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Focus on African freshwaters: hotspots of dragonfly diversity and conservation concern

Viola Clausnitzer^{1*}, Klaas-Douwe B Dijkstra², Robert Koch³, Jean-Pierre Boudot⁴, William RT Darwall⁵, Jens Kipping⁶, Boudjéma Samraoui^{7,8}, Michael J Samways⁹, John P Simaika⁹, and Frank Suhling³

This is the first continent-wide overview of insect diversity and status sufficiently fine-scaled to be used in conservation planning. We analyze patterns of richness and the conservation status of African dragonflies and damselflies (Insecta: Odonata), commonly referred to as dragonflies, to determine threats to species and freshwater habitats, location of diversity hotspots, necessary conservation actions, and research gaps. Major centers of dragonfly diversity in Africa are tropical forest areas that include highlands. Most threatened species – as classified by the International Union for Conservation of Nature global Red List – are concentrated in highlands from Kenya to South Africa (together with the Cape Floristic Region), western Africa (including mountains on the Cameroon–Nigeria border), and Ethiopia. Currently available knowledge can be applied throughout Africa's freshwater systems to help minimize or mitigate the impact of future development actions, allowing dragonflies to act as “guardians of the watershed”. The private sector can be advised to safeguard sensitive habitats and species when selecting sites for development. Key sites and species for monitoring can be identified by checking the distribution of threatened species at www.iucnredlist.org.

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Freshwater habitats represent one of the most imperiled ecosystems in the world (Dudgeon *et al.* 2006) and, despite occupying less than 1% of the Earth's surface, they contain 10% of all recorded species (Strayer and Dudgeon 2010). Protecting the world's freshwater resources is an urgent issue, and there is general agreement over the need to diagnose threats over a broad range of scales – from global to local and from social to biodiversity perspectives (Vörösmarty *et al.* 2010). However, the biodiversity component lacks even the most basic data on the most species-rich “group” – the invertebrates (see Cardoso *et al.* [2011] for an overview).

Here we provide the first continent-wide, fine-scale overview of African dragonfly diversity, as a blueprint for regional freshwater conservation. Inland waters are essential to the livelihoods of Africa's people (Figure 1a), while also supporting high levels of biodiversity and endemism

(Darwall *et al.* 2011). Management of water resources must take account of this wealth, while establishing sustainable development plans and monitoring schemes. However, with increasing development and population growth, water resources are under increasing pressure. Conservation actions are needed to ensure that ecosystem services are maintained and biodiversity is protected. Planning such actions – for example, establishing protected areas and conducting biological inventories (Gaston *et al.* 2008) – requires high-quality spatial data regarding patterns of biodiversity and threat. Unfortunately, prioritization has been largely directed at terrestrial habitats, focusing on vertebrates as target species (eg Rodrigues *et al.* 2004). Nonetheless, patterns of richness and threat for freshwater species differ from those of terrestrial animals, and surrogacy values (the use of terrestrial vertebrates as surrogates for the overall freshwater diversity in a given area) are usually low between taxa from different realms (Rodrigues and Brooks 2007). Moreover, it is not known whether global biodiversity hotspots (Mittermeier *et al.* 2004) apply to invertebrates, which make up over 95% of the Earth's known animal species' diversity (Gaston and Hudson 1994). Consequently, Conservation International's website of biodiversity hotspots (www.biodiversityhotspots.org) does not consider endemic insect species when describing hotspots.

Dragonflies (eg Figure 1, b and c) are excellent model organisms and flagship species in freshwater conservation because they are (1) a key component of species assemblages in freshwater ecosystems; (2) sensitive to changes in both aquatic and terrestrial environments (Figure 1a), because their larval phase is completed in water, while adults are mobile predators in the air and on land; (3) abundant on all continents except Antarctica, with tropical

¹Senckenberg Museum of Natural History, Görlitz, Germany (*viola.clausnitzer@senckenberg.de); ²Netherlands Centre for Biodiversity Naturalis, Leiden, The Netherlands; ³Institut für Geoökologie, TU Braunschweig, Braunschweig, Germany; ⁴LIMOS – UMR 7137 CNRS-Universités de Nancy, Faculté des Sciences, Vandoeuvre-lès-Nancy Cedex, France; ⁵Species Programme, International Union for Conservation of Nature, Cambridge, UK; ⁶Naturkundemuseum Mauritium Altenburg, Altenburg, Germany; ⁷Laboratoire de Recherche et de Conservation des Zones Humides, University of Guelma, Guelma, Algeria; ⁸Center of Excellence for Research in Biodiversity, King Saud University, Riyadh, Saudi Arabia; ⁹Department of Conservation Ecology and Entomology, Stellenbosch University, Matieland, South Africa



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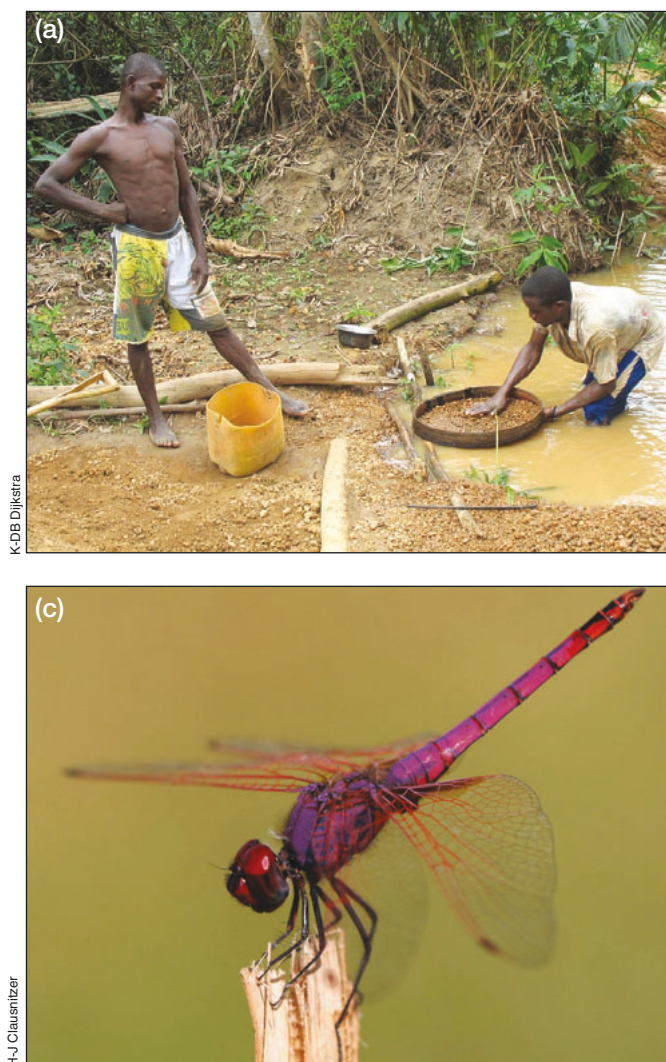


Figure 1. (a) Open pits, such as those created by diamond miners in Gola Forest, Sierra Leone, destroy the habitats of rainforest specialists like (b) the seepage pricklyleg (*Porpax bipunctus*, shown here in Liberia), which favors soaked leaf litter on the forest floor, and are colonized by species that are common throughout Africa, such as (c) the violet dropwing (*Trithemis annulata*), shown here in western Uganda.

forests being especially species-rich; and (4) taxonomically well-studied globally, in comparison to other invertebrate groups (Kalkman *et al.* 2008; Clausnitzer *et al.* 2009).

Methods

A database of point locality records was created, based on literature, collections, and field notes. Material was checked by experts, often resulting in revisions and taxonomic changes (Dijkstra *et al.* [2011] and references therein). The Odonata Database of Africa (ODA) is the first continent-wide, expert-reviewed database of freshwater insects. The database is updated continually and now contains over 80 000 records, representing 710 species from over 9000 localities (Figure 2a).

The distribution of each of 702 species (eight of the 710 species are not formally described or are of uncertain taxonomic status) was mapped to individual river/lake sub-basins, as delineated by the Hydro1K Elevation Derivative Database (US Geological Survey's Earth Resources Observation and Science). On the basis of known points of occurrence, expert knowledge of habitat requirements, and general biogeographic patterns, we

inferred the presence or absence of each species in each sub-basin of an edited version of the Hydro1K layer in ArcGIS (ESRI, Redlands, CA).

The risk of extinction for each species was assessed according to the International Union for Conservation of Nature (IUCN) Red List Categories and Criteria Version 3.1 (IUCN 2001). A species assessed as Critically Endangered (CR) is considered to be facing an extremely high risk of extinction in the wild, whereas a species assessed as Endangered (EN) or Vulnerable (VU) is considered at very high or at high risk of extinction in the wild, respectively. Diversity patterns of the different threat categories were estimated by overlaying the appropriate distributions. Preferred aquatic/larval habitat (standing versus flowing) and terrestrial/adult habitat (ie landscape) were recorded, based principally on field results. Data on habitat type were collated for each species on a coarse scale (forest, half-open, open), and numbers of species per habitat type were analyzed. All species assessments and species maps are available online (www.iucnredlist.org), and spatial data can be downloaded from the IUCN Red List website following www.iucnredlist.org/initiatives/freshwater/description/data-download, under the section "Dragonflies".

Results

The area of highest diversity – with over 100 species in each sub-basin, extending from Guinea and Angola on the Atlantic Ocean to Kenya and KwaZulu-Natal on the Indian

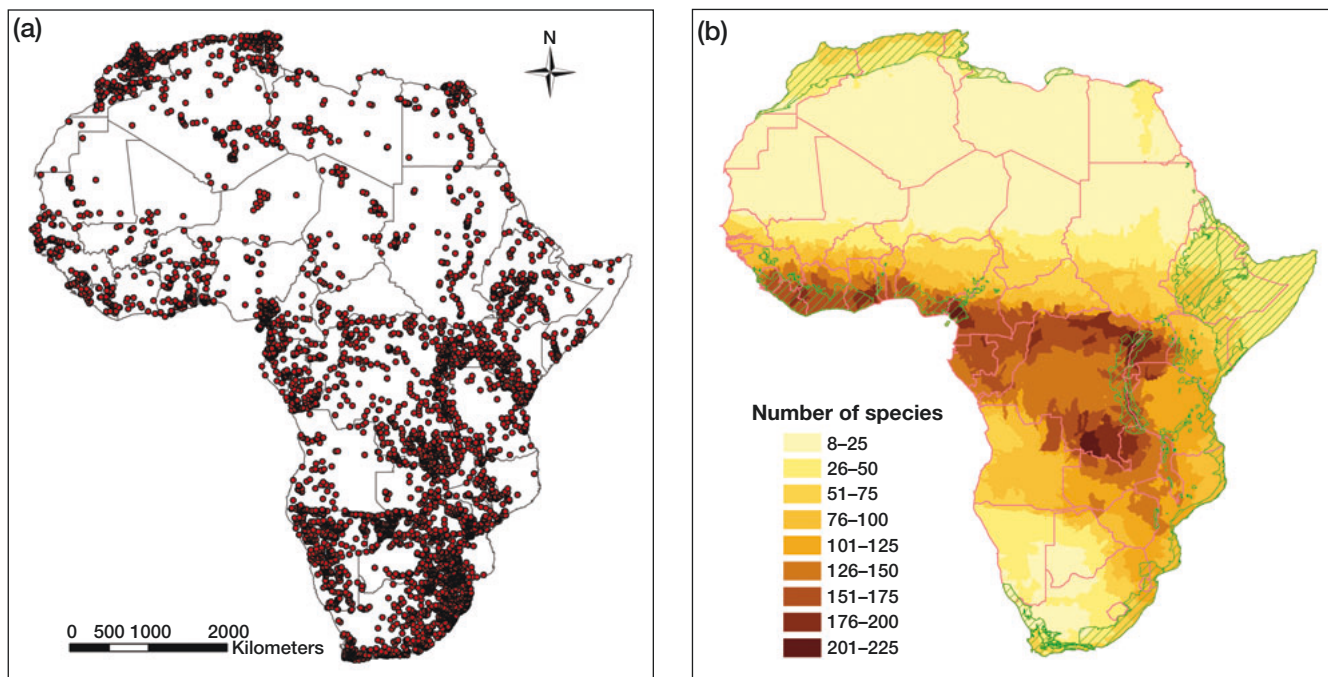


Figure 2. Species richness and sampling intensity of African dragonflies. (a) Distribution of locality data points throughout continental Africa. (b) Distribution of dragonfly (Odonata) diversity in continental Africa, mapped as the number of species per Hydro1K basin. Green hatching represents the global biodiversity hotspots according to Mittermeier *et al.* (2004).

Ocean – is flanked by two vast impoverished areas (containing fewer than 25 species locally) to the north (Sahara) and south (Namib-Kalahari), with rather abrupt diversity gradients in between (Figure 2b). In four core areas, local diversity reaches over 175 species: (1) in the west, from Sierra Leone to Togo; (2) centrally, from Nigeria to Congo; (3) northeast, including Uganda and northeastern Democratic Republic of Congo (DRC); and (4) southeast, including the Katanga Province of DRC and northwest Zambia.

Although the majority of all African continental dragonflies (74%) are classified by the IUCN as of Least Concern (LC), about 9% (65 species) were assessed as “threatened” – ie CR, EN, or VU – and almost 4% (25 species) as Near Threatened (NT; Table 1). The main concentrations of threatened and NT species are: (1) 17 species in the mountains and along the coast stretching from Kenya to northeastern South Africa; (2) 14 species in South Africa, especially the Cape Floristic Region; (3) 11 species in and around the mountains on the Cameroon–Nigeria border; (4) 11 species scattered from western Nigeria to Guinea, concentrated in the far west; and (5) 9 species in the Ethiopian highlands (Figure 3a). More than 12% (88 species) were categorized as Data Deficient (DD), meaning that insufficient information is available to assess them against the Red List criteria; most of these species are found in western and central Africa (Figure 3b). The breakdown of Red List threat categories is presented for all species, for continental endemics, and by major habitat types (Table 1). The highest total species diversity, as well as the greatest proportion of threatened, NT, and DD species, is found in forested streams and rivers.

Discussion

Patterns of diversity

In general, high dragonfly diversity coincides with the (formerly) continuously forested lowlands of western and central Africa, but richness spikes where important highland areas occur within this forest matrix (Figure 2b). The western and central core areas overlap with the global biodiversity hotspot “Guinean Forests of West Africa” (Upper and Lower Guinea), the northeastern area overlaps with “Eastern Afrotropical” (most notably the Albertine Rift), but the southeastern area (ie Katanga Province in Congo and northern Zambia) is not reflected in the hotspots designated by Mittermeier *et al.* (2004). This hotspot is often overlooked (Brooks *et al.* 2001), despite being the third-richest area of plant endemism and diversity in Africa (Linder 2001) and the most prominent center of overlooked bird diversity (Fjeldså 2003). The Congo Basin, another possible center of diversity and endemism, appears comparatively poor with around 125 dragonfly species locally, but includes some of the least-surveyed parts of Africa.

Higher habitat heterogeneity (a combination of rainforest and highlands) may explain not only areas of higher dragonfly diversity but also differences in diversity gradients. In the north, diversity rises steeply where deserts end (more than 25 species) and again where forests begin (more than 100 species), with a rather uniform and equally diverse fauna in the savanna and woodlands in between. However, rivers, swamps, and gallery forest (corridors of evergreen forest along rivers or wet-

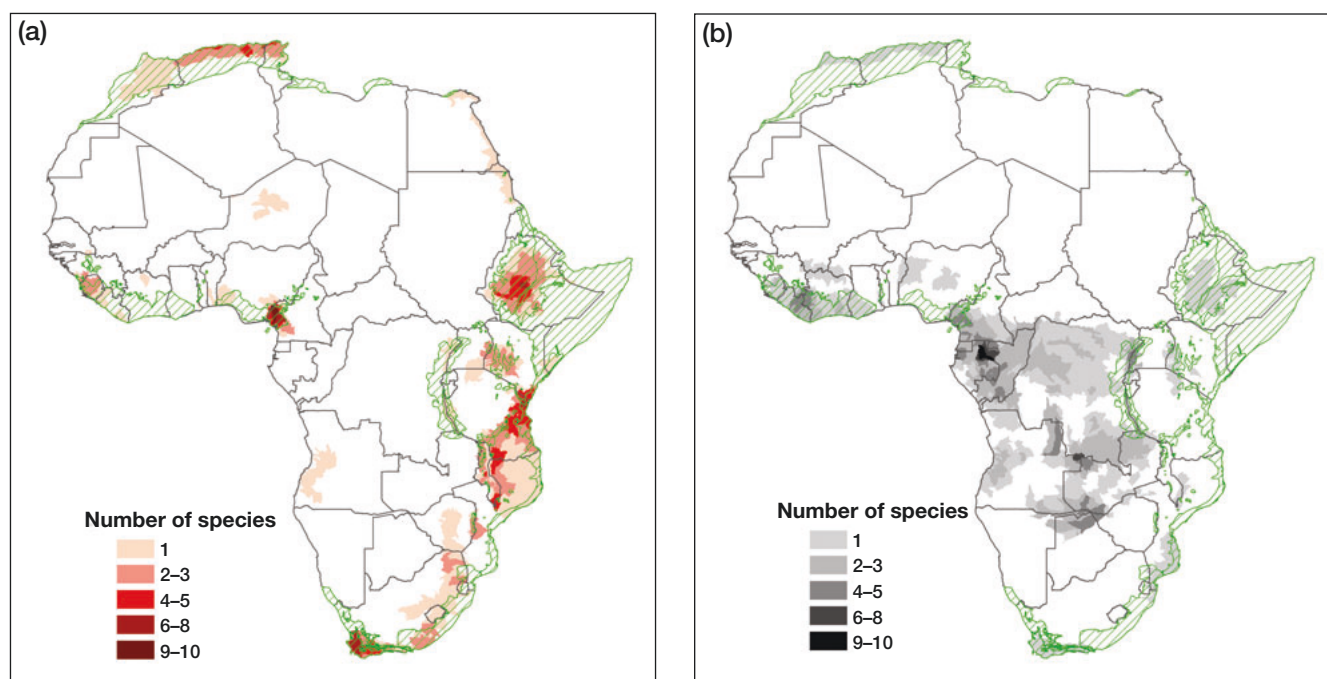


Figure 3. Distribution of (a) threatened species, mapped as the number of species listed in one of the threat categories VU, EN, and CR, and (b) DD species of dragonflies per basin in continental Africa. Green hatching represents the global biodiversity hotspots according to Mittermeier *et al.* (2004).

lands in sparsely treed landscapes) extend far from the wet center in the south – eg in the Okavango Delta. Even the Kalahari and Namib deserts, though species poor, profit from an irregular influx of more tropical species occurring along the rivers (Suhling *et al.* 2009). Furthermore, the eastern highlands provide a diversity (and perhaps stability) of habitats, allowing many species to extend their ranges well to the east and south.

Patterns of threat and data deficiency

Concentrations of threatened species show little overlap with centers of high species diversity (Figure 3a), except in the mountains on the Cameroon–Nigeria border. All 90 African species that are globally threatened or NT have a

restricted range, most being associated with the scarce and scattered high-elevation habitats. Species confined to running waters are much more likely to be threatened than those that prefer standing waters, especially if their habitat is forested (Table 1), the main reason being that species connected with running waters have smaller average ranges than those linked to standing waters. Moreover, many forest stream species are niche-conservative, adjusting poorly to changing ecological conditions, and are therefore sensitive to the rapid impacts of anthropogenic activity (Wiens and Graham 2005). Stagnant habitats are more often temporary, and associated species therefore depend more on dispersal for survival; consequently, they have larger ranges and are more tolerant of ecological change (see Dijkstra *et al.* 2011). This is demonstrated by the presence of adaptable species in the climatologically unstable areas of southern Africa (Samways and Niba 2010).

The distribution of DD species (Figure 3b) highlights some well-studied sites within (or at the edge of) presumably rich (Figure 3a) but generally poorly researched regions, such as Mount Nimba, northeastern Gabon, and northwestern Zambia. Many of the species are DD because they have not been reported since they were described from these localities. Thus, rather than identifying the most data-deficient regions, mapping DD species emphasizes foci of isolated taxonomic activity. Those places that genuinely lack information, and must therefore be prioritized for surveys, are those where potentially threatened species remain undiscovered. Identifying these is speculative, but known areas of endemism with limited associated data are logical targets (eg the Angolan highlands).

Table 1. Threat levels (expressed as percentages) for African dragonflies (Odonata), according to habitat types and continental endemism

	LC	NT	VU	EN	CR	DD	Total
All species	74.6	3.6	5.1	2.0	2.1	12.6	702
Africa endemic	72.0	3.4	5.6	2.0	2.5	14.5	592
Standing (lentic)	87.2	2.0	2.3	0.4	0.8	7.4	257
Flowing (lotic)	68.3	4.5	6.5	2.8	2.8	15.1	464
Open	86.1	3.0	5.0	1.5	1.0	3.5	201
Half-open	82.0	1.8	5.2	0.9	0.9	9.5	232
Forest	69.0	4.1	4.6	2.5	3.1	16.8	393

Notes: Habitat types were standing (lentic) versus flowing (lotic) and forest versus open or half-open, with multiple assignments possible. LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered; DD, Data Deficient.

Major threats

Transformation of the natural landscape – through deforestation, urbanization, and agricultural encroachment, and the subsequent alteration of water bodies – is the greatest threat to dragonflies in Africa. Forested streams and rivers, in particular, have been severely affected by human activities over recent decades (Dudgeon 2010). Sub-montane forest species, the habitats of which are naturally fragmented and lie in fertile and thus densely populated areas, are the most sensitive. Examples include *Amanipodagrion gilliesi* (CR) in Tanzania's East Usambara Mountains, and all Ethiopian endemics. Because of their comparatively dry and fire-prone surroundings, riparian forests are subject to disproportionately high human pressure for logging and agriculture, but such shaded refuges along rivers are important for many savanna and woodland dragonflies (see Dijkstra *et al.* 2011). Wetlands are also economically vital but poorly protected, and are therefore vulnerable to clearance and overuse, which might endanger a papyrus-endemic like *Agriocnemis palaeforma* (NT) in Uganda.

Specific threats to habitats include damming and mining. Mineral resources in Africa are often extracted by open-pit mining (Figure 1a). This is especially problematic in highlands composed largely of valuable deposits. In Malawi, for instance, the entire habitat of the endemic *Oreocnemis phoenix* (CR) could literally be removed if Mount Mulanje's bauxite plateaus are exploited. Dams can flood critical river habitat, such as rapids and gallery forests; for example, *Paragomphus cataractae* (NT) is confined to the rapids along large rivers. Dams also impact downstream flow regimes and sedimentation patterns. Damming in the Upper Gambia catchment may flood the habitat of *Elatoneura pluotae* (CR) upstream and create erratic water-level fluctuations downstream for *Mesocnemis dupuyi* (NT). Damming is not always harmful: the endemic *Africallagma sapphirinum* and *Proischnura rotundipennis* benefited from the construction of small dams in South Africa, as did the endemic *Enallagma deserti* in the Maghreb (see Dijkstra *et al.* 2011). Similarly, small-scale mining in rainforests can create valuable habitat when the canopy is left intact. The VU Upper Guinean populations of *Porpax bipunctus* (Figure 1b) require leaf litter on the forest floor soaked by seepage or streams, but without open water. This habitat is sensitive to desiccation, but may be created when deeply shaded mining pits become filled with fallen leaves. Exposed pits (Figure 1a), on the other hand, are colonized by highly mobile and ubiquitous species (Figure 1c).

Because fish are important predators of dragonfly larvae, the introduction of regionally alien species, particularly Nile perch (*Lates niloticus*) or brown trout (*Salmo trutta*), may have severe effects. In South Africa, introducing trout to formerly fish-free headwaters (or those with indigenous specialized fish) can have an impact on some species. Similarly, invasive alien trees can be a key threat:

riparian Australian wattles (*Acacia* sp) may overgrow the natural vegetation along streams, radically altering natural habitats and affecting many widespread dragonfly species and all localized endemics. However, removal of these alien species in South Africa resulted in a rapid recovery of the endemics *Metacnemis angusta* (VU), *Proischnura polychromatica* (CR), *Syncordulia legator* (VU), and *Pseudagrion newtoni* (VU) (see Dijkstra *et al.* 2011).

Human populations in many parts of Africa are still small, while industry and chemical-intensive agriculture are underdeveloped. Chemical and organic pollution are therefore mainly a local problem at present. Such impacts will also increase as pesticides are used increasingly against human disease vectors. Little is known about pollutant effects on dragonflies, but deltamethrin, which is used in aerial spraying for control of tsetse flies (*Glossina* spp) in the Okavango Delta, increases both adult and larval mortality under semi-artificial conditions (Schuran, Kipping unpublished data). River salination resulting from intensive agriculture, as reported in South Africa, may have a strong effect because many dragonfly larvae are salt-intolerant (Suhling *et al.* 2006). Similarly, water abstraction for consumption, irrigation, and industry – transforming perennial sources and rivers to ephemeral ones – is still a regional problem but is likely to increase. The effects of irresponsible use of freshwater resources are most critical in dry environments, especially in the densely populated Maghreb, where the narrow-range endemics *Calopteryx exul* (EN), *Gomphus lucasii* (VU), and *Cordulegaster princeps* (NT) are threatened. These impacts have direct and indirect effects, by destroying habitats and altering well-established patterns of inter-specific competition, respectively (Suhling *et al.* 2006).

Conservation recommendations

On the basis of our results, we can now prioritize catchments as freshwater conservation units and recommend actions to conserve habitats and species under threat, which will also cover other freshwater organisms. In general, it is necessary to maintain the structural integrity of both larval and adult habitats (ie water bodies and their surrounding landscapes). Many of the measures that can be taken to avoid erosion, siltation, and unnatural flow regimes (both daily and seasonal) are straightforward. When damming streams or piping springs, sufficient spillover and regular discharge must be maintained to avoid floods and droughts. The impact of drought on freshwater systems is obvious, but irregular water fluctuations may also seriously impact aquatic life cycles (eg by affecting the microclimate of breeding habitats and disrupting adult emergence). The impact of dams can be reduced, at least downstream, if a natural water flow regime with normal seasonal fluctuations is maintained. Intentional release of alien fish should be avoided, and invasive alien trees should be removed from stream banks and flood plains.

In the case of large-scale, landscape-altering projects like open-cast mining and agricultural plantations, damage to the watershed can be minimized by leaving broad buffer zones of natural vegetation around water bodies (eg rivers, inundation zones, swamps), although forest removal should generally be avoided. Where usage perturbs water, such as in irrigation and mining, measures should be instituted that avoid siltation of streams and rivers from the outflow; the simplest of these is to minimize outflow by water recycling and the use of settling ponds. Large-scale ecological networks can buffer the effects of extreme climatic events (eg El Niño, possible climate change) for an already climatically versatile dragonfly assemblage (Samways and Niba 2010).

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