (Clausnitzer et al. 2009). After data validation, a total of 23 241 records were available. Additional field data were collected from November 2017 to April 2019, and regions where data points were lacking and/or regions of high conservation interest were specifically targeted. These regions included: areas surrounding the Orange River and Vaal River (Northern Cape), the eastern and western slopes of the Cederberg mountain range (Western Cape), the Southern Cape coastal belt, the southern Free State (foothills of the Maloti mountain range), the Kwazulu-Natal Midlands, and the coastal and mountainous interior regions of the Eastern Cape, collectively comprising 1 336 distribution records at 133 localities (Appendix S3.1). Adult dragonflies were recorded by walking along pond and river margins for one hour at each locality, recording all observed species. Field data were collected on cloudless, windless days, between 10h30 and 15h30 when dragonflies were at their activity peak. One voucher specimen of each species is housed in the Stellenbosch University Entomological Museum.

All dragonfly distribution data were combined and transformed to quarter degree spatial resolution (QDSR), assigning dragonfly species presence/absence to each cell and removing all duplicate species records. Dragonfly species richness and national endemic species richness were determined for each cell based on the generated presence/absence dataset. Cells with <2 dragonfly species were excluded to correct for differences in sampling effort between assessors, and to account for regions with no water bodies, so improving overall reliability of distribution records (488 cells in total). We then calculated the proportion of national endemic species, and lentic, lotic and lentic/lotic species richness (based on larval biotopes from Chapter 1) for each cell relative to total species richness for each individual cell. Beta diversity (species assemblage turnover) was calculated between all cell-pair combinations, and represented by the Jaccard dissimilarity measure. We selected this dissimilarity measure, as it does not rely on abundance data to reflect similarity between assemblages, but rather uses presence/absence of species. The Jaccard dissimilarity measure is also effective in detecting underlying ecological patterns (Oksanen et al. 2017).

3.2.2 Environmental data and statistical analyses

To investigate the effects of environmental variables on dragonfly assemblage turnover, 28 interrelated spatial datasets were considered. These datasets included: latitude, longitude, elevation, 30-year monthly average rainfall (twelve spatial datasets), 30-year monthly average solar radiation (twelve spatial datasets), and 30-year average soil drain rate (Appendix S3.2). All spatial datasets were resampled to QDSR to match the generated dragonfly distribution dataset in QGIS (Quantum GIS Development Team 2017), and tested for covariation. Where there was high covariation among the 28 spatial datasets (Pearson correlation coefficient < -0.7 or > 0.7), only one of the spatial datasets in the pair was included for further analysis. After these considerations, eight variables were retained for final analysis: latitude, longitude, elevation, 30-year average rainfall for early summer (December) and mid-autumn (April), 30-year average solar radiation mid-summer (January) and mid-autumn (April), and 30-year average soil drain rate.

We used generalized linear modelling (GLM) and model selection to determine the environmental drivers most descriptive of spatial patterns related to total species richness, endemic species richness, proportion of endemic species, and lentic, lotic and lentic/lotic species richness (in terms of their larval habitat preferences). We then constructed GLMs for each response variable with all possible combinations of environmental variables. These models were overdispersed (Pearson's Test for overdispersion), and we used quasi-likelihood second-order Akaike's information criterion values (qAICc) to rank candidate models, and to extract the best model from each modelling scenario, using the *MuMIn* package for R (Barton 2019; R Development Core Team 2016). As a result, six independent GLMs containing a set of environmental variables with the lowest qAICc values were constructed in R (R Development Core Team 2016) for total species richness, endemic species richness, proportion of endemic species, and lentic, lotic, and lentic/lotic species richness, using the *lme4* package (Bates et al. 2014).

We used generalized dissimilarity modelling (GDM, Ferrier et al. 2007) to determine the importance of environmental variables in driving dragonfly assemblage-turnover rates, to extrapolate species assemblage composition in areas where data were lacking, and to identify assemblage-turnover boundaries across space, using the *gdm* package in R (Manion et al. 2017; R Core Development Team 2016). The set of environmental variables which explained dragonfly assemblage turnover the best was selected by 500 permutations of randomized backwards selection on 50% of the total data, using the *gdm.varImp* function. Only variables with significantly higher importance (highest percentage change in model deviance; $p < 0.05$) were retained, and three I-spline basis functions were used for each environmental variable to investigate their effects on the full dataset. The effect of each variable was evaluated based on ranges of the partial response plots (Overton et al. 2009). Variation partitioning (Borcard et al. 1992) was performed to determine the unique contribution of each environmental variable to total model deviance, and shared contribution between all combination of important variables to total model deviance, using the *vegan* package in R (Oksanen et al. 2017). Multidimensional scaling and principal component analysis (PCA) were used to visualize biological patterns between all cell pairs across space. Model outputs were transformed from environmental distances to biological distances, using the *transform* function. The first three PCA components were scaled to 8-bit format (1- 256 range) and assigned to a red, blue and green (RGB) colour palette, used to identify regions characterized by relatively similar environmental conditions and similar expected dragonfly assemblages, based on output values of each model scenario (Ferrier et al. 2007).

3.3 Results

3.3.1 Overall importance of environmental variables for species richness metrics

Overall, seven variables were selected as important in driving dragonfly species richness metrics across South Africa. These were latitude, longitude, elevation (m a.s.l.), average early summer and mid-autumn rainfall (mm/month), and average mid-summer and mid-autumn solar radiation (MJ/m^2/day). Spatial gradients of the significant variables are provided in Appendix S3.3.

Species richness overall increased from south to north, and was highest in the north-eastern region (Table 3.1; Figure 3.1a). Species richness decreased with increasing elevation, and high overall species richness was associated with areas with relatively higher mid-autumn rainfall, and relatively lower mid-summer solar radiation. Endemic species richness and proportion of endemic species richness were concentrated in the south-western region, and decreased from south to north overall (Figure 3.1b and c). Endemic species richness decreased from east to west, and was lowest in areas with relatively lower early summer rainfall and lower mid-summer solar radiation (Figure 3.1b). The proportion of endemic species was highest at high elevations, and was associated with areas with relatively high mid-summer solar radiation (Figure 3.1c).

Overall lentic, lotic, and lentic/lotic dragonfly species richness increased from south to north, and decreased with increasing elevation and increasing mid-summer solar radiation (Table 3.1; Figure 3.1d-f). Overall lentic species richness increased from east to west, and was highest in areas with relatively higher early summer rainfall and mid-autumn solar radiation (Figure 3.1d). Overall lotic species richness was highest in areas with relatively high early summer rainfall (Figure 3.1e), and overall lentic/lotic species richness was high in areas with relatively high mid-autumn rainfall (Figure 3.1f).

Table 3.1 Significant t-values of variables driving species richness, endemic species richness, proportion of endemic species, and lentic, lotic and lentic/lotic species richness between all populated grid cells.

Variables	**Species richness**	**Endemic species richness**	**Proportion endemic**	**Lentic species richness**	**Lotic species richness**	**Lentic/lotic species richness**
Latitude	(+) 5.01 ***	(-) -3.91 ***	(-) -6.56 ***	(+) 6.66 ***	(+) 4.56 ***	(+) 6.40 ***
Longitude		(-) -2.71 **		(+) 5.10 ***		
Elevation	(-) -3.25 **		(+) 3.44 ***	(-) -3.14 **	(-) -4.70 ***	(-) -1.99 *
Early summer rainfall		(-) 4.94 ***		(+) -4.83 ***	(+) 3.12 **	
Mid-autumn rainfall	(+) 4.28 ***					(+) 3.77 ***
Mid-summer radiation	(-) -2.35 *	(-) -4.01 ***	(+) -2.52 *	(-) 2.29 *	(-) -2.62 **	(-) -2.54 *
Mid-autumn radiation				(+) 6.58 ***		

(-) and (+) indicate trendline directions.
Significance levels: * : p < 0.05; ** : p < 0.01; *** : p < 0.001.

3.3.2 Overall importance of environmental variables for assemblage-turnover

Backwards selection identified four environmental variables as important for driving dragonfly assemblage-turnover at the national scale. These were mid-autumn solar radiation (MJ/m^2/day), average soil drain rate (mm/day), elevation (m a.s.l.) and geographical distance between cells (km) (Appendix S3.3). Total percentage explained deviance of the model was 31.7%, and individual fractions of explained deviance for each environmental variable was between 0.5% and 10.1%. Shared fractions of explained deviance between environmental variables was between 0% and 12.6% (Figure 3.2). Mid-autumn solar radiation explained 0.6% of total deviance in the generalized dissimilarity model containing the selected variables. Soil drain rate explained 1.4% of total deviance, elevation explained 1.7% of total deviance, and geographical distance between cells explained 10.1% of total model deviance. The interaction between mid-autumn solar radiation and geographical distance between cells explained 5.3% of total model deviance, while the interaction between mid-autumn solar radiation, elevation and soil drain rate explained 12.6% of total model deviance.

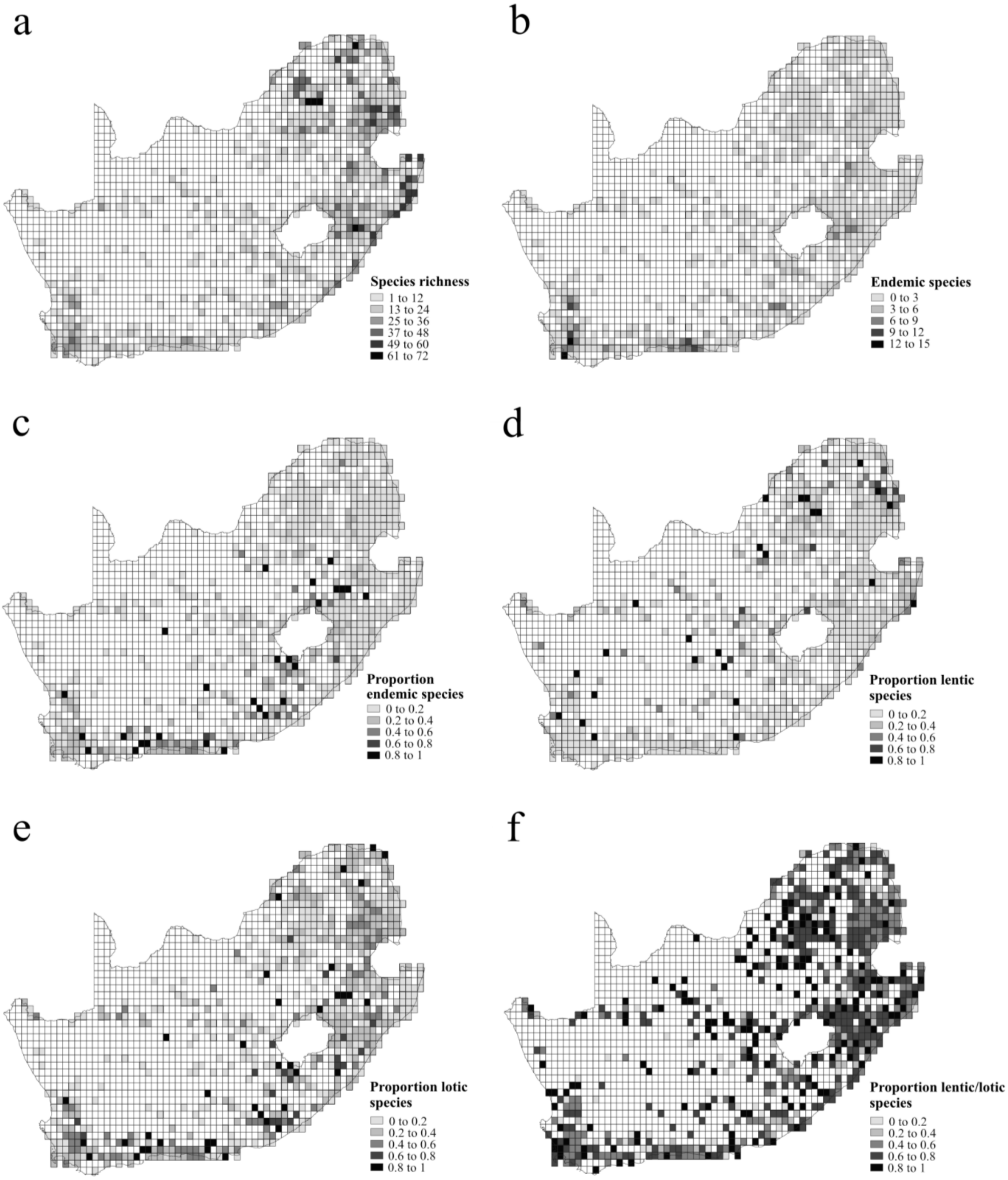


Figure 3.1 Spatial patterns of dragonfly species richness metrics across South Africa. Species richness (a), endemic species richness (b), proportion of endemic species (c), lentic species richness (d), lotic species richness (e) lentic/lotic species richness (f) are indicated. Spatial patterns c-f are shown as proportions (i.e. categorical richness relative to cell total species richness).

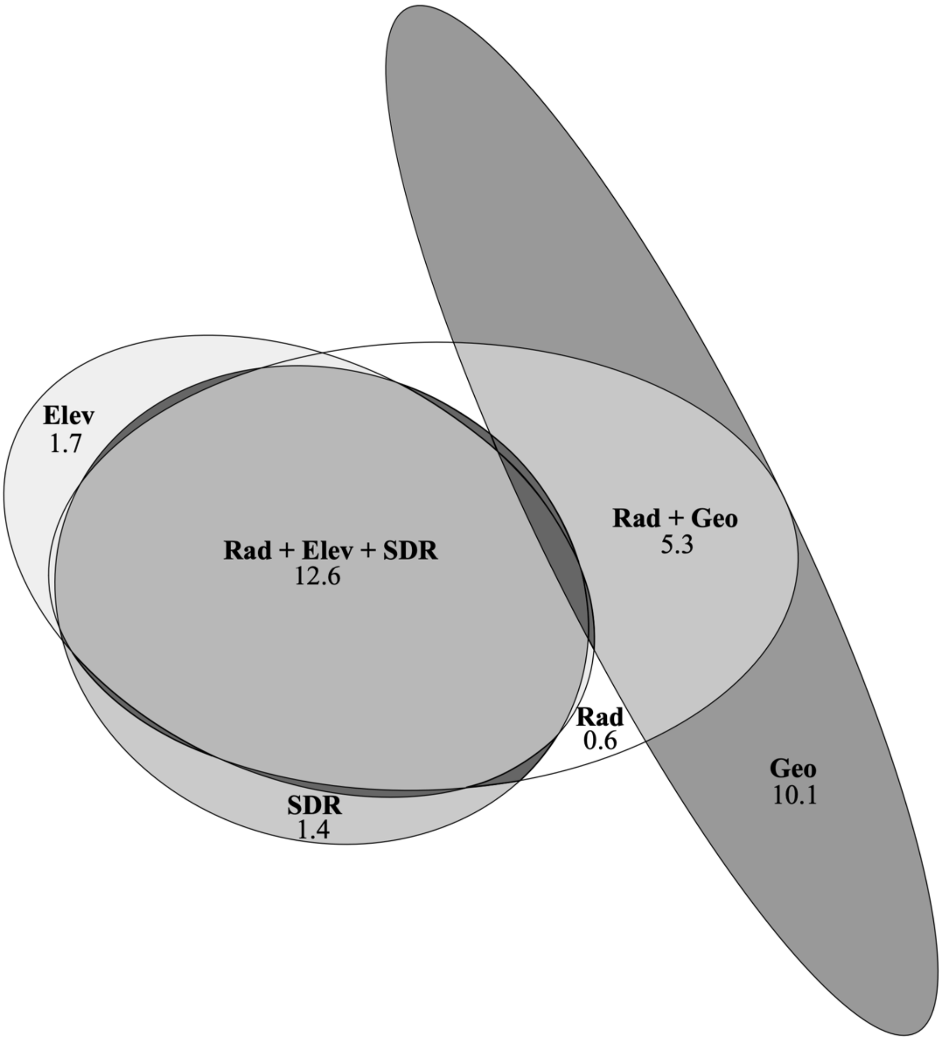


Figure 3.2 Variation partitioning of dragonfly species turnover among selected environmental variables. Values represent fractions of explained deviance as percentages. Only unique fractions and shared fractions > 5% are shown. Elev: elevation, Geo: geographical distance between cells, Rad: mid-autumn solar radiation, SDR: soil drain rate.

Dragonfly assemblage-turnover rate increased rapidly with increasing soil drain rate, until it reached 6 mm/day, after which assemblage-turnover rate slowed, and remained constant from 7 mm/day to 12 mm/day (Figure 3.3a). The effects of soil drain rate on assemblage-turnover was relatively even throughout the country, but lower in the north-western coastal region, and north-eastern mountainous region (Figure 3.3b). Assemblage-turnover rate remained constant with increasing mid-autumn solar radiation, until 23.2 MJ/m2/day was reached, after which assemblage-turnover rate increased rapidly until the maximum solar radiation value of 29.2 MJ/m2/day was reached (Figure 3.3c). The effect of solar radiation on dragonfly assemblage-turnover was highest in the arid, north-western regions (Figure 3.3d).

Assemblage-turnover rate increased steadily between 0 m a.s.l. and 250 m a.s.l., and there was a rapid increase in assemblage-turnover rate between 250 m a.s.l. and 3 000 m a.s.l (Figure 3.3e). The effects of elevation were highest in areas of sharp topographical gradients, especially the areas surrounding the Drakensberg Mountains and the Cape Fold Mountains. Elevation also had an effect on assemblage-turnover rate on the Highveld (high-elevation grassland region) and parts of the Northern Cape. (Figure 3.3f). Dragonfly assemblage-turnover rate increased rapidly throughout for geographical distance but slowed above 500 km and slowed further above 1 500 km (Figure 3.3g).

3.3.3 Assemblage-turnover boundaries across the region

Generalized dissimilarity models performed well in extrapolating assemblages across the country (Figure 3.3h), and landscape visualizations produced for observed and predicted assemblage turnover showed similar spatial patterns (Figure 3.4a and b). Both approaches showed an overall difference in species assemblage composition across the latitude gradient. Species assemblage composition was different between the north-eastern and south-eastern regions, and between the north-western and south-western regions. There was also an overall difference in species assemblage composition across the longitude gradient, where species assemblage composition was different between the north-western and north-eastern regions, as well as between the south-western and south-eastern regions.

Along the south-eastern coast, clear assemblage-turnover boundaries areas were difficult to discern, and assemblage-turnover was gradual along the south-eastern coast, following the southern slopes of the Great Escarpment (Figure 3.4a and b). From the south-eastern coast northwards, assemblage composition changed following the coastal-inland elevation gradient. Coastal assemblages were distinct from mountain assemblages, and there was an overall change in assemblage composition over the southern foothills of the Drakensberg Mountains, and over the Amatola and Cape Fold Mountains. Furthermore, dragonfly assemblages which occupied southern mountain slopes were different from dragonfly assemblages occupying northern mountain slopes along the east coast.

Along the west coast, a wide assemblage-turnover boundary coincided with the northern foothills of the Cederberg Mountains, and a second, wide turnover boundary was apparent along the lower reaches of the Orange River (Figure 3.4b). Species assemblage composition changed from west to east following the coastal-inland elevation gradient, and a change in species assemblage composition coincided with the wide areas between the Cederberg Mountains and the Kamiesberg Mountains. A transition in assemblage composition was also evident between the western and eastern slopes of the Cederberg Mountains, and between the eastern foothills of the Cederberg Mountains and the Karoo. Changes in species assemblage composition were highly gradual and variable across central South Africa. A biologically similar dragonfly assemblage occupied the southern rim of the Kalahari, but gradually changed in structure across the regions surrounding the middle reaches of the Orange River and the low reaches of the Vaal River. Species composition also changed gradually along the north-western slopes of the Waterberg Mountains, and the northern part of the Drakensberg Mountain escarpment towards the northwest.

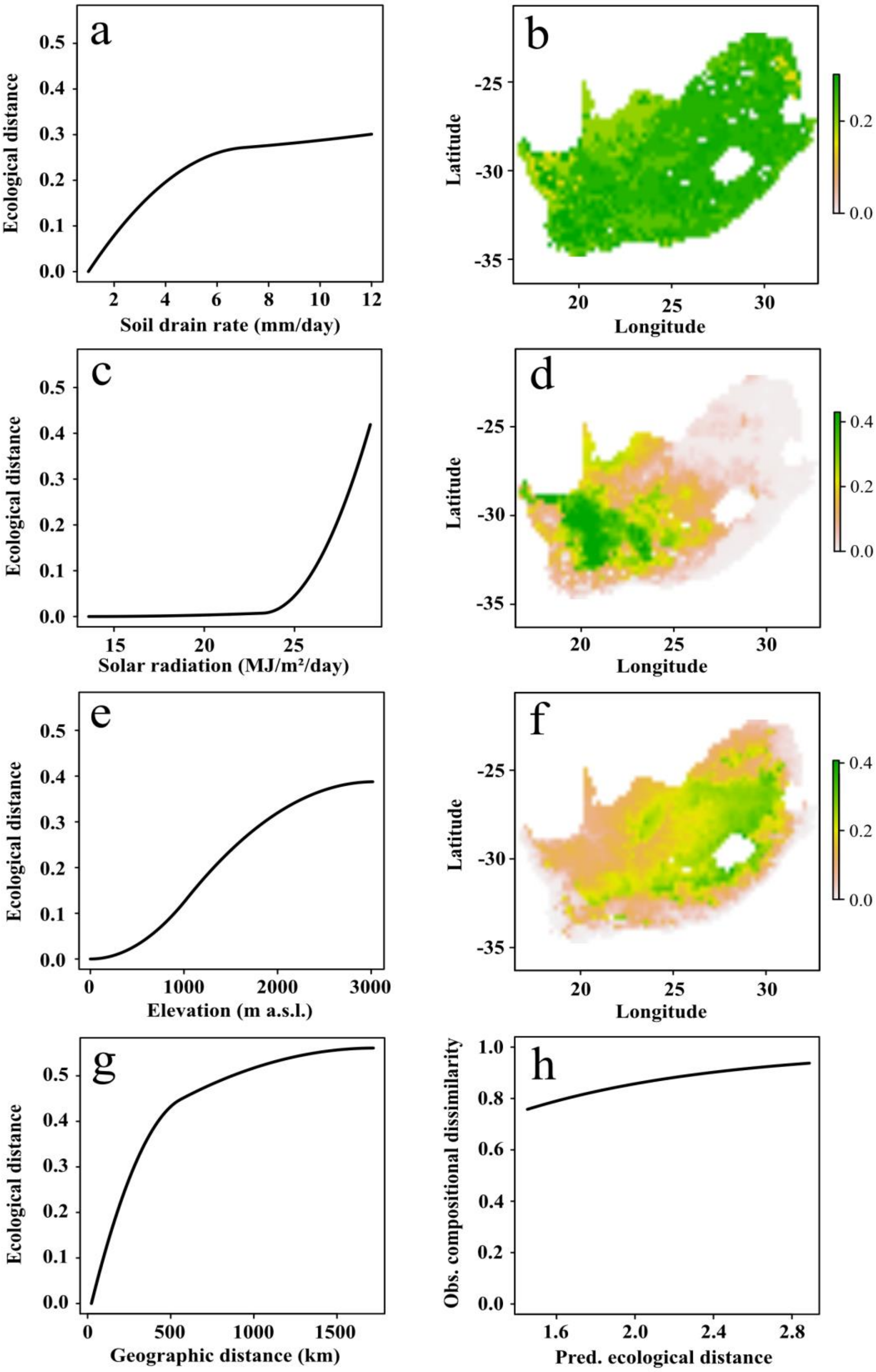


Figure 3.3 Generalized dissimilarity model transformations and fitting of selected environmental variables at the national scale. Average soil drain rate (a-b), average mid-autumn solar radiation (c-d), elevation (e-f), geographical distance between grid cells (g), and observed compositional dissimilarity against predicted ecological distance (h) are indicated.

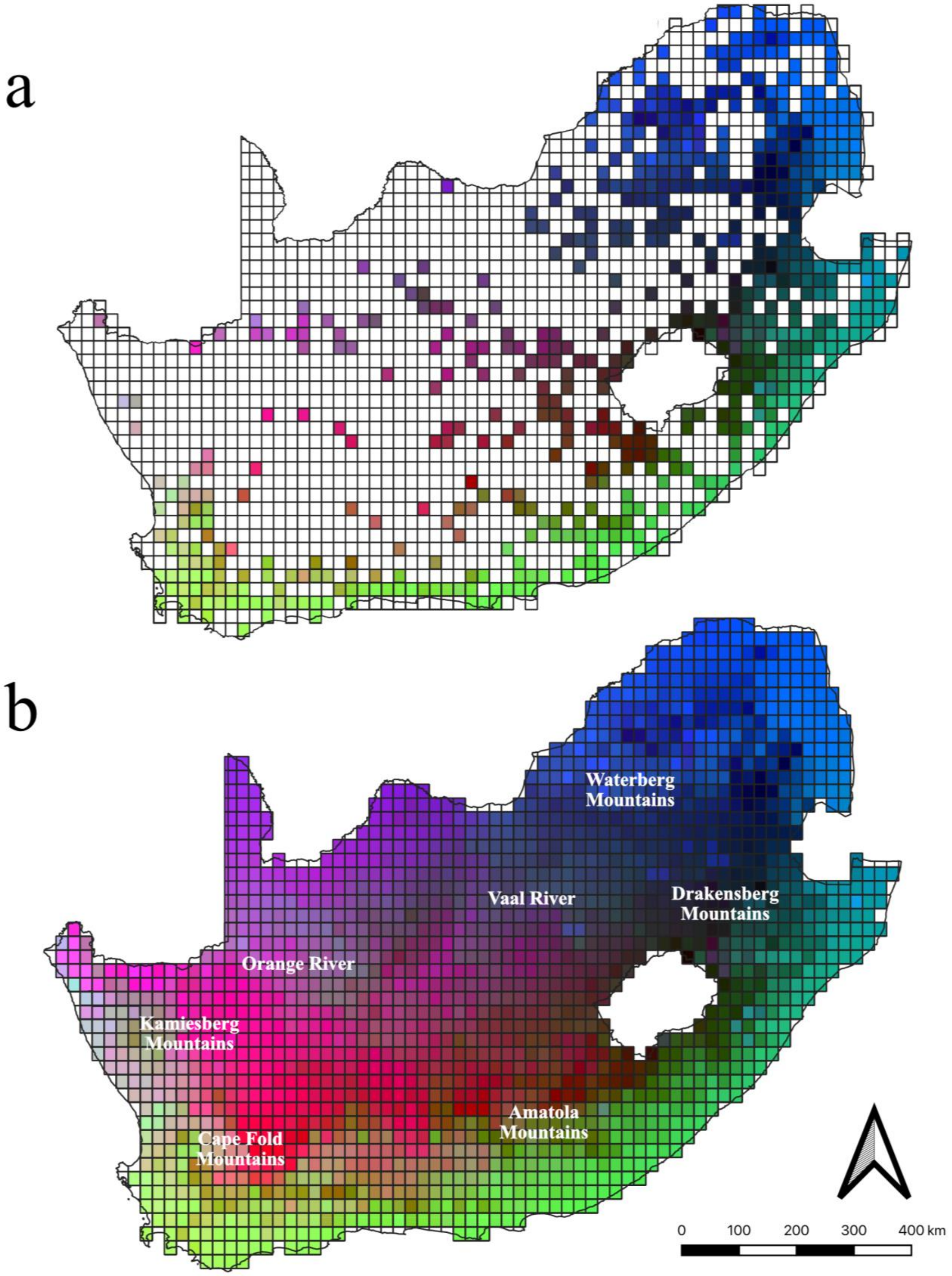


Figure 3.4 Observed (a) and predicted (b) spatial patterns of dragonfly assemblage-turnover across South Africa. Quarter degree cells with similar colours are predicted to be similar in dragonfly assemblage. Topographical features mentioned in text are indicated in white.

3.4 Discussion

Dragonfly species distribution patterns were complex across the southern tip of Africa, yet our results indicate strong latitudinal and longitudinal gradients in species richness, endemism and assemblage composition across the region. Furthermore, other regional factors related to climate (i.e. average seasonal rainfall and average seasonal solar radiation), underlying geology (i.e. soil type and drain rate), and topography (i.e. elevation gradients and geographical distance between cells) significantly determined overall dragonfly species distribution patterns. Dragonfly assemblage-turnover boundaries were gradual rather than sharp throughout the country, and most of these boundaries broadly coincided with prominent topographical features and/or areas where significant climatic factors changed from one condition to the next.

3.4.1 Significance of environmental variables for species richness metrics and assemblage turnover

Overall species richness decreased with increasing latitude, complementing findings for beetles, mayflies, stoneflies and dragonflies across Europe (Ribera et al. 2003), dragonflies across South America (Boyero 2002) and amphibians across south-eastern Africa (Poynton 1969). We also found that overall endemic species richness showed an inverse latitudinal trend, increasing from north to south, as well as from east to west across a longitudinal gradient. Patterns across longitudinal gradients have received much less research attention, yet east-to-west gradients in species richness have been found for beetles, mayflies, stoneflies and caddisflies across north Africa (Beauchard et al. 2003). These observed patterns suggest that species richness and assemblage patterns are likely driven by a combination of climatic, topographic and geological factors.

Average rainfall and seasonality have a strong influence on aquatic insect distribution through changes in hydrological regimes (Bêche and Statzner 2009), and dragonflies, being tropical of origin, favour warmer and wetter climatic conditions (Corbet 1999; Samways and Simaika 2016). Although we did not find a significant relationship between rainfall and dragonfly assemblage composition, high overall species richness was associated with warm sub-regions receiving much rain from late summer to mid-autumn, similar to previous findings for South Africa (Finch et al. 2006), and North America (Hassall 2012). These subtropical climatic conditions, together with diverse aquatic habitat types (e.g. rivers, wetlands, swamp forests), present a range of favourable conditions for dragonflies, many of which occur throughout the rich southern African savanna (Hart et al. 2015). Conversely, endemism was concentrated in the south-western sub-region with its arid summers, indicating that these species are biologically well-adapted to local conditions related to rainfall seasonality and seasonal habitat availability (Dijkstra et al. 2007).

Unsurprisingly, overall dragonfly species richness and endemism were lowest in the hot but dry areas, along with a clear distinction in assemblage composition between low and high rainfall sub-regions. Aquatic habitats in the arid areas are mostly seasonal, with the exception of the Orange and Vaal Rivers, being the only large perennial river systems. Most dragonfly species are well-adapted to harsh abiotic conditions through increased developmental rates to outlive seasonal habitats (McPeek and Peckarsky 1998), and/or have highly migratory behaviour to seek out favourable habitats, ensuring completion of their life cycles (Suhling et al. 2005). The effect of habitat permanency on species assemblage composition was further emphasized through the significance of underlying geology and soil drain rate. The north-western interior of South Africa is dominated by sandy desert soil with low water retention qualities, while soils in the coastal regions broadly consist of a mix between sand, loam and clay, with relatively higher water retention qualities (MacVicar 1977). In combination with average rainfall and temperature, soil type and the rate at which surface water is lost, influence habitat quality components and water permanency, shaping regional dragonfly assemblages.

It is well known that environmental conditions change with elevation across local and regional scales (Harrington et al. 2016). Our findings that high species richness was associated with low elevation overall, and that the proportion of endemic species increased overall with elevation, were consistent with other findings on local aquatic insects (Samways and Niba 2010) and aquatic insects in other regions (Finn et al. 2013; Harrington et al. 2016). Although hydrological conditions are variable at low elevations in general, primary production is often high, with lowland areas supporting a diverse range of aquatic habitats, so increasing overall species richness (Samways and Niba 2010; Hart et al. 2015). However, many endemic dragonfly species in South Africa are restricted to high elevation streams where hydrological conditions are more predictable, and many likely use habitats at high elevation as refuges against harsh environmental conditions (Dijkstra et al. 2007). Our results showed that assemblage-turnover rate increased with elevation, suggesting that heterogeneity among high elevation habitats provides a range of microhabitats and that several species are restricted to certain elevation ranges, which in turn, leads to high variation between aquatic communities across elevation gradients (Samways 1989a; Finn et al. 2013). Low assemblage-turnover rates at lower elevation may be a result of the presence of widespread species, capable of colonizing a wide variety of aquatic habitats.

We found that geographical distance was an important driver of dragonfly assemblage-turnover, and the importance of geographical distance can have three possible explanations (Fitzpatrick et al. 2017). Firstly, niche-based processes may be at play, where environmental dissimilarity increases as habitats become increasingly separated by geographical distance (Leibold et al. 2004). According to this explanation, species vary in their capability to perform well in relation to different environmental conditions between geographical areas (i.e. species sorting). Secondly, topographical processes may also be involved, which limit the ability of aquatic insects to reach suitable habitats (Garcillán and Ezcurra 2003). In other words, assemblage-turnover rates increase rapidly across landscapes characterised by significant dispersal barriers (e.g. mountains, deserts and oceans), as opposed to topographically similar landscapes. Thirdly, assemblage dissimilarity increases with distance, even across topographically similar landscapes, as a result of limited dispersal (Hubbell 2001). For South African dragonflies, the first two explanations seem most likely, with highly variable topography driving local ecological conditions, which greatly influences species occupancy (Samways and Simaika 2016), and although most dragonflies are highly mobile as adults, sharp topographic changes likely restrict dispersal, especially among Zygoptera (Heiser and Schmitt 2010).

Our results for assemblage turnover across the region left ~68% of deviance unexplained, thus we could not disregard the potential effect that historical factors may have had in honing current dragonfly assemblages (Huntley et al. 2016). This is emphasized by isolated mountain localities for some species such as *Chlorolestes fasciatus* in Mountain Zebra National Park, completely surrounded by the extensively arid Karoo (Samways 2008). Modelling dragonfly distribution relative to historical climate was beyond the scope of this study, but we found that endemic dragonfly assemblages were predominantly associated with the south-western area, especially the ancient Cape Fold Mountains, as was found for birds in the same area (Huntley et al. 2016). This could be related to the sub-region experiencing less climatic variability in the past, and its long history of being free of glaciation (Meadows and Baxter 1999). Conversely, tropical species associated with the north-eastern region of the country, and dryland species assemblages in the north-western region of the country likely persist by making regional movements in response to seasonal climatic variability, a fairly common phenomenon in the area (Ott and Samways 2010). Nevertheless, deeper investigation regarding the relationship between historical climate and its contribution to speciation would add to our current understanding of insect distribution patterns in general. Other factors not investigated here, related to habitat loss, habitat transformation, urbanisation, and complex predator/prey interactions likely also plays a key role in structuring dragonfly assemblages.

3.4.2 Dragonfly assemblage structuring across the southern tip of Africa

Dragonfly assemblage-turnover boundaries were gradual across the region, presumably related to high dispersal ability of dragonflies overall (Grönroos et al. 2013), and gradual spatial changes in climate. The gradual change in dragonfly assemblage composition along the east coast of South Africa likely results from the gradual change in climate, from subtropical in the northeast to Mediterranean in the southwest (Poynton 1961). Similar to the findings for frogs (Poynton 1969), the north-eastern coastal region of the country is rich in tropical dragonflies (e.g. *Zyxomma atlanticum, Parazyxomma flavicans, Tholymis tillarga*), but as climatic conditions change from sub-tropical to Mediterranean, many tropical lentic dragonflies (e.g. *Acisoma variegatum, Diplacodes luminans* and *Tetrathemis polleni*) drop out towards the south. In turn, several lotic Mediterranean-type climate dragonflies (e.g. *Ecchlorolestes peringueyi, Syncordulia legator* and *S. serendipator*) occupied only the south-western Cape, and some (e.g. *Chlorolestes umbratus, Pseudagrion furcigerum* and *E. nylephtha*) drop out from the south-western Cape along the south coast towards the east. In turn, many species (e.g. *Agriocnemis falcifera, C. tessellatus* and *P. kersteni*) have ranges across the entire east coastal band, evening out total species richness along the east coast, though there was an overall change from predominantly lentic/lentic species in the northeast to lotic species in the southwest.

From our results, the coastal-inland changes in dragonfly assemblage composition were mainly driven by the elevation gradient, and there was a gradual change in dragonfly assemblage composition from predominantly lowland lentic species to high elevation lotic species. Several lowland species (e.g. *Chalcostephia flavifrons, Hemistigma albipunctum* and *A. gratiosa*) drop out with increasing elevation, and are replaced by high elevation species (e.g. *Crenigomphus hartmanni, Notogomphus praetorius* and *C. draconicus*) in the Drakensberg Mountains. Lowland species are also replaced by moderate to high elevation species (e.g. *C. apricans, Metacnemis valida*) in the Amatola Mountains. Elevation gradient played an equally important role in structuring regional dragonfly assemblages in the Limpopo Province, where lowveld species gradually drop out with increasing elevation over the northern part of the Drakensberg escarpment (e.g. *Onychogomphus supinus, Paragomphus cognatus* and *P. sjoestedti*), and the Waterberg Mountains (e.g. *Palpopleura deceptor, Tholymis tillarga* and *O. guineense*).

Across the western region, there was a significant decrease in overall species richness together with a gradual change in dragonfly assemblage composition towards the north, and most lotic species in the Western Cape (e.g. *Ceratogomphus pictus*, *Zosteraeschna minuscula* and *P. cognatus*) were absent beyond the north-eastern foothills of the Cederberg Mountains. This is not surprising, as there is a strong aridification gradient northwards across the western region (de Jager and Ellis 2017), and aquatic habitats become increasingly seasonal and/or absent throughout. Consequently, the arid coastal region was mostly occupied by widespread and opportunistic lentic/lotic species (e.g. *Crocothemis erythraea*, *Sympetrum fonscolombii* and *P. massaicum*), which readily colonise seasonal rivers and pans during wet years. Dryland lotic species (e.g. *Mesocnemis singularis, Phyllomacromia picta*, *Platycypha caligata* and *P. vaalense*) only started appearing along the Orange River on the Namibian border, which consistently holds water throughout the year. The limited number of records across the interior of South Africa challenged our ability to discern assemblage turnover boundaries in this area, yet we expect the few scattered seasonal habitats across the region to be occupied by widespread and opportunistic lentic species (e.g. *Trithemis arteriosa*, *T. kirbyi*, *Orthetrum julia*) during wet years.

3.4.3 Implications for conservation

Identifying the centres of high species richness, endemism and assemblage-turnover, along with their underlying drivers, is an important step towards effective conservation action (Simaika and Samways 2009). Dragonflies are a valuable umbrella taxon for other aquatic insects (Bried et al. 2007; Smith et al. 2007), including those in the south-western Cape and the north-eastern area of South Africa (Samways et al. 2011; Kietzka et al. 2019), suggesting that areas defined here as either high in species richness, high in endemism or having high assemblage-turnover rates might well represent other aquatic insects (Wishart and Day 2002). These areas have high conservation value, and selecting protected areas based on dragonflies, especially Red-Listed species, can be highly representative of other freshwater taxa, as has been suggested previously for the biodiversity hotspots in South Africa (Simaika and Samways 2009). The south-western Cape is particularly significant, as many of the known dragonfly species, as well as several other taxa, have narrow geographical ranges.

Other dragonfly species might also await discovery in areas of high endemism and assemblage-turnover, as has been shown recently by the discovery of new dragonfly species (Dijkstra et al. 2007), and the re-discovery of dragonflies that were thought to be extinct from the south-western Cape (Samways and Tarboton 2006), underscoring merit in further focused field investigations. Large areas across South Africa are unexplored, mainly due to being arid, which attracts little attention from a freshwater research perspective. This does not imply that these areas are unimportant, since freshwater species may be localised to high elevation localities where water supply is more reliable. Artificial waterbodies in arid areas may also serve as stepping-stone habitats allowing some species to extend their range sizes (Samways 1989b). There is thus merit for further field investigations in under-represented areas, so as to improve overall reliability of distribution data and inform conservation planning throughout the country.

3.5 Conclusion

Overall dragonfly species richness and assemblage structure varied substantially across South Africa, and our results support previous findings on the relationship between latitude and longitude gradients and species richness for other regions. However, this was not the case for endemic species richness, which showed a converse tendency. These endemics are much richer in the south, due mainly to ancient mountains retaining sufficient ground water to continually feed small streams even during periods of drought. Furthermore, we found that overall dragonfly species richness and assemblage composition were driven by a combination of climatic factors related to rainfall and temperature gradients, as well as topographical factors related to elevation. The significance of these factors was further emphasized through their associations with aquatic habitat quality and permanency. There also appears much variation among current dragonfly assemblages, having been driven by local and/or historical factors, which warrants further detailed investigation. Although there were clear differences in assemblages over wide areas, we demonstrate that assemblage-turnover boundaries were mostly gradual throughout South Africa, likely related to the high mobility of dragonflies, and gradual changes in climatic conditions from one area to the next, and dynamics over time. We recommend that conservation efforts should be focused on areas characterised by high species richness and endemism, as well as those characterised by high dragonfly assemblage-turnover. Further searches across the country may also lead to new species being discovered, and allow improvement of current distribution data for known species.

3.6 References

Barton, K. 2019. MuMIn: Multi-model inference. R package version 1.42.1. Retrieved from https://CRAN.R-project.org/package=MuMIn

Basset, Y., Eastwood, R.G., Sam, L., Lohman, D.J., Novotny, V., Treuer, T., … Sakchoowong, W. 2011. Comparison of rainforest butterfly assemblages across three biogeographical regions using standardized protocols. *The Journal of Research on the Lepidoptera*, 44: 17-28.

Bates, D., Maechler, M., Bolker, B. and Walker, S. (2014). lme4: Linear mixed-effects models using S4 classes. R package version 1.1-7. Retrieved from https://CRAN.R-project.org/package=lme4.

Beauchard, O., Gagneur, J. and Brosse, S. 2003. Macroinvertebrate richness patterns in North African streams. *Journal of Biogeography*, 30: 1821-1833.

Bêche, L.A. and Statzner, B. 2009. Richness gradients of stream invertebrates across the USA: taxonomy- and trait-based approaches. *Biodiversity and Conservation*, 18: 3909-3930.

Borcard, D., Legendre, P. and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology*, 73: 1045-1055.

Boyero, L. 2002. Insect biodiversity in freshwater ecosystems: is there any latitudinal gradient? *Marine and Freshwater Research*, 53: 753-755.

Bried, J.T., Herman, B.D., and Ervin, G.N. 2007. Umbrella potential of plants and dragonflies for wetland conservation: A quantitative case study using the umbrella index. *Journal of Applied Ecology*, 44: 833-842.

Chase, B.M. and Meadows, M.E. 2007. Late Quaternary dynamics of southern Africa’s winter-rainfall zone. *Earth-Science Reviews*, 84: 103-138.

Clausnitzer, V., Dijkstra, K.-D.B., Koch, R., Boudot, J.-P., Darwall, W.R.T., Kipping, J., … and Suhling, F. 2012. Focus on African freshwaters: hotspots of dragonfly diversity and conservation concern. *Frontiers in Ecology and the Environment*, 10: 129-134.

Corbet, P.S. 1999. *Dragonflies: Behaviour and ecology of Odonata*. Harley Books, Colchester, UK.

de Jager, M. and Ellis, A.G. 2017. Evolutionary history of a keystone species pollinator parallels the biome occupancy of angiosperms in the Greater Cape Floristic Region. *Molecular Phylogenetics and Evolution*, 107: 530-537.

De Marco, P., Batista, J.D. and Cabette, H.S.R. 2015. Community assembly of adult odonates in tropical streams: an ecophysiological hypothesis. *PLoS ONE*, 10: e0123023.

Diekmann, B., Falker, M. and Kuhn, G. 2003. Environmental history of the south-eastern South Atlantic since the Middle Mioscene: evidence from the sedimentological records of ODP sites 1088 and 1092. *Sedimentology*, 50: 511-529.

Diester-Haass, L., Meyers, P.A. and Vidal, L. 2002. The late Miocene onset of high productivity in the Benguela current upwelling system as part of a global pattern. *Marine Geology*, 180: 87-103.

Dijkstra, K.-D.B., Samways, M.J. and Simaika, J.P. 2007. Two new relict *Syncordulia* species found during museum and field studies of threatened dragonflies in the Cape Floristic Region (Odonata: Corduliidae). *Zootaxa*, 1457: 19-34.

Diniz-Filho, J.A.F., De Marco, P. and Hawkins, B.A. 2010. Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity*, 3: 172-179.

Ferrier, S., Manion, G., Elith, J. and Richardson, K. 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, 13: 252-264.

Finch, J.M., Samways, M.J., Hill, T.R., Piper, S.E. and Taylor, S. 2006. Application of predictive distribution modelling to invertebrates: Odonata in South Africa. *Biodiversity and Conservation*, 15: 4239-4251.

Finn, D.S., Khamis, K. and Milner, A.M. 2013. Loss of small glaciers will diminish beta diversity in Pyrenean streams at two levels of biological organization. *Global Ecology and Biogeography*, 22: 40-51.

Fitzpatrick, M.C., Sanders, N.J., Normand, S., Svenning, J.-C., Ferrier, S., Gove, A.D. and Dunn, R.R. 2013. Environmental and historical imprints on beta diversity: insights from variation in rates of species turnover along gradients. *Proceeding of the Royal Society B*, 280: 20131201.

Garcillán, P.P. and Ezcurra, E. 2003. Biogeographic regions and β-diversity of woody dryland legumes in the Baja California peninsula. *Journal of Vegetation Science*, 14: 859-868.

Grönroos, M., Heino, J., Siqueira, T., Landeiro, V.L., Kotaken, J., and Bini, L.M. 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type and regional environmental context. *Ecology and Evolution*, 3: 4473-4487.

Harrington, R.A., Poff, N.L. and Kondratieff, B.C. 2016. Aquatic insect β-diversity is not dependent on elevation in Southern Rocky Mountain streams. *Freshwater Biology*, 61: 195-205.

Hart, L.A., Bowker, M.B., Tarboton, W. and Downs, C.T. 2014. Species Composition, Distribution and Habitat Types of Odonata in the iSimangaliso Wetland Park, KwaZulu-Natal, South Africa and the Associated Conservation Implications. *PLoS ONE*, 9: e92588.

Hassall, C. 2012. Predicting the distributions of under-recorded Odonata using species distribution models. *Insect Conservation and Diversity*, 5: 192-201.

Heino, J. 2001. Regional gradient analysis of freshwater biota: do similar biogeographic patterns exist among multiple taxonomic groups? *Journal of Biogeography*, 28: 69-76.

Heiser, M. and Schmitt, T. 2010. Do different dispersal capacities influence the biogeography of western Palearctic dragonflies (Odonata)? *Biological Journal of the Linnean Society*, 99: 177-195.

Henriques-Silva, R., Lindo, Z. and Peres-Neto, P.R. 2013. A community of metacommunities exploring patterns in spatial distributions across large geographic areas. *Ecology*, 94: 627-639.

Hillebrand, H. 2004. Strength, slope and variability of marine latitudinal gradients. *Marine Ecology Progress Series*, 273: 251-267.

Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.

Huntley, B., Collingham, Y.C., Singarayer, J.S., Valdes, P.J., Barnard, P., Midgley, G.F., … Ohlemüller, R. 2016. Explaining patterns of avian diversity and endemicity: climate and biomes of southern Africa over the last 140,000 years. *Journal of Biogeography*, 43: 874-886.

Kalkman, V.J., Clausnitzer, V., Dijkstra, K.-D.B., Orr, A.O., Paulson, D.R. and van Tol, J. 2008. Global diversity of dragonflies (Odonata) in freshwater. *Hydrobiologia*, 595: 351-363.

Kietzka, G.J., Pryke, J.S., Gaigher, R. and Samways, M.J. 2019. Applying the umbrella index across aquatic taxon sets for freshwater assessment. *Ecological Indicators*, 107 #105655. DOI: 10.1016/j.ecolind.2019.105655.

Leibold, M.A., Holyoak, M., Mougeut, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., … Loreau, M. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7: 601-613.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. and Gaston K.J. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, 70: 966-979.

MacVicar, C.N. 1977. *Soil classification. A binomial system for South Africa*. Department of Agricultural Technical Services.

Manion, G., Lisk, M., Ferrier, S., Nieto-Lugilde, D., Mokany, K. and Fitzpatrick, M.C. 2017. gdm: Generalized Dissimilarity Modelling. R package version 1.3.4. Retrieved from https://CRAN.R-project.org/package=gdm.

McPeek, M.A. and Peckarsky, B. 1998. Life histories and the strengths of species interactions: combining mortality, growth and fecundity effects. Ecology, 79: 867-879.

Meadows, M.E. and Baxter, A.J. 1999. Quaternary palaeoenvironments of the southwestern Cape, South Africa: a regional synthesis. *Quaternary International*, 57: 193-206.

Moir, M., Brennan, K. and Harvey, M. 2009. Diversity, endemism and species turnover of millipedes within the south-western Australian global biodiversity hotspot. *Journal of Biogeography*, 36: 1958-1971.

Mucina, L. and Rutherford, M.C. 2006. *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. South African National Biodiversity Institute, Pretoria.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'hara, R.B., Simpson, G.L., . . . Wagner, H. 2017. vegan: Community Ecology Package. R package version 2.4-2. Retrieved from https://CRAN.R-project.org/package=vegan.

Ott, J. and Samways, M.J. 2010. Effects of climate change on Odonata: are the impacts likely to be the same in the northern and southern hemispheres? In: Settele, J., Penev, L., Georgiev, T., Grabaum, R., Grobelnik, V., Hammen, V., Klotz, S., Kotarac, M. and Kuehn, I. (eds). *Atlas of Biodiversity Risk*. Pensoft Publishers, Sophia, Bulgaria. pp. 84-85.

Overton, J.M., Barker, G.M. and Price, R. 2009. Estimating and conserving patterns of invertebrate diversity: a test case of New Zealand land snails. *Diversity and Distributions*, 15: 731-741.

Pearson, R.G. and Boyero, L. 2009. Gradients in regional diversity of freshwater taxa. *Journal of the North American Benthological Society*, 28: 504-514.

Pires, M., Stenert, C. and Maltchik, L. 2018. Drivers of beta diversity of Odonata along a forest-grassland transition in southern Brazilian coastal ponds. *Freshwater Science*, 37: 357-366.

Poynton, J.C. 1961. Biogeography of south-east Africa. *Nature*, 189: 801-803.

Poynton, J.C. 1969. Optimum temperatures and amphibian distribution in south-east Africa. *Paleoecology Africa*, 4: 161-162.

Price, B.W., Barker, N.P. and Villet, M.H. 2007. Patterns and processes underlying evolutionary significant units in the *Platypleura stridula* L. species complex (Hemiptera: Cicadidae) in the Cape Floristic Region, South Africa. *Molecular Ecology*, 16: 2574-2588.

Quantum GIS Development Team. 2017. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. Available at: http://qgis.osgeo.org.

R Development Core Team. 2016. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/.

Ribera, I., Foster, G.N. and Vogler, A.P. 2003. Does habitat use explain large scale species richness patterns of aquatic beetles in Europe. *Ecography*, 26: 145-152.

Ricklefs, R.E. and Lovette, J. 1999. The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, 68: 1142-1160.

Ricklefs, R.E. and Schluter, D. 1993. *Species Diversity in Ecological Communities. Historical and Geographical Perspectives*. Chicago University Press, Chicago.

Samways, M.J. 1989a. Taxon turnover in Odonata across a 3000 m altitudinal gradient in southern Africa. *Odonatologica*, 18: 263-274.

Samways, M.J. 1989b. Farm dams as nature reserves for dragonflies (Odonata) at various altitudes in the Natal Drakensberg mountains, South Africa. *Biological Conservation*, 48: 181-187.

Samways, M.J. 2008. *Dragonflies and Damselflies of South Africa* (No. 70). Pensoft Publishers. Sophia, Bulgaria.

Samways, M.J. and Niba, A. 2010. Climate and elevation range of a South African dragonfly assemblage. *Biodiversity and Ecosystem Risk Assessment*, 5: 85-107.

Samways, M.J. and Simaika, J.P. 2016. *Manual of Freshwater Assessment for South Africa: Dragonfly Biotic Index*. Suricata 2. South African National Biodiversity Institute. Pretoria, South Africa.

Samways, M.J. and Tarboton, W. 2006. Rediscovery of *Metacnemis angusta* (Selys) in the Western Cape, South Africa, with description of male and redescription of female (Zygoptera: Platycnemididae). *Odonatologica*, 35: 375-378.

Samways, M.J., Sharratt, N.J. and Simaika, J.P. 2011. Effect of alien riparian vegetation and its removal on a highly endemic macroinvertebrate community. *Biological Invasions*, 13: 1305-1324.

Simaika, J.P. and Samways, M.J. 2009. Reserve selection using Red Listed taxa in three biodiversity hotspots: Dragonflies in South Africa. *Biological Conservation*, 142: 638-651.

Smith, J., Samways, M.J. and Taylor, S. 2007. Assessing riparian quality using two complementary sets of bioindicators. *Biodiversity and Conservation*, 16: 2695-2713.

Stuckenberg, B.R. and Kirk-Spriggs, A.H. 2009. Afrotropical Diptera - Rich savannas, poor rainforests. In: Diptera Diversity: Status Challenges and Tools. Koninklijke Brill. NV.

Suhling, F., Sahlén, G., Kasperski, J. and Gaedecke, D. 2005. Behavioural and life history traits in temporary and perennial waters: comparisons among three pairs of sibling dragonfly species. *OIKOS*, 108: 609-617.

van der Mescht, L., Matthee, S. and Matthee, C.A. 2015. Comparative phylogeography between two generalist flea species reveal a complex interaction between parasite life history and host vicariance: parasite-host association matters. *BMC Evolutionary Biology*, 15: 105.

Willig, M.R., Kaufman, D.M. and Stevens, R.D. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution and Systematics*, 34: 273-309.

Willows-Munro, S. and Matthee, C.A. 2011. Linking lineage diversification to climate and habitat heterogeneity: phylogeography of the southern African shrew *Myosorex varius*. *Journal of Biogeography*, 38: 1976-1991.

Wishart, M.J. and Day, J.A. 2002. Endemism in the freshwater fauna of the south-western Cape, South Africa. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 28: 1-5.

Chapter 4 Artificial reservoirs complement natural ponds to improve pondscape resilience in conservation corridors in a biodiversity hotspot

*Published as: Deacon, C., Samways, M.J. and Pryke, J.S. 2018. Artificial ponds complement natural ponds to improve pondscape resilience in conservation corridors in a biodiversity hotspot. PLoS One 13(9): e0204148. DOI: 10.1371/journal.pone.0204148.

Abstract

Natural ponds are rich in biodiversity, contributing greatly to regional aquatic biodiversity. Artificial reservoirs used for irrigation can be significant additional features of the landscape. They infill the local natural pondscape, and are attractors for aquatic insects. Here, we determine the extent to which artificial reservoirs represent the local natural pond biota, and how they contribute to the pondscape in conservation corridors used to mitigate the impact of plantation forestry in a global biodiversity hotspot. We did this by: 1) identifying the environmental factors, including plants, that drive dragonfly, water beetle, and water bug species richness, diversity and composition, and 2) determining the value of natural ponds vs. artificial reservoirs for maintaining the population size and expanding the area of occupancy for dragonflies, beetles and bugs in conservation corridors. While vegetation cover was central for maintaining species richness and composition of the assemblages in general, many other environmental variables are necessary to encourage the full suite of local diversity. Artificial reservoirs are attractive habitats to many species, overall increasing area of occupancy for 75% of them (ranging from 62–84% for different taxa). These reservoirs provide complementary alternative habitats to natural ponds, leading to improved ecological resilience across the pondscape. We conclude that maintaining a diverse and heterogeneous pondscape is important for conserving local aquatic insect diversity, and that artificial reservoirs increase the local area of occupancy for a range of pond insects in conservation corridors, and improve the biodiversity value of these pondscapes.

Keywords: aquatic insects, dragonflies, water beetles, water bugs, insect conservation, pond conservation

4.1 Introduction

Freshwater ponds are lentic water bodies <2 ha in size (Williams et al. 2016), common throughout the world (Holgerson and Raymond 2016). They contribute greatly to local ecology (Hill et al. 2016) and support high biodiversity, sometimes greater than that in larger water bodies such as rivers and lakes (Davies et al. 2008), due partly to their high habitat heterogeneity at the landscape scale (Davies et al. 2008). In transformed areas with limited numbers of natural ponds, artificial reservoirs can also provide refuge habitat for rare and threatened species (Chester and Robson 2013).

Artificial reservoirs are constructed for water storage (Bichel et al. 2015) and may replace small, natural wetlands and ponds, especially in agricultural and urban landscapes (Samways 1989a; Apinda-Legnouo et al. 2014). Compared to natural ponds, reservoirs are often of recent origin. Yet, reservoirs can support considerable freshwater biodiversity (Bichel et al. 2015; Oertli et al. 2010), and like natural ponds, can expand the area of occupancy for many aquatic species, often supporting rare species not in the immediate area (Samways 1989a; Oertli et al. 2010). This may come about through provision of essential physical characteristics, such as vegetation structure, substrate composition, and reservoir size (Oertli et al. 2002; Nicolet et al. 2004), or physicochemical characteristics such as elevation, temperature, and pH (Apinda-Legnouo et al. 2014).

Groups of ponds, natural and/or artificial, across a landscape are known as pondscapes (Hill et al. 2016). They are important in conservation efforts, as they support higher community diversity than single large ponds or reservoirs (Oertli et al. 2002; Martínez-Sanz et al. 2012). Pondscapes have been poorly explored in areas of the world with exceptionally high biodiversity. One of these areas is the Maputaland-Pondoland-Albany (MPA) biodiversity hotspot in South Africa, where large-scale conservation corridors of remnant land are in place to mitigate timber production (Pryke et al. 2015). These conservation corridors extend across the landscape to make up large-scale ecological networks (Samways and Pryke 2016). They have a rich toposcape of hills, wetlands, natural ponds, and artificial reservoirs (Kirkman and Pott 2002).

With increasing pressures on water resources, there has been much interest in aquatic insects occupying freshwater habitats (Bowd et al. 2006; Bonada et al. 2006; Mlambo et al. 2011), as a wide range of aquatic habitats lend themselves to understanding landscape ecology and contribute to conservation planning (McGeoch 2007). Aquatic insects make up much of the total freshwater fauna (Batzer and Wissinger 1996), fulfil many ecological roles (Bowd et al. 2006; Fairchild et al. 2003), and have the potential to reflect the physical and biological state of ecosystems (Ormerod et al. 2009; Gerlach et al. 2013; Guareschi et al. 2012; Valente-Neto et al. 2016). The aquatic insects that occupy ponds, natural and artificial, in the MPA biodiversity hotspot are poorly studied, yet their diversity is likely to be high in view of what is known for dragonflies in the area (Samways 2008).

Dragonflies are excellent model organisms for ecology (Clausnitzer et al. 2008; Samways and Simaika 2016), as they are taxonomically well-known, adults are easy to identify in field, they are highly mobile as adults, and they occupy almost any aquatic habitat. Furthermore, they are variously sensitive to environmental differences in relation to physical structure of the aquatic and aerial biotopes (Samways and Sharratt 2010) as well as in-water physicochemical conditions (Kietzka et al. 2016), leading to them being used in freshwater condition assessment, including in the MPA hotspot (Samways and Simaika 2016).

Two additional insect groups receiving increasing attention as indicators of water quality are aquatic beetles and bugs (Savage 1994; Dickens and Graham 2002; Kazangaki et al. 2008). Twenty-four families of strictly aquatic beetles (Griffiths et al. 2015) and 17 families of true bugs (Reavell 2003) are known from South Africa. Aquatic beetles and bugs are highly mobile as adults, possess several unique morphological characteristics, have adaptations to various ecological conditions (Hutchinson 1933; Savage 1989), and fulfil many roles in many aquatic ecosystems (Griffiths et al. 2015; Stals 2003). At the family level, water beetles and water bugs variously respond to physicochemical change and vegetation structure (Dickens and Graham 2002; Stals 2003; Samways 1991). However, especially in South Africa, their taxonomy and distribution are not well known, restricting their use as bioindicators.

Little research has been undertaken using a range of aquatic taxa for assessing natural vs. artificial ponds, especially in conservation corridors designed and managed principally using terrestrial taxa and interactions. One study considers the drivers of the composition of various aquatic insect taxa composition in the MPA hotspot (Briggs 2015), in addition to that of dragonflies (e.g. Samways 1991; Samways 1989b; Samways et al. 1996).

Here, we focus on the value of pondscapes as conservation clusters, and: 1) identify the physical and environmental variables driving dragonfly, water beetle, and water bug species richness, diversity, and composition in the MPA hotspot, and 2) determine the ecological value of artificial reservoirs vs. natural ponds for maintaining population sizes and expanding the local area of occupancy for dragonflies, beetles and bugs in conservation corridors. As conservation corridors have proven to be an effective conservation measure for terrestrial and aquatic ecosystems, we identify the important features of artificial reservoirs relative to natural ponds for maintaining aquatic insect diversity across this production landscape.

4.2 Sites, materials and methods

4.2.1 Study sites

Forty study sites were selected in the KwaZulu-Natal Midlands, South Africa: 20 natural ponds and 20 artificial reservoirs, in five geographical areas (Figure 4.1; Table 4.1). Sampling sites were selected to represent a spectrum of variation in natural quality, based on past records (obtained from satellite imagery) and initial inspection. Demarcation of natural pond sites was based on the presence/absence of hydrophilic plant species, benthic slow-flow characteristics of the water body, and the geomorphological setting. Only open grassland matrix valley bottoms and plains were considered, being the position of most ponds and reservoirs. Geomorphological data were obtained from the National Freshwater Ecosystem Priority Areas (NFEPA) database.

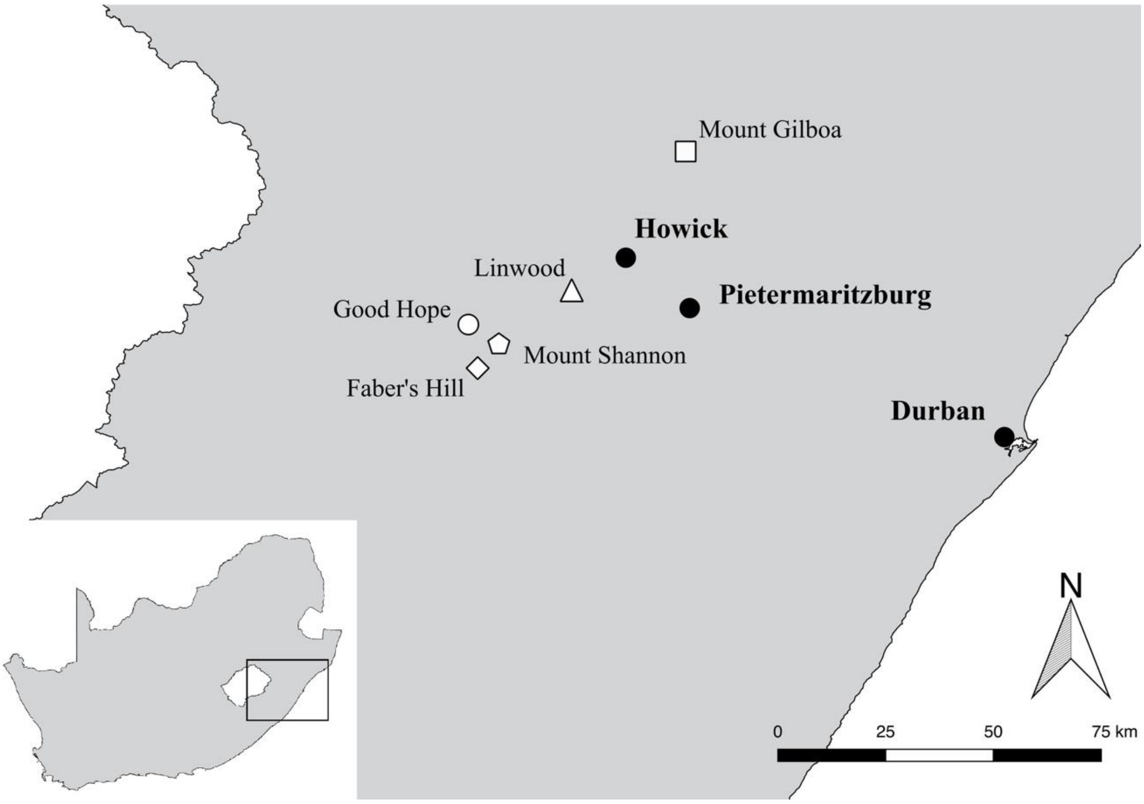


Figure 4.1 Locations of sampling areas in the Maputaland-Pondoland-Albany biodiversity hotspot. Pentagon: Mount Shannon Estate, diamond: Faber’s Hill Estate, circle: Good Hope Estate, triangle: Linwood Estate, and square: Mount Gilboa Estate. Black circles represent nearby towns.

Table 4.1 Geographic location and pond type of sampling sites in each sampling area.

Area	**Site**	**Latitude**	**Longitude**
Mount Shannon	Artificial reservoir 1	29° 42' 50" S	29° 59' 34" E
Mount Shannon	Natural pond 1	29° 42' 35" S	29° 58' 33" E
Mount Shannon	Natural pond 2	29° 42' 49" S	29° 59' 36" E
Mount Shannon	Natural pond 3	29° 42' 55" E	29° 59' 25" E
Faber's Hill	Artificial reservoir 1	29° 40' 26" S	29° 54' 57" E
Faber's Hill	Artificial reservoir 2	29° 40' 37" S	29° 56' 21" E
Faber's Hill	Artificial reservoir 3	29° 40' 20" S	29° 55' 10" E
Faber's Hill	Artificial reservoir 4	29° 44' 27" S	29° 54' 56" E
Faber's Hill	Natural pond 1	29° 40' 39" S	29° 55' 07" E
Faber's Hill	Natural pond 2	29° 40' 42" S	29° 54' 58" E
Faber's Hill	Natural pond 3	29° 40' 21" S	29° 56' 10" E
Faber's Hill	Natural pond 4	29° 40' 02" S	29° 56' 09" E
Faber's Hill	Natural pond 5	29° 40' 27" S	29° 56' 05" E
Faber's Hill	Natural pond 6	29° 44' 23" S	29° 55' 02" E
Mount Gilboa	Artificial reservoir 1	29° 14' 42" S	30° 20' 35" E
Mount Gilboa	Artificial reservoir 2	29° 14' 32" S	30° 19' 45" E
Mount Gilboa	Artificial reservoir 3	29° 14' 19" S	30° 20' 02" E
Mount Gilboa	Artificial reservoir 4	29° 15' 21" S	30° 19' 02" E
Mount Gilboa	Artificial reservoir 5	29° 14' 42" S	30° 17' 01" E
Mount Gilboa	Artificial reservoir 6	29° 14' 52" S	30° 19' 49" E
Mount Gilboa	Artificial reservoir 7	29° 15' 13" S	30° 18' 45" E
Mount Gilboa	Natural pond 1	29° 14' 44" S	30° 17' 40" E
Mount Gilboa	Natural pond 2	29° 15' 04" S	30° 15' 41" E
Mount Gilboa	Natural pond 3	29° 14' 59" S	30° 15' 05" E
Mount Gilboa	Natural pond 4	29° 14' 41" S	30° 19' 46" E
Mount Gilboa	Natural pond 5	29° 15' 15" S	30° 15' 37" E
Mount Gilboa	Natural pond 6	29° 15' 03" S	30° 14' 59" E
Mount Gilboa	Natural pond 7	29° 15' 02" S	30° 15' 03" E
Mount Gilboa	Natural pond 8	29° 14' 42" S	30° 19' 48" E
Good Hope	Artificial reservoir 1	29° 39' 18" S	29° 58' 12" E
Good Hope	Artificial reservoir 2	29° 39' 09" S	29° 58' 18" E
Good Hope	Artificial reservoir 3	29° 37' 40" S	29° 59' 06" E
Good Hope	Artificial reservoir 4	29° 40' 07" S	29° 58' 26" E
Good Hope	Natural pond 1	29° 39' 13" S	29° 57' 13" E
Good Hope	Natural pond 2	29° 39' 27" S	29° 58' 28" E
Good Hope	Natural pond 3	29° 40' 08" S	29° 58' 19" E
Linwood	Artificial reservoir 1	29° 33' 38" S	30° 05' 38" E
Linwood	Artificial reservoir 2	29° 32' 59" S	30° 06' 07" E
Linwood	Artificial reservoir 3	29° 33' 54" S	30° 06' 47" E
Linwood	Artificial reservoir 4	29° 33' 38" S	30° 05' 33" E

4.2.2 Data collection

Data were collected during two sampling seasons: early summer (January-February) and late summer (February-March). Adult dragonfly (Odonata), water beetle (Coleoptera), and water bug (Hemiptera) individuals were sampled on cloudless, windless days, 10h30-15h30, once during each sampling season. Each insect order was treated as a separate entity, as they differ substantially in terms of habitat requirements and traits. Ten quadrats of 4 m^2 were selected on the edge of the water body, and swept with an aquatic net (300 mm x 300 mm; 1000 micron mesh size) for 3 min to collect beetles and bugs. Quadrats were selected to represent all features of the water body at a depth of <1.2 m, below which aquatic insect diversity in this area drops off considerably (Samways et al. 1996). Collected individuals were identified to at least genus by making use of the Water Research Commission identification guides (Stals 2003), museum collections, and expert opinion (P. Reavell, pers. Comm.). In the case of adult dragonflies, two 50 m transects were selected per site, wherein all individuals were visually recorded for 30 min. Any other, large hawking species (e.g. *Anax imperator*) that were within 5 m of transects were also recorded. Dragonfly larvae were not included, as local larval taxonomy is not sufficiently well known to species level. To confirm the identity of species, individuals were collected with an insect net and identified using relevant field guides (Samways 2008; Samways and Simaika 2016). The procedure was repeated for the second sampling season. Two individuals of each species sampled are kept in a reference collection at the Stellenbosch University Entomological Museum.

At each study site, ten point measurements of physicochemical conditions were recorded at each sampling depth on cloudless, windless days, 10h30-15h30: dissolved oxygen (mg/L), water temperature (°C), conductivity (µs), turbidity (cm visibility, using a clarity tube), and sampling depth (m, using a measuring pole). In addition, water body size (m^2) and elevation (m a.s.l.) was recorded using Garmin eTrex 30 map data. Vegetation structure and composition was determined in five quadrats of 4 m^2 at the edge of each water body. Within each quadrat, the percentage grass cover, percentage reed cover, percentage forb cover, average vegetation height, and dominant marginal and submerged plant species were recorded.

Geomorphological data of each study site were obtained from the NFEPA database, and each site was ground-truthed. In the event of inaccurate classification in the NFEPA database due to coarse spatial scale, the particular site was reclassified in field by making use of geomorphological classification guidelines (Tooth et al. 2014).

4.2.3 Statistical analyses

In order to determine whether sampling was sufficient and that the subset of data was representative of the sampling area, two species estimators were calculated and compared with the number of observed species (Sobs):

$$S_{Chao2} = S_{obs} + \frac{Q_1^2}{2Q_2} \qquad \text{Chao2}$$

Where Q1 is species occurring exclusively in one sample and Q2 species occurring in two samples and,

$$S_{jack2} = S_{obs} + [\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)}] \qquad \text{Jackknife2}$$

Where m is the total number of samples collected.

The Chao2 species estimator is proven to be very effective for insect studies as non- parametric estimators are better for datasets with a large number of rare species. Jackknife2 species estimator is another effective non-parametric estimator, that is particularly unresponsive to sampling bias.

Generalized linear mixed modelling was used to pre-select and test the random and fixed effects of environmental variables on overall species richness and abundance, as well as within natural ponds and artificial reservoirs, using the *lme4* package in R (Bates and Sarkar 2007; R Core Team 2016). For species richness, the three separate models (overall effect, within natural ponds and within artificial reservoirs) were built with pond size, elevation, site type, geomorphological class of pond, vegetation height, percentage total cover, percentage reed cover, percentage forb cover, percentage grass cover, water depth, dissolved oxygen, water temperature, water conductivity, water pH, and turbidity as fixed variables, and the sampling season and area where the sites were located as random variables. For species abundance, a single overall model was built with pond type as fixed variable, and area where site is located, sampling season and site identity as random variables, to determine the difference in abundance between natural ponds and artificial reservoirs. All generalized linear mixed models were fitted by a Laplace approximation and a Poisson distribution. For all significant regressions, we used piece-wise regressions to segregate environmental data and determine the breakpoint in each regression using the *segmented* package in R (R Core Team 2016; Muggeo 2017).

The Shannon diversity index (hereafter referred to as “diversity”), accounting for species abundance and evenness, was calculated for each insect order at each sampling site in R using the *vegan* package (R Core Team 2016; Oksanen et al. 2017) and log-transformed. Linear mixed modelling was then used to pre-select and then test the random and fixed effect of environmental variables on overall insect diversity, as well as within natural ponds and artificial reservoirs. The three separate models (overall effect, within natural ponds and within artificial reservoirs) were again built with site size, elevation, site type, geomorphological class of site, vegetation height, percentage total cover, percentage reed cover, percentage forb cover, percentage grass cover, water depth, dissolved oxygen, water temperature, water conductivity, water pH, and turbidity as fixed variables, and the sampling season and area where the sites were located as random variables. The linear models were fitted by a Laplace approximation and a normal distribution. In the case of categorical fixed variables, categorical pairwise t-tests and Tukey post-hoc tests were used to determine significance. Again, for all significant regressions, we used piece-wise regressions to segregate environmental data and determine the breakpoint in each regression using the *segmented* package in R (R Core Team 2016; Muggeo 2017).

Distance-based linear modelling (DistLM), based on resemblance matrices and effects of multiple predictor variables, was performed to explain the variation in species composition using recorded environmental variables, in PRIMER version 6 (Clarke and Gorley 2006). Forward selection of environmental variables was used, meaning that each environmental variable was added into the analysis until no significant effect on the species composition was evident. In addition, permutational multivariate analyses of variance (PERMANOVA) were used to determine the difference in environmental variables between natural ponds and artificial reservoirs. 9999 permutations were used to determine effects of environmental variables on the overall species composition of the three orders, as well as within each water body type. Permutational analyses were used to randomize factors and to select the factors that explained species composition the best. The Bray-Curtis similarity measure (which measures species composition based on the abundance of each species) was used to evaluate species composition of all groups.

4.3 Results

A total of 61 lentic species were sampled (4 895 individuals), comprising 27 dragonfly species (1 053 individuals), 16 beetle species (658 individuals) and 18 bug species (3 184 individuals). The number of observed species (Sobs) neared the estimated number of species (Chao2 and

Jackknife2) across the insect orders, as well as within each pond type. This indicated that sampling was sufficient, and that the subset of data is representative (Appendix S4.1). For the complete list of species, refer to Appendix S4.2.

4.3.1 Influence of environmental variables on species richness, abundance and insect diversity

Overall dragonfly species richness and diversity increased with an increase in water temperature, but diversity decreased with an increase in % forb cover (Table 4.2). There was a significant negative relationship between water body size, and dragonfly species richness, although dragonfly diversity increased with water body size, until a size of about 20 260 m^2 was reached, after which diversity decreased significantly ($t = 10.4$; $p < 0.001$). There was no significant difference between dragonfly abundance for natural ponds and artificial reservoirs ($t = 0.6$; $p = 0.532$). For natural ponds, dragonfly species richness and diversity increased with an increase in water temperature and % reed cover. Natural ponds in valley bottoms had significantly higher dragonfly species richness and diversity over natural ponds on open plains. In the case of artificial reservoirs, dragonfly species richness decreased with an increase in water body size. An increase in dissolved oxygen, sampling depth, % reed cover, and % grass cover gave an increase in dragonfly species richness. Dragonfly diversity decreased with an increase in dissolved oxygen, and in the case of % forb cover, decreased until about 22% cover was reached, above which there was an increase in diversity ($t = 9.8$: $p < 0.001$). Dragonfly diversity increased with water body size until about 15 400 m^2, after which diversity decreased ($t = 11.5$; $p < 0.001$). For a summary on the ranges of measured environmental variables, consult Appendix S4.3.

Table 4.2 Effects of environmental variables on the overall species richness and diversity, and in the two water body types, natural vs. artificial.

		Overall		**Natural Ponds**		**Artificial reservoirs**	
		Species richness	**Shannon index**	**Species richness**	**Shannon index**	**Species richness**	**Shannon index**
Dragonflies	**Water body size**	(-)4.091*	(+/-)13.036***			(-)17.066***	(+/-)26.098***
	Temperature	(+)8.815**	(+)10.584**	(+)6.521*			
	Dissolved oxygen					(+)10.919***	(-)4.196*
	Depth					(+)6.64**	
	% Reed cover			(+)7.191*	(+)3.894*	(+)4.660*	
	% Grass cover					(+)3.928*	
	% Forbs cover		(-)4.104*				(-/+)5.284*
	Geomorph class		**-3.154****	**-2.26***	**-6.252*****		
Beetles	**Depth**	(-)9.376**		(-)4.403*			
	Temperature	(-)4.285*	(-)4.408*	(+)8.523**	(+)23.155***		
	Conductivity	(-)4.436*	(-)4.743*				
	pH				(+)15.795***		
	Dissolved oxygen				(-)17.851***		
	Elevation				(-/+)8.317**		
	% Forbs cover					(+)9.526**	(+)5.351*
	% Reed cover				(-)9.970**		
	Water body type	**3.070****	**2.636***				
Bugs	**Temperature**	(+)5.564*		(+)7.361*	(+)4.328*		
	Conductivity	(-)6.743*					
	% Grass cover					(-/+)9.814**	

Chi square values are indicated, and t-values are indicated in bold in the case of categorical variables. (+): positive correlation; (-): negative correlation; (+/-): initial positive correlation; (-/+): initial negative correlation. Significance levels *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

Type of water body (natural pond vs. artificial reservoir) had a significant effect on overall beetle species richness (Table 4.2), with natural ponds supporting more species. Overall beetle species richness increased with a decrease in water temperature and conductivity, while species richness decreased with an increase in water depth. There was no significant difference between beetle abundance for natural ponds and artificial reservoirs ($t = -0.3$; $p = 0.077$). For natural ponds, beetle species richness and diversity increased with water temperature, although beetle species richness decreased with increasing water depth. Beetle diversity increased with an increase in water pH, and decreased with increased dissolved oxygen and % reed cover. Beetle diversity decreased with increasing elevation, but above 1 500 m a.s.l., diversity increased ($t = 0.9$; $p = 0.036$). For artificial reservoirs, beetle species richness and diversity increased with increased % forb cover.

Overall bug species richness increased with water temperature but decreased with increased conductivity (Table 4.2). There was no significant difference between bug abundances for natural ponds and artificial reservoirs ($t = 0.1$; $p = 0.928$). For natural ponds, bug species richness and diversity increased with water temperature. For artificial reservoirs, bug species richness decreased with an initial increase % grass cover but increased above 13% grass cover ($t = 9.795$; $p < 0.001$).

4.3.2 Influence of environmental factors on dragonfly, beetle and bug assemblages

Pond type (natural vs. artificial) had a significant effect on dragonfly (pseudo-F = 3.08), beetle (pseudo-F = 3.12) and bug (pseudo-F = 2.97) assemblages, respectively. Within each water body type, the geomorphological class had no effect on the species assemblage of any of the three groups. Of the 13 environmental variables measured, distance based on linear modelling (DistLM) selected six variables as significant to overall aquatic insect species composition. These were water temperature, pH, conductivity, depth, pond size and elevation (Table 4.3; Figure 4.2). Water turbidity, dissolved oxygen, % reed cover, % forb cover, total % vegetation cover, and vegetation height did not influence species composition. For overall dragonfly species composition, 14.3% of the variation was explained by water temperature, 7.8% explained by water body size, 4.8% explained by elevation, and 1.9% explained by water depth.

Table 4.3 Distance based on linear modelling (DistLM) sequential results indicating environmental variables most descriptive of aquatic insect species composition structure between habitat types.

Group	**Type**	**Environmental variables**	**F**	**Variation explained (%)**	**Cumulative variation explained (%)**
Dragonflies	**Overall**	Temperature	5.181***	14.29	14.29
		Water body size	2.792**	7.83	22.12
		Elevation	2.437*	4.79	26.91
		Depth	2.692*	1.93	28.84
	Ponds	Temperature	4.556***	20.2	20.2
	Reservoirs	Temperature	3.177**	19.01	19.01
		Water body size	3.033**	27.87	46.88
Beetles	**Overall**	pH	3.522***	8.48	8.48
	Ponds	pH	2.288*	11.28	11.28
	Reservoirs	Depth	1.748*	8.85	8.85
Bugs	**Overall**	Temperature	3.535***	11.56	11.56
		Conductivity	3.032**	6.84	18.4
		Water body size	2.308*	2.13	20.53
	Ponds	Temperature	3.399***	15.89	15.89
	Reservoirs	% Grass cover	4.122*	18.63	18.63

Significance levels *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

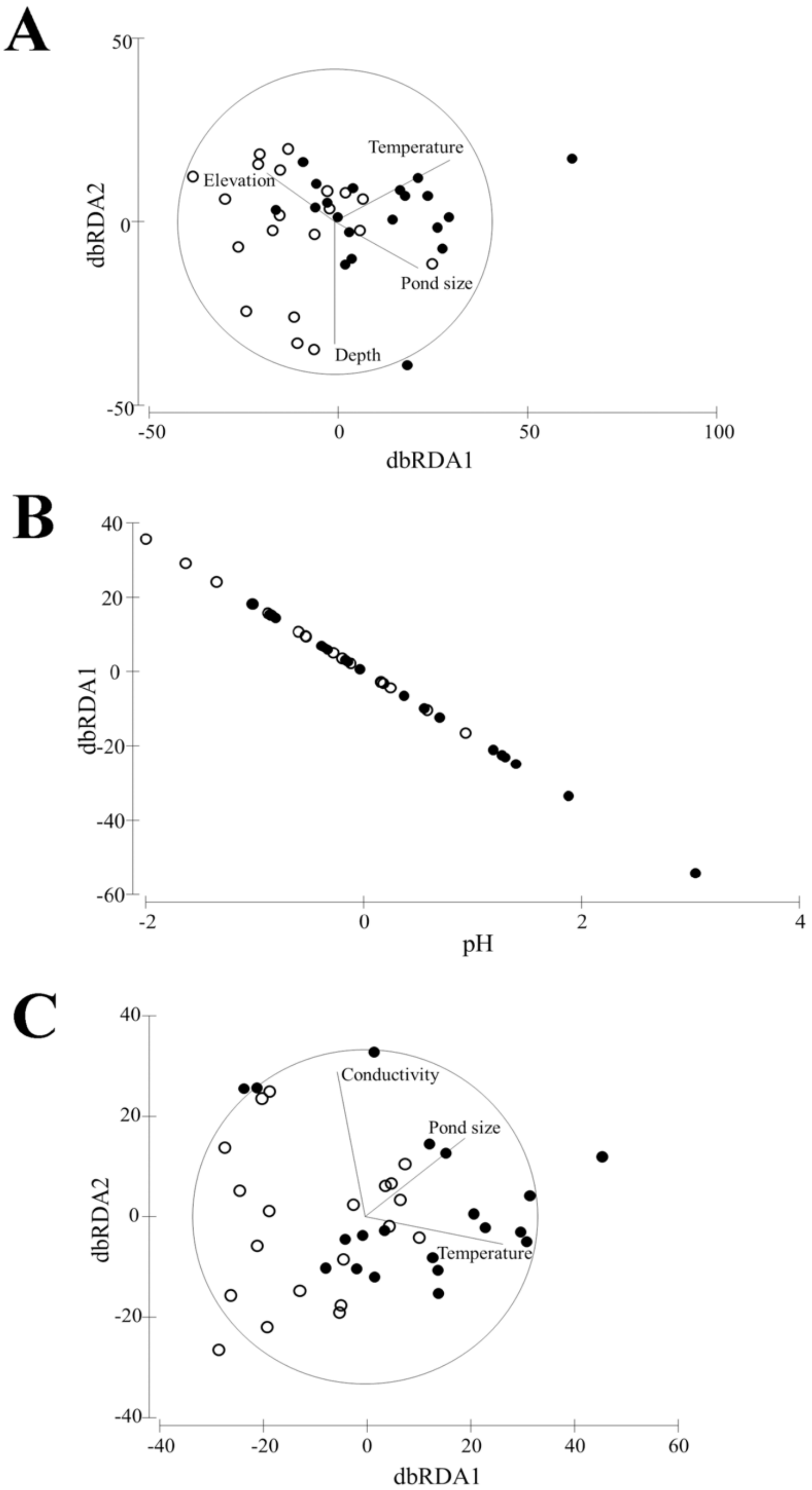


Figure 4.2 Distance-based redundancy analysis (dbRDA) results indicating significant effects of environmental variables on insect species composition. Vectors represent the effect of environmental variables on dragonfly (A), beetle (B) and bug (C) species composition between natural ponds (open circles) and artificial reservoirs (filled circles). Axes represent Bray-Curtis distance measure.

For overall beetle species composition, water pH explained 8.5% of total variation, and for overall bug species composition 11.6% of the variation was explained by water temperature, 6.8% by conductivity, and 2.1% by water body size. Two variables (water temperature and pH) influenced species composition in natural ponds (Table 4.3). Water temperature explained 20.2% of the variation in dragonfly species composition, and 15.9% of the variation in bug species composition. Water pH explained 11.3% of the variation in beetle species composition. Four environmental variables influenced species composition in artificial reservoirs. These were water temperature, depth, water body size, and % grass cover. Water temperature and water body size explained 19.0% of the variation and 27.9% of the variation in dragonfly species composition respectively. Sampling depth explained 8.9% of the variation in beetle species composition and % grass cover explained 18.6% of the variation in bug species composition.

15% of the sampled dragonfly species were unique to natural ponds (Figure 4.2). These were *Chlorolestes fasciatus*, *Elattoneura glauca*, *Proischnura rotundipennis* and *Zosteraeshna minuscula*. No dragonfly species was unique to the artificial reservoirs. 25% of beetle species was unique to natural ponds (Figure 4.2), and included *Amphiops* sp., *Aulonogyrus* sp. 1, *Copelatus* sp., *Derovatellus* sp. and *Orectogyrus* sp., and 13% unique to artificial reservoirs, and included *Aulonogyrus* sp. 2 and *Hydropeplus* sp. 28% of the bug species sampled was unique to natural ponds (Figure 4.2). These were *Borborophilus afzelii*, *Laccotrephes brachialis*, *Limnogonus capensis*, *Ranatra grandicollis* and *Sigara pectoralis*. No bug species were unique to the artificial reservoirs.

4.4 Discussion

4.4.1 Relative significance of the environmental variables

We found that any one of the investigated habitat descriptors cannot be substituted by another, and the focal taxa respond to each in different ways. As a result, high habitat heterogeneity created by the combination of environmental variables and pond types which maintain high insect diversity. Aquatic habitat heterogeneity in the form of vegetation complexity, substrate structure, and/or physicochemical characteristics are important for aquatic insects (Karaouzas and Gritzalis 2006; MacArthur and MacArthur 1961; Fairchild et al. 2000), and adult, terrestrial dragonflies (Kietzka et al. 2016), as we found here. This supports earlier studies (Mlambo et al. 2011; Fairchild et al. 2003; Kietzka et al. 2016; Drake 1990; Karaouzas and

Gritzalis 2006), whether at the regional scale (Scheffer et al. 2006), or at the finer scale of the pondscape (Hill et al. 2016; Samways and Pryke 2016).

Many dragonflies occupying lentic habitats require marginal and/or submerged vegetation (Mlambo et al. 2011; Samways 2008; Samways and Simaika 2016) as perching sites, substrate for larvae to seek refuge, and to emerge as adults (Osborn and Samways 1996). Furthermore, vegetation provides habitat for food items for both adult and larval dragonflies. Here, margins of natural ponds were predominantly covered by a mixture of grasses and forbs, with little variation between ponds, and were neither extensive, nor casting much shade which otherwise diminishes local dragonfly assemblages (Samways and Sharratt 2010).

Artificial reservoirs had less marginal grasses and forbs coverage, more reed coverage, and were rich in submerged aquatic weeds (dominated by *Elodea* spp.). These seemingly open habitats favour early aquatic beetle and bug colonization (Fernando 1958; Bloechl et al. 2010; Scheibler et al. 2016). However, consistent with recent suggestions (Mlambo et al. 2011; Fairchild et al. 2003; Juliano 1991), beetle species richness and diversity was positively correlated with increased forb cover in artificial reservoirs. Vegetation with complex growth forms allows Dytiscidae and Gyrinidae to exit the water when macerating prey (Balduf 1935), allows for the completion of their life cycles (Galewski 1971), and provides refuge against predators (Verberk et al. 2016), all of which are important for improving their persistence. As reeds are generally tall and throw much shade, few beetles select reedy stands as microhabitat. We found that only grass cover significantly drove bug species composition in artificial reservoirs, the reason for which is possibly the presences of some scavenger families (here, Hebridae, Hydrometridae and Veliidae) having a strong preference for vegetated margins, being surface dwellers that require emergent vegetation as refuge (Fairchild et al. 2003; Griffiths et al. 2015).

Consistent with previous studies, adult dragonflies (Kietzka et al. 2016; Simaika et al. 2016), aquatic beetles (Mlambo et al. 2011; Briggs 2015) and aquatic bugs (Karaouzas and Gritzalis 2006) respond to in-water physicochemical conditions. Although it has been suggested that adult dragonflies are likely unable to assess water biochemistry directly (Valente-Neto et al. 2016), it has been found that in South Africa they actually can do so (Kietzka et al. 2016), but this is secondary to the primary response to certain visual cues from vegetation (Osborn and Samways 1996; Michiels and Dhondt 1990; Schindler et al. 2003).

The beetles and most bugs sampled here are water-dwelling during their adult and larval stages, and might also be capable of assessing water biochemistry directly. Nevertheless, moderate water temperature increases activity (Samways et al. 1996; Scheibler et al. 1996) and shortens larval development time (Osborn and Samways 1996) for dragonflies, beetles and bugs occupying both natural ponds and artificial reservoirs. For these reasons, most aquatic beetles occupy ponds characterized by moderate water temperature, yet dragonflies (and their larvae) and bugs may be able to tolerate slightly elevated water temperature. The effect of dissolved oxygen on dragonflies was only detected in artificial reservoirs, where oxygen levels were much more variable. In general, dragonfly larvae are reliant on dissolved oxygen for respiration, unlike adult beetles and bugs, being atmospheric breathers (Griffiths et al. 2015; Skaife 1979). Artificial reservoirs rich in dissolved oxygen were predominantly occupied by zygopterans, as most anisopterans (the majority sampled here) are physiologically better equipped to tolerate low dissolved oxygen conditions. Furthermore, high aquatic beetle diversity in natural ponds was associated with lower dissolved oxygen, as higher dissolved oxygen might be synonymous with presence of predatory vertebrate species, although not directly measured here.

Fluctuating conductivity as a proxy for salinity (Bird et al. 2014) determines overall aquatic beetle and bug species richness, and shapes aquatic bug assemblages, as high salinity interferes with metabolic capabilities and water retention in aquatic insects (Baker and Christensen 1991). Here, only aquatic beetle diversity in natural ponds showed a response to water pH, suggesting that most of our aquatic beetles have a strong preference for slightly alkaline waters, related to their physiology and development (Friday 1987).

Overall, natural ponds and artificial reservoirs were clearly distinct in physical characteristics (size and depth). Artificial reservoirs here were much larger and deeper than the natural ponds. Island biogeography theory suggests that larger water bodies should sustain higher species richness and a more complex species composition (MacArthur and Wilson 1967). However, our findings suggest that dragonflies have a preference for maintained intermediate-sized natural ponds, as they provide a suitable number of microhabitats throughout the season, reducing competition for resources (Pryke et al. 2015; Kadoya et al. 2004). The water level of large artificial reservoirs may also fluctuate more than natural ponds as a result of agricultural abstraction and seasonal variation (Pryke et al. 2015; Samways 2008). Similarly, the water level of small natural ponds may fluctuate greatly between seasons. In both cases, marginal and submerged vegetation is exposed (Kadoya et al. 2004), increasing competition for suitable microhabitats, as was the case in our area (Shulze 1982).

We found that water body size and depth are less important to chance colonization by aquatic beetles and bugs. Most are highly mobile as adults and occupy mostly the shallow edges regardless of water body size (Fairchild et al. 2003; Davy-Bowker 2002). Water depth > 1.2 m sees a great drop in temperature and dissolved oxygen, combined with a decrease in aquatic insect richness and abundance in our area (Samways et al. 1996). Although size and depth are apparently of lesser importance to them than fine vegetation characteristics, larger and often deeper artificial reservoirs are still occupied by widespread generalist species (here, the largest proportion of beetles and bugs sampled), partly because larger size of a water body means a higher likelihood of being found by aerial and potential colonizing individuals moving across the landscape (MacArthur and Wilson 1967; Shieh and Chi 2010).

We found that geomorphology of natural ponds was a significant descriptor of dragonfly species richness and diversity, but not of aquatic beetle and bug species richness, diversity or composition, suggesting that most beetle and bug species here occupy both the grassy valley-bottom and open plain ponds. Geomorphology cannot fully be used as a measure of permanency, but remains important to consider as it is likely to be related to the relative age of ponds, determine variability in physicochemical characteristics (Kietzka et al. 2016) and climatic factors such as wind speed, surface water run-off, and variation in marginal/submerged vegetation structure (Tooth et al. 2014), all of which contribute to habitat heterogeneity.

Among the narrow range of elevations we investigated (~1100–1500 m), there was little effect of elevation on overall dragonfly species richness and diversity, but wide elevation gradients over hundreds of meters significantly influence dragonfly species assemblages in this region (Samways 1989b). Here, the three dragonfly species *C. fasciatus*, *A. nigridorsum* and *P. jucunda* were present only at the highest elevations, *A. pinheyi* and *Z. minuscula* at intermediate elevations, and *P. rotundipennis* only at low elevations. With changing elevation, habitat characteristics related to vegetation composition and temperature change, resulting in a subsequent change in dragonfly species' assemblages as different microhabitats become available/unavailable (Samways 1989b; Mendoza and Catalan 2010). Here, low beetle diversity was associated with natural ponds at intermediate elevations, but showed an increase at higher elevations. High beetle diversity probably arises from high species turnover between lentic and lotic habitats at higher elevations (Biggs et al. 2005; Picazo et al. 2010) and high microhabitat availability in natural ponds at low elevations respectively (Guareschi et al. 2012). Increased aquatic bug species richness and diversity can be associated with increased elevation (Scheibler et al. 2016), but we did not find that here across our short elevation range. Aquatic bugs in this area are mainly widespread generalists (Griffiths et al. 2015; Reavell 2003) possessing great plasticity (Polhemus 2008), allowing them to occupy a variety of aquatic environments. The range of elevations investigated here might simply have been too narrow to detect differences in bug species richness and assemblages.

4.4.2 Added ecological value of artificial reservoirs

Range-restricted species (e.g. *P. rotundipennis*, a localized endemic damselfly), habitat-specific species (e.g. deposition pools coupled with bushes for oviposition, *C. fasciatus* (a damselfly); cool, shallow water, *B. afzelii* and *L. brachialis*, both bugs) and nearly one third of beetles did not occupy the artificial reservoirs, as their preferred microhabitats were only available in natural ponds. Nevertheless, most of the sampled species were shared between natural ponds and artificial reservoirs (75% overall; 84% of dragonflies, 62% of beetles and 72% of bugs), including two South African endemic dragonflies (*A. sapphirinum* and *A. leucosticta*), and one endemic beetle (*Algophilus* sp.).

Comparatively, there was little difference in abundance between natural ponds and artificial reservoirs across all three insect taxa. This suggests that artificial reservoirs function well in maintaining local population sizes, expanding the area of occupancy and, as natural ponds and artificial reservoirs are interspersed and close together, improve functional connectivity for most pond species. However equally important is the landscape context, as many species require areas away from water to mature, forage, roost, and seek out hibernation sites (Conrad et al. 1999). The conservation management activity of setting aside remnant corridors in and among plantation compartments provides suitable habitats and makes up ecological networks (Samways and Pryke 2016) improving ecological resilience across the pondscape for aquatic insects. Although not directly measured here, dispersal ability should in part determine how well aquatic insects use landscape-scale ecological networks in addition to ecological preference (Vogler and Ribera 2003; Rundle et al. 2007). Most aquatic insects sampled here are highly mobile as adults, enabling them to move readily between interspersed lentic habitats and track favourable ecological conditions (Fairchild et al. 2003; Conrad et al. 1999; Landin 1980; Arribas et al. 2012).

4.5 Conclusion

The relatively similar environmental conditions in artificial reservoirs and natural ponds meant that most local species occupied the reservoirs (through similar levels of species richness, abundance and assemblage composition), emphasizing their great conservation value. Importantly however, it is the whole pondscape that is required to provide the wide range of environmental variables necessary to support this diversity. This is supported by no one environmental variable driving all the aquatic diversity in the same way. A range of pond types does this, as they provide a range of abiotic and biotic conditions. While the ideal is to achieve this with only natural ponds to support all the local diversity, reservoirs nevertheless go a long way to enhance the local abundance of most aquatic species.

Nearly a quarter of the species occupied only natural ponds, indicating the fundamental importance of natural ponds if we are to conserve all the local aquatic diversity. Yet, artificial reservoirs as part of a functioning pondscape in large-scale conservation corridors, improve much aquatic diversity and abundance, so contributing to improved resilience in the face of climate and land-use change. They do this principally by increasing the area of occupancy for most species.

4.6 References

Apinda-Legnouo, E.A., Samways, M.J. and Simaika, J.P. 2014. Value of artificial ponds for aquatic beetle and bug conservation in the Cape Floristic Region biodiversity hotspot. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24: 4522-4535.

Arribas, P., Valesco, J., Abellán, P., Sánchez-Fernández, D., Andujar, C., Calosi, P., … Bilton, D.T. 2012. Dispersal ability rather than ecological tolerance drives differences in range size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). *Journal of Biogeography*, 39: 984-994.

Baker, J.P. and Christensen, S.W. 1991. Effects of acidification on biological communities in aquatic ecosystems. In: Charles, D.F. (ed.). *Acidic deposition and aquatic ecosystems: regional case studies*. Springer-Verlag, New York, USA. pp. 83-106.

Balduf, W.V. 1935. *The bionomics of entomophagous Coleoptera*. John S. Swift, New York.

Bates, D.M. and Sarkar, D. 2007. lme4: Linear mixed-effects models using S4 classes. R package version 1.1-12.

Batzer, D.P. and Wissinger, S.A. 1996. Ecology of insect communities in non-tidal wetlands. *Annual Review of Entomology*, 41: 75-100.

Bichel, D., de Marco, P., Bispo, A.A. , Ilg, C., Dias-Silva, K., Vieira, T.B., Correa, C.C. and Oertli, B. 2015. Water quality of rural ponds in the extensive agricultural landscape of the Cerrado (Brazil). *Limnology*, 17: 1-9.

Biggs, J., Williams, P., Whitfield, P., Nicolet, P. and Weatherby, A. 2005. 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15: 693-714.

Bird, M.S., Day, J.A. and Malan, H.L. 2014. The influence of biotope on invertebrate assemblage in lentic environments: A study of two perennial alkaline wetlands in the Western Cape, South Africa. *Limnologica*, 48: 19-27.

Bloechl, A., Koenemann, S., Philippi, B. and Melber, A. 2010. Abundance, diversity and succession of aquatic Coleoptera and Heteroptera in a cluster of artificial ponds in the north German lowlands. *Limnologica*, 40: 215-225.

Bonada, N., Prat, N., Resh, V.H. and Statzner, B. 2006. Developments in aquatic insect biomonitoring: a comparative analysis of recent approaches. *Annual Review of Entomology*, 51:495-523.

Bowd, R., Kotze, D.C., Morris, C.D. and Quinn, N.W. 2006. Testing the applicability of the SASS5 scoring procedure for assessing wetland health: a case study in the KwaZulu-Natal Midlands, South Africa. *African Journal of Aquatic Science*, 31: 229-246.

Briggs, A.J. 2015. Pond biodiversity in a sugarcane-forestry mosaic in KZN. M.Sc. Thesis, Stellenbosch University, Stellenbosch, South Africa.

Chester, E.T. and Robson, B.J. 2013. Anthropogenic refuges for freshwater biodiversity: Their ecological characteristics and management. *Biological Conservation*, 166: 64-75.

Clarke, K.R. and Gorley, R.N. 2006. PRIMER v6: User manual/tutorial. PRIMER-E, Plymouth.

Clausnitzer, V., Kalkman, V.J., Ram, M., Collen, B., Baillie, J.E., Bebjanič, M., … Karube, H. 2009. Odonata enter the biodiversity crisis debate: The first global assessment of an insect group. *Biological Conservation*, 142: 1864-1869.

Conrad, K.F., Willson, K.H., Harvey, I.F., Thomas, C.J. and Sherratt, T.N. 1999. Dispersal characteristics of seven odonate species in an agricultural landscape. *Ecography*, 22: 524-531.

Davies, B.R., Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Sear, D. and Maund, S. 2008. Comparative biodiversity of aquatic habitats in the European agricultural landscape. *Agriculture, Ecosystems and Environment*, 125: 1-8.

Davy-Bowker, J. 2002. A mark and recapture study of water beetles (Coleoptera: Dytiscidae) in a group of semi-permanent and temporary ponds. *Aquatic Ecology*, 36: 435-446.

Dickens, C.W.S. and Graham, P.M. 2002. The South African Scoring System (SASS) Version 5 Rapid Bioassessment Method for Rivers. *African Journal of Aquatic Science*, 27: 1-10.

Drake, J.A. 1990. Communities as assembled structures: do rules govern patterns? *Trends in Ecology and Evolution*, 5: 159-164.

Fairchild, G.W., Faulds, A.M. and Matta, J.F. 2000. Beetle assemblages in ponds: effects of habitat and site size. *Freshwater Biology*, 44: 523-534.

Fairchild, G.W., Cruz, J., Faulds, M., Short, A.E.Z. and Matta, J.F. 2003. Microhabitat and landscape influences on aquatic beetle assemblages in a cluster of temporary and permanent ponds. *Journal of the North American Benthological Society*, 22: 224-240.

Fernando, C.H. 1958. The colonization of small freshwater habitats by aquatic insects. 1. General discussion, methods and colonization in the aquatic Coleoptera. *Ceylon Journal of Science: Biological Science*, 1: 117-154.

Friday, L.E. 1987. The diversity of macroinvertebrate and macrophyte communities in ponds. *Freshwater Biology*, 18: 87-104.

Galewski, K. 1971. A study on morphobiotic adaptations of European species of Dytiscidae (Coleoptera). *Polski Pismo Entomologiczne*, 41: 488-702.

Gerlach, J., Samways, M.J. and Pryke, J.S. 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation*, 17: 831-850.

Griffiths, C., Day, J. and Picker, M. 2015. *Freshwater Life. A field guide to the plants and animals of southern Africa*. Struik Nature. Cape Town, South Africa.

Guareschi, S., Gutiérrez-Cánovas, C., Picazo, F., Sanchéz-Fernández, D., Abellán, P., Velasco, J. and Millán, A. 2012. Aquatic macroinvertebrate biodiversity: patterns and surrogates in mountainous Spanish National Parks. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22: 598-615.

Hill, M.J., Ryves, D.B., White, J.C. and Wood, P.J. 2016. Macroinvertebrate diversity in urban and rural ponds: Implications for freshwater biodiversity conservation. *Biological Conservation*, 201: 50-59.

Holgerson, M.A. and Raymond, P.A. 2016. Large contribution to inland water CO_2 and CH_4 emissions from very small ponds. *Nature Geoscience*, 9: 222-226.

Hutchinson, G.E. 1933. The zoogeography of the African aquatic Hemiptera in relation to past climate change. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*, 28: 436-468.

Juliano, S.A. 1991. Changes in structure and composition of an assemblage of *Hydroporus* species (Coleoptera: Dytiscidae) along a pH gradient. *Freshwater Biology*, 25: 376-378.

Kadoya, T., Suda, S.-I., Tsubaki, Y. and Washitani, I. 2004. Dragonfly species richness on man-made ponds: effects of pond size and pond age on newly established assemblages. *Ecological Research*, 19: 461-467.

Karaouzas, I. and Gritzalis, K.C. 2006. Local and regional factors determining aquatic and semi-aquatic bug (Heteroptera) assemblages in rivers and streams of Greece. *Hydrobiologica*, 573: 199-212.

Kazangaki, A., Chapman, L.J. and Balirwa, J. 2008. Land use and the ecology of benthic macroinvertebrate assemblages of high-altitude rainforest streams in Uganda. *Freshwater Biology*, 53: 681-697.

Kietzka, G.J., Pryke, J.S. and Samways, M.J. 2016. Aerial adult dragonflies are highly sensitive to in-water conditions across an ancient landscape. *Diversity and Distributions*, 23: 14-26.

Kirkman, K.E. and Pott, R.M. 2002. Biodiversity conservation in plantation forestry. In: Pierce, S.M., Cowling, R.M., Sandwith, T. and MacKinnon, K. (eds). *Mainstreaming biodiversity in development case studies from South Africa*. The World Bank Environmental Department, Washington DC, USA. pp. 33-42.

Landin, J. 1980. Habitats, life histories, migration and dispersal by flight of two water-beetles *Helophorus brevipalpis* and *H. strigifrons* (Hydrophilidae). *Ecography*, 3: 190-201.

MacArthur, R.H. and MacArthur, J.W. 1961. On bird species diversity. *Ecology*, 42: 594-598.

MacArthur, R.H. and Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press, New Jersey.

Martínez-Sanz, C., Canzano, C.S.S., Fernández-Alaéz, M. and García-Criado, F. 2012. Relative contribution of small mountain ponds to regional richness of littoral macroinvertebrates and the implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22: 155-164.

McGeoch, M.A. 2007. Insects and bioindication: theory and progress. In: Stewart, A.J.A., New, T.R. and Lewis, O.T. (eds). *Insect Conservation Biology*. CABI Publishing, Oxfordshire, UK. pp. 144-174.

Mendoza, G. and Catalan, J. 2010. Lake macroinvertebrates and the altitudinal environmental gradient in the Pyrenees. *Hydrobiologica*, 648: 51-72.

Michiels, N.K. and Dhondt, A.A. 1990. Costs and benefits associated with oviposition site selection in the dragonfly *Sympetrum danae* (Odonata: Libellulidae). *Animal Behaviour*, 40: 668-678.

Mlambo, M.C., Bird, M.S., Reed, C.C. and Day, J.A. 2011. Diversity patterns of temporary wetland macroinvertebrate assemblages in the south-western Cape, South Africa. *African Journal of Aquatic Science*, 36: 299-308.

Muggeo, V.M.R. 2017. Regression Models with Break-Points / Change-Points Estimation. R package version 0.5-2.1.

Nicolet, P., Biggs, J., Hodson, M.J., Reynolds, C., Whitfield, M. and Williams, P. 2004. The wetland plant and macroinvertebrate assemblage of temporary ponds in England and Wales. *Biological Conservation*, 120: 261-278.

Oertli, B., Joye, D.A., Castella, E., Juge, R., Cambin, D. and Lachavanne, J.-B. 2002. Does size matter? The relationship between pond area and biodiversity. *Biological Conservation*, 104: 59-70.

Oertli, B., Indermuehle, N., Angélibert, S., Hinden, H. and Stoll, A. 2010. Macroinvertebrate assemblages in 25 high alpine ponds of the Swiss National Park (Cirque of Macun) and relation to environmental variables. *Hydrobiologica*, 597: 29-41.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. and Oksanen, M.J. 2017. Vegan: Community Ecology Package. R package version 2.4–2.

Ormerod, S.J., Durance, I., Terrier, A. and Swanson, A.M. 2009. Priority wetlands invertebrates as conservation surrogates. *Conservation Biology*, 24: 573-582.

Osborn, R. and Samways, M.J. 1996. Determinants of adult dragonfly assemblage patterns at new ponds in South Africa. *Odonatologica*, 25: 49-58.

Picazo, F., Moreno, J.L. and Millán, A. 2010. The contribution of standing waters to aquatic biodiversity: the case of water beetles in southeastern Iberia. *Aquatic Ecology*, 44: 205-216.

Polhemus, J.T. 2008. Aquatic and semiaquatic Hemiptera. In: Merrit, R.W., Cummins, K.W. and Berg, M.B. (eds). *An introduction to the aquatic insects of North America*. Kendall/Hunt Publishing Co., Dubuque, USA. pp. 385-423.

Pryke, J.S., Samways, M.J. and De Saedeleer, K. 2015. An ecological network is as good as a major protected area for conserving dragonflies. *Biological Conservation*, 191: 537-545.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reavell, P.E. 2003. Hemiptera. In: de Moor, I.J., Day, D.A. and de Moor, F.C. (eds). *Volume 8: Insecta II Guides to the freshwater invertebrates of southern Africa*. Water Research Commission, Pretoria.

Rundle, S.D., Bilton, D.T. and Foggo, A. 2007. By wind, wings or water: body size, dispersal and range size in aquatic invertebrates. In: Hildrew, A.G., Rafaelli, D.G. and Edmonds-Brown, R. (eds). *Body size: The structure and function of aquatic ecosystems*. Cambridge University Press, Cambridge, UK. pp. 186-209.

Samways, M.J. 1989a. Farm dams as nature reserves for dragonflies (Odonata) at various altitudes in the Natal Drakensberg Mountains, South Africa. *Biological Conservation*, 48: 181-187.

Samways, M.J. 1989b. Taxon turnover in Odonata across a 3000 m altitudinal gradient in southern Africa. *Odonatologica*, 18: 263-274.

Samways, M.J. 1991. Dragonfly conservation in South Africa: a biogeographical perspective. *Odonatologica*, 21: 165-180.

Samways, M.J. 2008. *Dragonflies and damselflies of South Africa*. Pensoft Publishers, Sofia, Bulgaria.

Samways, M.J. and Pryke, J.S. 2016. Large-scale ecological networks do work in an ecologically complex biodiversity hotspot. *Ambio*, 45: 161-172.

Samways, M.J. and Sharratt, N.J. 2010. Recovery of endemic dragonflies after removal of invasive alien trees. *Conservation Biology*, 24: 267-277.

Samways, M.J. and Simaika, J.P. 2016. *Manual of freshwater assessment for South Africa: Dragonfly Biotic Index*. Suricata 2. South African National Biodiversity Institute, Pretoria, South Africa.

Samways, M.J., Osborn, R. and van Heerden, I. 1996. Distribution of benthic invertebrates at different depths in a shallow reservoir in the KwaZulu-Natal Midlands. *Koedoe*, 39: 69-76.

Savage, A.A. 1989. Adults of the British aquatic Hemiptera Heteroptera: a key with ecological notes. *Freshwater Biological Association*.

Savage, A.A. 1994. The distribution of Corixidae in relation to the water quality of British lakes: a monitoring model. *Freshwater Reviews*, 4: 32-61.

Scheffer, M., van Geest, G.J., Zimmer, K., Jeppsen, E., Sondergaard, M., Butler, M.G. and De Meester, L. 2006. Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. *Oikos*, 112: 227-231.

Scheibler, S.S., Melo, M.C., Montemayor, S.I. and Scollo, A.M. 2016. Abundance, richness, seasonal and altitudinal dynamics of aquatic true bugs (Heteroptera) in mountain wetlands of Argentina. *Wetlands*, 36: 265-274.

Schindler, M., Fesl, C. and Chovanec, A. 2003. Dragonfly associations (Insecta: Odonata) in relation to habitat variables: a multivariate approach. *Hydrobiologia*, 497: 169-180.

Shieh, S.-H. and Chi, Y.-S. 2010. Factors influencing macroinvertebrate assemblages in artificial subtropical ponds of Taiwan. *Hydrobiologica*, 649: 317-330.

Shulze, R.E. 1982. *Agrohydrology and –climatology of Natal*. Water Research Commission, Pretoria, South Africa.

Simaika, J.P., Samways, M.J. and Frenzel, P.P. 2016. Artificial ponds increase local dragonfly diversity in a global biodiversity hotspot. *Biodiversity and Conservation*, 25: 1921-1935.

Skaife, S.H. 1979. *African Insect Life*. Struik, Cape Town, South Africa.

Stals, R. 2003. Coleoptera. In: Stals, R. and de Moor, I.J. (eds). *Volume 10: Coleoptera Guides to the Freshwater invertebrates of southern Africa*. Water Research Commission, Pretoria.

Tooth, S., Ellery, F., Grenfell, M., Thomas, A., Kotze, D. and Ralph, T. 2014. *10 reasons why the geomorphology of wetlands is important*. Climate Change Consortium of Wales, Wales.

Valente-Neto, F., de Oliveira Roque, F., Rodrigues, M.E., Juen, L. and Swan, C.M. 2016. Toward a practical use of Neotropical odonates as bioindicators: Testing congruence across taxonomic resolution and life stages. *Ecological Indicators*, 61: 952-959.

Verberk, W.C.E.P., van Duinen, G.-J.A., Peeters, T.M.J. and Esselink, H. 2001. Importance of variation in water-types for water beetle fauna (Coleoptera) in Korenburgerveen, a bog remnant in the Netherlands. *Proceedings of the Section Experimental and Applied Entomology*, 12: 121-128.

Vogler, A.P. and Ribera, I. 2003. Evolutionary analysis of species richness patterns in aquatic beetles: why macroecology needs a historical perspective. In: Blackburn, T.M. and Gaston, K.J. (eds). *Macroecology: causes and consequences*. Oxford Blackwell Science, Oxford, UK. pp. 17-30.

Williams, P., Biggs, J., Crowe, A., Murphy, J., Nicolet, P., Weatherby, A. and Dunbar, M. 2010. Countryside survey report from 2007, Technical report No 7/07. Pond Conservation and NERC/Centre for Ecology and Hydrology, Lancaster, UK.

Chapter 5 Aquatic insects decline in abundance and occupy low-quality artificial habitats to survive hydrological droughts

*Published as: Deacon, C., Samways, M.J. and Pryke, J.S. 2019. Aquatic insects decline in abundance and occupy low quality artificial habitats to survive hydrological droughts. Freshwater Biology 64: 1643-1654. DOI: 10.1111/fwb.13360.

Abstract

Hydrological extremes have negative impacts on natural, agricultural, and urban landscapes and place substantial ecological pressure on freshwater habitats. However, the role of artificial freshwater habitats during hydrological drought is poorly understood. Insects make up much of total aquatic fauna and lend themselves to understanding how drought impacts freshwater ecosystems. Using the Greater Cape Floristic Region as an example of a drought-prone area, we determined the effects of a severe drought on a subset of insects occupying lentic habitats in terms of their species richness, diversity, and assemblage composition. Here, we: 1) calculated the percentage change in average precipitation between a record dry season and the last consistently wet decade, 2) identified the environmental variables driving aquatic insect species richness, diversity and composition, 3) identified the environmental differences between natural ponds and artificial reservoirs, 4) determined whether artificial reservoirs act as suitable habitats for focal taxa during drought, and 5) compared these results to other, pre-drought studies. Environmental variables related to water chemistry and physical characteristics were drivers of species richness, diversity, and composition, yet vegetation cover remained a major driver. In terms of marginal vegetation cover, most artificial reservoirs did not resemble natural ponds, yet overall 38.4% of sampled aquatic insect species were shared between natural ponds and artificial reservoirs. We found some rare endemic species in artificial reservoirs that had never before been recorded in this habitat during wet years. When our drought findings were compared to earlier, wet years, species richness did not change significantly, although abundance was much lower during the drought year. We postulate that historically, these aquatic insects, which have been through many ecological filters such as drought, must have sought low-quality habitats to survive water stress periods. Artificial reservoirs, being novel landscape features, cannot fully replace natural ponds, but enable some aquatic insects to survive drought. Artificial reservoirs can be attractive habitats to aquatic insects when they resemble natural ponds, with specific reference to their marginal vegetation characteristics.

Keywords: climate change, community, conservation, invertebrates, physical environment, ponds

5.1 Introduction

Hydrological extremes are increasing in frequency and magnitude in the face of anthropogenically induced climate change and have negative impacts on natural and agro-ecosystems (Dai 2013). Future precipitation patterns are predicted to be highly variable (Trenberth et al. 2014) and their ecological effects are often only visible after environmental conditions recovered to the pre-impacted state (Bond et al. 2008; Mosley 2015). The effects of hydrological extremes on lotic ecosystems are fairly well understood (e.g. Bond et al. 2008; Dahm et al. 2003), yet their effects on biotic communities occupying lentic ecosystems have received much less research attention.

In its simplest terms, drought is defined as an extended period of below-average precipitation relative to the statistical multi-year mean for a particular region (Druyan 1996) and is characterised by its duration, intensity, and spatial extent. Most droughts in the southern hemisphere are linked to the El Niño/Southern Oscillation phenomenon (Pohl et al. 2009; Schiewer 1998) and can be separated into four categories: hydrological, meteorological, agricultural, and socio-economic (Bond et al. 2008). During hydrological droughts, substantial ecological pressure is placed on freshwater habitats through changes in the hydrological cycle and water levels, with cascading effects on water quality related to elevated water temperature, lower re-aeration, and changes in re-mineralisation processes (Bunn and Arthington 2002; Collinson et al. 1995; Mosley 2015).

Natural ponds, which are associated with drainage lines, are impacted by drought through decreased stream input and surface runoff, as well as increased evaporation rates (Bond et al. 2008). They are generally well vegetated, occupied by many permanent and semi-permanent aquatic populations and are high-quality habitat islands for several endemic aquatic plants and insects (Bilton et al. 2008; Mlambo et al. 2011). However, during drought periods, the drop in water level exposes the productive littoral zone (Furey et al. 2006) and diminishes aquatic and amphibiotic biological communities (Bond et al. 2008). These small and isolated lentic habitats are also extremely vulnerable to agricultural activity and urbanisation, especially so in interaction with anthropogenic climate change (Declerck et al. 2006; Kotze et al. 1995).

Artificial reservoirs are common modern landscape features in arid and semi-arid countries (Apinda-Legnouo et al. 2014) with the main function of storing water (Votruba and Broža 1989) to alleviate the effects of seasonal drought on the agricultural and socio-economic sectors. Some artificial reservoirs are constructed in ancient waterways, and are frequently disturbed, low-quality aquatic habitats, evident through their fluctuating water levels and general lack of marginal and submerged vegetation. However, artificial reservoirs with high water levels at the start of the wet season, and rich marginal vegetation, are attractive to aquatic biodiversity (Janssen et al. 2018; Nicolet et al. 2004; Oertli et al. 2002; Williams et al. 2008). These novel aquatic habitats increase the overall area of occupancy of several insect groups and can act as refuges by offering stable conditions during environmental stress (Osborn and Samways 1996; Samways 1989a).

Many aquatic taxa that occupy drought-prone lentic habitats have various resistance (related to life history) and resilience (related to dispersal and recolonisation) traits that enable them to survive droughts (Humphries and Baldwin 2003). However, some studies provide evidence that droughts have severe impacts on riparian and aquatic communities, leading to significant population declines (Jenkins and Boulton 2007; Osborn and Samways 1996; Samways and Niba 2010) and in some cases, local and regional extinctions (Boulton and Lake 2008). Aquatic insects make up much of total aquatic fauna (Batzer and Wissinger 1996) and fulfil several important biological and ecological roles. As such, aquatic insects can serve as indicators of environmental quality, and aid in understanding how droughts impact freshwater ecosystems (Apinda-Legnouo et al. 2014; Bird 2010; Mlambo et al. 2011; Simaika et al. 2016).

Dragonflies are excellent indicators of habitat quality as they are highly sensitive to local environmental changes, are well known taxonomically, are highly visible and widely distributed, and have life cycles with aquatic larval and terrestrial adult stages. Adults are highly mobile and respond strongly to vegetation composition (Kietzka et al. 2016; Samways and Niba 2010), allowing them to select suitable habitats (Samways and Sharratt 2010). As a result, diminishing or improving habitat conditions can be ascertained from the complement of dragonfly assemblages occupying various freshwater habitats.

Aquatic beetles and bugs are receiving increasing attention as indicators of water quality (Apinda-Legnouo et al. 2014; Mlambo et al. 2011) as most are highly mobile as adults and fulfil many roles in aquatic ecosystems as herbivores, detritivores, and predators (Scholtz and Holm 1985). Both groups are atmospheric breathers, have amphibious adult stages (although they spend most time in the water) and are sensitive to biotic (e.g. aquatic and/or marginal vegetation structure, conspecific densities, presence of predators) and abiotic factors (e.g. water chemistry, climatic factors, habitat change) within their aquatic and terrestrial habitats (Karaouzas and Gritzalis 2006; Lytle 2015; Yee and Kehl 2015). Aquatic beetles and bugs are good indicators of localised conditions of lotic ecosystems at coarse taxonomic scale (Dickens and Graham 2002), with different families responding to varying degrees of environmental change (Stals and de Moor 2007).

As there is limited information available on the response of lentic insect assemblages to drought events, we determined here whether artificial reservoirs, being novel landscape features, acted as supplementary habitats for dragonflies, beetles, and bugs occupying natural ponds using biological and environmental data obtained from the Greater Cape Floristic Region (GCFR) biodiversity hotspot (Mittermeier et al., 2004) during drought. We had five main objectives: 1) to calculate the percentage change in average precipitation between the sampling period and the last consistently wet decade, 2) to identify the environmental variables driving aquatic insect species richness and composition, 3) to identify environmental differences between natural ponds and artificial reservoirs, 4) to determine whether artificial reservoirs can act as suitable habitats for the focal taxa during drought; and, finally, 5) to compare our results with other, pre-drought studies on the focal insect taxa in the same study area. These results will identify the key environmental differences between natural ponds and artificial reservoirs, and identify the important features of lentic habitats for supporting high aquatic insect species richness and diversity under extreme drought conditions.

5.2 Methods

5.2.1 Study sites

The GCFR received highly variable precipitation during the last 2 decades (Botai et al. 2018) in combination with increasing intensity and frequency of heat addition (Dai 2013; Mosley 2015; Trenberth et al. 2014). As in many parts of the world, this has led to one of the driest hydrological years in the GCFR on record (years 2016–2017, Botai et al. 2018). Sixteen perennial natural ponds and 16 perennial artificial reservoirs were selected across the GCFR, from seven geographic locations, based on site availability and to represent regional biodiversity and a range of environmental conditions: Betty's Bay (two natural ponds), Cederberg (three natural ponds), Grabouw (five natural ponds, four artificial reservoirs), Franschhoek (four natural ponds), Stellenbosch (three artificial reservoirs), Somerset West (nine artificial reservoirs), and Worcester (two natural ponds; Figure 5.1).

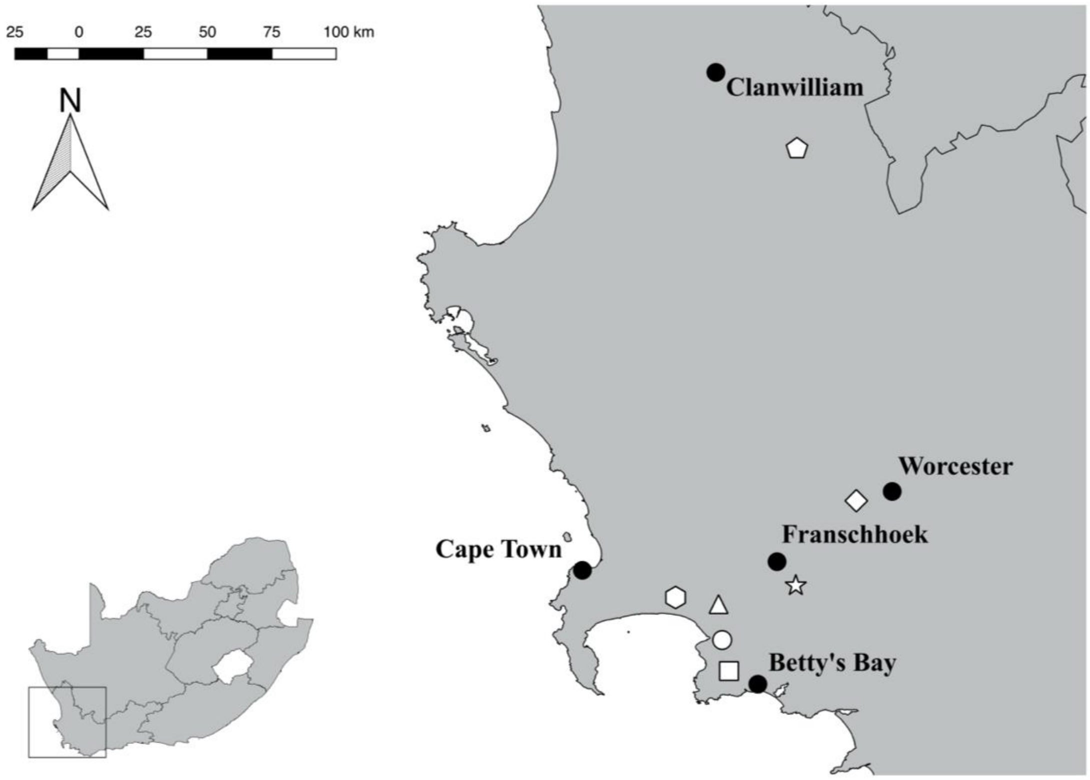


Figure 5.1 Locations of sampling sites in the Greater Cape Floristic Region. Pentagon: Cederberg; diamond: Worcester; star: Franschhoek; hexagon: Stellenbosch; triangle: Somerset West; circle: Grabouw and square: Betty's Bay. Filled circles represent nearby towns.

5.2.2 Precipitation anomalies

Merged microwave-infrared precipitation rate and root-mean-square precipitation-error estimated precipitation data (mm/month; quarter degree spatial resolution) were obtained from the NASA EarthData Portal (Tropical Rainfall Measuring Mission 2011) for March–August for the years 2000–2009 (the last consistently wet decade) and 2016–2017 (the dry sampling season). The average monthly precipitation was calculated for March–May (2000–2009 and 2016–2017, respectively), and June–August (2000–2009 and 2016–2017, respectively) in

QGIS (Quantum GIS Development Team 2017). To calculate the percentage precipitation change during 2016–2017, the monthly precipitation average of March–May and June–August were subtracted from the monthly precipitation average of March–May and June–August 2000–2009.

5.2.3 Field data collection

Sampling was over two seasons, spring 2016 (September– November) and autumn 2017 (February–April), on cloudless, windless days, between 10h30 and 15h30. All adult individuals of dragonflies (Odonata), water beetles (Coleoptera), and water bugs (Hemiptera) were sampled. Ten quadrats of 4 m^2 were selected along the edge of both natural ponds and artificial reservoirs, and swept with an aquatic net (300 mm × 300 mm; 1,000-μm mesh size) for 30 min to collect beetles and bugs. Quadrats were selected to represent all structural features of the water body and no deeper than 1.2 m, below which aquatic insect diversity declines significantly in the region (Samways, 1996). Collected individuals were identified to species using Stals and de Moor (2007) and Griffiths et al. (2015), as well as museum collections. For adult dragonflies, two 50-m long and 6-m wide transects were selected per site, in which all adult dragonflies were recorded for a total time of 30 min. Hawking dragonfly species (e.g. *Anax speratus*, *Zosteraeshna minuscula*) that were within a few metres of transects were also included. Reference individuals are housed in the Entomology Museum, Stellenbosch University.

At each study site, 10 point measurements of environmental parameters were recorded at the time of aquatic sweeping and averaged for each study site. These parameters were: water temperature (°C), dissolved oxygen (mg/L), conductivity (μS), pH, and water clarity (cm visibility). In addition, elevation (m above sea level), sampling depth (m), and water body size (m^2) were recorded. Vegetation community composition and structure was determined in five random quadrats of 4 m^2 along the edge of each water body. Within each quadrat, the % grass cover, % reed cover, % forbs cover, % total cover, and average vegetation height were recorded.

5.2.4 Statistical analyses

The Shannon diversity index (referred to as 'diversity' from here on), reflecting species dominance and relative abundance, was calculated for each insect order occupying each pond type in R using the *vegan* package (Oksanen et al. 2017; R Development Core Team 2016). Generalised linear mixed models with Poisson distribution were calculated for dragonfly, beetle, and bug species richness for all ponds as well as for each taxon in natural ponds and artificial reservoirs separately. Further depending on the distribution of the data, generalised linear models with binomial distribution or linear mixed models with Gaussian distribution were created for dragonfly, beetle and bug diversity overall for all ponds as well as for each taxon per natural ponds and artificial reservoirs to test the effects of environmental variables on species richness and diversity in R using the *lme4* package (Bates and Sarkar 2007; R Development Core Team 2016). These models were individually built for each focal taxon with pond size, elevation, pond type, vegetation height, % total vegetation cover, % reed cover, % forbs cover, % grass cover, sampling depth, dissolved oxygen, water temperature, water conductivity, water pH, and water clarity as fixed variables (18 separate models in total). The geographic distances between study sites were included as an additional fixed variable for all overall models. For generalised linear mixed models and generalised linear models, the seven locations where the sites were situated were included as a categorical spatial random variable as the data were spatially dependent, and these models were fitted by a Laplace approximation. In the case of categorical fixed variables, categorical pairwise *t*-tests and Tukey post hoc tests were used to test for significance. For all significant regressions for both species richness and diversity models, piecewise regressions were performed to determine whether regressions had break points in their relationships between environmental variables and response variables, using the *Segmented* package in R (Muggeo 2017; R Development Core Team 2016).

Principal coordinates of neighbourhood matrices (PCNMs) were used to determine the variation in species composition in relation to environmental variables and spatial structuring (i.e. geographic distances between sampling sites) in R using the *vegan* package (Oksanen et al. 2017; R Development Core Team 2016). To standardise biological datasets, Hellinger transformations were performed. The significant contribution to biological community variation, by each environmental variable and spatial structuring, was determined using 999 permutations of redundancy analyses for each focal taxon individually. Chi-squared tests were used to determine whether natural ponds and artificial reservoirs were significantly different in terms of physical and environmental properties.

Biological data were compared with pre-drought studies, following the same sampling methods, in the same geographic area for dragonflies (Simaika et al. 2016; field data obtained

2014– 2015), beetles and bugs (Apinda-Legnouo et al. 2014; field data obtained 2005–2006). Although the sampling period of Simaika et al. (2016) did not coincide with the last consistently wet decade (2000–2009), past rainfall data suggested that the period 2010–2015 had an average annual rainfall just below the historical annual average (Tropical Rainfall Measuring Mission 2011). As a result, the biological communities occupying lentic habitats in the study region during 2010–2015 were likely to be similar to those that were present during the last consistently wet decade. Average insect density for each taxon was calculated by dividing the abundance per taxon by the number of samples taken, for the pre-drought studies and biological data here, respectively. To calculate the change in average insect density between our data and the pre-drought studies, the average densities calculated here were divided by the average densities for the pre-drought studies, and converted to percentage change in density.

5.3 Results

5.3.1 Precipitation deficit in the GCFR

The average precipitation rate for March–May 2000–2009 (the last consistently wet decade) ranged between 25 mm/month in the northern (Cederberg) area and 73 mm/month in the southern (Betty's Bay) area (Table 5.1). For June–August 2000–2009, the average monthly precipitation rate ranged from 60 mm/month in the northern area to 163 mm/month in the southern area. For March–May 2016–2017, overall average precipitation was much lower than for 2000–2009 (Table 5.1), ranging from 8 mm/month below average in the northern area and 40 mm/month below average in the southern area. During June–August 2016–2017, precipitation deficit was magnified with 22 mm/month below average in the northern area and 43 mm/month below average in the southern area.

Table 5.1 Average rain season precipitation rate for the Greater Cape Floristic Region in mm/month and percentage difference (bold) of 2016–2017, for each sampling location.

	Betty's Bay	Cederberg	Worcester	Franschhoek	Grabouw	Stellenbosch	Somerset West
Average precipitation 2000-2009 (March to May)	82.22	25.02	42.93	50.45	52.44	55.44	72.73
Average precipitation 2000-2009 (June to August)	162.94	59.79	101.47	115.33	101.31	118.55	148.58
Average precipitation 2016-2017 (March to May)	46.00	17.10	25.01	29.22	27.09	29.27	39.88
Average precipitation 2016-2017 (June to August)	120.03	37.58	87.35	95.73	89.37	90.34	110.06
2016-2017 percentage difference (March to May)	**(-)44.1**	**(-)31.7**	**(-)41.7**	**(-)42.1**	**(-)48.3**	**(-)47.2**	**(-)45.2**
2016-2017 percentage difference (June to August)	**(-)26.3**	**(-)37.1**	**(-)13.9**	**(-)17.0**	**(-)11.8**	**(-)23.8**	**(-)25.9**

(-) Indicates below the monthly average of 2000–2009.

5.3.2 Species sampled in the GCFR

A total of 45 lentic species were recorded (5,069 individuals), comprising 22 dragonfly species (510 individuals; 20 species for natural ponds; 12 species for artificial reservoirs), 12 beetle species (665 individuals; 11 species for natural ponds; five species for artificial reservoirs), and 11 bug species (3,894 individuals; 11 species for natural ponds; four species for artificial reservoirs). The number of observed species approached the estimated number of species (Chao2 and Jackknife2) across all insect orders, indicating that sampling was sufficient and the subset of data representative (Appendix S5.1). For the full species list, refer to Appendix S5.2.

5.3.3 Environmental differences between natural ponds and artificial reservoirs

Out of the 13 environmental variables measured, four variables were significantly different between natural ponds and artificial reservoirs (Table 5.2). These were water body size, elevation, % grass cover, and % forbs cover. Natural ponds and artificial reservoirs were statistically identical in terms of temperature, dissolved oxygen, conductivity, pH, water clarity, sampling depth, % reed cover, % total cover, and average vegetation height.

Table 5.2 Means, standard errors (SE) and $\chi2$ test results indicating differences between natural ponds and artificial reservoirs for each physical and physicochemical variable.

	Natural ponds		Artificial reservoirs		X^2
	Mean	**SE**	**Mean**	**SE**	
Temperature (ºC)	20.79	1.11	19.69	0.56	0.03
Dissolved oxygen (mg/L)	10.75	2.78	8.32	0.75	0.31
Conductivity (µs)	163.36	27.57	177.04	42.87	0.55
pH	6.3	0.21	6.21	0.3	0
Water clarity (cm visibility)	66.12	4.82	51.52	6.35	1.81
Elevation (m a.s.l.)	371	61.9	319.13	49.47	3.89*
Sampling depth (m)	0.55	0.04	0.53	0.03	0
Water body size (m^2)	2662.66	752.18	168277.48	100771.33	16.04***
% Grass cover	6.84	3.84	22.13	8.79	8.06**
% Reed cover	6.32	5.26	5.75	2.88	0.03
% Forbs cover	38.42	9.19	16	7.82	9.23**
% Total cover	51.58	9.05	43.88	9.38	0.62
Vegetation height (m)	0.51	0.1	0.32	0.08	0.04

Significance levels: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

5.3.4 Influence of environmental variables on insect species richness and diversity

Overall, dragonfly species richness positively correlated to vegetation height until 0.14 m was reached, after which species richness increased at a lower rate (Table 5.3; Appendix S5.3). An increase in conductivity gave a positive correlation to overall dragonfly species richness until 115 µS was reached, after which species richness only increased steadily. In the case of natural ponds, dragonfly species richness positively correlated with water clarity initially, but decreased above 89 cm visibility. For artificial reservoirs, dragonfly species richness and diversity positively correlated to % reed cover and % grass cover, although marginally for dragonfly diversity. Dragonfly species richness was positively correlated with conductivity, and negatively correlated with water depth, until about 0.4 m was reached, after which dragonfly species richness increased.

Table 5.3 Significant effects of pre-selected environmental variables on overall species richness and Shannon diversity index, and within each water body type.

		Overall		**Natural ponds**		**Artificial reservoirs**	
		Richness	**Diversity**	**Richness**	**Diversity**	**Richness**	**Diversity**
Odonata	**Conductivity (µs)**	(+/+) 4.51 *				(+) 5.85 *	
	Water clarity (cm visibility)			(+/-) 3.93 *			
	Vegetation height (m)	(+/+) 5.46 *					
	% Reed cover					(+) 7.53 **	**(+) 1.73** *
	% Grass cover					(+) 9.62 **	**(+) 1.87** *
	Sampling depth (m)					(-/+) 9.57 **	
Coleoptera	**Elevation (m a.s.l.)**						(+) 10.73 **
	Conductivity (µs)					(-/+) 4.63 *	(+) 16.31 ***
	pH						(-) 6.25 *
	Pond size (m^2)					(+/-) 21.37 ***	
	% Total vegetation cover					(+) 18.03 ***	
	% Forb cover		**(+) 2.14** *				
	% Grass cover		**(+/+) 2.38** **				(+) 28.62 ***
	Pond type	*3.11* **					
Hemiptera	**Elevation (m a.s.l.)**					(-) 6.49 *	
	Temperature (°C)			(-/+) 5.68 *			
	Conductivity (µs)					(+) 5.33 *	
	Dissolved oxygen (mg/L)			(-) 9.21 **			
	% Reed cover			(-) 4.58 *			
	% Grass cover		**(+/+) 2.45** *	(-/+) 6.01 *			

Table displays pseudo-*F* values, *Z*-values (bold) and *t*-values (italics) in the case of categorical variables.
Significance levels: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$

Natural ponds had higher overall beetle species richness than artificial reservoirs (Table 5.3; Appendix S5.3). Beetle diversity was positively correlated with % forb cover and % grass cover, but increased at a higher rate above 47% grass cover. For natural ponds, no environmental variables had a significant effect on beetle species richness and diversity. In the case of artificial reservoirs, beetle species richness was positively correlated with % total cover, and initially to water body size until a size of 155,738 m^2 was reached, above which species richness decreased. Species richness was negatively correlated to conductivity until 53 µS was reached, above which beetle species richness then increased. Beetle diversity was positively correlated with elevation, conductivity and % grass cover, but negatively correlated with water pH.

Overall, no environmental variables had a significant effect on bug species richness, yet bug diversity was positively correlated with % grass cover, and increased at a higher rate above 24% grass cover (Table 5.3; Appendix S5.3). For natural ponds, bug species richness was negatively correlated with dissolved oxygen and % reed cover. Bug species richness was negatively correlated with water temperature and % grass cover, but increased above 17°C and 39% grass cover, respectively. For artificial reservoirs, bug species richness was positively correlated with conductivity and negatively correlated with elevation. No environmental variables had a significant effect on bug diversity in artificial reservoirs.

5.3.5 Influence of environmental variables on insect assemblage composition

Ten of the sampled dragonfly species (45.5%) only occupied natural ponds (Appendix S5.1). These were: *Africallagma sapphirinum*, *A. speratus*, *Ceriagrion glabrum*, *Chlorolestes umbratus*, *Elattoneura frenulata*, *Proischnura polychromatica*, *Spesbona angusta*, *Syncordulia legator*, *Trithemis annulata*, and *Crocothemis erythraea*. Two dragonfly species (9%; *Pinheyschna subpupillata* and *Syncordulia* venator) only occupied artificial reservoirs. Seven aquatic beetle species only occupied natural ponds (25.3%; *Agabus* sp., *Copelatus* sp. 1 and 2, *Darwinhydrus* sp., *Helochares* sp., *Hydropeplus* sp. and *Philaccolus* sp.). One aquatic beetle species, *Perovatellus* sp., only occupied artificial reservoirs (8.3%). Seven bug species (63.6%) only occupied natural ponds: *Appasus capensis*, *Gerris swakopensis*, *Laccocoris spurcus*, *Mesovelia vittigera*, *Ranatra* sp., *Rhagovelia maculate*, and *Tenagogonus* sp. No aquatic bug species exclusively occupied artificial reservoirs.

Out of the 14 variables measured, PCNM selected five significant variables for aquatic insect species composition. These were spatial structure, % total vegetation cover, temperature, conductivity, and pond type (Table 5.4). Pond size, elevation, sampling depth, dissolved oxygen, water pH, turbidity, vegetation height and % reed, % grass, and % total cover had no significant effect on species composition. For dragonfly composition, 20.50% of variation was explained by spatial structure, 6.90% explained by % total vegetation cover, and 5.08% explained by temperature, totalling 32.50% of variation explained. For beetle composition, pond type explained 9.31% of total variation, 6.00% explained by temperature, and 5.33% explained by conductivity, totalling 20.63% of variation explained. For bug composition, pond type explained 20.76% of total variation.

Table 5.4 Comparative abundance, number of observed species (S_{obs}) and average density (calculated as the number of individuals per sample) between results, Simaika et al. (2016) (for dragonflies) and Apinda-Legnouo et al. (2014) (for beetles and bugs).

	Dragonflies			**Beetles**			**Bugs**		
	Sobs	**Abundance**	**Density**	**Sobs**	**Abundance**	**Density**	**Sobs**	**Abundance**	**Density**
Results here	22	510 (140 samples)	3.64	12	665 (700 samples)	0.95	11	3 894 (700 samples)	5.56
Simaika et al. 2016	28	1905 (90 samples)	21.17						
Apinda-Legnouo et al. 2014				5	2 086 (504 samples)	4.14	14	8 140 (504 samples)	16.15
PERCENTAGE CHANGE			**83%**			**77%**			**66%**

Change in density during sampling period given as percentage change.

5.4 Discussion

5.4.1 Precipitation deficit

South Africa is considered a semi-arid country with precipitation below the global average and is characterised by highly variable precipitation from one season to the next (Botai et al. 2018). Our results indicate that most of the GCFR experienced major precipitation deficiency during 2016–2017, with below-average precipitation ranging from 8 mm/month in the northern area to 43 mm/month in the southern area. Although having great socio-economic impacts, the environmental impacts of hydrological droughts on lentic ecosystems are poorly understood. Similar to lotic ecosystems (Mosley 2015), hydrological droughts may result in substantial changes in habitat quality, related to physical transformation, and alteration of physicochemical processes.

5.4.2 Relative significance of vegetation

Lentic insects showed a positive response to vegetation cover and complexity across all three taxa, and vegetation remains among the primary drivers of aquatic insect diversity (Kadoya et al. 2004; Samways and Taylor 2004). Competition for suitable habitat is often high where vegetation cover and complexity is absent, leading to low species richness and diversity (Fairchild et al. 2003). Most dragonflies require emergent and marginal vegetation as perching sites, for thermoregulation, and as microhabitats for oviposition. Emergent and submerged vegetation also serve as substrate for dragonfly larvae from which to hunt, seek refuge from predators, and/or emerge to adulthood. Early colonising beetles and bugs, although having been described as being little affected by vegetation structure (Bloechl et al. 2010), favour vegetated margins of water bodies for oviposition (Fairchild et al. 2003), and similar to dragonfly larvae, vegetation provides refuge, and is also where prey most commonly occurs (Verberk et al. 2001). Artificial reservoirs characterised by little vegetation coverage and/or low vegetation complexity (most of the artificial reservoirs sampled here), had fewer natural resources available, resulting in low species richness and diversity (Fairchild et al. 2003).

5.4.3 Relative significance of environmental variables

Drought, in combination with anthropogenic influences, stimulates high stochasticity in water quality through climatic variation and hydrological shifts (Mosley 2015), and limits the delivery of water quality components from catchment areas (Olds et al. 2011; Worrall and Burt 2008). We found that water temperature was among the primary drivers of overall dragonfly composition. In general, speed of development for lentic dragonfly larvae increases under warmer conditions, within their thermal limits (Corbet et al. 2006; Suhling et al. 2015). Adult aquatic beetles and bugs are atmospheric breathers, and do not rely on dissolved oxygen directly, yet bug species richness showed some response to water temperature and dissolved oxygen. Most bug species are early colonisers of water bodies and are physically and physiologically enabled to occupy lentic habitats fluctuating in daily/seasonal water temperature and dissolved oxygen (Florencio et al. 2009; Scheibler et al. 2016), but high concentrations of dissolved oxygen and low water temperature create suitable conditions for predators, influencing the occupancy and diversity of aquatic bugs (Lytle 2015).

Water pH and conductivity (as a proxy for total dissolved solids) may increase slightly in lentic systems during extended droughts (Ludovisi and Gaino 2010; Mosley et al. 2012) and changes in pH and conductivity ranges shape aquatic insect communities (Kietzka et al. 2016; da Rocha et al. 2016). We found that dragonfly diversity in natural ponds and beetle diversity in artificial reservoirs were highest where pH was close to neutral, implying that habitats deviating from neutral pH were dominated by single, generalist species. Bugs are more robust to pH gradients, as most dwell just under the water surface, or spend some time outside the water where pH is likely to be a less critical factor (Griffiths et al. 2015). Consistent with findings for dragonflies occupying GCFR rivers (Kietzka et al. 2016), high aquatic insect species richness was associated with relatively higher conductivity. This suggests that increased levels of conductivity do not inhibit aquatic insects (at least in the GCFR) to be effective colonisers of aquatic habitats (Suhling et al. 2006).

High insect species richness, diversity, and abundance is associated with water clarity (O'Neill et al. 2015; da Rocha et al. 2016). Increased turbidity, as a result of lower frequencies of water replenishment, has a strong limiting effect on aquatic insect occupancy. Here, most dragonfly species preferred clear water, as turbid water interferes with the respiration efficiency of dragonfly larvae, and they rely on visibility to detect prey. Water clarity was expected to have an effect on beetle species richness and composition as they too, are visual predators that feed in water, yet this was unclear from our results, perhaps because there was great variation among species traits, e.g. with some feeding near the water surface. Bugs occupying natural ponds seemed to prefer turbid water to escape predation, as most are weak swimmers or surface dwellers in the region (Griffiths et al. 2015; Reavell 2003).

Large (and relatively deep) water bodies remain inundated for longer periods, and some female aquatic insects are probably able to assess survivorship of eggs and larvae based on the size and depth of water bodies (Wildermuth and Spinner 1991). Aquatic insects as adults are often capable of traveling long distances (Arribas et al. 2012; Samways 2008), and large water bodies have a higher chance of being found by moving individuals. Large and vegetated artificial reservoirs seem to function as supplementary habitats for generalist pond insect species (Simaika et al. 2016), especially when natural ponds experience stress as a result of climatic variation.

Elevation is an important driver of aquatic insect species richness and diversity in the region (Apinda-Legnouo et al. 2014; Samways and Niba 2010). Lentic and lotic habitats at high elevations share some structural and physicochemical similarities, they provide a range of high-quality microhabitats and often have high species turnover (Biggs et al. 2005). However, natural habitats at low elevations are highly variable, and have a higher risk of drying up completely during drought (Samways 1989a). Most of the sensitive endemic dragonfly species (e.g. *S. angusta*, *P. polychromatica*, and *Syncordulia legator*), as well as most bug species, were at elevations between 300 and 450 m above sea level, suggesting that the natural ponds (in the case of sensitive dragonflies) and artificial reservoirs (in the case of bugs) at intermediate elevations provide attractive habitats, as was found in another area of South Africa (Samways 1989b). This is probably due to the fact that lentic habitats at intermediate elevations have moderate natural variability, and as a result, provide a wide variety of microhabitats. Here, beetle diversity was highest at relatively high elevations, probably due to high competition for favourable microhabitats at low elevations (Ball-Damerow et al. 2014), especially so during drought. However, bug species richness was highest at relatively low elevations, as many bug species are highly opportunistic and require these highly variable habitats to mature and breed (Lytle 2015).

5.4.4 Complementarity among natural ponds and artificial reservoirs

The artificial reservoirs investigated here resembled natural ponds in that they had similar chemical properties (e.g. water temperature, dissolved oxygen content, conductivity, and pH), had moderately clear water and had fluctuating water levels (although mostly anthropogenically induced in the case of artificial reservoirs). However, artificial reservoirs were much larger than natural ponds, they were mostly found at relatively low elevations, and, as most artificial reservoirs are relatively novel, frequently disturbed habitats, they had much less marginal vegetation complexity (here, mostly limited to sparse cover by tall grasses).

In terms of aquatic insect occupancy, just under half (46%) of total sampled dragonflies and about a third of total beetles (34%) and total bugs (36%) were shared between natural ponds and artificial reservoirs. Seven of the 15 total endemic species recorded here occupied artificial reservoirs, including the dragonflies *P. draconis*, *P. furcigerum*, *Z. minuscula*, *P. subpupillata*, and *S. venator*, the beetle *C. brevicollis*, and the bug *N. lactitans*. Interestingly, *P. draconis*, *P. furcigerum*, *Z. minuscula*, *P. subpupillata*, and *S. venator* were previously only ever recorded from montane lotic habitats (Samways and Simaika 2016) and *C. erythraea* was found to only occupy natural ponds here, although being exceptionally tolerant of impacted freshwater habitats (Samways 2003). Furthermore, the beetle *C. brevicollis* and bug *N. lactitans* are only known to occupy natural ponds (Challet and Turner 2006; Mlambo et al. 2011).

From our results, artificial reservoirs, even with rich marginal vegetation, cannot fully replace the habitat function of natural ponds, but increase connectivity between isolated natural ponds and/or expand the area of occupancy for at least adult dragonflies. For adult beetles and bugs, spatial structuring of natural ponds and artificial reservoirs was a less critical factor. Instead, artificial reservoirs resembling natural ponds in terms of water chemistry (here, relatively higher water temperature and lower conductivity) were more attractive alternative habitats, at least in the case of beetles. Nevertheless, most beetle and bug species sampled here showed a strong preference for natural ponds, as these habitats provide the necessary resources that enable their survival and completion of their life cycles, most of which were limited in artificial reservoirs.

5.4.5 Relative effects of drought on local insect assemblages

For all three focal taxa, we recorded far lower individual densities in comparison to pre-drought studies. However, the number of aquatic insect species remained relatively similar for each focal taxon between the pre-drought and drought conditions, with the exception of beetles, being richer during drought conditions. These results indicate that the drought had little impact on the species richness of these three taxa. In the case of beetles, higher species richness during drought suggests that many species normally not found in lentic habitats may occupy ponds as they provide enough natural resources that enable them (at least the adults) to survive when natural resources become scarce in their natal habitats. Most of the aquatic insects investigated here can travel some distance to seek out favourable habitats in response to deteriorating ecological conditions (Lytle 2015), microhabitat availability (Kietzka et al. 2016), presence/absence of predators (Binckley and Resetarits 2005), and food availability (Yee and Kehl 2015), all of which are strongly affected by hydrological regimes. Occupancy at a particular pond type during stress periods does not imply effective reproduction, yet occupying a greater number of low-quality habitats at low densities could ensure natural resource availability and enable reproducing individuals to reach the next optimal breeding season to complete their life cycles. This may be a key strategy explaining why these species have persisted in the GCFR and other semi-arid regions where ecological filters such as hydrological extremes have been imminent in the past (Samways 2010). However, we did not investigate passively dispersing insects here, which may show different responses to climatic variation and adopt alternative survival strategies (e.g. life history strategies) for improved resilience against ecological stress periods.

5.5 Conclusion

In summary, there are many habitat characteristics related to physical and physicochemical characteristics that drive species richness, diversity, and composition of actively dispersing aquatic insects, yet vegetation cover remained a major driver. Using the GCFR as an example of a drought-prone region, artificial reservoirs share just under 40% of total sampled species with natural ponds, are attractive habitats to some rare endemic insects in times of drought, enabling an increase in the area of occupancy for some aquatic insects during drought. When their native habitats experience ecological pressure (in this case, extreme hydrological drought), some aquatic insects occupy low-quality habitats at low population levels, seemingly to sustain themselves until a wet season comes again. From a conservation perspective, artificial reservoirs, primarily constructed to store water for urban and agricultural use, cannot fully replace the functional value of natural ponds, but those artificial reservoirs resembling natural ponds (especially when having abundant marginal vegetation) contribute to providing supplementary habitats during drought for many widespread generalist insect species, and significantly, also for some of the rare endemics. Artificial reservoirs are common landscape features, especially in semi-arid regions, yet they differ fundamentally from natural ponds (at least in terms of their sizes, disturbance levels, vegetation composition and vegetation cover). There is merit in moving the characteristics of all artificial reservoirs closer towards those of natural ponds to further improve their effectiveness as conservation ponds for a range of highly mobile aquatic insects.

5.6 References

Apinda-Legnouo, E.A., Samways, M.J. and Simaika, J.P. 2014. Value of artificial ponds for aquatic beetle and bug conservation in the Cape Floristic Region biodiversity hotspot. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24: 4522-4535.

Arribas, P., Valesco, J., Abellán, P., Sánchez-Fernández, D., Andújar, C., Calosi, P., ... Bilton, D.T. 2012. Dispersal ability rather than ecological tolerance drives differences in range size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). *Journal of Biogeography*, 39: 984-994.

Ball-Damerow, J.E., M'Gonigle, L.K. and Resh, V.H. 2014. Local and regional factors influencing assemblages of dragonflies and damselflies (Odonata) in California and Nevada. *Journal of Insect Conservation*, 18: 1027-1036.

Bates, D.M. and Sarkar, D. 2007. lme4: Linear mixed-effects models using S4 classes. R package version 1.1-12.

Batzer, D.P. and Wissinger, S.A. 1996. Ecology of insect communities in non-tidal wetlands. *Annual Review of Entomology*, 41: 75-100.

Biggs, J., Williams, P., Whitfield, P., Nicolet, P. and Weatherby, A. 2005. 15 years of pond assessment in Britain: Results and lessons learned from the work of Pond Conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15: 693-714.

Bilton, D.T., McAbendroth, L.C., Nicolet, P., Bedford, A., Rundle, S.D., Foggo, A. and Ramsay, P.M. 2008. Ecology and conservation status of temporary and fluctuating ponds in two areas of southern England. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 19: 134-146.

Binckley, C.A. and Resetarits, W.J. 2005. Habitat selection determines abundance, richness and species composition of beetles in aquatic communities. *Biological Letters*, 1: 370-374.

Bird, M. 2010. Aquatic invertebrates as indicators of human impacts in South African wetlands. WRC Report No. TT 435/09. Water Research Commission, Pretoria, South Africa.

Bloechl, A., Koenemann, S., Philippi, B. and Melber, A. 2010. Abundance, diversity and succession of aquatic Coleoptera and Heteroptera in a cluster of artificial ponds in the north German lowlands. *Limnologica*, 40: 215-225.

Bond, N.R., Lake, P.S. and Arthington, A.H. 2008. The impacts of drought on freshwater ecosystems: An Australian perspective. *Hydrobiologia*, 600: 3–16.

Botai, C.M., Botai, J.O. and Adeola, A.M. 2018. Spatial distribution of temporal precipitation contrasts in South Africa. *South African Journal of Science,* 114: 1-9.

Boulton, A.J. and Lake, P.S. 2008. Effects of drought on stream insects and its ecological consequences. *Aquatic Insects: Challenges to Populations*, 2008: 81-102.

Bunn, S.E. and Arthington, A.H. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30: 492-507.

Challet, G. and Turner, C.R. 2006. Rediscovery of *Coelhydrus brevicollis* Sharp in South Africa with notes on *Andex insignis* Sharp (Coleoptera: Dytiscidae). *Latissimus*, 21: 21-24.

Collinson, N.H., Biggs, J., Corfild, A., Hodson, M.J., Walker, D., Whitfield, M. and Williams, P.J. 1995. Temporary and permanent ponds: An assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. *Biological Conservation*, 74: 125-134.

Corbet, P.S., Suhling, F. and Soendgerth, D. 2006. Voltinism of Odonata: A review. *International Journal of Odonatology*, 9: 1-44.

Dahm, C., Baker, M.A., Moore, D.I. and Thibault, J.R. 2003. Coupled biogeochemical and hydrological responses of streams and rivers to drought. *Freshwater Biology*, 48: 1219-1231.

Dai, A. 2013. Increased drought under global warming in observations and models. *Nature Climate Change*, 3: 52-58.

Declerck, S., De Bie, T., Ercken, D., Hampel, H., Schrijvers, S., van Wichelen, J. ... Martens, K. 2006. Ecological characteristics of small ponds: Associations with land-use practices at different spatial scales. *Biological Conservation*, 131: 523-532.

Dickens, C.W.S. and Graham, P.M. 2002. The South African Scoring System (SASS) Version 5 rapid bioassessment method for rivers. *African Journal of Aquatic Science*, 27: 1-10.

Druyan, L.M. 1996. Arid climates. In: Schneider, S.H. (ed), *Encyclopedia of climate and weather*. Oxford University Press, New York, USA. pp. 48-50.

Fairchild, G.W., Cruz, J., Faulds, M., Short, A.E.Z. and Matta, J.F. 2003. Microhabitat and landscape influences on aquatic beetle assemblages in a cluster of temporary and permanent ponds. *Journal of the North American Benthological Society*, 22: 224-240.

Florencio, M., Serrano, L., Gómez-Rodriguez, C., Millán, A. and Paz-Paniagua, C. 2009. Inter- and intra-annual variations of macroinvertebrate assemblages are related to the hydroperiod in Mediterranean temporary ponds. *Hydrobiologia*, 634: 167-183.

Furey, P.C., Nordin, R.N. and Mazumder, A. 2006. Littoral benthic macroinvertebrates under contrasting drawdown in a reservoir and a natural lake. *Journal of the North American Benthological Society*, 25: 19-31.

Griffiths, C., Day, J. and Picker, M. 2015. *Freshwater life: A field guide to the plants and animals of Southern Africa*. Struik Nature, Cape Town, South Africa.

Humphries, P. and Baldwin, D.S. 2003. Drought and aquatic ecosystems: An introduction. *Freshwater Biology*, 48: 1141-1146.

Janssen, A., Hunger, H., Konold, W., Pufal, G. and Staab, M. 2018. Simple pond restoration measures increase dragonfly (Insecta: Odonata) diversity. *Biodiversity and Conservation*, 27: 2311-2328.

Jenkins, K.M. and Boulton, A.J. 2007. Detecting impacts and setting restoration targets in arid-zone rivers: Aquatic micro-invertebrate responses to reduced floodplain inundation. *Journal of Applied Ecology*, 44: 823-832.

Kadoya, T., Suda, S. and Washitani, I. 2004. Dragonfly species richness on man-made ponds:

Effects of pond size and pond age on newly established assemblages. *Ecological Research*, 19: 461-467.

Karaouzas, I. and Gritzalis, K.C. 2006. Local and regional factors determining aquatic and semi-aquatic bug (Heteroptera) assemblages in rivers and streams of Greece. *Hydrobiologia*, 573: 199-212.

Kietzka, G.J., Pryke, J.S. and Samways, M.J. 2016. Aerial adult dragonflies are highly sensitive to in-water conditions across an ancient landscape. *Diversity and Distributions*, 23: 14-26.

Kotze, D.C., Breen, C.M. and Quinn, N. 1995. Wetland losses in South Africa. In: Cowan, G.I. (ed.), *Wetlands of South Africa*. Department of Environmental Affairs and Tourism, Pretoria, South Africa. pp. 263-272.

Ludovisi, A. and Gaino, E. 2010. Meteorological and water quality changes in Lake Trasimeno (Umbria, Italy) during the last fifty years. *Journal of Limnology*, 69: 174-188.

Lytle, D.A. 2015. Chapter 37: Order Hemiptera. In: Thorp, J.H. and Rogers, D.C. (eds). *Thorp and Covich's freshwater invertebrates: Ecology and general biology*. Elsevier, Amsterdam, The Netherlands. pp. 1953-1979.

Mittermeier, R.A., Patricio, R.G., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G. ... da Fonseca, G.A.B. 2004. *Hotspots revisited*. CEMEX, Mexico City, Mexico.

Mlambo, M.C., Bird, M.S., Reed, C.C. and Day, J.A. 2011. Diversity patterns of temporary wetland macroinvertebrate assemblages in the south-western Cape, South Africa. *African Journal of Aquatic Science*, 36: 299-308.

Mosley, L.M. 2015. Drought impacts on the water quality of systems; review and integration. *Earth-Science Reviews*, 140: 203-214.

Mosley, L.M., Zammit, B., Leyden, E., Heneker, T.M., Hipsey, M.R., Skinner, D. and Aldridge, K.T. 2012. The impact of extreme low flows on the water quality of the lower Murray River and Lakes (South Australia). *Water Resources Management*, 26: 3923-3946.

Muggeo, V.M.R. 2017. Regression models with break-points/change-points estimation. R package version 0.5-2.1.

Nicolet, P., Biggs, J., Hodson, M.J., Reynolds, C., Whitfield, M. and Williams, P. 2004. The wetland plant and macroinvertebrate assemblage of temporary ponds in England and Wales. *Biological Conservation*, 120: 261-278.

Oertli, B., Joye, D.A., Castella, E., Juge, R., Cambin, D., and Lachavanne, J.B. 2002. Does size matter? The relationship between pond area and biodiversity. *Biological Conservation*, 104: 59-70.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L. ... Wagner, H. 2017. Vegan: Community ecology package. R package version 2.4-2.

Olds, B.P., Peterson, B.C., Koupal, K.D., Farnsworth-Hoback, K.M., Schoenebeck, C.W. and Hoback, W.W. 2011. Water quality parameters of a Nebraska reservoir differ between drought and normal conditions. *Lake and Reservoir Management*, 27: 229-234.

O'Neill, B.J., Steffen, J. and Jakubauskas, M. 2015. Effects of sedimentation on the profundal benthic macroinvertebrates of a Great Plains Reservoir. *Transactions of the Kansas Academy of Science*, 117: 61-68.

Osborn, R. and Samways, M.J. 1996. Determinants of adult dragonfly assemblage patterns at new ponds in South Africa. *Odonatologica*, 25: 49-58.

Pohl, B., Fauchereau, N., Reason, C.J.C. and Rouault, M. 2009. Relationships between the Antarctic Oscillation, the Madden-Julian Oscillation, and ENSO, and consequences for rainfall analysis. *Journal of Climate*, 23: 238-254.

Quantum GIS Development Team. 2017. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. Retrieved from http://qgis.osgeo.org.

R Development Core Team. 2016. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/.

Reavell, P. 2003. Hemiptera. In: de Moor, I., Day, J. and de Moor, F. (eds). *Guides to the Freshwater invertebrates of Southern Africa: Insecta II Hemiptera, Megaloptera, Neuroptera, Trichoptera and Lepidoptera*. Water Research Commission, Pretoria, South Africa. pp. 16-71.

da Rocha, F.C., de Andrade, E.M., Lopes, F.B., de Paula Filho, F.J., Costa Filho, J.H. and da Silva, M.D. 2016. Physical-chemical determinant properties of biological communities in continental semi-arid waters. *Environmental Monitoring and Assessment*, 188: 1-15.

Samways, M.J. 1989a. Farm dams as nature reserves for dragonflies (Odonata) at various altitudes in the Natal Drakensberg mountains, South Africa. *Biological Conservation*, 48: 181-187.

Samways, M.J. 1989b. Taxon turnover in Odonata across a 3000 m altitudinal gradient in southern Africa. *Odonatologica*, 18: 263-274.

Samways, M.J. 1996. Dragonfly conservation in South Africa: A biogeographical perspective. *Odonatologica*, 21: 165-180.

Samways, M.J. 2003. Threats to the tropical island dragonfly fauna (Odonata) of Mayotte, Comoro archipelago. *Biodiversity and Conservation*, 12: 1785-1792.

Samways, M.J. 2008. *Dragonflies and damselflies of South Africa*. Pensoft, Sofia, Bulgaria.

Samways, M.J. 2010. Impacts of extreme weather and climate change on South African dragonflies. *Biodiversity and Ecosystem Risk Assessment*, 5: 73-84.

Samways, M.J. and Niba, A. 2010. Climate and elevational range of a South African dragonfly assemblage. *Biodiversity and Ecosystem Risk Assessment*, 5: 85-107.

Samways, M.J. and Sharratt, N.J. 2010. Recovery of endemic dragonflies after removal of invasive alien trees. *Conservation Biology*, 24: 267-277.

Samways, M.J. and Simaika, J.P. 2016. *Manual of freshwater assessment for South Africa: Dragonfly Biotic Index. Suricata 2*. South African National Biodiversity Institute, Pretoria, South Africa.

Samways, M.J. and Taylor, S. 2004. Impacts of invasive alien plants on Red-Listed South African dragonflies (Odonata): Working for water. *South African Journal of Science*, 100: 78-80.

Scheibler, S.S., Melo, M.C., Montemayor, S.I. and Scollo, A.M. 2016. Abundance, richness, seasonal and altitudinal dynamics of aquatic true bugs (Heteroptera) in mountain wetlands of Argentina. *Wetlands*, 36: 265-274.

Schiewer, U. 1998. 30 years' eutrophication in shallow brackish waters – Lessons to be learned. *Hydrobiologia*, 363: 73-79.

Scholtz, C.H. and Holm, E. 1985. *Insects of southern Africa*. Butterworths, Pretoria, South Africa.

Simaika, J.P., Samways, M.J. and Frenzel, P.P. 2016. Artificial ponds increase local dragonfly diversity in a global biodiversity hotspot. *Biodiversity and Conservation*, 25: 1921-1935.

Stals, R. and de Moor, I.J. 2007. *Coleoptera. Chapter 10. Guides to the freshwater invertebrates of Southern Africa*. Water Research Commission, Pretoria, South Africa. pp. 1-263.

Suhling, F., Sahlén, G., Martens, A., Marais, E. and Schütte, C. 2006. Dragonflies in arid tropical environments: A case study from Western Namibia. *Biodiversity and Conservation*, 15: 311-332.

Suhling, F., Suhling, I. and Richter, O. 2015. Temperature response of growth of larval dragonflies – An overview. *International Journal of Odonatology*, 18: 15-30.

Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R. and Sheffield, J. 2014. Global warming and changes in drought. *Nature Climate Change*, 4: 17-22.

Tropical Rainfall Measuring Mission. 2011. TRMM (TMPA/3B43) Rainfall Estimate L3 1 month 0.25 degree x 0.25 degree V7. Greenbelt, MD: Goddard Earth Sciences Data and Information Services Center (GES DISC).

Verberk, W.C.E.P., van Duinen, G.-J.A., Peeters, T.M.J. and Esselink, H. 2001. Importance of variation in water-types for water beetle fauna (Coleoptera) in Korenburgerveen, a bog remnant in the Netherlands. *Proceedings of the Experimental and Applied Entomology Section of the Netherlands Entomological Society*, 12: 121-128.

Votruba, L. and Broža, V. 1989. 1 Basic function of water reservoirs. In: Votruba, L. and Broža, V. (eds). *Water management in reservoirs*. Elsevier, Amsterdam, The Netherlands. pp. 19-60.

Wildermuth, H. and Spinner, W. 1991. Visual cues in oviposition site selection by *Somatochlora arctica* (Zetterstedt) (Anisoptera: Corduliidae). *Odonalologica*, 20: 357-367.

Williams, P., Whitfield, M. and Biggs, J. 2008. How can we make new ponds diverse? A case study monitored over 7 years. *Hydrobiologia*, 597: 137-148.

Worrall, F. and Burt, T. 2008. The effect of severe drought on the dissolved organic carbon (DOC) concentration and flux from British rivers. *Journal of Hydrology*, 361: 262-274.

Yee, D.A. and Kehl, S. 2015. Chapter 39: Order Coleoptera. In: Thorp, J.H. and Rogers, D.C. (eds). *Thorp and Covich's freshwater invertebrates: Ecology and general biology*. Elsevier, Amsterdam, The Netherlands. pp. 2056-2154.

Chapter 6 General discussion and conclusions

Freshwater insects and their associated habitats are in danger globally (Heino 2001), and several synergistic factors contribute to the overall vulnerability of freshwater ecosystems (Moilanen et al. 2008). Investigating insect biogeographical patterns across multiple spatial scales is timely and important, since local assemblage structures are determined by complex relationships between regional and local assemblages (Ricklefs and Schluter 1993). Having good understanding of the multi-scale drivers of distribution patterns is also fundamental for ensuring effective conservation among insects and their habitats. Yet, various aspects of biogeography are poorly investigated among aquatic insects, especially in terms of their underlying drivers (Willig et al. 2003). My overall aim was to investigate the significance of functional traits, contemporary climate and local environmental variables as drivers of aquatic insect species richness, diversity, and distribution across Africa. I approached this by investigating broad-scale, theoretical biogeography and local-scale, empirical ecology as related research topics, and in this chapter, I summarize my main findings from each data chapter, and discuss their implications for aquatic insect conservation (Figure 6.1).

Biological and ecological traits are highly interactive among insect taxa, and most are variably responsive to changes in environmental conditions, driven by the set of traits that defines any one species (Arribas et al. 2012). Species' traits determine their inherent capabilities to use a variety of resources, and are important drivers of their range sizes (Rundle et al. 2007). In conservation, this has led to species being binarily classified as 'widespread generalists' or 'narrow-range specialists' based on their habitat preferences, as a common currency that is easily translated to identifying the conservation requirements of species. Yet, several authors have suggested that ordering species along a generalist/specialist gradient is much more practical (Büchi and Vuilleumier 2014), since several other biological traits (e.g. those related to dispersal and fecundity) contribute to the variation in their range sizes (Rundle et al. 2007). Although habitat preference has been shown to be important for driving species range size in other regions (Hof et al. 2006), my study was one of the first to investigate the significance of the combination between ecological and biological traits in driving aquatic insect distribution across Africa. I expected ecological traits to be important drivers of dragonfly range sizes, but also expected other biological traits to contribute equally to the variation in range size among dragonfly species across the African continent.

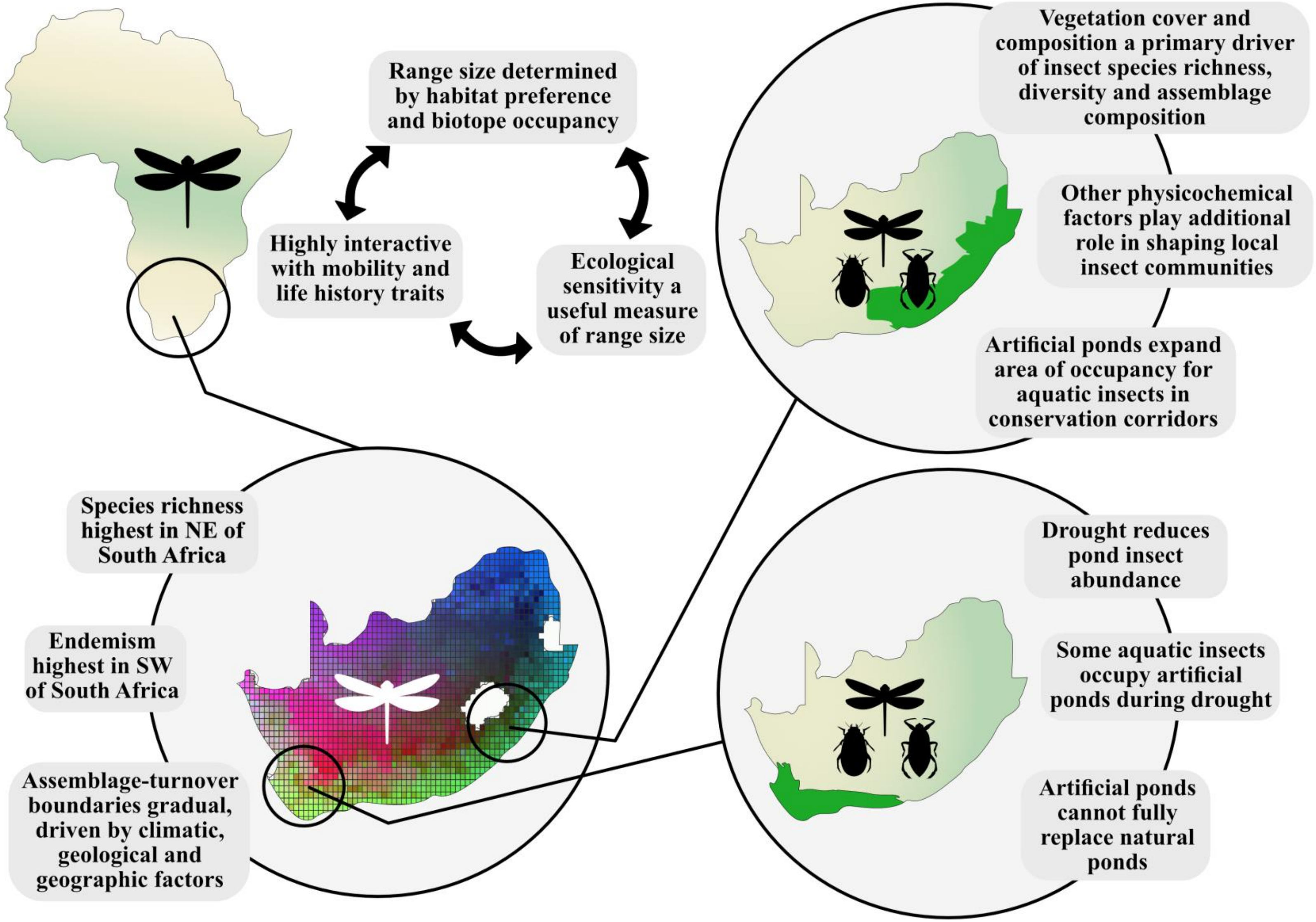


Figure 6.1 Summary of main findings from each data chapter.

My results presented in Chapter 2 indicated that overall, lentic dragonflies, and/or those that occupied more biotopes as adults (i.e. the generalists) had wider latitude, longitude and elevation ranges compared to lotic dragonflies, and/or those that occupied few biotopes (i.e. the specialists). In general, lentic habitats are short-lived and unpredictable compared to most lotic habitats (Ribera et al. 2001), and lentic species are well-adapted to outlive their habitats and migrate across the landscape to find other favourable habitats (Ribera and Vogler 2000). Likewise, generalist species are opportunistic, mostly robust to environmental change and highly migratory, allowing them to occupy a wide variety of biotopes (Julliard et al. 2006). Although the hard categorisation of species as ‘widespread generalists’ or ‘narrow-range specialists’ was mostly valid, there were many exceptions to this general premise. Some lentic dragonflies were confined to narrow regions, and some lotic dragonflies had wide ranges since their preferred habitats were common across wide geographical areas. In turn, some specialist dragonflies had wide ranges resulting from their favoured biotopes being common and widespread, while other seemingly generalist dragonflies had comparatively narrow ranges arising from their favoured biotopes being confined to small geographical areas and/or specific elevation ranges. Interestingly, my results have also shown that larval biotope occupancy was not significant for determining the range sizes of dragonflies, perhaps as a legacy of adults selecting for breeding habitats and so determined where the larvae were (Simaika and Samways 2009), or overall biotope relatedness within the various dragonfly families. The lesser importance of larval biotope occupancy may also simply be because the distribution data that were used focused on adult distribution points. Larval ecology and taxonomy are not as well-known as that of adult stages (Bried and Samways 2015), and larval distribution may differ slightly from adult distribution, yet only at the very local scale for most species except those that are highly migratory once having emerged as adults.

As expected, biological traits related to phenology and mobility also had significant relationships with the variation in range sizes among dragonfly species. I found that the duration of adult life stage and time of adult emergence were not significant drivers of dragonfly range size. However, the season in which adults died had a significant effect on their range sizes, related to the ability of overwintering adults to move across the landscape and breed as soon as environmental conditions become favourable (van Huyssteen and Samways 2009). My results have also shown that average wing and body sizes, as separate measures, were not significant drivers of dragonfly range sizes. Yet, the ratio of these two traits (i.e. wing-to-body ratios) had a strong effect on latitude and longitude range size, as higher wing-to-body ratios likely enhance dragonfly mobility, and enable them to reach favourable habitats (Rundle et al. 2007). Collectively, these results indicate that hard categorization of species as 'widespread generalists' or 'narrow-range specialists' based on ecological traits alone should be approached with caution. Since other biological traits were also significant in determining dragonfly range sizes, conservation efforts should be inclusive of multiple species with various combinations of traits, across all habitat types. There is merit for extension to other focal groups, given the high variation in ecological and biological traits among aquatic insect taxa.

Species traits also interact with local and regional climates, yet the significance of regional climates as drivers of broad-scale aquatic insect distribution patterns is poorly investigated (Heino 2011). Some previous investigations have indicated contemporary regional climate as a significant driver of aquatic insect migration and distribution patterns, although they are generally weaker compared to those of terrestrial taxa (Pearson and Boyero 2009). Nevertheless, regional climate is associated with hydrological regimes and availability of breeding habitats (Pedgley et al. 1995; Bêche and Statzner 2009), so determining areas of high species richness and diversity. In addition to its importance for determining regional richness and diversity, I expected regional climate, along with topography, both to be significant drivers of regional dragonfly assemblage structures through determining turnover boundaries among regional dragonfly assemblages, which I then addressed in Chapter 3.

My results presented in Chapter 3 indicated that there was a strong latitudinal trend for dragonflies across South Africa, and species richness decreased overall with increasing latitude, as was found for aquatic insects elsewhere (Boyero 2002; Ribera et al. 2003). Here, high overall species richness was associated with the subtropical, high summer rainfall regions of the country, where aquatic habitats are diverse and abundant, presenting a range of favourable ecological conditions to various dragonfly species (Hart et al. 2014; Samways and Simaika 2016). In turn, dragonfly endemism showed an opposite trend, and increased with increasing latitude. There was also a strong longitudinal trend for endemic species richness, where the proportion of endemic dragonflies (i.e. endemic species richness relative to total species richness) increased from west to east. The highest levels of endemism were predominantly associated with the Mediterranean, winter rainfall regions of the country, where topography is highly variable, and dragonflies, along with other insect taxa, were likely honed over countless generations to be well adapted to local conditions (Dijkstra et al. 2014).

To my knowledge, this study is the first to investigate assemblage-turnover boundaries for aquatic taxa across South Africa, and I expected assemblage-turnover boundaries to be discrete throughout the country. This was not the case for dragonflies, as assemblage-turnover boundaries were gradual throughout the country, with most broadly coinciding with significant topographical features and/or areas where regional climate changed from one condition to the next. The gradual changes in dragonfly assemblage composition resulted from gradual changes in climatic conditions throughout, and the overall high mobility of dragonflies, enabling most species to traverse wide geographical areas, so occupying fundamentally similar habitats across wide regions (Grönroos et al. 2013). It was however, clear that most lotic species occupied the coastal and mountainous regions, where rivers and streams are abundant and hold water throughout the year (Kietzka et al. 2015), while lentic species richness was highest in the north-eastern, subtropical regions, where coastal swamps and wetlands are abundant and highly variable in structure (Hart et al. 2014). Furthermore, the inland regions of the country were occupied mostly by opportunistic dragonflies having no specific habitat preferences (i.e. lentic/lotic species), since the South African interior is mostly arid throughout the year and aquatic habitats are spottily distributed throughout and are highly unpredictable in terms of hydrological regimes.

Despite the overall importance of regional climate, my results also indicated that geographical factors are highly significant in shaping regional dragonfly assemblages. This may result from local conditions being highly disparate between regions, since they are defined by the combination of climatic and topographical gradients, resulting in dragonfly species sorting occurring across the country (Leibold et al. 2004). Although adult dragonflies are generally mobile insects, the variable topography (e.g. the occurrence of mountain ranges) throughout the country may also impose upon their mobility, leading to assemblage structures being different between wider regions (Garcillán and Ezcurra 2003). Indeed, some dragonfly populations were geographically isolated, suggesting that the deep historical context of the overall landscape is an important consideration, as it relates to certain areas experiencing less climatic variation in the past.

At the local scale, small-sized ponds contribute greatly to overall biodiversity, and is often higher compared to that in large rivers and lakes (Williams et al. 2004). This is even more significant at the level of the pondscape, i.e. when ponds occur in networks, as individual ponds have different catchment areas and collectively contribute to overall habitat heterogeneity

(Biggs et al. 2005). The Maputaland-Pondoland-Albany (MPA) biodiversity hotspot was identified as an area of particular interest, since natural ponds and artificial reservoirs are interspersed and common in the ecological networks that make up much of the overall agricultural mosaic. Ecological networks have been shown to have high conservation value for several terrestrial insects (Gaigher et al. 2019; Joubert-van der Merwe et al. 2019), as well as some aquatic insects (Pryke et al. 2015; Briggs et al. 2019). In turn, natural ponds and artificial reservoirs are spottily distributed throughout the Greater Cape Floristic Region (GCFR), which also experienced a severe hydrological drought in recent years (Botai et al. 2018). Although some aquatic insects are adapted to climate extremes by having resistance and resilience traits, drought may lead to substantial population declines (Samways and Niba 2010), and when over extended periods, may lead to local and regional extinctions (Boulton and Lake 2008). Pond insects are poorly investigated in both regions, and I expected that artificial reservoirs occurring in ecological networks and in close association with natural ponds, as is the case for ponds in the MPA biodiversity hotspot, improve pondscape resilience. In the case of ponds in the GCFR, I expected artificial reservoirs to complement natural ponds during drought, and provide refuge habitats to widespread aquatic insects during ecological stress periods.

My results presented in Chapter 4 and Chapter 5 showed that high habitat heterogeneity among ponds maintain high species richness and diversity of dragonflies and beetles, and to a lesser extent, true bugs, as was found previously (Apinda-Legnouo et al. 2014; Kietzka et al. 2015; Briggs et al. 2018). In the case of both pond types and in both regions, habitat heterogeneity related to vegetation cover and composition was a key driver of species richness, diversity and assemblage variation. Most aquatic insects are associated with vegetated margins of ponds, as vegetation provides insects with, among others, breeding microhabitats and refuge against potential predators (Osborn and Samways 1996; Mlambo et al. 2011). The complement of aquatic insects investigated in these two regions also responded differently to variation in water chemistry across the range of ponds. Variation in water chemistry contributes to overall habitat heterogeneity across the pondscape, and provides a range of optimal conditions for species' physiological processes and development (Samways et al. 1996; Scheibler et al. 2016).

For dragonflies and aquatic beetles and true bugs in the MPA biodiversity hotspot (Chapter 4), there was no significant difference in abundance between natural ponds and artificial reservoirs in conservation corridors, indicating that artificial reservoirs, are novel landscape features that maintain local aquatic insect population sizes. Furthermore, three-quarters of all sampled species occupied both natural ponds and artificial reservoirs, indicating that artificial reservoirs expand the local area of occupancy for most widespread lentic insect species. Interestingly, some narrow-range endemic species also benefited by artificial reservoirs, but some insects with specific habitat requirements were confined to natural ponds, emphasizing the significance of naturalness if the ultimate goal is to conserve the full range of aquatic insects.

For dragonflies and aquatic beetles and true bugs in the GCFR biodiversity hotspot (Chapter 5), less than half of all sampled species occupied both natural and artificial pond types. Most dragonflies occupied both natural ponds and artificial reservoirs, and surprisingly, some endemic species, only ever recorded from rivers, were found to occupy artificial reservoirs during drought. Although the two pond types (natural and artificial) were relatively similar in terms of water chemistry, artificial reservoirs had much less marginal vegetation cover compared to natural ponds, and most beetles and true bugs exclusively occupied natural ponds. I also found that there was no significant difference in species richness compared to other, pre-drought studies that investigated the same taxa and used the same set of ponds, yet overall abundance was substantially lower. While drought no doubt exerts strong selection pressure, these findings suggest that actively dispersing aquatic insects occupy low-quality habitats at low abundance during environmental stress periods, seemingly as a survival strategy that allows breeding individuals to reach the next favourable breeding season. However, natural ponds are important habitats for most aquatic insects, and should be included in conservation efforts to preserve as many aquatic taxa as possible. There is also merit in moving the characteristics of artificial reservoirs closer to those of natural ponds, to create attractive habitats for a range of aquatic insects, so improving overall pondscape resilience.

In summary, having holistic understanding of species distribution patterns aids decision-making for effective conservation of insect taxa along with their associated freshwater habitats. Broad-scale investigations, especially for African freshwater insects are important, yet challenging, since their distributions, biological traits, and responses to regional climate gradients are not fully understood. Given their popularity and the substantial amount of information available with regards to their ecological responses, dragonflies are an exceptional group and have previously been suggested as an umbrella taxon for other freshwater taxa (Bried et al. 2007; Kietzka et al. 2019), thus justifying their use as model organisms. Here, I have made a novel contribution to theoretical biogeography and local ecology, so addressing the Wallacean, Raunkiæran, Eltonian and Hutchinsonian shortfalls. My results indicated that various aspects related to ecological and biological traits, climate, topography, and local environmental conditions drive dragonfly distribution at multiple spatial scales. My results further support the value of insect trait information, and emphasize the importance of large databases for detailing the distribution patterns of aquatic insects. Investigating other insect taxa also contributes to our increasing understanding of the drivers of insect distribution ranges, and my results have shown that aquatic beetles and true bugs respond to environmental variables, at least at local scale, complementing my findings for dragonflies. Therefore, I conclude that dragonflies are good model organisms, yet investigating other taxa is highly relevant. I recommend broad-scale investigations of other complementary taxa to determine their value for elucidating the drivers of overall insect distribution patterns, and so address our current shortfalls for all other taxa to improve conservation of scarce natural resources.

6.1 References

Apinda-Legnouo, E.A., Samways, M.J. and Simaika, J.P. 2014. Value of artificial ponds for aquatic beetle and bug conservation in the Cape Floristic Region biodiversity hotspot. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24: 522-535.

Arribas, P., Valasco, J., Abellán, P., Sánchez-Fernández, D., Andújar, C., Calosi, P., … Bilton, D.T. 2012. Dispersal ability rather than ecological tolerance drives differences in range size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). *Journal of Biogeography*, 39: 984-994.

Bêche, L.A. and Statzner, B. 2009. Richness gradients of stream invertebrates across the USA: taxonomy- and trait-based approaches. *Biodiversity and Conservation*, 18: 3909-3930.

Biggs, J., Williams, P., Whitfield, M., Nicolet, P. and Weatherby, A. 2005. 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15: 693-714.

Botai, C.M., Botai, J.O. and Adeola, A.M. 2018. Spatial distribution of temporal precipitation contrasts in South Africa. *South African Journal of Science*, 114: 1-9.

Boulton, A.J. and Lake, P.S. 2008. Effects of drought on stream in- sects and its ecological consequences. *Aquatic Insects: Challenges to Populations*, 2008: 81-102.

Boyero, L. 2002. Insect biodiversity in freshwater ecosystems: is there any latitudinal gradient? *Marine and Freshwater Research*, 53: 753-755.

Bried, J.T. and Samways, M.J. 2015. A review of odonatology in freshwater applied ecology and conservation science. *Applied Odonatology*, 34: 1023-1031.

Bried, J.T., Herman, B.D. and Ervin, G.N. 2007. Umbrella potential of plants and dragonflies for wetland conservation: A quantitative case study using the umbrella index. *Journal of Applied Ecology*, 44: 833-842.

Briggs, A., Pryke, J.S., Samways, M.J. and Conlong, D.E. 2019. Macrophytes promote aquatic insect conservation in artificial ponds. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29: 1190-1201.

Büchi, L. and Vuilleumier, S. 2014. Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. *The American Naturalist*, 183: 612-624.

Cardoso, P., Erwin, T. L., Borges, P.A.V. and New, T.R. 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, 144: 2647-2655.

Dijkstra, K.-D.B., Monaghan, M.T. and Pauls, S.U. 2014. Freshwater biodiversity and insect diversification. *Annual Review of Entomology*, 59: 143-163.

Gaigher, R., Pryke, J.S. and Samways, M.J. 2019. Divergent fire management leads to multiple beneficial outcomes for butterfly conservation in a production mosaic. *Journal of Applied Ecology*, https://doi.org/10.1111/1365-2664.13357.

Garcillán, P.P. and Ezcurra, E. 2003. Biogeographic regions and β-diversity of woody dryland legumes in the Baja California peninsula. *Journal of Vegetation Science*, 14: 859-868.

Grönroos, M., Heino, J., Siqueira, T., Landeiro, V.L., Kotaken, J. and Bini, L.M. 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type and regional environmental context. *Ecology and Evolution*, 3: 4473-4487.

Joubert-van der Merwe, L., Pryke, J.S. and Samways, M.J. 2019. Well-managed grassland heterogeneity promotes butterfly conservation in a corridor network. *Journal of Environmental Management*, *238*: 382-395.

Julliard, R., Clavel, J., Devictor, V., Jiguet, F. and Couvet, D. 2006. Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, 9: 1237-1244.

Hart, L.A., Bowker, M.B., Tarboton, W. and Downs, C.T. 2014. Species Composition, Distribution and Habitat Types of Odonata in the iSimangaliso Wetland Park, KwaZulu-Natal, South Africa and the associated conservation implications. *PLoS ONE*, 9: e92588.

Heino, J. 2001. Regional gradient analysis of freshwater biota: do similar biogeographic patterns exist among multiple taxonomic groups? *Journal of Biogeography*, 28: 69-76.

Heino, J. 2011. A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology*, 56: 1703-1722.

Hof, C., Brändle, M. and Brandl, R. 2006. Lentic odonates have larger and more northern ranges than lotic species. *Journal of Biogeography*, 33: 63-70.

Kietzka G.J., Pryke J.S. and Samways M.J. 2016. Aerial adult dragonflies are highly sensitive to in-water conditions across an ancient landscape. *Diversity and Distributions*, 23: 14-26.

Kietzka, G.J., Pryke, J.S., Gaigher, R. and Samways, M.J. 2019. Applying the umbrella index across aquatic insect taxon sets for freshwater assessments. *Ecological Indicators*, 107: 105655.

Leibold, M.A., Holyoak, M., Mougeut, N., Amarasekare, P., Chase, J. M., Hoopes, M.F., … Loreau, M. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7: 601-613.

Mlambo, M.C., Bird, M.S., Reed, C.C. and Day, J.A. 2011. Diversity patterns of temporary wetland macroinvertebrate assemblages in the south-western Cape, South Africa. *African Journal of Aquatic Science*, 36: 299-308.

Moilanen, A., Leathwick, J. and Elith, J. 2008. A method for spatial freshwater conservation prioritization. *Freshwater Biology*, 53: 577-592.

Osborn, R. and Samways, M.J. 1996. Determinants of adult dragonfly assemblage patterns at new ponds in South Africa. *Odonatologica*, 25: 49-58.

Pearson, R.G. and Boyero, L. 2009. Gradients in regional diversity of freshwater taxa. *Journal of the North American Benthological Society*, 28: 504-514.

Pedgley, D.E., Reynolds, D.R. and Tatchell, G.M. 1995. Long-range insect migration in relation to climate and weather: Africa and Europe. In: Drake, V.A. and Gatehouse, A.G. (eds.). *Insect migration: tracking resources through space and time*. Cambridge University Press, Cambridge, UK. pp. 3-29.

Pryke J.S., Samways M.J. and De Saedeleer, K. 2015. An ecological network is as good as a major protected area for conserving dragonflies. *Biological Conservation*, 191: 537-545.

Ribera, I. and Vogler, A.P. 2000. Habitat type as a determinant of species range sizes: the example of lotic-lentic differences in aquatic Coleoptera. *Biological Journal of the Linnaean Society*, 71: 33-52.

Ribera, I., Barraclough, T.G. and Vogler, A.P. 2001. The effect of habitat type on speciation rates and range movements in aquatic beetles: inferences from species-level phylogenies. *Molecular Ecology*, 10: 721-735.

Ribera, I., Foster, G.N. and Vogler, A.P. 2003. Does habitat use explain large scale species richness patterns of aquatic beetles in Europe. *Ecography*, 26: 145-152.

Ricklefs, R.E. and Schluter, D. 1993. *Species Diversity in Ecological Communities. Historical and Geographical Perspectives*. Chicago University Press, Chicago.

Rundle, S.D., Bilton, D.T. and Foggo, A. 2007. Chapter 10. By wind, wings or water: body size, dispersal and range size in aquatic invertebrates. In: Hildrew, A.G., Raffaelli, D.G. and Edmonds-Brown, R. (eds). *Body size: The Structure and Function of Aquatic Ecosystems*. Cambridge University Press, Cambridge, UK. pp. 186-209.

Samways, M.J. and Niba, A. 2010. Climate and elevational range of a South African dragonfly assemblage. *Biodiversity and Ecosystem Risk Assessment*, 5: 85-107.

Samways, M.J. and Simaika, J.P. 2016. *Manual of Freshwater Assessment for South Africa: Dragonfly Biotic Index*. Suricata 2. South African National Biodiversity Institute. Pretoria, South Africa.

Samways, M.J., Osborn, R. and van Heerden, I. 1996. Distribution of benthic invertebrates at different depths in a shallow reservoir in the KwaZulu-Natal Midlands. *Koedoe,* 39: 69-76.

Scheibler, S.S., Melo, M.C., Montemayor, S.I. and Scollo, A.M. 2016. Abundance, richness, seasonal and altitudinal dynamics of aquatic true bugs (Heteroptera) in mountain wetlands of Argentina. *Wetlands*, 36: 265-274.

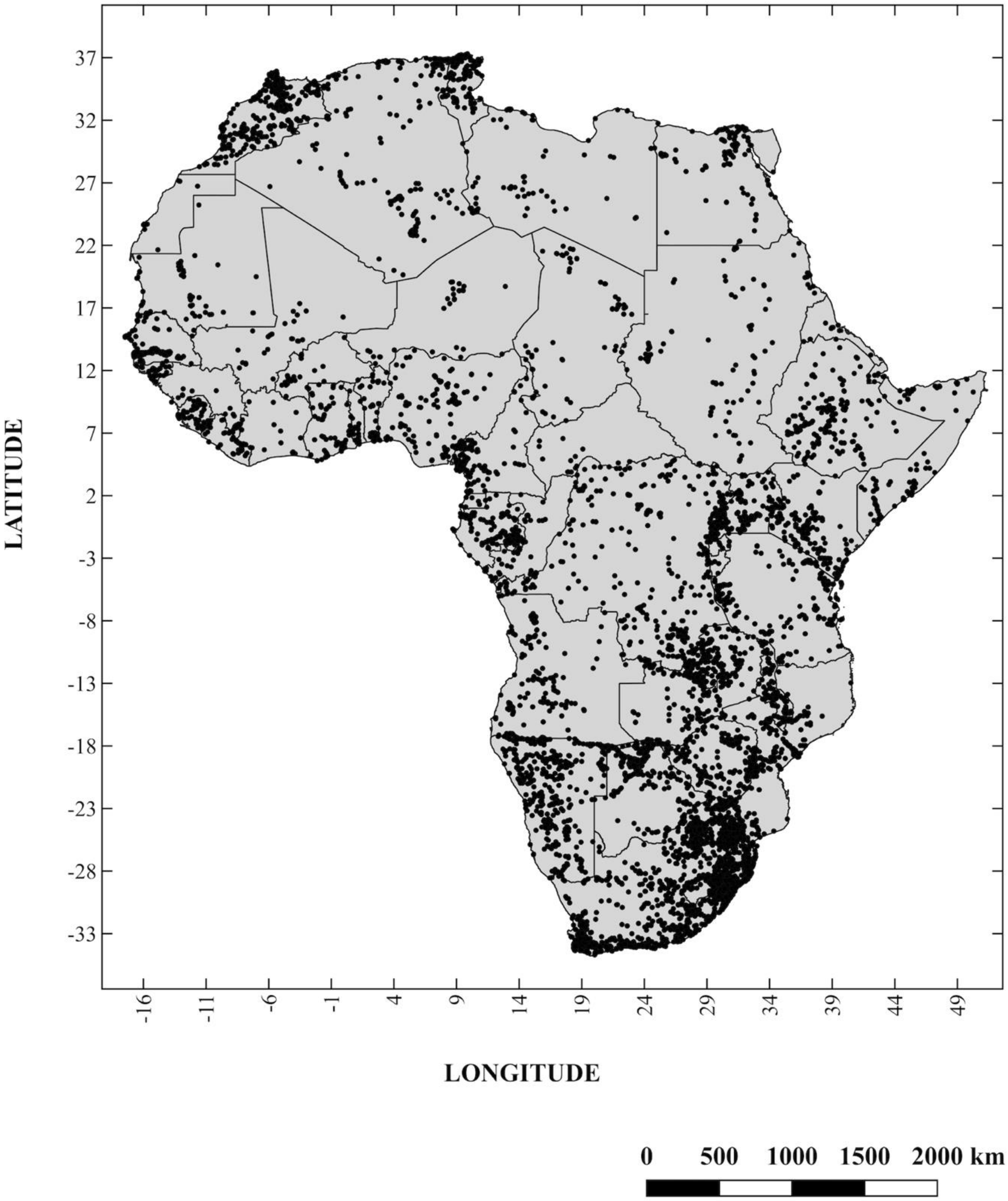
Simaika, J.P. and Samways, M.J. 2009. An easy-to-use index of ecological integrity for prioritizing freshwater sites and for assessing habitat quality. *Biodiversity and Conservation*, 18: 1171-1185.

van Huyssteen, P. and Samways, M.J. 2009. Overwintering dragonflies in an African savanna (Anisoptera: Gomphidae, Libellulidae). *Odonatologica*, 38: 167-172.

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P. and Sear, D. 2004. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation*, 115: 329-341.

Willig, M.R., Kaufman, D.M. and Stevens, R.D. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution and Systematics*, 34: 273-309.

Appendices



Appendix S2.1 African distribution records for dragonflies occurring in South Africa.

Appendix S2.2 Recently confirmed dragonfly species occurring in SA. * indicates endemics.

ZYGOPTERA

- **Calopterygidae**
  - *Phaon iridipennis*
- **Chlorocyphidae**
  - *Platycypha caligata*
  - *Platycypha fitzsimonsi* *
- **Synlestidae**
  - *Chlorolestes apricans* *
  - *Chlorolestes conspicuus* *
  - *Chlorolestes draconicus* *
  - *Chlorolestes elegans* *
  - *Chlorolestes fasciatus* *
  - *Chlorolestes tessellatus* *
  - *Chlorolestes umbratus* *
  - *Ecchlorolestes nylephtha* *
  - *Ecchlorolestes peringueyi* *
- **Lestidae**
  - *Lestes dissimulans*
  - *Lestes ictericus*
  - *Lestes pallidus*
  - *Lestes plagiatus*
  - *Lestes tridens*
  - *Lestes uncifer*
  - *Lestes virgatus*
- **Platycnemididae**
  - *Allocnemis leucosticta* *
  - *Elattoneura frenulata* *
  - *Elattoneura glauca*
  - *Mesocnemis singularis*
  - *Metacnemis valida* *
  - *Spesbona angusta* *
- **Coenagrionidae**
  - *Aciagrion dondoense*
  - *Aciagrion gracile*
  - *Africallagma fractum*
  - *Africallagma glaucum*
  - *Africallagma sapphirinum* *
  - *Africallagma sinuatum*
  - *Agriocnemis exilis*
  - *Agriocnemis falcifera* *
  - *Agriocnemis gratiosa*
  - *Agriocnemis pinheyi*
  - *Agriocnemis ruberrima*
  - *Azuragrion nigridorsum*
  - *Ceriagrion glabrum*
  - *Ceriagrion suave*
  - *Ischnura senegalensis*
  - *Proischnura polychromatica* *
  - *Proischnura rotundipennis* *
  - *Pseudagrion acaciae*
  - *Pseudagrion assegaii*
  - *Pseudagrion caffrum* *
  - *Pseudagrion citricola* *
  - *Pseudagrion coeleste*
  - *Pseudagrion commoniae*
  - *Pseudagrion draconis* *
  - *Pseudagrion furcigerum* *
  - *Pseudagrion gamblesi*
  - *Pseudagrion hageni*
  - *Pseudagrion hamoni*
  - *Pseudagrion inopinatum* *
  - *Pseudagrion kersteni*
  - *Pseudagrion makabusiense*
  - *Pseudagrion massaicum*
  - *Pseudagrion newtoni* *
  - *Pseudagrion salisburyense*
  - *Pseudagrion sjoestedti*
  - *Pseudagrion spernatum*
  - *Pseudagrion sublacteum*
  - *Pseudagrion sudanicum*
  - *Pseudagrion vaalense* *

ANISOPTERA

- **Aeshnidae**
  - *Anaciaeschnura triangulifera*
  - *Anax ephippiger*
  - *Anax imperator*
  - *Anax speratus*
  - *Anax tristis*
  - *Gynacantha manderica*
  - *Gynacantha usambarica*
  - *Gynacantha villosa*
  - *Pinheyschna subpupillata*
  - *Zosteraeschna minuscula*
- **Gompidae**
  - *Ceratogomphus pictus*
  - *Ceratogomphus triceraticus* *
  - *Crenigomphus hartmanni*
  - *Gomphidia quarrei*
  - *Ictinogomphus ferox*
  - *Lestinogomphus angustus*
  - *Neurogomphus zambeziensis*
  - *Notogomphus praetorius*
  - *Onychogomphus supinus*
  - *Paragomphus cognatus*
  - *Paragomphus elpidius*
  - *Paragomphus genei*
  - *Phyllogomphus selysi*
- **Corduliidae**
  - *Hemicordulia africana*
  - *Phyllomacromia contumax*
  - *Phyllomacromia monoceros*
  - *Phyllomacromia picta*
  - *Syncordulia gracilis* *
  - *Syncordulia legator* *
  - *Syncordulia serendipator* *
  - *Syncordulia venator* *
- **Libellulidae**
  - *Acisoma inflatum*
  - *Acisoma variegatum*
  - *Aethriamanta rezia*
  - *Brachythemis lacustris*
  - *Brachythemis leucosticta*
  - *Bradinopyga cornuta*
  - *Chalcostephia flavifrons*
  - *Crocothemis divisa*
  - *Crocothemis erythraea*
  - *Crocothemis sanguinolenta*
  - *Diplacodes lefebvrii*
  - *Diplacodes luminans*
  - *Diplacodes pumila*
  - *Hemistigma albipunctum*
  - *Nesciothemis farinosa*
  - *Notiothemis jonesi*
  - *Olpogastra lugubris*
  - *Orthetrum abbotti*
  - *Orthetrum caffrum*
  - *Orthetrum chrysostigma*
  - *Orthetrum guineese*
  - *Orthetrum hintzi*
  - *Orthetrum icteromelas*
  - *Orthetrum julia*
  - *Orthetrum machadoi*
  - *Orthetrum robustum*
  - *Orthetrum rubens* *
  - *Orthetrum stemmale*
  - *Orthetrum trinacria*
  - *Palpopleura deceptor*
  - *Palpopleura jucunda*
  - *Palpopleura lucia*
  - *Palpopleura portia*
  - *Pantala flavescens*
  - *Parazyxomma flavicans*
  - *Rhyothemis semihyalina*
  - *Sympetrum fonscolombii*
  - *Tetrathemis polleni*
  - *Tholymis tillarga*
  - *Tramea basilaris*
  - *Tramea limbata*
  - *Trithemis aconita*
  - *Trithemis annulata*
  - *Trithemis arteriosa*
  - *Trithemis donaldsoni*
  - *Trithemis dorsalis*
  - *Trithemis furva*
  - *Trithemis hecate*
  - *Trithemis kirbyi*
  - *Trithemis pluvialis*
  - *Trithemis stictica*
  - *Trithemis werneri*
  - *Urothemis assignata*
  - *Urothemis edwardsii*
  - *Urothemis luciana*
  - *Zygonoides fuelleborni*
  - *Zygonyx natalensis*
  - *Zygonyx torridus*
  - *Zyxomma atlanticum*

Appendix S2.3 Detailed list of lotic, lentic/lotic and lentic biotopes, and riparian/edge and features associated with open water occupied by adult dragonflies, along with the description of each biotope.

Biotope	**Description**
Lotic habitat and velocity	
Small stream	1st order stream and/or < 2 m channel size
Large stream	2nd order stream and/or 2 m to 5 m channel size
Small river	3rd order river and/or 5 m to 50 m channel size
Large river	4th order river and/or > 50 m channel size
Waterfall	River or stream crossing steep topography where water rushes down vertically into a waterfall pool or swift section of the river or stream, but excluding the pool deposition zone
Swift river or stream	Fast to medium flow velocity, includes both riffles (turbulent flow; >0.4 m/sec) and glides (laminar flow; 0.01-0.4 m/sec)
Sluggish river or stream	Slow flow velocity (<0.01 m/sec)
Shallow river or stream	Water depth of <1 m
Deep river or stream	Water depth of >1 m
Lentic/Lotic habitat	
Seep	Shallow water seeping out of rocks, often forming a well-vegetated pool, rich in organic matter, with no to minimal flowing according to rainy season
Wetland	Very slow or stagnant water (dependent on time of year)
Deposition pool	Pools along rivers and streams, often deep and rich in organic material. May flow during the rain season. Also including eddies
River bed pool	Pools with much vegetation that are left behind in savanna river beds when the water level of the river drops
Waterfall pool	Pool directly below waterfalls
Oxbow pond	Pools in meandering river channels, often deep and rich in organic material. May flow during the rain season.
Open swamp channel	Channels in swampy areas that connect swamps, flowing in the rainy season, and bordered by reeds, especially *Phragmites*
Canopied swamp channel	Channels in swampy areas that connect swamps, flowing in the rainy season, and bordered by trees and tall reeds
Lentic habitat	
Coastal swamp	An open swamp in coastal regions, often isolated from the ocean, which remains wet all year
Open swamp	A swamp with no canopy cover, and rich in low emergent vegetation
Marsh	Lowland areas (occasionally highland areas in the Cape) which are flooded during the wet season and remain wet for most of the year
Bog	Wet, soggy lentic water body with deep layers of decaying organic material
Pan	Large, shallow lentic water body. May or may not dry up during dry season
Waterhole	Muddy, shallow water body, trampled by game. Also referred to as a wallow
Dune pool	Small to medium-sized lentic water bodies formed between coastal dunes. May be spring or rain fed
Pothole	Small pools, ground into the rock surface by freely moving stones over many years, creating hollows in bare rock that fill from river splash and rainwater
Rock pool	Small pools in river channels, completely lined with bedrock and with no vegetation cover
Forest pool	Small pools, rich in organic matter, within forest
Perennial pond	Small to medium-sized lentic water bodies, rain or spring fed
Temporary pond	Ponds that vary greatly in water level, and may dry up completely. Also includes semi-permanent ponds
Lake	Large natural lentic water bodies away from the coast (> 2 ha)
Coastal lake	Large natural lentic water bodies along the coast (>2 ha)
Artificial farm or urban pond	Artificially-made ponds in agricultural or urban areas (< 2 ha)
Artificial reservoir	Artificially-made lentic habitats including municipal dams, often used for recreation (> 2 ha)
Riparian and edge characteristics	**Description**
Marshy edge	Shallow edge with abundant emergent and/or submerged vegetation
Flooded edge	Edge where water rises temporarily above the maximum level during times of high rainfall. Often with mud and abundant emergent vegetation

Grassy edge	Edge lined with short and tall grasses
Reedy edge	Edge lined with reeds, native or invasive
Palmiet edge	Edge lined specifically with Palmiet reed
Sedge edge	Edge lined with short and tall sedges
Bushy edge	Edge lined with bushy or shrubby vegetation
Wooded edge	Edge with single or clumps of small trees
Forested edge	Shaded edge with virtually no sunlight penetration and occasionally ferns in the understorey
Forest clearing	Shaded edge with openings in the canopy
Tree canopies	Edge with accessible tree canopies where some dragonflies forage or seek shade during very hot times
Open edge	Edge with limited vegetation and canopy cover, and mostly bare, compacted soil
Sandy edge	Sandy edge, beach-like in places, and also usually with scattered tufts of vegetation
Rocky edge	Edge with small to medium sized rocks and cobbles
Boulder-strewn edge	Edge with large, immobile boulders. Often with mossy covering in the case of montane rivers
Barringtonia forest	Shaded, dense forest, lining lowland streams and rivers, and floods during the wet season, with a predominantly *Barringtonia* tree canopy
Open grass/bush coastal dune	Areas covered mainly with coastal grasses and some bushes and small trees
Features associated with open water	
Open water	Water surface away from edges with no emergent vegetation, rocks and/or boulders
Boulders above water surface	Boulders exposed above the water surface away from the edge, more visible when the water level is low
Floating vegetation	Edge and parts away from the edges with vegetation floating on the surface, including *Aponogeton*, water lilies and organic debris
Submerged vegetation	Dense submerged vegetation reaching in the water surface, including *Stockenia*, excluding algal mats
Emergent vegetation	Edge and parts part away from the edges with vegetation penetrating the water surface. May included grasses, sedges and herbaceous plants
Stems over open water	Open water away from the edges with few reeds and stems emergent from the water surface
Algal mat	Mats of algae floating on the water surface, usually seen in ponds/reservoirs/streams where there is some fertilizer input

Appendix S2.4 Detailed list of lotic, lentic/lotic and lentic biotopes, and substratum type and marginal features occupied by larval dragonflies, along with the description of each biotope.

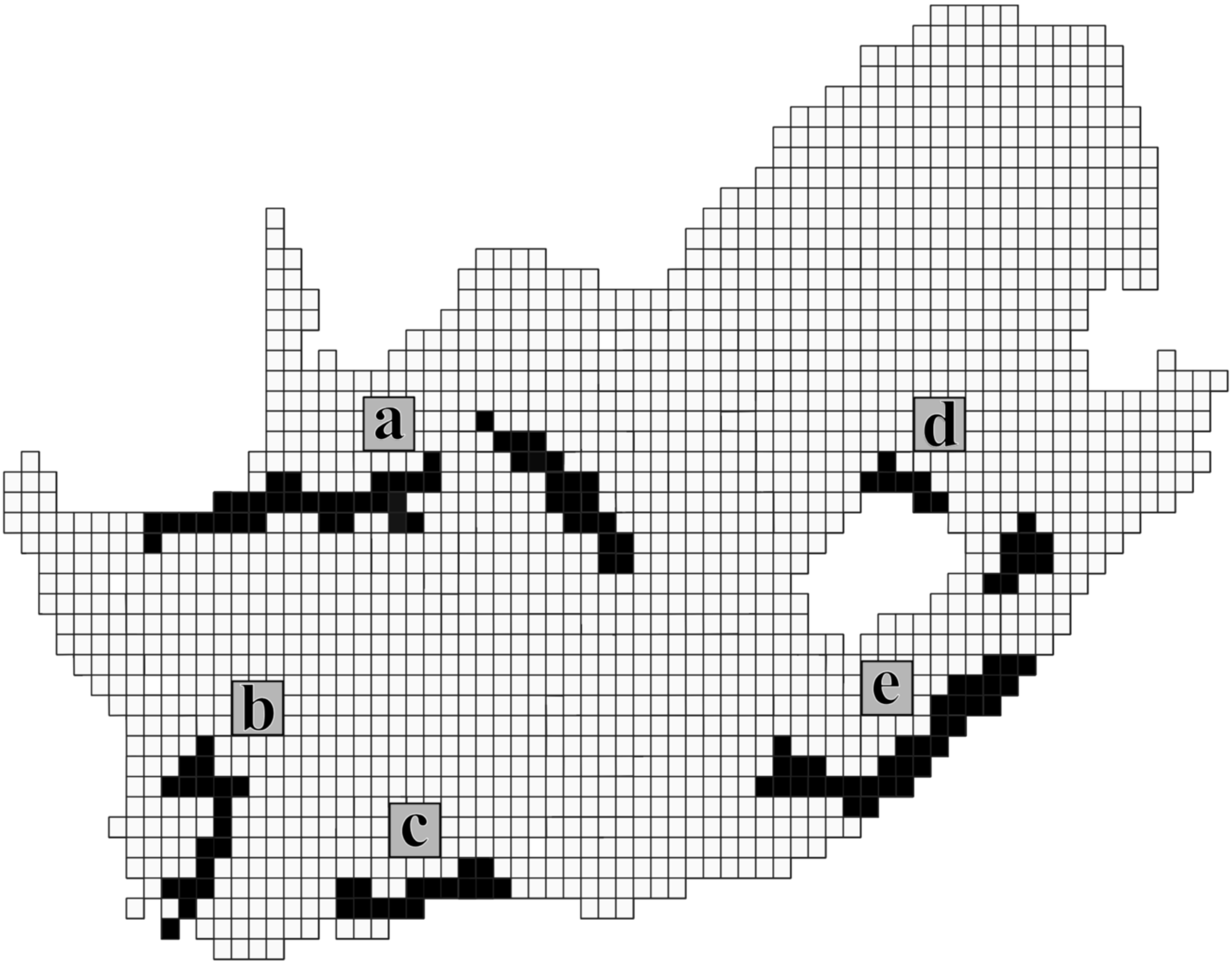
Biotope	**Description**
Lotic habitat and velocity	
Mountain trickle	Small flowing trickle from mountains, usually at steep gradients and/or over high elevation trails
Small stream	1st order stream and/or < 2 m channel size
Large stream	2nd order stream and/or 2 m to 5 m channel size
Small river	3rd order river and/or 5 m to 50 m channel size
Large river	4th order river and/or > 50 m channel size
Waterfall	River or stream crossing steep topography where water rushes down vertically into a waterfall pool or swift section of the river or stream, but excluding the pool deposition zone
Swift river or stream	Fast to medium flow velocity, includes both riffles (turbulent flow; >0.4 m/sec) and glides (laminar flow; 0.01-0.4 m/sec)
Sluggish river or stream	Slow flow velocity (<0.01 m/sec)
Lentic/Lotic habitat	
Seep	Shallow water seeping out of rocks, often forming a well-vegetated pool, rich in organic matter, with no to minimal flowing according to rainy season
Wetland	Very slow or stagnant water (dependent on time of year)
Deposition pool	Pools along rivers and streams, often deep and rich in organic material. May flow during the rain season. Also including eddies
River bed pool	Pools with much vegetation that are left behind in savanna river beds when the water level of the river drops
Waterfall pool	Pool directly below waterfalls, often with strong currents and multidirectional flows. Excluding deposition pools
Oxbow pond	Pools in meandering river channels, often deep and rich in organic material. May flow during the rain season.
Open swamp channel	Pools in meandering river channels, often deep, and rich in submerged vegetation and organic material. May flow during the rain season
Canopied swamp channel	Channels in swampy areas that connect swamps, flowing in the rainy season, and bordered by trees and reeds
Lentic habitat	
Coastal swamp	An open swamp in coastal regions, often isolated from the ocean, which remains wet all year
Open swamp	A swamp with no canopy cover, and rich in low emergent vegetation
Marsh	Lowland areas (occasionally highland areas in the Cape) which are flooded during the wet season and remain wet for most of the year
Bog	Wet, soggy lentic water body with deep layers of decaying organic material
Pan	Large, shallow lentic water body. May or may not dry up during dry season
Waterhole	Muddy, shallow water body, trampled by game. Also referred to as a wallow
Dune pool	Small to medium-sized lentic water bodies formed between coastal dunes. May be spring or rain fed
Pothole	Small pools, ground into the rock surface by freely moving stones over many years, creating hollows in bare rock that fill from river splash and rainwater
Rock pool	Small pools in river channels, completely lined with bedrock and with no vegetation cover
Forest pool	Small pools, rich in organic matter, within forest
Perennial pond	Small to medium-sized lentic water bodies, rain or spring fed
Temporary pond	Ponds that vary greatly in water level, and may dry up completely. Also includes semi-permanent ponds
Lake	Large natural lentic water bodies away from the coast (> 2 ha)
Coastal lake	Large natural lentic water bodies along the coast (>2 ha)
Artificial farm or urban pond	Artificially-made ponds in agricultural or urban areas (< 2 ha)
Artificial reservoir	Artificially-made lentic habitats including municipal dams, often used for recreation (> 2 ha)
Substratum	
Bedrock bottom	Very firm and smooth bottom with virtually no loose stones/boulders
Cobble bottom	Firm bottom covered with particles between a size of 5 cm and 25 cm
Gravel bottom	Fairly firm bottom covered with fine and coarse gravel or pebbles

Sandy bottom	Fairly firm bottom covered with fine and coarse sand particles
Muddy bottom	Soft bottom covered with mud and sometimes mixed with decaying organic material
Leaf litter and twig bottom	Bottom with twigs and leaves, making up high loads of organic material
Submerged vegetation	Dense submerged vegetation, usually in sluggish parts of rivers and still water, yet sometimes in fast flowing water. May or may not reach the water surface
Submerged roots	Submerged roots of grasses or sedges along the edge of flowing waters, or within the water course
Margin characteristics	
Bare margin	Margin mainly with mud, sand and/or gravel, and little to no vegetation
Rocky margin	Margin lined with small, medium and large sized rocks
Flooded margin	Temporary state of lotic habitat margin where water rises above the maximum level during times of high rainfall. Often with mud and abundant emergent vegetation
Marshy margin	Shallow margin with abundant emergent and/or submerged vegetation
Grassy margin	Margin lined with short and tall emergent grasses
Reedy margin	Margin lined with emergent reeds, native or invasive
Sedge margin	Margin lined with emergent sedges
Palmiet margin	Margin lined specifically with Palmiet reed
Bushy margin	Margin lined with emergent bushes
Forested margin	Shaded margin with virtually no sunlight penetration, usually from surrounding trees

Appendix S2.5 Significant t-values (plain), F-values (bold) z-values (cursive) of latitude, longitude and elevation ranges for a subset of dragonflies across Africa. (+) indicates positive correlations.

	Latitude range	Longitude range	Elevation range
Variable	**Test statistic**	**Test statistic**	**Test statistic**
Adult biotopes occupied	(+) 7.527 **	(+) 2.551*	(+)3.630 ***
Habitat preference	**15.778** ***	**15.405*****	
Lentic - Lotic	*-2.961* **	*-3.868* ***	
Lentic - Lentic/Lotic		*-2.587* *	
Lotic-Lentic/Lotic			
End of adult flight season	**9.083** ***	**8.367** ***	**7.138** ***
Late summer - Early autumn	*-4.586* ***	*-4.713* ***	
Late summer - Late autumn	*-5.231* ***	*-5.481* ***	*-2.632* *
Late summer - Early winter	*-4.229* ***	*-3.838* ***	
Early autumn - Late autumn			
Early autumn - Early winter			
Late autumn - Early winter			
Overwintering as adults			1.762 **.**
Wing-to-body ratio	(+) 22.923 ***	(+) 3.954 ***	

Significance levels: **.** : $p < 0.1$; * : $p < 0.05$; ** : $p < 0.01$; *** : $p < 0.001$.



Appendix S3.1 Sampling areas supplementing current dragonfly distribution records. Quarter degree grid cells visited from November 2017 – April 2019 indicated in black. (a) Orange River, Vaal River and surroundings, (b) Cederberg mountain range and surroundings, (c) Southern Cape coastal belt, (d) southern Free State and KwaZulu-Natal Midlands, and (e) coastal and interior parts of the Eastern Cape.

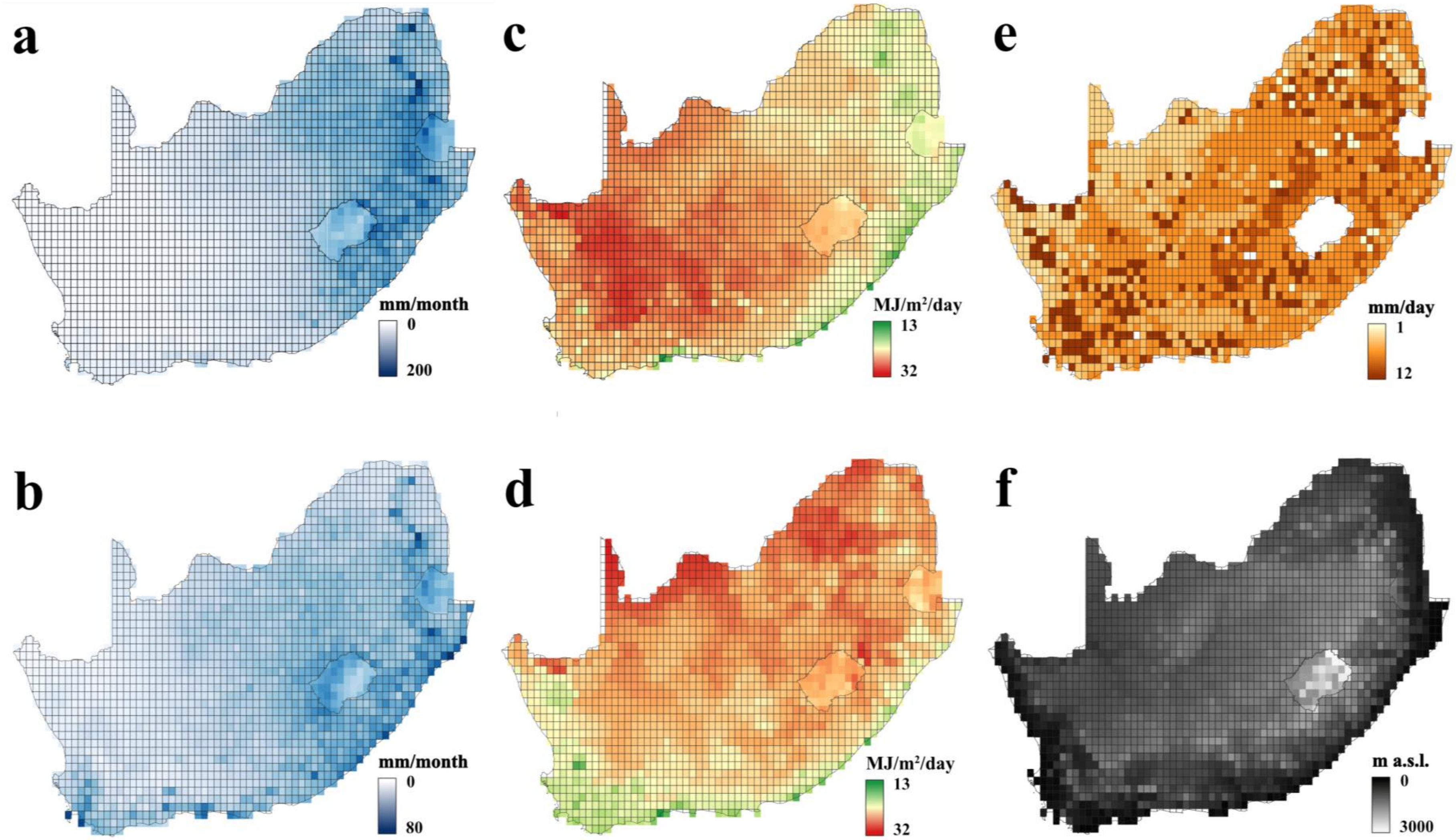
Appendix S3.2 List of considered spatial datasets, along with their type classifications and sources.

Variable	Data type	Source
Latitude	Topographic	Clausnitzer et al. 2009
Longitude	Topographic	Clausnitzer et al. 2009
Elevation	Topographic	van Niekerk, 2001
Seasonal average rainfall	Climatic	van Niekerk and Joubert, 2011
Early spring (September)		
Mid-spring (October)		
Late spring (November)		
Early summer (December)		
Mid-summer (January)		
Late summer (February)		
Early autumn (March)		
Mid-autumn (April)		
Late autumn (May)		
Early winter (June)		
Mid-winter (July)		
Late winter (August)		
Seasonal average solar radiation	Climatic	van Niekerk and Joubert, 2011
Early spring (September)		
Mid-spring (October)		
Late spring (November)		
Early summer (December)		
Mid-summer (January)		
Late summer (February)		
Early autumn (March)		
Mid-autumn (April)		
Late autumn (May)		
Early winter (June)		
Mid-winter (July)		
Late winter (August)		
Average soil drain rate	Geological	van Niekerk, 2001

Clausnitzer, V., Dijkstra, K.-D.B., Koch, R., Boudot, J.-P., Darwall, W.R.T., Kipping, J., … and Suhling, F. 2012. Focus on African freshwaters: hotspots of dragonfly diversity and conservation concern. *Frontiers in Ecology and the Environment*, 10: 129-134.

van Niekerk, A. 2001. *Western Cape digital elevation model: product description*. Centre for Geographical Analysis, Stellenbosch University, South Africa.

van Niekerk, A. and Joubert, S.J. 2011. Input variable selection for interpolating high-resolution climate surfaces for the Western Cape. *Water SA*, 37: 271-280.



Appendix S3.3 Spatial gradients of significant climatic and topographical factors identified by generalized linear modelling and generalized dissimilarity modelling. All spatial datasets are at quarter degree spatial resolution. (a) Early summer rainfall, (b) mid-autumn rainfall, (c) mid-summer solar radiation, (d) mid-autumn solar radiation, (e) average soil drain rate and (f) elevation

Appendix S4.1 Abundance, number of observed species (Sobs) and species estimators (Chao2 and Jackknife2).

Group	**Type**	**Abundance**	**Sobs**	**Chao2**	**Jackknife2**
Dragonflies	Overall	1129	27	26.67 (±1.31)	27.07
	Pond	438	27	38.25 (±13.15)	37.24
	Reservoir	691	23	30.00 (±11.66)	28.54
Beetles	Overall	658	16	16.00 (±0)	12.30
	Pond	415	14	14.00 (±0)	12.29
	Reservoir	243	12	13.50 (±2.29)	14.99
Bugs	Overall	3078	18	18.50 (±1.32)	19.00
	Pond	1038	18	18.67 (±1.31)	19.14
	Reservoir	2040	13	13.17 (±0.54)	12.29

Appendix S4.2 Species list of aquatic insect species sampled. * = South African endemic, ✓ = Occupying artificial reservoirs, ✗ = Occupying natural ponds

	Family	Artificial reservoir	Natural pond	Faber's Hill	Mount Gilboa	Good Hope	Linwood	Mount Shannon
Odonata								
Acisoma variegatum	Libellulidae	✓	✗			✓		✗
Africallagma glaucum	Coenagrionidae	✓	✗	✗	✓✗	✗	✓	✓✗
*Africallagma sapphirinum**	Coenagrionidae	✓	✗	✓✗	✓	✓		✓
Agriocnemis pinheyi	Coenagrionidae	✓	✗		✓	✗		
*Allocnemis leucosticta**	Platycnemididae	✓	✗	✗	✓	✗		✗
Anax imperator	Aeshnidae	✓	✗		✓✗	✓✗	✓	✓
Anax speratus	Aeshnidae	✓	✗	✗	✗		✓	✓✗
Azuragrion nigridorsum	Coenagrionidae	✓	✗	✓				
Chlorolestes fasciatus	Synlestidae		✗		✗			
Crocothemis erythraea	Libellulidae	✓	✗	✓✗	✓	✓✗	✓	✓✗
Ellatoneura glauca	Platycnemididae		✗	✗	✗			✗
Ischnura senegalensis	Coenagrionidae	✓	✗	✓✗	✓	✓✗	✓	✗
Lestes plagiatus	Lestidae	✓	✗	✓✗	✓	✓✗		✓✗
Nesciothemis farinosa	Libellulidae	✓	✗	✓✗	✓	✓✗	✓	
Notogomphus praetorius	Gomphidae	✓	✗	✓✗	✓✗	✓		✓
Orthetrum julia	Libellulidae	✓	✗	✓✗	✓✗	✓✗	✓	✗
Palpopleura jucunda	Libellulidae	✓	✗	✓✗				
Pantala flavescens	Libellulidae	✓	✗		✓✗	✓✗	✓	✓✗
Paragomphus cognatus	Gomphidae	✓	✗	✓	✓✗	✓✗		
*Proischnura rotundipennis**	Coenagrionidae		✗					✗
Pseudagrion caffrum	Coenagrionidae	✓	✗	✓	✓✗	✓		✗
Pseudagrion spernatum	Coenagrionidae	✓	✗	✗	✓✗	✗	✓	✓

Tramea limbata	Libellulidae	✓	✗	✓	✓	✓✗	✓	✓✗
Trithemis arteriosa	Libellulidae	✓	✗	✓✗			✓	
Trithemis furva	Libellulidae	✓	✗	✓✗	✓✗	✓✗	✓	✓✗
Trithemis stictica	Libellulidae	✓	✗	✓✗	✓✗	✗	✓	✓
Zosteraeshna minuscula	Aeshnidae		✗	✗		✗		✗
Coleoptera								
Algophilus sp.*	Hydrophilidae	✓	✗	✓	✓✗	✓✗	✓	✓✗
Amphiops sp.	Hydrophilidae	✓	✗	✗				✗
Aulonogyrus sp.	Gyrinidae		✗	✗		✗		
Aulonogyrus sp. 2	Gyrinidae	✓					✓	
Copelatus sp.	Dytiscidae		✗			✗		✗
Derovatellus sp.	Dytiscidae		✗		✗	✗		✗
Gyrinus sp.	Gyrinidae	✓	✗		✓✗	✗		✓
Helochares sp.	Hydrophilidae	✓	✗	✗	✓✗	✗		✗
Hydropeplus sp.	Dytiscidae	✓			✓			
Hyphydrus sp.	Dytiscidae	✓	✗	✗	✓✗			
Hyphydrus sp. 2	Dytiscidae	✓	✗	✓✗	✓✗	✓✗		✗
Hyphydrus sp. 3	Dytiscidae	✓	✗	✓✗	✓✗	✗		
Orectogyrus sp.	Gyrinidae		✗			✗		✗
Philaccolus sp.	Dytiscidae	✓	✗	✓	✗	✗		
Philaccolus sp. 2	Dytiscidae	✓	✗	✓✗	✓✗			✗
Rhantus concolorans	Dytiscidae	✓	✗	✓✗	✗	✗		✗
Hemiptera								
Agraptocorixa sp.	Corixidae	✓	✗	✓✗	✓✗	✓✗		✓
Anisops varia	Notonectidae	✓	✗	✓✗	✓✗	✓✗		✓✗
Appasus grassei	Belostomatidae	✓	✗	✓✗	✓✗	✓✗	✓	✓✗
Borborophilus afzelii	Nepidae		✗	✗		✗		✗
Enithares glauca	Notonectidae	✓	✗	✓✗	✓✗			✓✗
Hebrus sp.	Veliidae	✓	✗		✓✗	✓		
Hydrometra albolineata	Hydrometridae	✓	✗	✗	✓✗			
Laccocoris sp.	Naucoridae	✓	✗	✓✗	✓✗	✓✗		✗
Laccotrephes brachialis	Nepidae		✗	✗		✗		✗

Limnogonus capensis	Gerridae		✗	✗				
Micronecta sp.	Micronectidae	✓	✗	✓✗	✓✗	✓✗		✓
Neogerris severance	Gerridae	✓	✗	✓✗	✓✗	✗		✗
Plea pullula	Pleidae	✓	✗	✓✗	✓✗			✓✗
Ranatra franarantsoana	Nepidae	✓	✗		✓	✓✗		✗
Ranatra grandicollis	Nepidae		✗		✗			
Rhagovelia nigricans	Veliidae	✓	✗	✗	✗		✓	✗
Sigara pectoralis	Corixidae		✗	✗				✗
Sigara sp. 2	Corixidae	✓	✗	✓✗	✓✗	✓✗	✓	✓✗

Appendix S4.3 Summary statistics of environmental variables for artificial reservoirs and natural ponds.

	Mean	SE	Min.	Max.
Artificial reservoirs				
Size (m^2)	23933.7	7703.8	871.3	151604.6
Elevation (m a.s.l.)	1346.1	39.9	951.0	1584.0
Vegetation height (m)	0.8	0.1	0.2	2.5
Total cover (%)	65.4	6.5	18.0	100.0
Reeds cover (%)	14.0	4.8	0	90.0
Forbs cover (%)	38.9	8.2	0	100.0
Grasses cover (%)	12.8	3.7	0	60.0
Depth (m)	0.6	0.1	0.4	0.9
Dissolved oxygen (mg/L)	7.4	0.4	4.8	11.7
Temperature (°C)	24.8	0.8	20.7	37.5
Conductivity (µs)	61.6	5.9	31.7	119.0
pH	7.4	0.1	6.8	8.6
Turbidity (cm visibility)	57.0	6.0	5.0	100.0
Natural ponds				
Size (m^2)	7955.3	1925.7	213.5	30832.7
Elevation (m a.s.l.)	1435.3	33.1	950	1550.0
Vegetation height (m)	0.8	0.1	0.04	1.7
Total cover (%)	83.4	5.5	16.0	100.0
Reeds cover (%)	2.2	2.2	0.0	44.0
Forbs cover (%)	38.0	8.4	0.0	100.0
Grasses cover (%)	43.2	8.9	0.0	100.0
Depth (m)	0.5	0.1	0.1	1.2
Dissolved oxygen (mg/L)	6.2	0.4	2.8	8.8
Temperature (°C)	21.5	0.4	18.0	24.5
Conductivity (µs)	51.1	3.1	31.9	81.3
pH	7.1	0.1	6.4	7.6
Turbidity (cm visibility)	28.2	4.0	5.0	70.5

Appendix S5.1 Abundance, number of observed species (Sobs) and species estimators (Chao2 and Jackknife 2).

Group	**Type**	**Abundance**	**Sobs**	**Chao2**	**Jackknife2**
Odonata	Overall	510	22	24.08 (±2.51)	26.08
	Pond	278	20	3 (±3.24)	25.98
	Reservoir	232	12	12.17 (±0.54)	11.36
Coleoptera	Overall	665	12	13.5 (±2.29)	15.00
	Pond	622	11	15 (±5.29)	16.68
	Reservoir	43	6	6 (±3.74)	6.81
Hemiptera	Overall	3894	11	12.5 (±2.29)	14.00
	Pond	1072	11	13.67 (±3.49)	15.83
	Reservoir	2822	4	4.5 (±1.32)	5.00

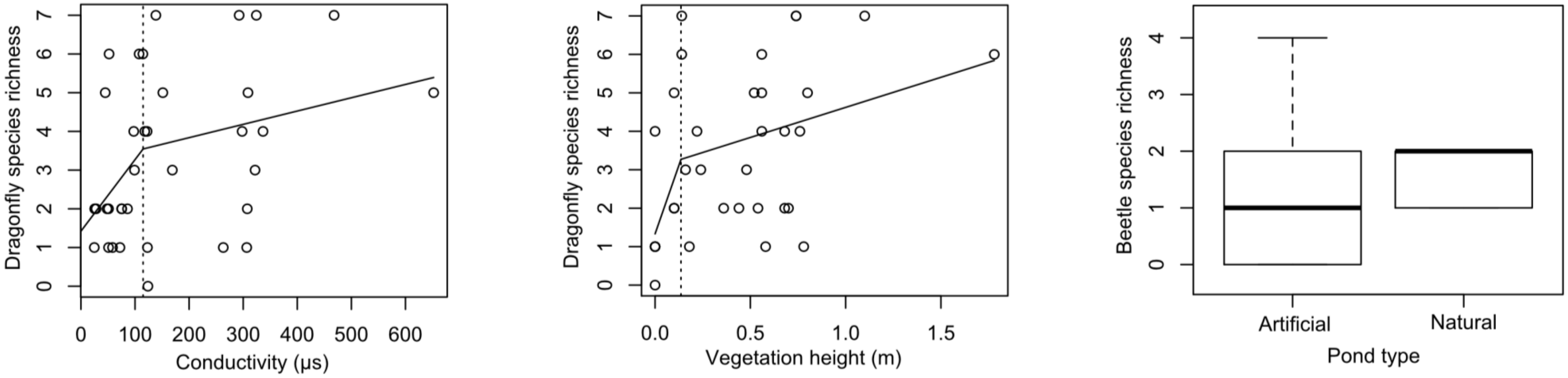
Appendix S5.2 Species list of aquatic insects sampled. ✓ Indicates occupancy at artificial reservoirs, × indicates occupancy at natural ponds.

	Common name	Artificial reservoir	Natural pond	Betty's Bay	Cederberg	Worcester	Franschhoek	Grabouw	Stellenbosch	Somerset West
Odonata										
Africallagma glaucum	Swamp Bluet	✓	×			×		×		✓
*Africallagma sapphirinum**	Sapphire Bluet		×		×					
Anax imperator	Blue Emperor	✓	×		×	×		×	✓	✓
Anax speratus	Orange Emperor		×	×			×			
Ceriagrion glabrum	Common Citril		×					×		
*Chlorolestes umbratus***	White Malachite		×					×		
Crocothemis erythraea	Broad Scarlet		×			×				
Crocothemis sanguinolenta	Little Scarlet	✓	×			×				✓
*Elattoneura frenulata***	Sooty Threadtail		×				×			
Ischnura senegalensis	Tropical Bluetail	✓	×	×		×	×	✓×	✓	✓
Orthetrum julia capicola	Julia Skimmer	✓	×		×		×	✓×		✓
*Pinheyschna subpupillata**	Stream Hawker	✓								✓
*Proischnura polychromatica***	Mauve Bluet		×		×		×			
*Pseudagrion furcigerum***	Palmiet Sprite	✓	×				×	×	✓	✓
*Pseudagrion draconis**	Mountain Sprite	✓	×		×		×	✓×	✓	
*Spesbona angusta***	Spesbona		×				×			
*Syncordulia legator***	Gilded Presba		×				×			
*Syncordulia venator***	Mahogany Presba	✓								✓
Trithemis annulata	Violet Dropwing		×				×			
Trithemis arteriosa	Red-Veined Dropwing	✓	×		×	×	×	✓×	✓	✓
Trithemis furva	Navy Dropwing	✓	×		×			✓	✓	✓

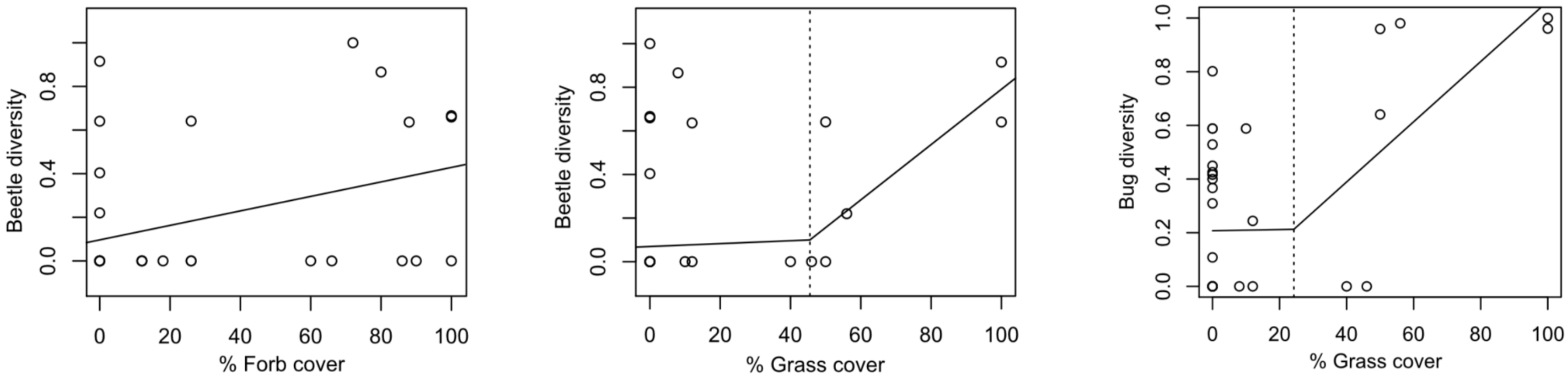
*Zosteraeshna minuscula**	Friendly Hawker	✓	✗		✗			✓✗		✓
Coleoptera										
Agabus sp.	Diving Beetle		✗		✗	✗				
Aulonogyrus sp. 2	Whirligig Beetle	✓	✗	✗			✗			
*Coelhydrus brevicollis***	Diving Beetle	✓	✗		✗					✓
Copelatus sp. 1	Diving Beetle		✗					✗		
Copelatus sp. 2	Diving Beetle		✗					✗		
Darwinhydrus sp.**	Diving Beetle		✗			✗	✗	✗		
Derovatellus sp.	Diving Beetle	✓							✓	✓
Helochares sp.	Water Scavenger Beetle		✗					✗		
Hydropeplus sp.**	Diving Beetle		✗					✗		
Hyphydrus signatus	Pigsnout Diving Beetle	✓	✗	✗			✗	✗		✓
Philaccolus sp.	Diving Beetle		✗		✗	✗		✗		
Rhantus concolorans	Speckled Diving Beetle	✓	✗							✓
Hemiptera										
Appasus capensis	Giant Water Bug		✗			✗		✗		
Enithares sobria	Common Backswimmer	✓	✗		✗	✗		✗	✓	✓
Gerris swakopensis	Water Strider		✗	✗						
Laccocorris spurcus	Saucer Bug		✗					✗		
Micronecta scutellaris	Pygmy Water Boatman	✓	✗			✗			✓	✓
*Notonecta lactitans**	Common Backswimmer	✓	✗					✗		✓
Ranatra sp.	Water Stick Insect		✗			✗		✗		
Rhagovelia maculata	Pygmy Water Cricket		✗				✗			
Sigara pectoralis	Water Boatman	✓	✗	✗	✗	✗	✗	✗	✓	✓
Tenagogonus sp.	Water Strider		✗					✗		
Tenagovelia vittigera	Water Cricket		✗		✗		✗	✗		

Appendix S5.3 Significant effects of pre-selected environmental variables on species richness and diversity for each focal taxon: (A) overall effects on species richness, (B) overall effects on diversity, (C) effects on species richness for natural ponds, (D) effects on species richness for artificial reservoirs and (E) effects on species diversity for artificial reservoirs. Dotted vertical lines indicate breakpoints in the case of piecewise regressions.

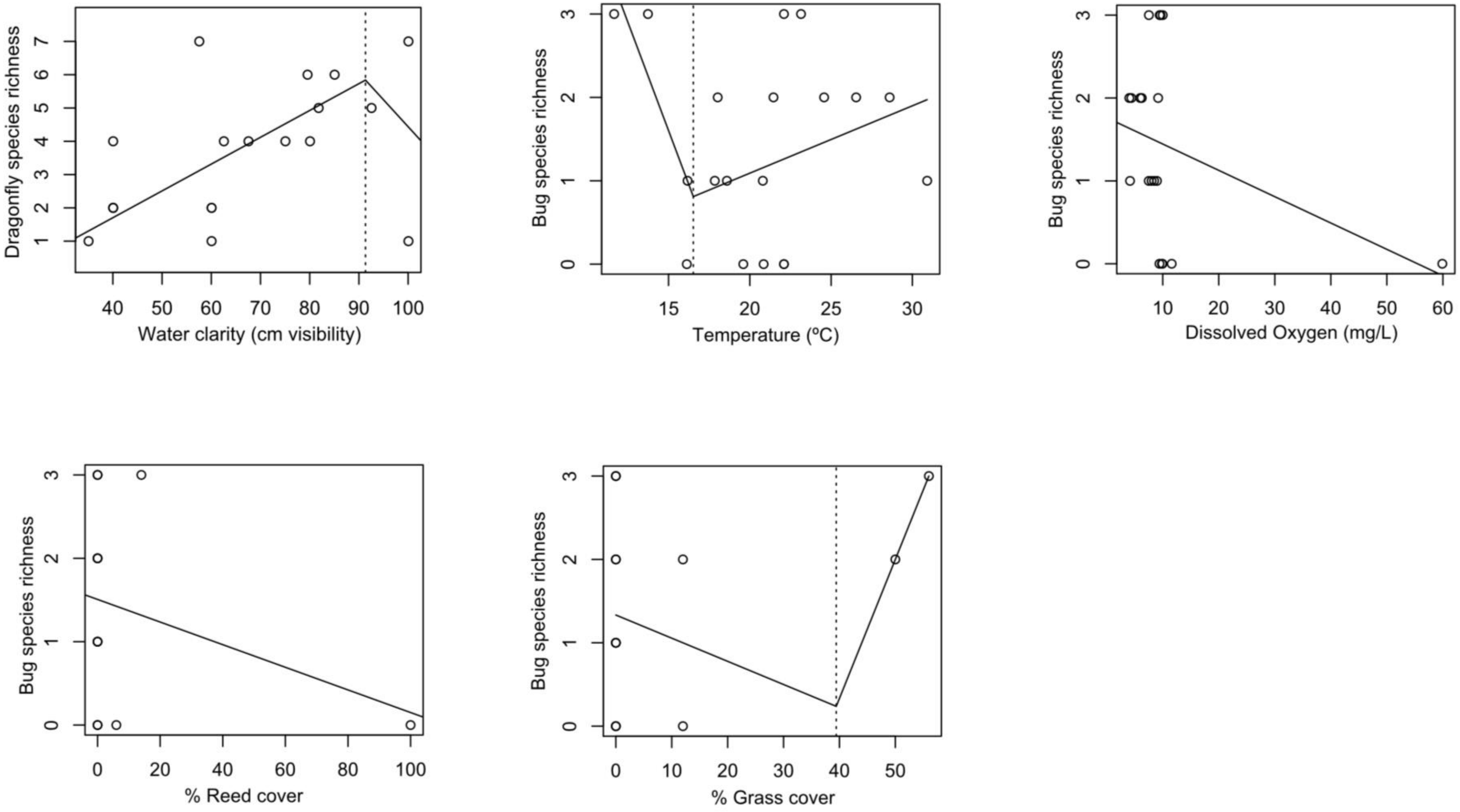
(A)



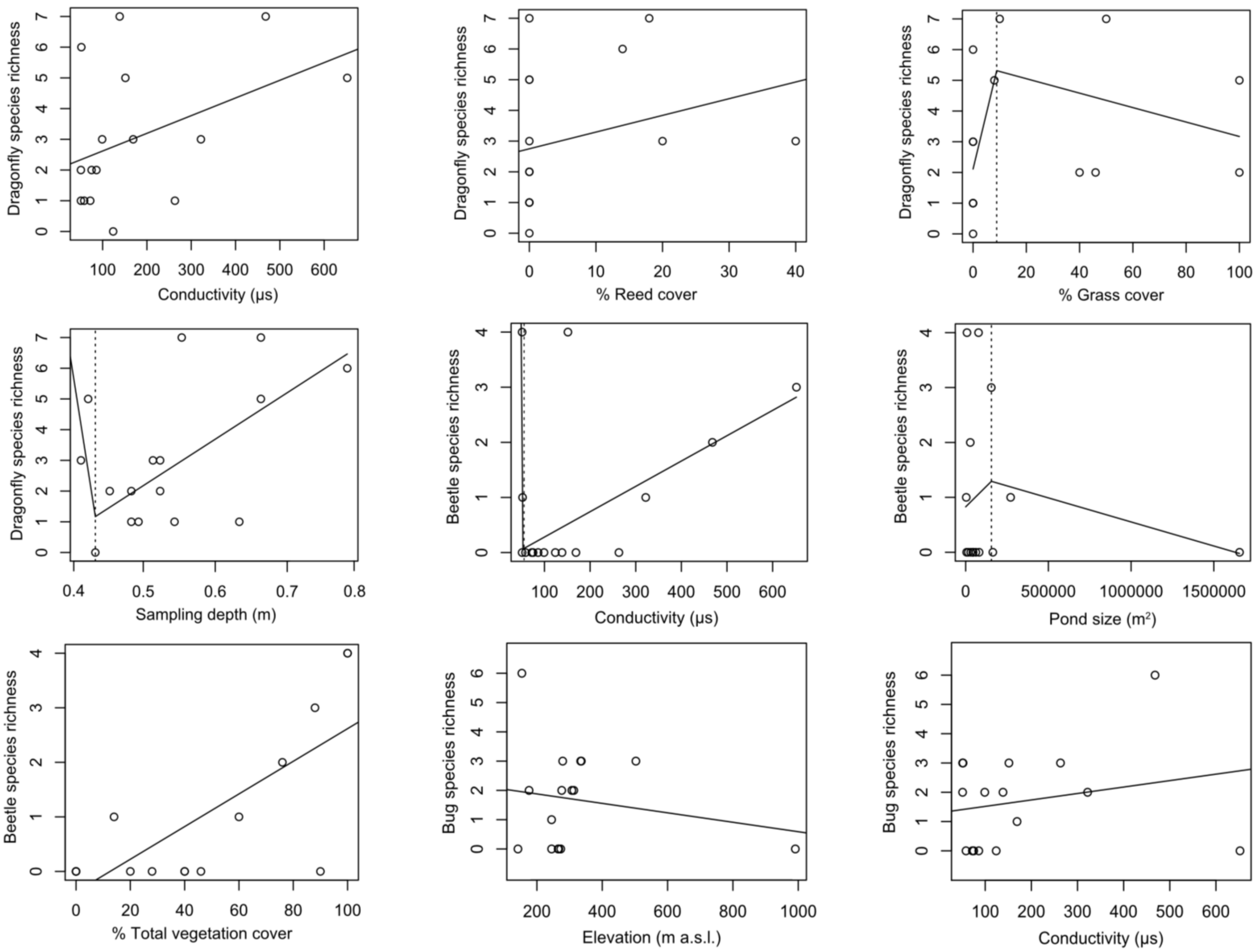
(B)


Beetle diversity
0.0
0.4
0.8
0
20
40
60
80
100
% Forb cover
Beetle diversity
0.0
0.4
0.8
0
20
40
60
80
100
% Grass cover
Bug diversity
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100
% Grass cover

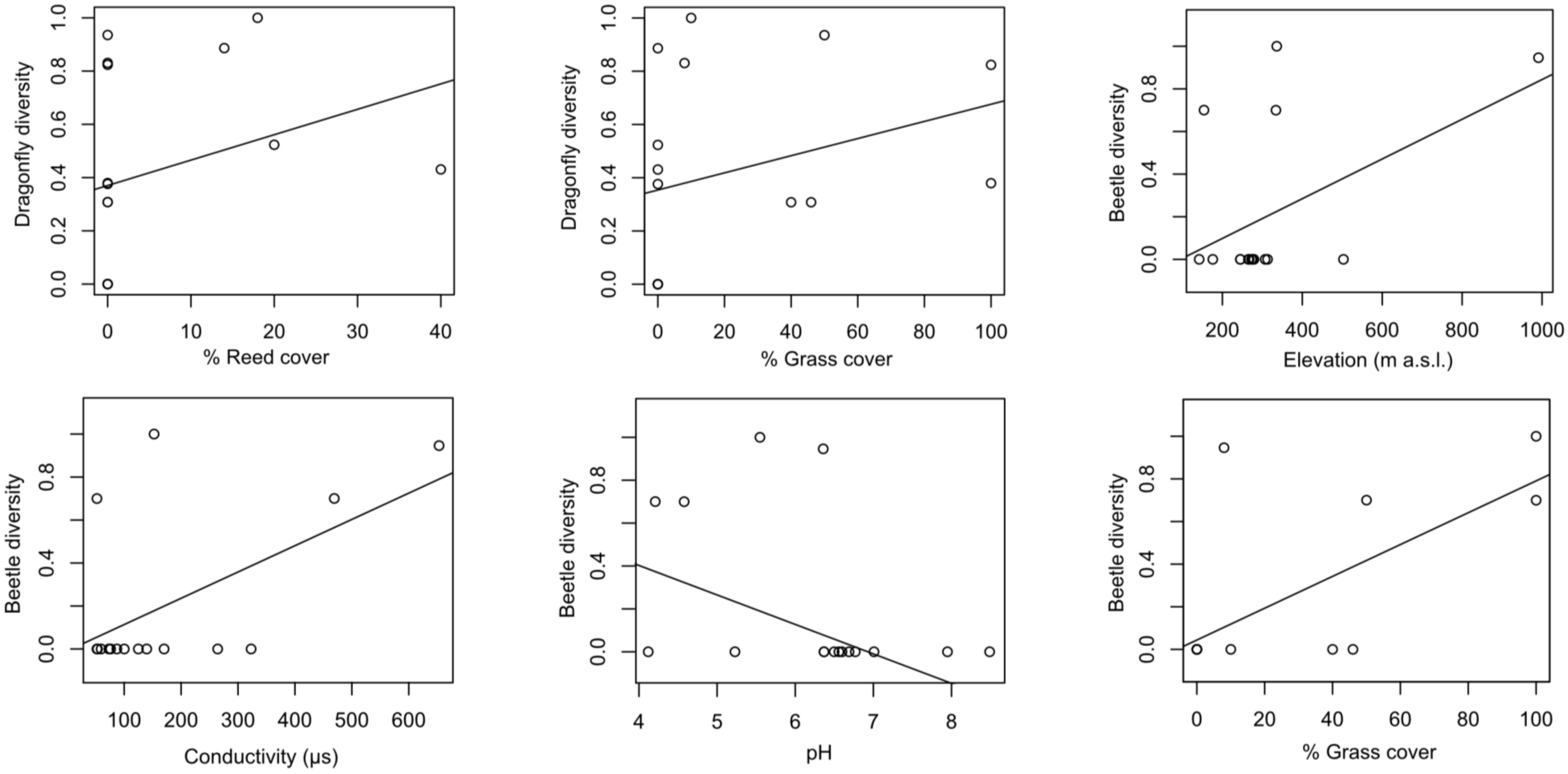
(C)


Dragonfly species richness
1
2
3
4
5
6
7
40
50
60
70
80
90
100
Water clarity (cm visibility)
Bug species richness
0
1
2
3
15
20
25
30
Temperature (ºC)
Bug species richness
0
1
2
3
10
20
30
40
50
60
Dissolved Oxygen (mg/L)
Bug species richness
0
1
2
3
0
20
40
60
80
100
% Reed cover
Bug species richness
0
1
2
3
0
10
20
30
40
50
% Grass cover

(D)


Dragonfly species richness
0 1 2 3 4 5 6 7
100 200 300 400 500 600
Conductivity (µs)
Dragonfly species richness
0 1 2 3 4 5 6 7
0 10 20 30 40
% Reed cover
Dragonfly species richness
0 1 2 3 4 5 6 7
0 20 40 60 80 100
% Grass cover
Dragonfly species richness
0 1 2 3 4 5 6 7
0.4 0.5 0.6 0.7 0.8
Sampling depth (m)
Beetle species richness
0 1 2 3 4
100 200 300 400 500 600
Conductivity (µs)
Beetle species richness
0 1 2 3 4
0 500000 1000000 1500000
Pond size (m²)
Beetle species richness
0 1 2 3 4
0 20 40 60 80 100
% Total vegetation cover
Bug species richness
0 1 2 3 4 5 6
200 400 600 800 1000
Elevation (m a.s.l.)
Bug species richness
0 1 2 3 4 5 6
100 200 300 400 500 600
Conductivity (µs)

(E)


Dragonfly diversity
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
% Reed cover
Dragonfly diversity
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100
% Grass cover
Beetle diversity
0.0
0.4
0.8
200
400
600
800
1000
Elevation (m a.s.l.)
Beetle diversity
0.0
0.4
0.8
100
200
300
400
500
600
Conductivity (μs)
Beetle diversity
0.0
0.4
0.8
4
5
6
7
8
pH
Beetle diversity
0.0
0.4
0.8
0
20
40
60
80
100
% Grass cover