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Continental-scale conservation prioritization of African dragonflies

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ABSTRACT

Indicators on the state of global biodiversity illustrate continued decline, while pressure on biodiversity keeps rising. This necessitates revisiting site prioritization and species protection for conservation. Patterns of richness and threat of four well-studied aquatic taxa, the fishes, crabs, molluscs and dragonflies largely coincide at the continental scale, at least in Africa. For this study, we focus on dragonflies, for which there is a point locality database, as a surrogate taxon, modeling the species at the fine-scale, using species distribution modeling. With this approach, we built a protected areas network using spatial planning software. Priority areas for dragonfly conservation largely coincided with analyses of global biodiversity hotspots. The Zambian swamps and woodlands, as well as the rainforests of the Lower Guinea and Congo Basin are emphasized as hotspots of dragonfly diversity. Among globally threatened species, 72% were recorded at least once in a protected area. Although the current reserve network covers 10.7% of the landscape, the proportional representation of species geographic distributions in reserves is only 1.2%. The reserve network is therefore inefficient concerning freshwater species, and many areas of conservation priority that are not formally protected remain. The advantage of operating at the fine scale, while covering a large geographic area is that it shifts the focus from the large-scale hotspots to smaller priority areas within and beyond hotspots. Also, by operating at the fine-scale for a large geographical area, the potential exists for local conservation managers to consider campaigning for the inclusion of the priority areas that are not formally protected, while adjacent to the existing reserve networks. Where this is not possible, we recommend monitoring these areas to detect future threats to the habitats that these might face.

1. Introduction

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

Biodiversity hotspots are areas of high priority for conservation (Myers et al., 2000). Hotspots may be selected on the basis of their local species richness, degree of concentration of rare species

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(Prendergast et al., 1993) or the two measures combined with some assessment of urgency for conservation action (Myers et al., 2000). Alternatively, biodiversity hotspots can be selected using the principle of complementarity, based on their relative contribution for attaining an overall conservation goal (Araújo, 2002). The selection and prioritization of conservation areas and design of reserve networks, depends in part, on good taxonomic knowledge of the surrogate used. Thus, the selection of freshwater protected areas is most commonly based on fish diversity, although biotic surrogate reserve selection studies have also used water beetles (Abellán et al., 2005) and dragonflies (Simaika and Samways, 2009). Indeed, in their study on the effectiveness of surrogate species and their representativeness of freshwater species on the African continent, Darwall et al. (2011a,b) found that dragonflies are effective surrogates for birds, mammals, and amphibians, but that the inverse of this relationship does not hold.

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

In this study, we model the distributions of African dragonflies, using predictive species distribution modeling software. Our objectives are firstly to build a hypothetical reserve network, based on maximal species representation, by identifying priority areas under the assumption that all areas are available for protection (unconstrained analysis). Secondly, the aim is to compare the efficiency of the existing continental reserve network as well as that of the global biodiversity hotspots at representing all species. Thirdly, our aim is to identify areas of conservation concern within and beyond reserves and hotspot areas.

2. Methods

2.1. The database

The database used here, the 'Odonata Database of Africa (ODA)', is the first continent-wide, expert-reviewed database of freshwater insects (Clausnitzer et al., 2012; Kipping et al., 2009; Dijkstra et al., 2011). The raw database is continually updated, and at the time of this analysis contained 77,369 records, representing 686 species. Of these, 581 are restricted to the African continent, and we term them here 'African endemics'. For modelling purposes, only georeferenced records were retained, with duplicates removed, which resulted in 50,485 unique presence records. Species that have low occurrence records tend to be rare, endemic species, or species that have a scant collection record. We therefore differentiated between species that were evaluated using the IUCN categories and criteria (IUCN, 2001) as data deficient (DD) and least concern (LC) and species that were near threatened (NT), vulnerable (VU), endangered (EN) and critically endangered (CR) at the global level. Species names, IUCN threat categories, relative geographic distributions on the African continent, and model performance information, are presented in Appendix S1. To maintain high model performance, only species with presences at >20 locations were used in species distribution modelling. Species with <20 locations were retained for inclusion in spatial modelling, termed species of special interest (Moilanen and Kujala, 2008).

2.2. Species distribution modeling

At the continental scale, climate can be considered the dominant factor driving species distributions (Pearson and Dawson, 2003). Here we obtained 2.5 arc-min, global climate raster datasets of the 19 bioclim variables, which are calculated from elevation, temperature and precipitation (Hijmans et al., 2005). In addition, we selected two topographical layers, namely slope and the compound topography index (CTI) often referred to as the wetness index, from the Hydro 1K database (USGS). As the climate raster grids were global in extent, we used the 'extract by mask' function in ArcMap to reduce the extent and resolution of the grids (0.042 cell resolution) to that of the mask (0.05 cell resolution), the equivalent to ca. 5 km^2 size grid cells. Topographical layers were aggregated from the initial resolution of 1 km^2 to that of the mask. To avoid multicolinearity, we chose only variables that were not highly intercorrelated ($-0.7 < r < 0.7$; Green, 1979). The final selection comprised nine variables (Appendix S2), and these layers were then used as environmental data input in BIOMOD/R (version 1.1-7.03, Thuiller et al., 2009; R Development Core Team, 2012).

BIOMOD/R is a species distribution modelling software that makes use of ensemble forecasting based on presence-only data, i.e., projections of several algorithms are combined into one final ensemble projection to reduce uncertainties derived from single algorithms (Thuiller et al., 2009). We created an ensemble model for each species consisting of four algorithms, namely Boosted Regression Trees (BRTs), Multivariate Adaptive Regression Splines (MARSs), Flexible Disciminant Ananlysis (FDA) and Random Forests (RFs). Here, each algorithm used the default settings of the BIOMOD package (Thuiller et al., 2009). For each species, we replicated 10 runs with 70% of a species' records randomly selected for model training and cross-validation, and 30% of the data set aside for model testing and independent validation (Fielding and Bell, 1997). To evaluate commission, 10,000 random background points were used. Model results were compared and validated using the true skill statistic (TSS), based on the sensitivity (true positive predictions) and specificity (true negative predictions). Allouche et al. (2006) have shown that TSS scores are superior for measuring the performance of SDMs when projections are expressed in binary presence–absence maps. A TSS score of 0 in the model would be equivalent to a random guess, while a value of 1.0 would indicate that the model can perfectly distinguish between presence and absence of a species.

Single algorithm models were merged to an ensemble model by giving them weights based on their predictive performance using a weight decay of 1.6 (default settings). This procedure minimizes uncertainties since weak models receive less weight in the final ensemble. Moreover, only models performing better than TSS >0.4 for at least two algorithms were included in the ensemble, otherwise no ensemble was created for the species (Araújo et al., 2011). The ensemble models were then projected on the entire study area, and maps indicating the probability of habitat suitability were transformed into binary presence–absence maps by applying a cut-off value which minimizes the difference between sensitivity and specificity (Liu et al., 2005).

In this study, species mean TSS scored averaged 0.999 ($n = 337$, range 0.971–1; Appendix S1). A total of 351 species were modelled in BIOMOD, 337 of them successfully (i.e., an ensemble was created), and an additional 335 species of special interest (SSI) retained for analysis in Zonation, including the species for which no ensemble could be created.

2.3. Spatial analysis and planning

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

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

An important step in Zonation analysis is specification of species-specific weights. These weights influence the balance that emerges between features (here species) in prioritization (e.g.

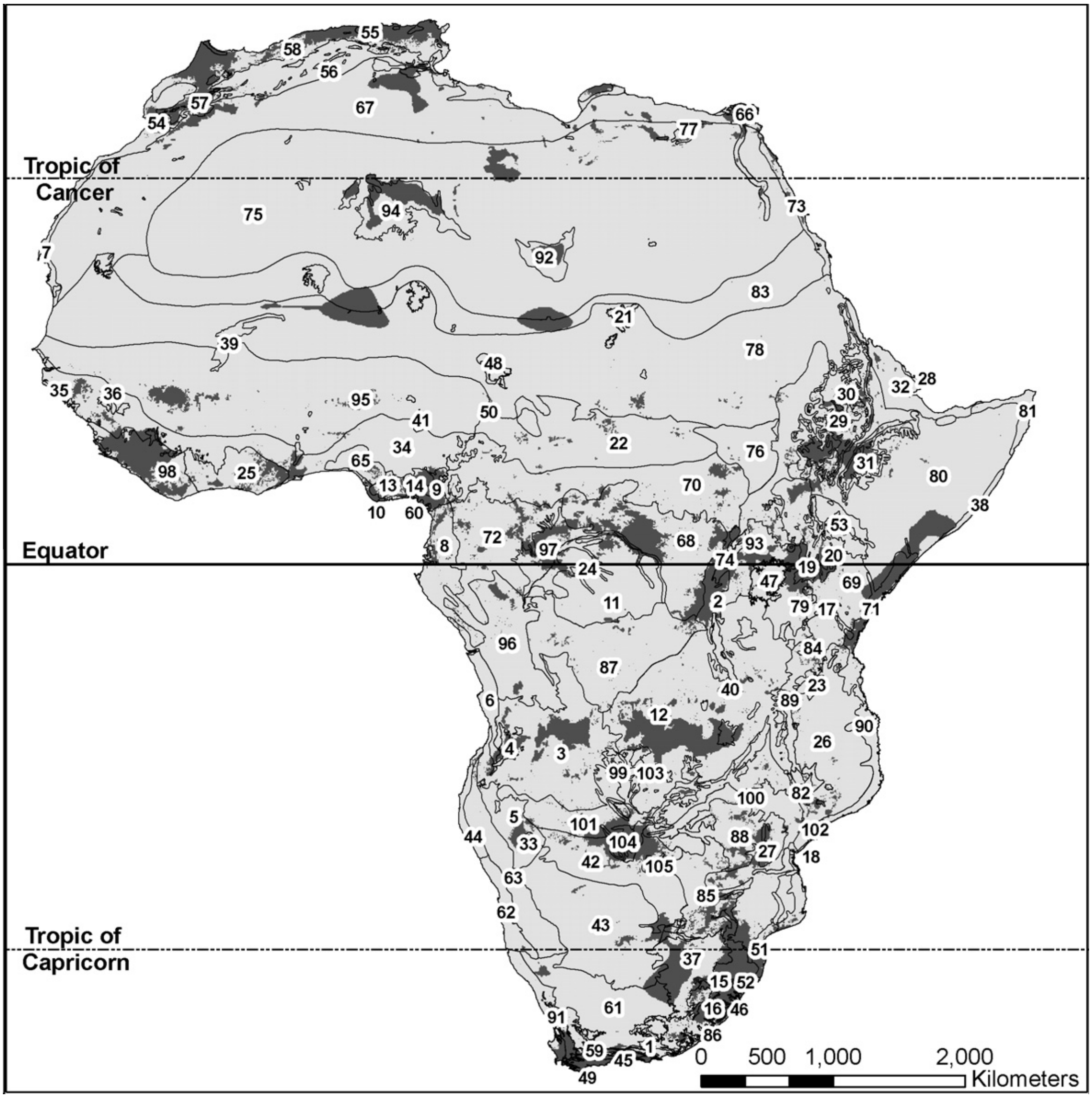

Fig. 1. Potential reserve network of 10% of the geographic distributions of dragonfly species (dark gray). This represents 12.7% of the top fraction of the African landscape. Annotations are for terrestrial ecoregions and described in Table 1.

Leathwick et al., 2008). Species were weighted according to whether or not they were globally threatened (IUCN, 2001). Species in the IUCN threat categories NT, VU, EN and CR were given a weight of 2. With respect to Zonation specific parameters, we used removal restricted to habitat edges (Moilanen et al., 2005) and set the analysis warp (acceleration) factor to 100 (Moilanen and Ball, 2009).

Three analyses were carried out with Zonation using the full species dataset (686 species) and the one containing only the African endemics (581). In the first analysis, Zonation was set to an unconstrained analysis in which it is assumed that there are no restrictions on how the landscape is to be prioritized. This is therefore the optimized reserve network. In the second and third analyses, mask files were included of protected areas (UNEP-WCMC, 2009), and global biodiversity hotspots (Mittermeier et al., 2004), respectively. We chose an arbitrary minimum size of 50 km^2 (ca. 7.1 × 7.1 km) for inclusion in the gap analysis, because we considered reserves of a smaller size unable maintain aquatic connectivity and therefore unable to significantly contribute to the protection of aquatic diversity. Areas of the mask file are prioritized or ‘locked into the landscape’ and the remainder of the analysis is carried out as under unconstrained conditions. All spatial work was carried out using ArcGIS 9.2 (ESRI, 2006).

For the resultant maps and discussion of biogeographic patterns, we chose to use terrestrial ecoregions (Olson, 2001) rather than freshwater ecoregions (Abell et al., 2008). This was done for two reasons: First, although the number of types of ecoregions are comparable for the maps (105 terrestrial types, 78 freshwater types), the number of distinct polygons is by an order of magnitude higher in the terrestrial ecoregions map (964 polygons) than the freshwater ecoregions map (78 polygons). In other words, the spatial resolution of the terrestrial ecoregions map is much higher. Secondly, the groupings of distinct vegetation types are ecologically meaningful, as they take habitat structure into consideration, and which drives presence or absence of dragonfly species in a local area in an African context (Clark and Samways, 1996). For example, some dragonfly species are particularly dependent on forests (Cordero-Rivera, 2006).

3. Results

3.1. Current reserve network

In total, dragonflies were recorded from 19.7% (431 of the 2185) of the currently recognized protected areas in Africa, representing 82.2% (564 of 686) of the dragonfly species overall. Of globally threatened species 72% (43 of 60 species) were recorded at least once in a protected area. Only 58% (7/12) critically endangered and 60% (8/13) endangered dragonfly species are found in formally protected areas, whereas 80% (28/35) of species listed as vulnerable occur in protected areas.

Table 1
Descriptions of annotations for terrestrial ecoregions as shown in Figs. 1, 2, 5 and 6.

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

3.2. Unconstrained analysis

An unconstrained analysis assumes that the entire landscape is available for protection. Setting aside 10% (100,057 of 1,000,569 grid cells) of the top fraction of the landscape for the conservation of dragonflies, would represent a 9.1% proportion of dragonfly species distributions overall, while a 10% proportion of the distribution of dragonfly species could be accommodated by setting aside 11.7% (117,314 grid cells) of the top fraction of the landscape (Fig. 1, Table 1). Considering only species endemic to the continent, a 10% fraction of the top landscape would represent 9.1% of endemic dragonfly species distributions, while a 10% proportion of the distribution of endemic dragonfly species could be accommodated by setting aside 10.6% (105,838 grid cells) of the landscape (Fig. 2, Table 1). Although the top areas cover several ecoregions, we note the 10 ecoregions that are most represented by area, for all species. Considering the number of selected cells in an ecoregion against all selected cells (Appendix S3), the most represented areas, standardized by size, are the Mediterranean woodlands and forests, the Central Zambezian Miombo woodlands, the Northeastern Congolian lowland forests, the Drakensberg montane grasslands, woodlands and forests, the Western Guinean lowland forests, the Angolan Miombo woodlands, the Sahara desert, the Somali Acacia-Commiphora bushalnds and thickets, the North Saharan steppe and woodlands, and the Highveld grasslands. Considering only species endemic to Africa, the first five most important for all species are still in the same place, and nearly as strongly represented as before. The Somali Acacia-Commiphora bushlands and thickets, and the Highveld grasslands remain among the top 10, but the remainder are replaced by the Ethiopian montane grasslands and woodlands, and the South Saharan steppe and woodlands.

3.3. Reserves

Protected areas represented 10.7% (106,561 of 1,000,569 grid cells) of the total landmass analyzed here. Reservation of the same area that protected areas represent would include only a 1.2% proportion of the distribution of dragonfly species overall, and 1.6% of the distribution of endemic dragonfly species. A 10% proportion of overall species distributions would require protection of 18.7% (187,389 grid cells) of the top-ranked fraction of landmass to be set aside (Fig. 3). Considering only endemic species distributions,

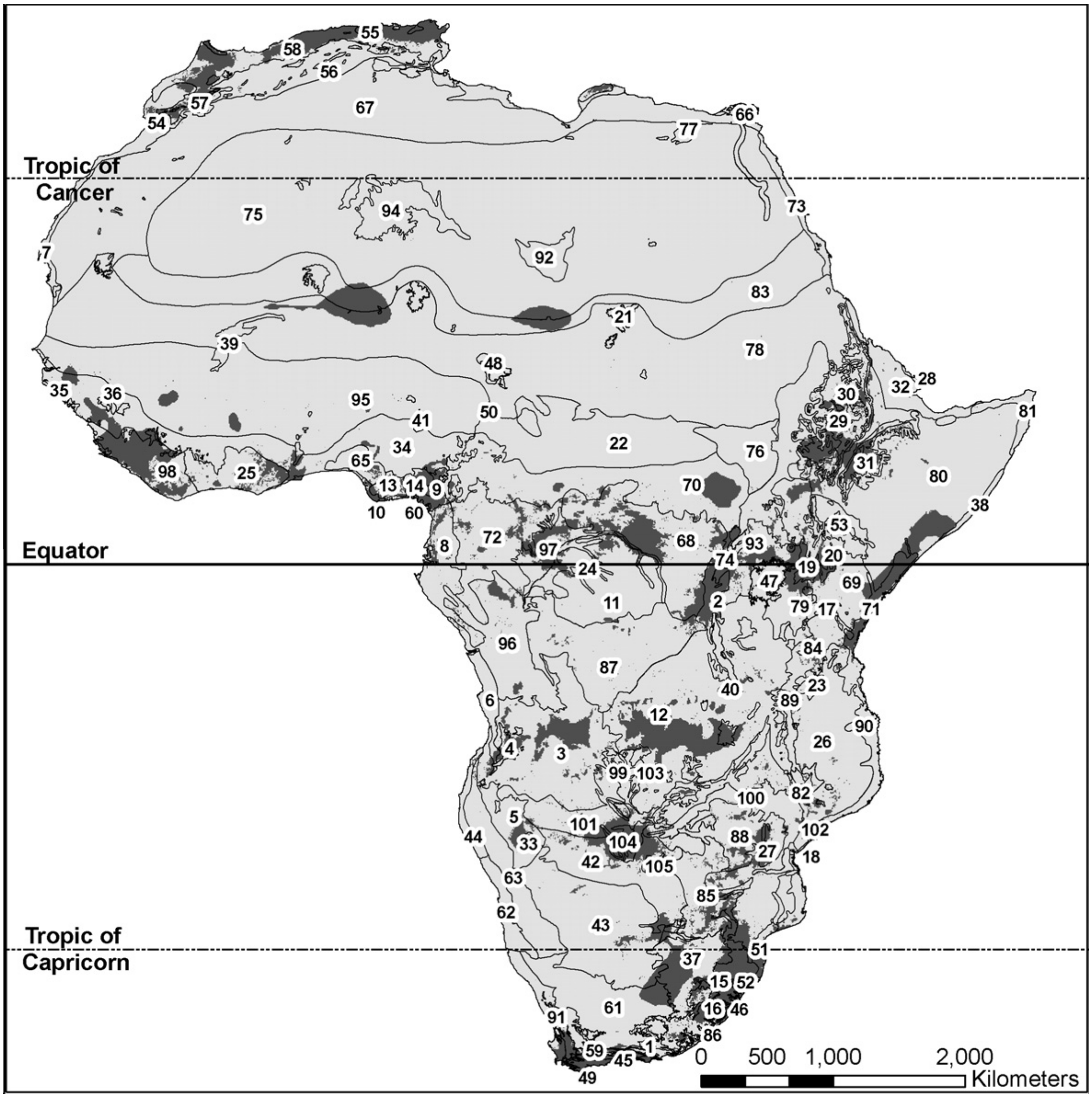

Fig. 2. Potential reserve network of 10% of the geographic distributions of endemic dragonfly species (dark gray). This represents 11.4% of the top fraction of the African landscape. Annotations are for terrestrial ecoregions and described in Table 1.

a top fraction of 18.1% (180,883 grid cells) of landmass would be required (Fig. 4). This represents 6.4% (63,569 grid cells) more than under the unconstrained analysis for all species, and 7.5% (75,045 grid cells) considering only African endemics.

3.4. Hotspots

African biodiversity hotspots represent 15% of the total available landmass (or 149,881 of 1,000,569 grid cells). However, protection of the area that hotspots represent would include only a 1.1% proportion of the geographic distribution of dragonfly species overall, and 1.1% of African endemics. To protect 10% of species distributions overall (Fig. 5, Table 1) and African endemics (Fig. 6, Table 1), a reserve network of hotspots would require a total selected landmass of 20.8% (207,694 grid cells) and 20.2% (202,011 grid cells), respectively.

4. Discussion

4.1. Overview of analyses

We found general agreement of the unconstrained network analysis with what might be expected in terms of biogeographical patterns of dragonfly distributions (Clausnitzer et al., 2012; Dijkstra et al., 2011) and accordingly, the priority areas (Figs. 1 and 2). The existing priority areas that fall outside the current hotspot areas and protected areas, are discussed in detail below. Nevertheless, under-sampled areas that are likely to yield new and rare and threatened species remain. In particular, these are the vast expanses of the Lower Guinea and Congo Basin rainforests, the Angolan and Albertine highlands, the highlands and woodlands of Mozambique, and eastern and north-eastern Tanzania.

4.2. Hotspots and beyond

Global biodiversity hotspots cover very large tracks of geographical regions without discriminating the finer details (Figs. 5 and 6). Setting aside entire hotspots would lead to a very inefficient representation of the geographic distribution of species, with nearly 17% of the landscape, slightly more efficient than the currently highly fragmented system of protected areas. The unconstrained analyses (Figs. 1 and 2) show that large portions of priority areas occur within the boundaries of the hotspot areas (Figs. 5 and 6). This is true for all hotspots except the dry Succulent Karoo and Horn of Africa, which have few suitable habitats for dragonflies and their aquatic larvae. At least in part, the Coastal Forests of Eastern Africa also have some importance to dragonflies. South Africa alone is home to three global biodiversity hotspots. In

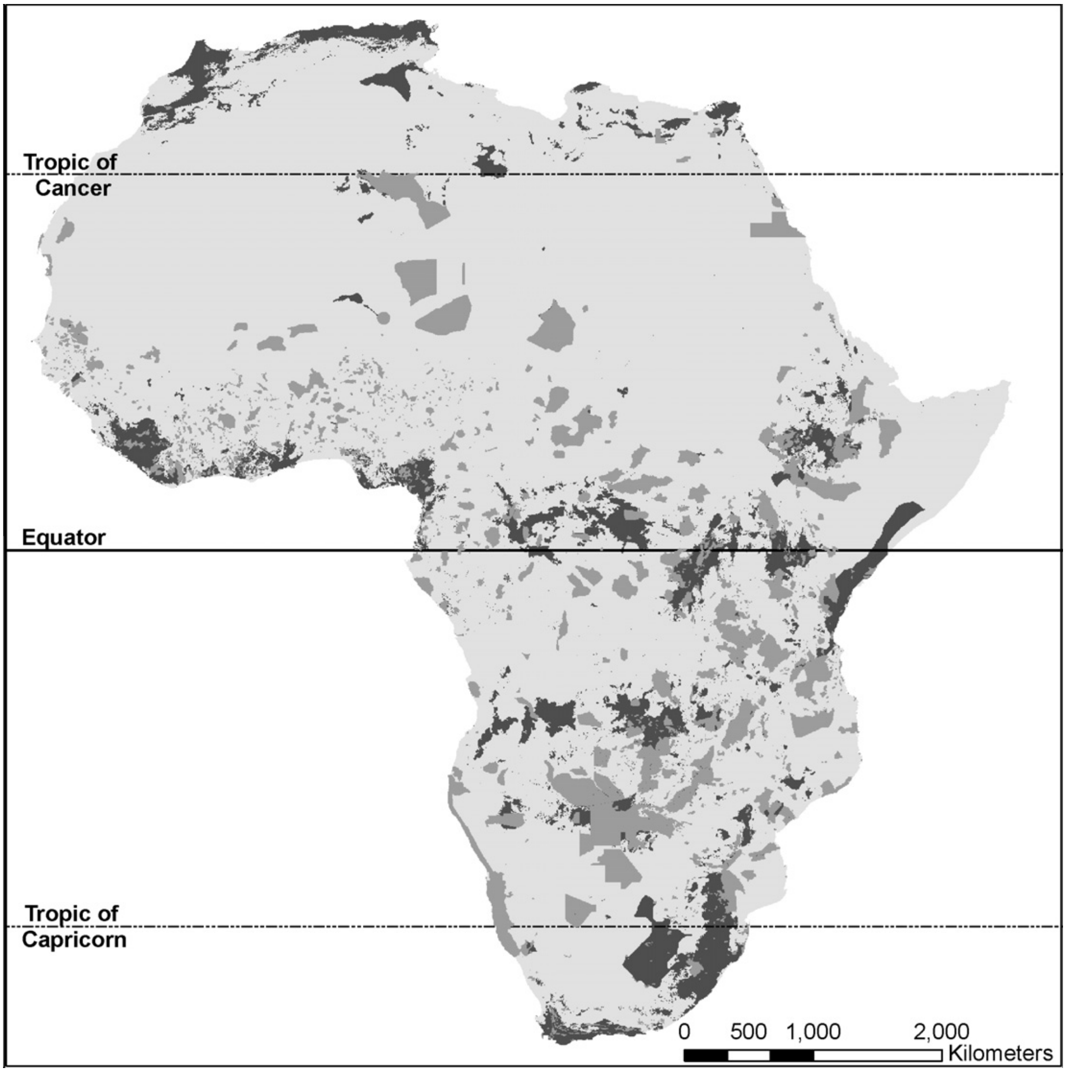

Fig. 3. Reserve network of 10% of the geographic distribution of dragonfly species (dark gray), with protected areas (light gray) (17.9% top fraction of landscape) included in the reserve network.

terms of dragonfly diversity, additional areas of conservation interest would be the Knysna-Amatole montane forests and Albany thickets. Also, the north-eastern expanse of the Maputo-Pondoland-Albany hotspot is flanked by priority areas represented by the Drakensberg montane ecoregion and Southern Africa bushveld. In addition, a large area of Highveld grasslands appears to be important. Several areas of priority extend beyond the fragmented portions of the Eastern Afromontane biodiversity hotspot of which the Victoria Basin forest-savanna mosaic ecoregion is most notable. Two major priority regions for freshwater conservation were identified well beyond the hotspots. These are Zambezia (incorporating large areas of Zambezian flooded grasslands, and Zambezian and Mopane woodland ecoregions) and, outside the Guinean Forests of West Africa biodiversity hotspot, the Lower Guinea and Congo Basin rainforests (e.g. large expanses of Atlantic Equatorial coastal forests, the Northwestern Congolian lowland forests and the Western Congolian swamp forests). In North Africa, small pockets of the (higher) Sahara and Sahel have conservation value for dragonflies that are marginal to the African continent and widespread elsewhere. Considering only species endemic to the continent, these areas do not have conservation value, however.

4.3. Protected areas

Although 10.7% of the African landscape is covered by reserves, these are widely dispersed and fragmented (Figs. 3 and 4). Thus, even a large and diverse taxonomic group composed of highly vagile generalist as well as specialist species such as the dragonflies are not particularly well protected. Our model shows that to protect a 10% proportion of the geographical distribution of dragonflies with the existing reserve network in place will require an additional 5.2% (or 4.2% for African endemics) of Africa to be set aside for the conservation of dragonfly species. This is significantly more than would be the case if the entire area was available for protection. The current reserve system is therefore inefficient, but demonstrates that dragonflies are nevertheless surviving well outside protected areas.

Our findings indicate that 82% of all dragonflies and 72% of globally threatened dragonflies occur at least once in a protected area. These results contrast with those of Darwall et al. (2011a) who in the same study area found high overlap between protected areas of all dragonfly species (86%), and perfect overlap (100%) with threatened dragonfly species, based solely on intersects between

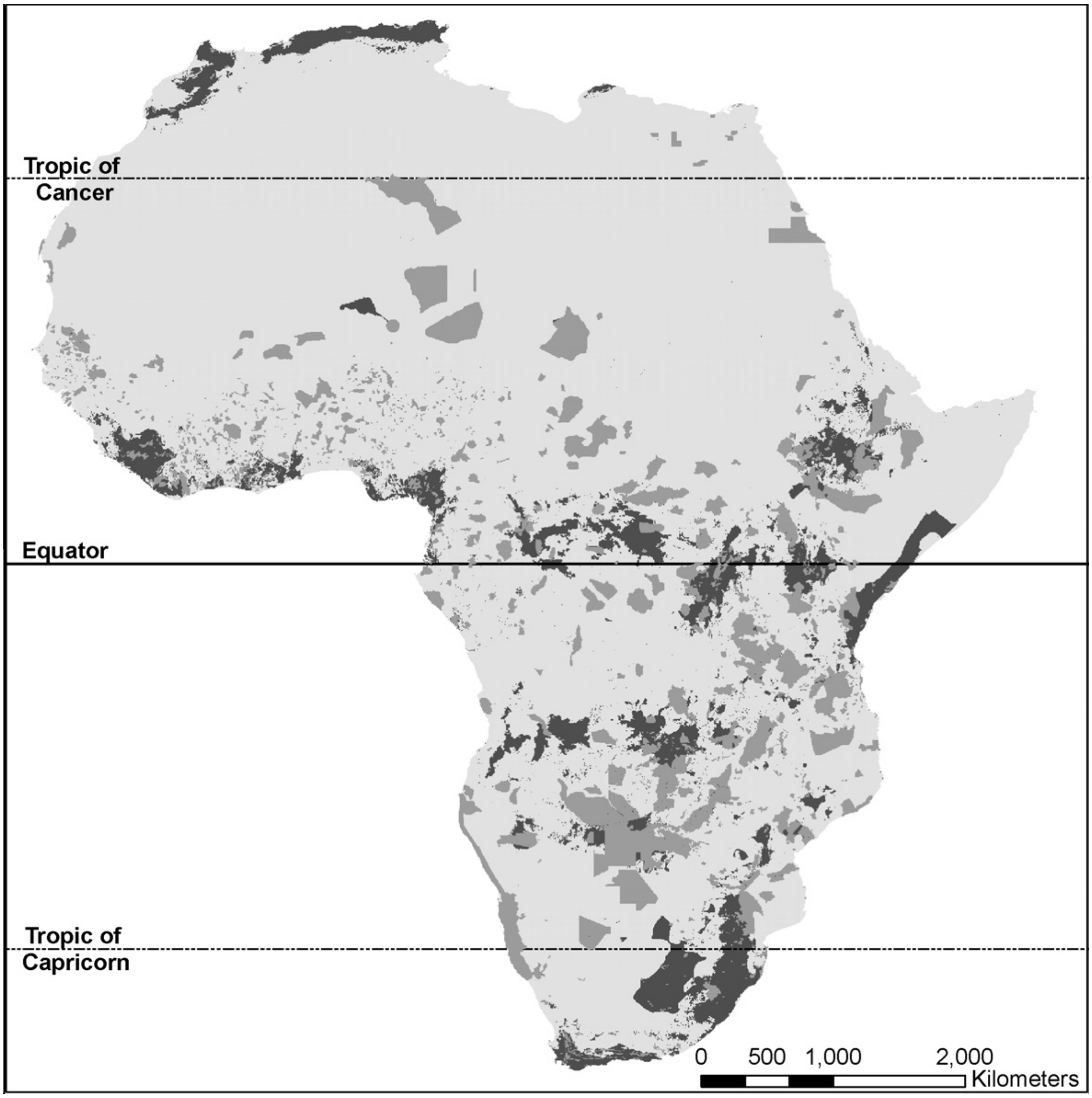

Fig. 4. Reserve network of 10% of the geographic distribution of endemic dragonfly species (dark gray), with protected areas (light gray) (17.9% top fraction of landscape) included in the reserve network.

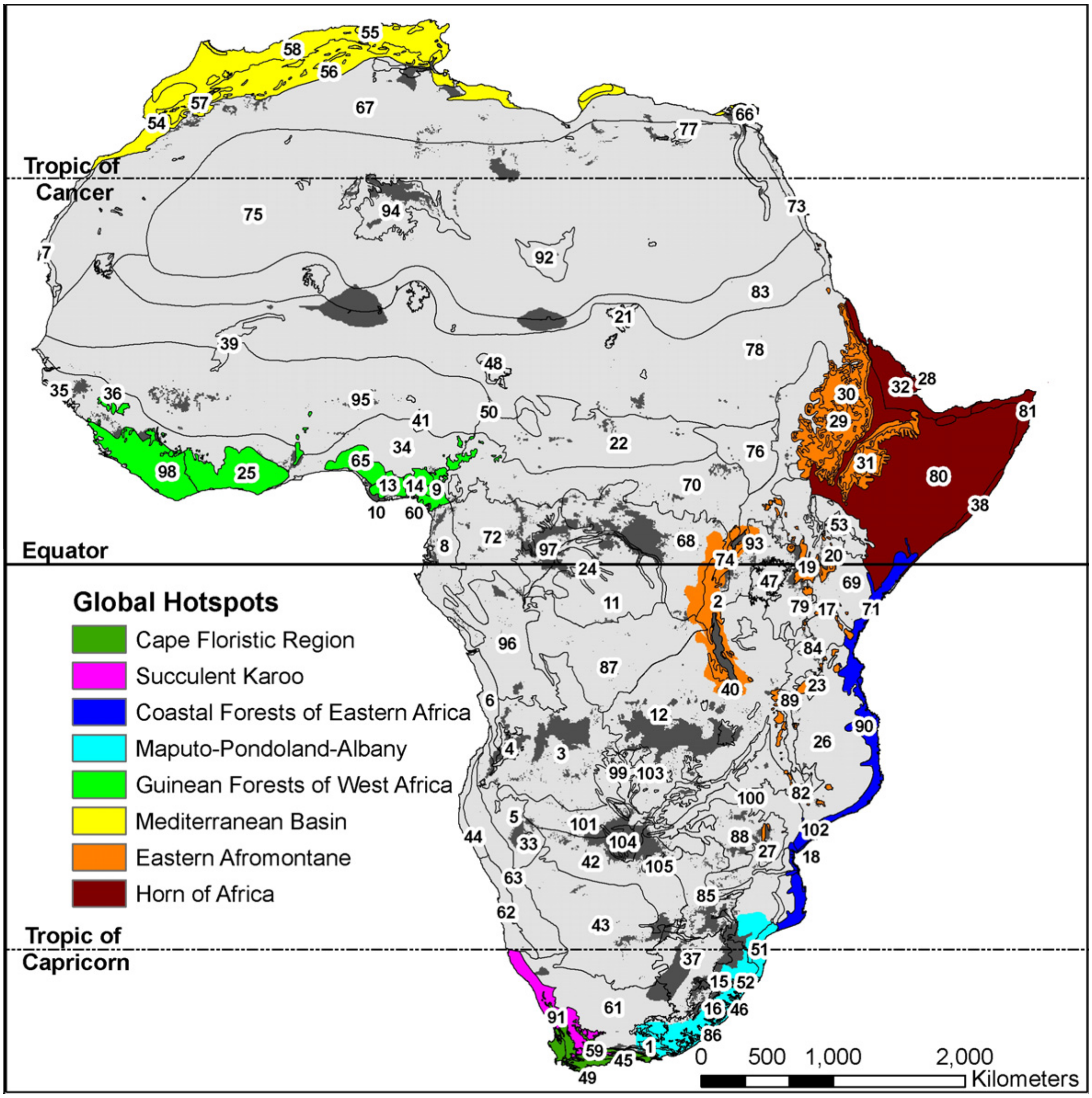

Fig. 5. Potential reserve network of 10% of the geographic distribution of dragonfly species (dark gray) with global biodiversity hotspots (17% top fraction of landscape) included in the network. Annotations are for terrestrial ecoregions and described in Table 1.

protected areas and species ranges. However, in catchments where 70% or more of the area falls within a protected area, Darwall et al. (2011a) found that more dragonfly species overall (74%) and fewer threatened taxa (50%) are represented. Although Darwall et al. (2011a) note that the intersect between a species range and a protected area will tend to overestimate the effective protection provided by the protected area network, we believe that this is additionally caused by the use of very large Hydro 1K catchments in obtaining these results. Indeed, Hydro 1K catchments tend to over-estimate species distributions, over-represent changes in distributions, and include large tracts of land unrepresentative of species habitat requirements (Simaika and Samways, 2010).

While our criteria for selecting protected areas for inclusion into the analysis was based solely on the size of existing reserves, this could have been based on other criteria such as designation or international convention (UNEP-WCMC, 2009). However, with few exceptions (Saunders et al., 2002; Darwall et al., 2011a), protected areas, even large ones, do not normally take freshwater biodiversity into account. The longitudinal nature of streams makes it difficult to include both headwaters and lower reaches in protected areas (Roux et al., 2008). For example, South Africa's Kruger National Park is oriented north–south, but cuts across the downstream sections of river catchments, which are oriented west–east. The result is that the perturbed inflows from upstream habitats outside the protected area negatively impact downstream habitat in the protected area (Skelton et al., 1995). In the case of Kruger National Park, Roux et al. (2008) recommend redesign of the park based on spatial prioritization of the riverine fauna that occurs there. Competing interests for freshwater may have negative impacts on freshwater species as well. Similarly, overexploitation of natural springs for water supply of tourist lodging has eradicated several dragonfly species from the Waterberg National Park in Namibia (Suhling et al., 2006).

5. Conclusions

While geographically hugely over-represented, many areas of high biodiversity fall within the boundaries of established global biodiversity conservation priorities. However, beyond global biodiversity hotspots, are also priority areas of significant conservation value. Furthermore, many under-sampled areas that are likely to

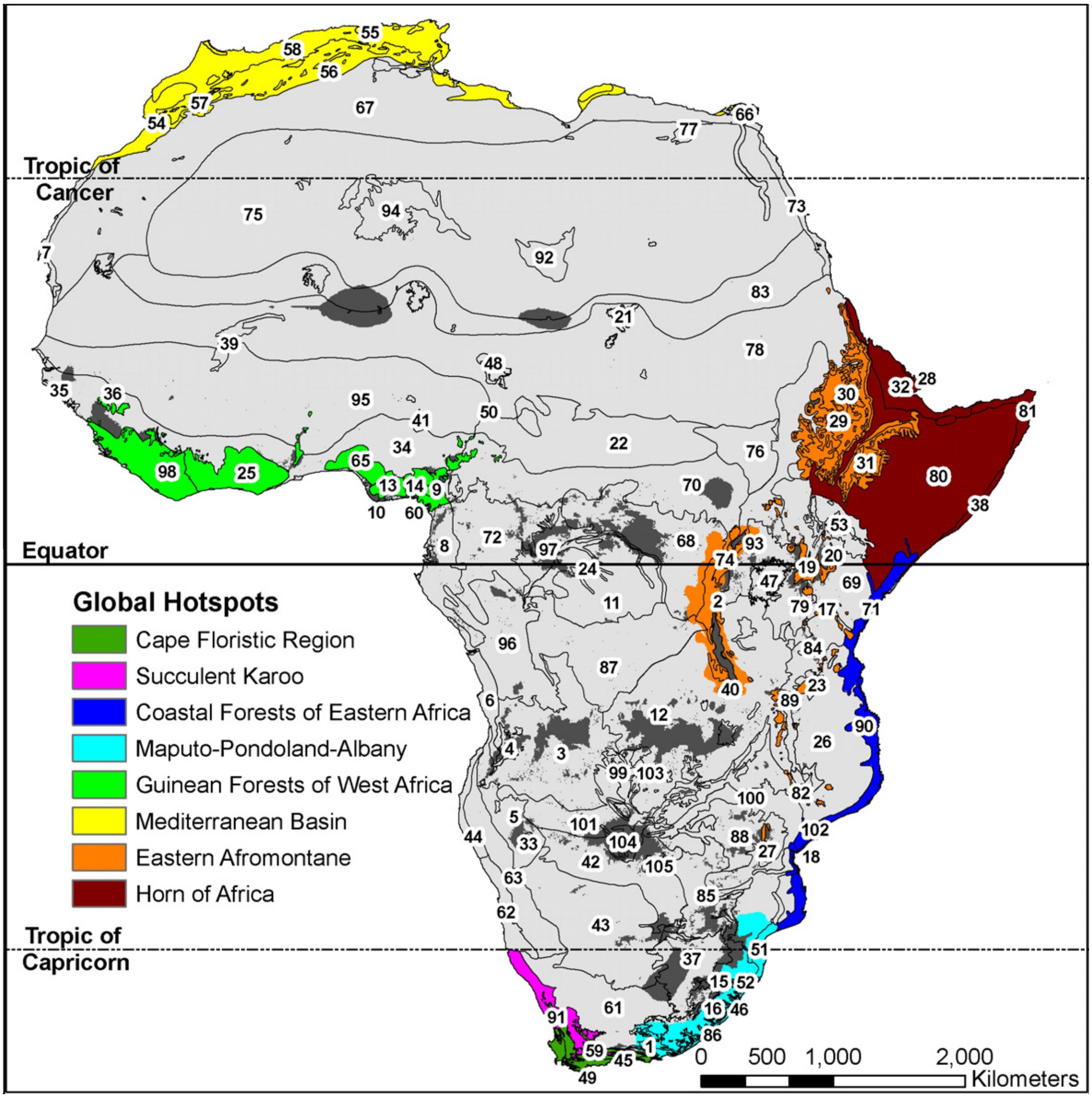

Fig. 6. Potential reserve network of 10% of the geographic distribution of endemic dragonfly species (dark gray) with global biodiversity hotspots (17% top fraction of landscape) included in the network. Annotations are for terrestrial ecoregions and described in Table 1.

yield new species remain. In particular, these are the vast expanses of the Congo Basin, the highlands of Angola, highlands and woodlands of Mozambique and eastern and north-eastern Tanzania. The fine-scale modeling approach presented here has two main advantages. Firstly, there is the benefit of a highly detailed, fine-scale representation of priority areas. This shifts the focus from the large-scale hotspots to smaller priority areas within and also beyond hotspots. Secondly, by operating at the fine-scale for a large geographical area, the potential exists for local conservation managers to consider campaigning for the inclusion of the priority areas that are not formally protected, and adjacent to the existing reserve networks. Where this is not possible, or where areas fall within the mosaic of different landscape uses, we recommend monitoring these areas to keep informed of future threats to the habitats that these might face.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.08.039.

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