Assemblage reorganization of South African dragonflies due to climate change

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Abstract

Aim: Climate change is expected to cause large shifts in species assemblages such as dragonflies and damselflies (Insecta: Odonata). Here, we assess the influence of environmental drivers of turnover on Odonata assemblages. Secondly, we map the predicted spatial variation in species composition, first as a gradient of assemblage similarity, and then as discrete bioregions delineating major areas of odonate endemism. Finally, we map the magnitude of expected change in species turnover in response to climate change under two emission scenarios.

Location: South Africa.

Methods: We used a spatial database comprising of 164 species of odonates and 20 covariates, to explore changes in compositional turnover using generalized dissimilarity models. Bioregions were compiled through various clustering techniques.

Results: Present-day odonate bioregions correspond to climatic zones and are clearly separated by transitional zones with rapid spatial turnover. Present odonate bioregions are projected to undergo extensive reorganization by 2050 and 2070. Temporal turnover in species composition is expected to reach up to 80% in the large arid interior and 64% along the coast. Half of all South Africa's protected areas are likely to experience climate induced changes to dragonfly bioregions in the near future.

Main conclusions: Species assemblages are rapidly changing. This work highlights future shifts in climate will result in complex and nonlinear responses in Odonata communities. With ongoing climate change, current odonate bioregions are predicted to expand while others will contract considerably in size within the next 30 years. The current demarcated protected areas may be inadequate to protect dragonflies as climates change. Odonata can be used to track frontiers of climate change, which will likely affect a larger array of taxa as well.

KEYWORDS
beta diversity, bioregions, climate change, generalized dissimilarity modelling, Odonata, turnover

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1 | INTRODUCTION

Understanding the drivers of species distributions is essential for implementing effective conservation strategies for climate change adaptation, protecting regional diversity and ecosystem function, and preventing further species loss (Socolar et al., 2016). While considering policies aimed at biodiversity loss, there is a parallel need to better understand the candidate mechanisms linked to the drivers of ongoing and future biodiversity change. Global indicators continue to show rapid declines in the state of biodiversity worldwide, with shifts in species distributions and community structures already observed in a variety of taxa (Newbold et al., 2015). Species turnover may reflect the potential breakdown of local assemblage-level community composition, with poorly known consequences. For instance, many species are threatened by the loss of climatically suitable habitat (Bush et al., 2014; Krechmer & Marchioro, 2020; Niskanen et al., 2019). Changes in climate suitability are predicted to increase dispersion pressure in the future and may result in the substantial reorganization of many assemblages (Flenner & Sahlén, 2008; Wauchop et al., 2017).

In the light of these concerns, what approaches might best inform conservation planning and action? The collective diversity of a region cannot be adequately measured by site-level diversity indices, such as alpha and gamma diversity, as they do not explain patterns of spatial and temporal turnover (McGeoch et al., 2019). When assessing the impact of environmental change, knowing which species are present (i.e., species composition) is more informative than simply knowing how many species are present (i.e., species richness) (Hillebrand et al., 2018; Jones et al., 2017). Compositional turnover, or beta diversity, captures how fast local assemblages change their species composition over space and time (Socolar et al., 2016). The term beta diversity was first introduced by Whittaker (1960) and is defined as the “extent of change in community composition” among sites. Indices of beta diversity can therefore reveal how biodiversity is organized in space and over time (Socolar et al., 2016). While variation in local community composition is typically thought to be driven by species sorting along often spatially autocorrelated environmental gradients, other spatial processes such as dispersal limitation can further affect local community composition (Cottenie, 2005). Consequently, when explored together with environmental and geographical gradients between sites, beta diversity can further reveal the underlying drivers of compositional turnover. A better understanding of large-scale patterns in community turnover and how these may shift with time can thus provide conservation-relevant insights about the maintenance and management of species over large areas.

Historical taxonomic biases in conservation focus have targeted charismatic large-bodied vertebrates, undermining the conservation of invertebrate taxa (Donaldson et al., 2016). These biases have resulted in invertebrates being inadequately managed and overlooked when facing challenges such as climate change. For instance, rising temperatures and a shift in rainfall are predicted for South Africa, which will likely threaten insects such as dragonflies (Odonata: Anisoptera) and damselflies (Odonata: Zygoptera), and for simplicity hereafter jointly termed dragonflies (Samways, 2010). Dragonflies are widely used for freshwater assessments (Kietzka et al., 2017; Nasirian & Irvine, 2017; Schindler et al., 2003; Simaika & Samways, 2011). Just under 20% of the national fauna of South Africa’s dragonfly species is endemic to the country (Samways et al., 2016). As a result of their narrow habitat tolerances and localized geographical ranges, endemic species are likely to be more susceptible to global changes than widespread species (Simaika & Samways, 2015; Vincent et al., 2020). In the face of increasing environmental change such as climate, the survival of dragonfly species will continue to be threatened unless intervention measures are put in place by conservation agencies to ensure the longevity of threatened species and cohesion of local assemblages (Nóbrega & De Marco Jr, 2011). As such, to assess how best to conserve biodiversity, and to predict how local assemblages may reshuffle due to environmental change, we first need to understand the processes that maintain diversity at regional scales. With such knowledge on the drivers of regional diversity at hand (Deacon et al., 2020), we are equipped to explore anticipated community reorganization under different future climate change scenarios.

Changes in local temperature and precipitation regimes alter habitat suitability and consequently drive local and regional species turnover (Bush et al., 2013; Shah et al., 2012). Range-shifts in dragonflies are an adaptive response to this change in climate (Flenner & Sahlén, 2008; Hassall et al., 2007; Hickling et al., 2005). A biome covers regions with a similar climate, vegetation, disturbance regime and geography and will therefore also influence species composition as the disparity in resource and niche availability between biomes can drive selection (Stein et al., 2014). As all species within the order Odonata are dependent on water for their egg and larval phase, they are also particularly sensitive to water condition (Samways et al., 2016). This makes dragonfly assemblages excellent indicators of water quality change for aquatic ecosystem assessments (Kietzka et al., 2017; Schindler et al., 2003; Simaika & Samways, 2011). Dragonflies have also been successfully used as model organisms to explore impacts of climate change (Bush et al., 2013; Hassall & Thompson, 2008; Simeika et al., 2013). Furthermore, research has indicated high congruence of odonate species richness and patterns of threat with that of other taxonomic groups, like mammals, birds and amphibians, which implies that odonates are an effective surrogate taxon (Darwall et al., 2011; Pinkert et al., 2020). Odonates could therefore act as a useful indicator for other taxonomic groups.

This study has three key objectives. Firstly, to assess the importance of environmental drivers of turnover on Odonata assemblages in South Africa. By relating species turnover of local assemblages to environmental gradients and geographical distance, we aim to uncover what processes are responsible for assemblage composition. These relationships can also provide an indication of how the rate of compositional turnover varies along the gradients concerned. As the relationship between compositional turnover and environmental distance is not constant over the entire range of environmental gradients, we determine not only what covariates are important...
for maintaining turnover but also at which points along the grad-
ents is turnover most sensitive. We achieve this using generalized
dissimilarity modelling (GDM), which models spatial gradients of
compositional turnover between pairs of geographical sites (Ferrier
et al., 2007). Our second objective is to map predictions of com-
positional turnover across the entire region, first as a continuous
gradient of assemblage similarity, and then as discrete bioregions
depicting major areas of endemism based on clustering results under
present climate conditions. For these present-day bioregions, we
assess what species are representative of each bioregion by compiling
a species list for conservation purposes, as well as a list of those
narrow-ranged species that exist in only one of the identified biore-
gions. Thirdly, with space-for-time substitution (Blois et al., 2013), we
estimate and map the magnitude of expected change in species turn-
over in response to climate change under two future climate condi-
tions (i.e., RCP 4.5 and RCP 8.5) for years 2050 and 2070. With this,
we also assess the stability of present-day bioregions under these
future climate change scenarios and develop an index of bioregion
instability. Results from this study carry important implications for
conservation planning by providing information regarding biodiver-
sity drivers, assemblage persistence and change as well as ecological
integrity.

2 | METHODS

2.1 | Study region

Our study is focused in South Africa at the southernmost tip
of the African continent. South African climate ranges from a
Mediterranean type in the southwest, temperate in the interior, and
subtropical in the northeast. Average annual rainfall is c. 450 mm
but varies considerably from west (100 mm) to east (900 mm) (see
Figure S1-BIO12 in Appendix S1), with some desert regions along
the western edge of the country. The weather is largely influenced
by ENSO (El Niño–Southern Oscillation) events, which result in cycli-
cal drought and flood conditions (Dilley & Heyman, 1995). Published
predictions of global warming are cause for concern as even a small
temperature increase will place considerable stress on South African
insect populations (Samways, 2010).

2.2 | Odonata dataset

The spatial dataset of South African Odonata, described in detail
by Simaika and Samways (2009) and Samways et al. (2016), is based
on a compilation of monitoring and museum collections and sight-
ings data from the 1900s to present, as well as records published in
Pinhey (1984, 1985). Records are also continually updated with the
most recent maps published in the handbook on freshwater
assessment for South Africa (Samways et al., 2016). At the time of
writing, the dataset comprised 164 species and over 25,000 pres-
ence records throughout South Africa, around 17,000 of which were
collected after year 2000. South Africa is one of the most signifi-
cant centres of dragonfly endemism in the world as it contains most
relictual species on the African continent (Clausnitzer et al., 2012;
Simaika et al., 2013). The dataset’s large sample size and expert veri-
fication of all insects collected makes this an ideal dataset to focus
efforts to predict assemblage reorganization of South African drag-
onflies induced by climate change.

2.3 | Environmental covariates

The choice of climatic variables should aim for ecological relevance
(Araújo et al., 2019). Environmental variables were therefore se-
lected based on the large body of odonate literature focused on
understanding dragonfly assemblage structure. For example, cli-
mate can be considered a dominant factor driving insect distribu-
tions (Bush et al., 2013; Hassall & Thompson, 2008). The life cycle of
dragonflies is primarily governed by temperature and water availabil-
ity that are essential for larval development and breeding. Annual
temperatures as well as temperature range are also known to af-
fact dragonfly physiology, such as phenology, seasonal regulation,
immune function and pigment production used for thermoregula-
tion (Hassall & Thompson, 2008). Precipitation of the driest quarter
was selected as prolonged periods of drought are known to drasti-
cally impact larvae survival (Pernecker et al., 2020). Thus, we ex-
ttracted four present-day bioclimatic variables, with two describing
air temperature and two describing precipitation (www.worldclim.
org; Hijmans et al., 2005), over the period from 1970 to 2000. These
climatic variables comprise annual mean temperature – “BIO1,” tem-
perature annual range – “BIO7,” annual precipitation – “BIO12” and
precipitation of the driest quarter – “BIO17.”

Secondly, data characterizing river conditions were obtained from
the National Freshwater Ecosystem Priority Areas (NFETPA) database
available through SANBI’s Biodiversity GIS portal (bgis.sanbi.org/
SpatialDataset; Council for Scientific & Industrial Research, 2011).
Because dragonflies are susceptible to changes in the quality of
aquatic systems, dragonfly response has been used extensively as an
indicator of ecological integrity (Simaika & Samways, 2011). River
condition was categorised into five classes: unmodified/largely natu-
ral with few modifications – “AB,” moderately modified – “C,” largely
modified – “D,” extremely modified – “EF” or tributary condition
modelled as no longer intact – “Z” (see Table S2 in Appendix S1).
Length of each river condition was calculated per grid cell (cells de-
scribed in detail below under generalised dissimilarity modelling).

Thirdly, we included human population density data for 2010,
obtained from NASA’s open data portal (beta.sedac.ciesin.colum-
bia.edu/data; Ciesin, 2016). Population density was used as human
presence (and density thereof) is largely associated with biodiversity
loss. We explored a long list of other anthropogenic factors, such as
human footprint and human influence index, but found they were
largely correlated with human population density (Variance Inflation
Factor >7) and yet less intuitive to interpret and were therefore not
included.
Lastly, we sourced data on vegetation types, including the percentage cover of each biome (n = 9, see Appendix S1) within each geographical grid cell for the year 2011 (bgis.sanbi.org/SpatialDataset; South African National Parks, 2011). We specifically used vegetation types as we expect species-specific habitat requirements to drive dragonfly diversity and distribution patterns (Schindler et al., 2003). Indeed, vegetation gradients have been found to be an important driver of assemblage patterns (Osborn & Samways, 1996).

2.4 RCP-related future environmental covariates

Future climate covariates were included in response to the report of climate trends and scenarios in South Africa (DEA, 2013) that warn of significant warming (as high as 5–8°C) expected over South Africa’s interior by the end of this century. As it is impossible to predict future emissions with any precision, a range of representative concentration pathway (RCP) scenarios have been developed with different degrees of change and likelihood (Van Vuuren et al., 2011). The RCP 4.5 represents a scenario where greenhouse emissions are weakly mitigated and is described by the IPCC as an intermediate scenario, while RCP 8.5 represents a Pre-Paris Accord or unmitigated scenario with high global greenhouse gas emissions. For analysis under these future climate change scenarios, we obtained the same climatic variables as for the present-day climate (BIO1, BIO7, BIO12, BIO17), but for the time period 2050 (average for 2041–2060) and 2070 (average for 2061–2080) under the RCP 4.5 and RCP 8.5 predictions (GCM-BCC-CSM2-MR; www.worldclim.org). In total, four sets of variables (two RCPs×two periods) were included to predict dragonfly assemblage reorganization under future climates in South Africa. Climate predictions from an additional General Circulation Model (GCM), namely CNRM-CM6-1, were also considered, although analyses using this GCM produced rather similar results (see Appendix S3 and Figure S10) and therefore were not discussed in the main text.

2.5 Generalized dissimilarity modelling

Generalized dissimilarity modelling (GDM) is formulated as a non-linear extension of the more traditional distance approach of linear matrix regression (Ferrier et al., 2007). It is a statistical method for analysing and predicting patterns of compositional turnover in species assemblage, usually in response to environmental gradients that vary in space. GDM uses the compositional dissimilarity between all site pairs and fits these dependent variables as a function of the difference in environmental and geographical covariates between these site pairs (Ferrier et al., 2007). Unlike in the case of species distribution models (SDMs), GDM does not target the presence and absence of individual species but rather species turnover of the entire assemblage between sites. For this reason, SDMs typically require a comprehensive geographical coverage of records for estimating the representative niche of the focal species; in contrast, GDM requires a representative list of species for sites of interest to compute realistic level of turnover in the model.

All analyses were carried out in R (version 3.6.1; R Development Core Team, 2019). South Africa was divided into 1,978 quarter degree cells in accordance with national atlas data resolution standards of previous projects (Harrison & Cherry, 1997). Each cell was considered a site and characterized by its central geographical coordinates; species composition (presence and pseudo-absence) and associated environmental covariates were summarized using the "LetS(R)" R package (Vilela & Villalobos, 2015). Since species presence/absence can be sensitive to sampling effort, we removed cells with low sampling counts (less than ten records/observations, which is the median number of records per quarter degree cell across South Africa) (Figure 1) leaving 351 quarter degree cells containing 22,552 dragonfly records to model representative dragonfly assemblages (Appendix S2). To further assess the role of sampling effort on observed local species composition, we included the total number of Odonata records in each cell as a surrogate for sampling effort in our analyses; this means that a higher number of Odonata records in a grid cell is likely to reflect a higher survey effort and thus yield a higher number of discovered species. Increased sampling efforts will yield overall a more representative species list of local assemblages (Hortal & Lobo, 2005) (Appendix S2; Figure S2) and will ideally reduce issues related to sampling inadequacy (e.g., pseudo-absences; Hui et al., 2011). Geographical distance was calculated as orthodromic distance between pairs of cells to account for changes in turnover resulting from the decay of compositional similarity with distance (Morlon et al., 2008; Soininen et al., 2007). This distance decay can be a product of multiple mechanisms, such as ecological filtering through spatially autocorrelated environmental gradients (the Moran effect; Hansen et al., 2020) and dispersal limitation (Latombe et al., 2019).

All covariates showing excessive skewness were transformed and only those where this transformation increased data symmetry were retained (See Appendix S1 for detail; Figure S1 for transformed variables). Variance Inflation Factor (VIF) measures how much the variance of a regression coefficient is inflated due to multicollinearity within the model. All covariates were tested for multicollinearity at a quarter degree scale by computing the VIF using the "car" R package (Fox et al., 2012). In general, a VIF value that exceeds five or in some cases ten indicates a problem with multicollinearity (Kutner et al., 2005). To be conservative we removed all variables with a VIF exceeding five, which was only the percentage cover of grasslands within the biome data. The final selection comprised 20 explanatory variables, including geographical distance and sampling effort, which were used as environmental predictors in the GDM (see Appendix S1 for data layer sources, projections and transformations as well as Table S1 for a summary of the twenty covariates used in the model).

The differences in species composition between two sites were expressed as a single ecological distance, the Jaccard distance metric. To explain compositional dissimilarity between pairs of cells, we transformed each covariate into five monotonic I-splines with three
internal knots using generalized linear models embedded in the GDM (using the "gdm" R package; Manion et al., 2018). The number of I-splines determines the precision of pinpointing the response along the environmental gradient represented by a covariate, while the number of knots determines the number of interlinked spline pieces and was kept low to avoid overfitting (Perperoglou et al., 2019). The percentage contribution of each explanatory variable to the variation of Jaccard dissimilarity was then estimated from 20 separate models (removing one predictor at a time). The variance explained by the full GDM model was then compared to each of the partial models to evaluate the importance of each explanatory variable (Table 1). The uncertainty in the fitted I-splines was assessed using bootstrapping of 70% of the sample site pairs with 50 bootstrap iterations (Appendix S3; Figure S5). The absolute model error of the observed versus predicted partial ecological distance was calculated and mapped for each cell (Appendix S3; Figure S6). A set of Bayesian Bootstrap Generalized Dissimilarity Models (BBGDMs) were also run to assess the robustness of the response curves for key model predictors (see Figure S9 in Appendix S3) (Woolley et al., 2017).

Results from the GDM were presented as response curves, where firstly the height of the response curve of each predictor provides an indication of the total amount of compositional turnover associated with a specific environmental gradient. Secondly, the slope of the response curve at a specific point provides an indication of how the rate of compositional turnover varies along the environmental gradient concerned. Additionally, to assess whether estimated turnover reflects true turnover (i.e., species gain and loss) or nested structure (i.e., narrow-ranged species are geographically nested within the range of wide-ranged species), we partitioned dissimilarity between all site pairs into total beta diversity, true turnover and nestedness components, using the Sørensen dissimilarity index, the Simpson dissimilarity index and the difference of the two (sensu Soininen et al., 2018; see Figure S8 in Appendix S3).

### 2.6 Assemblage composition mapping

Once the GDM was fitted to observed data, we used the fitted model to predict dissimilarity for unobserved locations in South Africa (cells without dragonfly records, or fewer than 10). For this we used all data layers within the GDM as well as a simulated constant layer representing "adequate sampling" (75 records per quarter degree grid cell) to replace that of real sampling effort. The level of adequate sampling was obtained from the I-spline analysis of the response curve (the number of records when the dissimilarity prediction levels off). This allows us to predict "true" turnover especially in under-sampled regions. We used the "gdm.transform" function, which uses the observed dissimilarity matrix and predictors as an
input to produce a predicted dissimilarity matrix (N-by-N in dimension), with its element depicting pairwise dissimilarity between sites. For dimensionality reduction and visualization, we used the Principal Component Analysis (PCA) of the predicted dissimilarity matrix and assigned the first three principal components (PCs) to a Red-Green-Blue (R-G-B) colour palette for mapping (Koubbi et al., 2011; Ramette, 2007). Principal Coordinates Analysis (e.g., Picazo et al., 2020) and PCA are both popular methods; however, as we are mapping the predicted dissimilarity matrix, not the observed dissimilarity matrix from co-occurrence matrix, we opted to use the PCA. When mapping the PCs, we weighted each PC to reflect the different proportions of variance explained by each PC (see the subsection below titled “Current and possible shifts in dragonfly assemblage composition relative to bioregion”). Two areas with similar colours show similar species compositions, whereas two areas with different colours represent different species compositions.

Discrete bioregion boundaries were delineated by classifying the first three PC values (represented as three bands: R-G-B) using the R packages “vegclust” (De Cáceres et al., 2010) and “diceR” (Chiu & Talhouk, 2019). Specifically, we first identified eight cluster prototypes from the present-day R-G-B scenario using a simple K-means clustering algorithm (De Cáceres et al., 2010). The significance of these cluster results was then assessed using the SigClust K-Means algorithm (Chiu & Talhouk, 2019). The choice of eight clusters/bioregions was based on exploratory analyses that identified the clearest clusters. For practical application, we further determined what species exist within each of these eight present-day bioregions and selected the top ten species occurring within a particular bioregion as representative species for each (Table 2). In contrast, a species occurring in only one bioregion was considered a narrow-ranged species (see Table S3 in Appendix S4).

To explore anticipated spatial turnover in future climates, we assessed how dragonfly assemblages would potentially respond to future climate change scenarios by re-running the fitted GDM with all previously included environmental layers but with climate layers from RCP 4.5 and RCP 8.5 scenarios for 2050 and 2070 instead of present-day climate layers. The R-G-B of the principal components of these pairwise dissimilarities were then classified using a hard noise clustering (HNC) algorithm where sites were assigned from one to eight prototype clusters (those from the present-day K-means clustering) or a new “noisy” cluster based on a threshold distance (0.8) to all cluster centroids (De Cáceres et al., 2010). Each of the outputs was then plotted to produce five maps representing bioregions of the present-day, RCP 4.5 for 2050, RCP 8.5 for 2050, RCP 4.5 for 2070 and RCP 8.5 for 2070. Note, as no new “noise” cluster was found, each future bioregion was linked precisely to one specific present-day bioregion (i.e., bioregions of the same colour in the maps represent the same bioregion shifted in future climate scenarios). Through this technique, we can view the reorganization of bioregions under different emission scenarios and years. A summary of the above methodology is provided in Figure S7 (Appendix S3). From these maps, we also developed a bioregion instability index where the number of times a site was reclassified as a different bioregion from the present-day scenario is computed and mapped. To provide insight into the potential threat to present-day protected areas, we also compared this bioregion instability index to the present-day network of formally protected areas in South Africa according to the World Database on Protected Areas (UNEP-WCMC & IUCN, 2020).

Lastly, to explore temporal turnover in future climates we utilized the GDM “predict” function, under space-for-time substitution (available in the “GDM” package). In this case, raster predictions were provided for the two time periods of interest (2050 and 2070) and the two climate change scenarios (RCP 4.5 and RCP 8.5) to estimate the magnitude of expected temporal turnover in dragonfly communities within a grid cell in response to environmental change associated with the four selected climate change scenarios. Outputs were then plotted to produce four additional maps.

### 3 | RESULTS

#### 3.1 | Drivers of dragonfly assemblage composition turnover

The observed beta turnover, measured by the Sørensen index, reflects largely true turnover of species gain and loss between sites.

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### TABLE 1 The percentage contribution (R^2) of each predictor variable in explaining compositional turnover in the generalized dissimilarly model

| Predictor variable                  | Percentage (%) contribution to R^2 (standard deviation) |
|------------------------------------|---------------------------------------------------------|
| Sampling effort                    | 31.44 (3.60)                                            |
| BIO1 – Annual mean temperature     | 20.48 (6.15)                                            |
| Geographical distance              | 4.61 (2.79)                                             |
| Savanna                            | 3.06 (0.43)                                             |
| BIO7 – Temperature annual range    | 3.06 (0.31)                                             |
| D – Largely modified river condition | 2.89 (0.10)                                          |
| Forest                             | 2.80 (0.30)                                             |
| Coastal belt                       | 2.66 (0.05)                                             |
| Fynbos                             | 2.60 (0.11)                                             |
| Albany thicket                     | 2.56 (0.08)                                             |
| EF – Extremely modified river condition | 2.51 (0.04)                                      |
| BIO17 – Precipitation of driest month | 2.49 (0.08)                                       |
| Human population density           | 2.42 (0.06)                                             |
| AB – Unmodified/largely natural river condition | 2.42 (0.03)                                      |
| Desert                             | 2.38 (0.03)                                             |
| C – Moderately modified river condition | 2.35 (0.03)                                     |
| Z – River condition no longer intact | 2.33 (0.03)                                      |
| BIO12 – Annual precipitation       | 2.31 (0.00)                                             |
| Nama Karoo                         | 2.31 (0.00)                                             |
| Succulent Karoo                    | 2.31 (0.00)                                             |

Note: Variables are shown in order of importance in describing percentage contribution to the model. The standard deviation of a predictor’s contribution is also shown in brackets.
by the full GDM (Pearson’s \(R^2\)) was 35.5% (\(<0.05\)). The relationship between observed dragonfly compositional dissimilarity of each site pair and the linear prediction of the regression equation from the GDM (otherwise known as the predicted ecological distance between unique regional dragonfly assemblages) is shown in Figure S3 (Appendix S3). Sampling effort (31%) and annual mean temperature (21%) contributed the most to explain species turnover of South African dragonflies (Table 1). This was followed by geographical distance (5%), savanna biome type (3%) and temperature annual range (3%) (Table 1).

According to the response curves, annual mean temperature evokes the largest turnover in community composition, followed by sampling effort and then geographical distance between sites measured in quarter degrees (Figure 2). We find annual mean temperature exceeds all other environmental explanatory variables at explaining turnover in community composition by at least four times, meaning it is the principal abiotic variable driving turnover between sites (Figure 2a). The slope of this relationship is roughly linear, suggesting compositional turnover increased with increasing annual mean temperature at a rate of c. 8.6% per °C (Figure 2a). For sampling effort, turnover in community composition stabilizes once the effort of 75 records per quarter degree cell is reached (Figure 2b). For geographical distance between sites, at around seven quarter degrees (c. 175 km) compositional turnover also stabilizes (Figure 2c). This indicates that beyond c. 175 km, complete turnover is driven by environmental gradients and not geographical distance. Compositional turnover is also sensitive to small, as well as large, changes in percentage savanna coverages (Figure 2d). When comparing the various levels of water condition, class D (the largely modified class) had the greatest amount of associated compositional dissimilarity as well as the most rapid rate of change (Figure 2e). Compositional turnover is only affected by temperature annual range above 24°C and increases further above 30°C range (Figure 2f). The response of compositional turnover to other predictors is shown in Figure S4 (Appendix S3). In addition, the BBGDM confirmed these response curves but suggested a smaller effect size for sampling effort (Appendix S3; Figure S9).

### Table 2

| Cluster 1 | Cluster 2 | Cluster 3 | Cluster 4 |
|-----------|-----------|-----------|-----------|
| Microgomphus nyassicus (1) | Pseudagrion vaalense (7) | Sperberia angustata (1) | Aciagrion dondoense (1) |
| Trithemis aconita (5) | Pseudagrion citricola (6) | Syncordulia serendipitor (1) | Gynacantha villosa (1) |
| Tetrahemis polleni (6) | Symperum forscolumbii (8) | Syncordulia legator (3) | Hemicordulia africana (1) |
| Pseudagrion assegai (4) | Trithemis kirbyi (8) | Pseudagrion newtonii (2) | Macrodilax cora (1) |
| Crocothemis divisa (2) | Africallagma sapphirinum (6) | Poischneria polychromatica (2) | Orthetrum monarda (1) |
| Bradinopyga cornuta (5) | Ischnura senegalensis (8) | Syncordulia gracios (3) | Urothemis luciana (1) |
| Phaon iridipennis (5) | Mesocnemis singularis (6) | Ecchlorelestes peringueyi (3) | Gynacantha usambarica (2) |
| Lestes tridens (5) | Crocothemis erythraea (8) | Chlorolestes umbratus (3) | Orthetrum robustum (3) |
| Gomphidia quareli (4) | Pantala flavescens (8) | Ettatoneura frenulata (4) | Neurogompus zambeziensis (2) |
| Pseudagrion sjoestedti (3) | Pseudagrion massacum (7) | Orthetrum rubens (2) | Aethriamanta rezia (3) |

(continued)
Under the RCP 4.5 scenario, we can see a large spatial shift in dragonfly bioregions between present and 2050 predictions (Figure 3c,d) but less so between 2050 and 2070 predictions (Figure 3d,f). The same trend was found under the RCP 8.5 scenario where we see a major shift of ecotones and bioregions between now and 2050 (Figure 3c,e) but less so between 2050 and 2070 (Figure 3e,g). The major bioregions at risk of change are cluster 1, 4, and 7. Cluster 1 of the present-day bioregions is present in Limpopo, the North West, Northern Cape as well as the far north of Mpumalanga (Figure 3c). This bioregion is predicted to contract its size by 80% under all future
scenarios (Figure 3d–g). In fact, for three of the four future scenarios this bioregion (cluster 1) is reduced to a small area in the Northern Cape alone (Figure 3e–g). The bioregion of cluster 7 contracted by 66% coverage and the bioregion of cluster 4 by 61% under all future scenarios (Figure 3d–g). Contrastingly cluster 3 has expanded primarily northward by 30% under all future scenarios (Figure 3d–g). Cluster 6 also shows a northward and coastal expansion, and in future scenarios takes up most of Limpopo and the coast of KwaZulu Natal (Figure 3d–g).

These bioregion shifts are further captured by the bioregion instability index (class 0, 1, 2, 3, 4) in Figure 3h, where the number of times a site is reclassified as a different bioregion from the present-day scenario is computed and mapped for each cell. That is, class 0 represents a cell not reclassified in any of the four future scenarios, while class 4 is a cell reclassified in all four future scenarios. The percentages shown in brackets in the map legend of Figure 3h indicate the percentage covers of a specific class in South Africa. That is, 45% of South Africa is classified as class 0, representing no change expected, 6% shows a low probability of bioregion change (class 1), 4% a moderate probability of change (class 2), 9% a high probability of change (class 3) and finally 36% of South Africa showing a very high probability of bioregion change (class 4, Figure 3h). Note that areas belonging to class 0 (i.e., those areas that were not reclassified as a different bioregion in any of the four future climate scenarios) are not necessarily exempt from temporal dragonfly turnover, only that future predictions of bioregion boundaries do not deviate substantially from today’s bioregions of species composition. One example of this is where species move within a bioregion, thus maintaining the bioregion’s inherent species composition, while the temporal
turnover of local assemblages can still be high (see detail in the section below).

When comparing our instability index map (Figure 3h) with present protected area networks in South Africa (UNEP-WCMC & IUCN, 2020), we found that alarmingly 47% of formally protected areas in South Africa today have a high to very high likelihood (class 3 and 4) of climate-related change to dragonfly bioregions in the future. While 34% of these protected areas have a low to moderate likelihood (class 1 and 2) and only 19% have no changes expected at least at the bioregion level (class 0).

Table 2 shows the representative species making up each of the bioregions. Narrow-ranged species which exist in only one of the eight bioregions in South Africa amount to 12 of the total 164 species (Appendix S4, Table S3). Specifically, the narrow-ranged species *Microgomphus my assicus* is present only in cluster 1, *Chlorolestes draconicus* in cluster 5 and *Crenigomphus cornutus* in cluster 6. Cluster 3 has two narrow-ranged species (*Spes bona angusta* and *Syncordulia serendipator*), so does cluster 7 holding *Macrodiplax cora* and *Trithemis monardi*. Cluster 8 has no narrow-ranged species, while cluster 4 holds the highest number of narrow-ranged species: *Aciagrion dondoense*, *Gynacantha villosa*, *Hemicordulia africana*, *Orthetr um monardi* and *Urothemis luciana*. In terms of localized South African endemics, the Western Cape is home to several ancient relict species, such as the Malachites (*Chlorolestes* species; Simaika et al., 2020) as well as *Spes bona angusta* and *Syncordulia serendipator* (Samways et al., 2016), while the genus of *Syncordulia* is nearly entirely endemic to the Cape Floristic Region (Dijkstra et al., 2007). Lastly, *Urothemis luciana* is endemic to the KwaZulu Natal. These species range from Endangered to Least Concern according to the IUCN Red List and are likely to become more localized due to their narrow habitat tolerances and restricted geographical ranges (IUCN, 2020).

### 3.3 Magnitude of temporal turnover of dragonfly assemblages

Figure 4a shows the magnitude of expected temporal turnover between present and RCP 4.5 for 2050, while Figure 4c shows the temporal turnover between present and RCP 4.5 for 2070. Both maps show inland patches could experience 72%–73% temporal turnover of local assemblages, with some pockets of areas reaching up to 77%–80% change by 2070. While the coasts show a lesser magnitude of temporal turnover, the minimum expected change is still 64%. Figure 4b shows the magnitude of expected change between present and RCP 8.5 for 2050, while Figure 4d shows the change between present and RCP 8.5 for 2070. RCP 8.5 shows the greatest magnitude and extent of temporal turnover. The hotspots of temporal turnover in all future scenarios are consistently concentrated in the centre of the Northern Cape, the border between the North West and Limpopo, as well as the far north of the Free State (Figure 4).

### 4 | DISCUSSION

#### 4.1 Major drivers of compositional turnover

The trends visible in the I-spline response curves in Figure 2 give us insight into the manner in which turnover varies along the gradient concerned. Our results show that turnover in dragonfly community composition increased with increasing annual mean temperature at a rate of c. 8.6% per °C. As temperature governs development rates and is known to affect dragonfly physiology (Hassall & Thompson, 2008), the behaviour of dragonflies and their survival depend largely on temperature (Gilbert & Raworth, 1996). As such, we see a steady effect of temperature on compositional turnover. Therefore, it is likely that even small changes in annual mean temperature will cause notable responses in dragonfly communities, such as range shifts and consequently species turnover.

The other major predictor of observed species turnover was sampling effort, making it a confounding factor that could strongly hinder our ability to accurately predict spatial patterns. By including sampling effort in our model, we were able to compensate for areas with lower sampling effort (sampling inadequacy) and determine whether sampling had been done adequately enough to predict turnover. Lastly, by determining the adequate sampling effort of 75 records in our predictions, we reduced sampling biases. Research by Finch et al. (2006) also used predictive models to generate maps in areas where there was inadequate sampling of Odonata to allow large-scale atlassing using the stacked Species Distribution Models of individual species (e.g., BIOCLIM-type approach). Based on our results, we urge the inclusion of sampling effort in predictive models in future, especially in the case of large areas where sampling effort is varied, as well as in the case of presence only data where precautionary model design becomes increasingly important.

Of all considered variables annual mean temperature and sampling effort had the greatest relative contribution to variance explained in compositional turnover. Water condition, only contributed marginally to turnover (Table 1; Appendix S3, Figure S4). At the scale of quarter degrees with a cell roughly 30 × 30 km, climatic drivers become dominant for odonates (de Oliveira-Junior & Juen, 2019). We stress that aquatic conditions and land use could become much stronger in dictating the distributions of Odonata at much finer local scales (de Oliveira-Junior et al., 2017).

In the response curve for geographical distance, the slope is steepest at lower distances but reaches a plateau around seven quarter degree cells (c. 175 km) (Figure 2c). This suggests that turnover beyond this distance is restrained, and notable distance decay of similarity only occurs within 175 km. This is most likely a reflection of disparity in niche requirements and the mobility of Odonata species. Sites that are closer to each other often share similar environmental characteristics and thus harbour a similar species composition, whereas sites that are further apart with distinct environmental characteristics will harbour distinct assemblages. The plateauing of geographical distance also indicates that beyond this
geographical range of 175 km, the establishment and composition of dragonfly assemblages cannot be modified by distance-related processes, such as the dispersal capacity of dragonflies within the regional environmental context. Under the space-for-time substitution (Blois et al., 2013), this range thus reflects the limit that a dragonfly community can shift to retain its compositional similarity in response to climate change.

Using historical data of British Odonata, Hickling et al. (2005) demonstrated a shift of 74 km over 36 years between 1960 and 1995, or an annual range shift of merely 2.1 km. This corresponds to the upper dispersal ability of some extensively studied Zygoptera (Conrad et al., 1999; Watts et al., 2004). Some Anisoptera in Namibia, however, have shown the potential for longer dispersal distances (Suhling et al., 2017), such as *Phyllomacromia contumax*, *Phyllomacromia picta* and *Olpogastra lugubris*, which are also present in our dataset. Collectively, 175 km could mark the upper limit of dispersal distance, in the context of regional ecological and environmental heterogeneity, to contribute to compositional turnover; beyond this distance, environmental differences could be solely responsible for observed community dissimilarity. Dispersal distance is a complex phenomenon dependant on species traits, population structure and habitat complexity (e.g., river and habitat configuration), as well as the time-scale represented by records within grid cells, so this result of the distance decay of similarity reflects the emerged interplay of multiple factors and must be interpreted in this context, not necessarily a reflection of a species’ inner dispersal ability.

### 4.2 The future of dragonfly assemblages under climate change

We found mean annual temperature to be the greatest environmental predictor of compositional turnover. Under RCP 4.5, temperature changes are expected to reach just under 3°C towards the end of the 21st Century (relative to the 1971–2005 average). For RCP 8.5, this is expected to exceed 4°C in the same period. Considering Figure 4, our GDM predicts a magnitude of 64% change in species turnover in coastal regions and up to 78% turnover inland for the RCP 4.5 scenario. For RCP 8.5, we see even greater magnitudes of species turnover, that is between 65% and 80%, with the greatest magnitude shown in the year 2070 for RCP 8.5. The specific hotspots of concern are in the arid centre of the Northern Cape, the border between the North West and Limpopo as well as the far north of the Free State. Interestingly, these hotspots of concern mirror the findings of Coetzee et al. (2009) on the turnover of birds across Southern Africa. They also identified higher rates of species turnover in the central arid areas of South Africa. This is also consistent with other findings from the same region on a broad range of taxa (plants, mammals, reptiles, invertebrates; Broennimann et al., 2006; Erasmus et al., 2002; Foden et al., 2007). These hotspots of species turnover are typically described as having a unique climate compared to the rest of South Africa, with no or few species endemic to these areas. This will likely be retained should temperatures continue to rise (Coetzee et al., 2009).

Dornelas et al. (2014) showed that on a global scale, many species assemblages are rapidly changing, with an estimated mean of 10% turnover of montane species per decade. Gibson-Reinemer et al. (2015) predicted a similar level of 12% species turnover per decade in Asia, Europe, North America, South America and the Indo-Pacific as climates continue to warm. Species turnover is likely to be even greater for ectotherms, such as insects. This presents a great challenge for conservation planning as species assemblages that previously occurred in protected areas will not stay intact as species move in response to climate change, in different directions and at different rates. This will in turn also create new species interaction networks that may result in highly complex, nonlinear and sometimes extreme responses (Walther, 2010). This further emphasizes the demand for adaptive management strategies, as many species that occur in areas today will emigrate or worse, become extinct under future predicted temperature increases. Indeed, according to Bush, Nipperess, Theischinger et al. (2014) and also our results, major shifts in the distribution of Odonata are expected to occur because of climate change, which presents major challenges not only for Odonata but for conservation of freshwater biodiversity in general.

This complex, nonlinear response is echoed in Figure 3. These shifts indicate that even at the level of bioregions, 36% of South Africa will likely undergo a complete bioregion shift in the near future, signalling a highly unstable future for dragonfly assemblages. As bioregions represent areas of similar species compositions, we should expect major future alterations to present assemblages. Furthermore, comparing the present network of protected areas with our bioregion instability index, we found 47% of the total area covered by formally protected areas in South Africa today have a high to very high likelihood of anticipated climate-driven changes to dragonfly bioregions in the future. While 34% of these areas have low to moderate levels of change, only 19% have no likely changes expected to bioregions under protection. Current strategies involving protected areas are predominantly fixed in space and may therefore be inadequate under climate change conditions. Shifting areas under protection and shifting targeted species will need to be considered in present and future conservation planning. The National Protected Areas Expansion Strategy (NPAES) highlights ways in which we can expand protected areas in South Africa while enabling co-ordination between the many role players involved (Department of Environmental Affairs, 2016). The NPAES may thus be a good starting point for discussions, as protected area expansion requires careful consideration of surrounding land use and ownership.

Although we have identified the arid areas of South Africa as the hotspots of species turnover (Figure 4), it does not always result in a full bioregion shift (Figure 3). Within the hotspot, species appear to be moving within the confines of the bioregion, supporting a high rate of temporal turnover in local communities but retaining the assemblage integrity of the bioregion. Conservation planning therefore also needs to consider if the focus should be on overall bioregion shifts or local areas showing greater temporal turnover.
Overall, our results across all scenarios indicate that a rapid shift in dragonfly assemblages is likely to occur between now and 2050 in South Africa. Such assemblage reorganization is predicted due to either rapid species turnover (Flenner & Sahlén, 2008) or shifts in range margins (Hickling et al., 2005) from ongoing climate change.

4.3 Practical application of the bioregions

One may want to focus on species that are representative of a bioregion for tracking shifts in assemblage structure. These species that show the greatest sampling counts in each of their bioregions should be regularly assessed as early indicators of potential shifts in larger assemblage structures (Table 2). Narrow-ranged species, on the other hand, should be targeted for conservation efforts as they lack redundancy between bioregions. For example, cluster 4 holds five narrow-ranged species that occur only within this bioregion (Appendix S4; Table S3). This cluster therefore maintains a highly unique assemblage of species and should be targeted for conservation and reassessment efforts. Not all the species investigated are native however and should be tagged as an additional point of concern for conservationists. Aciagrion dondense is one such species in cluster 4. A recent colonizer into South Africa, possibly driven by floods farther North, and a possible facilitator of the local demise of Agrionemis ruberrima (Samways, 2010), also sampled within this cluster.

The findings presented here have direct implications for the selection of protected areas for conservation purposes in future. A principal goal of conservation planning is to establish a network of protected areas that represent the largest variety of species (Linke et al., 2007). In this case, bioregions (Figure 3 and Table 2) can be used to either establish appropriate reference sites or to define areas in which randomized sites for sampling should be selected (Hawkins et al., 2000). With the dragonfly’s ability to reflect changes in temperature, these monitoring programmes can further be used to track the species that are most sensitive to climate change such as Aciagrion dondense, an indicator species in cluster 4.

4.4 Modelling limitations

All models may be improved upon in future with greater sampling efforts and presence records, as well as more relevant or additional environmental data. Greater sampling effort would also reduce additional uncertainty in the dissimilarity predictions caused by older records. Furthermore, presence-only data can alter estimates of species turnover due to the issue of augmented pseudo-absences from low levels of sampling effort, especially when calculating the turnover between cells with uneven sampling efforts, which is the case here to some extent. Including absence data will help mitigate any over-estimates of occurrence probability typical of modelling techniques that make use of presence only data with environmental predictors (Finch et al., 2006; Pineda & Lobo, 2012). Although we account for a number of issues, such as sampling effort, incorporating multiple non-climatic variables, such as local habitat conditions, further considering individual species’ dispersal limitations as well as species interactions could help us develop a better understanding of the limits exerted on species movement between areas where the environment may be suitable (Bush, Nipperess, Duursma, et al., 2014). Furthermore, alternate clustering techniques as well as different RCP scenarios could lead to different cluster outcomes.

If the distance dragonfly species need to move in response to climate change exceeds their ability to disperse, many species may need to adapt or face extinction. Our model also assumed that species responses in the future are the same as they are now, which when coupled with adaptation may not always be the case (Stoks & Cordoba-Aguilar, 2012). Furthermore, we used a GDM which applies pairwise beta diversity as a measure of species turnover and thus only captures turnover between pairs of sites. Future research could extend this pairwise analysis to a multi-site biodiversity assessment, such as zeta diversity (Hui & McGeoch, 2014), which may provide a more informative approach to explaining the response of rare versus common species. Lastly our model assumptions were that climate will shift while our other variables remain the same in future years. To improve future models, we can (with the availability of such data) also include predicted change of these other variables such as river condition and human density. This will likely increase the robustness of the model prediction.

5 Conclusion

Our results show that the turnover in dragonfly community composition increased with rising annual temperature at a rate of 8.6% per °C. This indicates that South African dragonflies are vulnerable to the effects of climate change, specifically based on their sensitivity to changes in temperature. We also found that with sufficient sampling these insects may be valuable large-scale biological indicators of climate change.

When we mapped the predictions of compositional turnover across the region and delineated eight discrete bioregions based on compositional similarity of predicted dragonfly assemblages, there was clear turnover/transition of dragonfly assemblages expected across South Africa. These spatial clusters of similar assemblages are predicted to wax and wane in future climates, and similar patterns at a global scale are yet to be explored. Across these bioregions we found 12 species out of the 164 total were narrow ranging species, existing in only one of the eight present-day bioregions (Table 2). This list of narrow ranging species will be valuable for targeted conservation efforts as it highlights the lack of redundancy in these 12 species across the region. So too, can the representative species list of each bioregion be used to establish long-term monitoring sites, select new reserve boundaries and help track potential shifts in the distributional limits of some species (Appendix S4, Table S3).

When assessing temporal turnover, we detected the largest changes to be expected between now and the year 2050, with
predictions reaching up to 80% turnover, suggesting a need for the strategies of rapid response to be developed through coordinated conservation efforts. Indeed, when assessing how present-day bioregions may dissolve and shift, we observed major shifts between now and 2050, and less between 2050 and 2070. Present-day bioregions are highly unstable and may show nonlinear and rapid changes in assemblage compositions. Under all emission scenarios, we can expect far-reaching consequences from the large-scale reorganization of dragonfly assemblage due to climate change. Facing a rapidly changing climate, conservation planning that aims to mitigate climate change impacts and species loss, needs to be mindful of these anticipated shifts and reshuffles as currently demarcated protected areas may not be adequate as climate changes.

ACKNOWLEDGEMENTS
This work was supported by the National Research Foundation of South Africa (grant 89967) and the Global Insect Threat-Response Synthesis (GLITRS) from the UK Natural Environment Research Council (grant NE/V007548/1).

CONFLICT OF INTEREST
The author(s) declare(s) that there is no conflict of interest.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13422.

DATA AVAILABILITY STATEMENT
Original and generated data, as well as R scripts for data analyses, can be found at https://doi.org/10.5061/dryad.4mw6m90b9.

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**How to cite this article:** Basel, A. M., Simaika, J. P., Samways, M. J., Midgley, G. F., MacFadyen, S., & Hui, C. (2021). Assemblage reorganization of South African dragonflies due to climate change. *Diversity and Distributions*, 27, 2542–2558. https://doi.org/10.1111/ddi.13422

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**BIOSKETCH**

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