The natural drivers and the effects of landscape transformation for dragonflies of the Cape Floristic Region

by

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Declaration

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General summary

The Cape Floristic Region (CFR) is a biodiversity hotspot. The region has three established biosphere reserves, which all aim to alleviate the impacts that land transformation has on ecosystem integrity, without jeopardizing basic human needs. In addition to its unique plant diversity, the CFR has high endemism levels of other taxa, including dragonflies. Dragonflies are useful bioindicators of freshwater quality, which has led to the development of the Dragonfly Biotic Index (DBI), a biomonitoring tool for freshwater. The combined pressures of urbanisation and agricultural expansion in the CFR are a major concern for rare, endemic dragonfly species, as well as for overall river ecosystem integrity. In view of this, my study aims to determine which variables drive lotic dragonfly diversity in the CFR, and to assess the effects that land transformation has on this diversity.

I first determined which environmental parameters were consistently important so that they could be used as mesofilters to conserve dragonfly diversity (Chapter 2). Dragonfly assemblages and various environmental variables were recorded along the untransformed reaches of three CFR rivers. Heterogeneity of water parameters was found to be the most crucial variables for dragonfly assemblages and for affecting species richness. Here, heterogeneity is defined by the natural spatial and temporal variation of water temperature, dissolved oxygen, conductivity and pH. This differed from previous studies, which strongly suggest vegetation-related variables are the primary drivers of dragonfly diversity. However, these studies took place in transformed landscapes where the strong effects related to anthropogenic disturbances could override the importance of other more subtle natural variables. The maintenance of a gradient of water parameters, which accounts for the natural range of each of the selected water variables, would thus aid in the conservation of dragonflies in the CFR.

I also investigated the effects of urbanization and agricultural development on dragonfly diversity and DBI scores. Land transformation homogenized dragonfly assemblages as some endemic species could not persist in these areas. However, species richness was not always reduced, because disturbance allowed for additional widespread, generalist species to enter the system. Dragonfly assemblages differed between agricultural and urban sites but these sites were more similar to each other than to undisturbed sites. Each river supported a unique dragonfly assemblage, making it important to conserve each individual river. Mitigating the adverse influences of landscape transformation is essential for the conservation of rare and endemic taxa, particularly in areas of high conservation value, and the DBI provided an effective way to assess ecosystem integrity in the region.

In conclusion, land transformation negatively affects dragonfly diversity and ecosystem integrity in CFR rivers. Conservation efforts should aim to rehabilitate the natural heterogeneity of riparian ecosystems. However, conservation plans should not only focus on restoration of riparian vegetation, but also incorporate variation in water quality parameters. There is not a high possibility of reducing land transformation, with the requirements of an ever-increasing human population. An important alternative option, as I show here, is to protect ecological integrity within a biosphere reserve. The proclamation of more biosphere reserves in the CFR, that include other, additional river catchments, will allow for the conservation of more rare, endemic dragonflies and other taxa. Dragonfly assemblages and the DBI should be used in future monitoring programs and to guide conservation actions.

Algemene opsomming

Die Kaapse Floristiese Streek (KFR) is 'n biodiversiteit kernarea. Die streek besit drie gevestigde biosfeerreservate, wat poog om die impak van landtransformasie op die integriteit van ekosisteeme te verlig, sonder om basiese menslike behoeftes in gevaar te stel. Benewens sy unieke plantdiversiteit, het die die KFR ook besonderse hoë vlakke van ander endemisme taxa, insluitend naaldekokers. Naaldekokers is uiters nuttig as bioindikatos van varswater gehalte. Dit het geleei tot die ontwikkeling van die naaldekoker biotiese indeks (NBI), 'n biomoniterings hulpmiddel. Die gekombineerde druk vanaf verstedeliking en landbou-uitbreiding in die KFR is 'n groot bron van kommer vir die bewaring van skaars, endemiese naaldekokerspesies, sowel as vir algehele rivierekosisteem integriteit. In lig hiervan, het my studie gepoog om te bepaal watter spesefieke faktore naaldekokerdiversiteit dryf in die KFR. Die gevolge van land transformasie op hierdie diversiteit was ook geevalueer.

Eerstens het ek bepaal watter omgewingsfaktore deurgaans belangrik is om naaldekoker diversiteit te bewaar (Hoofstuk 2). Naaldekoker gemeenskappe en verskeie omgewings-veranderlikes was aangeteken langs die ongetransformeerde areas van drie KFR riviere. Heterogeniteit van waterveranderlikes was bevind as die mees kritieke faktore wat naaldekoker gemeenskappe en spesierykheid bepaal. Hierdie resultate verskil van vorige studies wat gewys het dat plantegroei verwante veranderlikes die primêre oorsake van verandering van naaldekoker diversiteit is. Hierdie vorige studies was egter gefokus op getransformeerde landskappe waar die sterk effekte van menslike versteurings die belangrikheid van ander, meer subtiele, natuurlike faktore kon oorheers. Die instandhouding van 'n wye verskeidenheid water veranderlikes blyk dus om die behoud van die naaldekoker gemeenskappe in die KFR the bevorder.

Ek het ook die gevolge van verstedeliking en landbouontwikkeling op die diversiteit van naaldekokers en die NBI bepaal. Landtransformasie het naaldekoker gemeenskappe gehomogeniseer deurdat sommige endemiese spesies nie kon bestaan in hierdie gebiede nie. Dit het egter nie altyd gepaard gegaan met ‘n vermindering in spesierykheid nie, want aandui dat addisionele, wydverspreide, generiese spesies versteurde habitatte binnedring. Naaldekoker gemeenskappe het tussen landbou en stedelike areas verskil, maar was steeds meer soortgelyk aan mekaar as aan ongestoorde areas. Elke rivier ondersteun 'n unieke naaldekoker gemeenskap, wat daarop wys dat dit belangrik is om elke individuele rivier te bewaar. Verligting van die negatiewe invloede van landskaptransformasie is noodsaaklik vir die bewaring van skaars en endemiese spesies, veral in gebiede van hoë bewaringswaarde. Die NBI verskaf 'n doeltreffende manier om die integriteit van die ekosisteem te evalueer in hierdie streek.

Ten slotte, land transformasie beïnvloed naaldekoker diversiteit en die integriteit van die ekosisteem in KFR riviere negatief. Bewaring moet poog om die natuurlike heterogeniteit van die rivieroewer ekosisteme te rehabiliteer. Bewaring moet egter nie uitsluitlik fokus op die herstel van oewerplantegroei nie, maar moet ook poog om variasie in water faktore te inkorporeer. Vermindering van transformasie area is nie werklik haalbaar in die streek nie aangesien 'n toenemende menslike bevolking se vereistes ook toeneem. 'n Belangrike alternatiewe opsie, soos ek hier uitwys, is om te verseker dat die ekologiese integriteit binne biosfeerreservaate beskerm word. Die proklamasie van meer biosfeerreservate in die KFR, wat bykomende rivieropvanggebiede insluit, sal voorsiening maak vir die bewaring van meer seldsaame en endemiese naaldekokers, asook ander taxa. Naaldekoker gemeenskappe en die NBI behoort gebruik te word in toekomstige moniterings programme en kan dus bewaringsoptredes lei.

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Chapter 1: General introduction

Biodiversity and the Cape Floristic Region

Biodiversity is the very basis of ecosystem function and production, which is why ameliorating the current biodiversity crisis is critical for human survival (Singh, 2002; CBD, 2011; Buckley, 2012). We have entered a mass extinction event, eradicating species at a much faster pace than any of the previous mass extinctions, and it is estimated that approximately half of earth's species will be lost during the 21st century (Singh, 2002). The ever-increasing human population has destroyed ecosystems and transformed approximately 90 % of the planets habitable land (European Commission Joint Research Centre, 2008). Only about 10 % of earth's land falls within protected areas and less than half of that is devoted to biodiversity conservation (Hoekstra et al., 2005; Fischer et al., 2006). Habitat loss is considered the primary factor driving the global biodiversity crisis (Sala et al., 2000). In biodiversity hotspots, habitat loss is a good predictor of the number of endemic species that are threatened or already extinct (Falcucci et al., 2007). Landscape transformation and the associated habitat homogenization are a consequence of anthropogenic developments (Pimm & Lawton, 1998; Sanderson et al., 2002; Falcucci et al., 2007). The outcome is homogenization of biotic components of ecosystems as sensitive, endemic species with specialized habitat requirements are lost and replaced by widespread, habitat generalists (Pimm et al., 1995; Vitousek et al., 1997; Tews et al., 2004). Thus in response to the habitat heterogeneity hypothesis, which postulates that structurally complex habitats will comprise of a greater range of niches and diverse ecological resources, we would expect these homogenised areas to have lower species diversity (MacArthur & Wilson, 1967; Bazzaz, 1975; Tews et al., 2004).

Biodiversity hotspots are by definition areas of exceptional diversity and endemism that are under severe pressures due to habitat loss (Myers et al., 2000). When hotspots are selected, the emphasis is on species rather than populations because they are identified as the most recognizable form of biodiversity (Myers et al., 2000). Currently, hotspots comprise 35 biogeographic regions, which together contain about 77% of all mammal, bird, reptile and amphibian species and approximately half of the world's plant species (Mittermeier et al., 2004). The Cape Floristic Region (CFR) is a proclaimed biodiversity hotspot and is limited to the southern tip of Africa. It is renowned for its incredible plant diversity and is the smallest of the world's six floral kingdoms (Day & Day, 2009). The region is inhabited by more than 9000 plant species, of which 70% are endemic (Goldblatt & Manning, 1999). It also has the highest number of rare species in the world, with 1406 Red Data Book plant species (Cowling & Hilton-Taylor, 1997; Rouget et al., 2013). Other than its international status as a biodiversity hotspot it has also been proclaimed a Global 200 Ecoregion, a Centre of Plant Diversity and an Endemic Bird Area (Bond & Goldblatt, 1984; Cowling & Pressey, 2003). In addition to its high floral diversity, it is also famous for its exceptionally high concentration of other endemic taxa (Born et al., 2007). The unique landscape provides specialized habitat conditions for various specialist fauna (Myers et al., 2000) and the degree of diversity and endemism for aquatic invertebrates in the CFR, compares to that of its terrestrial plants (Wishart & Day, 2002).

The relationship between the CFR, its history and climate are crucial to better understand the regions biodiversity patterns. The area has a Mediterranean climate with dry, warm summers and wet, cool winters (Cowling & Pressey, 2003). The mountains comprise hard, resistant, quartzitic sandstones of the Table Mountain Group (de Moor & Day, 2013). These ancient rocks are severely weathered and contain little minerals, resulting in low nutrient soils (de Moor & Day, 2013). Fire plays an important role in the ecology of the CFR (Goldblatt & Manning, 1999). It is involved in the construction of a diversity of habitats for the co-existence of many species and is therefore considered an evolutionary driving force for speciation (Goldblatt & Manning, 1999; Linder, 2005). Divergence of species, caused by adaptation to a mosaic of different physical environments (different soil types, complex topography and differential seasonality and variability in rainfall), has also played a major part in creating the high diversity of species in the region (Linder, 2003; van der Niet & Johnson, 2009). Four Biomes form part of the CFR namely; Fynbos, Succulent Karroo, Thicket and Forest. Of these, the Fynbos Biome is the most unique and species-rich and it comprises three vegetation types; Fynbos, Renosterveld and Strandveld (Mucina & Rutherford, 2006). Fynbos dominates the region and characteristically contains the families Proteaceae, Ericaceae and Restionaceae (Manning & Paterson-Jones, 2007).

The realization of the severity of the biodiversity crisis led to the resolution of the 17th General Assembly of the IUCN in 1988 to forge global cooperation in order to protect landscapes through the creation of biosphere reserves (Lucas, 1992). To select and prioritize specific areas to protect nature would be a successful approach; if it were not for the limitation of financial resources. Therefore, it was suggested that focus would be put onto the extant hotspots to effectively conserve biodiversity (Mittermeier et al., 1998; Myers et al., 2000). The biosphere reserve model works within a conceptual framework and aims to conserve ecological integrity without compromising the requirements of a growing human population. Biosphere reserves comprise a range of different land use types, from protected natural areas to landscapes that are moderately to heavily impacted by anthropogenic activities (Stanvliet & Parnell, 2006). Buffer areas of moderately impacted regions surround the heavily transformed sections to act as a cushion for the more pristine areas (Stanvliet & Parnell, 2006). Three biosphere reserves have been proclaimed in the CFR, which include the Kogelberg, Cape West Coast and Cape Winelands Biosphere Reserves.

Rivers of the CFR

The high faunal and floral diversity of the CFR provide numerous important ecosystem services that are essential for the functioning of Western Cape communities (Meek et al., 2010). Riparian zones are no different and are defined by Naiman and Décamps (1997) as stream portions of rivers, between the low and high water mark, including the adjacent influenced areas. They provide a wide range of ecosystem services including: maintaining water quality and quantity, ground water recharge, nutrient cycling and stream bank stabilization (Meek et al., 2010). Riparian habitats also provide refuge for biota in transformed landscapes and may act as corridors and transport for plant propagules (Botkin & Beveridge, 1997; Meek et al., 2010). In the CFR, rivers are characteristically short and flow off the Table Mountain Group sandstones (de Moor & Day, 2013). In response to low nutrient soils, plants have adapted to produce large quantities of carbon-rich substances known as secondary plant compounds. When fynbos biomass is broken down, the compounds act as weak organic acids, leaching into water sources and making them acidic (de Moor & Day, 2013). As a result, rivers in the CFR are often naturally acidic and darkly coloured. They are also poorly buffered due to the low concentrations of magnesium and calcium salts (Day & King, 1995; de Moor & Day, 2013). Despite these harsh conditions, the diversity and degree of endemism of river organisms is high (de Moor & Day, 2013).

The complex, mosaic structure of these rivers creates diverse ecosystems with high habitat heterogeneity (Meek et al., 2013). The range of habitats may be responsible for the disproportionately high levels of diversity and endemism of freshwater invertebrates (Louwe et al., 2008). Approximately two thirds of the aquatic macroinvertebrates are endemic to the region and represent over a third of the country's freshwater invertebrate species (Wishart & Day, 2002). Many of the species are ancient Gondwanan relicts, which have persisted for over 200 million years in a climatic and geological landscape that has undergone relatively little change (Stuckenberg, 1962). The upper reaches of these rivers are generally well conserved because they begin in the mountains where the topography is harsh and intensive anthropogenic developments rarely take place. The middle and lower reaches are often subjected to intense transformation, which negatively affects the water quality and the biota that would naturally inhabit these sections (Dawson, 2003).

Threats to CFR rivers

The CFR is severely transformed, with approximately 30% of its land occupied by alien invasive plants, agricultural and urban developments (Rebelo & Siegfried, 1992; Lombard et al., 2003; Rouget et al., 2013). To date these anthropogenic-related influences have caused the most profound ecological changes and contributed to a significant decline in good quality habitats required to maintain biodiversity (Eldredge, 2001; Singh, 2002; Rouget et al., 2013). Agricultural development is by far the most intensive transformation type, taking up almost a quarter of the CFR's land area (Rouget et al., 2013). This is dominated by the wine industry, with approximately 90% of South Africa's vineyards found in the CFR (Gaigher, 2008). A conflict of interest exists because the unique topography, climate and edaphic conditions that are responsible for the high biodiversity levels in the region, are also the optimal conditions for farming grapes (Fairbanks et al., 2004). Agricultural development not only replaces the areas unique vegetation, it also degrades soil and water sources to irreparable states (Gaigher, 2008). Additionally, these practices require large quantities of water and over extraction of rivers can have detrimental effects on riparian ecosystems (Gurr et al., 2003). Another major problem is pollution of rivers by agricultural runoff, which drastically decreases the quality of rivers and usually results in an increase of water level, nutrients and/or suspended solids (Wauchope, 1978; Cooper, 1993; Schulz et al., 2001). In the CFR, farmers often plough right up to the river's edge and the heavy machinery used to level river-beds completely modifies the structure of these ecosystems (Gaigher, 2008). Loss of natural riparian vegetation results in erosion of the banks, sedimentation and increases agrichemical runoff into the rivers (Dallas & Day, 1993).

Urbanisation currently covers only about 2 % of the CFR but development is increasing at an explosive rate, which also threatens the biodiversity of the area (Rouget et al., 2003). River ecosystems are put under immense stress from surrounding urban areas mainly in form of over extraction and pollution (Karr & Chu, 2000). Currently in the CFR, waste water treatment plants cannot handle the large quantities of waste produced by metropolitan areas and as a result inadequately treated effluent is discharged into rivers (Meek et al., 2010). Pollution from urban runoff as storm water also frequently ends up in these systems and can chemically alter the water, making it toxic for biota (Moore & Palmer, 2005; Meek et al., 2010).

Urban and agricultural developments also create opportunities for alien plant invasions (Wania et al., 2006). This is a critical problem in the CFR because the slow-growing fynbos species are readily replaced by woody invasives (van Wilgen et al., 1992). The invasion of catchment areas in the CFR decreases biodiversity and has already contributed to the extinction of 26 plant species, with an estimate of an additional 750 species currently at risk (Hall & Veldhuis, 1985; van Wilgen et al., 1992). This level of extinction is a great concern, especially given the current world-wide biodiversity crisis (Le Maitre et al., 1996). Catchment invasions are estimated to decrease catchment yields by 347 m^3 per hectare per year, which is more than 30% of the water supplied to the City of Cape Town (Le Maitre et al., 1996). Additionally, invasive aliens may increase fire intensity, subtract from the aesthetic appeal of landscapes, destabilize catchment areas, shade out habitats, cause erosion and drastically decrease water quality (Le Maitre et al., 1996; Meek et al., 2010). To productively manage and ensure the persistence of these sensitive and dynamic ecosystems, it is crucial to implement suitable monitoring and rehabilitation programs (Palmer et al., 2005; Morán-Tejeda et al., 2010).

Conserving riparian zones within transformed landscapes

A healthy riparian ecosystem provides numerous important ecological and social goods and services upon which humanity depends (Postel & Richter, 2003). This has become the force driving the sudden urgency to achieve a balance between transformation and ecosystem integrity (Carter, 2001). Educating communities and farmers on the benefits and importance of conserving ecosystem integrity is a crucial step in the right direction. For example, farmers are more likely to adopt conservation practices when they are aware of economic benefits involved. By conserving riparian ecosystems they are provided with natural services such as soil maintenance, which would not be possible in a degraded and intensively transformed landscape (Napier & Forster, 1982). Riparian areas are also not used for planting crops themselves so conserving them would not reduce their planting area or yields (Napier & Forster, 1982). Biosphere reserves have become one of the large scale methods striving to attain a balance (Grant & Samways, 2011). However, there are numerous other methods, at smaller scales that can also be put into play. Restoration of damaged riparian ecosystems is generally considered the best option. In a highly sensitive region, like the CFR, restoration goals need to be realistic and account for the current state of the surrounding area as well as the intended future use of the river system (King & Brown, 2006). A crucial first step in river restoration should be to obtain an in-depth description of how a dynamic, ecologically-healthy river should be at a given site (Postel & Richter, 2003). The most commonly suggested requirement in restoration programs is to allow for the recovery of riparian vegetation (Holmes et al., 2008). In cases where it is not possible more realistic goals would aim to restore basic ecosystem functions through providing a vegetation cover that is structurally similar to the absent natural riparian vegetation (Holmes et al., 2008). Fynbos riparian ecosystems are believed to be relatively ecologically resilient to alien plant invasions (Holmes et al., 2008). However, the removal of invasive woody plants is crucial in order for any form of restoration to occur (Galatowitsch & Richardson, 2005). Other commonly utilised practices for conserving river integrity in transformed areas include retaining riparian buffers, adding grass filter strips along drainage swales, actions that limit runoff and no-till farming (Ryan et al., 2003).

Measuring ecosystem health through bioindicators

Various methods can be utilised to assess or monitor the effects of transformation on ecosystems. Abiotic, environmental variables can be directly measured in river ecosystems and can supply accurate information on water quality (Grant, 2005). Various indirect methods are also commonly used. Many of these make use of specific organisms as biological indicators (Carignan & Villard, 2002). Bioindicators are defined as species or groups of species whose presence, population or function can readily reflect the physical or biotic state of an ecosystem, or are suggestive of the diversity of other taxa or of an region overall biodiversity (Gerlach et al., 2013). Arthropods in particular, have numerous qualities which make many of their taxa promising bioindicators. These characteristics include their small body size, high mobility and high sensitivity to changing conditions. In addition, they occupy a great variety of habitats around the world, have diverse food preferences as well as short lifecycles and are relatively easy and low-cost to sample (McGeoch, 2007). Unfortunately their incredible diversity can sometimes hinder their utilization as indicators due to the taxonomic challenge. This is often the case for rare, endemic species in biodiversity hotspots such as the CFR, where there is a lack of information and expertise on the identification of taxa (McGeoch, 2007; Gerlach et al., 2013).

Odonata are one of the few well-studied arthropod orders renowned for their potential use as bioindicators (Adams, 2011). Their lifecycles depend on both aquatic and terrestrial ecosystems and they are therefore excellent indicators of integrity in both environments (Clark & Samways, 1996; Grant, 2005; Adams, 2011). They are highly sensitive to environmental change and are thus useful for monitoring and rehabilitation programs. Ecological conditions that influence their assemblages include shade cover, water permanency and water flow rate (Clark & Samways, 1996), vegetation characteristics, particularly aquatic macrophytes and vegetation height (Dunkle, 1976; Corbet, 1999; Samways & Taylor, 2004; Samways & Sharratt, 2010), and elevation (Samways, 1989; Samways & Steytler, 1996; Hawking & New, 1999; Clausnitzer, 2003). In addition, some anthropogenic-related impacts that influence dragonfly assemblages include alien invasive vegetation (Samways & Taylor, 2004), the presence of dams (Samways 1989), pollution (Adams, 2011) and roads (Riffel, 1999; Varju, 2004; Soluk et al., 2011). This sensitivity to environmental conditions means that dragonfly assemblages are able to successfully mirror different biotopes along rivers within a range of anthropogenic disturbances (Bulankova, 1997). A study by Samways and Steytler (1996) for example compared dragonfly diversity relative to four landscape types (plantation forest, parkland, residential area, industrial area) along the Dorpspruit River in Pietermaritzburg, South Africa. Their results highlighted the negative impacts of transformation on dragonfly diversity and ecosystem integrity. They suggested that a strip of intact riparian vegetation with a width of 30 m between the water's edge and forestry plantations will help maintain dragonfly diversity. Furthemore, using dragonflies as bioindicators in South Africa showed that they can successfully be used to measure restoration success after alien plant removal (Samways & Taylor, 2004).

Dragonflies are not merely a promising group for use in bio-assessments, they are also important keystone species. Keystone species are defined as taxa whose interactions with other species produce effects disproportionately larger than their abundances (Lambeck, 1997; Noss, 1999; Simaika & Samways, 2009b). They play important ecological roles as predators by controlling insect populations and are also a valuable source of food for insectivores (Knight et al., 2005). They have been described as umbrella species, whose communities can successfully reflect the state of various other taxa (Lambeck, 1997). This means that environmental conditions that are suitable to sustain a good dragonfly assemblage may also protect the diversity of other taxa. For these reasons, conserving global dragonfly biodiversity is important. Globally it had been predicted, that faced with the current biodiversity crisis, one in ten dragonfly species are at risk of going extinct (Clausnitser, 2003). The CFR is a centre of endemism for dragonflies, which makes conserving the rare species found in this region a conservation priority.

It is clear that the presence of certain dragonfly taxa is directly related to ecosystem health and water quality (Watson et al., 1982; Corbet, 1999). Therefore to maintain biodiversity and ecosystem integrity may involve the identification of the key factors influencing their assemblages. This is best achieved through using information from a combination of measures, such as species richness, community composition and appropriate biological indices (Chovanec, 2000). Numerous biotic indices have been developed for freshwater ecosystems. These incorporate a range of criteria and may prove to be the most reliable and flexible measures (Boon & Pringle, 2009; Simaika & Samways, 2012). A composite index, that can successfully asses rehabilitation projects or prioritize sites for conservation action, needs to be reliable and simple to use (McGeoch, 2007; Simaika & Samways, 2009a). The Dragonfly Biotic Index (DBI) is one such biodiversity measure, which is based on the acknowledged potential of dragonflies as indicator species (Chovanec, 2000; Simaika & Samways, 2009a; 2011). Its initial purpose was as an easy-to-use, efficient and low-cost freshwater biomonitoring tool, which provides a measure of ecological integrity (Simaika & Samways, 2009a; 2012). It works at the species level, which makes it sensitive to subtle changes at multiple scales in a range of habitats (Smith et al., 2007; Simaika & Samways, 2009a). Each dragonfly species has a set score based on the professional, quantitative assessment of three sub-indices (Simaika & Samways, 2009a). Each sub-index score ranges from 0 to 3 and includes the species geographical range, threat status as determined by the IUCN Red List and sensitivity to ecological disturbance (Simaika & Samways, 2009a;

Kietzka et al., 2015). The sum of these gives a total score ranging from 0 to 9 for any one species (Simaika & Samways, 2009a). A score of zero comprises widespread, hardy, common habitat generalists and a score of nine comprises extremely threatened and sensitive habitat specialists (Dickens & Graham, 2002; Simaika & Samways, 2009a; 2011). The DBI has successfully been used to measure habitat recovery and in site selection and prioritization for conservation (Simaika & Samways, 2011; 2012; Harabiš & Dolný, 2012). Specifically, the DBI has been employed for assessing the success of stream restoration after the removal of invasive alien trees, a key threat to various aquatic organisms (Samways & Taylor, 2004). Additionally, a strong correlation has been found between adult dragonfly scores and macroinvertebrate scores (Smith et al., 2007; Simaika & Samways, 2009a). This suggests the DBI is not only a valuable tool for measuring environmental health but also demonstrates its potential to be used as a surrogate for other taxa and as an overall measurement of conservation actions.

Objectives and thesis outline

Since landscape transformation homogenizes habitats, it poses a major threat to biodiversity, especially in biodiversity hotspots like the CFR (Wilcove et al., 1998; Myers et al., 2000). Defining compensatory measures are vital for acquiring more sustainable practices, which conserve ecosystem integrity. Similarly to endemic plants of the CFR, numerous rare and sensitive dragonfly species are also confined to the region and ensuring their persistence should be a priority (Grant & Samways, 2007; Samways & Sharrat, 2010). Dragonflies play important biological roles and are reliable indicators of ecosystem quality as well as being umbrella species for other taxa (Schindler et al., 2003). Therefore, this study aims to determine what parameters are important in order to maintain the unique dragonfly diversity of the CFR and how this assemblage responds to landscape transformation. Specifically, evaluating which environmental parameters, associated with natural habitat heterogeneity in undisturbed reaches of CFR rivers, are vital for supporting a high dragonfly diversity (Chapter 2). In the event that certain variables consistently drive dragonfly communities it may be expected that habitat heterogeneity, through the presence of these parameters, may determine the occurrence of specific species.

A key challenge in landscape ecology involves understanding how landscape transformation influences species distribution patterns, which is considered essential for effective biodiversity conservation (Wiens et al., 1993; Hobbs, 1997). Therefore, the effects of landscape transformation on dragonfly assemblages in the CFR were investigated (Chapter 3). A better understanding of the effects of urbanisation and agriculture on dragonflies will improve the effectiveness of maintaining ecosystem health and the conservation management of dragonflies and other taxa within this production landscape. The value of the DBI for reflecting environmental change will also be determined so that it can be used for prioritizing conservation areas in the future. My "Final Discussion" (Chapter 4) incorporates the findings of the previous chapters and proposes management recommendations for obtaining a balance between environmental integrity and human demand in a way that conserves the high diversity of unique dragonfly species and other taxa of the CFR. As Chapters 2 and 3 are written as individual manuscripts for publication as separate papers, some repetition was unavoidable.

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Chapter 2: Heterogeneity of water parameters drive natural dragonfly diversity in a biodiversity hotspot

Abstract

Rivers of the Cape Floristic Region (CFR), South Africa, are naturally heterogeneous and complex ecosystems. Habitat heterogeneity is crucial for maintaining the high levels of biodiversity observed in these rivers. The CFR is a significant centre of local endemism for dragonflies. As keystone species in these ecosystems, dragonflies are excellent indicators of water quality and the species are variously sensitive to environmental conditions. However, the factors driving dragonfly assemblages in undisturbed rivers of the CFR has not been extensively studied. So here I determine which variables drive dragonfly assemblages in the CFR, and whether a mesofilter approach is a promising tool for conserving their diversity. Dragonfly assemblages were analysed along the untransformed regions of three CFR rivers. In undisturbed sections of the rivers, heterogeneity of water parameters was found to be the most important factor driving dragonfly assemblages and not variables associated with substrate or vegetation. This pattern was constant whether the rivers were similar or differed in terms of their environmental variables and dragonfly assemblages. Other studies probably failed to identify the great importance of water parameters because they included the effects of anthropogenic disturbances, which override these more subtle parameters. Thus, a mesofilter approach would aid in the conservation of dragonflies of the CFR by maintaining a gradient of water parameters within a river or between different rivers.

Keywords: Odonata; river; insect conservation; mesofilter; water quality; Cape Floristic Region

Introduction

Habitat heterogeneity has various interpretations (Palmer et al., 2010). It can refer to the different habitats in an ecosystem (habitat diversity), the spatial arrangement of patches (habitat complexity) or the environmental variability within a habitat over time (Li & Reynolds, 1995). The role of river habitat heterogeneity in supporting species diversity is a common concept in ecology (Ricklef & Schluter, 1993). The theory that high macroinvertebrate diversity levels in river ecosystems are a result of high habitat heterogeneity has been extensively studied (Hynes, 1970; Allan, 1975; Dallas, 2002; Palmer et al., 2010). Habitat heterogeneity allows for a greater range of physical refuges and offers a greater supply and variation of resources. This results in a wider range and higher number of ecological niches, thereby promoting diversity (Warfe et al., 2008; Palmer et al., 2010). Often it is difficult to separate the influence of habitat heterogeneity from other confounding factors that may affect diversity, such as the influence of anthropogenic actions. For example, humans can alter natural habitats and can cause them to become either more or less heterogeneous. Despite the outcome, diversity is usually negatively affected by anthropogenic interference (Negro et al., 2007; Ponti et al., 2011).

Diversity of aquatic macroinvertebrates can be influenced by biogeographic factors, evolutionary aspects or biotic interactions (Crowl et al., 1997; Wishart & Day, 2002). In mountainous landscapes, local conditions such as flow rate, substrate type, temperature and habitat availability can change regional patterns in ecosystem assemblages (Hawkins et al., 1997). To conserve diversity, various methodologies which operate at different spatial scales have been designed. Among them is the concept of the mesofilter, which involves the conservation of specified ecosystem elements or features, which are important for the maintenance of certain species within an area (Hunter, 2005; Crous et al., 2013). Within a region, geographically isolated areas that experience similar environmental conditions are generally expected to have similar biotic assemblages. However, in some instances aquatic taxa under these circumstances have proven to be distinct (Dallas & Day, 2007). Rivers that may appear similar and occur in close proximity to one another can contain totally different assemblages of species. This phenomenon is described by King and Schael (2001) as 'catchment signature' (Dallas & Day, 2007). However, the influence of spatial scale is a variable that cannot be ignored. Environmental variables that constrain communities at smaller scales can differ significantly between areas that are thought to be environmentally similar and thereby change assemblage compositions (Bonada et al., 2008). Recent studies based in the Cape Floristic Region (CFR), South Africa, have shown that there are morphological and genetic differences between endemic, aquatic invertebrates that were previously thought to be of the same species occurring in environmentally similar headwaters (Stevens & Picker, 1999; Stewart & Griffiths, 2001). However, it remains unclear whether this is due to heterospecific species that fulfil similar ecological roles, and their presence in that particular niche is due to past chance events or whether their presence or absence is determined by a suite of biotic or abiotic river characteristics (mesofilters).

Rivers in the CFR are naturally heterogeneous, with a range of environmental conditions responsible for their remarkably high macroinvertebrate diversity (Dudgeon et al., 2006; Dallas & Day, 2007). Typically, these rivers begin high in the mountains and are characterized as having upper reaches that are low in discharge and turbulent, with boulder beds that are largely shaded by a canopy of trees (de Moor & Day, 2013). The upper reaches are physically complex and vary greatly with respect to hydraulic, substrate and biotope characteristics (Dallas & Day, 2007). These sections are generally the least affected by anthropogenic activities and are crucial as they can be inhabited by rare, endemic species (Palmer et al., 2005). As rivers approach their middle and lower reaches they become wider, decrease in velocity, lack a tree canopy cover and have pebbled or sandy beds (de Moor & Day, 2013). The mosaic structure of these rivers is a main cause of their patchy distribution of macroinvertebrates (Pringle et al., 1988; Dallas & Day, 2007). Various concepts aim to describe the biological changes of a river from source to mouth. These typically involve the differentiation of zones based on geomorphological attributes along a river and combine the stochastic, abiotic and deterministic, biotic (trophic relationships) aspects (Humphries et al., 2014). The longitudinal changes in macroinvertebrate communities between the zones of a river has been extensively researched and is an important concept in river ecology (King, 1983).

Although biodiversity studies in the CFR have suggested that river catchment, habitat heterogeneity and local environmental conditions can all influence river macroinvertebrate communities; this has only been extensively evaluated for a few taxa (Dallas & Day, 2007).

Of these, dragonflies have received focused attention. This charismatic group is recognized for the numerous important roles they play in both terrestrial and aquatic ecosystems (Remsburg & Turner, 2009; Samways et al., 2010). This order is well-known taxonomically, comprises species that are easily identifiable and common in aquatic ecosystems. They inhabit a wide range of biotopes and at the species level are variously sensitive to environmental change (Simaika & Samways, 2011). These characteristics are what make them valuable bioindicators in aquatic ecosystems, whether for assessing ecosystem changes or ecological integrity (Clark & Samways, 1996; Kietzka et al., 2015; Pryke et al., 2015). However, in areas such as the CFR, the factors that determine the natural distribution and diversity of dragonfly communities are still poorly known, despite the great number and high abundance of local endemic species (Grant & Samways 2007; 2011).

The mountainous areas of the CFR are a major centre of endemism for dragonflies, and as many are under threat, it also has a high number of Red Listed species (Samways, 1992). For example, in the CFR Kogelberg Biosphere Reserve, 53% of dragonfly individuals and 26% of the taxa recorded were national endemics. Three of the species are also Red Listed and require immediate conservation attention (Grant & Samways, 2007; 2011; Samways & Grant, 2007). This emphasizes the great conservation value of CFR rivers for sustaining this irreplaceable fauna. Furthermore, endemic species are particularly vulnerable to environmental change and should therefore receive conservation priority (Simaika & Samways, 2009). Due to their dependence on a particular resource or small area of occupancy, even a minor change could result in a species becoming extinct (Schindler et al., 2003; Simaika & Samways, 2009).

Although numerous studies on the factors that influence dragonfly assemblages in the CFR have been undertaken, these have focused only on assemblages of a single river (Grant & Samways, 2007) or have focused on areas facing anthropogenic disturbances (Samways & Sharratt, 2010; Grant & Samways, 2011). This study aims to determine whether there are parameters linked to natural habitat heterogeneity that are crucial for supporting a high diversity of dragonfly assemblages in undisturbed reaches of CFR rivers. If certain variables consistently influence these assemblages, then we can assume that habitat heterogeneity, through the presence of specific features, determines the presence of certain dragonfly species. However, if none are found we can assume that their presence may be due to river signature. Furthermore, if features can be identified as mesofilters for dragonflies of CFR rivers this will help focus future conservation efforts for this specialized fauna.

Methods

Study areas and sampling design

Study sites were selected along three Western Cape rivers, all within the Cape Floristic Region (CFR) biodiversity hotspot (Figure 2.1) (Mittermeier et al., 2004). Sites were established on the upper reaches of the Eerste River in the Jonkershoek Nature Reserve, Stellenbosch; the upper reaches of the Lourens River on Lourensford Farm, Somerset West and on the lower reaches of the Palmiet River in the Kogelberg Reserve, near Kleinmond. Sites were carefully chosen to include sections of the rivers that were as close to their natural, undisturbed state as possible.

A total of 108 sampling units (SUs), 36 per river, were identified. Each SU consisted of a 100 m stretch of river and included 3 m to either side of the river's edge. A distance of approximately 100 m was maintained between sites to minimise the chances of pseudo replication. Each SU was sampled twice, once during December 2014 and again during April 2015, to account for seasonal changes in assemblages. Adult, male dragonflies were recorded on clear, windless days by two observers, for a period of 30 min per SU. The observers were positioned 10 m apart as they walked the length of each SU and made use of visual scanning to record dragonflies. This method was previously found to be 100% accurate for Anisoptera and 80% accurate for Zygoptera, which was made even more accurate by using close-focus binoculars (Moore, 1991). Species that could not be identified on site were caught using a net and identified using a hand lens and a guidebook (Samways, 2008).

Environmental variables

A total of 21 environmental variables (EVs) were recorded at each SU (Table 2.1). River catchment (Eerste, Lourens or Palmiet) was recorded as a categorical variable. Elevations were determined using Google maps and an error margin of approximately 30 m (Google Maps, 2015) and site positions were determined through the use of a handheld GPS. The percentage of shade covering each SU was estimated at the time of data collection. Measuring of water variables (temperature, dissolved oxygen, conductivity and pH) was achieved by using a handheld multi-parameter water quality meter (Model: YSI 556 Multi Probe System; Make: YSI Fondriest Environmental). The percentage of each SU covered by rocks, sand or detritus was visually estimated by both observers and averaged. Vegetation data contained both continuous and categorical variables. The average height of the vegetation, percentage alien plant cover and percentage indigenous plant cover were estimated by two observers. Categorical data were recorded as presence or absence of indigenous and alien trees, shrubs and grass. Presence of aquatic macrophytes was also recorded but excluded *Prionium serratum* (Palmiet reed). The presence of *P. serratum* was chosen as a separate variable as it often blanket covers wetland areas and is an important plant species in the natural regions of CFR rivers. Dragonfly species patterns have previously been associated with high levels of *P. serratum* (Samways & Sharratt, 2010).

Data analyses

Non-parametric species estimators of Chao2, ICE and Jackknife2 were calculated using EstimateS version 9.1 (Colwell, 2013). Non-parametric species estimators are used for insect assemblages where a large number of rare species are present (Novotny & Basset, 2000; Hortal et al., 2006). Statistica version 9 (StatSoft Inc., USA) was used to calculate the summary statistics of the EVs measured at each river. Analyses to determine the influence of the EVs on species richness were carried out within R software (R Development Core Team, 2013). General linear mixed models (GLMMs) were calculated with the MASS package (Bates, 2005) using the penalized quasi-likelihood (PQL) estimation method, and fitted with a Poisson distribution (Bolker et al., 2009). The analyses were conducted for combined river assemblages for overall Odonata and then again for Anisoptera and Zygoptera separately, as well as for each of the three rivers individually. Seasonal data were pooled for all analyses. These data were tested using a semivariogram and showed no signs of spatial autocorrelation (Dormann et al., 2007). A limitation of the GLMM.pql method is that three level factors cannot be compared (Bolker et al., 2009). Therefore, to determine the effect of river catchment on species richness, GLMMs using the *lme4* package within R software were carried out (Bates & Sarkar, 2006). A Laplace approximation was used and data fitted to a

Poisson distribution (Bolker et al., 2009). Elevation was included as a random variable and Tukey posthoc tests determined the pairwise differences in species richness between rivers.

Canonical Correspondence Analyses (CCAs) were used to correlate species compositional data with EVs in CANOCO 5 (ter Braak & Šmilauer, 2012). This was done for overall species and separately for Anisoptera and Zygoptera with river catchment used as a nominal variable. Further analyses were carried out for each of the rivers independently. Summaries of the constrained analyses gave the marginal/simple effects of all the variables on the assemblages. This gave the independent effect of each EV on the assemblage in question. However, this method creates a type 3 error with the likelihood of correlated EVs being false positive. With a large number of variables there is the possibility of many of them being highly correlated and this could severely distort the ordering of objects in the CCAs. Thus, interactive forward selection analyses (ter Braak, 1990) were also used to select the best group of EVs, according to the amount of variation in dragonfly data that they explained. Selection stopped when there was no significant increase in explained assemblage variation, tested by Monte Carlo permutation. Analyses were permutated 499 times to normalize distribution and allow comparisons of variables (Lepš & Šmilauer, 2003). This method involves a direct gradient analysis that uses multiple regressions to determine the linear combinations of EVs that are responsible for the variation observed in species assemblages on each axis. This type of analysis accounts for skewed species distributions and covariant as well as incomplete environmental variables (Palmer, 1993). Quantitative variables included elevation, average vegetation height, water parameters (water temperature, conductivity, dissolved oxygen and pH), percentage cover at each SU (rock, sand, detritus, exotic plant species, indigenous plant species and shade) and the presence or absence of vegetation categories (macrophytes, *P. serratum* and alien and indigenous trees, shrubs and grass).

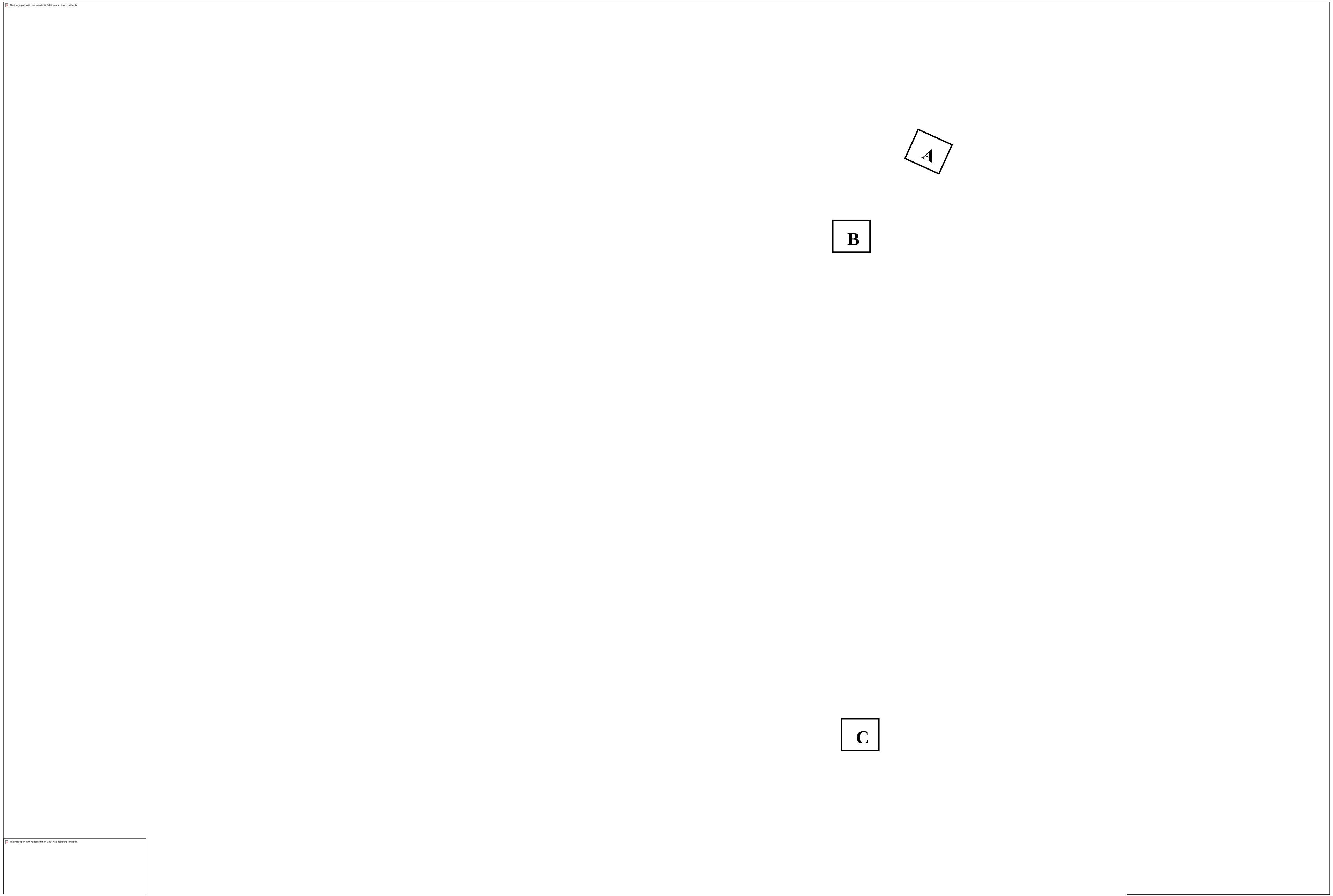

Figure 2.1. Areas selected for sites along the A) Eerste River, B) Lourens River and C) Palmiet River

Table 2.1. Environmental variables measured at each sampling unit

Variable	Measurement unit
River catchment	categories: Eerste River (E), Lourens River (L), Palmiet River (P)
Elevation	metres above sea level (m asl)
Shade	% cover
Water measures	
Water temperature	°C
Dissolved oxygen	mg/L
Conductivity	mS/cm
pH (acidity)	pH
Substrate cover	
Detritus	% cover
Sand	% cover
Rock	% cover
Vegetation	
Average veg height	metres (m)
Indigenous cover	% cover
Alien cover	% cover
Prionium serratum	presence/absence
Aquatic macrophytes	presence/absence
Indigenous trees	presence/absence
Alien trees	presence/absence
Indigenous shrubs	presence/absence
Alien shrubs	presence/absence
Indigenous grass	presence/absence
Alien grass	presence/absence

Results

Species richness and abundance

A total of 30 Odonata species (7109 individuals) were sampled, made up of 18 Anisoptera species (3646 individuals) and 12 Zygoptera species (3463 individuals) (species list in Appendix 1). The species accumulation curves flattened for all three of the rivers (Figure 2.2). Dragonfly species estimates neared observed species richness when pooled and for each river individually (Table 2.2). This indicates that sampling effort was sufficient to collect majority of the species present in the rivers. Seven of the 30 species I recorded here are endemic to the CFR and they made up of almost 30% of the observed individuals. Seasonally, all three species estimators produced similar results on observed species richness, with a much higher species richness and abundance in summer than in autumn.

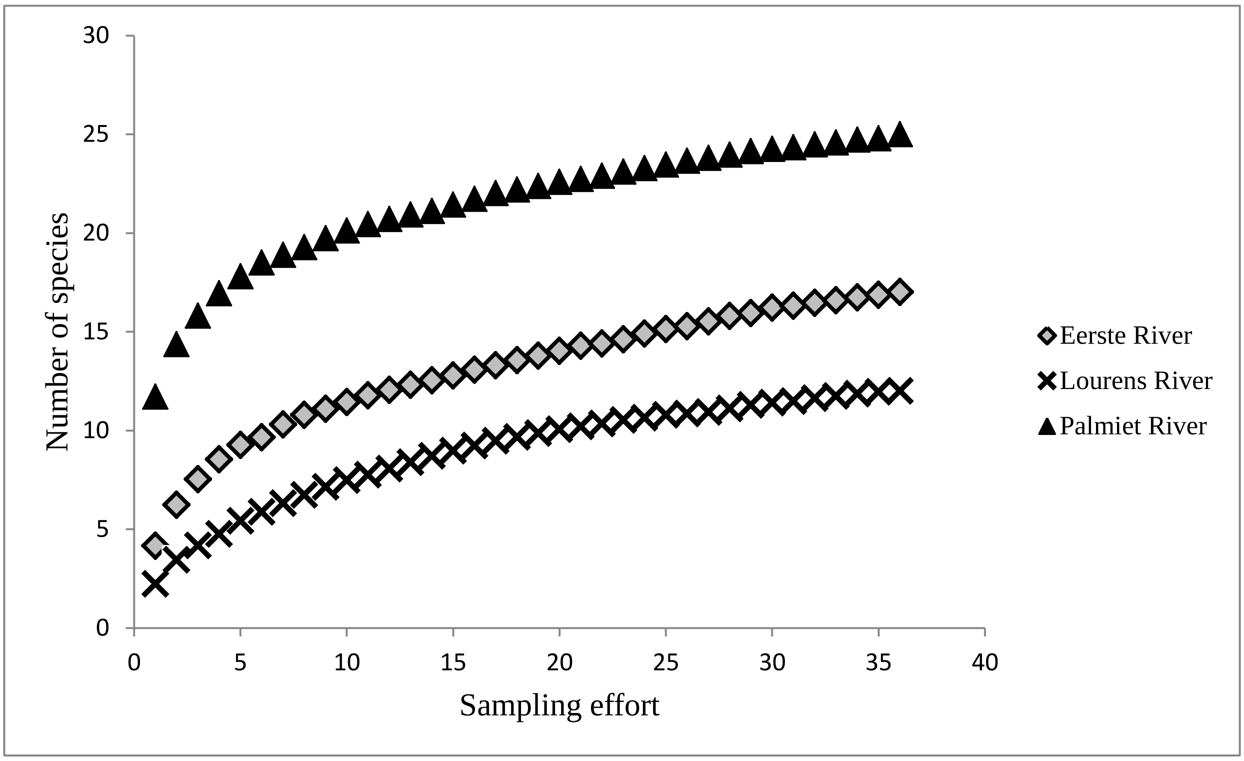

Figure 2.2. Rarefied species accumulation curves for the Eerste River, Lourens River and Palmiet River

Table 2.2. Species estimators and abundances

Estimators	Abundance	Species richness	Chao2	ICE	Jackknife2
Overall	7109	30	37.90(±10.25)	31.42(±4.84)	37.86±(6.96)
Anisoptera	3646	18	17.97(±4.50)	17.05(±3.09)	22.91(±4.61)
Zygoptera	3463	12	10.00(±0.48)	10.30(±1.39)	11.97(±2.38)
CFR endemics	2049	7	6.99(±2.23)	7.89(±1.84)	9.94(±3.07)
Summer	6282	28	32.94(±7.22)	29.28(±4.29)	34.89(±6.82)
Autumn	827	18	27.9(±10.18)	23.67(±2.57)	26.86(±4.11)
Eerste River	1120	17	20.24(±4.02)	23.67(±2.38)	24.75(±3.39)
Lourens River	893	12	12.73(±1.39)	13.83(±1.37)	15.00(±2.11)
Palmiet River	5096	26	34.72(±10.05)	30.36(±2.24)	34.58(±2.92)

Differences in environmental variables between rivers

Summary statistics of the EVs for each of the rivers showed the Eerste and Lourens rivers to be more similar to each other than to the Palmiet River (Table 2.3). In terms of water parameters, higher temperatures and lower pH values occured in the Eerste River than in the Lourens River. With respect to vegetation variables, the Lourens River had a higher percentage of alien vegetation cover, mainly from alien grasses. The Palmiet River differed from the Eerste and Lourens Rivers in majority of the selected EVs

Table 2.3. Summary statistics of the environmental variables for the Eerste River, Lourens River and Palmiet River. SE = standard error of the mean

Variable	Eerste River				Lourens River				Palmiet River			
	Mean	SE	Min	Max	Mean	SE	Min	Max	Mean	SE	Min	Max
Elevation	426.43	6.73	343.90	517.20	429.37	9.45	344.30	572.90	48.03	1.32	30.00	58.30
Shade	30.69	2.52	0.00	88.00	31.53	3.12	1.00	90.00	12.13	1.98	0.00	72.00
Water measures												
Water temperature	14.01	0.23	10.56	17.47	12.81	0.15	10.66	14.66	19.27	0.21	16.34	22.10
Dissolved oxygen	8.15	0.08	7.50	8.80	8.15	0.07	7.60	8.70	9.07	0.12	7.80	10.10
Conductivity	0.04	0.00	0.03	0.05	0.04	0.00	0.03	0.05	0.13	0.00	0.05	0.17
pH	6.80	0.01	6.70	6.90	6.91	0.03	6.60	7.20	7.02	0.02	6.80	7.20
Substrate cover												
Debris	2.15	0.52	0.00	20.00	5.81	0.83	0.00	20.00	5.74	1.18	0.00	40.00
Sand	2.78	1.36	0.00	50.00	1.94	0.38	0.00	10.00	11.61	2.22	0.00	63.75
Rock	94.61	1.34	52.00	100.00	91.94	1.91	0.00	100.00	10.03	1.93	0.00	74.50
Vegetation												
Avge veg height	3.27	0.11	2.05	5.00	2.84	0.12	1.78	5.80	2.54	0.11	1.58	6.20
Indigenous cover	52.64	2.27	24.80	100.00	50.88	2.54	24.35	100.00	51.66	1.73	25.75	73.33
Alien cover	0.83	0.41	0.00	20.00	11.91	1.85	0.00	50.00	3.81	0.89	0.00	30.00
P.serratum#	47.22				41.67				91.67			
Aquatic macrophytes#	55.56				66.67				27.78			
Indigenous trees#	100.00				100.00				80.56			
Alien trees#	5.56				27.78				19.44			
Indigenous shrubs#	61.11				63.89				88.89			
Alien shrubs#	2.78				8.33				8.33			
Indigenous grasses#	19.44				47.22				47.22			
Alien grasses#	0.00				8.33				0.00			

Environmental variables represented as percentage of sampling units where vegetation category is present

Effect of environmental variables on Odonata species richness

River catchment had a significant influence on dragonfly richness when included as an EV (Table 2.4). Other than that, water parameters were mostly responsible for changes observed in species richness. Species richness increased with an increase in water temperatures and dissolved oxygen content but decreased with an increase in pH. Anisoptera and Zygoptera species richness were evaluated separately and few differences were observed. Zygoptera species were more responsive to decreases in pH and Anisoptera species richness was positively correlated with detritus cover.

Average dragonfly species richness was significantly different between all three rivers, with the Palmiet River having significantly more species than either the Eerste or Lourens Rivers, and the Eerster River had significantly more species than the Lourens River (Figure 2.3). When river catchment was excluded as an EV, elevation was more important and was negatively correlated with species richness in the Lourens and Palmiet Rivers (Table 2.4). Despite this, water parameters were still the most influential factors affecting species richness in all three rivers. In the Eerste River, increases in both water temperature and dissolved oxygen had a positive influence on species richness, whereas an increase in pH had a negative influence. In the Lourens River, conductivity was significantly and positively correlated to species richness. Species richness in the Palmiet River was also positively related to conductivity but was negatively correlated with pH. Other than water parameters, only species richness in the Palmiet River showed positive correlations with percentage shade and percentage sand.

Table 2.4. Effects of environmental variables on combined species richness (overall, Anisoptera and Zygoptera) and for each of the individual rivers. The test-statistics for river catchment are displayed as x_2 values and all other test-statistics are displayed as t-values

Variable		**Overall**	**Anisoptera**	**Zygoptera**	**Eerste River**	**Lourens River**	**Palmiet River**
	River catchment	**33.4*** **	**37.70*** **	**26.7*** **	-	-	-
	Elevation	1.58	0.31	2.41*	1.58	**-3.22** **	**-2.88** **
	% shade	0.76	0.32	0.89	0.76	1.23	**3.16** **
Water measures							
	Water temperature	**8.12*** **	**7.36*** **	**6.24*** **	**8.12*** **	-0.68	-1.41
	Dissolved oxygen	**5.65*** **	**4.26*** **	**5.11*** **	**5.65*** **	0.91	0.64
	Conductivity	1.57	1.04	1.57	1.57	**3.76** **	**2.18***
	pH	**-2.32***	-1.06	**-2.96***	**-2.32***	-0.73	**-1.86***
Substrate cover							
	% debris	1.84	**1.99***	1.05	1.84	0.11	-1.32
	% sand	0.57	0.57	0.17	0.57	-0.09	**3.77*** **
	% rock	1.31	1.19	1.08	1.31	-0.08	-0.21
Vegetation							
	Avge veg height	1.86	1.35	1.58	1.86	-0.02	0.22
	% indigenous cover	-1.66	-1.17	-1.61	-1.66	-0.43	-0.36
	% alien cover	0.75	0.12	1.21	0.75	0.78	-0.08
	P.serratum	0.30	-0.95	1.52	0.30	0.51	1.65
	Aquatic macrophytes	1.10	1.22	0.66	1.10	1.05	0.40
	Indigenous trees	-0.78	-1.02	-0.12	-0.78	-	-0.33
	Alien trees	-0.35	0.36	-0.99	-0.35	-0.77	-0.79
	Indigenous shrubs	1.13	0.54	1.23	1.13	-1.67	0.62
	Alien shrubs	0.41	0.93	-0.42	0.41	-0.82	0.10
	Indigenous grasses	-0.92	-1.14	-0.38	-0.92	0.88	0.50
	Alien grasses	-0.52	0.38	-1.34	-0.52	-0.80	-

* = p < 0.05, ** = p < 0.01, *** = p < 0.001

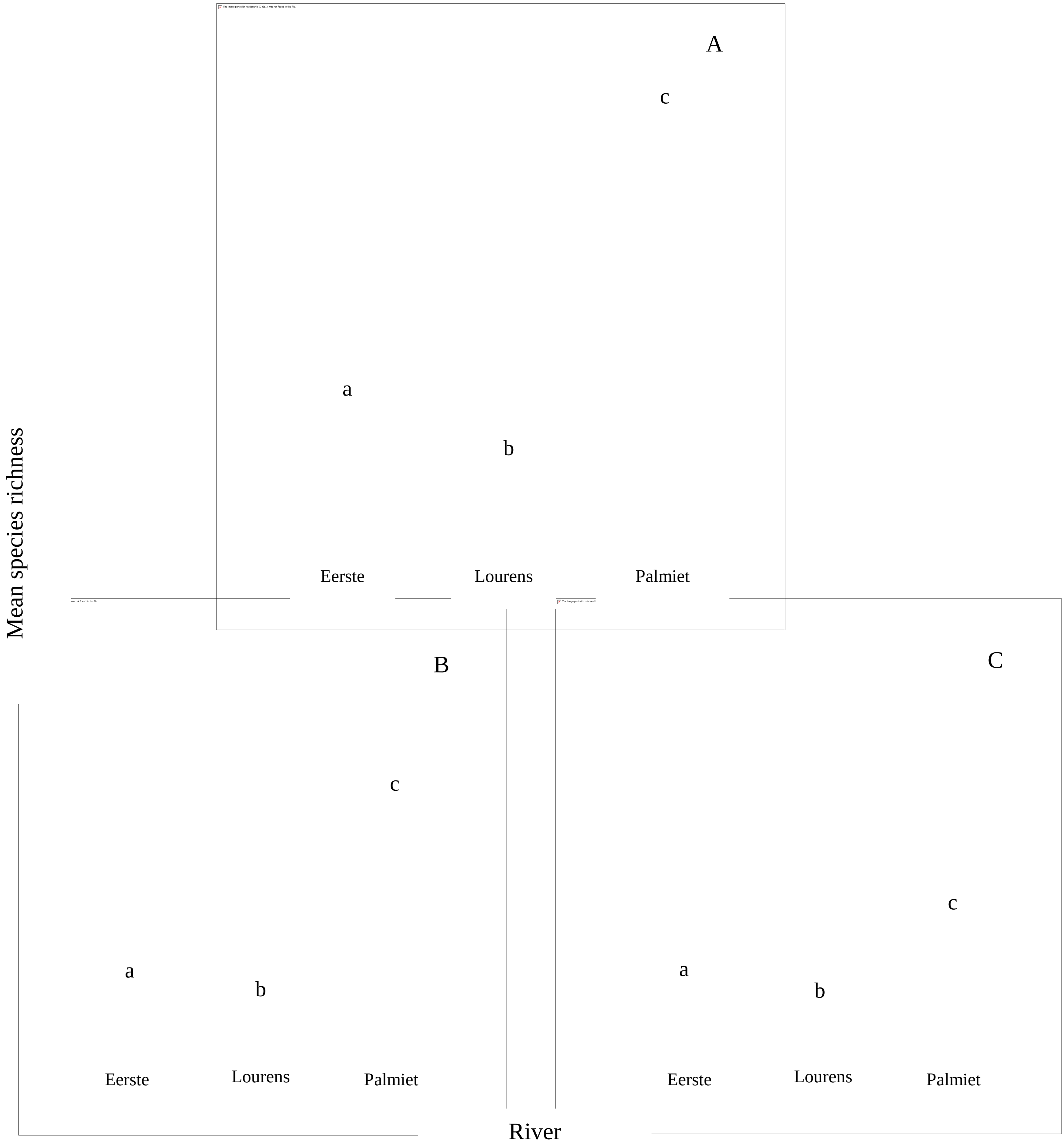

Figure 2.3. Mean species richness between three rivers for A) overall, B) Anisoptera, C) Zygoptera. Mean (±1 SE), different letters above bars represent significantly different means.

Factors effecting compositional shifts in dragonfly assemblages

Whether accounting for dragonflies overall or those at each river separately, elevation and water parameters were the most significant EVs driving dragonfly assemblages (Table 2.5). Substrate and vegetation characteristics were less important, except for the presence of *P. serratum*, which was significant in all respects except for the Palmiet River.

Of the 23 EVs initially considered for inclusion in the CCA, 14 were retained by the forward selection procedure for overall dragonfly composition. When separated into suborders, 14 were retained for Anisoptera and six for Zygoptera (Table 2.5; Figure 2.4). Overall dragonfly composition and the explanatory variables were significantly related ($P < 0.05$) for the first axis eigenvalue (pseudo-F = 34.1). In all, 35.8% of the variance of dragonfly species was accounted for by EVs and axis 1 explained 20.0% of the total variation in dragonfly composition. Of the selected variables, river catchment and elevation, which were closly correlated, were the most important factors driving dragonfly assemblages (Table 2.5; Figure 2.4). Together, they explained 25.1% of the variation. Of the three catchments, the Palmiet River had the largest influence on dragonfly assemblages, particulary for Zygoptera. The Palmiet River also had the most unique dragonfly assemblage. The grouping of the rivers relative to eachother showed dragonfly assemblages between the Eerste and Lourens Rivers were very different, but more similar to eachother when compared to the Palmiet River. Water parameters were the next most important EVs, explaining 6.3% of the variation in the overall dragonfly assemblage. Interestingly, rock cover was vital for overall dragonfly assemblages but not when rivers were evaluated separately. Correlations between CCA's EVs is given in Appendix 3.

From the 18 EVs initially considered for inclusion in the CCA for the Eerste River, five were retained by the forward selection procedure (Table 2.5). Indigenous trees and alien grass species were not present at any of the SUs and were therefore excluded as variables in the CCA. In all, 30.7% of the variance in the dragonfly assemblage was accounted for by EVs and axis 1 explained 12.0 % of the total variation in dragonfly assemblage composition. Of the selected EVs, water parameters were the most important factors driving dragonfly assemblages, together explaining 10.2% of assemblage variation. Although elevation was the next most important EV, without river catchment influencing it as a parameter it explained only 4.6% of the variation.

For the Lourens River, 19 EVs were initially considered for inclusion in the CCA but only 14 were retained by the forward selection procedure (Table 2.5). Indigenous trees were not present at any of the SUs and was therefore excluded as a variable in the CCA. In all, 48.8% of the variance in the dragonfly assemblage was accounted for by EVs and axis 1 explained 12.3% of the total. Of the selected EVs, water parameters were the most important factors driving dragonfly assemblages, together explaining 15.3% of assemblage variation. The water parameter pH was excluded from the forward selection analysis due to its collinearity with dissolved oxygen. Elevation was the next most important EV and explained 6.1% of the variation.

Table 2.5. CCA results for the influence of environmental variables on dragonfly assemblages. Pseudo-F values displayed for simple effects of variables (SS) and forward selection of variables (FS)

Variable	Overall		Anisoptera		Zygoptera		Eerste River		Lourens River		Palmiet River	
	SS	FS	SS	FS	SS	FS	SS	FS	SS	FS	SS	FS
River catchment							-	-	-	-	-	-
Eerste	**16.2****	**6.8****	**12.2****	**3.2****	**15.9****	-	-	-	-	-	-	-
Lourens	**16.0****	**3.4****	**7.6****	**3.2****	**17.5****	-	-	-	-	-	-	-
Palmiet	**35.4****	**3.4****	**20.0****	**20.0****	**42.3****	**42.3****	-	-	-	-	-	-
Elevation	**35.8****	**35.8****	**19.8****	1.2	**42.1****	-	**4.0****	**2.5***	**2.5****	**2.8****	**2.4****	**2.5****
% shade	**6.3****	-	**2.1***	1.7	**8.8****	-	1.0	-	**2.4***	1.4	1.1	1.4
Water measures												
Water temperature	**27.5****	**7.3****	**13.9****	**5.3****	**36.7****	**10.4****	**3.7****	-	**1.8***	0.7	**7.0****	**7.0****
Dissolved oxygen	**4.5****	**3.3****	**3.2****	-	**6.1****	**2.8****	**4.9****	**4.9****	**2.8****	**2.8****	**4.8****	**1.9***
Conductivity	**29.0****	-	**15.4****	-	**36.7****	-	**2.9****	-	0.7	-	**3.6****	**1.9***
pH	**8.6****	**2.4****	**5.6****	1.1	**8.9****	**8.4****	**4.9****	-	**2.6****	**3.1****	**6.1****	**2.5****
Substrate cover												
% debris	1.8	-	1.7	-	1.6	-	2.1	2.0	0.5	0.8	1.4	-
% sand	**3.8****	**2.3***	**2.8***	2.0	**4.0****	-	1.3	-	1.8	1.5	**1.8***	**1.9***
% rock	**29.9****	-	**17.2****	-	**35.5****	-	0.6	-	0.8	1.5	1.3	-
Vegetation	-	-	-	-	-	-						
Avge veg height	**3.0****	1.4	**2.5***	1.6	**3.3****	-	0.9	-	1.2	1.3	1.3	1.5
% indigenous cover	1.6	**2.1****	1.5	1.7	1.2	-	1.9	-	0.8	-	**1.7***	**1.7***
% alien cover	1.0	-	1.1	-	0.7	-	0.4	-	**2.5***	0.9	0.5	-
P.serratum	**12.2****	**1.8***	**6.0****	**2.5***	**15.5****	**3.1****	**4.3****	**4.6****	**1.8***	-	1.3	1.5
Aquatic macrophytes	**3.7****	-	**1.8***	-	**4.8****	-	0.9	-	1.7	-	1.2	-
Indigenous trees	**3.3****	1.7	1.2	1.5	**5.8****	**3.5****	-	-	-	-	**1.6***	**1.8***
Alien trees	1.1	-	1.1	1.4	0.9	-	1.6	-	1.2	1.6	0.8	-
Indigenous shrubs	**3.4****	1.6	1.5	-	**5.1****	-	**1.7***	**1.9***	1.7	1.3	1.0	1.3
Alien shrubs	0.7	-	0.5	-	0.8	-	0.5	-	1.8	1.6	0.6	-
Indigenous grasses	**1.8***	**2.2****	1.7	1.8	1.7	-	0.6	-	1.3	-	**1.9***	-
Alien grasses	0.9	-	0.8	-	0.8	-	-	-	1.8	1.4	-	-

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

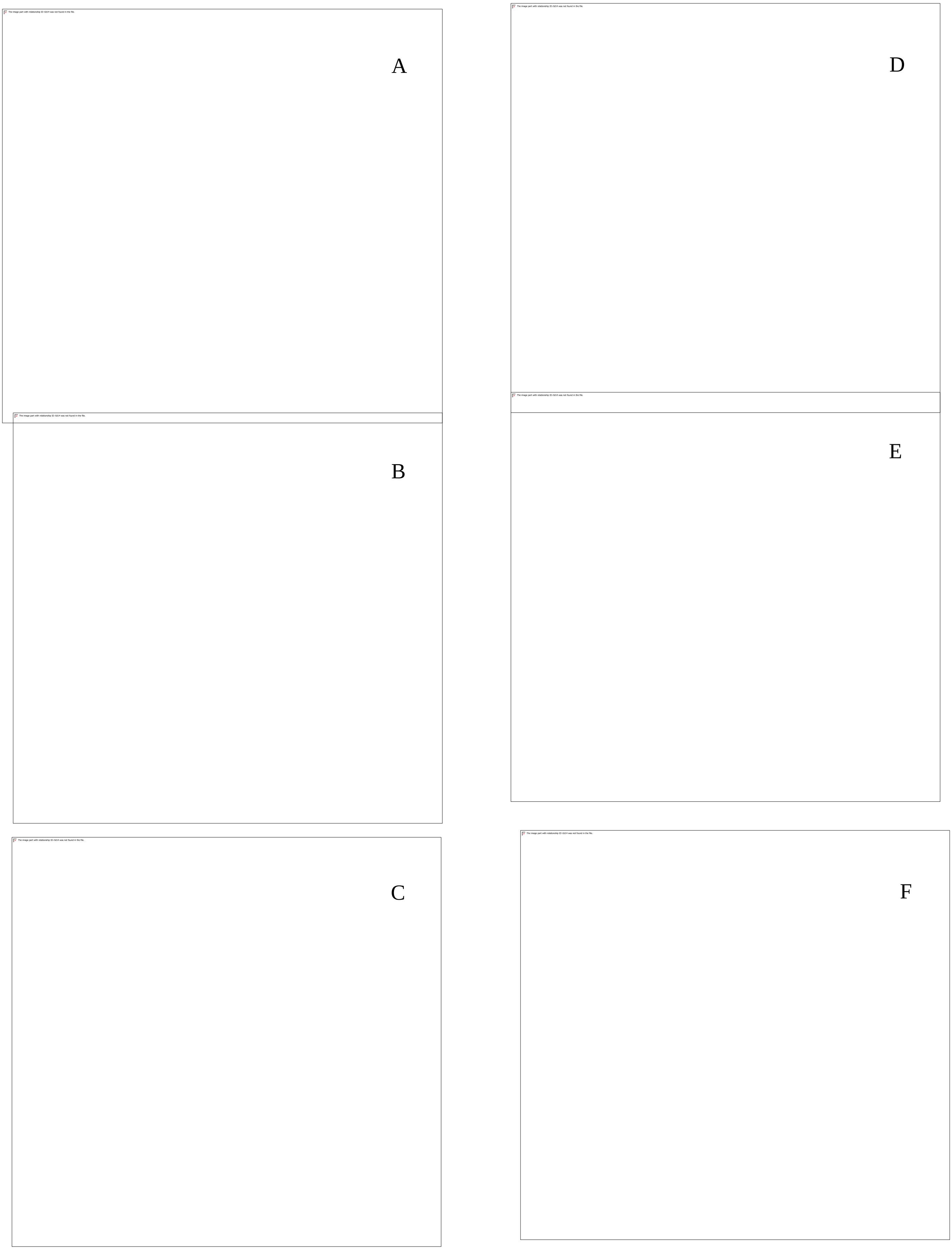

Figure 2.4. Canonical analysis of principal coordinates ordination forward selection for Odonata assemblage composition for A) overall community, B) Anisoptera, C) Zygoptera, D) Eerste River, E) Lourens River, F) Palmiet River

Discussion

Each of the rivers had its own particular dragonfly assemblage, driven mainly by water parameters. Vegetation and substrate characteristics that are often thought to be the main factors contributing to habitat heterogeneity and differences in dragonfly assemblages were not important for dragonfly diversity of natural, undisturbed CFR rivers. Other factors that may have an influence on water parameters also significantly influenced dragonfly assemblages. For example, changes in elevation led to changes in water temperature and dissolved oxygen. The natural areas of the Eerste and Lourens Rivers are similar in their environmental variables, whether water, substrate or vegetation characteristics. Yet these rivers differed in species richness and assemblage composition. These differences were driven by the individual river's water variables, specifically pH, conductivity, dissolved oxygen and temperature. The Palmiet River differed from the other rivers in its physical characteristics, dragonfly species richness and assemblage composition. However, the same water parameters were also key in influencing its dragonfly assemblage.

The habitat-heterogeneity hypothesis, developed by MacArthur and MacArthur (1961), proposes that an increase in the number of different habitats can lead to an increase in species diversity. Most often, studies refer to structural variation, such as those relating to vegetation and substrate characteristics, as the central components contributing to habitat heterogeneity. In river systems, more emphasis may need to be placed on the importance of the role of heterogeneity in terms of water parameters, such as those highlighted here. Conserving for heterogeneity is strongly linked to the concept of the mesofilter. This would entail conserving specified ecosystem elements which are important for the maintenance of dragonfly species. Thus conserving a gradient of water parameters is critical for the conservation of dragonflies in the CFR.

Previous studies in the CFR may not have recognised the importance of water variables in defining habitat heterogeneity for two possible reasons. Many studies fail to account for water parameters in assessments, as this requires specialised and expensive equipment. These parameters may also be disregarded because they are not visible to the naked eye and it is well-known that dragonflies respond largely to visual cues (Michiels & Dhondt, 1990; Schindler et al., 2003). Other studies probably failed to identify the great importance of water parameters because they included the effects of anthropogenic disturbances, which override the more subtle, natural variables. For example, Samways and Sharrat (2010) showed that within four rivers in the CFR, disturbance regimes (alien invaded, cleared of alien vegetation and natural vegetation) were more important than natural variables in defining dragonfly assemblages. Nevertheless, the next most important variables for dragonfly assemblages were dissolved oxygen and pH, and then water temperature and conductivity, as well as other significant EVs (Samways & Sharratt, 2010). Alien invasive trees, as with other anthropogenic disturbances, alter numerous components of natural systems to such an extent that their influences may override the role of water parameters in heterogeneity. Therefore, without disturbances, EVs like those related to vegetation dynamics, become less important in CFR rivers. Instead, EVs associated with water parameters are the most important in explaining dragonfly assemblage patterns, as is shown here.

Dragonflies spend the majority of their life cycle as aquatic nymphs (Corbet, 1962; Paulson & Jenner, 1971). In the CFR, they are exposed to the temperate conditions of a typical Mediterranean climate (Midgley et al., 2003). In such regions, the terrestrial, winged adult phase of most dragonfly species lasts only a few weeks. The main purpose of this short-lived phase is to reproduce (Corbet, 1962). Females, after selecting a suitable mate, select appropriate oviposition sites and deposit their eggs (Corbet, 1962). Males, patrol oviposition habitats, are often territorial and attempt to mate with as many females as possible (Buskirk & Sherman, 1985). Benke and Benke (1975) showed that during the aquatic phase of their lives, there can be up to 99.9% mortality rate. Therefore, the most important factors ensuring the persistence of dragonfly species and assemblages are those that act on larvae. Different species require different ranges of water parameters for larval survival (Buskirk & Sherman, 1985). Ensuring heterogeneity in water parameters and not just terrestrial variables would allow for the persistence of numerous species.

Adult dragonflies make use of visual cues to select territories and oviposition sites (Michiels & Dhondt, 1990; Schindler et al., 2003). This means that there is strong selection pressure to choose the best oviposition sites to maximise larvae survival. These sites should provide favourable physical conditions for development, supply ample food for larvae and contain few predators and minimal competition. However, females are unable to directly assess water parameters, food supply or predator density and can only choose the best oviposition sites based on general visual characteristics of habitats (Buskirk & Sherman, 1985). A female dragonfly will likely not choose an oviposition site based on the pH of the water, despite the apparent importance of this variable. However, dragonflies that breed in isolated or restricted permanent habitats, such as the rivers evaluated in this study, will remain close to the sites from which they emerged (Corbet, 1962). This means that oviposition sites are not solely based on visual EVs favoured by female dragonflies. By choosing sites close to where they successfully survived the aquatic stage of their life cycle, there is a greater chance that the conditions will be right for their own offspring to survive (Watson et al., 1982).

The role of spatial scale has been investigated for aquatic macroinvertebrates (Dallas & Day, 2007). There is a possibility that if a sampling area is too big it could fail to effectively capture the effect of habitat heterogeneity based on extra-aqueous variables. The larger the scale of a study the more similar parameters such as vegetation height or cover are likely to be. Water parameters are likely stay unchanged over longer distances due to constant directional movement and manifest at larger scales than the other variables tested. Defining the scale necessary for assessing dragonfly assemblages could be an important consideration for future studies.

My study is at variance with previous studies in the CFR which highlight the importance of vegetation, substrate and other variables for dragonfly assemblages. These EVs may indeed be more important in more disturbed habitats where anthropogenic disturbances alter dragonflies' natural habitats. However, for dragonflies in their more natural habitats faced with little disturbance, water related EVs become more important for driving their assemblages. This study has shown that although vegetation and other previously mentioned factors are important for dragonfly communities, numerous unseen or unmeasured variables can be just as vital or even more important for their conservation.

Conclusion

My results show that certain water parameters consistently influence dragonfly assemblages in natural sections of CFR rivers. We can therefore assume that habitat heterogeneity, as defined by variation of the water parameters, temperature, conductivity, dissolved oxygen and pH, are features that determine the presence of particular dragonfly species. These features can be identified as mesofilters for dragonflies of CFR rivers, which can be applied to future conservation efforts. Conserving rivers that differ in these parameters or even those that are more variable in these parameters should help to conserve a greater overall diversity of dragonfly species.

As overall species richness increases with increased dissolved oxygen and decreased pH, which are characteristically related to more pristine areas, focus should be on conserving natural areas with these features. Water temperature was positively correlated to an increase in overall species richness. Since water temperature characteristically is higher in downstream areas, historic, lower lying areas should be a conservation priority. For management of these systems, activities that can negatively influence variability in these water parameters should be avoided. For example, agricultural developments result in runoff, which leads to decreases in dissolved oxygen and increases in pH. Where avoiding these activities is not possible or in areas that require rehabilitation, conservation actions should focus on the factors that lead to changes in water parameters and not just restoration of riparian vegetation, as has been proposed by various programs.

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Chapter 3: Response of dragonfly assemblages and endemic species to urban and agricultural transformation in the Cape Floristic Region biodiversity hotspot

Abstract

Rivers of the Cape Floristic Region (CFR) are threatened by anthropogenic land transformation. The CFR is a centre of endemism for many taxa, including dragonflies. These insects are highly sensitive to water quality changes, which make the presence of narrow-range endemic and threatened species useful indicators of habitat integrity. The Dragonfly Biotic Index (DBI) uses the presence of ecologically-sensitive dragonfly species to measure ecosystem integrity. This study investigated the effects of agricultural and urban land transformations on dragonfly species richness, assemblage composition and DBI scores in three rivers in the CFR. Land transformation significantly influenced dragonfly assemblages but did not always reduce species richness. Agricultural and urban areas had different dragonfly assemblages but were more similar to each other than to natural areas. Both transformation types reduced opportunities for some endemic species but provided for the establishment of widespread, generalist species; as emphasized by great changes in DBI values. Different rivers supported different dragonfly assemblages, which emphasizes the importance of conserving the complementarity among rivers. Mitigating the adverse influences of landscape transformation is essential for the conservation of rare and endemic taxa, particularly in areas of high conservation value. Dragonflies are good bioindicators and their assemblage composition as represented by the DBI is an effective way to assess ecosystem integrity in the CFR with its large component of irreplaceable species.

Keywords: biodiversity hotspot; rivers; biological indicator; anthropogenic disturbance; water quality

Introduction

To meet the requirements of an ever-increasing human population, transformation of natural landscapes is inevitable, usually at the expense of ecosystem health and native biodiversity (Monteiro-Júnior et al., 2013). Transformation of land for urbanisation and agriculture results in a loss of habitat heterogeneity and leads to biotic homogenization (Olden & Rooney, 2006). Habitat loss has been recognized as the primary threat to global biodiversity (McKinney & Lockwood, 1999; Rouget et al., 2003; McKinney, 2006), and is particularly problematic in regions with high beta-diversity and rich in endemic taxa, such as the Cape Floristic Region (CFR), South Africa. Of concern is that these irreplaceable, endemic species dominate the global patterns of extinction (Pimm et al., 1995).

Biodiversity hotspots, including the CFR, have been identified in view of their extraordinarily high concentrations of endemic taxa under anthropogenic threat (Cowling et al., 2003; Myers et al., 2000; Goldblatt & Manning, 2002; Pressey et al., 2003). Like other biodiversity hotspots, the CFR has been extensively transformed, largely by urbanization and agricultural developments, which have put immense pressure on local biodiversity (Rebelo, 1992; Pressey et al., 2003; Lombard et al., 2003). The region is renowned for its great plant species richness and level of endemism (Bond & Goldblatt, 1984; Day & Day, 2009). However, its conservation value is not limited to the uniqueness of its vegetation. For example, the diversity and endemism of aquatic arthropods in the CFR compares to that of its terrestrial plants (Wishart & Day, 2002).

River catchments of the CFR comprise complex landscape mosaics that offer a range of habitat types and environmental gradients (Allan & Flecker, 1993; Ward et al., 2002). The variety of biotopes and the variability in these mosaics may be responsible for the high biodiversity levels (Meek et al., 2010), with the CFR having been identified as one of the world's 200 most significant Freshwater Ecoregions (Cowling et al., 2003). All rivers are affected by the landscapes through which they flow, with anthropogenic disturbances at the landscape scale being a major threat to the ecological integrity of rivers (Allan, 2004; Darwell et al., 2009). Rivers of the CFR characteristically begin in mountainous terrains and due to the rugged topography, these sections tend to be largely undisturbed by anthropogenic activities. However, the lower reaches generally occur on fairly rich soils on gradual slopes and often experience high levels of transformation (Dallas & Day, 2007; de Moor & Day, 2013).

Urbanization severely reduces water quality in lotic systems (Morley & Karr, 2002). Urban development puts immense pressure on river systems through various related disturbances such as effluent and urban runoff, which increase nutrient input and decrease river health (Schulz, 2001). Nutrient dynamics are poorly studied for rivers of the CFR, despite the obvious deteriation of water quality observed over the last few decades (Schulz, 2001; Struyf et al., 2012). Furthermore, riparian vegetation is often replaced with aesthetically-pleasing exotic grasses, shrubs and trees (Walsh, 2004). The CFR landscapes are also intensively transformed for crop production (mostly vineyards, orchards and wheat fields), which severely reduces river quality (Schulz et al., 2001). Land is often ploughed up to the river's edge and the heavy machinery that is used to level river-beds can completely destroy riparian systems (Medina-Vogel et al., 2003). Loss of natural riparian vegetation results in erosion of river banks, in sedimentation, and increases agrichemical runoff into the rivers (Schulz et al., 2001; Richardson et al., 2007). Transformation that leaves bare river banks allows for the establishment of alien woody invasive trees. In the CFR, the major invasive tree species, Acacia longifolia and A. mearnsii, can severely alter river ecosystem functioning (Galatowitsch & Richardson, 2005). These disturbances cause changes in water chemistry, for example, pH levels in agricultural landscapes have been recorded to increase to levels that are fatal to acidophilic, endemic arthropods (de Moor & Day, 2013).

In a highly sensitive region, like the CFR, restoration goals need to be realistic and account for the current state of the surrounding area as well as the intended future use of the riparian zone (King & Brown, 2006). In highly transformed landscapes, where ecological integrity is low, restoration of natural riparian vegetation is often not possible. In such cases, more realistic goals would aim to restore basic ecosystem functions through providing a vegetation cover that is structurally similar to the absent natural riparian vegetation. It should comprise non-invasive, possibly indigenous plant species, which are robust against flooding and re-invasion by alien species (Holmes et al., 2008). The functions restored would include the buffering of the river through erosion control and a return of more natural flow dynamics (King & Brown, 2006; Holmes et al., 2008). Fynbos riparian ecosystems are considered to be relatively ecologically resilient to alien plant invasions (Holmes et al., 2008). However, their removal is crucial and has been the motivation behind the national program, Working for Water, since 1995 (Galatowitsch & Richardson, 2005). Invasive plants have been, and continue to be, systematically removed from watercourses, and thereafter, cleared sites are generally left to recover without further intervention (Galatowitsch & Richardson, 2005). The most utilised practices for conserving river integrity in transformed areas include; restoration where possible, retaining riparian buffers, adding grass filter strips along drainage swales and no-till farming (Ryan et al., 2003).

The urgency to achieve a balance between transformation and environmental health is increasingly being realized (Carter, 2001). One approach aimed at achieving this in the CFR is the establishment of biosphere reserves. These enable the co-existence of both protected, natural areas as well as transformed areas of land that are separated by buffer zones (Grant & Samways, 2011). Activities should utilise the best possible practices in order to maintain ecosystem integrity for the sake of biodiversity and human wellbeing (Díaz et al., 2006). Buffer zones achieve this because they are areas subjected to anthropogenic influences of a low to moderate intensity. They are designed to cushion the impact of the more intense surrounding anthropogenic disturbances and improve the quality of the core zone (Simaika & Samways, 2009b). Recent research has focussed on the essential value of biodiversity to sustain stability and long term productivity in agricultural systems (Altieri, 1999; Gaigher, 2008). Riparian zones are heavily influenced by agricultural development, even though they are generally non-crop habitats. Often farmers are more likely to adopt conservation practices when there are economic benefits involved and conserving these non-crop habitats should come into being without reducing their planting area (Napier & Forster, 1982). Therefore, establishing biosphere reserves within production landscapes will be beneficial for famers as well as for biodiversity. The riparian zones of urban areas are often maintained for aesthetic reasons, and human community education and involvement can aid in preserving rivers and their biodiversity (Purcell et al., 2002). Species richness is often high in urban areas but usually have reduced sensitive and rare species (Findlay & Taylor, 2006). A way to overcome this limitation is by connecting these sections to more natural reaches that may serve as species sources and encourage re-colonization by endemic species (Morley & Karr, 2002). Additionally, river integrity will also improve by establishing such connections because water flow and sediment loads are likely to be in balance (Brierley & Fryirs, 2000; Findlay & Taylor, 2006).

Activities that restore or protect river health also alleviate some of the detrimental impacts of landscape transformation on river invertebrates. Restoring riparian vegetation will benefit organisms chiefly by creating a more heterogeneous environment. When restoration is not an option, habitat heterogeneity can be increased using other techniques. For example dragonfly diversity was increased in urban areas when a range of perching sites were provided (Sternberg, 1994; Suh & Samways, 2005). However, for different species, the effect of habitat heterogeneity differs depending on spatial scale. This reiterates the importance of conserving heterogeneity at all scales or defining certain keystone structures (Tews et al., 2004).

It is essential to define the effects of urbanization and agricultural developments on aquatic arthropods to understand their responses to these changes and to help development of compensatory measures. Dragonflies are highly sensitive to environmental conditions, which makes them good indicators of ecosystem health (Catling, 2005). Their diversity can be altered by water quality and their assemblages can mirror different biotopes within a range of anthropogenic disturbances (Watson et al., 1982; Takamura, 1991; Bulankova, 1997; Corbet, 1999). Dragonflies are therefore often used as bioindicators of ecological conditions in aquatic habitats (Clark & Samways, 1996; Monteiro-Júnior et al., 2013). Their use as surrogates for ecosystem health has gained popularity and they are now recognized as umbrella species whose conservation can lead to the conservation of other taxa (Noss, 1990; Schinder et al., 2003). In light of this, the Dragonfly Biotic Index (DBI) was developed as an efficient, low-cost method that uses the presence of dragonfly species as a measure of ecological integrity (Simaika & Samways, 2009a; Simaika & Samways, 2011). This index is a quantitative measure based on the assessment of three sub-indices of species geographic range, sensitivity to disturbance and threat status according to the Red List (Simaika & Samways, 2009a). A strong correlation exists between the DBI and other macroinvertebrate scores, which confirms its value as a bioindicator (Smith et al., 2001). In the Western Cape, the DBI has been used to prioritize conservation sites and measure habitat recovery (Simaika & Samways 2009a; Simaika & Samways, 2009b).

In many areas of the world, dragonflies have been extensively studied and are used as bioindicators, and to explore the impacts of anthropogenic disturbances on ecosystem health (Clark & Samways, 1996). The CFR is a centre of endemism for dragonflies of South Africa, which makes dragonfly conservation and the preservation of their habitats even more crucial in this region (Simaika & Samways, 2009b). Despite this, the influence of anthropogenic activities on their assemblages in the CFR has only been shown relative to invasive alien trees (Samways & Sharratt, 2010). Thus, the objective of this study is to determine the effect of landscape transformation on dragonfly diversity in the CFR. Specifically, my aim is to assess the extent to which dragonflies reflect the different land transformation types. Special focus will be on the effect of transformation on the persistence of endemic species. Furthermore, I assess the ability of the DBI to reflect the impact of the main types of transformation and to prioritize conservation sites. In short, my aim is to test the DBI as an assessment tool on the dragonfly assemblages of the CFR hotspot. I hypothesize that landscape transformation will reduce the presence of some endemic species and yet promote presence of the widespread, generalist species. I also expect the DBI to successfully demonstrate the negative effects of transformation and confirm the use of dragonflies as bioindicators.

Methods

Study sites and sampling design

Three Western Cape Rivers were chosen as focal areas for this study. These comprised sections of the Eerste, Lourens and Palmiet rivers, which were selected for having large areas of undisturbed as well as transformed land. An important selection criterion was to select sites along each river that maintained 10 m of semi-natural vegetation between the river's edge and the prevailing landscape disturbance. This was so as to standardize the size of the buffer areas between the rivers' edges and the start of the transformation for comparative results.

108 sampling units (SUs) were selected for each of the Eerste and Lourens rivers. These SUs were equally divided into 36 SUs per land use category (agriculture, urban, and the natural, untransformed condition) per river. The source of the Eerste River lies in the Jonkershoek Nature Reserve, Western Cape Province, South Africa (34°00'28.1952"S; 19°00'6.4656"E) and the Lourens River originates within the Hottentots Holland Nature Reserve, Western Cape, South Africa (34°00'56.9016"S; 18°58'42.5424"E) (Figure 3.1). Both rivers fall within the Cape Winelands Biosphere Reserve and are characteristically typical Western Cape mountainous rivers (Swilling & Sebitosi, 2012). At these two rivers the natural SUs were

confined to the upper reaches of the rivers and the urban and agriculture SUs to the middle and lower reaches. The third river, Palmiet River, forms an important part of the Kogelberg Biosphere Reserve and its source is within the Hottentots Holland Nature Reserve, Western Cape Province, South Africa (34°03'24.9516"S; 19°00'48.5244"E) (Figure 3.1). Due to limited sections of the river flowing through flowing through urban areas, only 72 SUs were chosen for the Palmiet River (Figure 3.1). These consisted of 36 natural SUs along the lower reaches of the river and 36 agricultural SUs along the upper reaches. The Palmiet River differs from the other two rivers because the natural, undisturbed sections occur in the lower reaches of the river, within a protected area, and the upper reaches are disturbed by agriculture (Ollis, 2005). Each SU consisted of a 100 m stretch of river and included the area 3 m on either side of the river's edge (i.e. total SU size 100 x 6 m = 600 m^2). For a more detailed explanation of the rivers used in this study refer to Appendix 2.

Sampling of adult dragonflies

Two observers recorded all the adult, male dragonfly species and their abundance for 30 min per SU using visual scanning and close focus binoculars. Only mature, male individuals were noted, as adult females and tenerals are not confined to riverside territories and are difficult to identify (Corbet, 1962). Individuals that were challenging to identify in the field were caught and their identities confirmed by referring to Samways (2008). Sampling took place twice per SU, during summer and autumn, to account for the effect of season. According to Schmidt (1985) the best time to sample dragonfly species is when they are most abundant at riverside territories. Therefore, sampling took place on warm, windless days between 09:00 and 14:00.

Environmental variables

Variables were selected based on their association to anthropogenic disturbances and land transformation. River catchment and surrounding land use category were recorded as categorical variables. Elevations were determined using Google Maps (Google Maps, 2015) and a handheld GPS was utilized to record positions. The percentage of alien plant cover and vegetation height were visually estimated by both observers and averaged for each SU.

Data analysis

For analyses, data from the two collection seasons were pooled. EstimateS version 9.1 (Cowell, 2013) was used to determine whether sampling effort was adequate. Samples were randomised 999 times and the non-parametric species estimators of Chao2, ICE, Jackknife2 and Bootstrap were calculated for the rivers combined and for each independently. Non-parametric estimators are recommended for insect assemblages, particularly in biodiversity hotspots, where a large number of rare, endemic species are present (Novotny & Basset, 2000; Hortal et al., 2006).

Analyses of species richness and DBI scores, were carried out within R software (R Development Core Team, 2013), using the *lme4* package (Bates & Sarkar, 2006). Analyses were conducted for the rivers separately and combined. Species richness and DBI scores were analyzed for overall Odonata, separately for Anisoptera and Zygoptera, and for species endemic to the CFR and wider endemics to South Africa. Analyses of DBI scores showed the data were normally distributed and thus linear mixed-effect models (LMMs) were used. Species richness data were non-normal, although fitted a Poisson curve, thus a GLMM with a Laplace approximation and a Poisson distribution was used (Bolker et al., 2009). Aikake Information Criterion (AIC) analyses were conducted to determine the best fit general linear mixed models (GLMMs) for the data. As these analyses showed no over dispersion of variances compared to the models, χ^2- and P-values were calculated (Bolker et al., 2009). Elevation was included as the random effect for all analyses. Three other variables, associated with landscape transformation, were included as fixed effects. These comprised the categorical variable of land use and the continuous variables of percentage alien cover and average vegetation height. When river data were combined, the possibility of a significant interaction between river catchment and land use category was tested. When necessary, Tukey *post hoc* tests in the *R* package *multcomp* were used to determine the pairwise differences in species richness and DBI scores between land use categories (Hothorn et al., 2008).

To determine differences in dragonfly assemblage composition, permutational multivariate analyses of variance (PERMANOVA) were conducted in *PRIMER 6* (Primer- E, 2008). These were performed using 9999 permutations to determine F- and P-values, as well as pairwise differences within significant tests to measure changes in the selected variables. For these analyses, the two continuous variables of percentage alien plant cover and average plant height were categorised. Unrestricted permutations of raw data were used, which is considered conservative regarding type I error (Anderson et al., 2008). Canonical analyses of principal coordinates (CAP) were used to detect trends of similarity in species assemblage data for the different land use categories and rivers. A CAP analysis locates an axis through the multivariate cloud of points which best separates predefined groups (Anderson et al., 2008). Data used in the PERMANOVA and CAP routines were square-root transformed to reduce the weight of common species and similarity matrices were derived using Bray-Curtis similarity coefficients (Anderson, 2001). Species data for the different transformation types were used in constructing Venn diagrams for the river data combined and for each river separately. The Jaccard Index (Cj) of similarity was calculated using the formula:

$$\mathrm{J(A,B)} = \frac{|\mathrm{A} \cap \mathrm{B}|}{|\mathrm{A} \cup \mathrm{B}|}$$

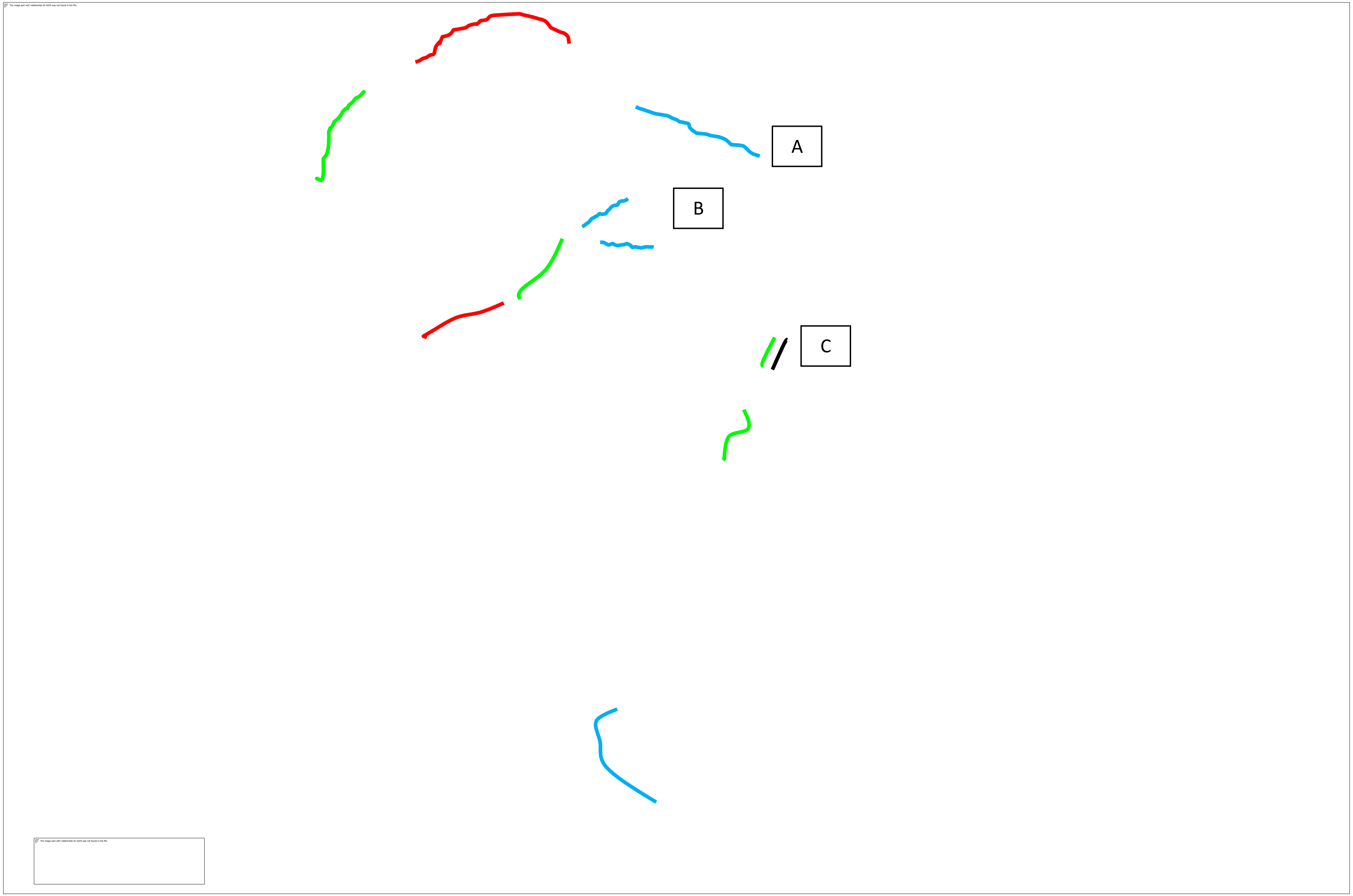

Figure 3.1. Areas selected for sites along the A) Eerste River, B) Lourens River and C) Palmiet River coloured lines represent land use categories with blue representing the natural sites, green the agricultural sites and red the urban sites

Results

Species richness and abundance

A total of 37 Odonata species (22 Anisoptera and 14 Zygoptera), comprising 10 711 individuals were recorded throughout the study (species list in Appendix 1) (Table 3.1). Seven of the 37 species are CFR endemics and made up 35% of the observed individuals. In addition to these species, another seven species were South African endemics (excluding the CFR endemics), which means 14 species, over half of all the observed individuals, were endemic to South Africa. Observed species richness neared species estimates when pooled, as well as for each river individually. This indicates that sampling effort was representative of the local dragonfly assemblage. The Palmiet River had by far the highest observed species richness (31 species) and abundance (5669 individuals) compared to either the Eerste (22 species, 1995 individuals) or Lourens Rivers (24 species, 3047 individuals) (Table 3.1). When the data of all three rivers were combined, natural areas had much higher species richness (30 species) and abundance (7109 individuals) than the urban (23 species, 1933 individuals) or agricultural sites (21 species, 1669 individuals) (Table 3.1). Endemic species richness was low in transformed areas, especially in urban regions (Table 3.1).

Factors influencing species richness

Overall, species richness was most strongly affected by land use category and river catchment, and their interaction was significant for overall species richness, Anisoptera and CFR endemic species richness (Table 3.2). Vegetation height was negatively correlated with species richness for Zygoptera and both categories of endemic species (Table 3.2). Pairwise comparisons of land use category showed natural sites generally had the highest species richness and agricultural sites the lowest (Table 3.3). When rivers were analysed separately, land use category stood out as the most influential factor affecting species richness (Table 3.2). For the rivers individually, overall species richness was always negatively correlated with vegetation height and alien vegetation cover. In the Eerste River, species richness of the natural sites was always equal to that of the urban sites and the agricultural sites had lower species richness (Table 3.3). In the Lourens River, urban sites usually had the highest species richness but for South African endemic species, richness was the same between all land use categories. For the Palmiet River, species richness was generally highest in the natural sites, except for CFR endemic species richness, which remained the same regardless of landscape transformation. Vegetation height was an important variable in the Palmiet River and was always negatively correlated with species richness (Table 3.2).

Factors influencing DBI scores

When river data were pooled or analysed separately, land use category was the main variable influencing DBI scores, with higher scores always at natural sites (Table 3.2; Table 3.3). When data were combined, river catchment did not influence DBI scores and the interaction between river catchment and land use category was not significant (Table 3.2). In the Eerste River, DBI scores were not significanlty different between the natural and urban sites but agricultural sites had significantly lower scores (Table 3.3). For the Lourens River higher scores occurred in the natural areas and scores did not differ between the transformation types. For the Palmiet River, vegetation height had a strong, negative correlation with DBI scores for all the groups (Table 3.2).

Table 3.1. Various species richness estimates and observed richness and abundance. CFR = Cape Floristic Region, SA = South African.

Estimators	Abundance	Observed richness	ICE	Chao2	Jackknife2	Bootstrap
Rivers combined						
Overall	10711	37	40.52	39.14±(4.20)	44.97	38.65
Anisoptera	5635	22	26.99	25.32±(4.12)	29.97	24.12
Zygoptera	5076	14	13.54	13.00±(1.94)	14.99	13.39
CFR endemics	3725	7	6.00	6.00±(0.94)	6.00	6.02
SA endemics	6767	14	13.28	13.00±(1.67)	14.99	13.4
Agriculture						
Overall	1669	21	20.55	20.00±(0.08)	17.11	21.08
Anisoptera	1220	13	12.00	12.00±(0.68)	8.11	12.54
Zygoptera	449	8	7.79	7.00±(0.25)	8.00	7.55
CFR endemics	627	6	5.80	5.00±(0.53)	6.97	5.41
SA endemics	1093	8	7.77	7.00±(0.53)	8.97	7.41
Urban						
Overall	1933	23	20.05	19.33±(0.92)	21.00	20.00
Anisoptera	773	12	11.49	11.00±(0.25)	12.00	11.5
Zygoptera	1160	8	7.47	7.00±(0.48)	8.96	7.37
CFR endemics	568	3	2.00	2.00	2.00	2.00
SA endemics	1080	6	6.93	6.00±(0.48)	7.96	6.37
Natural						
Overall	7109	30	35.38	49.80±(17.30)	42.80	31.63
Anisoptera	3642	18	24.33	26.91±(10.18)	26.86	18.89
Zygoptera	3467	12	12.18	11.99±(2.25)	14.94	11.74
CFR endemics	2530	7	6.91	6.00±(0.48)	7.97	6.37
SA endemics	4594	14	13.91	13.99±(2.26)	16.94	13.75
Eerste River						
Overall	1995	22	23.5	21.74±(1.41)	24.00	21.54
Agriculture	241	10	10.70	9.49±(1.27)	11.92	9.90
Urban	634	15	16.02	15.46±(2.53)	18.83	15.32
Natural	1120	18	20.55	17.94±(2.82)	21.83	17.79
Lourens River						
Overall	3047	24	23.96	23.2±(0.62)	23.06	24.31
Agriculture	855	11	11.11	10.97±(2.21)	13.83	10.73
Urban	1299	18	17.44	17.00±(0.16)	17.08	17.65
Natural	893	12	12.02	11.19±(0.61)	11.17	12.25
Palmiet River						
Overall	5669	31	36.48	40.35±(10.44)	42.75	32.79
Agriculture	573	18	19.10	17.73±(1.39)	20.00	18.60
Natural	5096	27	33.23	46.42±(16.96)	39.42	28.60

Table 3.2. Effects of anthropogenic-related variables on species richness and Dragonfly Biotic Index (DBI) scores for the rivers combined and for each individually. The test-statistics are displayed as χ^2 values. CFR = Cape Floristic Region, SA = South African.

Variables	Overall	Anisoptera	Zygoptera	CFR endemics	SA endemics	DBI
Combined						
River	**20.55*** **	**11.47** **	**37.55*** **	**21.16*** **	**36.68*** **	0.95
Land use	**15.02*** **	**14.17*** **	**39.13*** **	**17.83*** **	**19.73*** **	**15.22*** **
Alien cover	0.26	0.26	0.50	0.17	0.07	0.12
Veg height	**5.27* **	0.18	**7.67** **	**9.59** **	**5.25* **	3.61
River*land use	**31.78*** **	**48.12*** **	0.25	**14.02* **	6.55	6.13
Eerste River						
Land use	**11.48** **	3.85	**15.84*** **	**16.3*** **	**18.45*** **	**10.56** **
Alien cover	**12.79** **	1.61	0.01	0.00	0.70	0.14
Veg height	**12.19** **	0.33	2.49	0.23	0.70	0.01
Lourens River						
Land use	**20.90*** **	**24.04*** **	**14.63*** **	**6.87* **	0.83	**36.77*** **
Alien cover	**22.13*** **	0.08	1.35	1.22	2.15	6.39
Veg height	**22.87*** **	2.73	0.41	0.01	1.58	0.01
Palmiet River						
Land use	**24.25*** **	**21.90*** **	**6.65** **	0.19	**7.96** **	**7.51** **
Alien cover	**29.88*** **	1.54	0.06	1.53	0.58	2.34
Veg height	**35.96*** **	**5.07* **	**8.00** **	**18.26*** **	**14.98*** **	**11.43*** **

* P<0.05, ** P<0.01, *** P<0.001

Table 3.3. Results of pair-wise tests of dragonfly richness (R) and Dragonfly Biotic Index (DBI) scores between the different land use categories; natural (N), agriculture (A) and urban (U). Values are arranged from highest to lowest. > indicates that value on left is signifficantly larger than that on the right, = indicates that values did not signifficantly differ. CFR = Cape Floristic Region, SA = South African.

River	Overall R	Anisoptera R	Zygoptera R	CFR endemics R	SA endemics R	DBI
Combined	N = U > A	N = U = A	N = U > A	N > U > A	N = U >A	N > U = A
Eerste River	N = U > A	U = N = A	N = U > A	N = U > A	N = U > A	N = U > A
Lourens River	U > A > N	U = A > N	U > N > A	U > N = A	U = N = A	N > A = U
Palmiet River	N > A	N > A	N > A	N = A	N > A	N > A

Dragonfly assemblage composition

River catchment and land use category had the greatest influence on overall assemblage composition (Table 3.4). The dragonfly assemblages of the natural sections differed between all rivers (Figure 3.2). However, the Eerste and Lourens rivers clustered closer together than to the Palmiet River, which had a unique dragonfly assemblage. Assemblages between and within rivers were more similar and grouped closer together in transformed sites, although they were all significantly different. Alien plant cover was the least influential factor on most dragonfly assemblages but did significantly influence overall, Zygoptera and CFR endemic species assemblages (low and high percentage categories). Zygoptera assemblages and species endemic to the CFR and South Africa, were more sensitive to changes in land use than Anisoptera assemblages. When rivers were analysed separately, land use category remained the largest driver of dragonfly assemblages, whether considering Odonata overall, separate suborders or endemic species. In the Eerste and Palmiet Rivers, vegetation height was also a significant factor influencing species composition, although it was much less significant than land use category. In the Lourens River, high percentages of alien plant cover had significantly different dragonfly assemblages to sites with less alien cover.

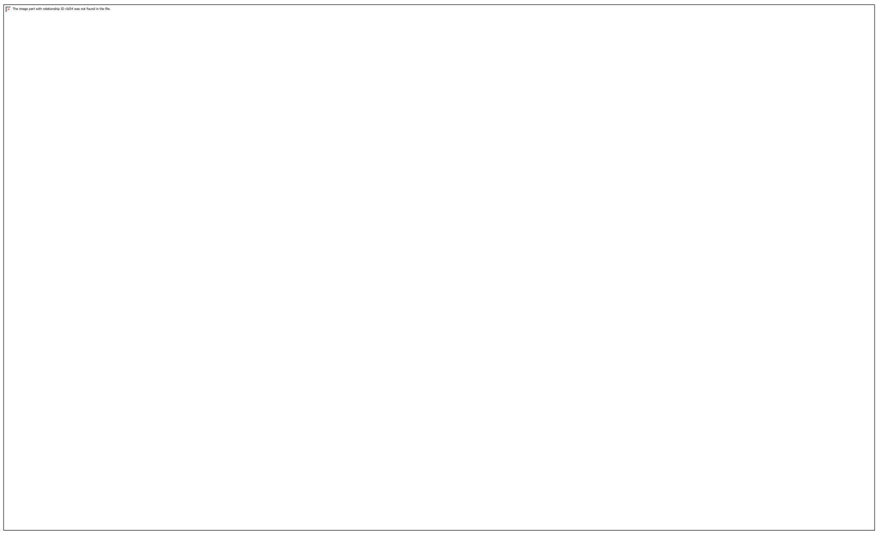

Figure 3.2. Canonical analysis of principal coordinates ordination plot of dragonfly assemblage data for the different land use categories and rivers. Triangles represent the Eerste River, open squares represent the Lourens River and circles represent the Palmiet River, with blue representing the natural sites, green agricultural sites and red the urban sites.

When rivers were combined, 16 of the 37 species were observed at all three land use categories and half of these were endemic to South Africa (Figure 3.3). Many species were shared between agriculture and urban sites (Cj = 0.76). Together, the transformed sites only had seven species that were not observed in the natural areas, all of which have low DBI scores and none were endemic species (Appendix 1). The natural sites were inhabited by 12 species that were absent from the other land use categories. Five of these were South African endemics, one of which (*Syncordulia venator*) only occurs within the CFR.

In the Eerste River, all three land use categories had quite different species compositions but the urban and agriculture sites were the most similar to each other (Cj = 0.56) (Figure 3.3). All three land use categories only shared six of the 22 species observed along the river. Three of these were South African endemics (Appendix 1). Six species only occurred in the natural areas and five of them were endemic to South Africa. Five species, comprising two South African endemics were shared between the natural and urban sites and absent from the agricultural areas. In the Lourens River, the natural and agricultural sites were very similar to each other in terms of their shared species (Cj = 0.77) (Figure3.3). All three land use categories shared seven species and three of these were the same endemic species found in all three land use categories of the Eerste River. The natural sites were inhabited by five unique species, three of these were endemic to South Africa (Appendix 1), and the urban sites housed eight unique species, two of which were South African endemics. In the Palmiet River, the natural and agricultural sites were quite different from each other and shared only 14 of the 31 observed species (Cj = 0.45) (Figure 3.3). The natural sites had 13 unique species, five of these were endemic to South Africa (Appendix 1). The agricultural sites had four species that were not observed in the natural areas but none of these were South African endemics.

Table 3.4. Comparisons of species composition in relation to anthropogenic-related variables. Main test represents a Pseudo-F value calculated using a Permutational Multivariate Analyses of Variance (PERMANOVA) for categorical variables and pairwise represents results from a PERMANOVA pairwise test, ≠ represents significantly different assemblages and ALL represents significant differences between all the categories in question

	Overall		**Anisoptera**		**Zygoptera**		**CFR endemics**		**SA endemics**	
	Pseudo-F	**Pairwise**	**Pseudo-F**	**Pairwise**	**Pseudo-F**	**Pairwise**	**Pseudo-F**	**Pairwise**	**Pseudo-F**	**Pairwise**
Combined										
River	**38.95*** **	ALL	**32.03** **	ALL	**50.10*** **	ALL	**68.46*** **	ALL	**50.59*** **	ALL
Land use	**31.53*** **	ALL	**11.15** **	ALL	**54.82*** **	ALL	**28.67*** **	ALL	**42.41*** **	ALL
Alien cover	**2.42** **	L ≠ H, M	1.89		**2.84** **	L ≠ H, M	**2.86* **	L ≠ H, M	0.79	
Vegetation height	**6.63*** **	S ≠ T	**4.12** **	S ≠ T	**7.82*** **	S ≠ T	**10.09*** **	S ≠ T	**1.88*** **	S ≠ T
River*Land use	**21.30*** **	ALL	**24.18** **	ALL	**16.87*** **	ALL	**15.27*** **	ALL	**19.16*** **	ALL
Eerste River										
Land use	**13.56** **	ALL	**6.09*** **	ALL	**23.35*** **	ALL	**14.51*** **	ALL	**16.83** **	ALL
Alien cover	1.23		1.20		1.73		0.20		0.79	
Vegetation height	**3.17** **	S ≠ M	0.85		**4.20** **	S ≠ M	**5.14** **	S ≠ M	**4.65* **	S ≠ M
Lourens River										
Land use	**28.8*** **	ALL	**17.90*** **	ALL	**38.10*** **	ALL	**18.76*** **	ALL	**34.46*** **	ALL
Alien cover	**3.18** **	H ≠ L, M	**2.21* **	H ≠ L	**4.13*** **	H ≠ L, M	**2.55* **	H ≠ L, M	**2.59* **	H ≠ L, M
Vegetation height	0.90		1.18		1.92		1.81		1.86	
Palmiet River										
Land use	**24.75*** **	ALL	**31.95*** **	ALL	**27.79*** **	ALL	**20.05*** **	ALL	**19.79*** **	ALL
Alien cover	1.13		1.05		1.51		**2.47* **	H ≠ L	1.72	
Vegetation height	**9.39*** **	S ≠ T	**5.17*** **	S ≠ T	**10.87*** **	S ≠ T	**15.15*** **	S ≠ M, T	**10.34*** **	S ≠ T

S = short; M = medium; T = tall; L = low; H = high
* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

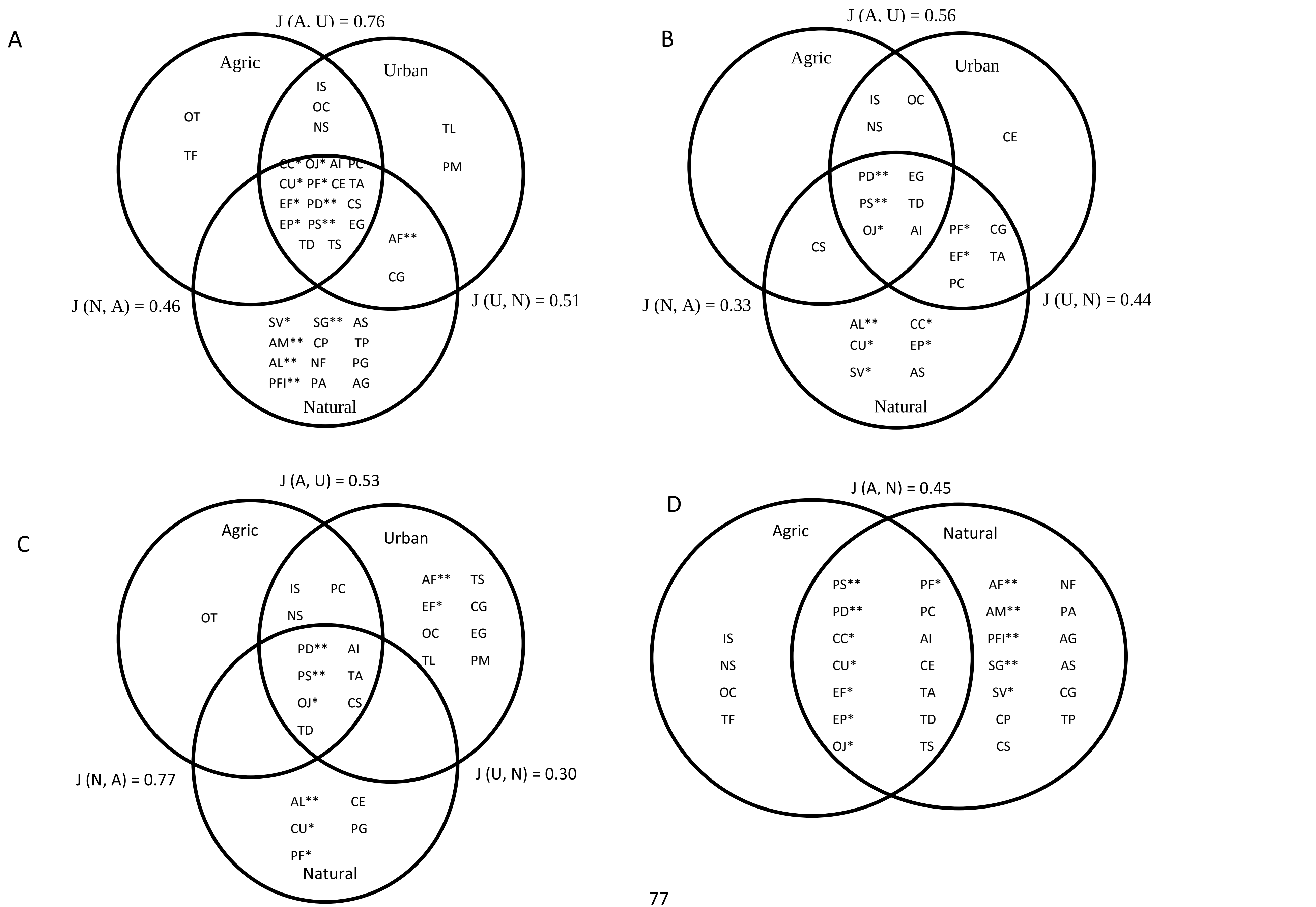

Figure 3. Venn diagrams and Jaccard's similarity index values of dragonfly species shared between land use types for A) combined rivers, B) Eerste River, C) Lourens River and D) Palmiet River. * = CFR endemic; ** = South African endemic. Species names for abbreviations are given in Appendix 1

Discussion

I aimed to investigate the effects of agriculture and urban land transformation on dragonfly assemblages, notably on the endemic species, in the Cape Floristic Region. Dragonfly assemblages were significantly influenced by landscape transformation, with endemic species commonly found in more natural areas and largely excluded from transformed areas. Widespread, habitat generalists were prevalent in transformed landscapes. This impact on rare and endemic species highlights the importance of correct management along CFR rivers for dragonfly biodiversity. If actions are not put in place to manage rivers, numerous taxa stand the chance of becoming locally extinct in the near future (Pressey et al., 2003). Rivers that are known to contain numerous sensitive and rare species, such as the Palmiet River identified here, should be considered conservation priorities.

Dragonfly assemblages in the agricultural and urban areas were more similar to each other than to assemblages in the untransformed areas, which is expected when habitats become homogenized (Olden & Rooney, 2006). Landscape transformation destroys natural riparian vegetation and creates a homogeneous environment, which reduces species diversity (Samways & Steytler, 1996). In this case, homogenization of riparian vegetation was in the form of replacement of natural, low- to medium growing natural riparian communities by tall alien invasive trees in agricultural areas and exotic aesthetic trees in the urban areas. Dragonfly assemblages also reflected the type of transformation, with each land use having a characteristic species assemblage. The influence of geomorphological zones in shaping dragonfly communities is a factor that cannot be ignored. Although both transformation types homogenized and decreased river system quality, slight differences in the severity of the impact were present. For example, agricultural transformation decreased river ecosystem quality through various processes such as over abstraction of water, pollution in the form of agricultural products, effluent discharge, and disturbances that result in river bank erosion, canalization and sedimentation (Allan, 2004). The level of impact of each of these will differ according to the specific land use category. This will result in a different range of biotopes and environmental variables associated with each land use category that are suited for specific assemblages of species (Samways & Steytler, 1996). This not only confirms the use of dragonflies as good indicators of the condition of aquatic and terrestrial ecosystems but also their potential use to reflect the type and intensity of landscape transformation (Sahlen & Ekestubbe, 2001).

Another important result of this study was that each river comprised distinct species assemblages. This validates the importance of conserving individual rivers in the CFR to prevent the extinction of rare species that may be confined to a single river. For example, the Palmiet River flows through the Kogelberg Biosphere Reserve (KBR) and had its own dragonfly assemblage. It also had a much higher species richness and abundance than the other two rivers. This included the presence of three national endemics and seven other dragonfly species that were absent from all other rivers assessed. As dragonflies are seen as umbrella species, their persistence likely reflects the conservation of other taxa (Noss, 1990). Furthermore, my results emphasize that it is crucial to conserve the natural remnant areas of rivers that are rich in endemic taxa.

Land transformation along the Palmiet River severely negatively affected dragonfly diversity. Nine of the ten unique species recorded in this river only occurred at sites within the core (natural) zone. The core zone of biosphere reserves (in this case the Kogelberg Biosphere Reserve (KBR)) are shielded from human interference (Simaika & Samways, 2009b). This emphasizes the importance of excluding high-impact, anthropogenic influences and maintaining pristine areas in order to conserve crucial source habitat for unique species. Despite this, I recorded some national and CFR endemics in the agricultural sites of the Palmiet River but these were absent in the transformed sites of the Eerste and Lourens Rivers. Agricultural areas in the Palmiet River sampled here fell within the buffer and transitional zones of the KBR reserve that is in close proximity to the core zone and to other protected areas such as the Hottentots-Holland Nature Reserve. Buffer and transition zones are designed to cushion the impact of the surrounding anthropogenic influences and improve the quality of the core zone (Simaika & Samways, 2009b). The effectiveness of this cushioning effect depends on the availability of suitable habitat, gradient of change between the areas, as well as the mobility of the individual species (Smith et al., 2001). Mobile organisms, such as dragonflies, seem to be able to easily disperse between core zones and other zones in this reserve. Even though anthropogenic influences in the buffer and transition zones make these areas unsuitable for some specialist dragonfly species, diversity in landscapes often leads to overall increased species richness (Grant & Samways, 2011). By creating diversity in biotopes (in the form of different land uses), habitat for an additional four species, that are not associated with natural sites, has been created. Although they were all widespread, generalist species they increased the dragonfly compositional biodiversity of the reserve.

Changes in dragonfly assemblages from those consisting of many threatened, sensitive, habitat specialists to assemblages consisting of mostly widespread, eurytopic individuals were also fairly accurately reflected in the DBI scores of the various land use categories (Simaika & Samways, 2009a). As expected, DBI scores were always lower in transformed landscapes compared to more natural areas. This indicates the effectiveness of this index for identifying priority sites for conservation action. The DBI, in some instances, could also distinguish between the severity of the impact on particular river sections. For example, in the Eerste River, urban sites had a higher mean DBI score than agricultural sites, as is expected from the added impacts of the urban and agricultural transformations. This indicates that this measure could be useful as measure of ecological integrity and useful for prioritizing conservation sites in the CFR (Simaika & Samways, 2009b). However, the DBI was not able to detect significant differences between the mean scores for natural and urban sites in the Eerste River, even though numerous endemic taxa were lost in these highly transformed areas.

Comparisons of dragonfly assemblages of these areas revealed significant differences. The use of the DBI alone should therefore not be the sole tool used for evaluation of habitat integrity in CFR rivers. Similarly, habitat transformation did not always lead to a decrease in species richness. Species with narrow geographical ranges (endemics) usually have more specific habitat requirements, are generally the most sensitive to disturbance and at risk of becoming extinct at disturbed sites (Simaika & Samways, 2009b). These sensitive species seem to be replaced by widespread, eurytopic species in CFR rivers, which leads to non-significant changes in species richness. Therefore, species richness alone is also not a good indicator of ecosystem integrity and other measures such as assemblage compositional changes should be included in thorough evaluations.

Implications for riparian management

My results show that CFR rivers may each have their own unique dragonfly assemblages. This has also been found for other benthic macroinvertebrate fauna and this individuality of rivers is termed "catchment signature" (King & Schael, 2001; Samways et al., 2011). Western Cape Rivers are extremely heterogeneous and renowned for their large species turnover between catchments (Samways et al., 2011). This spatial distinctness results from the typical high level of endemism in the region combined with a long history of climatic and geological stability and the isolation of individual catchments (King & Schael, 2001; Wishart et al., 2003; Samways et al., 2011). This means that every river is important for maintaining dragonfly diversity and the high levels of endemism in the CFR. Conservation priorities and requirements need to be identified to suit the needs of individual rivers. Another clear finding was that the Palmiet River is important for numerous endemic species. It had a unique dragonfly assemblage and a notably high species richness and abundance. It forms an important part of the KBR, which was designed to protect the high plant diversity of the area yet it also maintains an irreplaceable dragonfly assemblage. This reiterates the importance of biosphere reserves for protecting an array of taxa. The proclamation of more biosphere reserves in the CFR, that include other river catchments, will allow for the conservation of more rare and endemic dragonflies and other taxa. Biosphere reserves opposed to conservation areas consider the needs of the surrounding communities by incorporating buffer and transition zones into planning to allow for agricultural and urban development. Monitoring these zones, particularly the buffer zone, will effectively cushion the core zone and minimize the biodiversity losses that could result from intensive development practices in unmanaged regions outside conservation areas.

Dragonfly assemblages here were negatively affected by landscape transformation. Dragonfly assemblages became more similar in areas where agricultural and urban developments are present. Biotic homogenization occurred due to a loss of unique species and the persistence and introduction of generalist, eurytopic species. Landscape transformation severely impacted both CFR and national endemic species. Dragonfly assemblages were able to reflect differences in the type of anthropogenic interference, more so than the DBI. The value of dragonflies as bioindicators in the CFR is clear and the general accuracy of the DBI for assessing habitat integrity confirmed this. This rapid, easy to use method should be used in monitoring for rapidly assessing the severity of landscape transformations along individual rivers, although for more reliable assessments, a detailed account of which species were gained or lost from the focal system should also be included.

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Chapter 4: Conclusion

My study identified the crucial need to conserve as many individual rivers in the CFR as possible. Each of the studied rivers had its own specific dragonfly assemblage. Furthermore, to maintain the high dragonfly diversity in the region, appropriate, river-specific management applications are vital (Chapter 2). This means that the identification of separate conservation management requirements are even necessary for rivers which are in close proximity to each other and have similar environmental characteristics, such as the Eerste and Lourens Rivers. All three rivers studied here fall within biosphere reserves and their unique communities validate the success of these reserves. The proclamation of more biosphere reserves that incorporate other river systems would be beneficial for additional, sensitive dragonfly species, other endemic taxa and also for the security of water resources in the CFR.

Dragonflies are a well-studied group of insects and numerous studies have defined their relationships with various environmental variables (Clark & Samways, 1996; Catling, 2005; Kietzka et al., 2015). The majority of these studies suggest that the main factors that influence dragonfly assemblages comprise a range of vegetation-related characteristics (Corbet, 1999; Samways & Taylor, 2004; Samways & Sharratt, 2010). As a result, numerous studies suggest that restoration of natural riparian vegetation is the main requirement needed to conserve ecosystem integrity and dragonfly diversity (Mabry & Dettman, 2010; Magoba & Samways, 2010; Samways & Sharrat, 2010; Adams, 2011). Similarly, this study also found that certain vegetation characteristics are important, but usually only when the river ran through transformed landscapes (Chapter 3). In the natural, untransformed river reaches, heterogeneity of water parameters were the primary drivers of dragonfly assemblages (Chapter 2). These variables included dissolved oxygen, pH, water temperature and conductivity. Previous studies may not have identified the importance of these water parameters because they included effects related to anthropogenic disturbances, which override the more subtle, natural variability in water parameters. Female dragonflies select suitable nurseries largely based on visual cues but the water conditions are more likely to be suitable at sites close to where they successfully survived the larval stage of their life cycles (Watson et al., 1982).

In undisturbed reaches, water parameters were also important for driving dragonfly species richness, which was positively correlated with dissolved oxygen and negatively correlated with pH (Chapter 2). These conditions (increased oxygen levels and lower pH) are characteristics usually associated with more pristine areas. Therefore, natural areas with these features should be conservation priorities. Another clear result was that the Palmiet River is important for numerous endemic species (Chapter 2). It had a unique dragonfly assemblage and an unusually high species richness and abundance. The major difference of this river compared to the other rivers was that the natural sites occurred at the lower reaches, where water temperatures were comparably warmer. Water temperature was positively correlated with species richness. Since water temperature is typically higher in lower reaches of rivers, this reiterates the importance of correctly managing historic, downstream sections by avoiding anthropogenic activities that may negatively influence variability in water parameters.

Dragonfly assemblages successfully reflected differences in the land transformation types (Chapter 3). This agrees with previous results that suggest that dragonfly assemblages along rivers experiencing various anthropogenic disturbances can successfully reflect differences in biotopes (Bulankova, 1997). The value of using dragonflies as bioindicators in the CFR was clarified, and the general accuracy of the DBI for assessing ecosystem integrity confirmed this result. The DBI, used in combination with a detailed account of the species introduced or lost from the focal system, should be used in conservation planning to successfully and rapidly assess the severity of disturbances along rivers.

In transformed river sections, although alien vegetation cover and vegetation height were important factors for dragonfly assemblages, neither were nearly as influential as the negative effects of land transformation (Chapter 3). Dragonfly assemblages became more similar in areas where agricultural and urban developments were present (Chapter 3). This biotic homogenization occurred due to a loss of unique species and the persistence and colonization by generalist, eurytopic species. Anthropogenic disturbances also influence river ecosystem function, such as the effects of runoff on water quality and chemistry. For dragonflies this results in unsuitable habitat conditions for the terrestrial and aquatic stages of their life cycles. Transformation of land decreases habitat heterogeneity. For example, riparian vegetation can be readily replaced by tall alien invasive plant species such as Australian *Acacia* species. In production landscapes, management recommendations for riparian zones all suggest the rehabilitation of riparian vegetation as the primary requirement for restoring ecosystem integrity (Dallas & Day, 1993). Although the presence of alien vegetation was important, my study showed vegetation height had a greater influence. A dragonfly would probably not be able to differentiate between which plants are alien invasive species and which are not (Samways, 2003). The influence of alien invasive species and vegetation height is likely due to the sensitivity of dragonflies to shading and a loss of habitat heterogeneity when tall, alien invasive trees dominate riparian zones and prevent the establishment of under story plants (Samways & Taylor, 2004; Samways et al., 2005; Remsburg et al., 2008; Magoba & Samways, 2010; Samways & Sharratt, 2010). Some riparian zones have been so degraded that restoration of riparian vegetation is not possible. However, the removal of alien invasive plant species and by providing vegetation cover that is structurally similar to the absent natural riparian vegetation could restore habitat heterogeneity as experienced by dragonflies (Holmes et al., 2008).

Successfully restored riparian vegetation along a river within a transformed landscape may appear to harbour a healthy ecosystem that can maintain a diverse dragonfly assemblage. However, as my results show, the detrimental effects caused by transformation may be so severe that they direct attention away from other crucial parameters that are needed to maintain high dragonfly diversity (Chapter 3). For dragonflies in the undisturbed reaches of CFR rivers, heterogeneity of water parameters were the most important variables. It can thus be assumed that in order to conserve the unique dragonfly diversity of the CFR, conservation actions should also focus on heterogeneity of water parameters (Chapter 2). Agricultural and urban developments have numerous, drastic effects on water quality. For example runoff, pollution and over extraction of rivers all alter chemical components of the water in these systems. Dragonflies have life cycles that depend on terrestrial and aquatic life stages. Therefore, to ensure their persistence, conditions need to be suitable in both habitat types. I therefore endorse the use of dragonfly assemblages and the DBI in future river quality monitoring programmes.

In transformed landscapes it would prove extremely difficult to achieve near pristine riparian zones. Despite this, sustainable transformation practices such as organic fertilizers, extraction restrictions; no-till farming and the inclusion of buffer zones would promote a healthier ecosystem and allow for the survival of some rare, endemic dragonfly species. Additionally, to maintain the dragonfly diversity in the CFR conservation requirements should be determined for individual rivers and with the formation of additional biosphere reserves. Ultimately, this study suggests the crucial role of habitat heterogeneity for sustaining dragonfly diversity in transformed landscapes (Chapter 2). Transformation homogenizes various ecosystem components and reduces habitat integrity (Chapter 3). Future planning for biodiversity conservation within production landscapes should therefore account for the importance of maintaining heterogeneity in all its natural forms.

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Appendix 1. Species list of dragonflies recorded at the study sites

Letters represent land use types dragonflies occurred at A = agriculture, U = urban, N = natural

Scientific name	Species code	Range	DBI	Eerste River	Lourens River	Palmiet River
Suborder ZYGOPTERA						
Family CHLOROCYPHIDAE						
Platycypha fitzsimonsi fitzsimonsi	PFI	**	4			N
Family SYNLESTIDAE						
Chlorolestes conspicuus	CC	*	7	N		A, N
Chlorolestes umbratus	CU	*	7	N	N	A, N
Ecchlorolestes peringueyi	EP	*	7	N		A, N
Family PROTONURIDAE						
Elattoneura glauca	EG	****	1	A, U, N	U	
Elattoneura frenulata	EF	*	5	U, N	U	A, N
Family PLATYCNEMIDIDAE						
Allocnemis leucosticta	AL	**	5	N	N	
Family COENAGRIONIDAE						
Ceriagrion glabrum	CG	****	0	U, N	U	N
Pseudagrion draconis	PD	**	4	A, U, N	A, U, N	A, N
Pseudagrion furcigerum	PF	*	7	U, N	N	A, N
Pseudagrion massaicum	PM	****	1		U	
Africallagma glaucum	AG	****	1			N
Agriocnemis falcifera	AF	**	4		U	N
Ischnura senegalensis	IS	****	0	A, U	A, U	A
Suborder ANISOPTERA						
Family AESHNIDAE						
Zosteraeschna minuscula	AM	**	5			N
Pinheyschna subpupillata	PS	**	4	A, U, N	A, U , N	A, N
Anax imperator	AI	****	1	A, U, N	A, U , N	A, N
Anax speratus	AS	****	2	N		N
Family GOMPHIDAE						
Ceratogomphus pictus	CP	****	2			N
Paragomphus cognatus	PC	****	1	U, N	A, U	A, N
Paragomphus genei	PG	****	3		N	
Family CORDULIIDAE						
Syncordulia gracilis	SG	**	7			N
Syncordulia venator	SV	*	7	N		N
Family LIBELLULIDAE						
Orthetrum julia capicola	OJ	*	4	A, U, N	A, U, N	A, N
Orthetrum caffrum	OC	****	3	A, U	U	A
Orthetrum trinacria	OT	****	1		A	
Nesciothemis farinosa	NF	****	1			N
Crocothemis erythraea	CE	****	0	U	N	A, N
Crocothemis sanguinolenta	CS	****	3	A,N	A, U, N	N
Trithemis arteriosa	TA	****	0	U, N	A, U, N	A, N
Trithemis dorsalis	TD	****	0	A, U, N	A, U, N	A, N
Trithemis furva	TF	****	1			A
Trithemis pluvialis	TP	****	2			N
Trithemis stictica	TS	****	1		U	A, N
Zygonyx natalensis	NS	****	2	A, U	A, U	A
Pantala flavescens	PA	****	0			N
Tramea limbata	TL	****	0		U	

Levels of endemism
* Endemic to Cape Floristic Region
** Endemic to South Africa
*** Endemic to southern Africa
**** Widespread species in Africa

Appendix 2. Detailed descriptions of rivers used in study

The source of the Eerste River lies at 530 m asl in the Jonkershoek Nature Reserve, Western Cape Province, South Africa (34° 0' 28.1952"S; 19° 0' 6.4656"E). It is approximately 40 km long, with a catchment area of 420 km^2. The first 6 km of river is mostly undisturbed and surrounded by natural fynbos vegetation. The river is impounded by the Kleinplaas Dam, which regulates the upper reaches of the river. During summer, a municipal weir situated above the dam directs the river into the Ida's Valley Dam, which supplies water to Stellenbosch (Brown & Magoba, 2009). The river then flows through a few kilometres of vineyards and through the town of Stellenbosch. This section has undergone considerable canalization over the years, which has resulted in steep, bare river banks and the replacement of indigenous riparian trees by English oaks (*Quercus robur*) and other alien taxa (Brown & Magoba, 2009). Just past Stellenbosch, the Eerste River merges with the Blouklippen River after which it flows through numerous farms (mostly vineyards), where water is extracted and also polluted by agricultural runoff (Thomas & Ayuk, 2010). Treated municipal effluent flows into the river through the Veldwagters tributary. It then merges with Kuils River just before it passes through the small town of Macassar and meets the Atlantic Ocean in False Bay (Meek et al., 2013).

The Lourens River originates at an elevation of 1110 m a.s.l, within the Hottentots Holland Nature Reserve, Western Cape, South Africa (34° 0' 56.9016"S; 18° 58' 42.5424"E). It acts as the boundary separating two large wine farms, Lourensford and Vergelegen. The river is approximately 20 km in length with a catchment area of about 92 km^2. The upper reaches are relatively pristine, except for a few commercial plantations (Dabrowski et al., 2002). Not far from its source, the natural fynbos is replaced by agriculture, which consists predominantly of vineyards and orchards. This section is exposed to intensive farming and the water is extracted and polluted by chemical residues from pesticides and fertilizers (Schulz, 2001). A large portion of the natural riparian vegetation has been replaced by alien invasive species. The alien species, in combination with forestry plantations significantly, reduce river flow, especially during summer. Hereafter, the river's course runs through the large suburban town of Somerset West. The water in these lower reaches is of a poor quality, which is made worse by the impacts of alien willow trees (*Salix babylonica*), gabions and infilling. The river continues through to the small seaside town of Strand, where if forms a small estuary before discharging into False Bay (Dabrowski et al., 2002). Both the Eerste and Lourens rivers fall within the recently established Cape Winelands Biosphere Reserve.

The Palmiet River forms an important part of the Kogelberg Biosphere Reserve. Its source occurs at 1010 m a.s.l within the Hottentots Holland Nature Reserve, Western Cape Province, South Africa (34° 3' 24.9516"S; 19° 0' 48.5244"E). It is approximately 70 km in length, is fed by numerous streams and drains a catchment area of 500 km² (Grant, 2005). The river falls rapidly over the first couple of kilometres as it flows through orchards and forestry plantations. About four kilometres from its source, it flows into the Elgin Valley, where it is impounded by the Eikenhof and Nuweberg dams. From here it travels between more agricultural land and is severely degraded by the time it passes through the small town of Grabouw. After another stretch of farmed land (orchards and vineyards) the river is impounded by three large in-channel dams; the Kogelberg, Appelthwaite and Arieskraal dams (Dawson, 2003). The Kogelberg Dam differs from the others because it is operated according to recommended in-stream flow requirements and aims to imitate natural environmental conditions. It thus reduces the effects of flow patterns on the river as well as reducing eutrophication, due to runoff, by minimizing the quantities of hydride and salts of nitrogen that enter the lower reaches of the river (Dawson, 2003). Downstream of the Arieskraal Dam, the river is joined by the Klein Palmiet River and after six kilometres exits the Elgin Valley. Water quality drastically improves in its lower reaches before reaching the Palmiet Estuary (Dawson, 2003). This is largely as a result of the high quality water that enters the Palmiet River from the Louws and Dwars rivers (Dawson, 2003). This section falls within the core zone of the biosphere reserve and is protected from major anthropogenic disturbances. The narrow coastal plain is situated in a valley and causes the Palmiet River to change from a mountain stream to an estuary with no intervening stretch. This is known as a “South Cape acid river” and is typical of lower rivers and different from both the Eerste and Lourens rivers (Noble & Hemens, 1978).

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Appendix 3. Correlations between environmental variables for CCAs

A) overall Odonata, B) Anisoptera, C) Zygoptera, D) Eerste River, E) Lourens River, F) Palmiet River

A)

	Lourens	Palmiet	Eerste R	WatrTemp	Conductv	DissOxyg	PH	Altitiud	%Shade	%Debris	%Rock	%Sand	%AlieCo	%IndiCo	AvgVegHe	IndgTree	AlieTree	IndgShrb	AlieShrb	IndgGras	AlieGras	AquaMacr	PSerrt
Lourens	1.00	-0.54	-0.16	-0.56	-0.51	0.00	-0.39	0.51	0.24	0.00	0.50	-0.15	0.33	-0.03	0.07	0.14	0.09	-0.16	0.02	0.05	0.27	0.21	-0.28
Palmiet	-0.54	1.00	-0.75	0.85	0.92	-0.05	0.27	-0.98	-0.40	0.13	-0.93	0.28	-0.08	0.02	-0.28	-0.27	0.07	0.24	0.05	0.16	-0.14	-0.31	0.47
Eerste R	-0.16	-0.75	1.00	-0.55	-0.67	0.07	-0.02	0.75	0.27	-0.15	0.70	-0.21	-0.16	-0.01	0.27	0.20	-0.15	-0.16	-0.07	-0.22	-0.04	0.20	-0.33
WatrTemp	-0.56	0.85	-0.55	1.00	0.92	-0.39	-0.11	-0.85	-0.36	0.05	-0.79	0.23	-0.11	-0.03	-0.26	-0.24	0.03	0.22	0.02	0.12	-0.13	-0.26	0.48
Conductv	-0.51	0.92	-0.67	0.92	1.00	-0.35	0.00	-0.89	-0.32	0.09	-0.85	0.24	-0.06	0.00	-0.24	-0.21	0.07	0.20	0.04	0.21	-0.14	-0.29	0.38
DissOxyg	0.00	-0.05	0.07	-0.39	-0.35	1.00	0.82	0.03	-0.01	-0.18	0.06	-0.15	0.00	0.19	0.04	-0.07	0.00	0.01	0.02	-0.28	0.01	-0.12	0.03
PH	-0.39	0.27	-0.02	-0.11	0.00	0.82	1.00	-0.27	-0.12	-0.06	-0.25	0.04	-0.13	0.10	-0.03	-0.10	-0.02	0.06	0.03	-0.14	-0.16	-0.16	0.15
Altitiud	0.51	-0.98	0.75	-0.85	-0.89	0.03	-0.27	1.00	0.44	-0.11	0.92	-0.26	0.02	-0.02	0.28	0.28	-0.11	-0.24	-0.05	-0.15	0.10	0.30	-0.54
%Shade	0.24	-0.40	0.27	-0.36	-0.32	-0.01	-0.12	0.44	1.00	-0.07	0.36	-0.27	0.08	0.28	0.40	0.35	0.14	-0.30	0.03	0.00	-0.05	-0.03	-0.64
%Debris	0.00	0.13	-0.15	0.05	0.09	-0.18	-0.06	-0.11	-0.07	1.00	-0.20	0.36	-0.11	-0.38	-0.29	0.19	-0.21	-0.10	0.09	0.53	0.05	0.33	0.11
%Rock	0.50	-0.93	0.70	-0.79	-0.85	0.06	-0.25	0.92	0.36	-0.20	1.00	-0.24	0.03	-0.02	0.30	0.14	-0.13	-0.18	0.05	-0.25	0.12	0.23	-0.45
%Sand	-0.15	0.28	-0.21	0.23	0.24	-0.15	0.04	-0.26	-0.27	0.36	-0.24	1.00	-0.18	-0.30	-0.08	-0.17	-0.19	-0.03	0.07	0.18	-0.05	0.22	0.07
%AlieCo	0.33	-0.08	-0.16	-0.11	-0.06	0.00	-0.13	0.02	0.08	-0.11	0.03	-0.18	1.00	0.08	0.15	0.20	0.69	0.09	0.17	0.08	0.48	-0.10	0.05
%IndiCo	-0.03	0.02	-0.01	-0.03	0.00	0.19	0.10	-0.02	0.28	-0.38	-0.02	-0.30	0.08	1.00	0.56	-0.07	0.23	-0.19	-0.02	-0.50	-0.12	-0.50	-0.30
AvgVegHe	0.07	-0.28	0.27	-0.26	-0.24	0.04	-0.03	0.28	0.40	-0.29	0.30	-0.08	0.15	0.56	1.00	0.31	0.29	-0.22	-0.06	-0.31	-0.07	-0.34	-0.54
IndgTree	0.14	-0.27	0.20	-0.24	-0.21	-0.07	-0.10	0.28	0.35	0.19	0.14	-0.17	0.20	-0.07	0.31	1.00	0.19	-0.20	0.13	0.25	0.04	0.17	-0.21
AlieTree	0.09	0.07	-0.15	0.03	0.07	0.00	-0.02	-0.11	0.14	-0.21	-0.13	-0.19	0.69	0.23	0.29	0.19	1.00	0.07	-0.14	-0.10	-0.04	-0.22	-0.03
IndgShrb	-0.16	0.24	-0.16	0.22	0.20	0.01	0.06	-0.24	-0.30	-0.10	-0.18	-0.03	0.09	-0.19	-0.22	-0.20	0.07	1.00	-0.04	0.06	0.04	0.06	0.16
AlieShrb	0.02	0.05	-0.07	0.02	0.04	0.02	0.03	-0.05	0.03	0.09	0.05	0.07	0.17	-0.02	-0.06	0.13	-0.14	-0.04	1.00	0.15	-0.03	-0.16	0.15
IndgGras	0.05	0.16	-0.22	0.12	0.21	-0.28	-0.14	-0.15	0.00	0.53	-0.25	0.18	0.08	-0.50	-0.31	0.25	-0.10	0.06	0.15	1.00	0.11	0.30	0.10
AlieGras	0.27	-0.14	-0.04	-0.13	-0.14	0.01	-0.16	0.10	-0.05	0.05	0.12	-0.05	0.48	-0.12	-0.07	0.04	-0.04	0.04	-0.03	0.11	1.00	0.12	0.04
AquaMacr	0.21	-0.31	0.20	-0.26	-0.29	-0.12	-0.16	0.30	-0.03	0.33	0.23	0.22	-0.10	-0.50	-0.34	0.17	-0.22	0.06	-0.16	0.30	0.12	1.00	0.01
PSerrt	-0.28	0.47	-0.33	0.48	0.38	0.03	0.15	-0.54	-0.64	0.11	-0.45	0.07	0.05	-0.30	-0.54	-0.21	-0.03	0.16	0.15	0.10	0.04	0.01	1.00

B)

	Lourens	Palmiet	Eerste R	WatrTemp	Conductv	DissOxyg	PH	Altitiud	%Shade	%Debris	%Rock	%Sand	%AlieCo	%IndiCo	AvgVegHe	IndgTree	AlieTree	IndgShrb	AlieShrb	IndgGras	AlieGras	AquaMacr	PSerrt
Lourens	1.00	-0.52	-0.10	-0.53	-0.48	-0.04	-0.26	0.49	0.18	0.00	0.47	-0.12	0.34	-0.05	0.05	0.12	0.08	-0.10	0.04	0.05	0.30	0.19	-0.23
Palmiet	-0.52	1.00	-0.79	0.80	0.88	0.02	0.23	-0.98	-0.38	0.12	-0.91	0.24	-0.08	-0.01	-0.28	-0.23	0.03	0.24	0.05	0.15	-0.16	-0.27	0.45
Eerste R	-0.10	-0.79	1.00	-0.56	-0.68	0.01	-0.08	0.80	0.31	-0.14	0.73	-0.19	-0.14	0.05	0.29	0.18	-0.09	-0.21	-0.08	-0.21	-0.03	0.18	-0.36
WatrTemp	-0.53	0.80	-0.56	1.00	0.91	-0.40	-0.26	-0.80	-0.32	0.02	-0.72	0.19	-0.11	-0.05	-0.23	-0.21	0.00	0.19	0.01	0.10	-0.14	-0.22	0.43
Conductv	-0.48	0.88	-0.68	0.91	1.00	-0.35	-0.12	-0.85	-0.28	0.06	-0.80	0.19	-0.05	-0.03	-0.22	-0.17	0.04	0.18	0.05	0.22	-0.14	-0.24	0.34
DissOxyg	-0.04	0.02	0.01	-0.40	-0.35	1.00	0.87	-0.04	-0.04	-0.16	-0.01	-0.14	0.00	0.21	0.02	-0.08	0.01	0.03	0.02	-0.28	0.00	-0.15	0.08
PH	-0.26	0.23	-0.08	-0.26	-0.12	0.87	1.00	-0.23	-0.08	-0.05	-0.21	0.00	-0.09	0.11	-0.04	-0.08	0.00	0.05	0.01	-0.14	-0.14	-0.14	0.12
Altitiud	0.49	-0.98	0.80	-0.80	-0.85	-0.04	-0.23	1.00	0.41	-0.08	0.90	-0.21	0.03	0.00	0.27	0.24	-0.07	-0.23	-0.05	-0.12	0.12	0.27	-0.51
%Shade	0.18	-0.38	0.31	-0.32	-0.28	-0.04	-0.08	0.41	1.00	-0.05	0.33	-0.26	0.12	0.29	0.41	0.36	0.21	-0.27	0.02	0.05	-0.03	-0.02	-0.63
%Debris	0.00	0.12	-0.14	0.02	0.06	-0.16	-0.05	-0.08	-0.05	1.00	-0.20	0.37	-0.13	-0.42	-0.29	0.21	-0.25	-0.15	0.11	0.57	0.04	0.36	0.12
%Rock	0.47	-0.91	0.73	-0.72	-0.80	-0.01	-0.21	0.90	0.33	-0.20	1.00	-0.18	0.02	0.01	0.30	0.08	-0.11	-0.17	0.08	-0.26	0.13	0.18	-0.42
%Sand	-0.12	0.24	-0.19	0.19	0.19	-0.14	0.00	-0.21	-0.26	0.37	-0.18	1.00	-0.21	-0.35	-0.05	-0.15	-0.22	-0.03	0.05	0.16	-0.05	0.28	0.01
%AlieCo	0.34	-0.08	-0.14	-0.11	-0.05	0.00	-0.09	0.03	0.12	-0.13	0.02	-0.21	1.00	0.11	0.16	0.22	0.71	0.08	0.14	0.09	0.44	-0.14	0.01
%IndiCo	-0.05	-0.01	0.05	-0.05	-0.03	0.21	0.11	0.00	0.29	-0.42	0.01	-0.35	0.11	1.00	0.56	-0.05	0.23	-0.14	-0.01	-0.53	-0.11	-0.53	-0.32
AvgVegHe	0.05	-0.28	0.29	-0.23	-0.22	0.02	-0.04	0.27	0.41	-0.29	0.30	-0.05	0.16	0.56	1.00	0.31	0.29	-0.20	-0.07	-0.31	-0.06	-0.35	-0.60
IndgTree	0.12	-0.23	0.18	-0.21	-0.17	-0.08	-0.08	0.24	0.36	0.21	0.08	-0.15	0.22	-0.05	0.31	1.00	0.22	-0.21	0.14	0.28	0.04	0.14	-0.20
AlieTree	0.08	0.03	-0.09	0.00	0.04	0.01	0.00	-0.07	0.21	-0.25	-0.11	-0.22	0.71	0.23	0.29	0.22	1.00	0.08	-0.15	-0.09	-0.04	-0.24	-0.08
IndgShrb	-0.10	0.24	-0.21	0.19	0.18	0.03	0.05	-0.23	-0.27	-0.15	-0.17	-0.03	0.08	-0.14	-0.20	-0.21	0.08	1.00	-0.08	0.03	0.04	0.03	0.11
AlieShrb	0.04	0.05	-0.08	0.01	0.05	0.02	0.01	-0.05	0.02	0.11	0.08	0.05	0.14	-0.01	-0.07	0.14	-0.15	-0.08	1.00	0.17	-0.02	-0.16	0.13
IndgGras	0.05	0.15	-0.21	0.10	0.22	-0.28	-0.14	-0.12	0.05	0.57	-0.26	0.16	0.09	-0.53	-0.31	0.28	-0.09	0.03	0.17	1.00	0.10	0.34	0.08
AlieGras	0.30	-0.16	-0.03	-0.14	-0.14	0.00	-0.14	0.12	-0.03	0.04	0.13	-0.05	0.44	-0.11	-0.06	0.04	-0.04	0.04	-0.02	0.10	1.00	0.11	0.03
AquaMacr	0.19	-0.27	0.18	-0.22	-0.24	-0.15	-0.14	0.27	-0.02	0.36	0.18	0.28	-0.14	-0.53	-0.35	0.14	-0.24	0.03	-0.16	0.34	0.11	1.00	0.03
PSerrt	-0.23	0.45	-0.36	0.43	0.34	0.08	0.12	-0.51	-0.63	0.12	-0.42	0.01	0.01	-0.32	-0.60	-0.20	-0.08	0.11	0.13	0.08	0.03	0.03	1.00

C)

	Lourens	Palmiet	Eerste R	WatrTemp	Conductv	DissOxyg	PH	Altitiud	%Shade	%Debris	%Rock	%Sand	%AlieCo	%IndiCo	AvgVegHe	IndgTree	AlieTree	IndgShrb	AlieShrb	IndgGras	AlieGras	AquaMacr	PSerrt
Lourens	1.00	-0.52	-0.24	-0.57	-0.52	0.07	-0.53	0.50	0.28	0.01	0.49	-0.17	0.33	0.01	0.09	0.16	0.12	-0.20	0.00	0.06	0.24	0.22	-0.31
Palmiet	-0.52	1.00	-0.70	0.89	0.94	-0.19	0.28	-0.98	-0.39	0.14	-0.95	0.32	-0.08	0.04	-0.30	-0.31	0.10	0.25	0.05	0.17	-0.13	-0.35	0.47
Eerste R	-0.24	-0.70	1.00	-0.53	-0.64	0.16	0.12	0.70	0.21	-0.17	0.67	-0.22	-0.19	-0.05	0.26	0.22	-0.21	-0.11	-0.05	-0.25	-0.06	0.21	-0.28
WatrTemp	-0.57	0.89	-0.53	1.00	0.93	-0.43	0.04	-0.89	-0.38	0.09	-0.84	0.28	-0.11	-0.03	-0.30	-0.28	0.06	0.24	0.03	0.14	-0.13	-0.29	0.52
Conductv	-0.52	0.94	-0.64	0.93	1.00	-0.42	0.09	-0.92	-0.33	0.12	-0.90	0.28	-0.07	0.02	-0.26	-0.26	0.10	0.22	0.04	0.22	-0.12	-0.33	0.40
DissOxyg	0.07	-0.19	0.16	-0.43	-0.42	1.00	0.71	0.18	0.06	-0.24	0.20	-0.18	-0.01	0.17	0.08	-0.03	-0.03	-0.04	0.02	-0.28	0.02	-0.07	-0.06
PH	-0.53	0.28	0.12	0.04	0.09	0.71	1.00	-0.27	-0.14	-0.10	-0.25	0.07	-0.20	0.08	-0.01	-0.11	-0.08	0.08	0.04	-0.13	-0.18	-0.18	0.15
Altitiud	0.50	-0.98	0.70	-0.89	-0.92	0.18	-0.27	1.00	0.45	-0.13	0.93	-0.31	0.01	-0.01	0.30	0.32	-0.14	-0.26	-0.06	-0.18	0.08	0.32	-0.55
%Shade	0.28	-0.39	0.21	-0.38	-0.33	0.06	-0.14	0.45	1.00	-0.09	0.37	-0.27	0.04	0.28	0.38	0.34	0.05	-0.33	0.04	-0.05	-0.06	-0.06	-0.64
%Debris	0.01	0.14	-0.17	0.09	0.12	-0.24	-0.10	-0.13	-0.09	1.00	-0.20	0.33	-0.07	-0.34	-0.27	0.16	-0.15	-0.02	0.05	0.48	0.07	0.29	0.08
%Rock	0.49	-0.95	0.67	-0.84	-0.90	0.20	-0.25	0.93	0.37	-0.20	1.00	-0.29	0.04	-0.04	0.31	0.21	-0.14	-0.20	0.03	-0.25	0.10	0.27	-0.46
%Sand	-0.17	0.32	-0.22	0.28	0.28	-0.18	0.07	-0.31	-0.27	0.33	-0.29	1.00	-0.14	-0.25	-0.12	-0.19	-0.14	-0.03	0.10	0.20	-0.05	0.15	0.14
%AlieCo	0.33	-0.08	-0.19	-0.11	-0.07	-0.01	-0.20	0.01	0.04	-0.07	0.04	-0.14	1.00	0.05	0.15	0.17	0.65	0.09	0.21	0.06	0.53	-0.05	0.10
%IndiCo	0.01	0.04	-0.05	-0.03	0.02	0.17	0.08	-0.01	0.28	-0.34	-0.04	-0.25	0.05	1.00	0.58	-0.09	0.21	-0.26	-0.04	-0.47	-0.13	-0.45	-0.30
AvgVegHe	0.09	-0.30	0.26	-0.30	-0.26	0.08	-0.01	0.30	0.38	-0.27	0.31	-0.12	0.15	0.58	1.00	0.31	0.28	-0.25	-0.05	-0.31	-0.09	-0.33	-0.48
IndgTree	0.16	-0.31	0.22	-0.28	-0.26	-0.03	-0.11	0.32	0.34	0.16	0.21	-0.19	0.17	-0.09	0.31	1.00	0.16	-0.18	0.11	0.20	0.04	0.19	-0.21
AlieTree	0.12	0.10	-0.21	0.06	0.10	-0.03	-0.08	-0.14	0.05	-0.15	-0.14	-0.14	0.65	0.21	0.28	0.16	1.00	0.07	-0.13	-0.11	-0.04	-0.20	0.02
IndgShrb	-0.20	0.25	-0.11	0.24	0.22	-0.04	0.08	-0.26	-0.33	-0.02	-0.20	-0.03	0.09	-0.26	-0.25	-0.18	0.07	1.00	0.02	0.09	0.05	0.10	0.22
AlieShrb	0.00	0.05	-0.05	0.03	0.04	0.02	0.04	-0.06	0.04	0.05	0.03	0.10	0.21	-0.04	-0.05	0.11	-0.13	0.02	1.00	0.13	-0.03	-0.15	0.16
IndgGras	0.06	0.17	-0.25	0.14	0.22	-0.28	-0.13	-0.18	-0.05	0.48	-0.25	0.20	0.06	-0.47	-0.31	0.20	-0.11	0.09	0.13	1.00	0.13	0.25	0.13
AlieGras	0.24	-0.13	-0.06	-0.13	-0.12	0.02	-0.18	0.08	-0.06	0.07	0.10	-0.05	0.53	-0.13	-0.09	0.04	-0.04	0.05	-0.03	0.13	1.00	0.12	0.06
AquaMacr	0.22	-0.35	0.21	-0.29	-0.33	-0.07	-0.18	0.32	-0.06	0.29	0.27	0.15	-0.05	-0.45	-0.33	0.19	-0.20	0.10	-0.15	0.25	0.12	1.00	-0.01
PSerrt	-0.31	0.47	-0.28	0.52	0.40	-0.06	0.15	-0.55	-0.64	0.08	-0.46	0.14	0.10	-0.30	-0.48	-0.21	0.02	0.22	0.16	0.13	0.06	-0.01	1.00

D)

	WatrTemp	Conductv	DissOxyg	Altitiud	%Shade	%Debris	%Rock	%Sand	%IndiCo	AvgVegHe	AlieTree	IndgShrb	AlieShrb	IndgGras	AquaMacr	PSerrt
WatrTemp	1.00	0.19	0.17	-0.59	-0.29	-0.04	-0.01	0.17	-0.52	-0.29	-0.16	0.05	0.09	0.09	0.14	0.64
Conductv	0.19	1.00	0.69	0.44	-0.02	0.15	0.21	-0.17	-0.04	-0.05	-0.23	0.41	-0.01	-0.07	-0.16	-0.22
DissOxyg	0.17	0.69	1.00	0.16	0.05	0.10	0.03	-0.05	0.06	0.10	-0.12	0.08	0.05	0.02	-0.15	-0.09
Altitiud	-0.59	0.44	0.16	1.00	0.07	0.31	0.29	-0.27	0.28	0.08	-0.31	0.44	-0.02	-0.15	-0.27	-0.62
%Shade	-0.29	-0.02	0.05	0.07	1.00	0.06	0.10	-0.04	0.45	0.32	0.55	-0.16	0.48	-0.15	-0.26	-0.42
%Debris	-0.04	0.15	0.10	0.31	0.06	1.00	0.00	-0.10	0.06	-0.09	-0.11	0.28	-0.10	0.12	-0.08	-0.31
%Rock	-0.01	0.21	0.03	0.29	0.10	0.00	1.00	-0.10	-0.09	-0.01	-0.20	0.47	0.09	-0.61	-0.14	-0.09
%Sand	0.17	-0.17	-0.05	-0.27	-0.04	-0.10	-0.10	1.00	-0.01	-0.20	-0.05	-0.31	-0.04	0.46	0.18	0.19
%IndiCo	-0.52	-0.04	0.06	0.28	0.45	0.06	-0.09	-0.01	1.00	0.68	0.44	-0.35	-0.07	-0.13	-0.31	-0.48
AvgVegHe	-0.29	-0.05	0.10	0.08	0.32	-0.09	-0.01	-0.20	0.68	1.00	0.45	-0.29	0.03	-0.19	-0.66	-0.14
AlieTree	-0.16	-0.23	-0.12	-0.31	0.55	-0.11	-0.20	-0.05	0.44	0.45	1.00	-0.36	-0.05	-0.11	-0.04	-0.25
IndgShrb	0.05	0.41	0.08	0.44	-0.16	0.28	0.47	-0.31	-0.35	-0.29	-0.36	1.00	0.14	-0.31	0.06	-0.09
AlieShrb	0.09	-0.01	0.05	-0.02	0.48	-0.10	0.09	-0.04	-0.07	0.03	-0.05	0.14	1.00	-0.10	-0.25	0.20
IndgGras	0.09	-0.07	0.02	-0.15	-0.15	0.12	-0.61	0.46	-0.13	-0.19	-0.11	-0.31	-0.10	1.00	0.07	0.24
AquaMacr	0.14	-0.16	-0.15	-0.27	-0.26	-0.08	-0.14	0.18	-0.31	-0.66	-0.04	0.06	-0.25	0.07	1.00	-0.03
PSerrt	0.64	-0.22	-0.09	-0.62	-0.42	-0.31	-0.09	0.19	-0.48	-0.14	-0.25	-0.09	0.20	0.24	-0.03	1.00

E)

	WatrTemp	Conductv	DissOxyg	PH	Altitiud	%Shade	%Debris	%Rock	%Sand	%AlieCo	%IndiCo	AvgVegHe	AlieTree	IndgShrb	AlieShrb	IndgGras	AlieGras	AquaMacr	PSerrt
WatrTemp	1.00	0.48	0.82	-0.88	0.13	0.08	-0.11	-0.02	-0.20	-0.09	-0.15	-0.22	-0.33	0.01	-0.08	0.19	0.18	0.00	0.01
Conductv	0.48	1.00	0.19	-0.23	0.25	0.26	-0.06	-0.14	-0.34	-0.33	-0.17	-0.27	-0.44	0.10	-0.17	0.28	0.03	0.09	-0.08
DissOxyg	0.82	0.19	1.00	-0.95	0.08	-0.01	0.03	-0.04	-0.20	-0.02	-0.03	-0.08	-0.14	0.05	0.03	0.10	0.08	0.06	0.07
PH	-0.88	-0.23	-0.95	1.00	-0.01	0.09	-0.03	0.09	0.18	-0.10	0.10	0.14	0.13	-0.11	0.02	-0.15	-0.23	-0.12	-0.16
Altitiud	0.13	0.25	0.08	-0.01	1.00	0.75	-0.34	0.19	-0.48	-0.63	0.29	-0.01	-0.45	-0.59	-0.22	-0.30	-0.27	-0.49	-0.53
%Shade	0.08	0.26	-0.01	0.09	0.75	1.00	-0.28	0.15	-0.50	-0.55	0.54	0.34	-0.22	-0.79	-0.35	-0.50	-0.26	-0.78	-0.74
%Debris	-0.11	-0.06	0.03	-0.03	-0.34	-0.28	1.00	-0.53	-0.11	0.11	-0.24	-0.04	0.14	0.29	-0.25	0.14	0.21	0.26	-0.04
%Rock	-0.02	-0.14	-0.04	0.09	0.19	0.15	-0.53	1.00	0.39	-0.20	0.38	0.26	0.05	-0.33	0.14	-0.31	-0.39	-0.27	-0.25
%Sand	-0.20	-0.34	-0.20	0.18	-0.48	-0.50	-0.11	0.39	1.00	0.37	-0.09	0.11	0.53	0.25	0.27	-0.13	-0.19	0.22	0.26
%AlieCo	-0.09	-0.33	-0.02	-0.10	-0.63	-0.55	0.11	-0.20	0.37	1.00	-0.13	0.01	0.41	0.32	0.24	0.04	0.71	0.29	0.59
%IndiCo	-0.15	-0.17	-0.03	0.10	0.29	0.54	-0.24	0.38	-0.09	-0.13	1.00	0.89	0.30	-0.80	-0.05	-0.62	-0.28	-0.74	-0.47
AvgVegHe	-0.22	-0.27	-0.08	0.14	-0.01	0.34	-0.04	0.26	0.11	0.01	0.89	1.00	0.47	-0.62	-0.03	-0.50	-0.26	-0.63	-0.45
AlieTree	-0.33	-0.44	-0.14	0.13	-0.45	-0.22	0.14	0.05	0.53	0.41	0.30	0.47	1.00	-0.02	-0.20	-0.58	-0.18	-0.04	0.20
IndgShrb	0.01	0.10	0.05	-0.11	-0.59	-0.79	0.29	-0.33	0.25	0.32	-0.80	-0.62	-0.02	1.00	0.24	0.70	0.21	0.96	0.70
AlieShrb	-0.08	-0.17	0.03	0.02	-0.22	-0.35	-0.25	0.14	0.27	0.24	-0.05	-0.03	-0.20	0.24	1.00	0.34	-0.10	0.23	0.34
IndgGras	0.19	0.28	0.10	-0.15	-0.30	-0.50	0.14	-0.31	-0.13	0.04	-0.62	-0.50	-0.58	0.70	0.34	1.00	0.30	0.67	0.30
AlieGras	0.18	0.03	0.08	-0.23	-0.27	-0.26	0.21	-0.39	-0.19	0.71	-0.28	-0.26	-0.18	0.21	-0.10	0.30	1.00	0.20	0.31
AquaMacr	0.00	0.09	0.06	-0.12	-0.49	-0.78	0.26	-0.27	0.22	0.29	-0.74	-0.63	-0.04	0.96	0.23	0.67	0.20	1.00	0.67
PSerrt	0.01	-0.08	0.07	-0.16	-0.53	-0.74	-0.04	-0.25	0.26	0.59	-0.47	-0.45	0.20	0.70	0.34	0.30	0.31	0.67	1.00

F)	WatrTemp	Conductv	DissOxyg	PH	Altitiud	%Shade	%Debris	%Rock	%Sand	%AlieCo	%IndiCo	AvgVegHe	IndgTree	AlieTree	IndgShrb	AlieShrb	IndgGras	AquaMacr	PSerrt
WatrTemp	1.00	0.77	-0.81	-0.91	-0.02	0.03	-0.10	0.02	-0.03	0.01	0.03	0.00	-0.04	0.04	0.01	-0.05	-0.01	-0.01	-0.01
Conductv	0.77	1.00	-0.79	-0.74	0.37	0.18	-0.09	0.00	-0.05	0.09	-0.07	0.08	0.08	0.06	-0.11	0.01	0.21	0.00	-0.19
DissOxyg	-0.81	-0.79	1.00	0.96	-0.45	-0.05	-0.20	0.03	-0.14	0.01	0.26	0.02	-0.09	0.02	0.01	0.02	-0.32	-0.17	0.10
PH	-0.91	-0.74	0.96	1.00	-0.23	-0.02	-0.09	0.01	-0.04	0.00	0.12	0.01	-0.03	-0.01	-0.01	0.03	-0.16	-0.07	0.05
Altitiud	-0.02	0.37	-0.45	-0.23	1.00	0.16	0.49	-0.11	0.46	-0.14	-0.57	-0.10	0.25	-0.22	-0.11	0.09	0.65	0.54	-0.24
%Shade	0.03	0.18	-0.05	-0.02	0.16	1.00	0.00	-0.07	-0.23	0.26	0.17	0.34	0.39	0.23	-0.05	0.05	0.26	0.00	-0.56
%Debris	-0.10	-0.09	-0.20	-0.09	0.49	0.00	1.00	-0.24	0.38	-0.20	-0.52	-0.31	0.25	-0.29	-0.28	0.13	0.60	0.49	0.17
%Rock	0.02	0.00	0.03	0.01	-0.11	-0.07	-0.24	1.00	0.09	-0.19	0.00	0.11	-0.33	-0.20	0.08	0.31	-0.26	-0.19	-0.02
%Sand	-0.03	-0.05	-0.14	-0.04	0.46	-0.23	0.38	0.09	1.00	-0.25	-0.43	0.03	-0.11	-0.26	-0.10	0.07	0.12	0.39	-0.17
%AlieCo	0.01	0.09	0.01	0.00	-0.14	0.26	-0.20	-0.19	-0.25	1.00	0.21	0.27	0.26	0.87	0.07	0.08	0.06	-0.31	-0.11
%IndiCo	0.03	-0.07	0.26	0.12	-0.57	0.17	-0.52	0.00	-0.43	0.21	1.00	0.50	-0.09	0.19	0.04	-0.01	-0.61	-0.55	-0.25
AvgVegHe	0.00	0.08	0.02	0.01	-0.10	0.34	-0.31	0.11	0.03	0.27	0.50	1.00	0.31	0.30	-0.01	-0.06	-0.25	-0.39	-0.70
IndgTree	-0.04	0.08	-0.09	-0.03	0.25	0.39	0.25	-0.33	-0.11	0.26	-0.09	0.31	1.00	0.25	-0.19	0.17	0.35	0.11	-0.15
AlieTree	0.04	0.06	0.02	-0.01	-0.22	0.23	-0.29	-0.20	-0.26	0.87	0.19	0.30	0.25	1.00	0.17	-0.15	-0.07	-0.29	-0.10
IndgShrb	0.01	-0.11	0.01	-0.01	-0.11	-0.05	-0.28	0.08	-0.10	0.07	0.04	-0.01	-0.19	0.17	1.00	-0.16	-0.02	0.01	-0.10
AlieShrb	-0.05	0.01	0.02	0.03	0.09	0.05	0.13	0.31	0.07	0.08	-0.01	-0.06	0.17	-0.15	-0.16	1.00	0.15	-0.20	0.09
IndgGras	-0.01	0.21	-0.32	-0.16	0.65	0.26	0.60	-0.26	0.12	0.06	-0.61	-0.25	0.35	-0.07	-0.02	0.15	1.00	0.40	-0.10
AquaMacr	-0.01	0.00	-0.17	-0.07	0.54	0.00	0.49	-0.19	0.39	-0.31	-0.55	-0.39	0.11	-0.29	0.01	-0.20	0.40	1.00	0.18
PSerrt	-0.01	-0.19	0.10	0.05	-0.24	-0.56	0.17	-0.02	-0.17	-0.11	-0.25	-0.70	-0.15	-0.10	-0.10	0.09	-0.10	0.18	1.00