

Practical Conservation Planning from Local to Continental Scales Using Freshwater Invertebrates

by
John Pascal Simaika

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Promoter: Prof. Michael John Samways
Faculty of AgriSciences
Department of Conservation Ecology and
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Declaration

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Abstract

Dragonflies (Insecta: Odonata) are a valuable tool for assessing aquatic systems and have been used as indicators of ecological health, ecological integrity, and environmental change, including climatic change. In four separate studies I explored the usefulness of dragonflies as surrogates in biomonitoring, site prioritization and indication of global climate change. In the use of dragonflies for biomonitoring, I field-tested a freshwater ecological integrity index, the Dragonfly Biotic Index (DBI), based on dragonfly assemblages at the local scale, and compared the DBI to a standard freshwater benthic macroinvertebrate-based freshwater health index. Overall, dragonflies were more sensitive to changes in river condition than were macroinvertebrates, and the DBI site value and macroinvertebrate scores were highly significantly correlated. I conclude that dragonfly assemblages in the form of a DBI are an excellent tool for environmental assessment and monitoring freshwater biodiversity, with the potential to replace benthic macroinvertebrate-based freshwater quality assessments.

In the second study, I used the DBI to prioritize sites for conservation action in South Africa. Using a selected set of top prioritized sites, I compared the DBI's performance to that of a rarity-complementarity algorithm. Site prioritization using the DBI reveals that CFR sites protect Red Listed taxa rather well. The rarity-complementarity algorithm represents all species, but without greater emphasis on the rare and threatened species. I conclude that the DBI is of great value in selecting biodiversity hotspots, while the algorithm is useful for selecting complementarity hotspots.

The third study was made possible by the recent completion of a continental assessment of freshwater biodiversity, which revealed that patterns of richness and threat of four well-studied aquatic taxa largely coincide at the continental scale. Using only dragonflies, I built a protected areas network for Africa using spatial planning software. I then compared the performance of the existing African reserve network and that of known global biodiversity hotspots against the model, and identified sites of conservation concern. Although the current reserve network covers 10.7% of the landscape, the proportional representation of species geographic distributions in reserves is only 1.1%. The reserve network is therefore inefficient, and many areas of conservation priority that are not formally protected remain. The advantage of operating at the fine scale, while covering a large geographic area is that it shifts the focus from the large-scale hotspots to smaller priority areas within and beyond hotspots.

In the fourth study, I created species distribution models of dragonflies in an El Niño-prone biodiversity hotspot in South Africa, and predicted the changes in species richness, geographic range and habitat suitability, forty and eighty years from now. According to the model results of

two different emissions scenarios, at least three species will be lost from the area by 2050, and four by 2080. The remaining species are predicted to persist with reduced geographical ranges, at generally higher elevations. Most species presented here thrive quite well in artificial environments, that is, engineered ponds or dams. It is therefore unlikely that loss in connectivity will play a role for these species.

Opsomming

Naaldekokers (Insecta:Odonata) is waardevolle instrumente om akwatiese sisteme te assesser, en is al gebruik as aanwysers van ekologiese gesondheid, ekologiese integriteit en omgewingsverandering, insluitend klimaatsverandering. In vier studies het ek die nut van naaldekokers as surrogate in biomonitoring, area prioritisering en indikatie van globale klimaatsverandering ondersoek. In die benutting van naaldekokers in biomonitoring, het ek 'n varswater ekologiese integriteits indeks, die Dragonfly Biotic Index (DBI), wat gebaseer is op naaldekokergemeenskappe op die plaaslike skaal, getoets en dit vergelyk met 'n standaard bentiese makroinvertebraat-gebaseerde varswater gesondheids index. Naaldekokers was meer sensitief vir veranderinge in rivierstoestand as makroinvertebrate, en die DBI lokaliteit waarde en makroinvertebraat telling was beduidend gekorreleer. Die gevolgtrekking was dat naaldekoker gemeenskappe in die vorm van die DBI 'n uitstekende instrument is vir omgewings assessering en die monitering van varswater biodiversiteit, met die potensiaal om bentiese makroinvertebraat-gebaseerde varswaterkwaliteit assessering te vervang.

In die tweede studie, het ek die DBI gebruik om areas te prioriseer vir bewaringsaksie in Suid Afrika. Met die gebruik van 'n geselekteerde set top prioriteit areas, het ek die DBI se prestasie vergelyk met die van 'n rariteit-komplementariteit algoritme. Area prioritisering met die gebruik van die DBI het aangedui dat CFR areas taxa op die Rooi Lys goed beskerm. Die rariteit-komplementariteit algoritme verteenwoordig alle spesies, maar beklemtoon minder skaars en bedreigde spesies. Die gevolgtrekking was dat die DBI van meer waarde is in die selektering van biodiversiteits 'hotspots', terwyl die algoritme nuttig is vir die selektering van komplementariteits 'hotspots'.

Die derde studie was moontlik gemaak deur die onlangse voltooiing van 'n kontinentale assessering van varswater biodiversiteit, wat aangedui het dat patrone van rykheid en bedreiging van vier goed-bestudeerde akwatiese taxa grootliks ooreenstem op die kontinentale skaal. Met die gebruik van naaldekokers, het ek 'n beskermde area netwerk gebou vir Afrika met ruimtelike beplannings sagteware. Ek het die prestasie van die bestaande Afrika reservaatnetwerk en die van bekende globale biodiversiteit 'hotspots' vergelyk teen die model, en het areas van bewaringsbelang geïdentifiseer. Alhoewel die bestaande reservaatnetwerk 10.7% van die landskap dek, is die proporsionele verteenwoordiging van spesies se geografiese verspreiding net 1.1%. Die reservaatnetwerk is dus onvoldoende en baie areas van bewaringsbelang is nie formeel beskerm nie. Die voordeel van op die fyn skaal werk terwyl 'n groot geografiese are gedek word, is dat dit die fokus van groot skaal 'hotspots' na kleiner prioriteits areas binne en buite 'hotspots' verskuif.

In die vierde studie, het ek spesies verspreidingsmodelle van naaldekokers geskep in 'n El Niño-geneigde biodiversiteits 'hotspot' in Suid Afrika, en het veranderinge in spesies rykheid, geografiese verspreiding en habitatsgeskiktheid voorspel, veertig en tagtig jaar van nou af. Volgens die modelresultate van twee verskillende emissie scenarios, sal ten minste drie spesies verlore gaan uit die area teen 2050, en vier teen 2080. Daar word voorspel dat die oorblywende spesies sal voortduur in verkleinde geografiese areas, by groter hoogte bo seespieël. Die meeste spesies hier verteenwoordig floreer in kunsmatige omgewings, soos mensgemaakte damme. Dit is dus onwaarskynlik dat 'n verlies in konnektiwiteit 'n rol sal speel vir hierdie spesies.

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Table of Contents

DECLARATION.....	ii
ABSTRACT.....	iii
OPSOMMING.....	v
ACKNOWLEDGEMENTS.....	vii
TABLE OF CONTENTS.....	viii
List of Figures.....	xi
List of Tables.....	xiv
List of Supplementary materials.....	xvi
CHAPTER 1: GENERAL INTRODUCTION.....	1
ABSTRACT.....	1
1.1. Threats to freshwater biodiversity.....	1
1.2. Dragonflies as flagships for freshwater conservation.....	2
1.3. Dragonflies as bioindicators.....	2
1.4. Dragonflies as tools in site prioritization.....	3
1.5. Research aims.....	3
REFERENCES.....	5
CHAPTER 2: COMPARATIVE ASSESSMENT OF INDICES OF FRESHWATER HABITAT CONDITIONS USING DIFFERENT INVERTEBRATE TAXON SETS	
ABSTRACT.....	9
1. INTRODUCTION.....	10
2. METHODS.....	11
2.1. Environmental variables.....	11
2.2. Dragonfly collection.....	12
2.3. Dragonfly Biotic Index.....	14
2.4. Sampling for the South African Scoring System.....	14
2.5. Average Taxonomic Distinctness.....	15
2.6. Statistical Analyses.....	15
2.6.1. Canonical Correspondence Analysis.....	15
2.6.2. BIOENV.....	15
2.6.3. Similarity.....	16
2.6.4. RELATE analysis.....	16
2.6.5. Cluster analysis.....	16
2.6.6. Spearman rank correlation.....	16

3. RESULTS.....	17
3.1. Environmental variables.....	17
3.2. Relatedness of the biotic assemblages.....	17
3.3. Cluster analyses of the biotic assemblages.....	17
3.3.1. Dragonflies.....	18
3.3.2. Benthic macroinvertebrates.....	21
3.3.3. Dragonflies compared to benthic macroinvertebrates.....	21
3.4. Average taxonomic Distinctness (AvTD).....	23
3.4.1. Dragonflies.....	23
3.4.2. Benthic macroinvertebrates.....	23
3.5. Biotic index scores.....	26
4. DISCUSSION.....	29
4.1. Environmental variables, relatedness and cluster analyses.....	29
4.2. Average taxonomic distinctness and biotic index scores.....	29
4.3. Performance of the DBI and SASS.....	30
5. CONCLUSION.....	31
REFERENCES.....	33

CHAPTER 3: RESERVE SELECTION USING RED LISTED TAXA IN THREE GLOBAL BIODIVERSITY HOTSPOTS: DRAGONFLIES IN SOUTH AFRICA

ABSTRACT.....	38
1. INTRODUCTION.....	39
1.1. Reserve selection.....	39
1.2. Red Listing.....	40
1.3. Objectives.....	41
2. METHODS.....	42
2.1. Statistical analysis.....	44
3. RESULTS.....	44
3.1. Sampling gaps.....	44
3.2. Richness, endemism and threat.....	45
3.3. Protected areas and threatened, endemic species.....	51
3.4. Comparison of value-based index with algorithm.....	54
4. DISCUSSION.....	59
4.1. Sampling gaps.....	59
4.2. Comparison of richness, endemism and threat.....	60
4.3. Protected areas and threatened, endemic species.....	61
4.4. Comparison of value-based index with algorithm.....	62
5. CONCLUSION.....	64
REFERENCES.....	65

CHAPTER 4: CONTINENTAL-SCALE ASSESSMENT OF FRESHWATER CONSERVATION AREAS USING FINE-SCALE MODELING

ABSTRACT.....	71
1. INTRODUCTION.....	72
2. METHODS.....	73
2.1. <i>The database</i>	73
2.2. <i>Species habitat modeling</i>	74
2.3. <i>Spatial analysis and planning</i>	75
3. RESULTS.....	76
3.1. <i>Current reserve network</i>	76
3.2. <i>Unconstrained analysis</i>	78
3.3. <i>Reserves</i>	82
3.4. <i>Hotspots</i>	82
4. DISCUSSION.....	87
4.1. <i>Overview of analyses</i>	87
4.2. <i>Hotspots and beyond</i>	87
4.3. <i>Protected areas</i>	88
5. CONCLUSION.....	89
REFERENCES.....	90

CHAPTER 5: PREDICTED RANGE SHIFTS OF VAGILE ORGANISMS ALONG AN ELEVATION GRADIENT

ABSTRACT.....	97
1. INTRODUCTION.....	98
2. METHODS.....	99
2.1. <i>Study area and sampling records</i>	99
2.2. <i>Environmental variables</i>	101
2.3. <i>Species habitat modelling</i>	101
2.4. <i>Spatial analysis</i>	102
3. RESULTS.....	102
3.1. <i>Models and variables</i>	102
3.2. <i>Species richness</i>	103
3.3. <i>Geographic range and elevation</i>	103
3.4. <i>Change in habitat suitability</i>	109
4. DISCUSSION.....	111
5. CONCLUSION.....	113
REFERENCES.....	114

CHAPTER 6: GENERAL DISCUSSION..... 119

6.1 <i>Dragonflies as tools in biomonitoring</i>	120
6.2 <i>Dragonflies as surrogates for site prioritization in South Africa</i>	120
6.3 <i>Dragonflies as surrogates for site prioritization for Africa</i>	121
6.4 <i>Dragonflies as indicators of climate change</i>	122
REFERENCES.....	123

List of Figures

- FIGURE 2.1.** CLUSTER DENDROGRAM OF SITES BASED ON EUCLIDEAN DISTANCES, SHOWING THE DISTANCES OF THE SITES BASED ON THE ENVIRONMENTAL VARIABLES. FULL NAMES OF ABBREVIATED SAMPLES ARE GIVEN IN TABLE 1.1. 19
- FIGURE 2.2.** CLUSTER GRAPH OF SAMPLING SITES BASED ON DRAGONFLY SPECIES ABUNDANCE. PERCENT SIMILARITIES ARE GIVEN FOR EACH JUNCTION. FULL NAMES FOR SAMPLE ABBREVIATION NAMES ARE GIVEN IN TABLE 1.1. 20
- FIGURE 2.3.** CLUSTER GRAPH OF SAMPLING SITES BASED ON BENTHIC MACROINVERTEBRATE TAXA ABUNDANCE. PERCENT SIMILARITIES ARE GIVEN FOR EACH JUNCTION. FULL NAMES FOR SAMPLE ABBREVIATION NAMES ARE GIVEN IN TABLE 1.1. 22
- FIGURE 2.4.** FUNNEL PLOT OF AVERAGE TAXONOMIC DISTINCTNESS (AVTD) OF SAMPLING SITES BASED ON DRAGONFLY SPECIES ABUNDANCE. FULL NAMES FOR SAMPLE ABBREVIATION NAMES ARE GIVEN IN TABLE 1.1. 24
- FIGURE 2.5.** FUNNEL PLOT OF AVERAGE TAXONOMIC DISTINCTNESS (AVTD) OF SAMPLING SITES BASED ON BENTHIC MACROINVERTEBRATE TAXA ABUNDANCE. FULL NAMES FOR SAMPLE ABBREVIATION NAMES ARE GIVEN IN TABLE 1.1. 25
- FIGURE 2.6.** TWO-TAILED SPEARMAN RANK CORRELATION ($R_s = 0.561$, $N = 20$, $P < 0.005$) OF THE SQUARE-ROOT TRANSFORMED DRAGONFLY BIOTIC INDEX (DBI) SITE VALUE AND AVERAGE SCORE PER TAXON (ASPT). 28
- FIGURE 3.1.** GLOBAL HOTSPOTS AND PRIMARY CATCHMENT REGIONS OF SOUTH AFRICA. HIGHLIGHTED AREAS (DARK GRAY) SHOW SAMPLED QUATERNARY CATCHMENTS. ABBREVIATIONS ARE AS FOLLOWS: A (LIMPOPO), B (OLIFANTS), C (VAAL), D (ORANGE), E (OLIFANTS), F (BUFFELS), G (BERG/BOT/POTBERG), H (BREDE), J (GOURITS), K (KEURBOOM/STORM/KROM), L (GAMTOOS), M (SWARTKOPS), N (SUNDAYS), P (BUSHMANS), Q (FISH), R (KEISKAMMA), S (KEI), T (MZIMVUBU), U (MKOMAZI), V (TUGELA), W (MFOLOZI/PONGOLA), AND, X (KOMATI/CROCODILE). 46
- FIGURE 3.2.** DRAGONFLY SPECIES RICHNESS ACROSS SOUTH AFRICA. CLASSES ARE BASED ON NATURAL GROUPINGS INHERENT IN THE DATA, ESTABLISHED USING THE NATURAL BREAKS FUNCTION IN ARCGIS (2006). LETTERS INDICATE PRIMARY CATCHMENT REGIONS: ABBREVIATIONS FOR THE PRIMARY CATCHMENT ZONES ARE AS FOLLOWS: A (LIMPOPO), B (OLIFANTS), C (VAAL), D (ORANGE), E (OLIFANTS), F (BUFFELS), G (BERG/BOT/POTBERG), H (BREDE), J (GOURITS), K (KEURBOOM/STORM/KROM), L (GAMTOOS), M (SWARTKOPS), N (SUNDAYS), P (BUSHMANS), Q (FISH), R (KEISKAMMA), S (KEI), T (MZIMVUBU), U (MKOMAZI), V (TUGELA), W, (MFOLOZI/PONGOLA) AND X (KOMATI/CROCODILE). 48

FIGURE 3.3. NUMBER OF NATIONAL ENDEMIC DRAGONFLY SPECIES ACROSS SOUTH AFRICA. CLASSES ARE BASED ON NATURAL GROUPINGS INHERENT IN THE DATA, ESTABLISHED USING THE NATURAL BREAKS FUNCTION IN ARCGIS (2006). LETTERS INDICATE PRIMARY CATCHMENT REGIONS: A (LIMPOPO), B (OLIFANTS), C (VAAL), D (ORANGE), E (OLIFANTS), F (BUFFELS), G (BERG/BOT/POTBERG), H (BREDE), J (GOURITS), K (KEURBOOM/STORM/KROM), L (GAMTOOS), M (SWARTKOPS), N (SUNDAYS), P (BUSHMANS), Q (FISH), R (KEISKAMMA), S (KEI), T (MZIMVUBU), U (MKOMAZI), V (TUGELA), W, (MFOLOZI/PONGOLA) AND X (KOMATI/CROCODILE). 49

FIGURE 3.4. NUMBER OF RED LISTED (THREATENED) NATIONAL ENDEMIC DRAGONFLY SPECIES ACROSS SOUTH AFRICA, USING THE IUCN CATEGORIES AND CRITERIA (IUCN 2001). CLASSES ARE BASED ON NATURAL GROUPINGS INHERENT IN THE DATA, ESTABLISHED USING THE NATURAL BREAKS FUNCTION IN ARCGIS (2006). LETTERS INDICATE PRIMARY CATCHMENT REGIONS: A (LIMPOPO), B (OLIFANTS), C (VAAL), D (ORANGE), E (OLIFANTS), F (BUFFELS), G (BERG/BOT/POTBERG), H (BREDE), J (GOURITS), K (KEURBOOM/STORM/KROM), L (GAMTOOS), M (SWARTKOPS), N (SUNDAYS), P (BUSHMANS), Q (FISH), R (KEISKAMMA), S (KEI), T (MZIMVUBU), U (MKOMAZI), V (TUGELA), W, (MFOLOZI/PONGOLA) AND X (KOMATI/CROCODILE). 50

FIGURE 3.5. PROTECTION STATUS AND DRAGONFLY BIOTIC INDEX (DBI) VALUE OF CATCHMENTS IN WHICH GLOBALLY RED LISTED SPECIES OCCUR. CLASSES ARE BASED ON NATURAL GROUPINGS INHERENT IN THE DATA, ESTABLISHED USING THE NATURAL BREAKS FUNCTION IN ARCGIS (2006). 53

FIGURE 3.6. TWENTY-THREE HIGHEST VALUE DRAGONFLY BIOTIC INDEX (DBI) CATCHMENTS (DARK GREY OUTLINES) AND TOP CATCHMENT CHOSEN BY THE RESNET ALGORITHMS (BLACK OUTLINES). 55

FIGURE 3.7. FREQUENCY DISTRIBUTION OF THE GLOBALLY RED LISTED DRAGONFLY FAUNA IN COMPARISON TO ITS REPRESENTATION BY THE DRAGONFLY BIOTIC INDEX (DBI) AND THE RESNET ALGORITHMS. 57

FIGURE 3.8. FREQUENCY DISTRIBUTION OF THE GLOBALLY RED LISTED DRAGONFLY TAXA IN COMPARISON TO EACH SPECIES' REPRESENTATION BY THE DRAGONFLY BIOTIC INDEX (DBI) AND THE RESNET ALGORITHMS. 58

FIGURE 4.1. POTENTIAL RESERVE NETWORK OF 10% OF THE GEOGRAPHIC DISTRIBUTIONS OF DRAGONFLY SPECIES (DARK GRAY). THIS REPRESENTS 12.7% OF THE TOP FRACTION OF THE AFRICAN LANDSCAPE. ANNOTATIONS ARE FOR TERRESTRIAL ECOREGIONS AND DESCRIBED IN TABLE 4.2. 79

FIGURE 4.2. POTENTIAL RESERVE NETWORK OF 10% OF THE GEOGRAPHIC DISTRIBUTIONS OF ENDEMIC DRAGONFLY SPECIES (DARK GRAY). THIS REPRESENTS 11.4% OF THE TOP FRACTION OF THE AFRICAN LANDSCAPE. ANNOTATIONS ARE FOR TERRESTRIAL ECOREGIONS AND DESCRIBED IN TABLE 4.2. 81

FIGURE 4.3. RESERVE NETWORK OF 10% OF THE GEOGRAPHIC DISTRIBUTION OF DRAGONFLY SPECIES (DARK GRAY), WITH PROTECTED AREAS (LIGHT GRAY) (17.9% TOP FRACTION OF LANDSCAPE) INCLUDED IN THE RESERVE NETWORK. 83

- FIGURE 4.4.** RESERVE NETWORK OF 10% OF THE GEOGRAPHIC DISTRIBUTION OF ENDEMIC DRAGONFLY SPECIES (DARK GRAY), WITH PROTECTED AREAS (LIGHT GRAY) (17.9% TOP FRACTION OF LANDSCAPE) INCLUDED IN THE RESERVE NETWORK. 84
- FIGURE 4.5.** POTENTIAL RESERVE NETWORK OF 10% OF THE GEOGRAPHIC DISTRIBUTION OF DRAGONFLY SPECIES (DARK GRAY) WITH GLOBAL BIODIVERSITY HOTSPOTS (17% TOP FRACTION OF LANDSCAPE) INCLUDED IN THE NETWORK. ANNOTATIONS ARE FOR TERRESTRIAL ECOREGIONS AND DESCRIBED IN TABLE 4.2. 85
- FIGURE 4.6.** POTENTIAL RESERVE NETWORK OF 10% OF THE GEOGRAPHIC DISTRIBUTION OF ENDEMIC DRAGONFLY SPECIES (DARK GRAY) WITH GLOBAL BIODIVERSITY HOTSPOTS (17% TOP FRACTION OF LANDSCAPE) INCLUDED IN THE NETWORK. ANNOTATIONS ARE FOR TERRESTRIAL ECOREGIONS AND DESCRIBED IN TABLE 2. 86
- FIGURE 5.1.** THE STUDY AREA, IN KWAZULU-NATAL, SOUTH AFRICA. WHITE DOUBLE-CIRCLES ARE SAMPLING LOCATIONS. SHADED AREAS INDICATE INCREASING ELEVATION FROM LOW (LIGHT GRAY) TO HIGH ELEVATIONS (DARK GRAY). 100
- FIGURE 5.2.** PREDICTED CURRENT DISTRIBUTIONS OF DRAGONFLY SPECIES IN THE STUDY AREA. 105
- FIGURE 5.3.** PREDICTED SPECIES RICHNESS PATTERNS FOR 2050 AND 2080 UNDER THE A2 (LEFT) AND B2 (RIGHT) CLIMATE SCENARIOS. 106
- FIGURE 5.4.** RANGE OF HABITAT CHANGE FROM THE CURRENT PREDICTION COMPARED TO THE FUTURE (2050 AND 2080) UNDER THE A2 (LEFT) AND B2 (RIGHT) CLIMATE SCENARIOS. 110

List of Tables

- TABLE 2.1.** DETAILS OF SAMPLING SITES (TSITSIKAMMA REGION, WESTERN AND EASTERN CAPE PROVINCES, SOUTH AFRICA), INCLUDING RIVER NAME, SAMPLING SITE ABBREVIATION, SITE COORDINATE (WGS 1984), TRANSECT LENGTH AND ELEVATION OF SITE. 13
- TABLE 2.2.** DBI AND SASS SCORES FOR EACH SITE (TSITSIKAMMA REGION, WESTERN AND EASTERN CAPE PROVINCES, SOUTH AFRICA): DRAGONFLY SPECIES RICHNESS, DBI SCORE, DBI SITE VALUE, AVERAGE MACROBENTHIC TAXA RICHNESS (SASS), AVERAGE SASS SCORE, AND AVERAGE ASPT SCORE. ABBREVIATIONS: AV. = AVERAGE. SITE NAME ABBREVIATIONS ARE EXPLAINED IN TABLE 1.1. 27
- TABLE 3.1.** THE SUB-INDICES OF THE DRAGONFLY BIOTIC INDEX (DBI) RANGE FROM 0 TO 3. IT IS BASED ON THE THREE SUB-INDICES RELATING TO GEOGRAPHICAL DISTRIBUTION, LEVEL OF THREAT, AND SENSITIVITY TO HABITAT CHANGE, WITH PARTICULAR REFERENCE TO INVASIVE ALIEN RIPARIAN TREES. THE DBI IS THE SUM OF THE SCORES FOR THE THREE SUB-INDICES, AND RANGES FROM 0 TO 9. A COMMON, WIDESPREAD, NOT-THREATENED AND HIGHLY-TOLERANT (OF DISTURBANCE) SPECIES WOULD SCORE 0 (0 + 0 + 0), WHILE A HIGHLY RANGE-RESTRICTED, THREATENED AND SENSITIVE SPECIES WOULD SCORE 9 (3 + 3 + 3). ABBREVIATIONS: IUCN SPECIES STATUS (IUCN, 2001): LC = LEAST CONCERN, NT = NEAR THREATENED, VU = VULNERABLE, CE = CRITICALLY ENDANGERED, EN = ENDANGERED, GS = GLOBAL STATUS, AND NS = NATIONAL STATUS. 43
- TABLE 3.2.** COUNT OF SAMPLED QUATERNARY CATCHMENTS IN EACH PRIMARY CATCHMENT ZONE. 47
- TABLE 3.3.** GLOBALLY RED LISTED TAXA (I.E. IUCN THREAT CATEGORY OF VU, EN, CR), AND THEIR PROTECTION STATUS. QUATERNARY CATCHMENTS WERE FOUND TO BE ONLY PARTIALLY PROTECTED. TAXA PRESENTED IN BOLD ARE NOT IN A PROTECTED AREA. ALTHOUGH CURRENTLY NOT ON THE GLOBAL RED LIST, *ORTHETRUM RUBENS* BARNARD, 1937 AND *SYNCORDULIA VENATOR* (BARNARD, 1993) ARE SCHEDULED TO BE LISTED IN FUTURE (SAMWAYS, 2006) AND ARE THUS INCLUDED IN THIS TABLE. SUBHEADINGS: PP: PARTIALLY PROTECTED; NP: NOT PROTECTED. 52
- TABLE 4.1.** DISTRIBUTION OF THREATENED DRAGONFLIES IN THE LANDSCAPE (OVERALL) AND IN PROTECTED AREAS. ABBREVIATED IUCN CATEGORIES (2001) ARE AS FOLLOWS: CR = CRITICALLY ENDANGERED, EN = ENDANGERED, VU = VULNERABLE. 77
- TABLE 4.2.** DESCRIPTIONS OF ANNOTATIONS FOR TERRESTRIAL ECOREGIONS AS SHOWN IN FIGURES 4.1, 4.2, 4.5 AND 4.6. 80

TABLE 5.1. SELECTED BIOCLIM VARIABLES (HIJMANS ET AL., 2005) AND THEIR USE IN SPECIES DISTRIBUTION MODEL BUILDING (M1 – M8). THE FOUR MOST FREQUENTLY USED VARIABLES ARE INDICATED IN BOLD. ALL VARIABLES ARE CONTINUOUS DATA, EXCEPT FOR CATCHMENT BOUNDARIES (MIDGLEY, 1994), WHICH ARE CATEGORICAL DATA. 104

TABLE 5.2. GEOGRAPHIC RANGES OF MODELED SPECIES, EXPRESSED HERE AS NUMBER OF GRID CELLS, UNDER CURRENT AND FUTURE (2050, 2080) PREDICTED GLOBAL CLIMATE CHANGE SCENARIOS. PREDICTED CHANGES ARE EXPRESSED AS PERCENTAGES. ABBREVIATIONS: N.A. = NOT APPLICABLE. 107

TABLE 5.3. CURRENT AND FUTURE PREDICTED ELEVATION TOLERANCES OF SPECIES UNDER TWO CLIMATE SCENARIOS, A2 AND B2 FOR 2050 AND 2080. MINIMUM, MAXIMUM AND RANGE OF ELEVATIONS ARE GIVEN IN METERS. RANGE MEANS HERE THE DIFFERENCE BETWEEN THE MINIM AND MAXIMUM RECORDED ELEVATION. ABBREVIATION N.A. = NOT APPLICABLE. 108

LIST OF SUPPLEMENTARY MATERIALS

TABLE 4.S1. LIST OF DRAGONFLY SPECIES USED IN THE MAXENT AND ZONATION ANALYSES. SAMPLES REFER TO THE NUMBER OF UNIQUE RECORDS PER SPECIES. THREAT STATUS REFERS TO THE IUCN THREAT CATEGORIES. ABBREVIATED IUCN CATEGORIES (2001) ARE AS FOLLOWS: CR = CRITICALLY ENDANGERED, EN = ENDANGERED, VU = VULNERABLE. THE ABBREVIATION N.A. (= NOT APPLICABLE) DENOTES SPECIES THAT WERE NOT MODELED IN MAXENT. THE ‘PERCENTAGE OF DISTRIBUTION ON AFRICAN CONTINENT’ IS AN ESTIMATE BASED ON THE EXPERT OPINION OF ODONATOLOGISTS WORKING ON THE FAUNA OF THE CONTINENT.

..... SEE DISK.

TABLE 4.S2. LIST OF BIOCLIM VARIABLES. THESE ARE BIOLOGICALLY MEANINGFUL VARIABLES, WHICH ARE CALCULATED FROM ELEVATION, TEMPERATURE AND PRECIPITATION. SEE DISK.

TABLE 4.S3. SPECIES REPRESENTATIONS IN TERRESTRIAL ECOREGIONS, FOR TWO ANALYSES: ALL DRAGONFLY SPECIES, AND AFRICAN ENDEMICS ONLY.

..... SEE DISK.

Chapter 1

GENERAL INTRODUCTION

1.1 Threats to freshwater biodiversity

Anthropogenic global climatic change and habitat destruction have emerged as the greatest threats to global biodiversity (e.g. Opdam and Wascher, 2004). Freshwater ecosystems are not exempted, and declines in biodiversity are estimated to be up to five times greater in some freshwaters than in the most affected terrestrial ecosystems (Dudgeon et al., 2006). Indeed, the WWF Living Planet Report (WWF, 2010) documents a 69% decline in tropical freshwater areas, but a 36% improvement in temperate areas, using a freshwater index based on vertebrate species over the period of 1970-2007.

Among the greatest global threats to the functioning of freshwater ecosystems is the destruction or degradation of habitat, invasion by alien species, overexploitation, water pollution, and flow modification. Superimposed upon these interacting threats are global environmental changes such as nitrogen deposition, temperature warming and shifts in precipitation and runoff patterns. Indeed, climate change coupled with loss in connectivity are likely to prevent freshwater species from adapting at a rate fast enough to cope with local and regional changes (Dudgeon et al., 2006).

Already a water-scarce country, the future climate of South Africa is predicted to increase in temperature and decrease in precipitation (Driver et al., 2005). Rivers are the primary source of water (85%) for agricultural, domestic and industrial uses. Dams provide the remainder (15%) and the water stored in dams accounts for 67% of the total annual run-off in all rivers. A 2007 study that assessed the status of main river ecosystems in South Africa found that 23% of the length of the country's main rivers has been irreversibly transformed (Nel et al., 2007). Coupled with ever-increasing water withdrawals and effluent discharge, aquatic diversity is bound to decline further in other systems, causing associated losses in ecosystem services (Driver et al., 2005). Some of these ecosystem services provided by freshwater biodiversity include the provisioning of clean water, food (e.g. rice, fish), and goods to humans (e.g. reeds as building material) and resilience to anthropogenic impacts (e.g. pollution or excessive nutrient release). Other services include the suppression of water-borne diseases, flood attenuation, and delivery of sediment to coastal areas. Additionally, the recreational and spiritual value of wetlands cannot be denied (Millennium Ecosystem Assessment, 2005). These findings highlight the need to systematically protect freshwater biodiversity. In this study, I used dragonflies (Odonata) as model organisms for conservation research.

1.2 Dragonflies as flagships for freshwater conservation

Dragonflies (Insecta: Odonata) are a well-studied group of invertebrates (Córdoba-Aguilar, 2008), with their increasing recognition in conservation worldwide (Samways, 2008). In a regional context, this fact is reflected in dragonflies being the only insect group that are currently being globally assessed by the International Union for the Conservation of Nature (IUCN). Indeed, dragonflies have already been the subject of a continental African (Dijkstra et al., 2011) and regional southern African freshwater assessment (Suhling et al., 2008). They have also been nationally assessed in South Africa for Red List status (Samways, 2006). The Red List of the national (which also includes globally Red Listed taxa) conservation status of the South African dragonfly fauna, using current IUCN categories and criteria, resulted in a total of 42 odonate taxa being Red Listed (Samways, 2006). The IUCN Red List categories of threat are Critically Endangered (CR), Endangered (EN) or Vulnerable (VU) (IUCN, 2006). Thus 25% of the national total of 162 taxa (i.e. species and subspecies) are Red Listed. In terms of endemic dragonfly taxa in South Africa, fourteen out of 33 taxa are globally Red Listed. Threats to these globally Red Listed taxa appear to come mainly from riverine invasive alien trees, especially wattle (*Acacia* spp.), and which have dense canopies that shade out the habitat (Samways and Taylor, 2004).

Of the 28 remaining nationally Red Listed taxa, six are marginal in South Africa; seven threatened mainly by habitat loss through urbanization, industrialization and pollution; and, nine by habitat loss through invasive alien trees. Many of the species on the national, but also global Red List, are further affected by a synergy of threats. Synergistic impacts include habitat disturbance by cattle that use invasive alien trees for shade. Cattle trampling causes direct destruction of the river bank and riparian vegetation, trampling of the larval habitat, and siltation of the stream (Kinvig and Samways, 2000). In some cases, there may be possible predation by trout, especially rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)). Detergent pollution, mine effluent and agricultural run-off, and over-abstraction of water are also of concern (Samways and Taylor, 2004).

1.3 Dragonflies as bioindicators

The use of adult dragonflies as bioindicators is well established (Oertli, 2008; Simaika and Samways, 2009), and dragonflies have become an essential tool for assessing aquatic systems (Schindler et al., 2003). Dragonflies can be used as indicators of ecological health (Moore, 1997; Trevino, 1997), ecological integrity (Clark and Samways, 1996; Osborn and Samways, 1996; Von Ellenrieder, 2000; Smith et al., 2007; Simaika and Samways, 2008, 2009), and environmental change, whether climatic (Ott, 2009) or in the recovery of habitats (Samways and Taylor, 2004). Dragonflies are frequently identified as bioindicators for several reasons: (a) they are well known taxonomically; (b) most are readily identifiable in the field; (c) they occupy a spectrum of habitats;

(d) they are sensitive to changes in water quality and the ecological conditions of their habitats; and, (e) their species assemblages are large enough for assessments (Samways and Steytler, 1996; Chovanec and Waringer, 2001). The above mentioned characteristics make dragonflies, especially the adults, valuable candidates for medium to long-term monitoring programs (Smith et al., 2007).

1.4 Dragonflies as tools in site prioritization

Reserve designs can be based on two major methodological approaches, (i) scoring procedures; or, (ii) species complementarity (Abellán et al., 2005; Gaston et al., 2001). Scoring procedures rank sites in order of value or priority according to one or several criteria, such as richness, rarity or threat status (e.g. Orme et al., 2005), and have been traditionally used in area selection (Abellán et al., 2005). The principle of complementarity was first coined by Vane-Wright et al. (1991). The complementarity value of a site relative to an existing set of prioritized sites is defined as its quantitative contribution to the representation of biodiversity features that are not adequately represented in the existing set (Sarkar et al., 2006). Methods based on complementarity are more recent than scoring procedures (Abellán et al., 2005), and are frequently based on the use of algorithms (e.g. Margules and Pressey, 2000).

The Dragonfly Biotic Index, a scoring procedure that uses dragonflies as an indicator taxon to identify sites for conservation action, is designed to assign conservation (biodiversity) value to individual species. Intrinsic to the DBI is the targeting of rare, endemic, or Red Listed taxa, or species that are sensitive to habitat disturbance, by assigning a higher score to such species than those that are common and widespread (Simaika and Samways, 2008a). The IUCN Red Listing process, an expert-based classification method (Gärdenfors, 2001), is integral to functioning of the index, as the DBI incorporates a score for each Red List status (both global and national categorization) of an individual species. The DBI therefore has practical potential in reserve selection.

1.5 Research aims

This thesis focuses on three areas of conservation research, spread over four chapters. Namely, these are bioindication for ecological integrity (Chapter 2), site prioritization at the national (Chapter 3) and continental scale (Chapter 4) and bioindication for climate change (Chapter 5).

In Chapter 2, I field test the Dragonfly Biotic Index (DBI), an ecological integrity measure developed for South African freshwaters (Simaika and Samways, 2008, 2009). I compare the performance of the DBI, to a biodiversity index (average taxonomic distinctness; AvTD) as well as

to a standard freshwater benthic macroinvertebrate-based freshwater health index (South African Scoring System, using Average Score Per Taxon; ASPT).

In Chapter 3, I test the use of the DBI (Simaika and Samways, 2008a, b) to prioritize sites for conservation action, with special emphasis on species occurrence in three global hotspots in southern Africa. Before employing the DBI, I first identify species sampling gaps and biases, and patterns of richness, endemism and threat in a dataset of South African dragonflies. Second, using the DBI, I make recommendations for which areas require further recording effort. Third, I identify areas for conservation action based on existing reserve networks. Finally, I compare site selection in the DBI and the ResNet rarity-complementarity algorithm with special emphasis on globally Red Listed species.

In Chapter 4, I modeled the distributions of a continent-wide dataset of African dragonflies at the fine-scale, using predictive species distribution modeling software. My objectives were to first build a hypothetical reserve network, based on maximal species representation, by identifying priority areas under the assumption that all areas are available for protection (unconstrained analysis). Second, the aim was to compare the efficiency of the existing continental reserve network as well as that of the global biodiversity hotspots at representing all species. Third, my aim was to identify areas of conservation concern within and beyond reserves and hotspot areas.

Finally, in Chapter 5, I investigate the effect that climate change may have on a selected assemblage of dragonflies, along an El Niño elevational gradient in the South African province of KwaZulu-Natal. The objectives of the study are first to understand how the geographic spread and richness patterns of dragonflies will be affected by global climate change in the medium to long term, and second what influence different global climate change scenarios may have on these predictions.

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Chapter 2

Comparative assessment of indices of freshwater habitat conditions using different invertebrate taxon sets*

Abstract: *Monitoring changes in population levels of a wide range of species in biodiversity research and conservation requires practical, easy-to-use and efficient assessment and monitoring methods. Dragonflies (Insecta: Odonata) are a valuable tool for assessing aquatic systems and have been used as indicators of ecological health, ecological integrity, and environmental change, including climatic change, as well as indicators of habitat recovery. I field-tested a freshwater ecological integrity index, the Dragonfly Biotic Index (DBI), based on dragonfly assemblages at the local scale, and compared the DBI to a biodiversity index (average taxonomic distinctness; AvTD) as well as to a standard freshwater benthic macroinvertebrate-based freshwater health index (South African Scoring System, using Average Score Per Taxon; ASPT). I sampled 20 river sites, selected a priori. Adult dragonflies and benthic macroinvertebrates were collected using standardized methods. Environmental variables were collected in situ, and water samples taken. Temperature and pH were the most important physical environmental variables in explaining the assemblage structure, and I found significant abiotic-biotic relationships, as well as biotic-biotic relationships. Overall, dragonflies were more sensitive to changes in river condition than were macroinvertebrates, in part because they were responding at the species rather than higher taxonomic level. AvTD scores did not show any significant relationship with changes in river condition. Furthermore, sites with low biotic scores (indicating disturbance) had high AvTD values. In contrast, DBI site value and ASPT scores were highly significantly correlated. I conclude that dragonfly assemblages in the form of a DBI are an excellent tool for environmental assessment and monitoring freshwater biodiversity, with the potential to replace benthic macroinvertebrate-based freshwater quality assessments such as SASS.*

Keywords: ecological integrity, biomonitoring, freshwater, dragonflies, Odonata, Dragonfly Biotic Index, benthic macroinvertebrates, taxonomic distinctness

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1. Introduction

Freshwater ecosystems, especially rivers, are central to the process of economic and social development (Boon et al., 2000). Yet freshwaters are the most threatened ecosystems in the world (Abell, 2002). Among the most harmful anthropogenic impacts to these ecosystems is the introduction of alien organisms, dam construction, habitat modification and alteration of water chemistry (Malmqvist and Rundle, 2002). Conservationists are faced with limited time, funding and personnel, and thus rely on surrogate approaches to species inventories for biodiversity assessment (e.g. Lawler et al., 2003, Kati et al., 2004). This creates the need to rapidly inventory biodiversity and to monitor changes, particularly declines in biodiversity. One way of doing this is to focus on selected taxa as bioindicators. McGeoch (1998) suggests that a good biological indicator (a) readily reflects the state of an environment, (b) represents the impact of environmental change at a variety of scales, or (c) is a useful surrogate or umbrella of other taxa. Bioindicators can be used in measuring any of the three indicator categories: biological diversity, environmental, and ecological.

The use of adult dragonflies (Insecta: Odonata) as bioindicators in any of these categories is well established (Simaika and Samways, 2009a, 2009b), and dragonflies have become an essential tool for assessing aquatic systems (Schindler et al., 2003). Dragonflies can be used as indicators of ecological health (Carle, 1979; Moore, 1997; Trevino, 1997), ecological integrity (Clark and Samways, 1996; Osborn and Samways, 1996; Von Ellenrieder, 2000; Smith et al., 2007; Simaika and Samways, 2008, 2009a, 2009b), and environmental change, whether climatic (Ott, 2009) or in the recovery of habitats (Samways and Taylor, 2004). Dragonflies are frequently identified as bioindicators for several reasons: (a) they are well known taxonomically; (b) most are readily identifiable in the field; (c) they occupy a spectrum of habitats; (d) they are sensitive to changes in water quality and the ecological conditions of their habitats; and, (e) their species assemblages are large enough for assessments (Samways and Steytler, 1996; Chovanec and Waringer, 2001). The above mentioned characteristics make dragonflies, especially the adults, valuable candidates for medium to long-term monitoring programs (Smith et al., 2007). Monitoring abundant resident species may be important for detecting the early decline of a habitat (Hawking and New, 2002), while monitoring rare species can be indicative of relict or undisturbed conditions and used to rate the importance of a site (Eyre et al., 1986).

It is also important to identify species that are restricted to a narrow range of conditions, as they may be good indicators of change (Smith et al., 2007). Numerous studies have sought to find unique species assemblages which could then be used to characterize unique habitats or habitat quality (Schmidt, 1985). In Europe, Chovanec and Waringer (2001) developed the Odonata Habitat Index

(OHI), a measure of ecological integrity. The index is a weighted measure based on habitat type (i.e. the spread of species in different habitat types), abundance, and indication (i.e. weighted specificity to identify sensitivity of species). For South Africa, the Dragonfly Biotic Index (DBI) was developed, also a measure of wetland ecological integrity (Simaika and Samways, 2008, 2009a, 2009b).

In development testing, the DBI was found to be very useful for site selection, as well as for measuring ecological integrity at the global and regional scale. It is a low-cost, easy-to-use method. Another biodiversity index, Average Taxonomic Distinctness (AvTD) was also proposed as an alternative to species richness (Warwick and Clarke, 1995), and has gained popularity in environmental assessment (Warwick and Clarke, 1998, Ellingsen et al., 2005, Mouillot et al., 2005, Heino et al., 2007). Simaika and Samways (2009a) tested the AvTD with the DBI in nation-wide site selection, and found that the AvTD had good potential in regional, but not global site selection, while the DBI was found to be useful at both spatial scales. The subsequent recommendation was that the DBI should be integrated into freshwater quality assessment schemes that use macroinvertebrates.

In this study, I tested the DBI at the local scale. The objectives of this study were to (a) field-test the DBI as a measure of ecological integrity, (b) compare the DBI to a biodiversity index (AvTD) and, (c) compare the DBI to a freshwater macroinvertebrate-based health index (South African Scoring System).

2. Methods

Sampling was done according to a strict schedule of four two-week site visits, spaced six weeks apart, during the 2008-09 field season. This ensured detection of seasonal changes in populations and their associated habitats. Sampling dates were 1 to 11 April 2008, 3 to 13 July 2008, 1 to 11 October 2008, and 15 January – 31 January 2009. Twenty river sites were chosen, at Tsitsikamma, South Africa, with each river represented by one upper and one lower sampling site (Table 1.1). Where possible, these sites were at the main-stem of the river, but lack of accessibility to main rivers in the rocky ravines sometimes required the use of close proximity tributaries as surrogates.

2.1. Environmental variables

At each site, the pH, water temperature, DO (dissolved oxygen), electrical conductivity and TDS (total dissolved solids) were measured using a handheld multiparameter water quality meter (Model: YSI 6920 V2 Sonde; Make: YSI Environmental). Elevation was measured using a handheld GPS unit

(Model: ETrex Legend, Make: Garmin). In addition, water samples were collected from each site using 2l plastic jugs, and frozen until these could be analyzed in the laboratory by Talbot Laboratories (Pietermaritzburg, South Africa). Laboratory analysis measured 27 environmental variables (EVs), which for 11 EVs, there was lack of sample size to make the measurement. A further three were analyzed only in any one of the four sampling seasons, and five were analyzed twice out of the four sampling seasons. In total therefore, only nine of the laboratory analyzed EVs were included in the analysis. These laboratory tested EVs were: ammonia (mg N/l), chloride (mg Cl/l), dissolved magnesium (mg Mg/l), fluoride (μg F/l), nitrate/nitrite (mg N/l), orthosulphate (mg P/l), sodium (mg Na/l), sulphate (mg SO_4 /l), and total dissolved iron (mg Fe/l).

In addition to continuous EVs, also categorical information was collected on percentage canopy shade cover, dominant flow regime (pool, run, riffle), and disturbance regime (natural, near natural (i.e. <10% alien vegetation cover), alien (>75% alien vegetation cover)). Percent shade was measured as the percentage of the stream that was shaded at mid-day. Flow regime was characterized as in Dickens and Graham (2002).

2.2. Dragonfly collection

Adult male dragonflies were counted along transects. The length of transects varied according to habitat accessibility (Table 1.1). Therefore, sampling was standardized to one hour of intensive sampling, by a two-person team. To avoid duplication of counts, specimens were collected and later released. Where abundance was very high, estimates were made of the relative abundance of species encountered. Where identification could not be made directly by use of close-focus binoculars, the individuals were caught, identified in-hand, and released. Voucher specimens were collected from each site for reference. Point counts were conducted along both river banks, including the margins up to 2 m from the edge and across the river itself. Sampling of adult dragonflies was conducted on fine, windless days between 9:00 and 17:00 hr. Only male abundance was recorded. Male adult dragonflies are more easily identified than females in the field, as the latter are rather cryptic, or are not found at the water. Especially females of Zygoptera species are easily misidentified or missed. Indeed, Moore (1991) states that counts of Anisoptera are almost 100% accurate, while counts of Zygoptera are 80% accurate, the latter either being missed or counted twice. Furthermore, unlike males, females and teneral males tend to leave the water to mature and return only to water to mate, while adult males generally set up territories in wait for females to return (Corbet, 1999). Adult specimens were identified using Samways (2008) and Tarboton and Tarboton (2002).

Table 2.1. Details of sampling sites (Tsitsikamma region, Western and Eastern Cape Provinces, South Africa), including river name, sampling site abbreviation, site coordinate (WGS 1984), transect length and elevation of site.

River	Abbreviation	Co-ordinates	length (m)	Elevation (m)
Bloukrants River, Lower	BLU(L)	33°57'21"S; 23°38'19"E	500	40
Bloukrants River, Upper	BLU(U)	33°55'04"S; 23°38'20"E	500	276
Bobbejaans, Upper	BOB	33°53'47"S; 23°33'20"E	150	414
Buffels River, Lower	BUF(L)	33°59'8"S; 23°27'49"E	300	32
Buffels River, Upper	BUF(U)	33°58'57"S; 23°28'44"E	300	61
Elands River, Lower	ELW(L)	34°01'03"S; 24°03'39"E	200	56
Elands River, Upper	ELW(U)	33°57'47"S; 24°03'09"E	300	313
Elandsbos River, Lower	ELL(L)	33°58'01"S; 23°46'30"E	500	215
Elandsbos River, Upper	ELL(U)	33°55'57"S; 23°46'58"E	300	254
Groot River East, Lower	GRE(L)	34°02'5"S; 24°12'27"E	500	39
Groot River East, Upper	GRE(U)	33°58'21"S; 24°07'16"E	200	275
Groot River West, Lower	GRW(L)	33°59'8"S; 23°27'49"E	500	14
Groot River West, Upper	GRW(U)	33°54'46"S; 23°34'37"E	150	312
Lottering River, Lower	LOT(L)	33°58'24"S; 23°44'51"E	350	218
Lottering River, Upper	LOT(U)	33°55'59"S; 23°43'46"E	200	267
Matjies River	MAT	33°58'51"S; 23°27'28"E	300	51
Salt River, Lower	SLT(L)	33°58'28"S; 23°31'20"E	500	47
Salt River, Upper	SLT(U)	33°55'36"S; 23°29'23"E	500	265
Storms River, Lower	STR(L)	33°59'19"S; 23°55'09"E	300	65
Storms River, Upper	STR(U)	33°56'57"S; 23°54'55"E	150	285

2.3. Dragonfly Biotic Index

The Dragonfly Biotic Index (DBI) (Simaika and Samways, 2008, 2009a, 2009b) is used here as an ecological habitat integrity measure. The DBI relies on dragonfly species presence-absence data. The DBI comprises three sub-indices: a species relative geographic distribution, threat status based on IUCN Categories and Criteria (IUCN, 2008), and species sensitivity to habitat disturbance (Simaika and Samways, 2009a). Each sub-value ranges from 0 to 3. The sum of the sub-values for any one species is the standard DBI score, which can range from 0 to 9. The standard DBI for all known South African dragonfly species is given in Samways (2008). To arrive at a DBI score per site, I divided the total of all the species DBIs by the total number of species. This method thus standardized the DBI score to give the DBI site value, which now ranged between 0 and 9, allowing us to compare DBI site values to one another. The conditions needed to arrive at the correct DBI values are outlined in Simaika and Samways (2009a).

2.4. Sampling for the South African Scoring System

The South African Scoring System (SASS5) was used to assess benthic macroinvertebrates (including dragonfly larvae) using the protocol of Dickens and Graham (2002), by a team of SASS specialists provided to the project by the national Department of Water Affairs and Forestry (DWAF). The SASS method involves sampling of aquatic macroinvertebrates in riffles, glides and deposition zones. Scores are assigned to each taxon according to its sensitivity or tolerance to disturbance or pollution (Dallas, 2000). Unlike the DBI, in SASS, the sensitivity scores are based only on the tolerance of taxa to disturbance. High sensitivity scores are allocated to the most sensitive benthic macroinvertebrate taxa, and lowest scores to those which are least susceptible. The sum of the individual scores is the macroinvertebrate (SASS) score, which gives a preliminary index of water condition. However, the average score per taxon (ASPT) is the most standardized measure, and is calculated by dividing the macroinvertebrate score by the number of sampled taxa. The ASPT score is equivalent to the DBI site value, as both have been standardized in the same manner.

Benthic macroinvertebrate samples at each site were taken during each sampling season. All available microhabitats were sampled: stones, both in and out of current, vegetation (marginal and aquatic vegetation), and gravel, sand and mud. All samples from all biotopes were kept and preserved in 90% ethanol.

2.5. Average Taxonomic Distinctness

Average Taxonomic Distinctness (AvTD) was used here as a biodiversity measure. I found in a previous study that AvTD performed well at the regional scale and I now aimed to test AvTD at the local scale (Simaika and Samways, 2009a). The AvTD measure calculates the average taxonomic distance between any two species chosen at random from a sample (Warwick and Clarke, 1995; Clarke and Warwick, 1998, 2001). In contrast to other diversity measures, AvTD can be used in situations where sampling is uncontrolled, unknown or unequal, and where data are nominal, i.e. species are present or absent. Using species lists (presence-absence) has the advantage of ensuring that no one species can dominate contributions to the index (Clarke and Warwick, 1998, 2001). For each of the biotic assemblages, I used five taxonomic levels in the aggregation file for the analysis. For the Odonata, these levels were Order, Suborder, Family, Genus, and Species, and for the macrobenthic invertebrates, these were Phylum, Class, Order, Suborder, and Family. Funnel plots of taxonomic distinctness and species richness were constructed with 95% confidence envelopes. The limits of the funnel plot become increasingly wide as sample size decreases, which increases uncertainty. Significantly disturbed sites should fall below the lower 95% confidence.

2.6. Statistical Analyses

The software packages PRIMER V6 (Clarke and Warwick, 2001), CANOCO V4.5 (ter Braak and Smilauer, 2002) and SPSS V13 (SPSS Inc., 2004) were used for statistical analyses.

2.6.1. Canonical Correspondence Analysis

Canonical Correspondence Analysis (CCA) is a direct gradient analysis technique that uses multiple regression to select linear combinations of EVs that account for most of the variation in the assemblage structure (ter Braak, 1986). Forward selection was used to rank EVs in order of importance according to the eigenvalues produced (i.e. variation in the species data accounted for by that variable) when each variable was considered individually. Monte Carlo permutation tests, using 999 unrestricted random permutations, were performed to test the significance of the EVs on faunal distribution patterns.

2.6.2. BIOENV

The BIOENV selects EVs, or species best explaining community pattern, by maximizing a rank correlation between their respective resemblance matrices (Clarke and Warwick, 2001). Prior to analysis using BIOENV, EVs were visualized using a correlation matrix. Non-normally distributed variables were log-transformed. The EVs were then normalized to allow comparison at the same scale.

A new correlation matrix was generated, and strongly correlated values identified (matrix value > 0.95). Strongly collinear EVs were removed from subsequent analyses.

2.6.3. *Similarity*

As biotic data were collected seasonally, the datasets were first averaged, representing the entire study period. Species abundance data were square-root transformed. Subsequent to transformation, a Bray-Curtis similarity was performed to assess the similarity between sites. Clarke and Warwick (2001) recommend Bray-Curtis similarity to assess similarity in ecological studies, as this similarity is not affected by absences and gives more weight to abundance in comparing species. Similarity based on Euclidean distances was also performed on treated (averaged, transformed and normalized) abiotic data.

2.6.4. *RELATE analysis*

The RELATE function in PRIMER V6 allows a user to compare two sets of multivariate data based on a matching set of samples, by calculating a rank correlation coefficient between all the elements of their similarity matrices (Clarke and Warwick, 2001). In this study, abiotic-biotic and biotic-biotic relatedness was analyzed using the similarity matrices produced in the previous steps. The RELATE analysis was also used to test the seriation of samples spatially, to detect any trends in taxon turnover that may be present.

2.6.5. *Cluster analysis*

After computation of similarity, a cluster analysis was performed in PRIMER V6 (Clarke and Warwick, 2001) using the triangular matrix generated through Bray-Curtis similarity. Cluster analysis forms a natural grouping of data based on similarity amongst separate samples, where samples within a group are more similar than samples from a different group. Clustering using group averages was used to plot the cluster dendrograms.

2.6.6. *Spearman rank correlation*

The following biotic scores were tested for correlations between pairs. These included the DBI, DBI site value, AvTD, SASS, ASPT, dragonfly species richness and macroinvertebrate taxa richness. Biotic scores were square-root transformed. Two-tailed Spearman rank correlation analyses were produced,

and scatter plots generated for significant correlations, in SPSS V13. Spearman rank correlations were used as these assume non-normality of data.

3. Results

3.1. Environmental variables

Based on a CCA, the only EVs found to be significant in structuring the dragonfly assemblages were pH ($F = 3.63$, $p < 0.001$) and water temperature ($F = 3.86$, $p < 0.001$). The findings of the BIOENV analysis supported the CCA. The pH and water temperature explained 70% of the structure of the dragonfly assemblage. Similarly, for the benthic macroinvertebrates, pH alone explained 64% of the variability in this assemblage. A cluster analysis of the abiotic EVs revealed a structuring of sites similar to that explained in detail for the biotic analyses (Figure 2.1). RELATE analysis confirmed that the abiotic EVs and biotic assemblages were significantly related, both for dragonflies ($\rho = 0.47$, $p < 0.001$) and benthic macroinvertebrates ($\rho = 0.51$, $p < 0.002$). Of interest is that the BUF(L), BUF(U), and MAT sites were, based on the abiotic information alone, very different from the other sites. Of note is also that the ELW(L) and SLT(L) grouped together. As shown below, this latter grouping was also reflected in the cluster analysis on benthic macroinvertebrates (Figure 2.3). Also, the BLU(U) site does not group with any other site, which was not reflected by the biotic assemblages. The remaining sites clustered closely together, and there was no clear pattern.

3.2. Relatedness of the biotic assemblages

The RELATE analysis revealed that the dragonfly species assemblage and benthic macroinvertebrate taxa assemblage were significantly related. The same result was found, whether using relative abundance data ($\rho 0.55$, $p < 0.001$) or presence-absence ($\rho 0.45$, $p < 0.001$) data, for the assemblages.

3.3. Cluster analyses of the biotic assemblages

It should be noted that for ease of description, the following cluster dendrograms are presented using groupings. These do not, however, represent any statistical significance, but are used to accentuate patterns in the resultant analyses.

3.3.1. Dragonflies

The overall groupings of the dendrogram produced by the cluster analysis combined into six major groups (Figure 2.2). Group 1 consisted of four sites, ELW(L), BUF(U), BUF(L) and MAT, all of which were more similar (66.07% similarity) to each other than sites of any other grouping. Indeed, the sites of Groups 2 to 6 shared only 30.73% similarity with those of Group 1. All remaining groups shared 37.46% similarity. Groups 2 and 3 were overall more similar (49.11%) than Groups 4, 5 and 6 (41.57%). The sites of Group 2, GRE(L), GRW(L), ELL(U) and STR(L), were more similar (58.23%) than the sites SLT(L), BLU(L) and BOB of Group 3 (54.02%). Group 4 was distinct from all other groupings in that it only consisted of one site, STR(U). Group 5 and 6 shared 58.38% similarity. Group 5 consisted of six sites, making it the largest grouping, with 60.13% similarity. The two sites BLU(U) and LOT(U) of Group 6 were 57.40% similar.

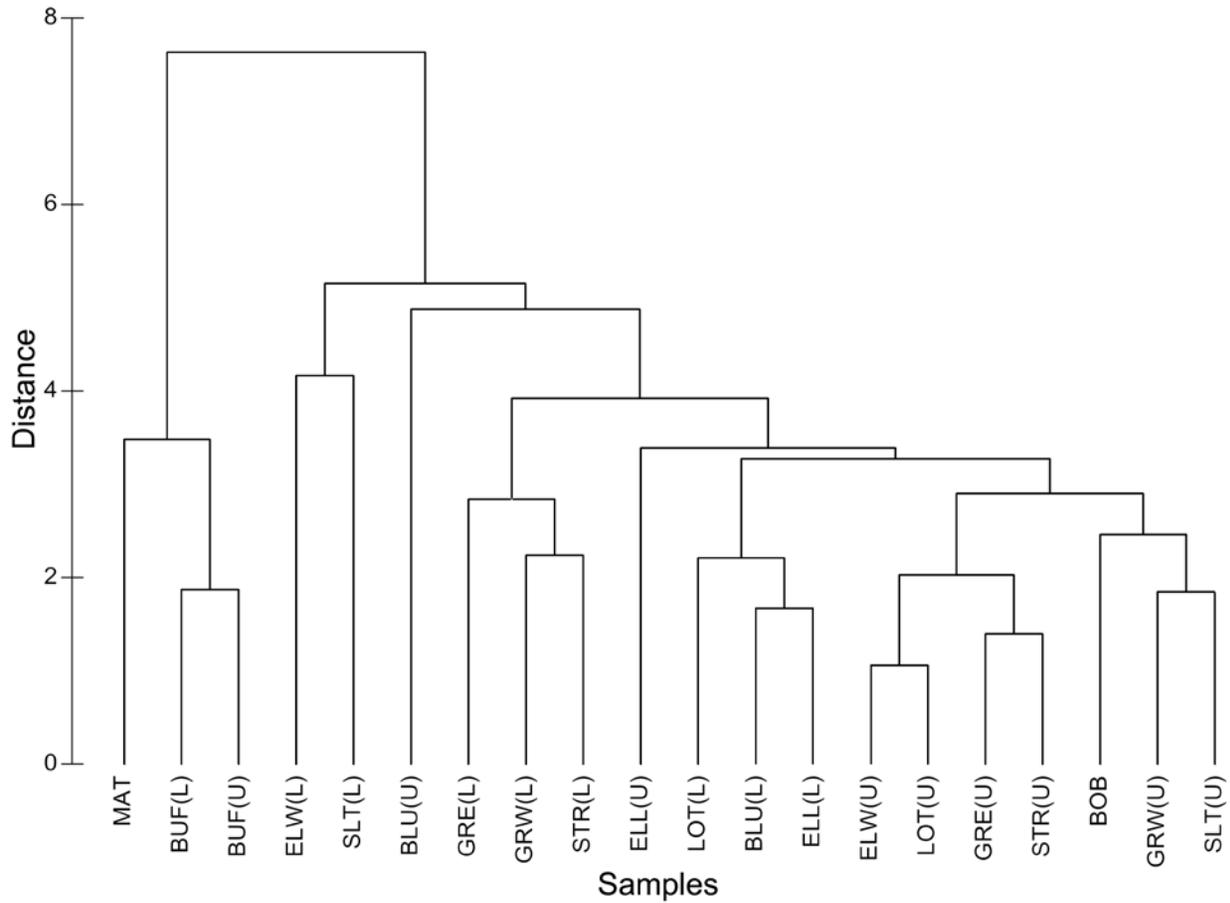


Figure 2.1. Cluster dendrogram of sites based on Euclidean distances, showing the distances of the sites based on the environmental variables. Full names of abbreviated samples are given in Table 2.1.

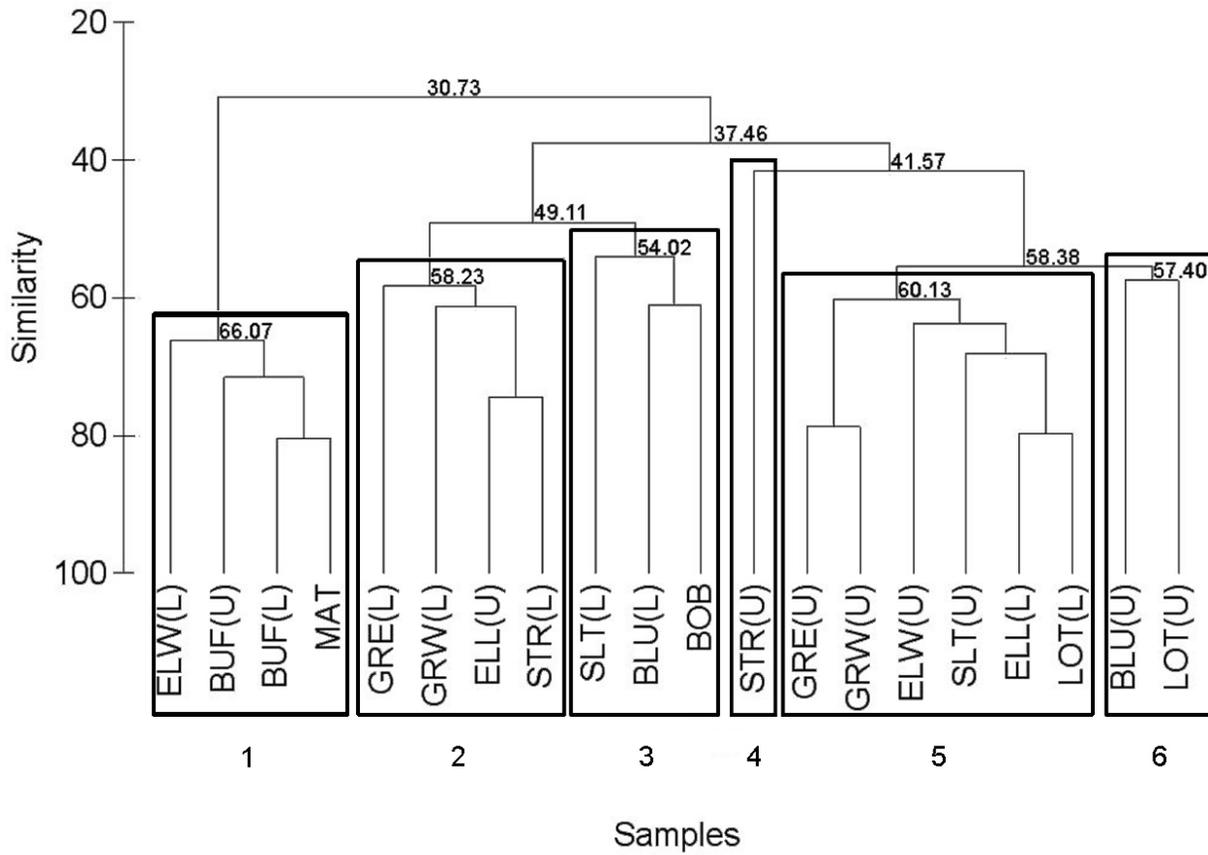


Figure 2.2. Cluster graph of sampling sites based on dragonfly species abundance. Percent similarities are given for each junction. Full names for sample abbreviation names are given in Table 2.1.

3.3.2. *Benthic macroinvertebrates*

The cluster dendrogram of similarities based on benthic macroinvertebrates (Figure 2.3) showed that these were overall more similar than those based on dragonflies (Figure 2.2). Groups 7 to 12 shared 50.65% similarity. The three sites of Group 7, BUF(U), BUF(L) and MAT were most similar (68.62% similarity). Group 8 shared only 53.07% similarity with Groups 9 to 12, but the two sites that made up Group 8, ELW(L) and SLT(L) share 67.28% similarity. Group 9 shared only 56.29% similarity with Groups 10 to 12, but the two sites, ELW(U) and STR(U) shared 67.35% similarity. Group 10 consisted of only one site, STR(L), and shared 62.21% similarity with Groups 11 and 12, while the latter share 65.53% similarity. Group 11 was the largest, consisting of eight sites, which were 67.77% similar. The four sites of Group 12, GRE(L), GRW(L), BLU(L) and SLT(U) were 66.62% similar.

3.3.3. *Dragonflies compared to benthic macroinvertebrates*

The dendrograms of the dragonfly assemblage compared to those of the benthic macroinvertebrates revealed that the dragonfly assemblage was overall more dissimilar than that of the benthic macroinvertebrates, with the dragonflies being 69.27% dissimilar, while the benthic macroinvertebrates were 49.35% dissimilar (Figures 2.2 and 2.3). Similarity of groups for dragonflies ranged from 41.57% to 66.07%, while for benthic macroinvertebrates, the range was 62.21% to 68.62%. Of interest is that Groups 1 and 7 were least similar to the other groups in both dendrograms, having three sites in common (BUF(U), BUF(L) and MAT). Although site ELW(L) fell within group 1 for the dendrogram based on dragonflies, site ELW(L) was more similar to the SLT(L) site in group 8 based on benthic macroinvertebrates than the three sites of group 7 (Figure 2.3). Groups 2 and 12 both consisted of four sites, having only two sites, GRE(L) and GRW(L), in common. Site STR(L) was part of group 2 for dragonflies, but was a distinct group (Group 10) in the dendrogram based on benthic macroinvertebrates. Although the STR(U) site (Group 4) was similar to groups 5 and 6, it formed its own distinct group for dragonflies. The differences between the remaining sites were less clear, as sites became more similar.

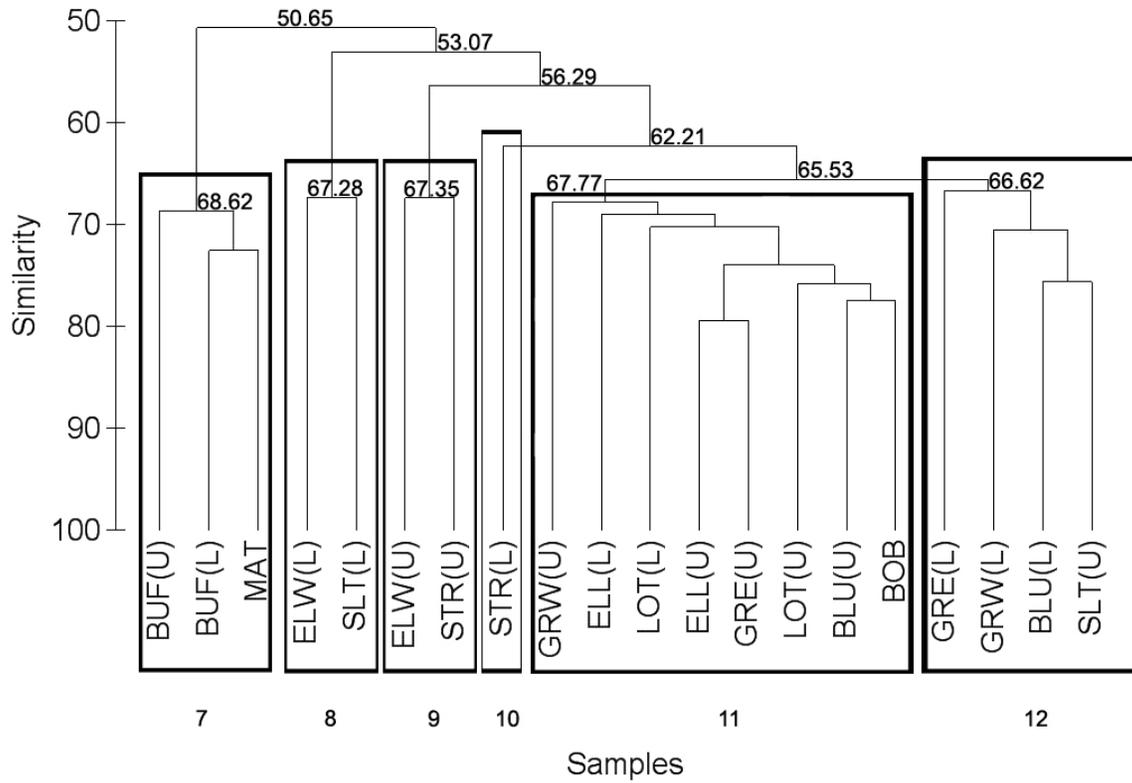


Figure 2.3. Cluster graph of sampling sites based on benthic macroinvertebrate taxa abundance. Percent similarities are given for each junction. Full names for sample abbreviation names are given in Table 2.1.

3.4. Average taxonomic Distinctness (AvTD)

A Spearman-rank correlation test, used to determine whether the AvTD values of dragonflies and benthic macroinvertebrate assemblages were correlated, was not significant. The funnel plots of the AvTD scores based on the abundances and species compositions of dragonflies and benthic macroinvertebrates are shown in Figures 2.4 and 2.5 respectively.

3.4.1. Dragonflies

The majority of sites (14) in the funnel plot fell above the mean and within the 95% confidence interval (Figure 2.4). This indicates that diversity at these sites was within expected limits. However, three sites scored particularly low. These were, in decreasing order of number of species GRE(U), GRW(U) and STR(U). The GRE(U) site fell below the lower 95% confidence envelope, indicating lower diversity than expected by chance. As fewer species were recorded at a site, the lower the possibility of assigning a value with high confidence, and thus the funnel plot broadened to the left of the graph (Clarke and Warwick, 2001). At site STR(U), only two species were recorded, and thus the AvTD score was very low at this site. Two other sites, SLT(U) and GRE(L) scored below the mean, but within the 95% confidence envelopes. The MAT, BUF(U) and BUF(L) sites fell above the mean in the funnel envelope, while BLU(U), BLU(L) and BOB scored well above the mean.

3.4.2. Benthic macroinvertebrates

The funnel plot based on benthic macroinvertebrates was almost the opposite to the that based on dragonflies, in that seven sites fell above the mean, while, 13 sites fell below the mean (Figure 2.5). The BUF(L) site fell above the upper 95% limit of the envelope. The BUF(U) and MAT sites fell above the mean, but within the limits of the envelope, as did STR(U) (but see the dragonflies above), ELW(U), ELW(L) and SLT(L). Four sites fell outside the lower 95% limit of the envelope. These were, in decreasing order of number of species, ELL(L), BLU(L), LOT(U) and GRW(L).

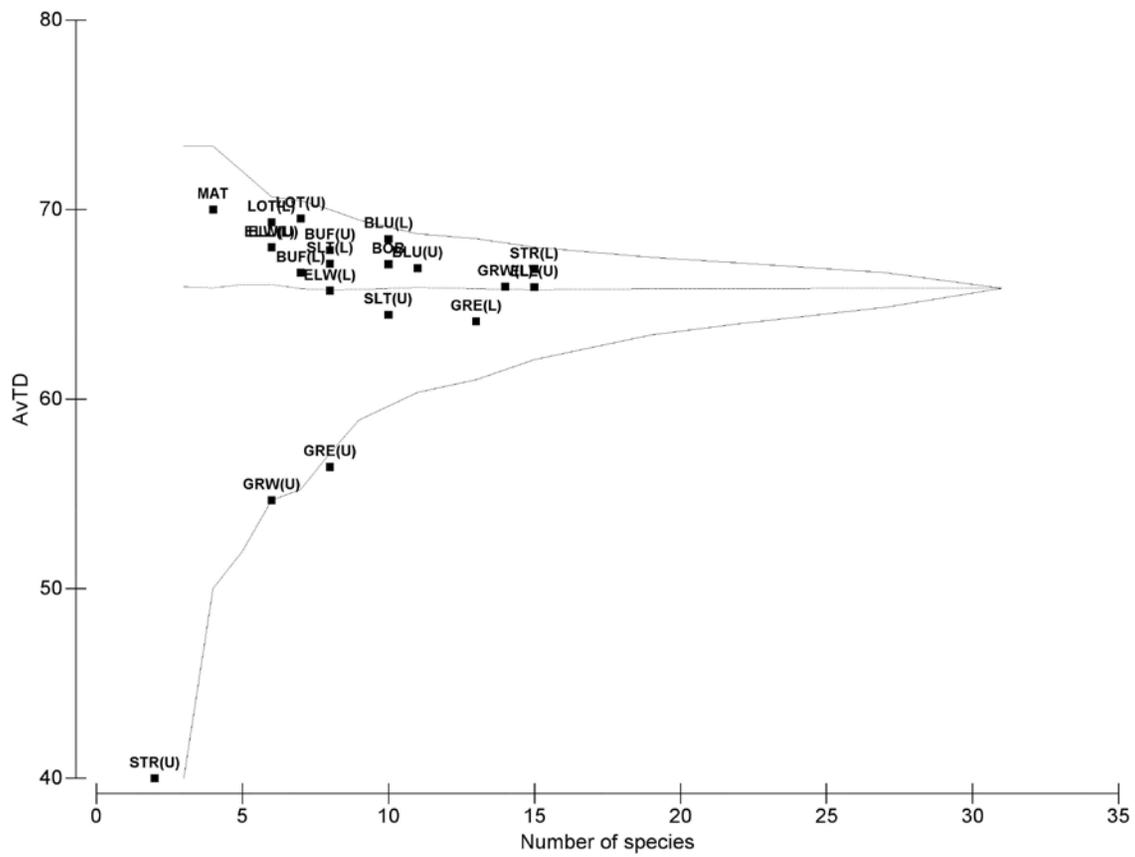


Figure 2.4. Funnel plot of average taxonomic distinctness (AvTD) of sampling sites based on dragonfly species abundance. Full names for sample abbreviation names are given in Table 2.1.

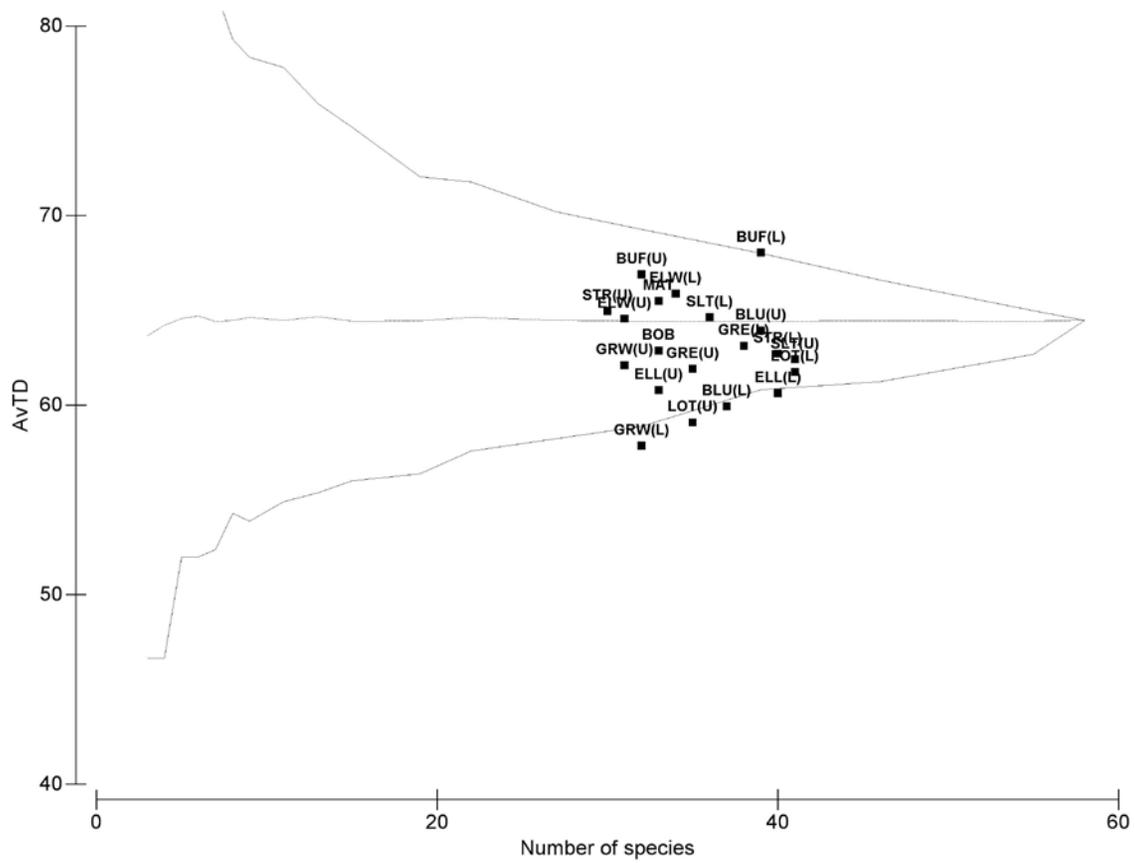


Figure 2.5. Funnel plot of average taxonomic distinctness (AvTD) of sampling sites based on benthic macroinvertebrate taxa abundance. Full names for sample abbreviation names are given in Table 2.1.

3.5. Biotic index scores

A comparison of the resultant biotic scores, the Dragonfly Biotic Index (DBI) and South African Scoring System (SASS) are shown for each site in Table 2.2. Significant correlations were found between the DBI site value and ASPT ($r_s = 0.561$, $n = 20$, $p < 0.005$) (Figure 2.6), as well as the SASS score and ASPT ($r_s = 0.624$, $n = 20$, $p < 0.003$) scores. The DBI site value and SASS scores were found to be significantly correlated at the 0.05 level ($r_s = 0.402$, $n = 20$, $p < 0.04$), but not the 0.01 level. No significant correlations were found in comparisons of any of the other biotic scores based on the dragonfly or benthic macroinvertebrate assemblages.

Table 2.2. DBI and SASS scores for each site (Tsitsikamma region, Western and Eastern Cape Provinces, South Africa): Dragonfly species richness, DBI score, DBI site value, average macrobenthic taxa richness (SASS), average SASS score, and average ASPT score. Abbreviations: Av. = average. Site name abbreviations are explained in Table 2.1.

Site	Dragonfly species richness	DBI score	DBI site value	Av. macrobenthic taxa richness	Av. SASS score	Av. ASPT score
BLU(L)	10	44	4.4	23.5	179	7.675
BLU(U)	11	56	5.09091	25	186.75	7.4875
BOB	10	40	4	19.5	156.75	7.735
BUF(L)	7	24	3.42857	24.75	158.5	6.4075
BUF(U)	8	22	2.75	20.75	127.5	6.15
ELW(L)	6	29	4.83333	25.25	192.5	7.635
ELW(U)	15	53	3.53333	20.75	156	7.525
ELL(L)	8	30	3.75	17.5	96.75	5.6
ELL(U)	6	22	3.66667	18.25	138.5	7.6675
GRE(L)	13	33	2.53846	24.25	159.25	7.05
GRE(W)	8	40	5	23.75	181	7.625
GRW(L)	14	45	3.21429	20.25	147	7.125
GRW(U)	6	38	6.33333	22.5	169.75	7.5875
LOT(L)	6	31	5.16667	24.5	202	8.275
LOT(U)	7	35	5	23.75	186	7.8125
MAT	4	12	3	18.25	114	6.05
SLT(L)	8	38	4.75	22	149.5	6.825
SLT(U)	10	37	3.7	25.5	198.25	7.8
STR(L)	15	54	3.6	25	190	7.62
STR(U)	2	14	7	17.75	136.25	7.675

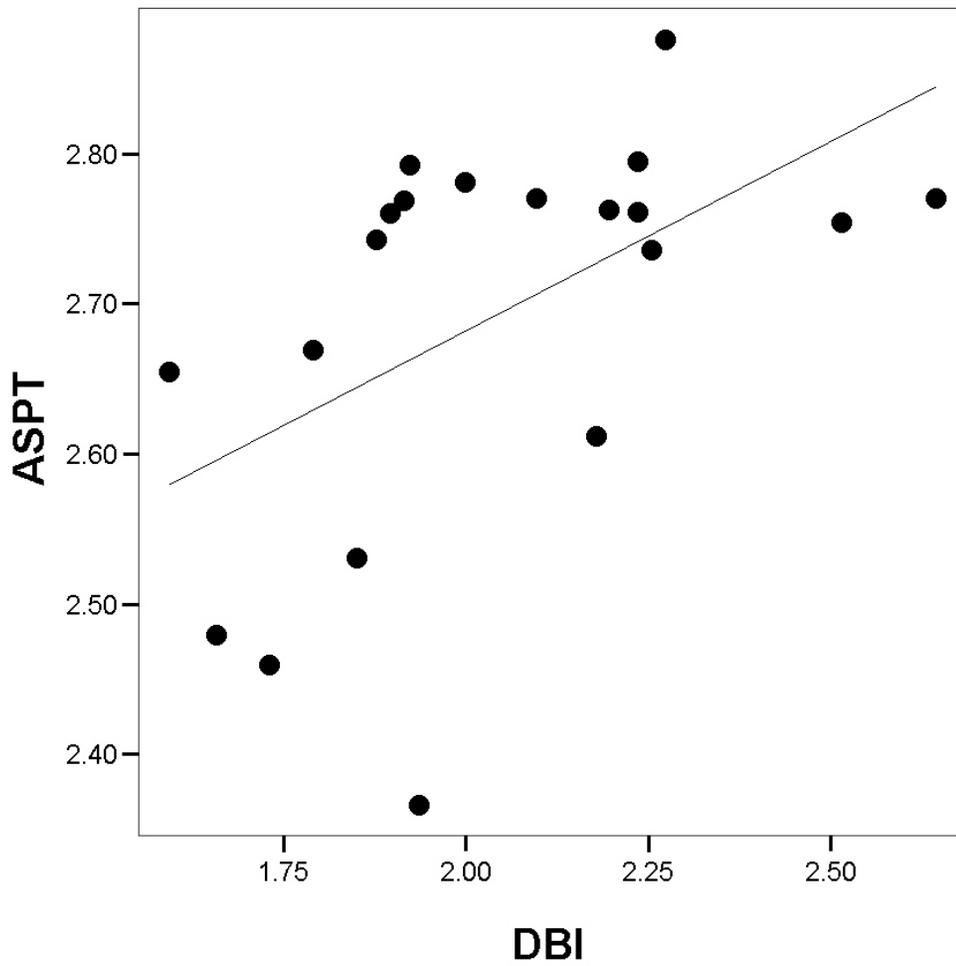


Figure 2.6. Two-tailed Spearman rank correlation ($r_s = 0.561$, $n = 20$, $p < 0.005$) of the square-root transformed Dragonfly Biotic Index (DBI) site value and Average Score Per Taxon (ASPT).

4. Discussion

4.1. Environmental variables, relatedness and cluster analyses

The results of the multivariate tests (both CCA and BIOENV) revealed that water temperature and pH were very important for structuring the adult dragonfly assemblage, accounting for 70% of the variability in the structure of that assemblage, while for the benthic macroinvertebrate assemblage, pH alone was significant, accounting for 64%. The RELATE analysis confirmed that the biotic assemblages were significantly related to the EVs. Furthermore, the clustering of sites using EVs was remarkably similar to that based on taxa (Figures 2.1, 2.2 and 2.3), and the RELATE analysis supported this result. The seriation analysis of both the dragonfly and benthic macroinvertebrate assemblages revealed that there was no significant taxon turnover across the sites, and the great overall similarity of sites as shown in the cluster dendrograms, particularly those of the macrobenthic invertebrates, strongly suggested that there was no trend in species composition change across sites.

More importantly, however, the RELATE analysis revealed that the dragonfly assemblage of the sites directly reflected that of the benthic macroinvertebrates. However, the cluster dendrograms of the dragonfly assemblage compared to that of the benthic macroinvertebrates indicated that the dragonfly assemblage were overall more dissimilar than that of the macroinvertebrate assemblage, and that within groups, for dragonflies, the range was broader and lower (Figure 2.2), while for benthic macroinvertebrates, it was comparatively short and high (Figure 2.3). This may indicate that the dragonfly assemblage is more responsive to habitat changes than those of the benthic macroinvertebrates. This characteristic makes the DBI an excellent tool for environmental assessment and monitoring freshwater biodiversity, especially as a complement to freshwater quality assessments, such as SASS (Smith et al., 2007; Simaika and Samways, 2009a).

4.2. Average taxonomic distinctness and biotic index scores

Taxonomic distinctness has been tested with success in environmental assessment of marine invertebrate assemblages to disturbance (Warwick and Clarke, 1995; Clarke and Warwick, 1998; Mouillot et al., 2005; Campbell and Novelo-Gutiérrez, 2007; but see Ellingsen et al., 2005). However, taxonomic distinctness has found little support in studies using freshwater organisms. In studies on aquatic beetles (Abellán et al., 2006), fish (Bhat and Magurran, 2006) and stream macroinvertebrates (Heino et al., 2007) taxonomic distinctness did not give any indication of anthropogenic degradation.

In this study I showed that dragonfly and benthic macroinvertebrate assemblages were significantly related. I therefore expected to find that the AvTD scores would also be significantly

related among assemblages. Based on the highly significant relationship between the DBI site value and ASPT score, I also expected that sites with lower DBI site values and ASPT scores would fall below the mean AvTD, if not below the lower 95% confidence limit of the funnel plot envelope. However, the sites that should have scored lower, based on the DBI site values and ASPT scores (Table 2.2), especially the MAT, BUF(U) and BUF(L), fell above the AvTD means in the funnel plots for dragonflies, as well as for macroinvertebrates (Figures 2.4 and 2.5). The sites with the highest DBI scores, BLU(U), BLU(L) and BOB, however, also scored well above mean taxonomic distinctness for dragonflies. The same sites also scored well using the SASS and ASPT, but scored below mean taxonomic distinctness. Indeed, BLU(L) scored lower than expected by chance, below the lower bounds of the 95% confidence envelope (Figure 2.5).

The poor performance of taxonomic distinctness in this study may be due to the several reasons suggested by the other freshwater studies. Bhat and Magurran (2006) suggest that the longitudinal patterns in the river course are responsible for the variability in taxonomic distinctness. Heino et al. (2007) suggest that in their study multiple environmental gradients, including water chemistry, substratum characteristics and stream size were responsible for generating variability in taxonomic distinctness, and that these masked any environmental perturbations. Ellingsen et al. (2005) suggest that the usefulness of taxonomic distinctness depends on how consistently Linnean ranks are applied, and changes in classification may change their meaning and usefulness. However, the most plausible explanation is given by Abellán et al. (2006), in that it is not always the case that disturbed assemblages are composed of more closely related species than unperturbed assemblages, resulting in higher taxonomic distinctness. It may also happen that species disappear that are representative of the richer taxa, causing taxonomic distinctness to increase (Abellán et al. 2006). That is why in subsequent studies, perturbation was manifested as an increase or lack of response of the average taxonomic distinctness index. In the study by Abellán et al. (2006) taxonomic distinctness was found to be less sensitive than species richness or rarity, and no relationship was found between the recorded biodiversity measures and disturbance level. I suggest that caution must be exercised when using taxonomic distinctness to complement biodiversity studies or environmental assessments, and that more reliance should be placed on scoring methods.

4.3. Performance of the DBI and SASS

The advantage of dragonfly surveys over benthic macroinvertebrate surveys is that they provide a quick, and therefore low-cost, indication of the health or richness of freshwaters (Moore, 1997). This makes sense, as adult dragonflies are more easily observed and identified in the field (Simaika and

Samways, 2009a). Furthermore, SASS operates at the family and other higher taxon level, while dragonfly surveys are at the species level. Thus adult dragonfly surveys can detect changes at this lower taxonomic level, an advantage when it comes to conserving point endemic biota (Smith et al., 2007; Samways and Sharratt, 2009). In this study, I showed that the use of dragonflies, and in particular that of the DBI in comparison to the SASS, is of great value in environmental monitoring. Although the DBI site value and SASS scores were weakly correlated, I recommend not to compare them, as one score is standardized and the other is not. When both scores are standardized, as is the case for the DBI site value and the ASPT, then the scores are highly significantly correlated at the $p < 0.01$ level, and comparative use of these standardized scores makes sense.

The correlation of the DBI site value and ASPT indicates that the DBI method is at least as sensitive as the SASS method. The MAT, and the related BUF(U) and BUF(L) sites are genuinely biologically impoverished, as is reflected in the SASS and ASPT scores. However, at the STR(U) site, which scored high using the SASS and ASPT, only two dragonfly species were recorded over the entire sampling period, and because these are endemics, the DBI site value is also unusually high (7.00 score) (Table 2.2). This score is unrealistic, and thus it is important to use it in conjunction with dragonfly species richness, when interpreting the results. Low species richness and an unusually high DBI would suggest an impoverished site.

The DBI is useful for measuring ecological integrity but, as this study suggests, will also prove useful for the measurement of ecological health, including water quality. Specifically for South Africa, the DBI could be used alongside SASS, and indeed could be used in lieu of SASS, especially as adult dragonflies are much easier and faster to sample than benthic macroinvertebrates.

5. Conclusion

In this study, I found that pH and temperature are most important for structuring dragonfly assemblages, while for the benthic macroinvertebrate assemblage pH alone was significant. Furthermore, the dragonfly assemblages of the sites directly reflect those of the benthic macroinvertebrates. However, dragonfly assemblages are overall more dissimilar. This may indicate that the dragonfly assemblage is more responsive to habitat changes than those of the benthic macroinvertebrates. This characteristic makes the Dragonfly Biotic Index an excellent tool for environmental assessment and monitoring freshwater biodiversity, especially as a complement to freshwater quality assessments, such as SASS. In addition, the advantage of dragonfly surveys over benthic macroinvertebrate surveys is that they

provide a quick, and therefore low-cost, indication of the health or richness of freshwaters. This makes sense, as adult dragonflies are more easily observed and identified in the field. Furthermore, SASS operates at the family and other higher taxon level, while dragonfly surveys are at the species level. Thus adult dragonfly surveys can detect changes at this lower taxonomic level, an advantage when it comes to conserving point endemic biota. The DBI could be used alongside SASS, and indeed could be used in lieu of SASS, especially as adult dragonflies are much easier and faster to sample than benthic macroinvertebrates.

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Chapter 3

Reserve selection using Red Listed taxa in three global biodiversity hotspots: dragonflies in South Africa*

Abstract: *The Red List can be used as a gauging tool by conservationists to assess which species require focused conservation attention. Mapping the relative distributions of species, and identification of centers of richness, endemism and threat are a first step towards site-oriented conservation action. I use here a specially developed biodiversity index, based on three weighted sub-components assigned to each species: geographical distribution, Red List status, and sensitivity to habitat change. I test this approach using what is called here the Dragonfly Biotic Index (DBI) to prioritize sites for conservation action, with special emphasis on species occurrence in three global hotspots in southern Africa. Using a selected set of the 23 top prioritized sites, I compare the DBI's performance to that of a rarity-complementarity algorithm. As with several other taxa, local endemism levels are highest in the Cape Floristic Region (CFR), while richness is highest in the north west, particularly in the stream systems of the Maputaland-Pondoland-Albany (MPA) hotspot. Red Listed Odonata species are also concentrated in the CFR, while richness is highest in the MPA hotspot. Site prioritization using the DBI reveals that CFR sites protect Red Listed taxa rather well. The DBI demonstrates high levels of redundancy in representing Red Listed species, in other words, the same species are represented in several catchments. The value in the DBI thus lies in maximizing redundancy (i.e. representation) of globally Red Listed species. The rarity-complementarity algorithm represents all species, but without greater emphasis on the rare and threatened (i.e. Red Listed) species. I conclude that the DBI is of great value in selecting biodiversity hotspots, while the algorithm is useful for selecting complementarity hotspots. I identify protection gaps and thus recommend continued searches in centers of endemism and existing reserves, as well as gap areas.*

Keywords: biodiversity; hotspots; concordance; species richness; endemism; threat; Red List; conservation; dragonfly; Odonata; South Africa

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1. Introduction

Mapping the relative distributions of species, in this case of dragonflies, and identification of centers of endemism and species richness are a first step towards site-oriented conservation action. However, an approach is needed in which places are prioritized based on their biodiversity value (Abellán et al., 2005). This requires, first, a spatially explicit gap analysis from which I can determine which areas have not been sampled or require more sampling; second, a comparison of present reserves and species distributions in a hierarchal fashion.

1.1. Reserve selection

Reserve designs can be based on two major methodological approaches, (i) scoring procedures; or, (ii) species complementarity (Abellán et al., 2005; Gaston et al., 2001). Scoring procedures rank sites in order of value or priority according to one or several criteria, such as richness, rarity or threat status (e.g. Orme et al., 2005), and have been traditionally used in area selection (Abellán et al., 2005). The principle of complementarity was first coined by Vane-Wright et al. (1991). The complementarity value of a site relative to an existing set of prioritized sites is defined as its quantitative contribution to the representation of biodiversity features that are not adequately represented in the existing set (Sarkar et al., 2006). Methods based on complementarity are more recent than scoring procedures (Abellán et al., 2005), and are frequently based on the use of algorithms (e.g. Margules and Pressey, 2000).

Biodiversity hotspots are areas of high priority for conservation (Myers et al. 2002). They may be selected on the basis of their local species richness, degree of concentration of rare species (Prendergast et al., 1993) or the two measures combined with some assessment of urgency for conservation action (Myers et al., 2000). The Dragonfly Biotic Index, an expert-based scoring procedure that uses dragonflies (Odonata) as an indicator taxon to identify sites for conservation action, is designed to assign conservation (biodiversity) value to individual species. Intrinsic to the DBI is the targeting of rare, endemic, or Red Listed taxa, or species that are sensitive to habitat disturbance, by assigning a higher score to such species than those that are common and widespread (Simaika and Samways, 2009). The IUCN Red Listing process, an expert-based classification method (Gärdenfors, 2001), is integral to functioning of the index, as the DBI incorporates a score for each Red List status (both global and national categorization) of an individual species. The DBI is thus designed to identify biodiversity hotspots.

Araújo (2002) argues that ‘more targeted’ approaches identify complementarity hotspots, based on their relative contribution to attaining an overall conservation goal. Heuristic selection algorithms use complementarity, ordering places according to their biodiversity content, a process that is known as the ‘site prioritization problem’ (Kelley et al., 2002). ResNet, is a software package that implements algorithms based on the principles of rarity, complementarity, and richness (Garson et al., 2007). Richness is only used in the initialization part of the algorithms, as it results in inefficient place selection (Garson et al., 2007). Indeed, Abellán et al. (2005) found that the richness-based algorithm in ResNet was more efficient for their dataset on water beetles in Spain than the rarity-based algorithm. The rarity-complementarity-based algorithm continues site prioritization until a target is met (i.e. minimum species are represented, or the maximum allowed area or cost is exceeded). Biodiversity content is thus implicitly defined by the algorithm, and the intuition behind this approach is that diversity is adequately captured by rarity and complementarity (Garson et al., 2007).

1.2. Red Listing

The Red List is highly effective and authoritative, and may be used as a gauging tool by conservationists to assess which species require conservation attention (Gärdenfors et al., 1999). Of particular concern to the Red List are small, fragmented or declining populations, and range restricted species (Ginsburg, 2001). Thus, endemism per se has high conservation priority (Grill et al., 2002). The often extremely restricted range of endemic species, gives countries or regions that they inhabit a particular conservation responsibility, as disappearance from that area means their global extinction. The dependence on particular resources makes them especially vulnerable to changes in land use or habitat management. Even small alterations could lead to extinction (Grill et al., 2002).

Dragonflies are a well-studied group of invertebrates (Córdoba-Aguilar, 2008), with their increasing recognition in conservation worldwide (Samways, 2008a). In a regional context, this fact is reflected in dragonflies being the only insect group besides butterflies that are currently being assessed by the World Conservation Union (IUCN). For example, in an African context, dragonflies have been the subject of a regional southern African freshwater assessment (Suhling et al., 2008), and have been assessed in South Africa for Red List status (Samways, 2006). This knowledge base is continually expanded and refined, with recent discoveries of new species (Dijkstra et al., 2007), and re-discoveries of species (Samways and Tarboton, 2006), as well as numerous range-extensions.

Dragonflies are highly vagile, generalist predators, and thus tend to show lesser levels of endemism than many other insect taxa, and little dependency on plant composition (Grant and

Samways, 2007). Additionally, areas of high richness and endemism do not necessarily correspond (Prendergast et al., 1993). Indeed, Wishart and Day (2002) found that for a subset of the South African freshwater invertebrate fauna, species richness tends to be concentrated in the north east of the country, while endemism is highest and concentrated in the south western Cape Floristic Region (CFR). In South Africa, Red Listed dragonflies occur mostly in the mountainous regions of the CFR, also considered a centre of endemism for the group (Samways, 1992; Grant and Samways, 2007).

The Red List of the national (which also includes globally Red Listed taxa) conservation status of the South African dragonfly fauna, using current IUCN categories and criteria, resulted in a total of 42 odonate taxa being Red Listed (Samways 2006). The IUCN Red List categories of threat are Critically Endangered (CR), Endangered (EN) or Vulnerable (VU) (IUCN, 2006). Thus 25% of the national total of 162 taxa (i.e. species and subspecies) are Red Listed. In terms of endemic dragonfly taxa in South Africa, fourteen out of 33 taxa are globally Red Listed. Threats to these globally Red Listed taxa appear to come mainly from riverine invasive alien trees, especially wattle (*Acacia* spp.), and which have dense canopies that shade out the habitat (Samways and Taylor, 2004).

Of the 28 remaining nationally Red Listed taxa, six are marginal in South Africa; seven threatened mainly by habitat loss through urbanization, industrialization and pollution; and, nine by habitat loss through invasive alien trees. Many of the species on the national, but also global Red List, are further affected by a synergy of threats. Synergistic impacts include habitat disturbance by cattle that use invasive alien trees for shade. Cattle trampling causes direct destruction of the river bank and riparian vegetation, trampling of the larval habitat, and siltation of the stream (Kinvig and Samways, 2000). In some cases, there may be possible predation by trout, especially rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)). Detergent pollution, mine effluent and agricultural run-off, and over-extraction of water are also of concern (Samways and Taylor, 2004; Samways, 2004).

1.3. Objectives

I test the use of a newly developed, sensitive, easy-to-use and robust biodiversity index, the Dragonfly Biotic Index (Simaika and Samways, 2008, 2009). Before employing the DBI, I firstly identify species sampling gaps and biases, and patterns of richness, endemism and threat in a dataset of South African dragonflies. Secondly, using the DBI, I make recommendations for which areas require further recording effort. Thirdly, I identify areas for conservation action based on existing reserve networks. Finally, I compare site selection in the DBI and the ResNet rarity-complementarity algorithm with special emphasis on globally Red Listed species.

2. Methods

Biogeographic information on South Africa (including Lesotho and Swaziland) was used here. This area is unique in that such information is not only available to potential users worldwide, via the internet (SANBI, 2008), but that many taxa, including the dragonflies, are well sampled. A spatial-relational database was constructed from point-locality records of odonatological collections and sightings. The database consists of a merger between the unpublished Stellenbosch University database of collections and sightings (from 1988 to present) and a database of Pinhey's (1984, 1985) records. Additional records came from insect collections housed at the Iziko Museum (Cape Town), Albany Museum (Grahamstown), Northern Flagship Institution (Pretoria), National Museum (Bloemfontein) and National Insect Collection (Pretoria). Museum visits included verification of old records and identification of new specimens accessioned since 1984. Additional records came from new collection efforts, with special emphasis on endemic species sampling, during the field seasons from 2005-8 in the Western and Eastern Cape. These new records extend the known geographical range of the endemic Red Listed *Ecchlorolestes peringueyi* (Ris, 1921) and *E. nylephtha* (Barnard, 1937), and *Syncordulia venator* (Barnard, 1933) and the discovery of two new species, *Syncordulia legator* (Dijkstra, Samways and Simaika, 2007) and *S. serendipator* (Dijkstra, Samways and Simaika, 2007) (Dijkstra et al., 2007). In total, the current database now consists of 9945 species records from 897 locations.

From the resultant database, species distribution maps were constructed using both ArcView GIS 3.2a and ArcGIS 9.2 (Environmental Systems Research Institute 1999, 2006). The point-locality information was checked and verified, and has been used in the making of the southern African IUCN freshwater assessment (Suhling et al., 2008) and the field guide *Dragonflies and Damselflies of South Africa* (Samways, 2008b). The quaternary catchments map of South Africa was used for distribution mapping (SANBI, 2008).

The Dragonfly Biotic Index (DBI) (Simaika and Samways, 2008, 2009) is used here for identifying areas for conservation action, especially in the case of globally Red Listed taxa. The DBI relies on species presence/absence data. The DBI is comprised of three sub-indices (Table 3.1): a species relative geographic distribution, threat status based on IUCN Categories and Criteria (IUCN, 2001), and species sensitivity to habitat disturbance (Simaika and Samways, 2009). Each sub-value ranges from 0 to 3. The sum of the sub-values for any one species is the standard DBI score, which can range from 0 to 9. The standard DBI for all known South African odonate species is given in Samways (2008b).

Table 3.1. The sub-indices of the Dragonfly Biotic Index (DBI) range from 0 to 3. It is based on the three sub-indices relating to geographical distribution, level of threat, and sensitivity to habitat change, with particular reference to invasive alien riparian trees. The DBI is the sum of the scores for the three sub-indices, and ranges from 0 to 9. A common, widespread, not-threatened and highly-tolerant (of disturbance) species would score 0 (0 + 0 + 0), while a highly range-restricted, threatened and sensitive species would score 9 (3 + 3 + 3). Abbreviations: IUCN species status (IUCN, 2001): LC = Least Concern, NT = Near Threatened, VU = Vulnerable, CE = Critically Endangered, EN = Endangered, GS = Global Status, and NS = National Status.

Score	Sub-Indices		
	Distribution	Threat	Sensitivity
0	Very common throughout South Africa and southern Africa.	LC; GS	Not sensitive; little affected by habitat disturbance and may even benefit from habitat change due to alien plants; may thrive in artificial waterbodies.
1	Localized across a wide area in South Africa, and localized or common in southern Africa; or very common in 1-3 provinces and localized or common in southern Africa.	NT; GS or VU; NS	Low sensitivity to habitat change from alien plants; may occur commonly in artificial waterbodies.
2	National endemic confined to 3 or more provinces; or widespread in southern Africa but marginal and very rare in South Africa.	VU; GS or CR; NS or EN; NS	Medium sensitivity to habitat disturbance such as from alien plants and bank disturbance; may have been recorded in artificial waterbodies.
3	Endemic or near-endemic and confined to only 1 or 2 Provinces.	CR; GS or EN; GS	Extremely sensitive to habitat change from alien plants; only occurs in undisturbed natural habitat.

To arrive at a DBI score per site, I divided the total of all the species DBIs by the total number of species. This method thus standardized the DBI site values, which now ranged between 0 and 9, allowing us to compare site values to one another.

I chose ResNet 1.2 (Garson et al., 2007) and ResNet 2.1 (GUI) (Kelley et al., 2007) to calculate and visualize optimal reserve networks in ArcView 3.2a (Environmental Survey Research Institute, 1999). ResNet software is easily learned and used, and I therefore chose ResNet as a surrogate for other complementarity software for comparison with the DBI. I also used Randomize_ResNet_Input 1.0 for randomizing the input file 100 times. ResNet solutions generated from different randomizations of the same input file represent different ways to satisfy the same target of biodiversity representation (Fuller, 2005). For the purpose of site prioritization, I selected assemblages of at least 10 species (see also Simaika and Samways, 2009). I thus selected 213 catchments for analysis.

2.1. Statistical analysis

Primer V6 was used in correlating ResNet and the DBI using a Pearson correlation (Clarke and Warwick, 2001).

3. Results

3.1. Sampling gaps

Sampling gaps are shown in Figure 3.1, and quantitatively compared in Table 3.2. Only 21% of the countries' primary river systems have been sampled to date. The well-studied primary systems include the Limpopo (A), Olifants (B), Tugela (V), Mfolozi/Pongola (W), Komati/Crocodile (X), and Mkomazi (U) in the north east, the Keurboom/Storm/Krom (K), Swartkops (M) and Keiskamma (R) on the eastern Coast, and the Berg/Bot/Potberg (G) and Breede (H) in the south western Cape. However, even in this top category, only 38-46% of these primary catchment areas have been sampled. Even less (15-22%) of the inland Vaal (C), and the near-coastal and costal Sundays (N), Bushmans (P), Fish (Q), Kei (S) and Mzimvubu (T) have been sampled. By far the largest area, the vast inland Orange system (D), is among the least sampled (9%). This lowest category of representation (7-11%) includes the smaller systems of the Olifants (E) and Buffels (F) in the north west, and J (Gouritz) and L (Gamtoos) of the inland south east.

3.2. Richness, endemism and threat

All major aquatic regions have at least 1 to 17 species (Figure 3.2). The Limpopo, Mkomazi, Mfolozi/Pongola, and Komati/Crocodile (A, U, W and X) are the most species rich, with at least 50 or more species in a given river system. Intermediate regions of richness are the Olifants, Breede, Mzimvubu and Tugela (B, H, T and V). Low regions of richness are the remaining systems (C, D, E, F, G, J, K, L, M, N, P, Q, R and S).

Endemic species occur in all primary aquatic regions (Figure 3.3). The center of highest endemism occurs in regions G and H, the south western Cape, in which up to 16 endemic species can occur per catchment. Most river systems are intermediate in endemism (5-9 species) (A, B, C, D, E, J, K, L, P, R, S, T, U, V, and W). Systems low in endemism are the Swartkops, Sundays, Fish and Komati/Crocodile (M, N, Q and X).

Comparison of the categories of richness and endemism reveals that, in both cases, the Swartkop, Sundays, Fish and Buffels (M, N, Q (and F)) systems fall in the lowest category. Very likely, these are under-sampled systems. The Komati/Crocodile, while among the most species rich system in the country, is low in endemism (Figure 3.3), but the Limpopo, Mkomazi, and Mfolozi/Pongola (A, U and W) is intermediate in endemism. Also of interest is the Breede (H), which is high in endemism but intermediate in species richness, while the Berg/Bot/Potberg (G) is also high in endemism but low in species richness. The Olifants (E) and Gouritz (J) are intermediate in endemism and low in richness.

Threatened (i.e. Red Listed) species are found throughout the country, with the highest concentration in the Cape (Figure 3.4). The Berg/Bot/Potberg (G) and Breede (H) are the richest in threatened species, and the Olifants (E), Gourits (J), and Keurboom/Storm/Krom (K) are intermediate.

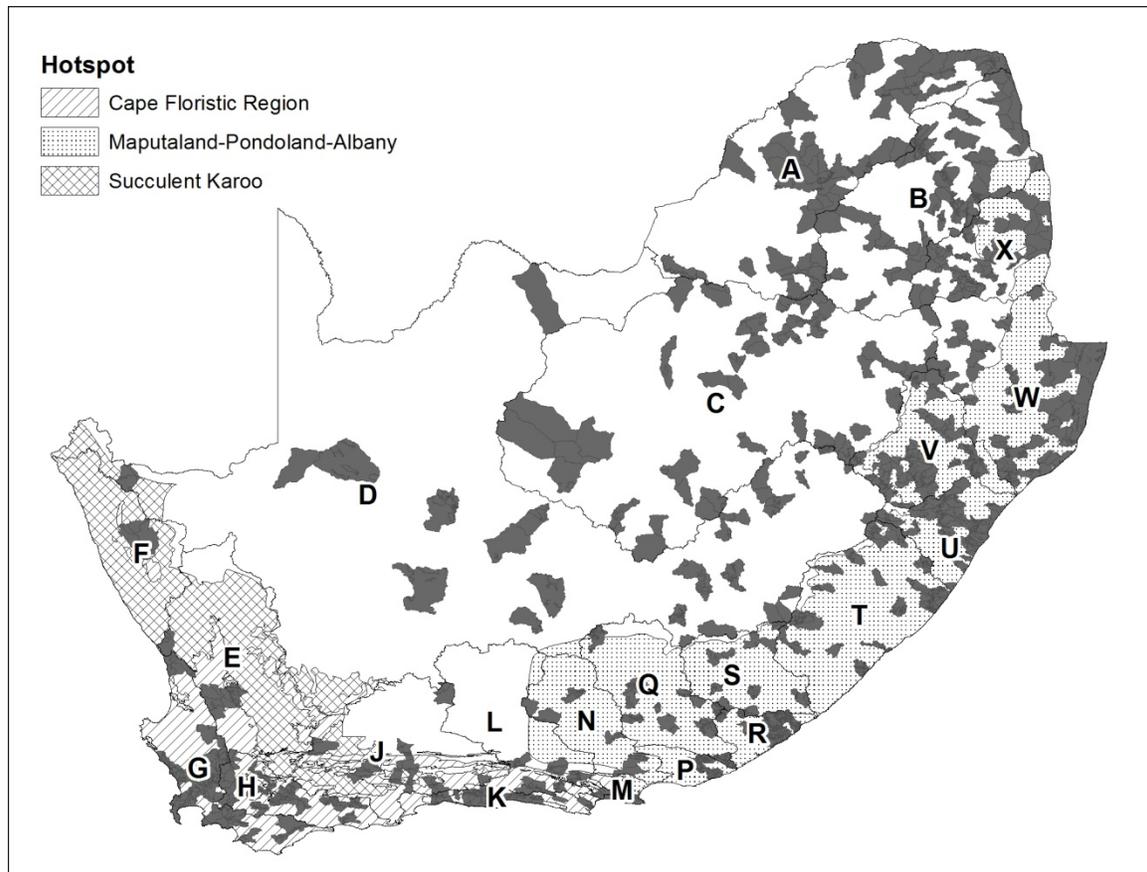


Figure 3.1. Global hotspots and primary catchment regions of South Africa. Highlighted areas (dark gray) show sampled quaternary catchments. Abbreviations are as follows: A (Limpopo), B (Olifants), C (Vaal), D (Orange), E (Olifants), F (Buffels), G (Berg/Bot/Potberg), H (Breede), J (Gourits), K (Keurboom/Storm/Krom), L (Gamtoos), M (Swartkops), N (Sundays), P (Bushmans), Q (Fish), R (Keiskamma), S (Kei), T (Mzimvubu), U (Mkomazi), V (Tugela), W (Mfolozi/Pongola), and, X (Komati/Crocodile).

Table 3.2. Count of sampled quaternary catchments (QC) in each primary catchment zone.

Primary Catchment	QC Sampled	QC	% QC Count	% QC Area
A (Limpopo)	52	139	37	36
B (Olifants)	47	145	32	35
C (Vaal)	43	193	22	22
D (Orange)	31	288	11	9
E (Olifants)	8	75	11	7
F (Buffels)	2	35	6	9
G (Berg/Bot/Potberg)	30	58	52	42
H (Breede)	29	69	42	39
J (Gourits)	11	92	12	11
K (Keurboom/Storm/Krom)	18	40	45	45
L (Gamtoos)	7	58	12	9
M (Swartkops)	3	8	38	42
N (Sundays)	6	36	17	15
P (Bushmans)	4	16	25	23
Q (Fish)	12	71	17	17
R (Keiskamma)	12	30	40	40
S (Kei)	10	58	17	17
T (Mzimvubu)	26	134	19	20
U (Mkomazi)	28	62	45	45
V (Tugela)	33	86	38	40
W (Mfolozi/Pongola)	43	151	28	38
X (Komati/Crocodile)	42	104	40	46
Total	497	1948	26	21

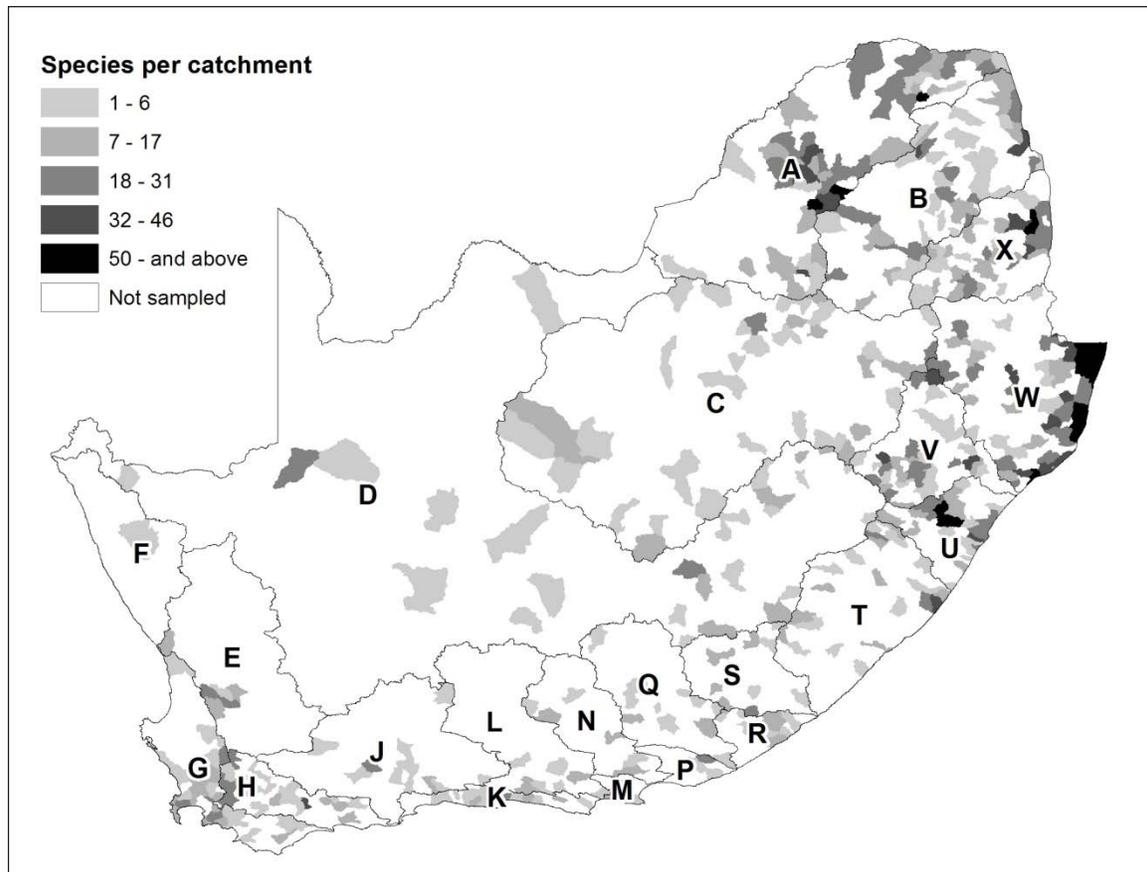


Figure 3.2. Dragonfly species richness across South Africa. Classes are based on natural groupings inherent in the data, established using the natural breaks function in ArcGIS (2006). Letters indicate primary catchment regions: Abbreviations for the primary catchment zones are as follows: A (Limpopo), B (Olifants), C (Vaal), D (Orange), E (Olifants), F (Buffels), G (Berg/Bot/Potberg), H (Breede), J (Gourits), K (Keurboom/Storm/Krom), L (Gamtoos), M (Swartkops), N (Sundays), P (Bushmans), Q (Fish), R (Keiskamma), S (Kei), T (Mzimvubu), U (Mkomazi), V (Tugela), W, (Mfolozi/Pongola) and X (Komati/Crocodile).

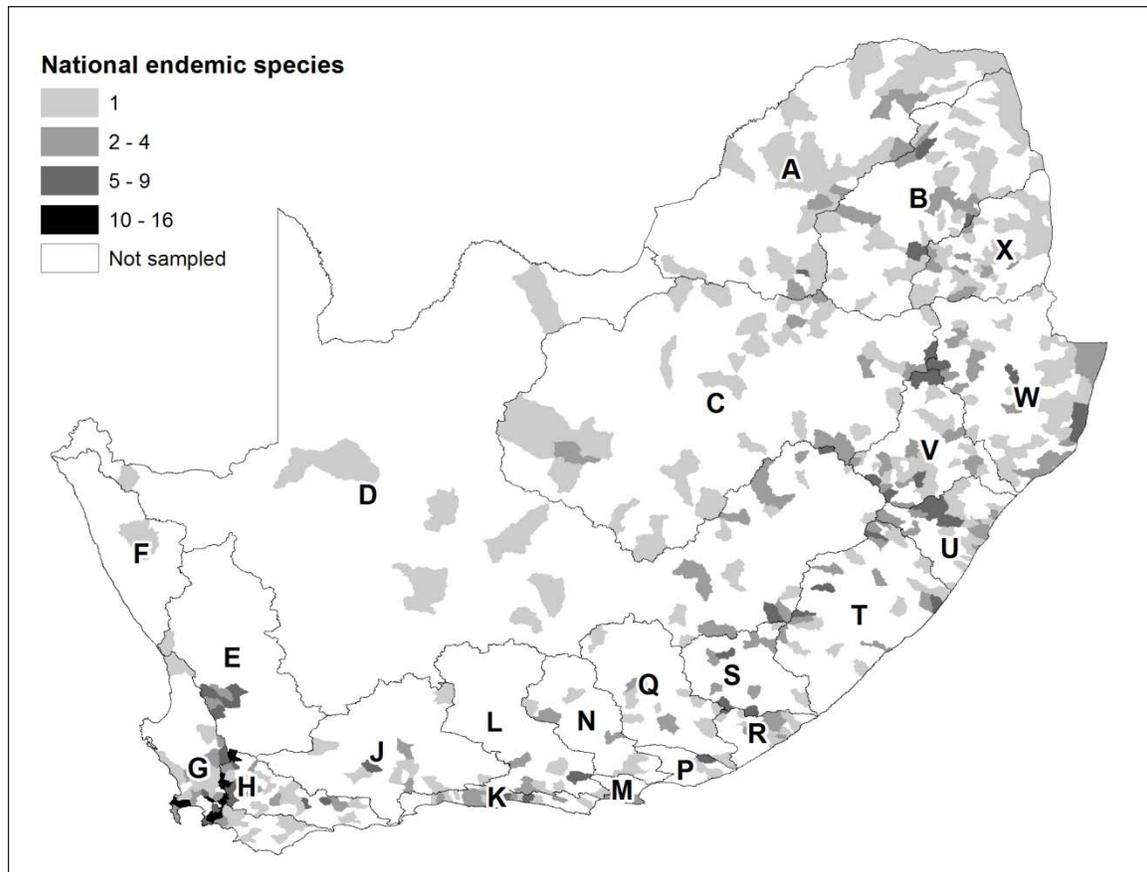


Figure 3.3. Number of national endemic dragonfly species across South Africa. Classes are based on natural groupings inherent in the data, established using the natural breaks function in ArcGIS (2006). Letters indicate primary catchment regions: A (Limpopo), B (Olifants), C (Vaal), D (Orange), E (Olifants), F (Buffels), G (Berg/Bot/Potberg), H (Breede), J (Gourits), K (Keurboom/Storm/Krom), L (Gamtoos), M (Swartkops), N (Sundays), P (Bushmans), Q (Fish), R (Keiskamma), S (Kei), T (Mzimvubu), U (Mkomazi), V (Tugela), W, (Mfolozi/Pongola) and X (Komati/Crocodile).

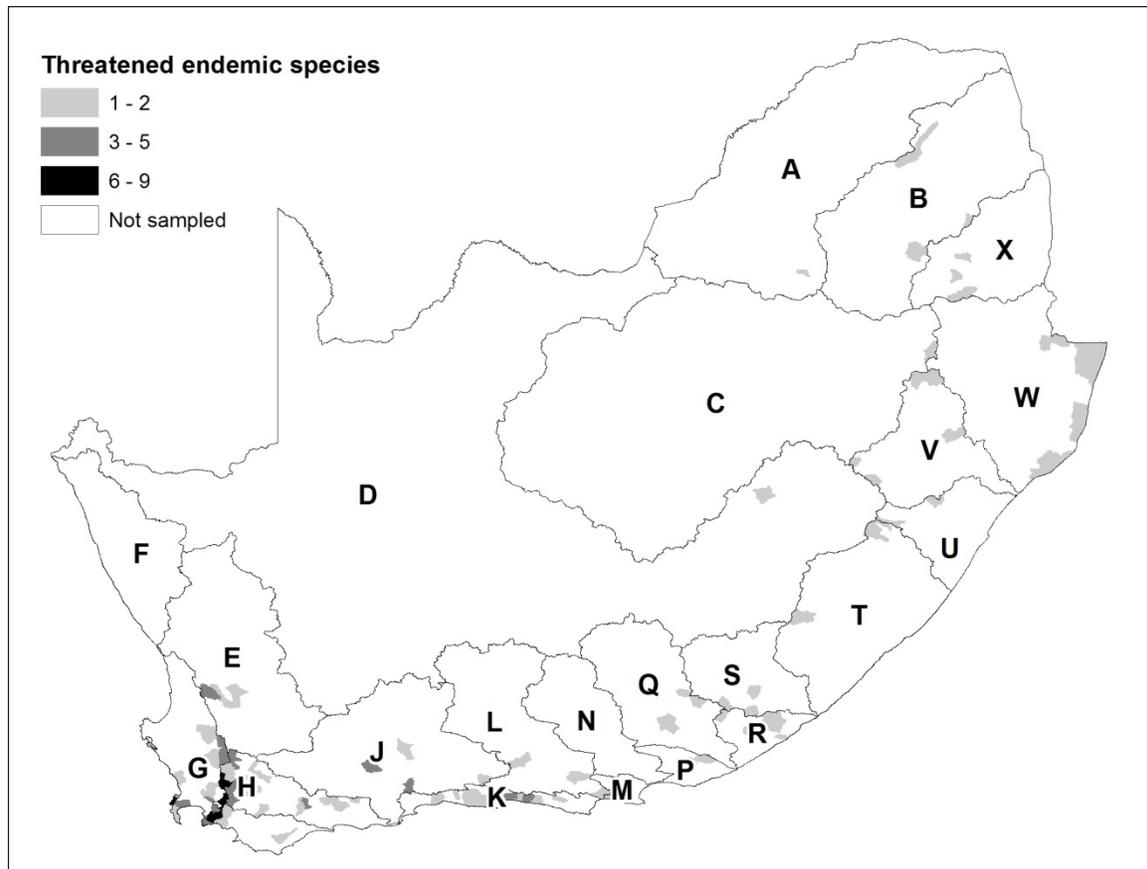


Figure 3.4. Number of Red Listed (threatened) national endemic dragonfly species across South Africa, using the IUCN categories and criteria (IUCN 2001). Classes are based on natural groupings inherent in the data, established using the natural breaks function in ArcGIS (2006). Letters indicate primary catchment regions: A (Limpopo), B (Olifants), C (Vaal), D (Orange), E (Olifants), F (Buffels), G (Berg/Bot/Potberg), H (Breede), J (Gourits), K (Keurboom/Storm/Krom), L (Gamtoos), M (Swartkops), N (Sundays), P (Bushmans), Q (Fish), R (Keiskamma), S (Kei), T (Mzimvubu), U (Mkomazi), V (Tugela), W, (Mfolozi/Pongola) and X (Komati/Crocodile).

3.3. Protected areas and threatened, endemic species

Of 897 recorded sites for all species, 270 sites occur in formally protected areas. Eleven of the 162 taxa occurring in South Africa do not occur in protected areas. Three include the non endemic, not threatened *Africallagma sinuatum* (Ris, 1921), *Crocothemis divisa* Karsch, 1898, *Proischnura subfurcatum* (Sélys, 1876) and *Orthetrum guineense* Ris, 1910, the nationally Red Listed, non-endemic taxa *Aeshna ellioti* Kirby, 1896, *Chlorolestes elegans* Pinhey, 1950 and *Phyllomacromia monoceros* (Förster, 1906), and the endemic *Agriocnemis falcifera transvaalica* Pinhey, 1974. The globally Red Listed *Chlorolestes apricans*, *Pseudagrion inopinatum* Balinsky, 1971 and *P. newtoni* Pinhey, 1962 also do not occur in any known reserves. All globally Red Listed taxa are listed in Table 3.3. Less than 25% of the sites in which *Metacnemis valida* Hagen in Sélys, 1863 and *Proischnura rotundipenne* (Ris, 1921) occur are protected. For the remaining globally Red Listed taxa, 50% or more of the sites are protected.

In terms of quaternary catchments, no catchments are fully protected, with the (near) exceptions being the Cape Peninsula, Table Mountain National Park (NP), Kogelberg Nature Reserve (NR), Hawekwas Conservation Area (CA), and Groot Winterhoek Wilderness Area (WA) in the south western Cape, the proposed Garden Route NP in the south eastern Cape, the Ukhahlamba Drakensberg Park and the iSimangaliso Wetland Park in KwaZulu-Natal, and the Kruger NP in Mapumalanga.

In Figure 3.5 I show prioritization of sites using the Dragonfly Biotic Index. All taxa were considered in calculating the DBI, but only catchments that have at least one of the globally Red Listed taxa are presented. Catchments that are partially protected, and fall into the high DBI category are the Table Mountain NP, Kogelberg NR, Hottentots-Hollands NR, the Hawekwas CA, Garden Route NP and iSimangaliso Wetland Park. The Drakensberg falls into the middle category. The Groot Winterhoek WA does not fall into any category, because the area is under-sampled. By contrast, the well-sampled Kruger NP does not fall into any DBI priority category as the area is not home to any Red Listed, nor to more than one endemic species.

Table 3.3. Globally Red Listed taxa (i.e. IUCN threat category of VU, EN, CR), and their protection status. Quaternary catchments were found to be only partially protected. Taxa presented in bold are not in a protected area. Although currently not on the global Red List, *Orthetrum rubens* Barnard, 1937 and *Syncordulia venator* (Barnard, 1993) are scheduled to be listed in future (Samways, 2006) and are thus included in this table. Subheadings: PP: Partially protected; NP: not protected.

Species	Quaternary catchments			Point Localities		
	PP	NP	Total	PP	NP	Total
<i>Aciagrion pinheyi</i> Samways, 2001	2	0	2	2	0	2
<i>Agriocnemis ruberrima ruberrima</i> Balinsky, 1961	1	2	3	3	2	5
<i>Ceratogomphus triceraticus</i> Balinsky, 1963	7	6	13	8	7	15
<i>Chlorolestes apricans</i> Wilmot, 1975	0	8	8	0	13	13
<i>Ecchlorolestes peringueyi</i> (Ris, 1921)	9	3	12	15	3	18
<i>Metacnemis angusta</i> Sélys, 1863	1	1	2	2	1	3
<i>Metacnemis valida</i> Hagen in Sélys, 1863	2	7	9	2	9	11
<i>Orthetrum rubens</i> Barnard, 1937	4	3	7	4	3	7
<i>Proischnura polychromatica</i> (Barnard, 1937)	2	0	2	3	0	3
<i>Pseudagrion coeleste umsingaziense</i> Balinsky 1963	3	1	4	3	1	4
<i>Pseudagrion inopinatum</i> Balinsky, 1971	0	2	2	0	2	2
<i>Pseudagrion newtoni</i> Pinhey, 1962	0	3	3	0	4	4
<i>Syncordulia gracilis</i> (Burmeister, 1839)	7	4	11	8	4	12
<i>Syncordulia legator</i> Dijkstra, Samways & Simaika, 2007	3	1	4	4	1	5
<i>Syncordulia serendipator</i> Dijkstra, Samways & Simaika, 2007	2	1	3	2	1	3
<i>Syncordulia venator</i> (Barnard, 1933)	10	5	15	13	5	18

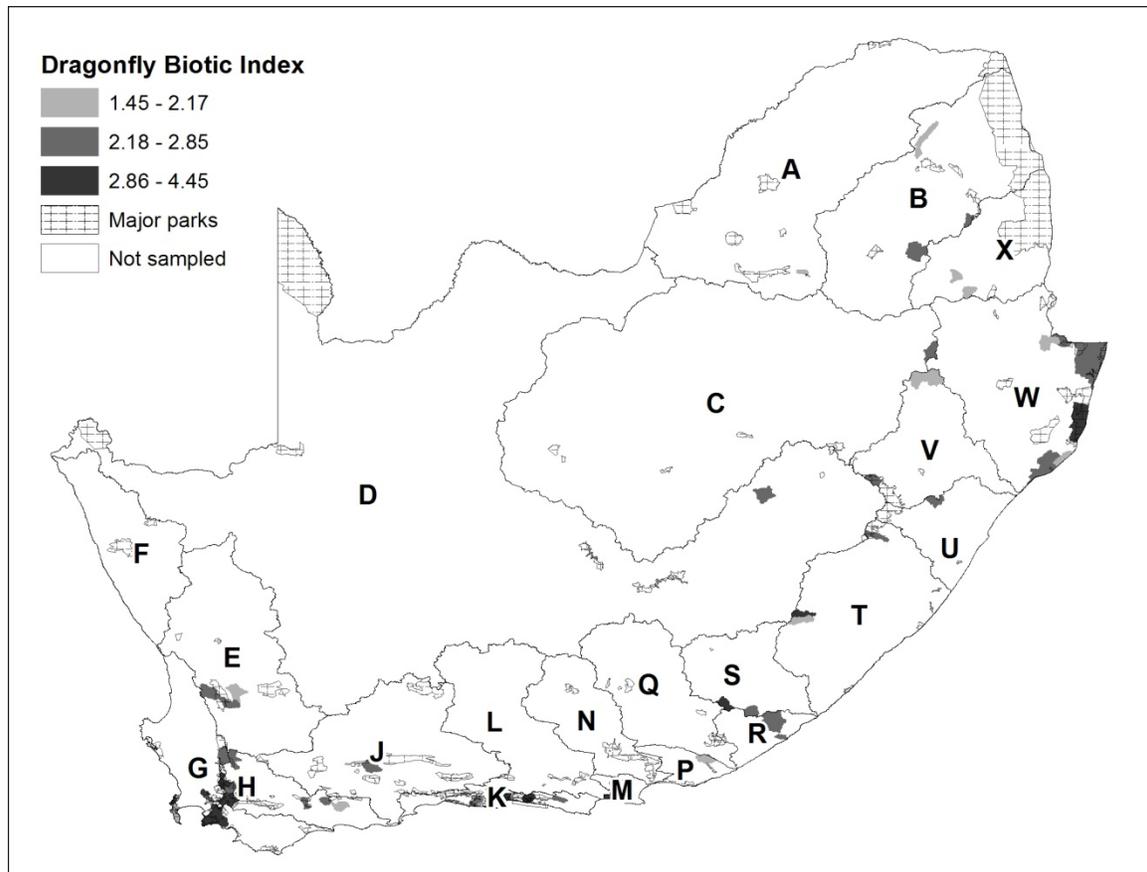


Figure 3.5. Protection status and Dragonfly Biotic Index (DBI) value of catchments in which globally Red Listed species occur. Classes are based on natural groupings inherent in the data, established using the natural breaks function in ArcGIS (2006).

Unprotected top DBI catchments are all in the Eastern Cape Province. These top sites are situated near Grahamstown, Clifton and Prentjiesberg. In the middle DBI category there are only partially protected catchments, but many protected record sites. Middle categories of note in the Western Cape Province include the Cederberg area in the north, Marloth NR and Towerkop NR, as well as Nature's Valley in the south east.

In the Eastern Cape Province the middle categories occur at the Kareedouw Pass and in Stutterheim and East London. Lesotho's middle category is represented by Maseru. KwaZulu-Natal's Blinkwater NR, Richard's Bay, Kosi Bay NR and Ndumo GR also fall into the middle category, as well as Mapumalanga's Wakkerstroom, Lydenburg and Pilgrim's Rest. The remaining catchments, those that fall in the low category, are found protected on the Cape Peninsula, and unprotected in the Cederberg, and Heidelberg in the south western Cape, Grahamstown and Prentjiesberg in the Eastern Cape, Wakkerstroom, and Richards Bay in KwaZulu-Natal, and Pretoria, Badplaas, and Duiwelskloof in Mapumalanga, and Kwaluseni in Swaziland.

3.4. Comparison of value-based index with algorithm

Using a target of one (i.e. a species must be represented at least once per catchment), ResNet 1.2 chose a network of 22 catchments in all 100 trials. In the trials, a total 31 catchments were used to complete the network of 22 cells at any one time. Of the 22 catchments that it took to complete a network, seventeen catchments were chosen 100 times (out of 100 randomizations), two were chosen 99, another two 53 times, and a final pair 47 times. The algorithm was thus tied in the frequency of use of the 22nd and 23rd top catchment. I thus chose the 23 most frequently used catchments to compare the algorithm and scoring method (Figure 3.6).

Of the 23 top sites chosen by each method, six are mutually shared. Comparison using a Pearson Correlation of the full dataset of 213 catchments with the top 23 sites selected by each method, revealed that there is a weak ($r = 0.1714$) but highly significant ($p < 0.001$) association between the DBI and the ResNet algorithms.

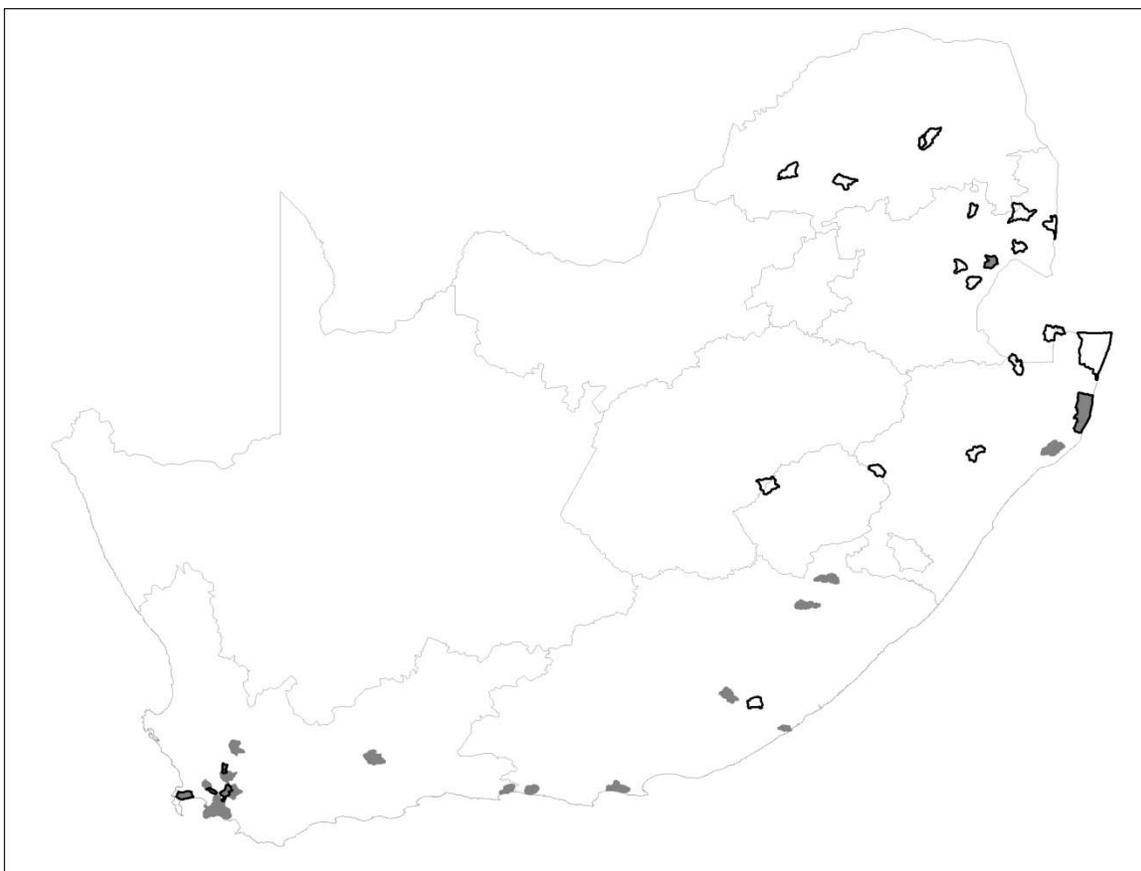


Figure 3.6. Twenty-three highest value Dragonfly Biotic Index (DBI) catchments (dark grey outlines) and top catchment chosen by the ResNet algorithms (black outlines).

Globally Red Listed taxa were found in 45 catchments. The DBI did not represent all globally Red Listed taxa, but many taxa several times. Indeed, 20 of the top 23 DBI catchments include at least one globally Red Listed taxon, while only 12 of the ResNet catchments do so. However, ResNet captures all the species, while the DBI does not. The following globally Red Listed species were not included by the top 23 sites: *A. pinheyi*, *P. inopinatum*, *P. newtoni*. Although the DBI did not include three of the 16 globally Red Listed species, it did represent the countries' remaining globally Red Listed fauna with 62.3% (48/77), and that of the Cape fauna specifically 69.7% (46/66). This is in contrast to ResNet, which represented the entire globally Red Listed fauna with 32.4% (25/77) and the Cape fauna with only 27.3% (18/66). The 20 top DBI sites are in the Cape, of which 12 are in the south west Cape, and the remainder in the eastern Cape. ResNet by contrast, only includes five catchments for the Cape, of which four are in the south west, and one in the eastern Cape. The overall frequency distribution of globally Red Listed catchments, and the DBI and ResNet catchments, is shown in Figure 3.7. The frequency distribution of globally Red Listed taxa and the DBI and ResNet is shown in Figure 3.8.

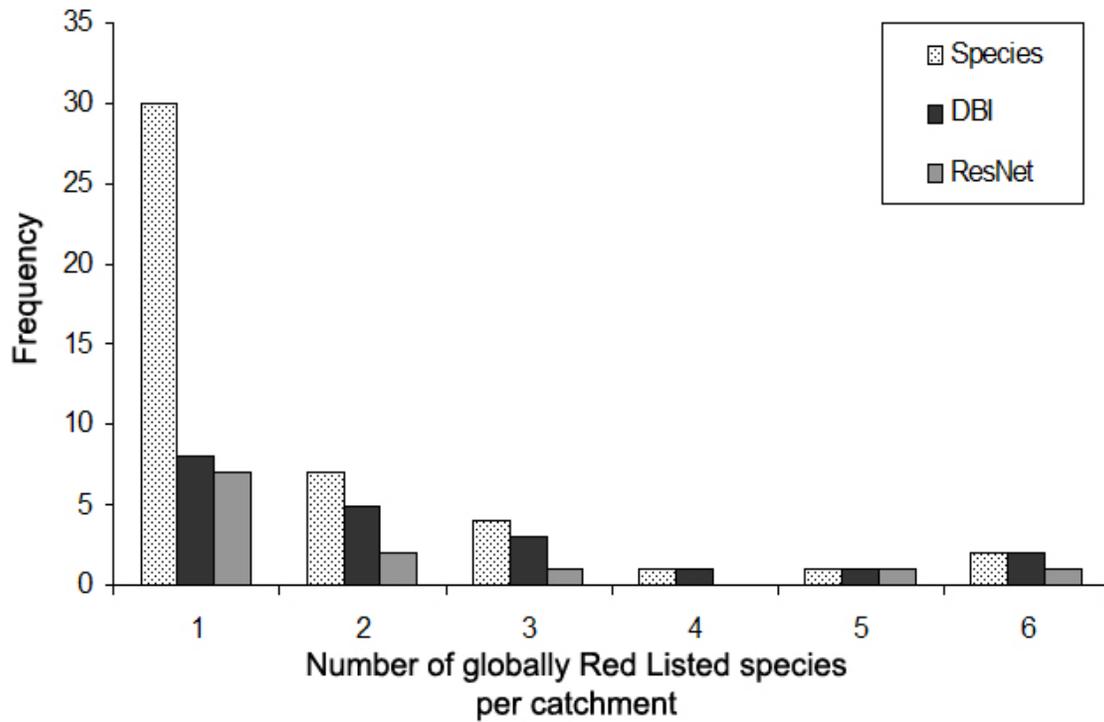


Figure 3.7. Frequency distribution of the globally Red Listed dragonfly fauna in comparison to its representation by the Dragonfly Biotic Index (DBI) and the ResNet algorithms.

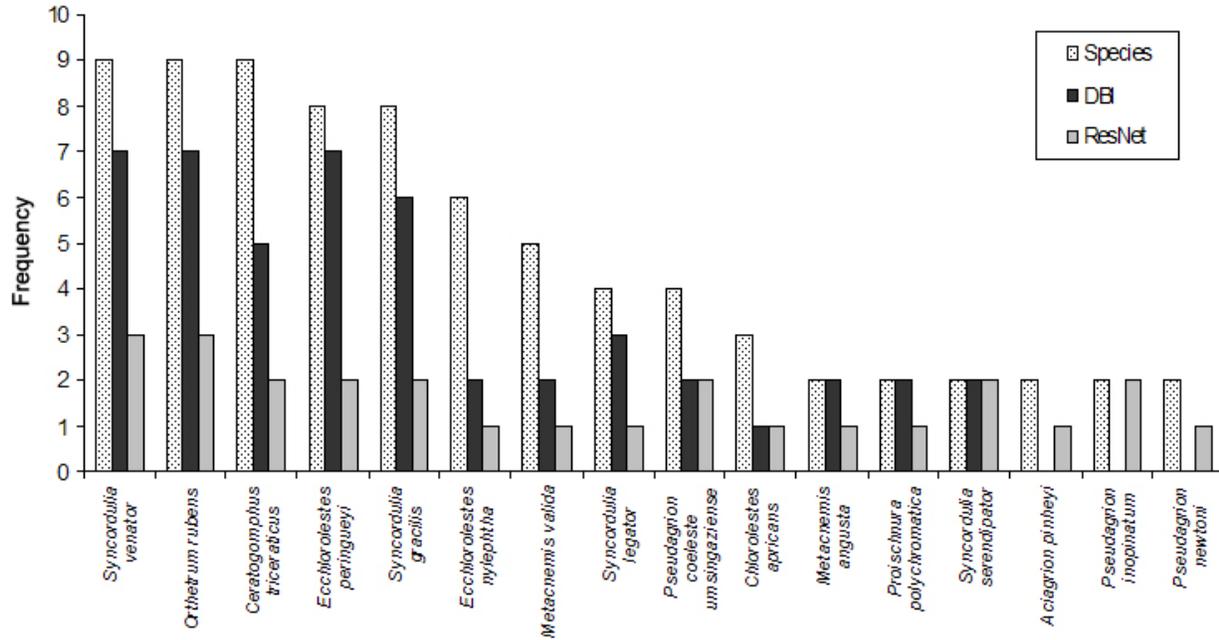


Figure 3.8. Frequency distribution of the globally Red Listed dragonfly taxa in comparison to each species' representation by the Dragonfly Biotic Index (DBI) and the ResNet algorithms.

4. Discussion

4.1. Sampling gaps

South African dragonflies are one among the most sampled and studied faunal taxa, along with the butterflies, fishes, amphibians and mammals. Yet, large areas in South Africa still remain unexplored, and there are large gaps in records of the distributions of many species. This is of great concern because of the persisting and growing anthropogenic pressure, especially on freshwater systems, and the resultant loss of habitat in the country (Davies and Day, 1998). In a study on South African dragonflies comparing habitat indices, Simaika and Samways (2009) were only able to use 213 of the 497 catchments identified here (Figure 3.1). Although this was done mainly to make the particular dataset more robust for testing, the severe reduction in the dataset also indicates that 43% of quaternary catchment areas are under-sampled. Thus, Figure 3.1 is a relatively optimistic representation of sampling effort.

For the south western Cape, sampling has been most intense in the Cape Floristic Region (CFR), a global biodiversity hotspot (Figure 3.1). The aquatic fauna of the Cape Fold Mountains has long been recognized as descending from the southern temperate Gondwanaland fauna (Balinsky, 1962; Stuckenberg, 1962), and for Odonata, this was confirmed with a phylogenetic analysis of the genus *Syncordulia* (Ware et al., 2009). As such, the CFR is probably the stock of the oldest and least disturbed of the continent's biomes (Wishart and Day, 2002). For these reasons, much attention has also been paid to sampling Odonata in the CFR (e.g. Grant and Samways, 2007; Simaika and Samways; 2008; Ware et al., 2009). However, much of the north west and south east of the CFR remains relatively unexplored. The Succulent Karoo, another global biodiversity hotspot, remains virtually un-sampled (Figure 3.1), being arid and generally having little to attract the attention of odonatologists.

The Cape Peninsula and Table Mountain have received much attention (Samways et al., 2008). However, other plateau areas, like the Groot Winterhoek Wilderness Area, have remained unexplored. Yet, the area is more continental, and forms part of the north-west CFR biodiversity hotspot. The CFR continues to yield new species, as exemplified by recent intense field searches (Dijkstra et al., 2007; Grant and Samways, 2007). Thus it is imperative that searches continue in this area. This is further supported by the frequent observation that long-known and studied centers of endemism continue to yield species that are new to science (Fjeldså and Tushabe, 2005). Much land beyond these areas, of the Orange and Vaal systems, remains unsampled. This is perhaps due to inaccessibility of habitat (fewer

road networks), and the propensity of dragonfly recorders to follow the coast, rather than venturing inland. Perhaps it is collectors' awareness that northern inland regions are very dry and are likely to yield mostly the widespread, vagrant species that have managed to spread by dam building over the last century. These artificial waterbodies serve as stepping stones for previously unrecorded Afro-tropical species into the Cape region (Samways, 1989).

The inland coastal areas also require more attention, as do areas that represent transitions in species ranges, such as the Swellendam/Bontebok area in the Gouritz system, which was found to be consistently intermediate in species richness, endemism and threat. The Eastern Cape may even yield new species, as well as range extensions as in the recent example of the Red Listed endemic *S. venator*. The Eastern Cape is also home to three of the top priority sites identified by the DBI.

The Maputaland-Pondoland-Albany region is also likely to yield new species, as in the case of *Aciagrion pinheyi* (Samways, 2001), as well as new national records (Samways, 2008a). The north east is particularly well-sampled. However, new species may be recorded here in future. This is because the area is home to many Afro-tropical species whose ranges extend south into the country. With global warming, additional Afro-tropical species may move south into South Africa, and at the same time, some specialized cold mountain stream dwellers may go extinct (Samways, 2008c).

4.2. Comparison of richness, endemism and threat

The most commonly used biodiversity measure in ecology is species richness (Jennings et al., 2008; Fleishman, 2006; Magurran, 2004). Yet, there are numerous intrinsic problems with the measurement of biodiversity based on simple species counts (Warwick and Clarke, 2001). Of most concern here is that areas of high richness and endemism will not necessarily correspond (Prendergast et al., 1993; Jennings et al., 2008). For South Africa also, richness, for freshwater invertebrates, including amphipods, ostracods, molluscs, trichoptera, ephemeroptera, and simuliids, is concentrated in the north east of South Africa, while endemism is highest and concentrated in the Cape region. The same pattern emerges for aquatic vertebrate taxa dependent on freshwater, such as fish and amphibians, but also millipedes, tortoises and terrapins, and other vertebrate taxa (Wishart and Day, 2002). Dragonflies follow this general pattern.

The most species rich areas are the Mkomazi, Mfolozi/Pongola, and Komati/Crocodile systems, in the north east, where 50 or more species have been recorded at a site (Figure 3.2). Most of these species are widespread Afro-tropical odonates, whose more northern ranges extend into South Africa. In contrast, the center of highest endemism occurs in the Berg/Bot/Potberg and Breede systems, in the

CFR of the south western Cape (Figure 3.3). Here, up to 16 endemic species can occur per catchment. The Berg/Bot/Potberg and Breede systems are also home to the highest number of threatened endemic taxa (Figure 3.4). Thus, from the perspective of conserving the most evolutionary history, these systems deserve much attention. The middle category of endemism, in which 5-9 species may occur, spreads across the country.

4.3. Protected areas and threatened, endemic species

In this study, I found that of all sites sampled in the country, 30% were protected. However, most of these are not major parks, and these are represented only 9% of the time in the sample. Eleven of 162 taxa occurring in South Africa are not protected. Of these, the non-endemic *C. elegans* and *P. subfurcatum* are nationally Red Listed and are recommended for conservation action, as are the globally Red Listed *C. apricans*, *P. inopinatum* and *P. newtoni* (Samways, 2006). Not a single catchment was found to be fully protected. Perhaps this is not surprising as freshwater habitats are often only protected as part of their inclusion with terrestrial reserves (Saunders et al., 2002). For example, the Kruger NP offers little protection to freshwater fishes because it cuts across the downstream portions of catchments, while the upstream habitats are vulnerable to disturbance (Skelton et al., 1995).

The Dragonfly Biotic Index was used here, as it has been identified as useful for prioritizing sites of global conservation interest. The DBI suggested that the partially protected quaternary catchments of Table Mountain NP, Kogelberg NR, Hottentots-Hollands NR, the Hawekwas CA, and the proposed Garden Route NP are of highest value for the protection of globally Red Listed taxa and their associated assemblages of species. The iSimangaliso Wetland Park was also identified as a top priority site although, in contrast, for its high number of marginal, nationally Red Listed species, and not for high endemism. Of concern is that the top conservation action sites, for globally Red Listed species, Grahamstown, Clifton and Prentjiesberg, remain completely unprotected. Interestingly, the largest protected area, the Kruger National Park is not home to any endemic or any Red Listed species. However, its conservation value lies in the high species richness of the area, and the representativeness of its distinctly Afro-tropical fauna.

Although detailed descriptions of the patterns of richness, endemism and threat are essential as a first step in conservation, this approach is far removed from prioritizing sites for conservation. There is the need for an index, like the DBI, that combines the measures of richness and endemism (geographic distribution of species), threat status and also the sensitivity of species to habitat

disturbance. The DBI, as shown here, is one step closer to prioritizing sites for habitat conservation. As a minimum first step towards conservation of all dragonfly species in South Africa, I recommend protection of the globally Red Listed taxa, with first priority given to the top DBI sites in the Eastern Cape.

4.4. Comparison of value-based index with algorithm

According to Abellán et al. (2005), the advantages of scoring methods are easy development, no need for computer software, and easy access to broad scale data for development. Their apparent disadvantages are inefficiency, subjectivity, and lack of accountability and transparency. There is no theoretical basis for producing composite scoring systems, and they are highly affected by sampling bias. Minimum reserve selection procedures have the advantage that some methods guarantee to meet their target with the most efficient (i.e. least area) selection possible (Sarkar et al., 2006; Garson et al., 2007). A disadvantage is that, although Garson et al. (2007) state that their algorithms make use of species *identities*, these are not more than simple species lists. Additionally, reserve selection algorithms tend to select areas of ecological transition, and thus species range edges. These are argued to be either of advantage or disadvantage for conservation (Araújo and Williams, 2001, Gaston et al., 2001), clearly a field in need of further exploration. Ironically, another potential draw-back of the algorithms is their efficiency (i.e. the selection of the least area to represent all species). I found that in the south west Cape only four catchments were selected by the rarity-complementarity algorithms, while the DBI selected 12 catchments for the same region. Thus, using the algorithms, few areas are selected for Red Listed species, affecting their viability.

The listed advantages and disadvantages are subjective assessments, in that they ignore the intrinsic differences between scoring procedures compared to that of reserve selection algorithms. Scoring procedures, by their nature, do not account for complementarity or representativeness. Thus, it is hardly surprising that they are inefficient at representing all species. For example, I found that of the globally Red Listed fauna, ResNet represented all 22 species, while the DBI only selected 16. This highlights, however, that from a conservation perspective, not all species, and not all areas are equal. Hence the terms ‘site prioritization’ are used, to indicate that conservation is in a state of emergency, where triage is commonly practiced. Adequate representation of globally Red Listed species must take precedence over nationally Red Listed species, these over other nationally Red Listed endemics and non-threatened endemics, and so on, until one reaches the most common and geographically most represented species. At the same time, important conservation resources for species whose long-term

viability is already severely compromised should be diverted to species further down the priority list. This ensures continuity in conservation effort, giving lower priority taxa the attention they need, at least to remain stable.

The Dragonfly Biotic Index, an index that uses dragonflies as an indicator taxon to identify sites for conservation action, is designed to assign conservation (biodiversity) value to individual species. Thus, it identifies sites with high value. The DBI is designed to target rare, endemic, or threatened (i.e. Red Listed) taxa, and/or species that are sensitive to habitat disturbance. Red Listed species are thus given conservation priority. This is in line with IUCN policy on species conservation, and explains why species that fall in such categories are Red Listed, while common, ubiquitous species are not on the Red List. These have, of course, also conservation value, but the idea of using the DBI as opposed to a complementarity-based index, is that the DBI gives conservationists a picture not only of the content, but also the value of the site, for conservation. This is because the DBI is also a habitat integrity index (Simaika and Samways, 2009), and presence of a high number of high value species, gives a site an overall high value.

The DBI is at least as transparent as the algorithm, because the values are assigned to each species, and the standardized DBI site values are derived from the species lists in each assemblage. One can therefore examine each list and determine exactly which species contributed, and why a site value is overall low or high. With the algorithm, although the output records which catchments were chosen or discarded while searching for the optimal set of cells, it does not record whether this is due to a particular species, an assemblage, the species ecology, or that of the assemblage. Thus, the notion that value-based indices lack accountability and are not transparent is, in this case, unfounded. Also, while users can visualize the site DBI values for all catchments at once, the ResNet algorithms can only present one optimal solution at a time. I found that finding all possible network solutions using the algorithm is a time consuming process, because input datasets need to be randomized to find all solutions (Fuller, 2005). Furthermore, a decision must then be made which network is optimal, as a combination of solutions would introduce redundancy (i.e. species are represented more often than the set target). Thus, Kelley et al.'s (2001) notion that reserve selection algorithms can be used to find quick solutions at planning meetings is thus far too optimistic.

There are also limitations to the DBI. First, it only focuses on the patterns of one taxon, although other vertebrate and invertebrate taxa follow the same patterns of richness and endemism (Wishart and Day, 2002). It would thus be useful to expand the index to include other taxa, as was done, for example, by Benayas and de la Montaña (2003), for a complete dataset of the vertebrate taxa

of Spain. Second, the DBI depends on our changing understanding of species distributions, their Red List status, and their sensitivity to disturbance or pollution. Perhaps this is an advantage of the DBI, since the algorithm can only make use of species presences or absences. Third, the DBI cannot be used to optimize reserve selection efficiently, requiring expert input. This is perhaps the greatest limitation of the DBI. A selected set of top DBI sites will not be complementary nor represent all species. On the other hand, common, widespread or vagrant species are often eurytopic, and thus likely to be represented by existing reserve networks, such as is the case in South Africa.

Reserve networks could be built on other surrogates of biodiversity. Other possible surrogates, which remain largely unexplored, are phylogenetic, taxonomic and functional diversity (e.g. Magurran, 2004; Warwick and Clarke, 2001). Reserve networks based on any of these surrogates are likely to be distinct from rarity-complementarity (e.g. ResNet) or threat-based (DBI) networks. Another consideration is viability, which Gaston et al. (2001) suggest should be incorporated in minimum representation sets, even if this results in more costly reserve networks. A method that encompasses the advantages of the different procedures is thus needed, while at the same time satisfying the different goals of conservation. In the short term, it makes sense to prioritize sites that are less represented globally, conserving globally Red Listed taxa and thus evolutionary history (Sechrest et al. 2002), without losing sight of long term conservation of larger tracts of land of the more commonly represented species.

5. Conclusion

The DBI is sufficiently sensitive, easy-to-use and robust to be of great value to conservation managers interested in wetland assessment, monitoring and restoration (Simaika and Samways, 2008, 2009). Employment of the DBI will aid in closing some of the sampling gaps identified here. I recommend continued field searches in centers of high endemism, in this case also the CFR. Reserve selection using the DBI is valuable if users recognize that it is a weighted scoring method used to identify globally threatened endemic biodiversity and not complementarity hotspots. The value of the DBI thus lies in maximizing redundancy (i.e. representation) of globally Red Listed species.

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Chapter 4

Continental-scale assessment of freshwater conservation areas using fine-scale modeling*

Abstract: *Indicators on the state of global biodiversity illustrate continued decline, while pressure on biodiversity keeps rising. This necessitates revisiting and honing site prioritization and species protection for conservation. Patterns of richness and threat of four well-studied aquatic taxa, the fishes, crabs, molluscs and dragonflies largely coincide at the continental scale, at least in Africa. I chose dragonflies, for which there is a point locality database, as a surrogate taxon, modeling the species at the fine-scale, using predictive species distribution modeling. With this approach, I built a protected areas network using spatial planning software. I then compared the performance of the existing reserve network and that of known global biodiversity hotspots against the model, and identified sites of conservation concern. Priority areas for conservation largely coincided with analyses of global biodiversity conservation priorities. Among globally threatened species, 72% were recorded at least once in a protected area. Although the current reserve network covers 10.7% of the landscape, the proportional representation of species geographic distributions in reserves is only 1.1%. The reserve network is therefore inefficient at conserving dragonfly diversity, and many areas of conservation priority that are not formally protected remain. The advantage of operating at the fine scale, while covering a large geographic area is that it shifts the focus from the large-scale hotspots to smaller priority areas within and beyond hotspots. Second, by operating at the fine-scale for a large geographic area, the potential exists for local conservation managers to consider campaigning for the inclusion of the priority areas that are not formally protected, while adjacent to the existing reserve networks. Where this is not possible, or where areas fall within the mosaic of different landscape uses, I recommend monitoring these areas to detect future threats to the habitats that these might face.*

Keywords: hotspots, freshwater, aquatic biodiversity, conservation planning, species distribution modeling, maximum entropy, protected area, reserve networks, continent, Africa

*Submitted: Simaika, J.P., Samways, M.J., Kipping, J., Suhling, F., Dijkstra, K.-D.B., Clausnitzer, V., Boudot, J.P.

1. Introduction

Indicators on the state of global biodiversity show continued decline at a rapid rate, while pressure on biodiversity keeps rising (Butchart et al. 2010). Threats to biodiversity include, among others, resource consumption, invasive alien species, pollution, overexploitation, and climate change (Tylianakis et al. 2008). Despite human dependence on aquatic resources, threats to freshwater areas are several and synergistic, and the decline in aquatic biodiversity is estimated to be up to five times greater in some freshwaters than in the most affected terrestrial ecosystems (Dudgeon et al. 2006; Dudgeon 2010; Sala et al. 2000). The WWF Living Planet Report (WWF 2010) documents a 69% decline in tropical freshwater areas, but a 36% improvement in temperate areas, using a freshwater index based on vertebrate species over the period of 1970-2007. Similar to the challenges for general biodiversity, freshwater biodiversity specifically faces loss of hydrologic connectivity (Pringle 2001), nitrogen pollution, resource over-exploitation, flow alteration and water over-extraction, invasion by alien species, and climate change impacts such as temperature warming and shifts in precipitation and runoff patterns (Abell et al. 2007).

Globally, biodiversity protection is poor (Rodrigues et al. 2004), with only 12% of the earth's surface covered by protected areas (Lee and Jetz 2007). Freshwater ecosystems are even more poorly protected, as most protected areas are aimed at protecting terrestrial and not aquatic biodiversity or hydrologic processes (Abell et al. 2007; Revenga et al. 2005; Dudgeon et al. 2006, but see Saunders et al. 2002 for notable exceptions), and thereby fail to maintain whole-catchment integrity (Simaika and Samways 2009, 2010). Global biodiversity assessments have long been biased to terrestrial vertebrates, although invertebrates account for a much bigger part of earth's biodiversity. Only recently have some invertebrate groups entered the global biodiversity crisis debate (Clausnitzer et al. 2009, Cumberlidge et al. 2009). Furthermore, global biodiversity assessments frequently ignore freshwater species despite evidence that aquatic organisms are highly imperilled and that terrestrial hotspots do not always overlap with freshwater hotspots (Strayer and Dudgeon 2010). In addition, present (e.g. Lamoreux et al. 2006) and future (Lee and Jetz 2007) global assessments, and indices such as the WWF's Living Planet Index (WWF 2010) with a freshwater component, are frequently based on assessments of vertebrate diversity alone.

Biodiversity hotspots are areas of high priority for conservation (Myers et al. 2000). They may be selected on the basis of their local species richness, degree of concentration of rare species (Prendergast et al. 1993) or the two measures combined with some assessment of urgency for conservation action (Myers et al. 2000), or alternatively, using the principle of complementarity, based on their relative contribution for attaining an overall conservation goal (Araújo 2002). The selection and prioritization of conservation areas and design of reserve networks, depends in part,

on good taxonomic knowledge of the surrogate used. Therefore, perhaps, the selection of freshwater protected areas is most commonly based on fish diversity, although biotic surrogate reserve selection studies have also used water beetles (Abellán et al. 2005) and dragonflies (Simaika and Samways 2009).

Dragonflies (Insecta: Odonata) make excellent model organisms. They have been used as indicators for monitoring both habitat and water quality change (e.g. Clausnitzer 2003; Simaika and Samways 2011; Suhling et al. 2006), and habitat recovery (Simaika and Samways 2008, 2011). Furthermore, dragonflies make useful surrogates in the selection and prioritization of sites for aquatic conservation (Simaika and Samways 2009). Indeed, the IUCN Southern African Freshwater Biodiversity Assessment (Darwall et al. 2009) was a baseline against which Simaika and Samways (2010) proposed a spatially explicit alternative to the freshwater mapping methods currently in use by IUCN, as well as an expansion of the conceptual basis on which such methods rest, and built an aquatic reserve network using these principles for South Africa (Simaika and Samways 2009). The Freshwater Biodiversity Assessment of Africa (Darwall et al. 2011) confirms that patterns of richness and threat are remarkably similar among dragonflies, fishes, molluscs and crabs at the continental scale, particularly in Mediterranean North Africa, the Cape region of South Africa, equatorial West Africa, and of the afro-montane regions of East Africa.

In this study I modeled the distributions of a continent-wide dataset of African dragonflies at the fine-scale, using predictive species distribution modeling software. My objectives were to first build a hypothetical reserve network, based on maximal species representation, by identifying priority areas under the assumption that all areas are available for protection (unconstrained analysis). Second, the aim was to compare the efficiency of the existing continental reserve network as well as that of the global biodiversity hotspots at representing all species. Third, my aim was to identify areas of conservation concern within and beyond reserves and hotspot areas.

2. Methods

2.1. The database

The database used here, the ‘Odonata Database of Africa (ODA)’, is the first continent-wide, expert-reviewed database of freshwater insects (Kipping et al. 2009; Dijkstra et al. 2011). The raw database is continually updated, and at the time of this analysis contained 77 369 records, representing 686 species. Of these, 581 are restricted to the African continent, and I therefore termed them here ‘African endemics’. For modelling purposes, only geo-referenced records were retained and duplicates removed, which resulted in 50 485 unique presence records. Species that

have low occurrence records tend to be rare, endemic species, or species that have a scant collection record. I therefore differentiated between species that were evaluated using the IUCN categories and criteria (IUCN 2001) as data deficient (DD) and least concern (LC) and species that were near threatened (NT), vulnerable (VU), endangered (EN) and critically endangered (CR) at the global level. Species names, IUCN threat categories, relative geographic distributions on the African continent, and model performance information, are presented in Table 4.S1. Only species with presences at >20 locations were used in species distribution modelling. Species with <20 locations were retained for inclusion in spatial modelling, termed species of special interest (Moilanen and Kujala 2008).

2.2. *Species habitat modeling*

At the continental scale, climate can be considered the dominant factor driving species distributions (Pearson and Dawson 2003). Here I obtained 2.5 arc-minute, global climate raster datasets of the 19 bioclim variables (Table 4.S2), which are calculated from elevation, temperature and precipitation (Hijmans et al. 2005). As the climate raster grids were global in extent, I used the ‘extract by mask’ function in ArcMap to reduce the extent and resolution of the grids (0.042 cell resolution) to that of the mask (0.05 cell resolution). The resultant rasters were then converted to .asc files for use as environmental data input in Maxent (version 3.3.3e, Phillips et al. 2006, Phillips and Dudik 2008). In model building I also included a dataset of the terrestrial ecoregions of Africa (Olson et al. 2001). I chose to use terrestrial ecoregions rather than freshwater ecoregions (Abell et al. 2008) for two reasons. First, although the number of types of ecoregions are comparable for the maps (105 terrestrial types, 78 freshwater types), the number of distinct polygons is by an order of magnitude higher in the terrestrial ecoregions map (964 polygons) than the freshwater ecoregions map (78 polygons). Second, the groupings of distinct vegetation types are ecologically meaningful. For example, some dragonfly species are particularly dependent on forests (Cordero Rivera 2006). Maxent is species distribution modeling software that facilitates the analysis of presence only data (Phillips et al. 2006). The software has been shown to produce higher quality predictive models compared to other presence only modeling methods (Elith et al. 2006). Maxent is insensitive to sample size, and performs well at $n = 10$ (Wisz et al. 2008) and even $n = 5$ (Pearson et al. 2007). Nevertheless, given the extent of the study area, I chose a more conservative approach, in which species with sample sizes of $n < 20$ were removed from distribution modelling. For each species, I replicated 10 runs with 75% of a species’ records randomly selected for model training and cross-validation, and 25% of the data set aside for model testing and independent validation. To evaluate commission, 10,000 random background points were used. Model results were compared and validated using the area under the receiver operating characteristic curve (AUC). According to Elith

et al. (2006) models with an AUC of >0.75 have a useful amount of discrimination. In this study, species mean AUCs averaged 0.94 ($n = 351$, range 0.79 to 0.99). Species mean AUC values, standard deviations of AUCs are presented in Table 4.S1. A total of 351 species were modelled in Maxent, and an additional 335 species of special interest (SSI) retained for analysis in Zonation.

2.3. Spatial analysis and planning

I used the Zonation framework and software to create a nested spatial conservation prioritization that serves as a basis for identifying a putative reserve network (Kremen et al. 2010; Moilanen et al. 2005, 2009; Moilanen and Kujala 2008). The broad strategy of Zonation can be described as maximal retention of weighted range-size normalized (rarity corrected) richness. "Maximal retention" means that the computational strategy operates via minimization of marginal loss that follows from the removal of an area from conservation. "Richness" here implies that Zonation simultaneously considers many biodiversity features, such as species or habitat types. "Weighted" means that features are given numeric weights that influence the balance that emerges between features. At each step of the analysis, the maximum retention procedure aggregates across all features so that a planning unit (grid cell) that contains a relatively high proportion of the remaining distribution of many features will be retained (Moilanen 2007). The planning unit removed will be the one leading to lowest marginal loss, that is, the planning unit least important for remaining weighted range-size corrected feature richness. The removal order of planning units is converted to a priority ranking that informs conservation decision making. Thus Zonation allows the user to identify the proportion of the landscape (e.g. 10% target) of highest conservation value, at which a certain proportion of the geographic distribution of all species will remain.

Species of special interest (SSI) are treated in the same manner as modelled species in the Zonation process (Moilanen and Kujala 2008). The marginal loss following the removal of a cell is based on the fraction of the distribution of the species residing in the cell. Therefore, it can be expected that the full distributions of SSI species will be retained far into the cell removal process especially if there are relatively few locations with observations of these species.

An important step in Zonation analysis is specification of species-specific weights. These weights influence the balance that emerges between features (here species) in prioritization (see e.g. Leathwick et al. 2008). Species were weighted according to whether or not they were globally threatened (IUCN 2001). Species in the IUCN threat categories NT, VU, EN and CR were given a weight of 2. With respect to Zonation specific parameters, I used removal restricted to habitat edges (Moilanen et al. 2005) and set the analysis warp (acceleration) factor to 100 (Moilanen and Ball 2009).

Three analyses were carried out with Zonation using the full species dataset (686 species) and the one containing only the African endemics (581). In the first analysis, Zonation was set to an unconstrained analysis in which it is assumed that there are no restrictions on how the landscape is to be prioritized. This is therefore the optimized reserve network. In the second and third analyses, mask files were included of protected areas (UNEP-WCMC 2009), and global biodiversity hotspots (Mittermeier et al. 2004), respectively. I chose an arbitrary minimum size of 50 km² (ca. 7.1 x 7.1 km) for inclusion in the gap analysis, because I considered reserves of such a small size unable to maintain aquatic connectivity and therefore unable to significantly contribute to the protection of aquatic diversity. Areas of the mask file are prioritized or 'locked into the landscape' and the remainder of the analysis is carried out as under unconstrained conditions. All spatial work was carried out using ArcGIS 9.2 (ESRI 2006).

3. Results

3.1. Current reserve network

In total, dragonflies were recorded from 19.7% (431 of the 2185) of the currently recognized protected areas in Africa, representing 82.2% (564 of 686) of the dragonfly species overall. Of globally threatened species 72% (43 of 60 species) were recorded at least once in a protected area. The distribution of globally threatened species inside and outside protected areas is compared using IUCN Criteria (2001) in Table 4.1.

Table 4.1. Distribution of threatened dragonflies in the landscape (overall) and in protected areas. Abbreviated IUCN Categories (2001) are as follows: CR = Critically Endangered, EN = Endangered, VU = Vulnerable.

Species representation	IUCN threat categories		
	CR	EN	VU
Overall	12	13	35
Only reserves	7	8	28
Percent (%) in reserves	58	62	80

3.2. Unconstrained analysis

An unconstrained analysis assumes that the entire landscape is available for protection. Setting aside 10% (100028 of 999771 grid cells) of the top fraction of the landscape for the conservation of dragonflies, would represent a 6.8% proportion of dragonfly species distributions overall, while a 10% proportion of the distribution of dragonfly species could be accommodated by setting aside 12.7% (126772 grid cells) of the top fraction of the landscape (Figure 4.1, Table 4.2). Considering only species endemic to the continent, a 10% fraction of the top landscape would represent 9.1% of endemic dragonfly species distributions, while a 10% proportion of the distribution of endemic dragonfly species could be accommodated by setting aside 11.4% (114399 grid cells) of the landscape (Figure 4.2, Table 4.2). Although the top areas cover several ecoregions, I note the 10 ecoregions that are most represented by area, for all species. Considering the number of selected cells in an ecoregion against all selected cells (Table 4.S3), the most represented areas, standardized by size, would be the Mediterranean woodlands and forests, the Central Zambezian Miombo woodlands, the Highveld grasslands, the Western Guinean lowland forests, the Zambezian and Mopane woodlands, the West Saharan montane xeric woodlands, the Drakensberg montane grasslands, woodlands and forests, the Ethiopian montane grasslands and woodlands, and the Western Congolian swamp forests. Considering only species endemic to Africa, the Mediterranean woodlands and forests would still be in first place, but not be as strongly represented (63% from a previous 84% representation of the ecoregion's area), and the Saharan montane xeric woodlands would not be represented at all (Table 4.S3). In 10th place would be the Zambezian flooded grasslands.

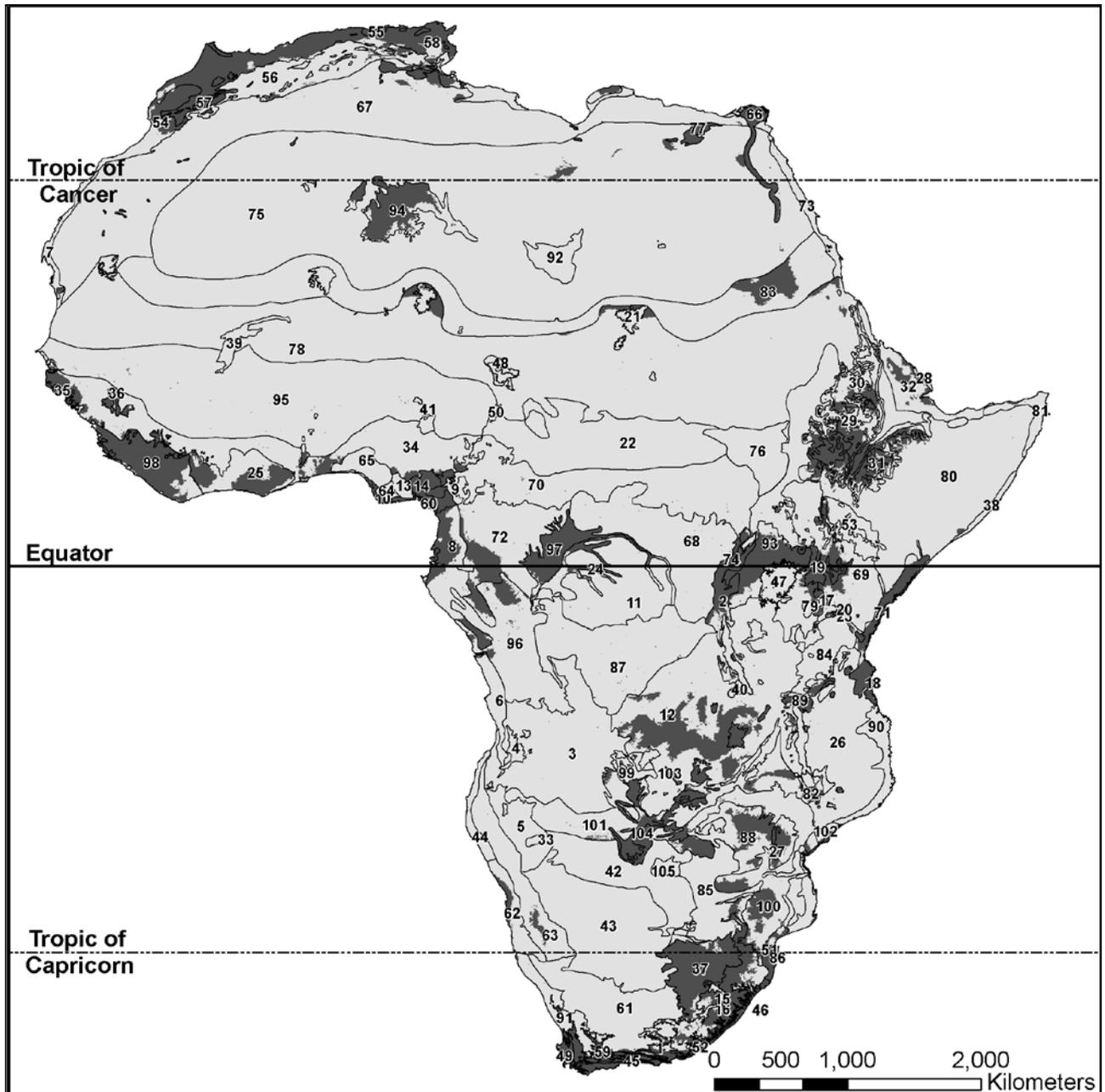


Figure 4.1. Potential reserve network of 10% of the geographic distributions of dragonfly species (dark gray). This represents 12.7% of the top fraction of the African landscape. Annotations are for terrestrial ecoregions and described in Table 4.2.

Table 4.2. Descriptions of annotations for terrestrial ecoregions as shown in Figures 4.1, 4.2, 4.5 and 4.6.

ID Terrestrial Ecoregion	ID Terrestrial Ecoregion (continued)
1 Albany thickets	53 Masai xeric grasslands and shrublands
2 Albertine Rift montane forests	54 Mediterranean acacia-argania dry woodlands & succulent thickets
3 Angolan Miombo woodlands	55 Mediterranean conifer and mixed forests
4 Angolan montane forest-grassland mosaic	56 Mediterranean dry woodlands and steppe
5 Angolan Mopane woodlands	57 Mediterranean High Atlas juniper steppe
6 Angolan scarp savanna and woodlands	58 Mediterranean woodlands and forests
7 Atlantic coastal desert	59 Montane fynbos and renosterveld
8 Atlantic Equatorial coastal forests	60 Mount Cameroon and Bioko montane forests
9 Cameroonian Highlands forests	61 Nama Karoo
10 Central African mangroves	62 Namib desert
11 Central Congolian lowland forests	63 Namibian savanna woodlands
12 Central Zambezian Miombo woodlands	64 Niger Delta swamp forests
13 Cross-Niger transition forests	65 Nigerian lowland forests
14 Cross-Sanaga-Bioko coastal forests	66 Nile Delta flooded savanna
15 Drakensberg alti-montane grasslands and woodlands	67 North Saharan steppe and woodlands
16 Drakensberg montane grasslands, woodlands and forests	68 Northeastern Congolian lowland forests
17 East African halophytics	69 Northern Acacia-Commiphora bushlands and thickets
18 East African mangroves	70 Northern Congolian forest-savanna mosaic
19 East African montane forests	71 Northern Zanzibar-Inhambane coastal forest mosaic
20 East African montane moorlands	72 Northwestern Congolian lowland forests
21 East Saharan montane xeric woodlands	73 Red Sea coastal desert
22 East Sudanian savanna	74 Rwenzori-Virunga montane moorlands
23 Eastern Arc forests	75 Sahara desert
24 Eastern Congolian swamp forests	76 Saharan flooded grasslands
25 Eastern Guinean forests	77 Saharan halophytics
26 Eastern Miombo woodlands	78 Sahelian Acacia savanna
27 Eastern Zimbabwe montane forest-grassland mosaic	79 Serengeti volcanic grasslands
28 Eritrean coastal desert	80 Somali Acacia-Commiphora bushlands and thickets
29 Ethiopian montane forests	81 Somali montane xeric woodlands
30 Ethiopian montane grasslands and woodlands	82 South Malawi montane forest-grassland mosaic
31 Ethiopian montane moorlands	83 South Saharan steppe and woodlands
32 Ethiopian xeric grasslands and shrublands	84 Southern Acacia-Commiphora bushlands and thickets
33 Etosha Pan halophytics	85 Southern Africa bushveld
34 Guinean forest-savanna mosaic	86 Southern Africa mangroves
35 Guinean mangroves	87 Southern Congolian forest-savanna mosaic
36 Guinean montane forests	88 Southern Miombo woodlands
37 Highveld grasslands	89 Southern Rift montane forest-grassland mosaic
38 Hobyo grasslands and shrublands	90 Southern Zanzibar-Inhambane coastal forest mosaic
39 Inner Niger Delta flooded savanna	91 Succulent Karoo
40 Itigi-Sumbu thicket	92 Tibesti-Jebel Uweinat montane xeric woodlands
41 Jos Plateau forest-grassland mosaic	93 Victoria Basin forest-savanna mosaic
42 Kalahari Acacia-Baikiaea woodlands	94 West Saharan montane xeric woodlands
43 Kalahari xeric savanna	95 West Sudanian savanna
44 Kaokoveld desert	96 Western Congolian forest-savanna mosaic
45 Knysna-Amatole montane forests	97 Western Congolian swamp forests
46 KwaZulu-Cape coastal forest mosaic	98 Western Guinean lowland forests
47 Lake	99 Western Zambezian grasslands
48 Lake Chad flooded savanna	100 Zambezian and Mopane woodlands
49 Lowland fynbos and renosterveld	101 Zambezian Baikiaea woodlands
50 Mandara Plateau mosaic	102 Zambezian coastal flooded savanna
51 Maputaland coastal forest mosaic	103 Zambezian Cryptosepalum dry forests
52 Maputaland-Pondoland bushland and thickets	104 Zambezian flooded grasslands
	105 Zambezian halophytics

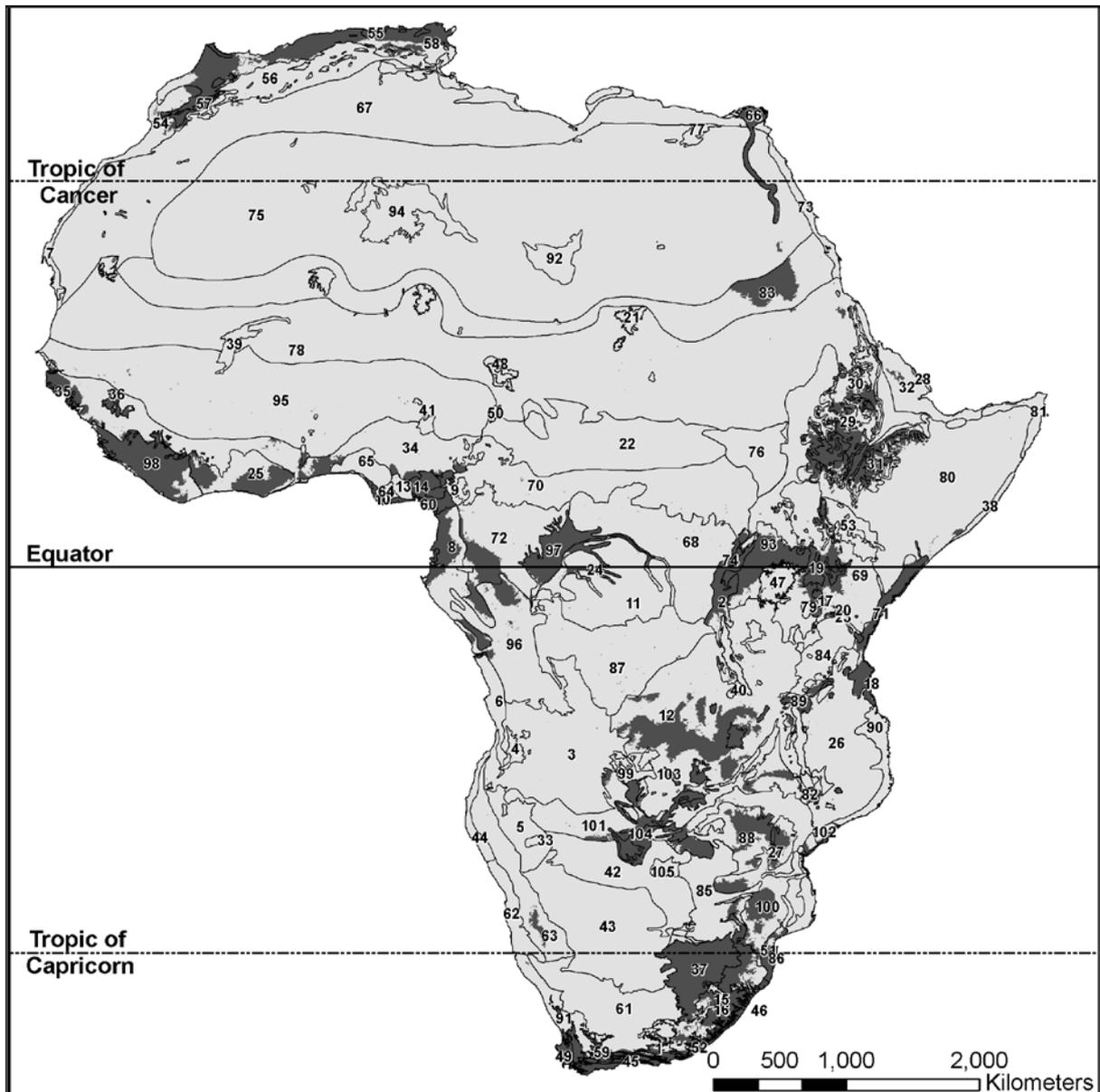


Figure 4.2. Potential reserve network of 10% of the geographic distributions of endemic dragonfly species (dark gray). This represents 11.4% of the top fraction of the African landscape. Annotations are for terrestrial ecoregions and described in Table 4.2.

3.3. Reserves

Protected areas represented 10.7% (106561 of 999771 grid cells) of the total landmass analyzed here. Reservation of the same area that protected areas represent would include only a 1.1% proportion of the distribution of dragonfly species overall, and 1.4% of the distribution of endemic dragonfly species. A 10% proportion of overall species distributions would require protection of 17.9% (178812 grid cells) of the top-ranked fraction of landmass to be set aside (Figure 4.3). Considering only endemic species distributions, a top fraction of 16.2% (162637 grid cells) of landmass would be required (Figure 4.4). This represents 5.2% (52040 grid cells) more than under the unconstrained analysis for all species, and 4.8% (48238 grid cells) considering only African endemics.

3.4. Hotspots

African biodiversity hotspots represent 15% of the total available landmass (or 149881 of 999771 grid cells). However, protection of the area that hotspots represent would include only a 2.6% proportion of the geographic distribution of dragonfly species overall, and 3.1% of African endemics. To protect 10% of species distributions overall (Figure 4.5, Table 4.2) and African endemics (Figure 4.6, Table 4.2), a reserve network of hotspots would require a total selected landmass of 17% (170205 grid cells) and 15.8% (158372 grid cells), respectively. However, considering all species, 2% (20324 grid cells) of high value area would occur outside the hotspot areas, and considering endemics, 0.8% (8491 grid cells) would occur outside the hotspot areas.

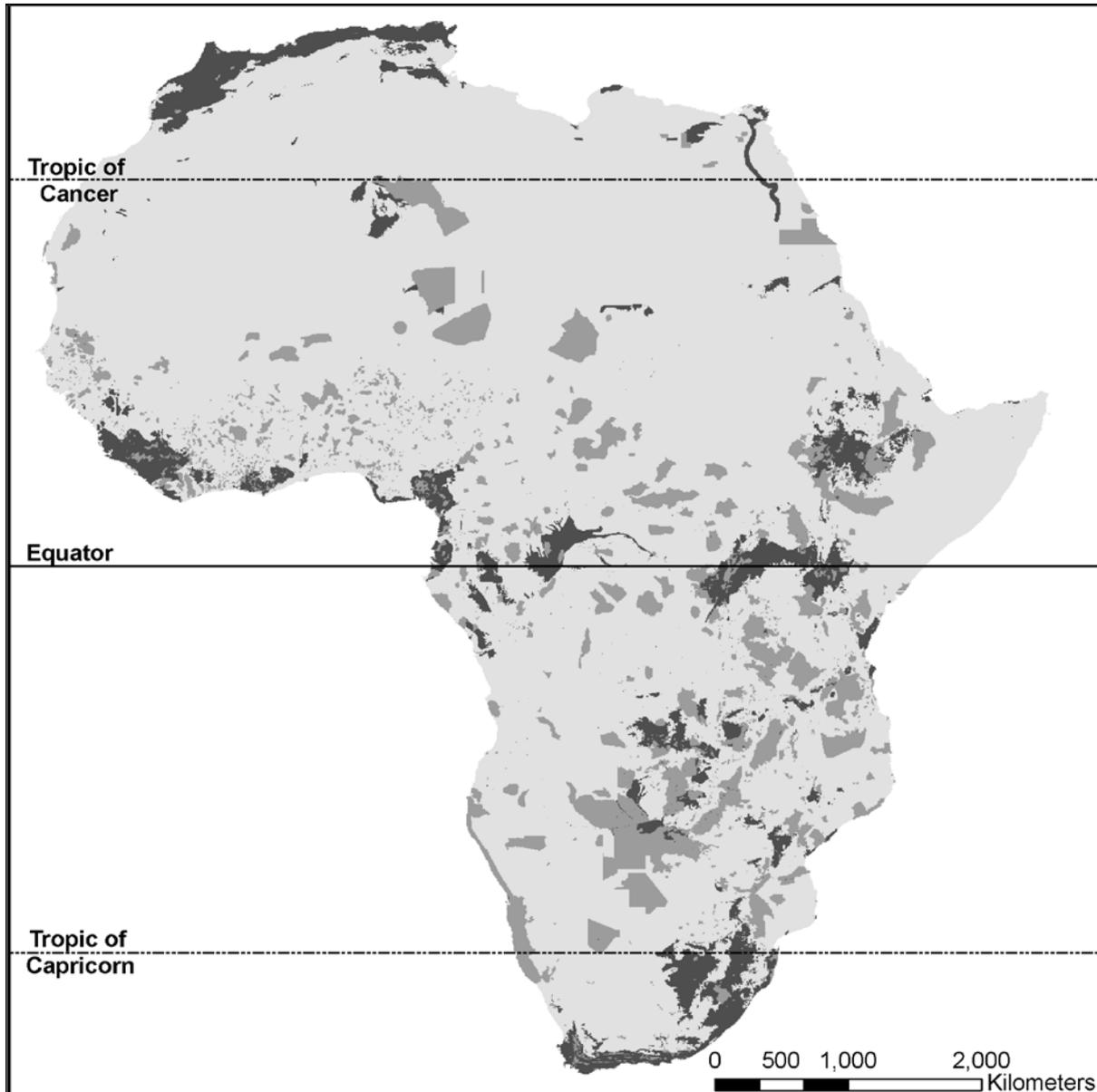


Figure 4.3. Reserve network of 10% of the geographic distribution of dragonfly species (dark gray), with protected areas (light gray) (17.9% top fraction of landscape) included in the reserve network.

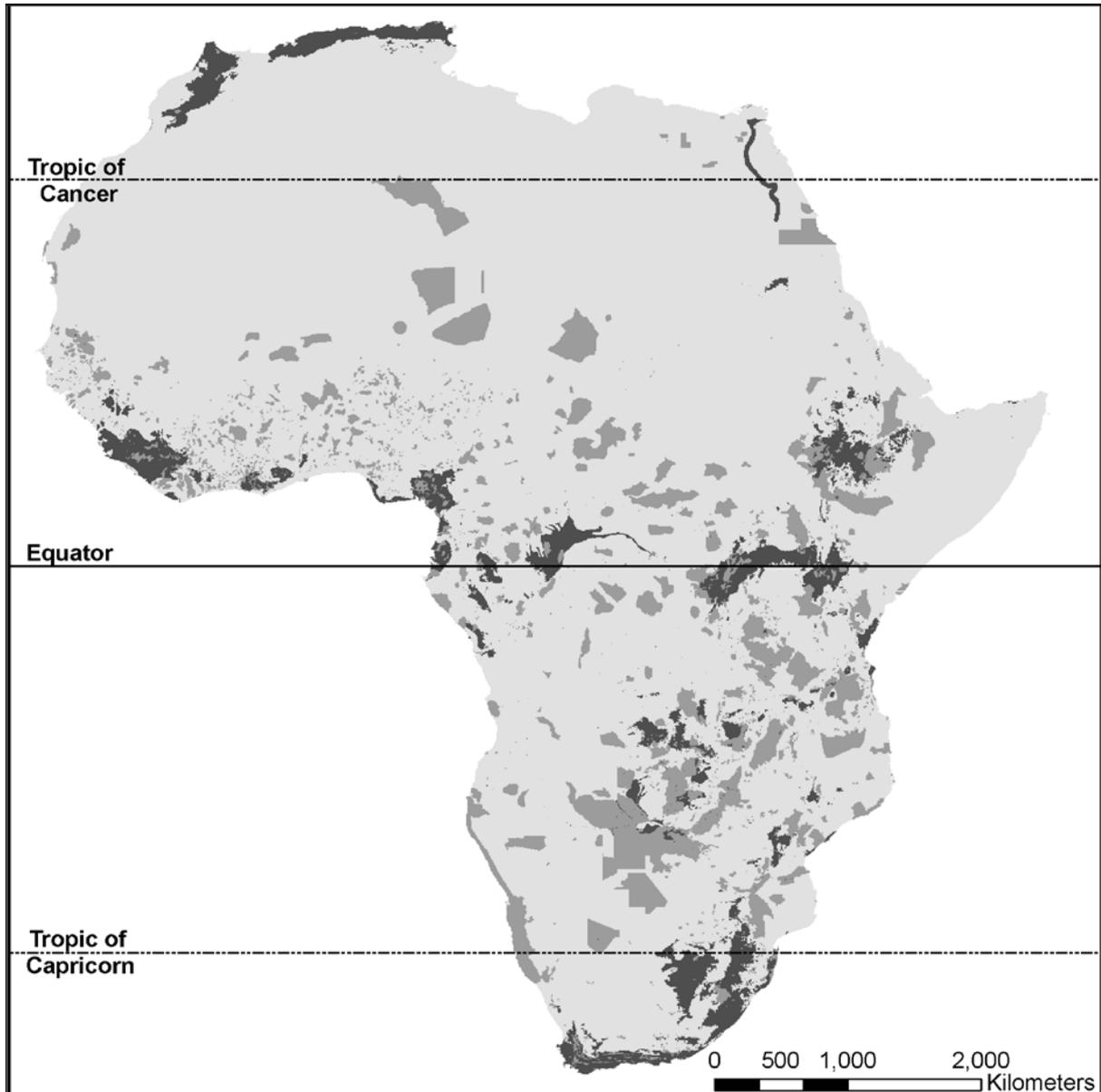


Figure 4.4. Reserve network of 10% of the geographic distribution of endemic dragonfly species (dark gray), with protected areas (light gray) (17.9% top fraction of landscape) included in the reserve network.

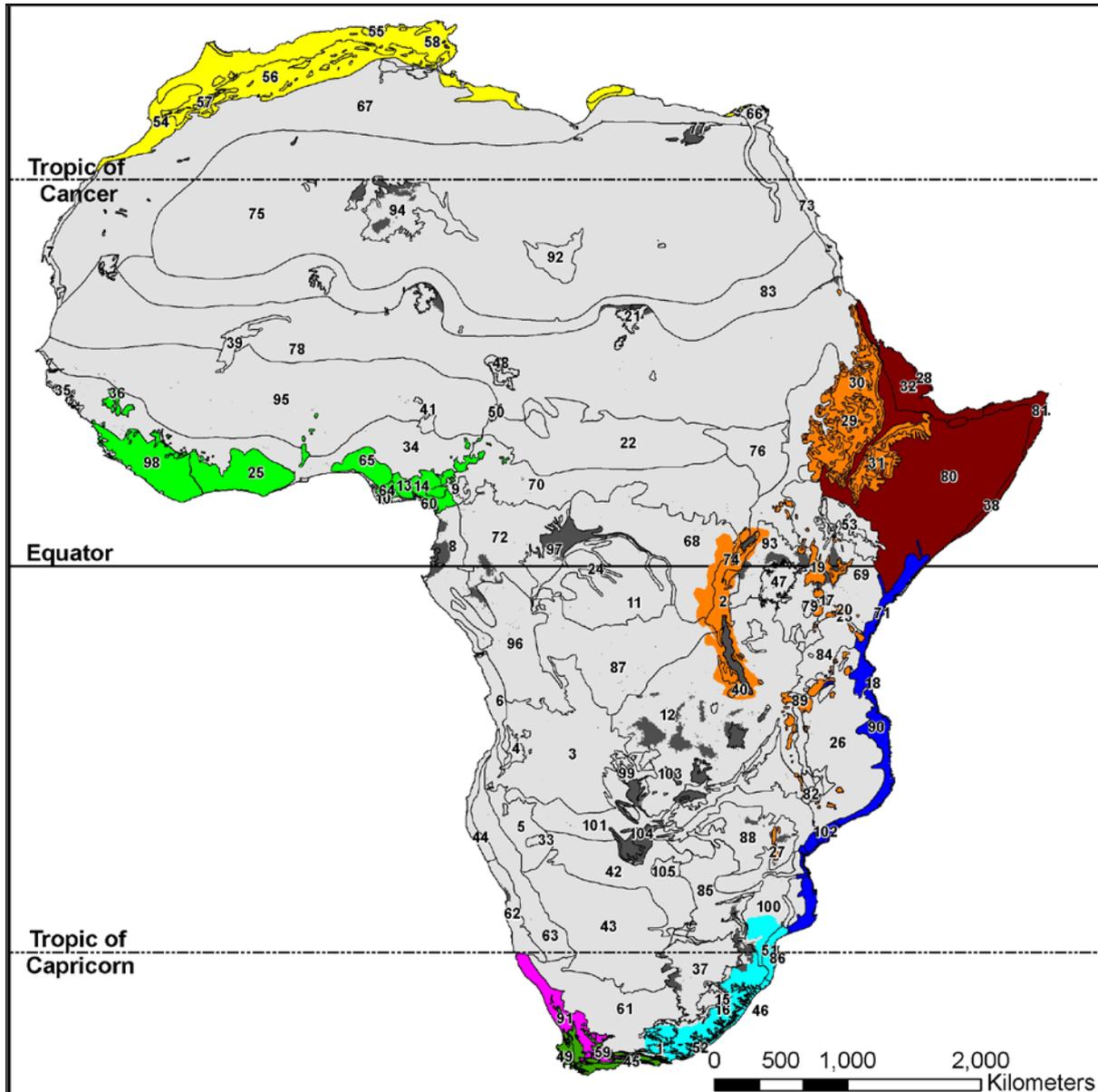


Figure 4.5. Potential reserve network of 10% of the geographic distribution of dragonfly species (dark gray) with global biodiversity hotspots (17% top fraction of landscape) included in the network. Annotations are for terrestrial ecoregions and described in Table 4.2.

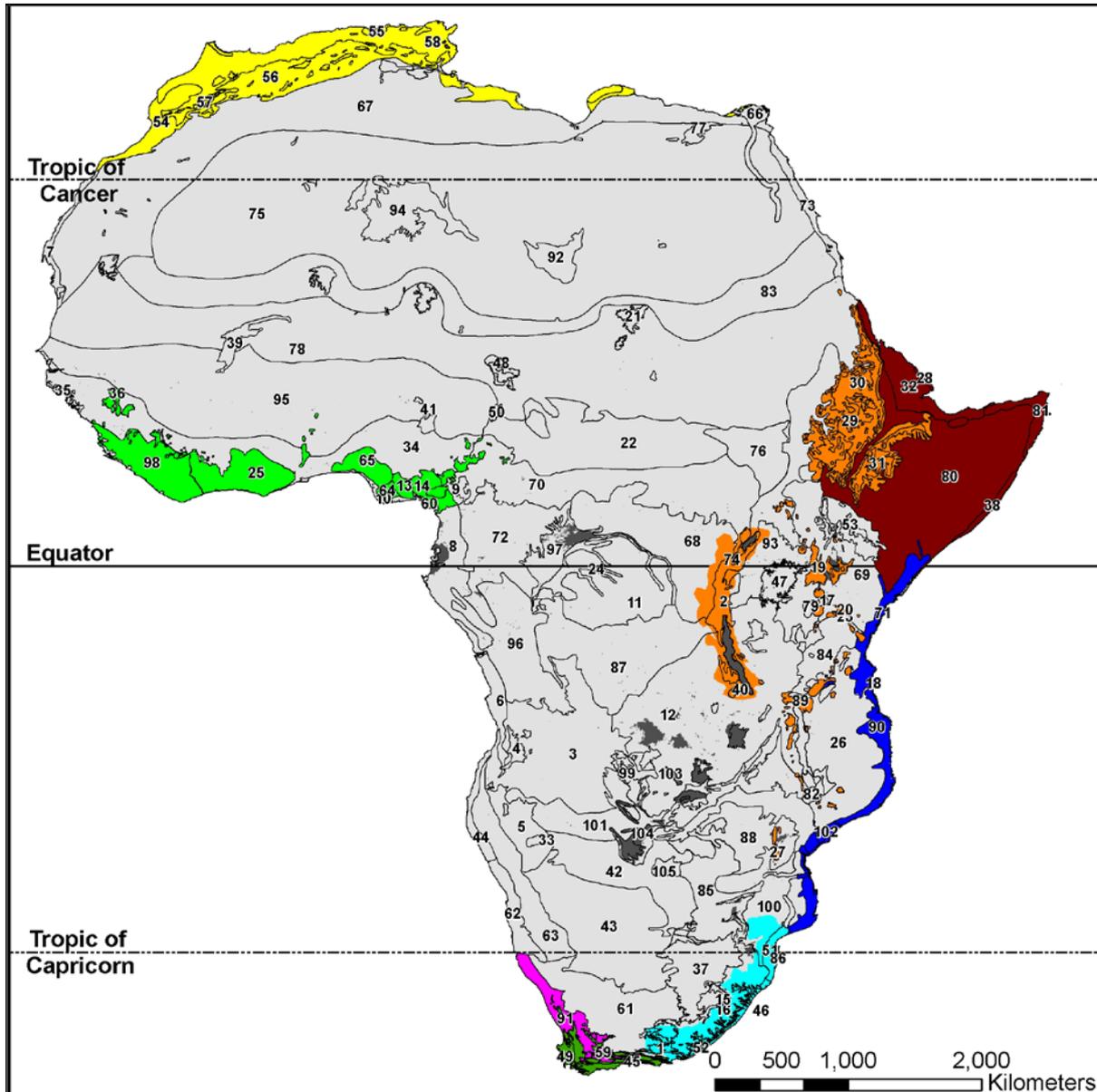


Figure 4.6. Potential reserve network of 10% of the geographic distribution of endemic dragonfly species (dark gray) with global biodiversity hotspots (17% top fraction of landscape) included in the network. Annotations are for terrestrial ecoregions and described in Table 2.

4. Discussion

4.1. Overview of analyses

I found general agreement of the unconstrained network analysis with what might be expected in terms of biogeographical patterns of dragonfly distributions and accordingly, the priority areas (Figures 4.1, 4.2). The existing priority areas that fall outside the current hotspot areas and reserves, are discussed in detail below. Nevertheless, under-sampled areas that are likely to yield new species remain. In particular, these are the vast expanses of the Congo Basin rainforests, the Angolan and Albertine highlands, the highlands and woodlands of Mozambique, and eastern and north-eastern Tanzania.

4.2. Hotspots and beyond

Global biodiversity hotspots cover very large tracks of geographical regions without discriminating the finer details (Figures 4.5, 4.6). Setting aside entire hotspots would lead to a very inefficient representation of the geographic distribution of dragonfly species, with nearly 17% of the landscape, slightly more efficient than the currently highly fragmented system of protected areas. The unconstrained analyses (Figures 4.1, 4.2) show that large portions of priority areas occur within the boundaries of the hotspot areas (Figures 4.5, 4.6). This is true for all hotspots except the dry Succulent Karoo and Horn of Africa, which have few suitable habitats for dragonflies and their aquatic larvae. At least in part, the Coastal Forests of Eastern Africa also have some importance to dragonflies. South Africa alone is home to three global biodiversity hotspots. In terms of dragonfly diversity, additional areas of conservation interest would be the Knysna-Amatole montane forests and Albany thickets. Also, the north-eastern expanse of the Maputo-Pondoland-Albany hotspot is flanked by priority areas represented by the Drakensberg montane ecoregion and Southern Africa bushveld. In addition, a large area of Highveld grasslands appears to be important. Several areas of priority extend beyond the fragmented portions of the Eastern Afromontane biodiversity hotspot. At the southern expanse of the hotspot, these are the Miombo woodlands and South Malawi montane forest-grassland mosaic. Towards the middle of the expanse, it is the Northern Acacia-Commiphora bushlands and thickets ecoregion, as well as the Victoria Basin forest-savanna mosaic ecoregion. Well beyond the hotspots, very large areas of Zambezian flooded grasslands, Zambezian and Mopane woodlands, as well as large portions of the Central Zambezian Miombo woodlands have priority areas of high conservation value for dragonflies. On the west coast, home to the Guinean Forests of West Africa biodiversity

hotspot, small portions of the central African mangroves and large expanses of Atlantic Equatorial coastal forests are of importance. Farther inland, it is the Northwestern Congolian lowland forests and the Western Congolian swamp forests that are important. In North Africa, the West Saharan montane xeric woodlands, small pockets of Saharan halophytics and Sahelian acacia savanna.

4.3. Protected areas

Although 10.7% of the African landscape is covered by reserves, these are widely dispersed and fragmented (Figures 4.3, 4.4). Thus, even a large and diverse taxonomic group composed of highly vagile generalist and specialist species such as the dragonflies are not particularly well protected. While 82% of globally threatened species are recorded to occur at least once in a protected area, only a 1.1% proportion of species geographic distributions are represented by reserves. To protect a 10% proportion of the geographic distribution of dragonflies would require an additional 5.2% (or 4.2% for African endemics) of Africa to be set aside for the conservation of dragonfly species, significantly more than would be the case if the entire area was available for protection. The current reserve system is therefore inefficient at conserving dragonfly diversity, and demonstrates that dragonflies survive outside protected areas. Furthermore, while my criteria for selecting protected areas for inclusion into the analysis was based solely on the size of existing reserves, this could have been based on other criteria, such as designation or international convention (UNEP-WCMC 2009). However, with few exceptions (Saunders et al. 2002), protected areas, even large ones, do not normally take freshwater biodiversity into account. The longitudinal nature of streams makes it difficult to include both headwaters and lower reaches in protected areas (Roux et al. 2008). For example, South Africa's Kruger National Park is oriented north-south, but cuts across the downstream sections of river catchments, which are oriented west-east. The result is that the perturbed inflows from upstream habitats outside the protected area negatively impact downstream habitat in the protected area (Skelton et al. 1995). In the case of Kruger National Park, Roux et al. (2008) recommend redesign of the park based on spatial prioritization of the riverine fauna that occurs there. Competing interests for freshwater may have negative impacts on freshwater species as well. Overexploitation of natural springs for water supply of tourist lodging has eradicated several dragonfly species from the Waterberg National Park in Namibia (Suhling et al. 2006).

5. Conclusions

While geographically hugely over-represented, many areas of high biodiversity fall within the boundaries of established global biodiversity conservation priorities (Brooks et al. 2006). However, beyond global biodiversity hotspots, are also priority areas of significant conservation value. Furthermore, many under-sampled areas that are likely to yield new species remain. In particular, these are the vast expanses of the Congo Basin, the highlands of Angola, highlands and woodlands of Mozambique and eastern and north-eastern Tanzania. The fine-scale modeling approach presented here has two main advantages. First, there is the benefit of a highly detailed, fine-scale representation of priority areas. This shifts the focus from the large-scale hotspots to smaller priority areas within and also beyond hotspots. Second, by operating at the fine-scale for a large geographic area, the potential exists for local conservation managers to consider campaigning for the inclusion of the priority areas that are not formally protected, and adjacent to the existing reserve networks. Where this is not possible, or where areas fall within the mosaic of different landscape uses, I recommend monitoring these areas to keep informed of future threats to the habitats that these might face.

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Chapter 5

Predicted range shifts of vagile organisms along an elevation gradient

Abstract: *The greatest threat to biodiversity is human-induced future climate change, especially when coupled with habitat destruction. Already a water-stressed country, precipitation in South Africa is predicted to decrease with increasing water demand. Dragonflies are a well-studied surrogate taxon for freshwater biodiversity. Here, I created species distribution models of 15 dragonfly species, and predicted the changes in species richness, geographic range and habitat suitability, forty and eighty years from now. According to the model predictions of two different emissions scenarios, at least three species will be lost from the area by 2050, and four by 2080. However, there is the possibility of some species that currently occur farther north in southern Africa and South Africa, moving southwards. The remaining species are predicted to persist with reduced geographical ranges, at generally higher elevations. Most species presented here thrive quite well in artificial environments, such as engineered ponds or dams, but also in roadside ditches and other temporary water features. It is therefore unlikely that, to a certain extent, loss in connectivity will play a role for these species. However, stream specialists are particularly vulnerable, due to the synergistic effects of climate change and loss of habitat.*

Keywords: climate change, freshwater, aquatic biodiversity, dragonfly, South Africa

1. Introduction

Anthropogenic climatic change, especially when synergistic with habitat destruction, has emerged as among the greatest threats to global biodiversity (e.g. Opdam and Wascher, 2004; Travis, 2003). Although climate changes all the time, it is the current and future rate and magnitude of change that is of concern. Globally, patterns in temperature and precipitation are predicted to change greatly, altering the distribution of rivers and wetlands (Carpenter et al., 1992; Dawson et al., 2003). In addition, climate change coupled with habitat destruction and loss in connectivity, invasion by alien organisms, water abstraction, and pollution are likely to prevent freshwater species from adapting at a rate fast enough to cope with local and regional changes (Dudgeon et al., 2006; Opdam and Wascher, 2004).

Already a water-scarce country, the future climate of South Africa is predicted to increase in temperature and decrease in precipitation (Driver et al., 2005). Rivers are the primary source of water (85%) for agricultural, domestic and industrial uses. Dams provide the remainder (15%) and the water stored in dams accounts for 67% of the total annual run-off in all rivers. A study assessing the status of main river ecosystems in South Africa found that 23% of the length of the country's main rivers has been irreversibly transformed (Nel et al., 2007). Coupled with ever-increasing water withdrawals and effluent discharge, aquatic diversity is bound to decline further in other systems, causing associated losses in ecosystem services (Driver et al., 2005; MA, 2005).

To monitor the effect on biodiversity of such large-scale and ubiquitous changes requires the careful selection of bioindicators. Adult dragonflies make excellent surrogates for the assessment of aquatic systems (Schindler et al., 2003). They are used as indicators of ecological health (Trevino, 1997), ecological integrity (Simaika and Samways, 2009a) and environmental change, including habitat recovery (Samways and Sharratt, 2010) and climate change (Hassall et al., 2007; Ott, 2011). Indeed, distributional changes in dragonflies due to anthropogenic climate change have been studied in Germany and Britain. In Germany, Ott (2011) demonstrated the expansion of Mediterranean species of dragonflies into Northern Europe. Furthermore, Hickling et al. (2005) showed that there was a trend towards a northward shift in range margins that occurred in Britain.

The dragonfly fauna of South Africa is composed of specialist and generalist species, showing lesser levels of endemism than many other insect taxa, and little dependency on plant composition (Grant and Samways, 2007). Nevertheless, the mountainous south west is a centre of endemism for dragonflies, while the species rich north east is dominated by Afrotropical species (Simaika and Samways, 2009b). This distribution pattern also reflects that found by Wishart and Day (2002) for

other freshwater invertebrates and vertebrates. Small reservoirs, such as pools or farm dams, are frequently encountered in the landscape and act as important reserves for dragonflies (Samways, 1989). Such reservoirs increase the area of occupancy of local, albeit generalist species, thus increasing the connectivity of the landscape, from a dragonfly's perspective. Furthermore, in KwaZulu-Natal, the dragonfly assemblages are known to be highly elevation tolerant and vagile (Samways and Niba, 2011).

Species distribution models are frequently used to model current and future distributions of species (Hijmans and Graham, 2006; Franklin, 2010). These models seek to predict habitat suitability at unsampled locations by combining the data on the observed location of a species (presence) with environmental data. The applications of such models are varied. For example, past studies have used models to guide field surveys (e.g. Bourg et al., 2005), predict species invasions (e.g. Ficetola et al. 2007), plan for conservation (e.g. Elith and Leathwick, 2009) and project potential impacts of climate change (e.g. Thomas et al., 2004). In this study, my objective is to understand how the distributions of dragonflies will be affected by global climate change in the medium to long term. I aim to investigate what effect climate change will have on (a) species geographic spread and elevation range (b) species richness patterns and (c) habitat suitability.

2. Methods

2.1. Study area and sampling records

The study area was located in the province of KwaZulu-Natal (South Africa), extending from the coast to the Drakensberg mountains. At sea level a sub-tropical to tropical climate prevailed, while at higher elevations was temperate. Elevation ranged from 0 to 3408 m.a.s.l. This is an ideal location for such an elevational study as the gradient runs from east to west, so not invoking the variable of changes in latitude, only longitude. Collection and observation records for this study were extracted from a larger, national dataset of dragonfly species (Simaika and Samways, 2009b). Additional data came from a study on the elevation tolerance of dragonflies in the same study area (Samways and Niba, 2011). Of 40 species initially selected for this study, only 15 could be retained for further analysis. In total, 280 records, representing 15 species and 77 unique sampling locations were used in this study (Figure 5.1).

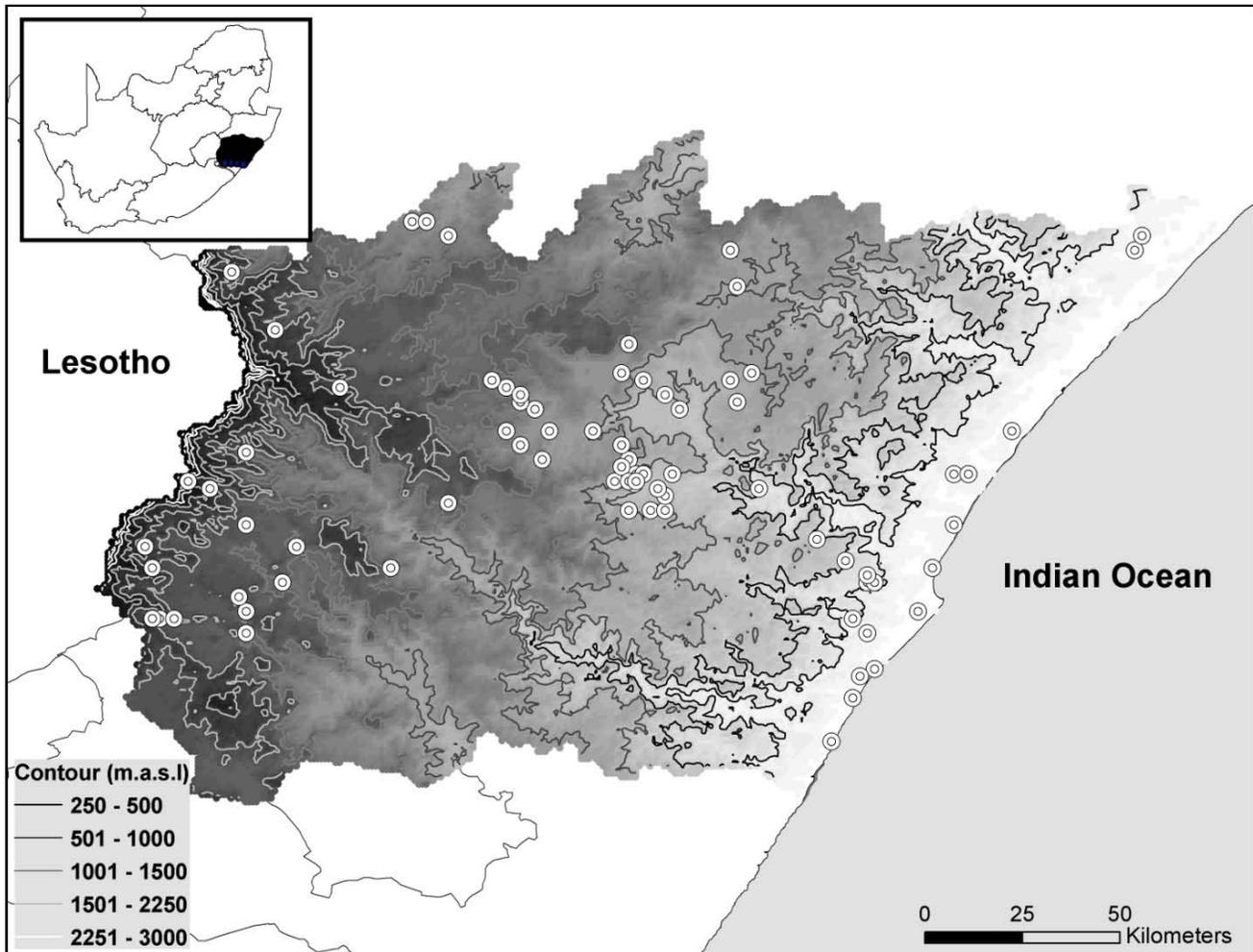


Figure 5.1. The study area, in KwaZulu-Natal, South Africa. White double-circles are sampling locations. Shaded areas indicate increasing elevation from low (light gray) to high elevations (dark gray).

2.2. *Environmental variables*

I obtained 30 arc-second (c.a. 1 km² cell size), climate raster datasets of bioclimate variables. These are biologically relevant variables, which are calculated from elevation, temperature and precipitation (Hijmans et al., 2005). In addition to current climate data (1950 to 2000 average), I also obtained coupled global climate data from the IPCC 4th Assessment (IPCC, 2007) of future climate projections for the years 2050 and 2080. The future climate projections came from three global climate models: the Canadian Centre for Global Climate Modeling and Analysis (CCCma), the Commonwealth Scientific and Industrial Research Organization (CSIRO) and Hadley Centre Coupled Model V3 (HADCM3). Each model was tested under two different emissions scenarios (A2 and B2). The A2 scenario assumes that population growth does not slow down and reaches 15 billion by 2100, and is associated with an increase in emissions. The B2 scenario assumes slower population growth, reaching 10.4 billion by 2100, and assumes that precautionary environmental practices are implemented (IPCC, 2007). In addition to the climate rasters, I used a river catchment areas map, at the quaternary scale (Midgley et al., 1994). Bioclim variables for the future scenarios were calculated using DIVA-GIS 7.2 (Hijmans et al., 2005).

2.3. *Species habitat modeling*

For this study, I used the species distribution modeling software package Maxent (version 3.3.3a; Philips et al., 2006; Philips and Dudik, 2008). Maxent was run using default parameters. Maxent has been shown to produce higher quality predictive models compared to other modeling methods (Elith et al., 2006), and is relatively insensitive to sampling size (Wisz et al., 2008). To check for multicollinearity, I used a Spearman rank correlation analysis on the normalized environmental variables. The use of multicollinear variables may cause overfitting of models, and makes the interpretation of variable importance impossible (Philips et al., 2006). Jackknife tests were used to remove variables that did not significantly contribute to model predictions. In this study a minimum of 20 unique locations (one presence per grid cell) were required for species to be admitted for modeling. For each species, I replicated 100 runs with 75% of a species' records randomly selected for model training and cross-validation, and 25% of the data set aside for model testing and independent validation. The importance of environmental variables will differ among species, and therefore, different models were built for each species. Model results were compared and validated using the area under the receiver operating characteristic curve (AUC). The AUC measures the ability of models to discriminate presence records from absence records. An AUC value of 0.5 in the model would be

equivalent to a random guess, while a value of 1.0 would indicate that the model can perfectly distinguish between presence and absence of a species (Elith et al., 2006). Suggestions on what minimum AUC values have a useful amount of discrimination vary from $AUC > 0.7$ (Pearce and Ferrier 2000) and the frequently quoted $AUC > 0.75$ (Elith et al. 2006) to $AUC > 0.85$ (Newbold, 2010). To take uncertainty into consideration, I selected species models that had an AUC value > 0.7 after subtraction of the lower 95% confidence interval. Thus of 40 species chosen for modelling in Maxent, only 15 were selected for further analysis. Selected model AUCs ranged from 0.76 – 0.96 or after subtraction of the lower 95% confidence interval, the lower AUC values ranged from 0.70 – 0.94.

2.4. Spatial analysis

In order to assess changes in species richness and geographic range, the species models were converted into presence-absence datasets. Species were considered present in a grid cell only above the training presence threshold, averaged over all 100 runs for each species. In addition to this criterion, at least two models would have to agree on the presence of a species in a grid cell to be considered a presence. Species geographic range was defined as the sum of the presence scores (i.e. number of grid cells) across the study area, and species richness as the number of species considered present in each grid cell. Species minimum and maximum elevations were calculated as the average of 10 grid cells of lowest or highest value, respectively. The potential change in species distribution under climate change was computed by differentially weighting grid cells of current and future suitable (current=1, future=4) and non-suitable habitat (current=0, future=2) for each prediction and then adding current predictions to future predictions. This method allowed me to classify areas as unsuitable (current and future), stable (suitable currently and in the future), increasing suitability in the future, and decreasing suitability in the future (unsuitable=2, stable=5, increasing=4, decreasing=3) under future climate scenarios. All spatial work was carried out using ArcGIS 9.2 (ESRI, 2006).

3. Results

3.1. Models and variables

Here, all variables used in model building were found to correlate ($p < 0.01$, $r > 0.08$), and thus interpretation of variable importance to models was not possible. Eight models were created for species under different climate scenarios. The most commonly used variables were the catchment area (all

models), minimum temperature of the coldest month (4 models), mean temperature of the driest month (4 models), and precipitation of the warmest quarter (4 models) (Table 5.1).

3.2. *Species richness*

In the current prediction, the richest area is in the midlands, with 13 species (Figure 5.2). Richness at the coast is lower, with eight species, and lowest in the highlands, where five to six species occur. Under the more severe emissions scenario A2 for the year 2050, few species (one to two) are predicted to occur at the coast (Figure 5.3), while in the other scenarios for 2050 and 2080, at least up to four species will occur. Species richness remains highest in the midlands, as it does in all modeled predictions. However, in all scenarios there is a loss of at least three species (Table 5.2). There is a general loss of extent in occurrence in the highland areas, especially in the 2050 models. In contrast, in both emissions scenarios for 2080, numbers of species are as high as in the current prediction.

3.3. *Geographic range and elevation*

Overall, species will undergo a reduction in extent of occurrence, with this decrease ranging from 28% to 35% in 2050 and 32% to 45% in 2080. Three species, *Brachythemis leucosticta*, *Hemistigma albipunctum* and *Palpopleura portia*, all widespread African species, will be extirpated from the study area by the year 2050 (Table 5.2). These species also have the most narrow elevation ranges of all species, from 458 – 1258 m (Table 5.3).

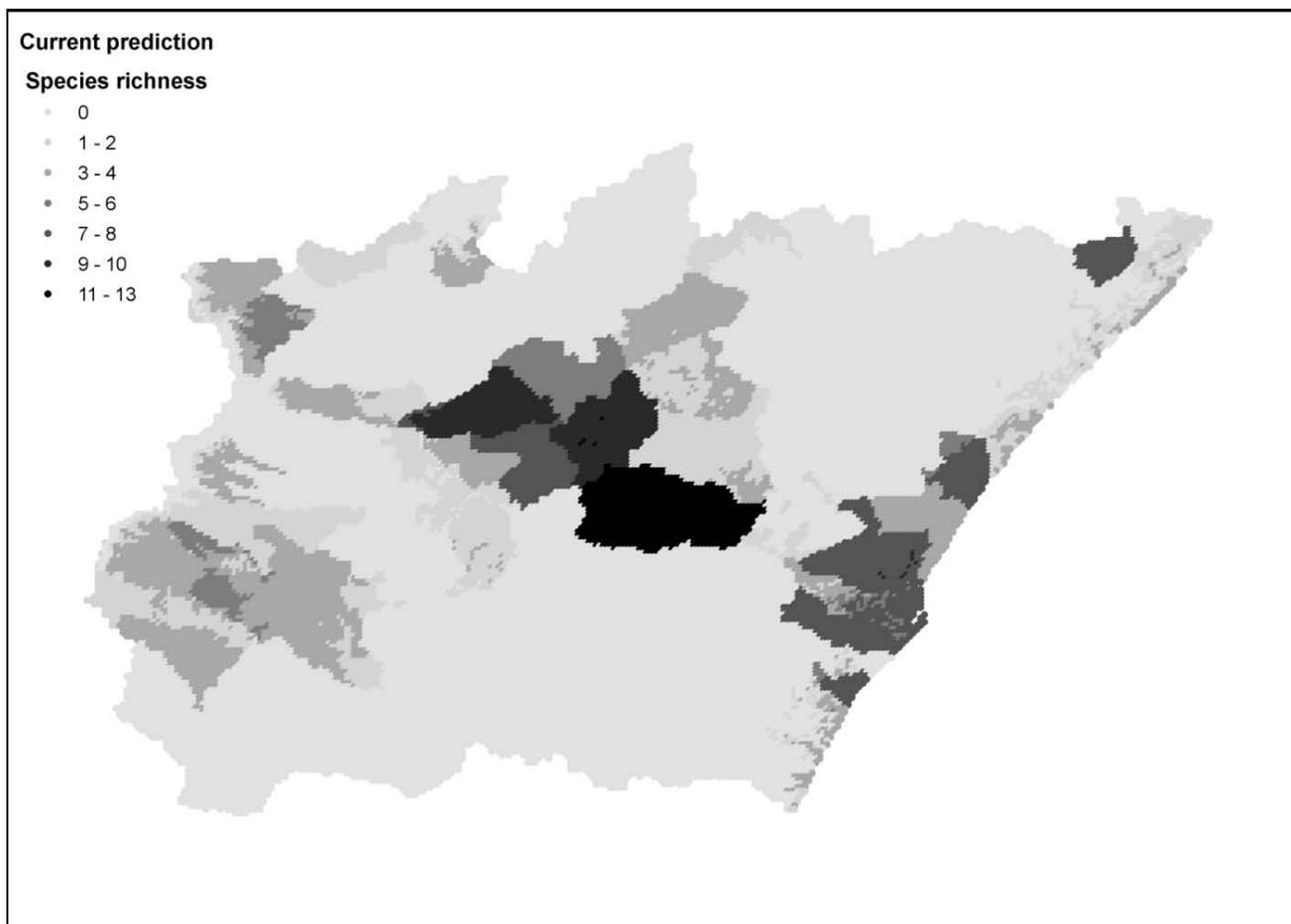


Figure 5.2. Predicted current distributions of dragonfly species in the study area.

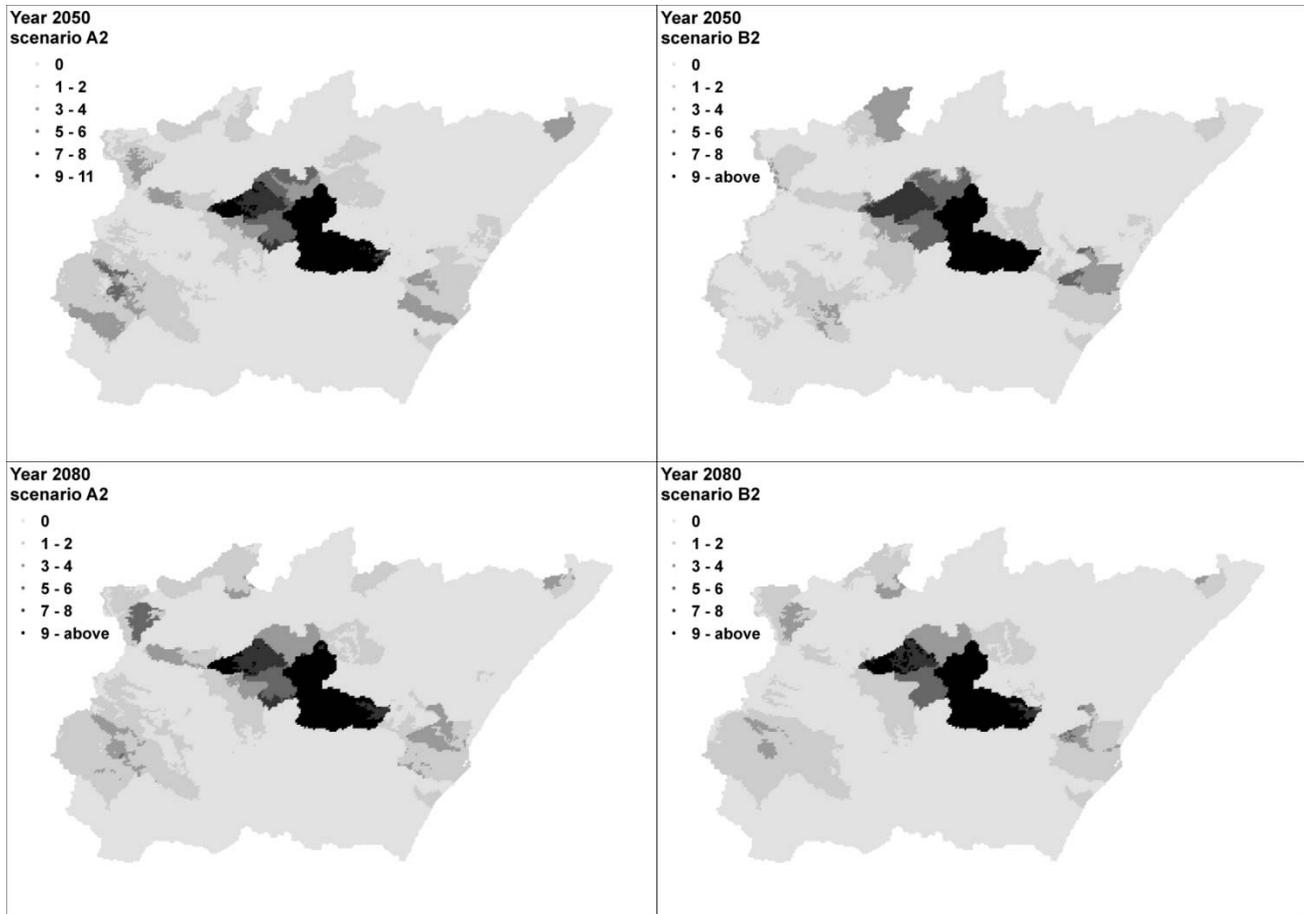


Figure 5.3. Predicted species richness patterns for 2050 and 2080 under the A2 (left) and B2 (right) climate scenarios.

Table 5.2. Geographic ranges of modeled species, expressed here as number of grid cells, under current and future (2050, 2080) predicted global climate change scenarios. Predicted changes are expressed as percentages. Abbreviations: n.a. = not applicable.

Species	Current	Scenario A2				Scenario B2			
		Current 2050	Current to 2050	Current 2080	Current to 2080	Current 2050	Current to 2050	Current 2080	Current to 2080
<i>Africallagma glaucum</i>	5200	4751	91	4329	83	5088	98	3194	61
<i>Brachythemis leucosticta</i>	1151	0	0	0	0	0	0	0	0
<i>Ceriagrion glabrum</i>	3295	1475	45	0	0	0	0	0	0
<i>Chlorolestes fasciatus</i>	4636	3283	71	4011	87	2117	46	880	19
<i>Chlorolestes tessellatus</i>	2640	2362	89	2352	89	2719	103	2352	89
<i>Hemistigma albipunctum</i>	1887	2	0	0	0	0	0	0	0
<i>Lestes virgatus</i>	2257	2257	100	2257	100	2257	100	2257	100
<i>Nesciothemis farinosa</i>	3543	2809	79	3135	88	1429	40	2890	82
<i>Palpopleura portia</i>	2497	0	0	0	0	0	0	0	0
<i>Pseudagrion kersteni</i>	3933	1855	47	1853	47	2956	75	2344	60
<i>Pseudagrion massaicum</i>	2123	1817	86	1077	51	1077	51	1077	51
<i>Pseudagrion spernatum</i>	3868	5145	133	5601	145	4461	115	5538	143
<i>Trithemis arteriosa</i>	5438	2990	55	2769	51	4036	74	2054	38
<i>Trithemis dorsalis</i>	4967	4978	100	4200	85	4151	84	5226	105
<i>Trithemis furva</i>	2945	2659	90	2780	94	2469	84	2916	99
Total species range	50380	36383	72	34364	68	32760	65	27812	55

Table 5.3. Current and future predicted elevation tolerances of species under two climate scenarios, A2 and B2 for 2050 and 2080. Minimum, maximum and range of elevations are given in meters. Range means here the difference between the minimum and maximum recorded elevation. Abbreviation n.a. = not applicable.

Species	Present			A2 2050			A2 2080			B2 2050			B2 2080		
	min	max	range												
<i>Africallagma glaucum</i>	13	2339	2326	27	2369	2342	26	2318	2292	14	3002	2988	27	3232	3205
<i>Brachythemis leucosticta</i>	20	990	970	n.a.	n.a.	n.a.									
<i>Ceriagrion glabrum</i>	4	1294	1290	70	1293	1223	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
<i>Chlorolestes fasciatus</i>	1045	2368	1323	999	3142	2143	1004	3132	2128	884	3248	2364	1074	2677	1603
<i>Chlorolestes tessellatus</i>	15	1768	1753	92	1768	1676	348	1768	1420	15	1768	1753	348	1768	1420
<i>Hemistigma albipunctum</i>	2	470	468	13	44	31	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
<i>Lestes virgatus</i>	4	1293	1289	4	1293	1289	4	1293	1289	4	1293	1289	4	1293	1289
<i>Nesciothemis farinosa</i>	4	1768	1764	12	1768	1756	10	1768	1758	348	1293	945	12	1768	1756
<i>Palpopleura portia</i>	4	1262	1258	n.a.	n.a.	n.a.									
<i>Pseudagrion kersteni</i>	4	1840	1836	441	2176	1735	345	2176	1831	12	2431	2419	528	2128	1600
<i>Pseudagrion massaicum</i>	12	1578	1566	4	1340	1336	39	1262	1223	39	1262	1223	39	1262	1223
<i>Pseudagrion spernatum</i>	583	2593	2010	348	3054	2706	348	3054	2706	348	2509	2161	385	2651	2266
<i>Trithemis arteriosa</i>	4	1835	1831	22	2437	2415	105	2657	2552	12	3004	2992	361	1895	1534
<i>Trithemis dorsalis</i>	250	3246	2996	242	3127	2885	547	2337	1790	371	3254	2883	250	3246	2996
<i>Trithemis furva</i>	12	1593	1581	10	1799	1789	68	1773	1705	15	1509	1494	12	1735	1723

Another narrow-elevation range species, *Ceriagrion glabrum* is predicted to persist under the more severe A2 2050 scenario, but with a range reduced to 45% of its former extent. By 2080, *C. glabrum* will be extirpated under the A2 scenario, and the B2 scenario predicts that the species will no longer be in the study area by 2050. In contrast, *Pseudagrion spernatum* is predicted to extend its range to 133% beyond its former extent under the A2 scenario, and by 2080 will have expanded to 144% over its former geographic range. The elevation range will increase in *P. spernatum* up to 630 m, with 400 m of that change towards the upper elevations (Table 5.3). Under the moderate emissions B2 scenario, the species range will also increase its geographic range, but with only a 160 - 260 m elevational change. The only unaffected species is *Lestes virgatus*. Both the geographic range and elevations remain the same for *L. virgatus* under all scenarios. The widespread endemic *Africallagma glaucum*, has an elevational range second only to *Trithemis dorsalis*, of 2320 m. Under the A2 scenario, the species' elevational range changes little, but under the moderate scenario, there is an upward trend in elevation from current conditions of 670 m in 2050 and 920 m in 2080. It is also under the moderate scenario in which *A. glaucum* is predicted to lose 39% of its former geographic extent. The endemic *Chlorolestes fasciatus* faces range reductions under all scenarios, but while under the severe emissions scenario the species initially declines 29% in 2050, there is a recovery to 87% of its former extent in 2080. Under the moderate scenario there is a decline of 54% in 2050 followed by a further decline to 19% in 2080. By contrast, the geographical range of the endemic *C. tessellatus*, remains relatively stable, ranging from 89% - 103%. Interestingly, it is only the lower range margin in *C. tessellatus* that moves upwards, by 330 m in 2080. In contrast the already high lower range margin of *C. fasciatus* moves only up to 160 m lower, whereas the upper range margin moves up to 880 m higher by 2080 under the severe emissions scenario. Interestingly, it is under the moderate emissions scenario, where *C. fasciatus* faces the greatest range loss, that the elevational range is similar to present conditions.

3.4. Change in habitat suitability

Under the more severe emissions scenario, both the 2050 and 2080 predictions have in common that there is a decrease in habitat suitability for species at the coast and the highlands, while in the midlands there is both a decrease and an increase in habitat suitability (Figure 5.4). The moderate scenario prediction changes the least from the current prediction, while the more severe scenario shows greater change, in particular in the highlands.

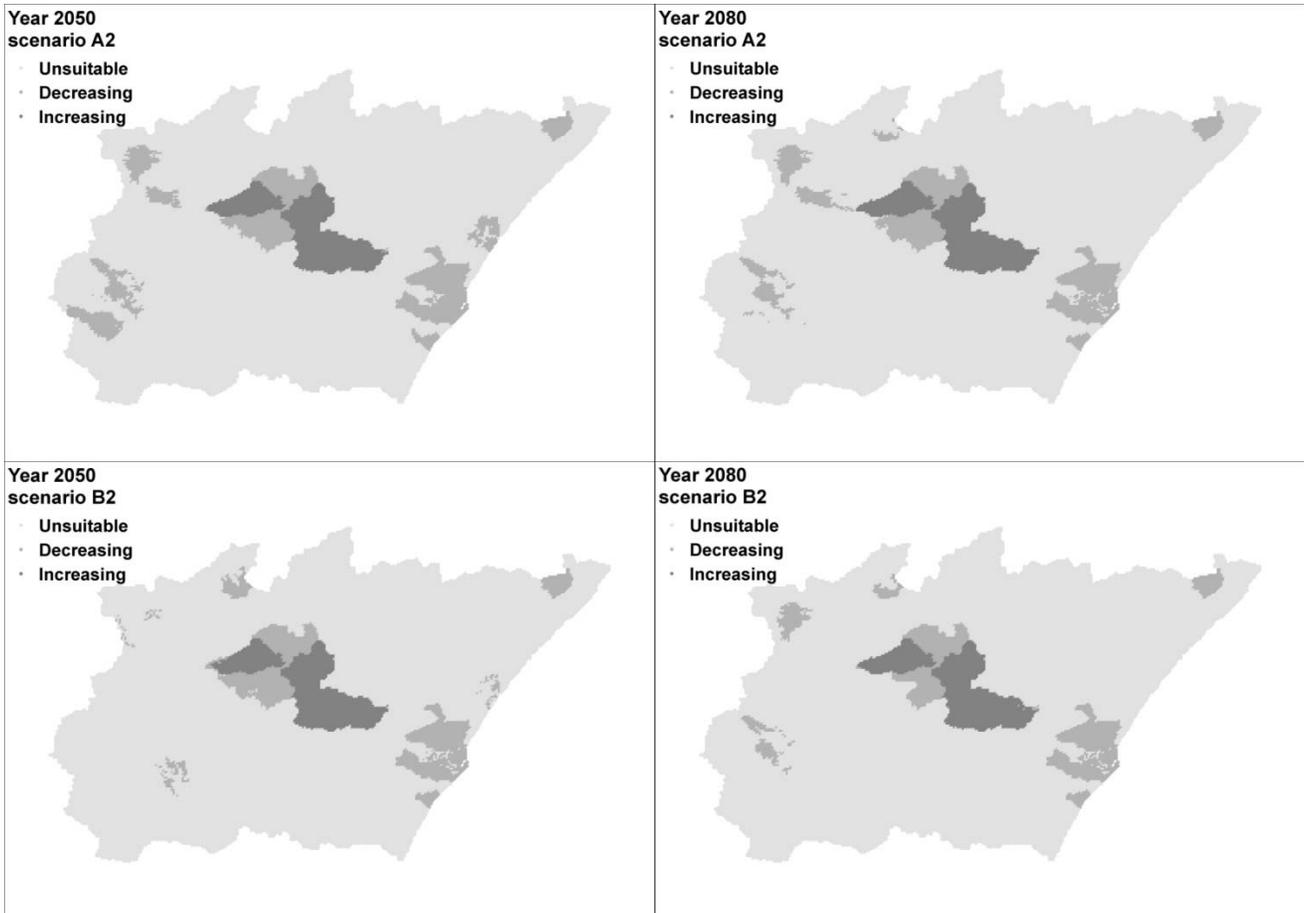


Figure 5.4. Range of habitat change from the current prediction compared to the future (2050 and 2080) under the A2 (left) and B2 (right) climate scenarios.

4. Discussion

Coope (1995) identified three ways in which a species may respond to persistent climate change: (a) the species can become extinct (b) the species can adapt *in situ*, or (c) the species can migrate to an area with a more tolerable climate. There is evidence that some species have gone extinct due to climate change (Pounds et al., 2006), and for the future at least, accelerated rates of extinction are likely (Thomas et al., 2004). In contrast, evolution plays a minor role in faunal responses to climate change (Coope, 1978). Unlike the first two scenarios, distributional changes are recorded and studied frequently (Hassall et al., 2007).

In their study on the responsiveness of 179 animal species from various taxa to climate change brought about by a doubling of CO₂ in South Africa, Erasmus et al. (2002) found that some 17% of species expanded their ranges, 78% displayed range contractions, varying from 4% to 98%, 3% showed no response, and 2% became locally extinct. More importantly, the majority of range shifts (41%) were in an easterly direction, and highest losses of species in the west.

In this study, all modeled species are widespread, and many are common where they occur. Only two species, *C. fasciatus* and *C. tessellatus* are national endemics (Samways, 2006). Nevertheless, climate change is predicted to affect most species negatively. The models for 2050 and 2080 consistently predict reductions in overall species ranges, with a minimum of 28% and a maximum of 35% in 2050 and 32% and 45%, respectively in 2080. Interestingly, species ranges decrease less under the more severe emissions A2 scenario for 2050 and 2080, than under the B2 scenario for the same time periods.

Four species, *B. leucosticta*, *C. glabrum*, *H. albipunctum*, and *P. portia*, face extirpation from the study area in the long term. All these are widespread species, but have relatively narrow elevation ranges compared to other species in the study. Nevertheless, the ranges of *B. leucosticta*, *H. albipunctum* and *P. portia* extend marginally into the study area, and therefore a loss of these species would most likely indicate that they are shifting out of the study area, most likely west. The predicted loss of *C. glabrum* from the study area is likely an artifact of sampling bias, as the distribution of samples mirrors that of the other marginal range species in the study area. However, *C. glabrum* is widespread in South Africa, including the Cape. Only *P. spernatum* will increase in geographic spread under any scenario. The species is widespread in Africa, with two subspecies further north, and in South Africa, is even present in the Western Cape. It is remarkably elevation tolerant, with an estimated range of 2000 m in present conditions. Although a stream specialist, its geographic spread

and remarkable elevation tolerance benefits *P. spernatum* in the changing climatic conditions. The only high-elevation specialist, *C. fasciatus*, is predicted to extend both to lower elevations and higher elevations, with most of the change to higher elevations. Under the more severe emissions scenario the species will initially face a reduced habitat range, followed by a recovery of some of that range. In contrast, under the more moderate emissions scenario the species faces a continued decline to up to 81% of its former range. The general range reduction of this habitat specialist, despite the increasing elevation range to higher elevations makes sense, since there is less available habitat at higher elevations, than at lower elevations.

It is clear from the predictions, that in this study, the majority of species will be reduced in extent of occurrence and become more localized, while at the same time species richness will decrease. Furthermore, the reduction in the number of species, and therefore competition for habitat, could cause some species to become more common. These changes will likely cause a change in community structures, although it is difficult to foresee that restructuring of the species assemblages would affect trophic interactions (e.g. Winder and Schindler, 2004), mainly because dragonflies have a non-specialist diet. A further consideration is that it is likely that several species that occur farther north in southern Africa, some of which extend just inside South Africa, may move southwards. This is highly likely as several species temporally extend and contract their ranges, mostly north-south, according to El Niño Southern Oscillation events, and regularly becoming present and then locally extinct (Samways 2010). In addition, there are also several species which move up and down in elevation on a temporary basis with prevailing climate (Samways and Niba 2010).

Most species presented here thrive quite well in artificial environments, such as engineered ponds or dams, but also in roadside ditches and other temporary water features. It is therefore unlikely that, to a certain extent, loss in connectivity will play a role for these species. Stream specialists, however, are far more vulnerable, such as *C. fasciatus* and *C. tessellatus*. Whereas *C. fasciatus* occurs at streams at higher elevations where development, forestry plantation or agriculture would be too costly and difficult to achieve, *C. tessellatus* occurs generally in streams at lower elevations, and will thus likely face the synergistic threats of habitat destruction and alien invasion, abstraction and pollution. Stream specialists in particular, such as *C. tessellatus* are therefore likely to benefit from the clearing of invasive alien woody plants, which not only aides the recovery of local biodiversity, but opens up riparian pathways along elevational gradients (Samways 2010).

5. Conclusion

Of 15 species modeled under two emissions scenarios, at least three will be lost from the area by 2050, and four by 2080. However, there is the possibility of some species that are currently occurring farther north in southern Africa and South Africa, moving southwards. Only one species is predicted to benefit greatly from climate change. The remaining species are predicted to persist with reduced geographical ranges, at generally higher elevations. Stream specialists, in particular are vulnerable, due to the synergistic effects of climate change and loss of habitat.

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Chapter 6

GENERAL DISCUSSION

Undoubtedly, anthropogenic global climatic change and habitat destruction are the greatest threats to global biodiversity (e.g. Opdam and Wascher, 2004). Freshwater ecosystems in particular are vulnerable to declines in biodiversity, and are estimated to be up to five times greater in some freshwaters than in the most affected terrestrial ecosystems (Dudgeon et al., 2006). Freshwater ecosystems face destruction or degradation of habitat, invasion by alien species, overexploitation, water pollution, and flow modification. Superimposed upon these interacting threats are global environmental changes such as nitrogen deposition, temperature warming and shifts in precipitation and runoff patterns. Climate change coupled with loss in connectivity are likely to prevent freshwater species from adapting at a rate fast enough to cope with local and regional changes (Dudgeon et al., 2006). Yet humanity depends on freshwater ecosystem services, for example on the provisioning of clean water, food (e.g. rice, fish), and goods to humans (e.g. reeds as building material) and resilience to anthropogenic impacts (e.g. pollution or excessive nutrient release). Other services include the suppression of water-borne diseases, flood attenuation, and delivery of sediment to coastal areas. Additionally, the recreational and spiritual value of wetlands cannot be denied (Millenium Ecosystem Assessment, 2005). These findings highlight the need to systematically protect freshwater biodiversity. In this study, I used dragonflies (Odonata) as model organisms for conservation research, since dragonflies are a well-studied group of invertebrates (Córdoba-Aguilar, 2008), with increasing recognition in conservation worldwide (Samways, 2008). Furthermore, the use of adult dragonflies (Insecta: Odonata) as bioindicators is well established (Oertli, 2008; Simaika and Samways, 2009), and dragonflies have become an essential tool for assessing aquatic systems (Schindler et al., 2003). Dragonflies can be used as indicators of ecological health, ecological integrity, and environmental change, whether climatic or in the recovery of habitats.

This study's findings and their implications for further study are listed below:

6.1 Dragonflies as tools in biomonitoring

1. I found that at the habitat scale, pH and temperature are most important for structuring dragonfly assemblages, while for the benthic macroinvertebrate assemblage pH alone was significant.
2. The dragonfly assemblages of local sites directly reflect those of the benthic macroinvertebrates. However, dragonfly assemblages are overall more dissimilar. This may indicate that the dragonfly assemblage is more responsive to habitat changes than those of the benthic macroinvertebrates.
3. The greater responsiveness of dragonfly assemblages makes the Dragonfly Biotic Index (DBI), a habitat integrity index, an excellent tool for environmental assessment and monitoring freshwater biodiversity, especially as a complement to freshwater quality assessments, such as the South African Scoring System (SASS).
5. The advantage of dragonfly surveys over benthic macroinvertebrate surveys is that they provide a quick, and therefore low-cost, indication of the health or richness of freshwaters. This makes sense, as adult dragonflies are more easily observed and identified in the field.
6. The South African Scoring System operates at the family and other higher taxon level, while dragonfly surveys are at the species level. Thus adult dragonfly surveys can detect changes at this lower taxonomic level, an advantage when it comes to conserving point endemic biota. The DBI could be used alongside SASS, and indeed could be used in lieu of SASS, especially as adult dragonflies are much easier and faster to sample than benthic macroinvertebrates.

6.2 Dragonflies as surrogates for site prioritization in South Africa

1. The Dragonfly Biotic Index is sufficiently sensitive, easy-to-use and robust to be of great value to conservation managers interested in wetland assessment, monitoring and restoration (Simaika and Samways, 2009).

2. Employment of the DBI will aid in closing some of the sampling gaps identified for South Africa.
3. I recommend continued field searches in centers of high endemism, in this case also the CFR.
4. Reserve selection using the DBI is valuable if users recognize that it is a weighted scoring method used to identify globally threatened endemic biodiversity and not complementarity hotspots. The value of the DBI thus lies in maximizing redundancy (i.e. representation) of globally Red Listed species.

6.3 Dragonflies as surrogates for site prioritization for Africa

1. While geographically hugely over-represented, many areas of high biodiversity fall within the boundaries of established global biodiversity conservation priorities (Brooks et al. 2006).
2. However, beyond global biodiversity hotspots, are also priority areas of significant conservation value.
3. Furthermore, many under-sampled areas that are likely to yield new species remain. In particular, these are the vast expanses of the Congo Basin, the highlands of Angola, highlands and woodlands of Mozambique and eastern and north-eastern Tanzania.
4. The fine-scale modeling approach presented here has two main advantages. First, there is the benefit of a highly detailed, fine-scale representation of priority areas. This shifts the focus from the large-scale hotspots to smaller priority areas within and also beyond hotspots. Second, by operating at the fine-scale for a large geographical area, the potential exists for local conservation managers to consider campaigning for the inclusion of the priority areas that are not formally protected, and adjacent to the existing reserve networks. Where this is not possible, or where areas fall within the mosaic of different landscape uses, I recommend monitoring these areas to keep informed of future threats to the habitats that these might face.

6.4 Dragonflies as indicators of climate change

1. Overall, species richness is predicted to decline significantly in 2050 and 2080. However, there is the possibility of some species that are currently occurring farther north in southern Africa and South Africa, moving southwards.
2. Most species are predicted to persist with reduced geographic ranges, at generally higher elevations.
3. Loss in connectivity will not affect the widespread, habitat generalist fauna of Afrotropical dragonflies, as these will make use of artificial structures, such as artificial dams and roadside ditches.
4. Stream specialists, in particular, are vulnerable due to the synergistic effects of climate change and loss in habitat.

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