Biodiversity in Southern Africa

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Patterns and Processes at Regional Scale

BIOTA

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Large-scale patterns

Dragonfly diversity from the Cape to the Kavango

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Summary: Dragonflies are amongst the most well-studied and most recognised insects and there is an ongoing worldwide initiative in which the diversity and conservation status of all species are being assessed. In Africa, where about 900 species of Odonata occur, the southern part of the continent is currently the best surveyed for Odonata. In this chapter we analyse and depict biodiversity distribution patterns in the BIOTA transect area, from the Cape in the south to the Okavango River in the north, using Odonata databases for Botswana, Namibia and South Africa. We counted species numbers in each WWF Terrestrial Ecoregion and freshwater basin. Species numbers were highest in the Zambezian ecoregions followed by the Cape ecoregions, whereas the drier ecoregions had fewer species, except for a few outstanding localities. The proportions of range-restricted species were highest in the Cape and Zambezian ecoregions accounting for at least one third of the species, whereas all other ecoregions were almost exclusively populated by widespread species.

Introduction

There is evidence and it is widely recognised that human impacts are causing a severe loss of biodiversity globally (Brooks et al. 2001). However, most biodiversity remains undetected, since many ecosystems are largely unexplored, particularly in the tropics where biodiversity is supposed to be highest (Gaston 2000). Biodiversity hotspot analyses are based on only a few taxonomic groups (Myers et al. 2000), which have been more widely explored, such as mammals, birds, amphibians and vascular plants. For prioritising conservation areas, multitaxonomic rather than single-taxon approaches are critical for identifying areas likely to promote the persistence of most species (Kremen et al. 2008). Estimates suggest that biodiversity loss is most severe in freshwater ecosystems, particularly in Africa (Thieme et al. 2005). A recent attempt at surveying freshwater biodiversity on a larger taxonomic scale is the Pan-Africa Freshwater Biodiversity Assessment (Darwall et al. 2009). This has included the Odonata, which have proved to be of good value for conservation assessment (Simaika & Samways 2009a, b, see also Box 1).

Odonata are amongst the most well-studied groups of insects and freshwater organisms (Box 1) and it is therefore not surprising that Odonata are the first insect group for which global conservation status has been assessed (Clausnitzer et al. 2009). In southern Africa, research on Odonata has a long tradition. The first overview was compiled by Ris (1921), followed by Barnard (1937) who published a comprehensive survey of the dragonfly fauna of the Cape region. Later, it was Elliot Pinhey in particular, who contributed to the knowledge about the Odonata of the region (e.g. Pinhey 1951, 1984b, 1985). To date, about 300 species have been recorded in southern Africa (Suhling et al. 2009a), and checklists have been published for most countries, including Botswana (Pinhey 1976), Mozambique (Pinhey 1981), Namibia (Martens et al. 2003, Suhling & Martens 2007), South Africa (Samways 1999, 2008), Zambia and Zimbabwe (Pinhey 1984a). Field guides have also been

Box 1
Dragon y biodiversity and conservation

Odonata have aquatic larvae (with a few exceptions) and terrestrial adults and are obligate predators. From a global perspective, Odonata are amongst the best-known insect groups with respect to taxonomy and distribution (Corbet 1999, Kalkman et al. 2008). Not many other insect groups receive so much attention from the general public and have so many organisations devoted to their study, for instance the Worldwide Dragonfly Association. This makes the Odonata a good agent for freshwater conservation, true "guardians of the watershed" (Clausnitzer & Jödicke 2004). At present 5,680 species of Odonata have been described, although the actual number of species may total 7,000. The rate of new descriptions is currently approximately 200 Odonata species per decade (Kalkman et al. 2008). The majority of species occur in the tropics, with the highest diversities in the Neotropical and Oriental regions, which harbour about 1,650 species each, while in the Afrotropics the diversity is lower with 890 species (Kalkman et al. 2008). According to IUCN criteria, only 10% of the globally assessed Odonata species are threatened, which is a relatively low figure compared with 31% for amphibians and 20% for mammals (Clausnitzer et al. 2009).

published (Tarboton & Tarboton 2002, 2005, Samways & Wilmot 2003, Suhling & Martens 2007, Samways 2008), which will surely improve the dragonfly survey in the region.

Brinck (1955) was the first to systematically analyse the patterns of dragonfly diversity of southern Africa from a biogeographical perspective. Based on generalised knowledge of dragonfly distribution patterns at the time, the author assumed that dragonfly species diversity is correlated with average annual precipitation. This led to the prediction that areas with higher rainfall would have higher dragonfly diversity than those with lower rainfall. This pattern was recently corroborated during the southern Africa freshwater assessment initiated by IUCN (Suhling et al. 2009a). More detailed analyses of diversity distribution in South Africa and Namibia have been presented by Simaika & Samways (2010) and Suhling et al. (2009b).

The aim of this contribution was to illustrate patterns of Odonata diversity for the region in which the BIOTA Southern Africa transects falls. The area stretched broadly from the Cape of Good Hope in South Africa, across Namibia to the Okavango River in Botswana, with branches into the Kalahari and Namib Deserts. For this we extracted the point locality distribution data from the Odonata species databases of Botswana, Namibia, and South Africa. The Namibia Odonata database was compiled as part of the BIOTA Southern Africa subproject S08. We analysed species numbers for WWF Terrestrial Ecoregions and freshwater basins, and summarised the conservation status of species according to IUCN criteria.

Databases and analysis

The analysis presented here is based on the Odonata records assembled by the authors from the databases of Botswana (J. Kipping), Namibia (F. Suhling) and South Africa (M. J. Samways & J. P. Simaika). Recently, all data from these three databases, in total ca 25,000 records, was transferred into the Africa Odonata database (administered by J. Kipping), which currently includes about 80,000 records. Thus, the three countries considered in

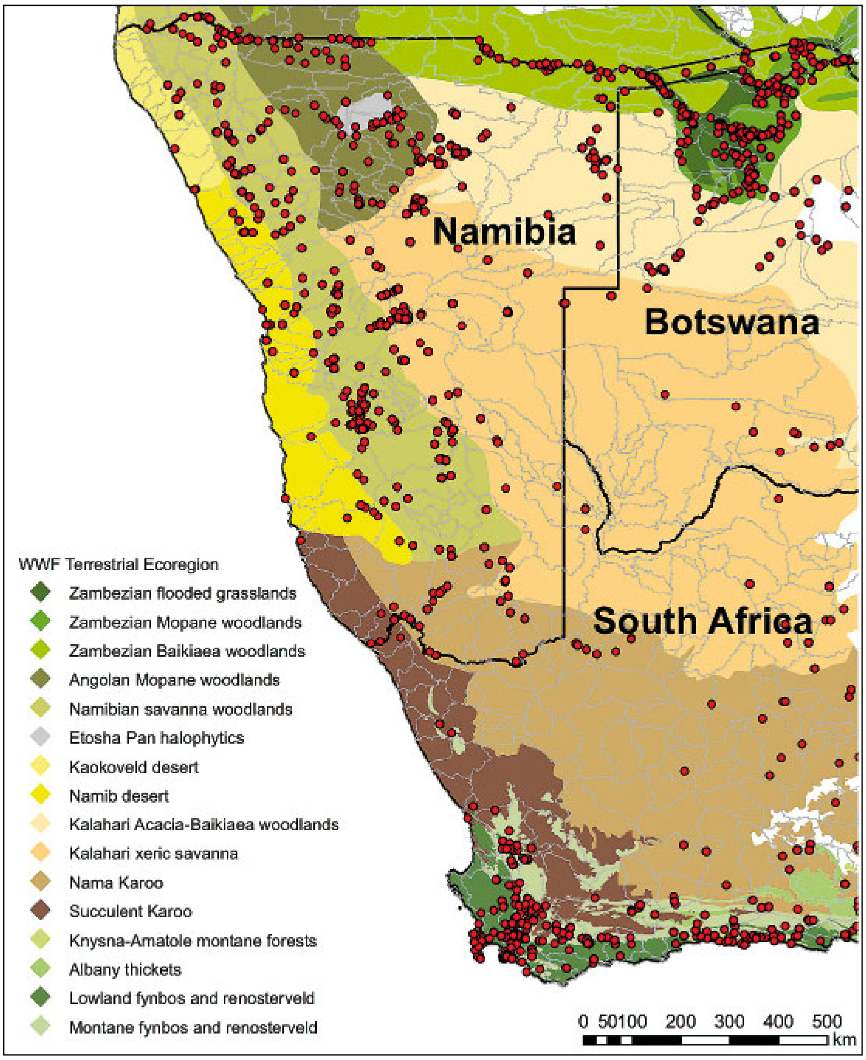

Fig. 1: Distribution of dragonfly records (red dots) in southwestern Africa overlaid on a map of the WWF Terrestrial Ecoregions. The thin grey lines indicate river basins.

Table 1: Overview of numbers of point locality records and numbers of species observed in the major WWF Terrestrial Ecoregions of southwestern Africa

WWF terrestrial ecoregion	Large ecoregion*	No. of species	No. of records
Albany thickets	Cape	31	109
Knysna-Amatole montane forests	Cape	26	149
Lowland fynbos and renosterveld	Cape	63	419
Montane fynbos and renosterveld	Cape	71	1,378
Nama Karoo	Karoo	53	333
Succulent Karoo	Karoo	33	94
Namib desert	Namib	23	167
Kaokoveld desert	Namib	11	31
Namibian savanna woodlands	Savanna	71	2,306
Etosha Pan halophytics	Savanna	21	85
Angolan Mopane woodlands	Savanna	48	275
Kalahari Acacia-Baikiaea woodlands	Kalahari	51	480
Kalahari xeric savanna	Kalahari	70	1,492
Zambezian Mopane woodlands	Zambezian	100	2,195
Zambezian Baikiaea woodlands	Zambezian	102	1,818
Zambezian flooded grasslands	Zambezian	112	3,383
Total		171	14,720

* for later analyses (see Figs. 3, 4) the ecoregions were combined to larger regions.

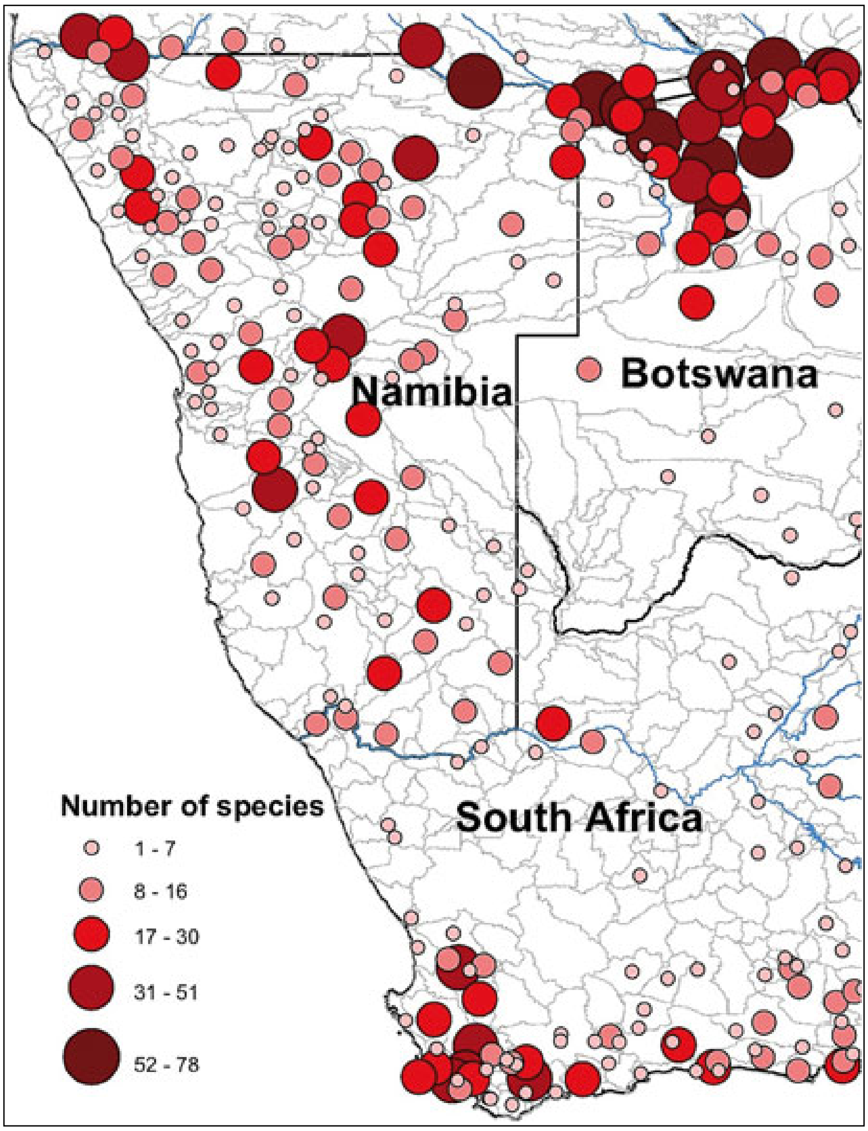

Fig. 2: Dragonfly species numbers per river basin. Basins intersected by ecoregions are represented by more than one dot. Basins with dots absent represent areas where the numbers of records were not sufficient for analysis.

this study have amongst the best records for the whole of Africa. All geographic analyses described below were carried out using ArcGIS 9.

For the purpose of this study we considered only the western part of southern Africa from the Cape of Good Hope in the south to the Okavango River in the north, and extending from the coastline in the west to 26° longitude (roughly a line from Kasane in Botswana to Port Elizabeth in South Africa) in the east (Fig. 1). We assigned all records to the 16 WWF Terrestrial Ecoregions (Olson et al. 2001) that were well represented in the region (Fig. 1). Records from marginal ecoregions were not considered (cf. white areas in Fig. 1). The numbers of records and the numbers of species per ecoregion were counted (Table 1) to identify broad scale patterns of species diversity. A more detailed spatial analysis of species diversity was carried out by counting species numbers in each river basin in the study area according to Darwall et al. (2009). However, certain river basins crossed more than one ecoregion (see Fig. 1). Therefore, in order to obtain polygons of subbasins that were only represented in one ecoregion, we intersected the shapes of the WWF Terrestrial Ecoregions with the river basins shapes (cf. Thieme et al. 2005). This procedure generated 1,077 polygons (subbasins), of which 282 had species records. Species numbers were then counted for those polygons, which had species records.

We also analysed the spatial diversity of range-restricted species in the region. In certain parts of the study area, namely the Cape and the Okavango Delta regions, the WWF ecoregions form comparatively small-scaled mosaics. Therefore, almost no species were identified that were restricted in occurrence to just one of the ecoregions. In order to analyse the diversity of range restricted species we therefore combined the ecoregions to form larger complexes (Table 1).

Spatial distribution of species diversity

A total of 171 species have until now been recorded in the study area (for species names cf. Electronic Appendix). The Zambezian ecoregions possessed the highest species diversities (Tab. 1), with 100 or more species records per ecoregion. In the drier parts of the study area and in the Cape, a maximum of 71 species per ecoregion occurred. The lowest species diversities were found in the Namib Desert and in the Etosha halophytic ecoregion.

On the subbasin scale, a maximum of 78 species was recorded. Highest species diversities occurred along the Okavango, Kwando and Zambezi Rivers (Fig. 2). However, relative high values of 3–51 species were also recorded in some subbasins along the Kunene River in the northwest and the Cape in the south. In addition, at two localised subbasins in Namibia, namely in the Otavi Mountains and the upper Swakop River catchment around a large impoundment, relatively high species numbers were also recorded.

Range restricted and widespread species

Range-restricted species were only recorded in the Zambezian and Cape ecoregions (Fig. 3). The only exception was the Gariep River endemic *Pseudagrion vaalense*, which was restricted to the Karoo in the region considered. All of the species restricted to the Cape were true endemics. By contrast, most of the

Zambezian range restricted species also occur outside the region, particularly in the Palaeo-Chambeshi-Katanga-Region, to which the Okavango and Kwando River swamps belong. The proportion of range-restricted species was 37% in the Cape and 33% in the Zambezian ecoregions.

Seven groups of species were categorised from their biogeographical backgrounds (Fig. 4). Besides the range restricted species mentioned above, we observed patterns of distribution, which suggest that several species entered the other ecoregions mainly from the Zambezian or the Cape ecoregions. Hence, these species had their centre of occurrence in either the Zambezian or the Cape ecoregions. Other species occurred in most ecoregions and these we considered to be widespread species (Fig. 4).

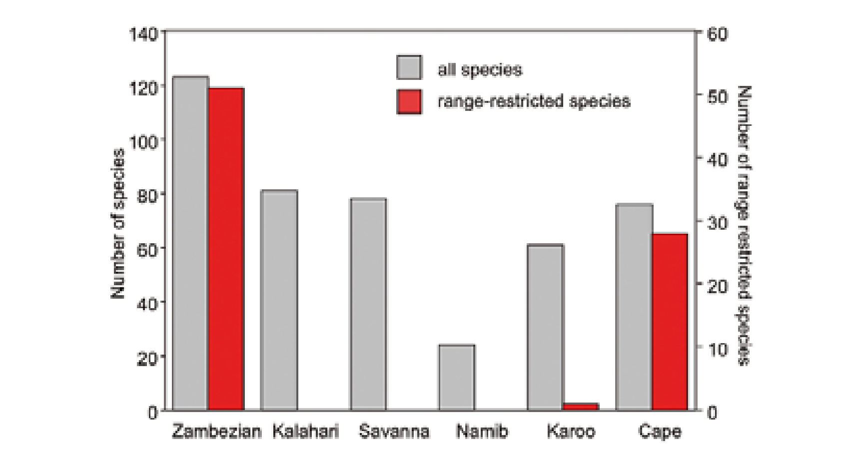

Fig. 3: Numbers of dragonfly species restricted to ecoregion complexes compared to total species numbers. Note that a high proportion of restricted species occur in the Zambezian and Cape complexes, whereas only one restricted species, the Gariep River endemic *Pseudagrion vaalense*, occurs in the other regions.

Which environmental variables govern the different patterns identified?

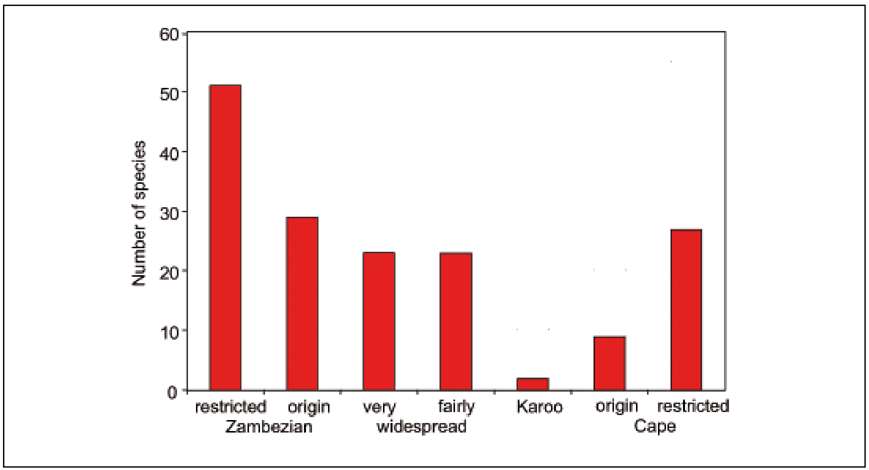

Fig. 4: Biogeographical classification of the dragonfly species occurring in the study area. The number of restricted species matches those in the ecoregion complexes depicted in Fig. 3. Those of Zambezian and Cape origin are mainly recorded in either of these regions but also occur in the drier ecoregions. Thus, their origin has been assumed from a distribution gradient. They broadly match species of category 4 and most of category 6 of Suhling et al. (2009). The widespread species occur in most or all ecoregions, and the fairly widespread species at least in each of the larger ecoregion complexes, although they are less common (categories 1–3 and 5). The two species classed under ‘Karoo’ are one range restricted species and *Pseudagrion salisburyense*, of which most records are from the Karoo ecoregions.

The diversity of dragonflies in the region is influenced by two major determinants. Firstly, two biogeographical realms converge in the region, which both contribute assemblages that differ in their radiation history. Although the Cape is not zoologically recognised as a realm on its own, relatively high numbers of endemic dragonflies occur (Grant & Samways 2007), i.e. 16.5% of the species in the region. This includes, for example, most species of the family Synlestidae, the genus *Syncordulia* among the Corduliidae, and others (Samways 2009). For instance, *Syncordulia* is likely to have diverged in the region 60 million years ago (Ware et al. 2009). Moreover, some other species, which are more widespread in the region, such as *Aeshna minuscula*, are likely to have originated from the Cape (Fig. 4; cf. Suhling et al. 2009). However, the majority of species are of Afrotropical origin of which a high number are restricted to the Zambezian ecoregions.

Secondly, the diversity of dragonflies, being dependent on freshwater habitats, corresponds broadly with humidity gradients, as suggested by Brinck (1955).

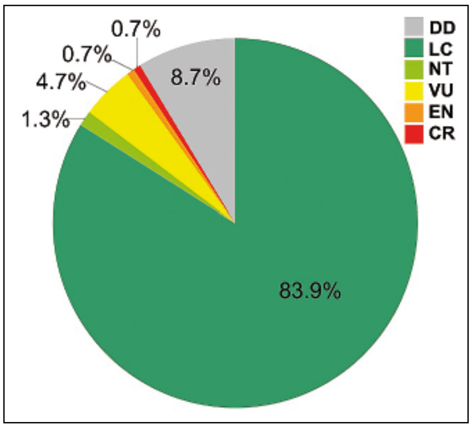

Fig. 5: The proportions of dragonfly species in each Red List category (CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern, DD = Data Deficient) in the study area according to the regional southern African IUCN Red List (cf. Suhling et al. 2009).

Highest diversities occur in the humid northeast of the region, particularly along the large perennial rivers, such as the Okavango, Kwando and Zambezi. Other centres of diversity are in the Cape winter rainfall area and along the Kunene River. The lower species diversity in the arid regions can broadly be explained by the increasing sparseness of freshwater habitats with increasing aridity. However, species numbers in the arid regions are still surprisingly high. Suhling et al. (2009b) tried to explain why so many species occur in the Namibian deserts. They identified six categories of species occurring in the arid landscape:

1. widespread desert-biased Namibian species regularly breeding in the desert;
2. widespread non-desert-biased Namibian species regularly breeding in the desert;
3. widespread species that have been observed entering the desert seasonally;
4. species, which immigrate from neighbouring regions and sometimes breed in the desert locally;
5. species with highly localised breeding populations in the desert (usually at streams), which are widely isolated from potential source populations;
6. species restricted to one of the allochthonous perennial rivers, with no breeding populations away from the river.

Many species of dragonfly are highly mobile and distances of several hundred kilometers can be covered within a few days (cf. Corbet 1999). This applies, in particular, to species belonging to categories 1–4 and especially to members of the family Libellulidae, which make up almost 60% of the species in the desert (Suhling et al. 2009b). These mobile species are able to enter the desert from different neighbouring regions rapidly, and may reproduce if the conditions allow. Such immigration occurs annually during seasonal long-distance mass-migration events at the beginning of the rainy season as with *Pantala flavescens* and some other dragonflies known as obligate migrants (cf. Anderson 2009, see also Article III.2.7). Other species may expand their ranges into the desert during wetter years and contract their ranges again in dry years. In addition, species that have relict populations dating back to wetter periods (category 5) contribute to the diversity. These species have developed mechanisms to avoid intraguild predation by the immigrants (see Article III.2.7). Finally, a few species may have evolved under arid conditions. The late Miocene ancestors of the genus *Trithemis* may have bred in temporary pools (Damm et al. 2010) and *Trithemis kirbyi*, a typical dragonfly of the Namib Desert, may have evolved with ongoing aridification of the continent.

Besides the two major Odonata diversity ‘hot spots’ in the region (Zambesian and Cape regions), a few local ‘hot spots’, where relatively high species diversity was recorded in one subbasin, can be identified in the arid ecoregions (Fig. 2). Two of these local ‘hot spots’ are along the Kunene River, which hosts several species restricted to large perennial rivers, and which therefore enter the otherwise highly arid landscape along the river line. Three more similar local ‘hot spots’ are scattered over Namibia. One in the northeast is in the Otavi Mountains, which receives the highest rainfall in Namibia, and thus conforms with the general humidity-species richness gradient. Another is in central Namibia at the S. von Bach dam, a large impoundment supplying Windhoek with water, where 46 species of dragonfly have been recorded. Leaks in the dam have formed a swampy wetland colonised by several species, including some otherwise confined to swamps along large tropical rivers, such as *Acisoma panorpoides* and *Hemistigma albipunctum* (cf. Suhling et al. 2009b). The habitat is obviously suitable and still within reach for those species likely dispersing there from the Okavango River. The last ‘hot spot’ is in the Naukluft Mountains, where at least 32 species occur close to the Namib Desert. Here several small perennial streams originate, which host a set of stream species. In addition, not only has this area been colonised by species from the Cape such as *Aeshna minuscula* and *Trithemis stictica*, possibly during wetter periods, but also by widespread desert species and by those originating from the Zambezian ecoregions.

The conservation status of southwest African dragonflies

The conservation status of Odonata in the region is relatively good with only 6.1% of all species listed as either critically endangered, endangered, or vulnerable on the IUCN regional southern Africa Red List (Fig. 5), in comparison to approximately 10% of dragonflies globally (Clausnitzer et al. 2009). However, all of the threatened species are Cape endemics (cf. Samways 2004, 2006, Suhling et al. 2004) and, compared to the species numbers in the Cape ecoregions, the proportion of threatened species in this subregion is comparatively high (14.1%). The major threats to dragonfly diversity in southern Africa are deforestation, habitat destruction due to water extraction and damming of large rivers, and invasion of alien plants and fish, while pollution is currently only a local problem (Suhling et al. 2009a). In particular, invasive alien plants are a major cause of the red listed Cape endemics, which have been negatively affected as a result of shading of their stream habitats (Samways & Taylor 2004). In the more tropical parts of the region, however, deforestation causes habitat loss of forest-adapted species. For instance, along the Okavango River in Namibia, felling of riverine forests has likely caused local extinctions of species that spend most of their adult life in the shade, such as *Phaon iridipennis*. Habitat destruction due to water extraction is an important factor in the arid ecoregions where certain species are regionally threatened and locally extinct in Namibia (Suhling et al. 2006).

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Corrections brought to our attention will be published at the following location: http://www.biota-africa.org/biotabook/

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