

Predicted range shifts of dragonflies over a wide elevation gradient in the southern hemisphere

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Abstract: Human-induced climate change is among the greatest threats to biodiversity, especially when coupled with habitat destruction. For an already water-stressed country like South Africa, changes in temperature and precipitation regimes, coupled with increasing water demands, are likely to lead to losses in biodiversity. Dragonflies are a well-studied surrogate taxon for aspects of freshwater biodiversity. We created species distribution models for 14 dragonfly species, and predicted the changes in species richness, extent of occurrence, and habitat suitability for the years 2050 and 2080 in South Africa, a poorly studied area for range-change predictions for insects. Model predictions for 2 different emissions scenarios suggest that at least 2 species will be lost from the area by 2050, and 3 by 2080. All are widespread Afrotropical species, but with narrow elevation ranges in South Africa. Only 1 species is predicted to benefit greatly from climate change. The remaining species are predicted to persist with reduced extents of occurrences at higher elevations. Most species we studied (12 of 14) thrive in artificial environments. Therefore, to a certain extent, loss in connectivity is unlikely to play a role for these species. However, the 2 stream specialists that occur in the area are particularly vulnerable because of loss of habitat. Species that currently occur farther north in southern Africa and South Africa also are likely to move southward in the future. Thus, species richness may not necessarily decrease, but replacement of species within communities will be significant.

Key words: climate change, freshwater, aquatic biodiversity, dragonfly, South Africa

Anthropogenic climatic change, especially when synergistic with habitat loss, has emerged as among the greatest threats to global biodiversity (e.g., Brooke 2008, Bellard et al. 2012). Climate changes all the time, but the current and future rate and magnitude of change is of concern. Global patterns of temperature and precipitation are predicted to change greatly, altering the distribution of rivers and wetlands (Dawson et al. 2003, Middleton and Kleinebecker 2012). In addition, climate change coupled with habitat loss and reduced 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; but see Stuart et al. 2014 on rapid evolutionary change on observable time scales).

The future climate of South Africa, already a water-scarce country, 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 use. Dams provide the remainder (15%), and the water stored behind dams accounts for 67% of the total

annual runoff in all rivers. In a study assessing the status of major river ecosystems in South Africa, Nel et al. (2007) found that 23% of the length of the country's main rivers has been irreversibly transformed. 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).

Monitoring the effect on biodiversity of such large-scale and ubiquitous changes requires careful selection of bio-indicators. Adult dragonflies make excellent surrogates for the assessment of aquatic systems (Schindler et al. 2003, Darwall et al. 2011). They are used as indicators of ecological health (Trevino 1997), ecological integrity (Simaika and Samways 2009a), and environmental change, including habitat recovery (Samways et al. 2011) and climate change (Hassall and Thompson 2008, Bush et al. 2013). Distributional changes in dragonflies caused by anthropogenic climate change have been studied in Europe. Ott (2011) demonstrated the expansion of Mediterranean species into northern Europe. Compared with baseline data from 1988,

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13 species of Mediterranean origin have expanded their range, and 2 more were assessed as having a greater tendency to migrate or invade. Species from the dragonfly genera *Aeshna* (2), *Anax* (3), *Boyeria* (1), *Crocothemis* (1), *Erythromma* (2), *Gomphus* (1), *Oxygastra* (1), and *Sympetrum* (2) were well represented on this list of species, but some damselfly species from the genera *Coenagrion* and *Lestes* also are expanding their ranges. Most of the expansions are into northern Germany, the UK, Finland, Denmark, Sweden, and Poland. Ott (2011) also showed that the ranges of several Eurosiberian species *Coenagrion hastulatum*, *Aeshna juncea*, *Somatochlora arctica*, and *Leucorhinia dubia* are contracting and that some local or regional populations are extinct.

The dragonfly fauna of South Africa is composed of specialist and generalist species that show lower levels of endemism than many other insect taxa and little dependence on plant composition (Grant and Samways 2007). The mountainous southwestern area of the country is a center of endemism for dragonflies, whereas the species-rich northeastern area is dominated by Afrotropical species (Simaika and Samways 2009b). This distribution pattern reflects patterns found by Wishart and Day (2002) for other freshwater invertebrates and vertebrates. Small reservoirs, such as pools or farm reservoirs, are encountered frequently on the landscape and are important reserves for dragonflies (Samways 1989). Such reservoirs increase the area of occupancy of local, albeit generalist species, and from a dragonfly's point of view, increase the connectivity of the landscape. Furthermore, in KwaZulu-Natal, the dragonfly assemblages are highly elevation tolerant and vagile, traits apparently honed by past El Niño Southern Oscillation (ENSO) events (Samways and Niba 2011).

Species distribution models (SDMs) are frequently used to model current and future distributions of species (Franklin 2010, Simaika et al. 2013, De Marco et al. 2015). 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. Investigators have used SDMs 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). Our objective was to understand how the distributions of a subset of South African dragonflies will be affected by global climate change in the medium to long term.

For South African Odonata, we expect the Afrotropical, largely habitat-tolerant species to increase their extent of occurrence because additional suitable climate spaces will become available for Afrotropical species as temperatures undergo expected increases and precipitation undergoes expected decreases. Furthermore, we predict that endemic habitat specialists (usually stream species) will have dimin-

ished extents of occurrence as they move to higher elevations where less habitat is available in their climate envelope. In addition, adverse changes to habitats that arise from climate change (increased woody vegetation growth, sedimentation, flood events) are expected to have further adverse effects on larval habitats. We expect species richness to remain similar to current conditions as specialist species are replaced by an increasingly generalist fauna. Last, we expect habitat suitability (i.e., available climate envelopes) to decrease for the dragonfly fauna overall. The goal of our study was to investigate the effect of climate change on: 1) species geographic spread and elevation range of endemic habitat specialist species in comparison to Afrotropical generalist species, 2) species richness patterns, and 3) habitat suitability (i.e., climatic suitability).

METHODS

Study area and sampling records

Our study area was in the province of KwaZulu-Natal (South Africa) and extended from the coast to the Drakensberg mountains. At sea level, a subtropical to tropical climate prevails, whereas higher elevations are temperate to alpine. Elevation range is 0 to 3408 m asl. The location is ideal for such an elevation study because the gradient runs from east to west. Thus, the gradient does not include changes in latitude. We extracted collection and observation records for our study from a larger, national data set of dragonfly species (Simaika and Samways 2009b). We obtained additional data from a study on the elevation tolerance of dragonflies in the same area (Samways and Niba 2010). As a minimum selection criterion, we used species with ≥ 20 unique sampling locations (i.e., 1 sampling location/grid cell), resulting in 14 species representing a total of 259 records and 77 unique sampling locations (Fig. 1). A list of the species and a faunal description is given in Table 1.

Environmental variables

We obtained 30-arc-second ($\sim 1\text{-km}^2$ cell size), climate raster data sets of bioclimatic variables, which are biologically relevant variables calculated from elevation, temperature, and precipitation (Hijmans et al. 2005a). In addition to current climate data (1950–2000 average), we 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 3 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 2 emissions scenarios (A2 and B2). The A2 scenario assumes that population growth does not slow down and the population reaches 15 billion by 2100, and is associated with an increase in emissions. The B2 scenario assumes slower population growth, reach-

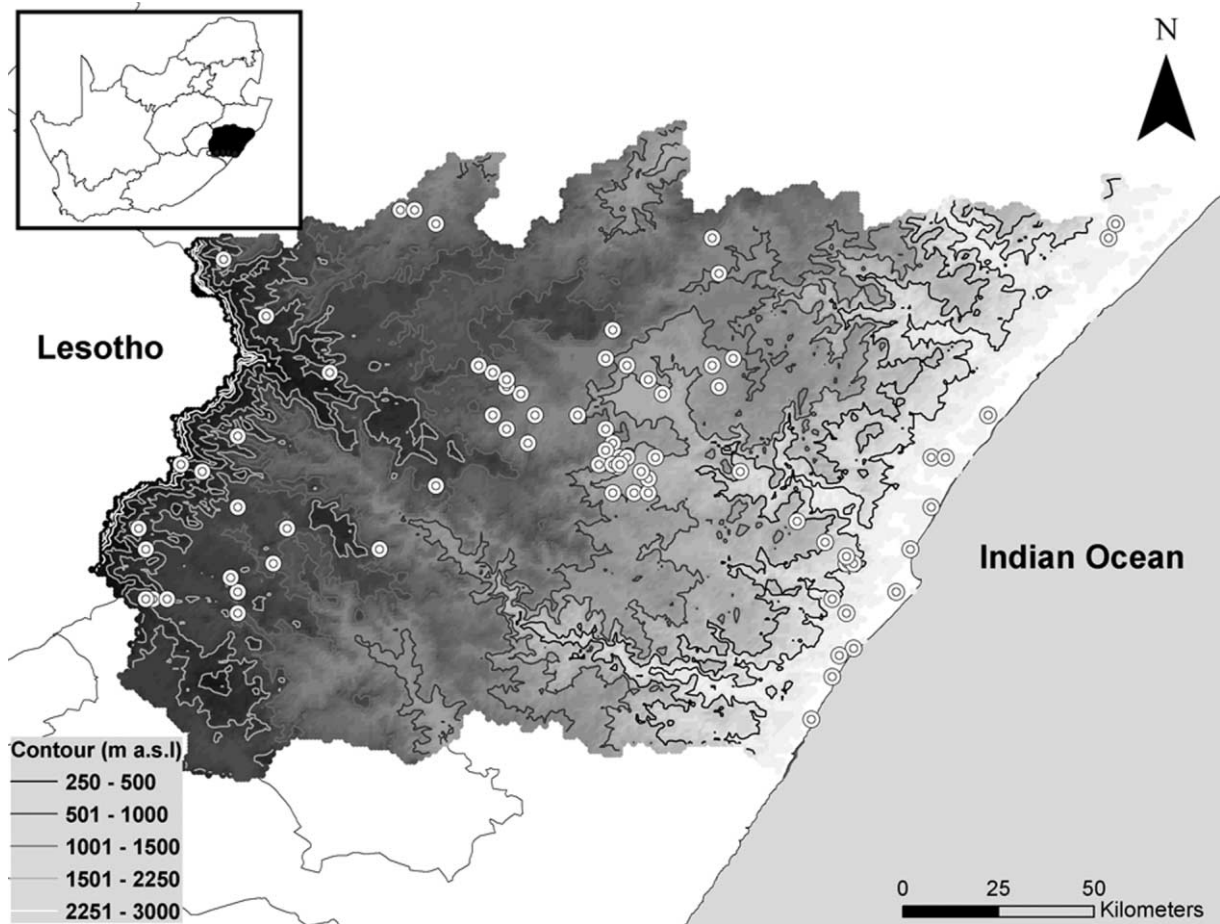


Figure 1. The study area, in KwaZulu-Natal, South Africa. White double circles are sampling locations. Shaded areas indicate increasing elevation from low (light gray) to high (dark gray).

ing 10.4 billion by 2100, and assumes that precautionary environmental practices are implemented (IPCC 2007). In addition to the climate rasters, we used a river catchment areas map, at the Quaternary scale (Midgley et al. 1994). Bioclimatic variables for the future scenarios were calculated using DIVA-GIS (version 7.2; Hijmans et al. 2005b).

Species habitat modeling

For this study, we used the species distribution modeling (SDM) software package MaxEnt (version 3.3.3a; Phillips et al. 2006, Phillips and Dudík 2008). MaxEnt has been used extensively for constructing SDMs, including in studies on dragonflies (e.g., Shah et al. 2012, Weltenreuther et al. 2012, De Marco et al. 2015). MaxEnt was run using default parameters. To check for multicollinearity, we 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 (Phillips et al. 2006). We used jackknife tests to re-

move variables that did not significantly contribute to model predictions. In our study, a minimum of 20 unique locations (1 presence per grid cell) was required for species to be admitted for modeling. For each species, we replicated 100 runs with 75% of a species' records randomly selected for model training and cross-validation, and we set aside 25% of the data for model testing and independent validation. The importance of environmental variables will differ among species, and therefore, we built different models for each species. We compared and validated model results using the area under the receiver operating characteristic curve (AUC). The AUC measures the ability of models to discriminate presence from absence records. An AUC value of 0.5 in the model would be equivalent to a random guess, whereas 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, we selected spe-

Table 1. Descriptions of species geographic ranges, habitat preferences, and flight season (season). SA = South Africa.

Species	Range	Habitat	Season
<i>Africallagma glaucum</i>	Throughout SA to tropical Africa	Marshy areas with emergent vegetation	All year
<i>Brachythemis leucosticta</i>	Northeastern SA to eastern and western Africa	Pools, dams, sluggish rivers	November–May
<i>Chlorolestes fasciatus</i>	Endemic to SA	Streams and rivers	December–May
<i>Chlorolestes tessellatus</i>	Endemic to SA	Forested streams and rivers	December–May
<i>Hemistigma albipunctum</i>	KwaZulu–Natal coast to central Africa	Pools with emergent vegetation	November–May
<i>Lestes virgatus</i>	SA to northern and western Africa	Pools with emergent vegetation	November–May
<i>Nesciothemis farinosa</i>	SA to Egypt and southern Arabia	Pools, pans, sluggish rivers	October–May
<i>Palpopleura portia</i>	Northeastern SA to eastern and western Africa	Ponds, pools, pans, swamps, marshes, sluggish rivers	October–May
<i>Pseudagrion kersteni</i>	Throughout SA to tropical Africa, rare at coast	Vegetated banks of streams and rivers	All year
<i>Pseudagrion massaicum</i>	Throughout SA to tropical Africa, north to Ethiopia and Uganda	Ponds, pools, sluggish rivers	October–May
<i>Pseudagrion spernatum</i>	Mountains of SA, >800 m asl	Fast-flowing montane streams and rivers	October–May
<i>Trithemis arteriosa</i>	Throughout SA to tropical Africa and Asia	Pools, dams, still reaches of rivers	All year
<i>Trithemis dorsalis</i>	Throughout SA to tropical Africa and Asia	Lakes, dams, still reaches of rivers	November–May
<i>Trithemis furva</i>	<700 m asl, throughout SA to Ethiopia and western Africa	Rocky, shallow rivers	All year

cies models that had an AUC value >0.7 after subtraction of the lower 95% confidence interval of the average model species AUCs, calculated from the model test samples and related standard deviation. Selected model AUCs ranged from 0.76 to 0.96. After subtraction of the lower 95% confidence interval, the lower AUC values ranged from 0.70 to 0.94.

Spatial analysis

To assess changes in species richness and geographic range, we converted the species models meeting the AUC criteria into presence–absence (binary) data sets. The binary maps were created using the minimum logistic presence threshold; i.e., we considered suitable all sites that were at least as suitable as those where a species presence was recorded in the training set. This threshold is considered conservative because it identifies the minimum predicted area possible while maintaining 0 omission error in the training data set. 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, ≥ 2 models had 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 unsuitable habitat (current = 0, future = 2) for each prediction and then adding current predictions to future predictions. This method allowed us to classify areas as unsuitable (current and future), stable (suitable currently and in the future), increasingly suitable in the future, and decreasingly suitable in the future (unsuitable = 2, stable = 5, increasing = 4, decreasing = 3) under future climate scenarios. All spatial work was carried out using ArcGIS (version 9.2; Environmental Systems Research Institute, Redlands, California).

RESULTS

Models and variables

All variables used in model building were correlated ($r > 0.8$, $p < 0.01$), and thus, interpretation of variable importance to models was not possible. Eight models were created for species under different climate scenarios. The most com-

monly used variables were 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 2).

Species richness

In the current situation, using predicted distributions, species richness is and will be highest in the midlands (13 species; Fig. 2). Richness at the coast is lower (8 species), and richness is lowest in the highlands (5–6 species). Under the more severe emissions scenario (A2) for the year 2050, few species (1–2) are predicted to occur at the coast (Fig. 3A), whereas in the other scenarios for 2050 and 2080, at least up to 4 species will occur (Fig. 3B–D). All models predict that species richness will remain highest in the midlands. However, in all future scenarios, at least 3 species will be lost (Table 3). A general loss of extent in occurrence is predicted in the highland areas, especially in

Table 2. Selected bioclimatic variables (Hijmans et al. 2005a, b) and their use in species distribution model building (M1–M8). The 4 most frequently used variables are in bold. All variables are continuous data, except for catchment area (Midgley et al. 1994), which is categorical.

Variable description	M1	M2	M3	M4	M5	M6	M7	M8
Temperature								
Minimum temperature of coldest month			Yes	Yes		Yes	Yes	
Mean temperature of driest quarter			Yes			Yes	Yes	Yes
Mean temperature of coldest quarter						Yes	Yes	Yes
Precipitation								
Annual precipitation				Yes				
Precipitation of wettest month					Yes			
Precipitation of driest month							Yes	
Precipitation seasonality (coefficient of variation)		Yes						
Precipitation of wettest quarter	Yes	Yes						Yes
Precipitation of driest quarter		Yes						Yes
Precipitation of warmest quarter		Yes	Yes	Yes				Yes
Precipitation of coldest quarter		Yes						
Landscape								
Catchment area	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes

the 2050 models. In contrast, in both emissions scenarios for 2080, numbers of species are as high as in the current prediction.

Geographic range and elevation

Overall, species will undergo a reduction in extent of occurrence. The decrease will range 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 3). These species also have the narrowest elevation ranges of all species (468–1258 m; Table 4). 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 143% beyond its former geographic range. *Pseudagrion spernatum*'s elevation range will increase up to 696 m, with 461 m of that change toward the upper elevations (Table 4).

Under the moderate emissions scenario (B2), species geographic ranges will increase, but with only a 160- to 260-m elevation change. The only unaffected species is *Lestes virgatus*, for which both geographic range and elevations remain the same under all scenarios. The widespread endemic *Africallagma glaucum* has an elevation range of 2326 m that is 2nd only to the elevation range for *Trithemis dorsalis*. Under the A2 scenario, *A. glaucum*'s elevation range will change little, but under the B2 scenario, the species will undergo an upward trend in elevation range from current conditions of 662 m in 2050 and 879 m in 2080. Under the B2 scenario, *A. glaucum* is predicted to lose 39% of its former geographic extent. The endemic *Chlorolestes fasciatus* faces range reductions under all scenarios. However, under the A2 scenario, the species will initially decline 29% in 2050 and then recover to 87% of its former extent in 2080. Under the B2 scenario, a decline of 54% in 2050 is followed by a further decline to 19% in 2080. In contrast, the geographic range of the endemic *C. tessellatus* will remain relatively stable at ~216 km² and will range from 89 to 103%. The lower range margin for *C. tessellatus* will move upward by 333 m by 2080. In contrast, the already high lower range margin of *C. fasciatus* will move to only 161 m lower, whereas the upper range margin will move up to 880 m higher by 2050 under the B2 scenario. *Chlorolestes fasciatus* faces the greatest geographic range loss under the B2 scenario where the elevation range is similar to present conditions (Table 3).

Change in habitat suitability

Under the A2 scenario, the 2050 and 2080 predictions have in common a decrease in habitat suitability for species at the coast and the highlands, whereas in the midlands, habitat suitability both decreases and increases (Fig. 4). The

CCCMA a2a current

Species richness

- 0
- 1 - 2
- 3 - 4
- 5 - 6
- 7 - 8
- 9 - 10
- 11 - 13

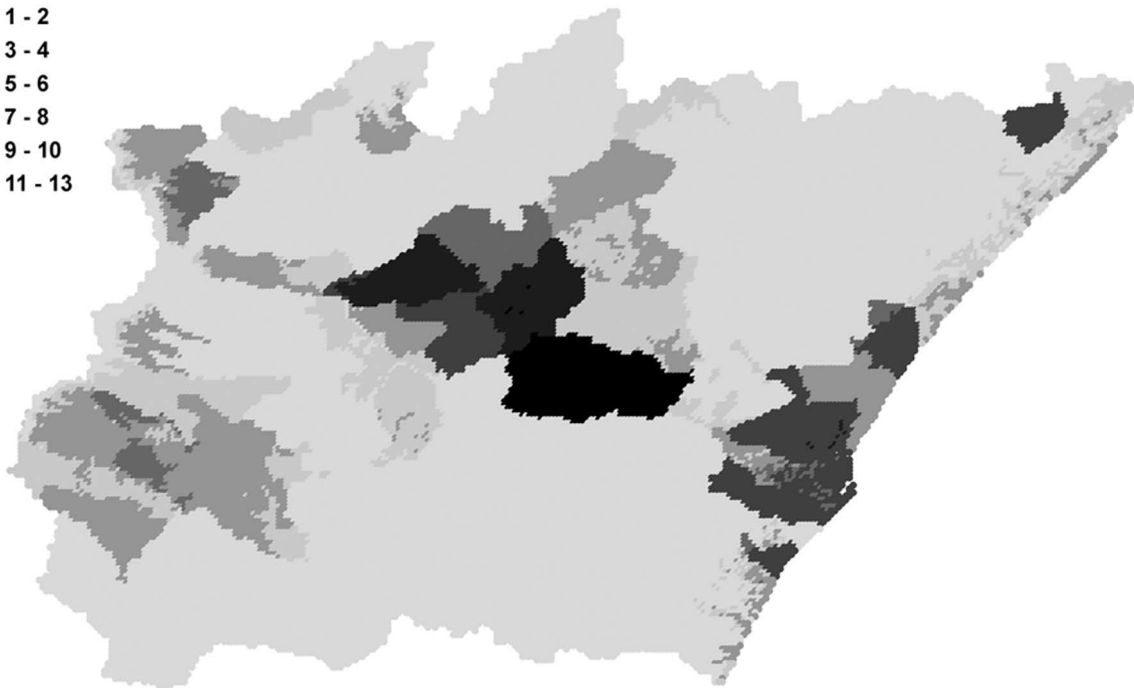


Figure 2. Predicted current distributions of dragonfly species in the study area.

B2 scenario changes the least from the current prediction, whereas the A2 scenario shows greater change, in particular in the highlands.

DISCUSSION

Coope (1995) identified 3 ways in which a species may respond to persistent climate change: 1) the species can become extinct, 2) the species can adapt in situ, or 3) the species can migrate to an area with a more tolerable climate. Evidence does exist that some insect species have become extinct because of recent climate change, and that 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, with insect species in the past tending to have shifted their geographical ranges according to changing climatic conditions (Coope 1978, Ponel et al. 2003). This tendency does not exclude the possibility of rapid evolutionary change under future scenarios, especially when there are strong and even synergistic drivers of change (Williams 2002, Murcia et al. 2014). Unlike the first 2 responses listed above, distributional changes are recorded and studied frequently (Hassall et al. 2007).

In their study on the responsiveness of 179 animal species from various taxa (mammals, birds, reptiles, butterflies, various other invertebrate species) to climate change brought

about by a doubling of CO₂ in South Africa, Erasmus et al. (2002) found that 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, most range shifts (41%) were in an easterly direction, and highest losses of species occurred in the west. Along the Durban–Sani Pass gradient (the one we used), Erasmus et al. (2002) showed that butterflies, while slightly fewer in numbers, were overall more widely distributed in the area, as were what they classed in their analysis as ‘other invertebrate taxa’ (Scarabainae beetles, antlions [Neuroptera], buprestid beetles, and termites).

In our study, all modeled species are widespread, and many are common where they occur. Only 2 species, *C. fasciatus* and *C. tessellatus* are national endemics (Samways 2006), and their future in South Africa appears to be assured. This stability may be because the endemic species have been through many climatic bottlenecks in the past without being obliterated by glaciations, which have not occurred in the area for >200 my. 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.

Species ranges decrease less under the A2 scenario for 2050 and 2080 than under the B2 scenario for the same time periods. This prediction would seem counter-intuitive

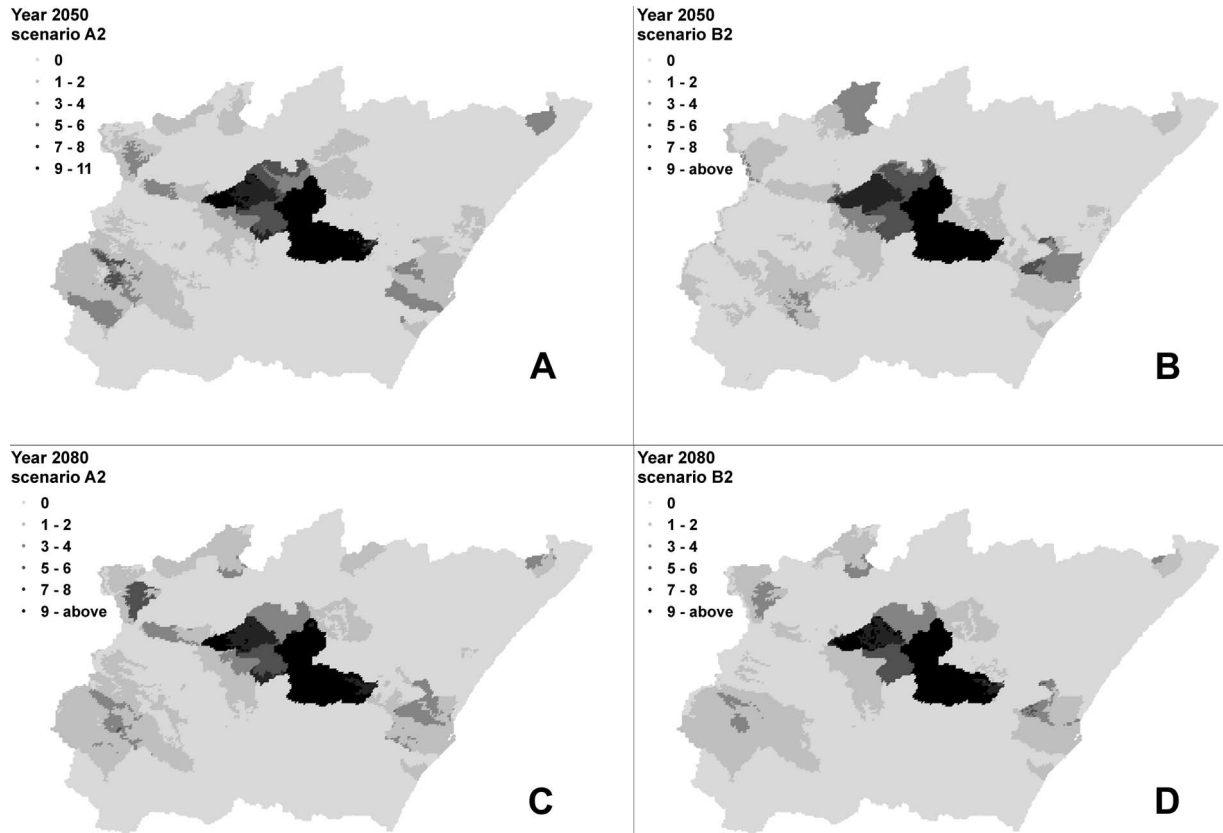


Figure 3. Predicted species richness patterns for 2050 (A, B) and 2080 (C, D) under the A2 (A, C) and B2 (B, D) climate scenarios.

because the A2 scenario is considered more severe than the B2 scenario. This prediction does make ecological sense because most of the species considered here are widespread and tolerant of water-scarce environments and, therefore,

should be able to breed in temporary habitats including small ponds and pools and artificial reservoirs. In other words, these less-sensitive species stand to benefit from the deterioration of permanent lotic habitat, such as the

Table 3. 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.

Species	Now	Scenario A2				Scenario B2			
		2015	Now–2050	2080	Now–2080	2015	Now–2050	2080	Now–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>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	5583	143
<i>Trithemis arteriosa</i>	5438	2990	55	2769	51	4036	7	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	47085	34908	74	34364	73	32760	70	27812	59

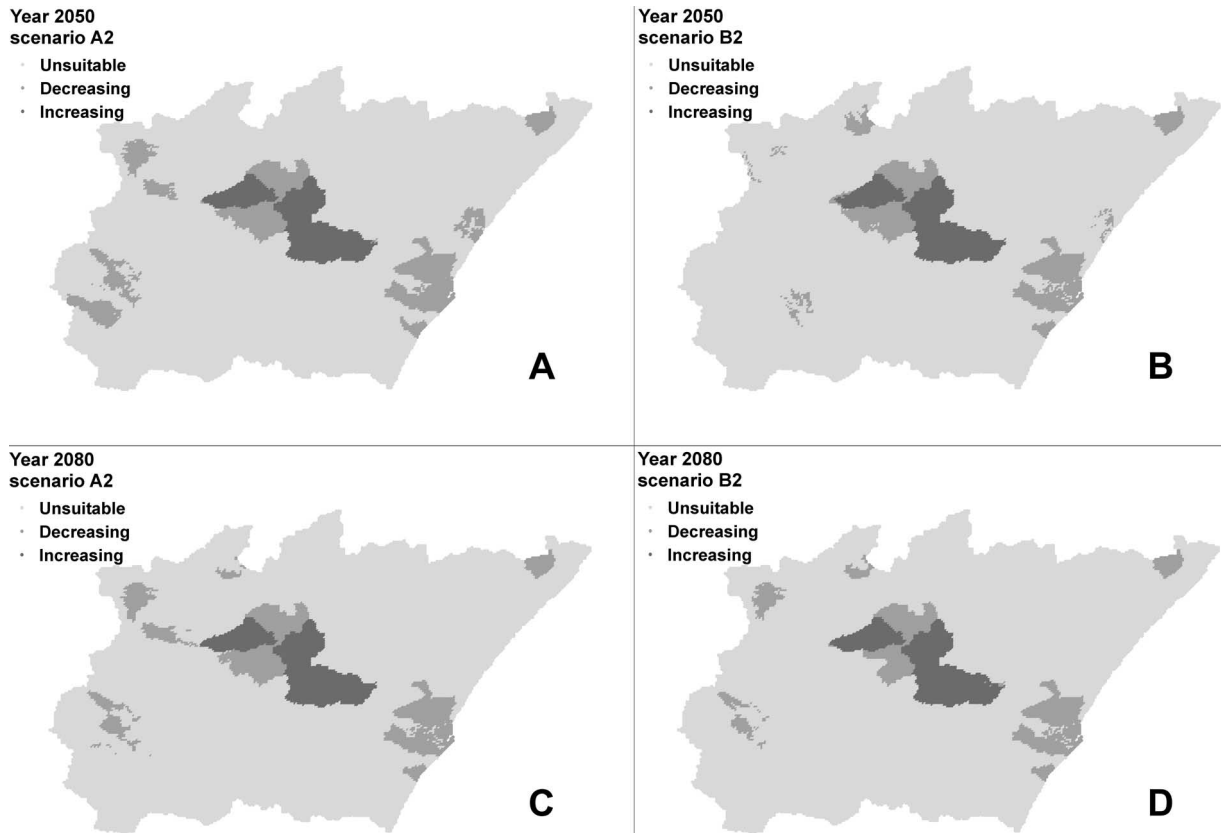


Figure 4. Predicted range of habitat change for 2050 (A, B) and 2080 (C, D) under the A2 (A, C) and B2 (B, D) climate scenarios from the current prediction.

change of perennial streams to ephemeral habitats. In addition, as water shortages increase, so too will the number of reservoirs used for irrigation, further giving habitat opportunities to tolerant species.

Three species, *Brachythemis leucosticta*, *Hemistigma albigunctum*, and *Palpopleura portia*, face local extinction from the study area in the long term. All these species are widespread, but have relatively narrow elevation ranges compared to other species in the study. The ranges of these 3 species extend marginally into our study area, and therefore, a loss of these species probably would indicate that they are shifting out of the study area, most likely westward. *Pseudagrion spernatum* is a stream specialist, but its geographic spread and remarkable elevation tolerance will give it an advantage in the changing climatic conditions. The only high-elevation specialist, *C. fasciatus*, is predicted to extend to lower and to higher elevations, with most of the change to higher elevations.

Species at high elevations tend to be thermally tolerant because of the breadth of climatic conditions encountered at higher elevations. Indeed, this tolerance is supported by the climatic variability hypothesis (Stevens 1992, Gaston and Chown 1999) that an increase in the elevation range of occurrence of a species in an assemblage with increasing elevation can be explained as a consequence of individuals

having to withstand a broader range of climatic conditions. Gaston and Chown (1999) tested this hypothesis on an assemblage of 26 scarab dung beetle species along an elevation transect of 2500 m by using thermal tolerance as a measure of climatic tolerance. They found evidence for a general increase in temperature-tolerance range of the dung beetles across the elevation gradient, a result that supports the climate variability hypothesis. Therefore, ecological support may exist for the model results, in that because *C. fasciatus* occurs at higher elevations, the species' altitudinal range also would increase.

Under the A2 scenario, *C. fasciatus* will initially face a reduced geographic range, followed by a recovery of some of that range. In contrast, under the B2 scenario, the species faces a continued decline of up to 81% of its former range. The general range reduction of this habitat specialist, despite the increasing elevation range to higher elevations, will occur because less-suitable habitat is available at higher than at lower elevations. This conclusion is supported by preliminary evidence that this species has, to some extent, a glacial-relict distribution. For example, it occurs in the low, but watered mountain peaks of the Mountain Zebra National Park, is absent from the extensive and totally surrounding lower and drier areas (Samways 2006), and occurs in some locations, such as at Umtamvuna, at sea

Table 4. Current and future predicted elevation tolerances of species under 2 climate scenarios, A2 and B2, for 2050 and 2080. Minimum (min), maximum (max), and range of elevations are given in meters. Range = difference between the minimum and maximum recorded elevation, na = not applicable. Habitat codes: * = endemic, g = habitat generalist, s = habitat specialist, l = lentic, o = lotic, c = localized, w = widespread, f = forest habitat – = narrow elevation range, + = wide elevation range.

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

level (Samways and Simaika 2015). This distribution pattern suggests that *C. fasciatus* has remarkable elevation tolerance that might have been honed by deep history and by more recent ENSO events.

The model predictions in our study clearly indicate that most species will experience reduced extent of occurrence and will become more localized, while at the same time, species composition will change. Furthermore, the reduction in the number of species and, therefore, competition for habitat, could cause some species to become more common. These changes probably will cause a change in local community structure, but 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 nonspecialist diets (but see Knight et al. 2005 on trophic effects across ecosystems). A further consideration is that several species that occur farther north in southern Africa, some of which have ranges that currently extend south to just inside South Africa, may move farther southward in the country. This situation is highly likely because several species temporally extend and contract their ranges mostly north–south according to ENSO events and regularly become present and then locally extinct (Samways 2010). In addition, several species move up and down in elevation on a temporary basis depending on prevailing climate (Samways and Niba 2010).

Most species in our study thrive in artificial environments, such as reservoirs, but also in roadside ditches and other artificial water features. Therefore, to a certain extent, loss in connectivity or changes in hydrological con-

ditions are unlikely to affect these species. However, stream specialists, such as the nationally endemic species *C. fasciatus* and *C. tessellatus*, are far more vulnerable. These species are adapted to cool, oligotrophic, acidic stream conditions (Samways and Simaika 2015). Coastal habitats are predicted to become warmer, resulting in increased evaporation (Schulze et al. 2011). Intensified coastal winds are likely to increase this effect. Increases in rainfall volume and intensity, and consequently increased sedimentation, are likely to result in negative changes to stream geomorphology and, thus, to affect the ability of larvae to cope in their aquatic habitats. In addition, stream species (*C. fasciatus* at higher elevations and *C. tessellatus* at lower ones) are vulnerable to the effects of forestry and invasive alien woody plants. This threat is real because increasing CO₂ concentrations in the atmosphere are predicted to dramatically contribute to woody plant growth (Wigley et al. 2010). Both species benefit from clearing of invasive alien tree and creation of large-scale natural corridors (ecological networks) along streams in their natural habitat. These corridors will be increasingly important in the future as a means of maintaining connectivity across the landscape and for allowing these species and others to track climate change without the inhibition of a fragmented landscape (Samways 2010).

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