Impacts of extreme weather and climate change on South African dragonflies

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Abstract
The absence of ice sheets for many millions of years, yet variable topography and changing climate, has generated considerable biodiversity in South Africa. There is no evidence to date that anthropogenic climate change has affected odonate populations in the region. One reason is that the highly varying weather and climate constitutes considerable background noise against which any effects of modern climate change must be measured. Evidence is accumulating that the Holocene interglacial and gradual warming has left some species with isolated populations in montane areas among a matrix of arid land. Many South African odonate species are remarkably vagile and elevationally tolerant, readily immigrating into and emigrating from pools during wet and dry phases respectively. Some species take this movement to greater extremes by moving the southern margins of their geographical range back and forth with varying climate. After floods, populations of riverine odonates can recover within a year, although where the riparian corridor has been stripped of its trees, the recovery is very slow. Various synergistic impacts, particularly from invasive alien woody plants, are having a severe impact on many riverine species, and reducing their ability to respond positively to changing environmental conditions. Large-scale removal of these woody aliens is greatly benefiting the odonates’ ability to survive in the short-term and to restore natural corridors for movement in the face of possible future climatic changes.

Keywords
Climate change, extreme weather, dragonflies, South Africa
Introduction

The last 130,000 years has seen three major events in the earth’s climatic history. During the Eemian (130,000 – 110,000 years BP) the climate was a major driver of plant populations and their evolution. During the glacial period (110,000 – 10,000 years BP) there were alternating cold and temperate conditions with major shifts in insect assemblages at any one location (Elias 1994, Coope 1995, Ponel et al. 2003). In the current interglacial (10,000 years BP to Present) there has been a general warming of the earth’s climate (with minor cool periods) when human pressure on the landscape increased considerably, especially in localized areas (Fagan 2004).

This natural background warming has accelerated in recent years through the impacts of the industrial age. The important point here is that in very recent years, it has been a combination of global climate change and anthropogenic landscape fragmentation that has caused considerable stress on insect populations (Warren et al. 2001, Travis 2003).

While the southern hemisphere has been subject to the various climatic changes as in the north, it has not had a major glaciation event for over 200 million years. This lack of cold sterilization, combined with milder climatic variations, various orographic conditions and much soil variation, has been the background for considerable speciation and the evolution of many localized endemics (Fjeldsa and Lovett 1997a,b; Goldblatt 1997; Jürgens 1997). Additionally, the historical human impact on the landscape has only been intensive over wide areas in the last 200 years, but still leaving today many areas that are only minimally disturbed. These various factors have all played a major role in determining the local distribution of the biota. Yet there is another factor that is part of this backdrop when assessing any contemporary climate change on dragonflies in the region. This is the ‘El Niño Southern Oscillation’ (ENSO), which produces alternately droughts and floods, often devastatingly so. ENSO, in addition to the overall warming during the current interglacial, constitutes the background noise against which we must measure the localized effects of anthropogenic climate change.

What the botanists have to say

Rutherford et al. (1999) undertook an interesting study on the effect that current anthropogenic climate change may have on floristic composition in reserve areas in South Africa. A climate change scenario of increased temperature but no change in precipitation would result in an increased growing season in some areas and a decrease in others. In this latter group is a reserve in the Northern Cape (Augrabies Falls National Park) which could lose a third of its plant species. However, such extinctions depend on the tolerances of the focal species, and their departure may be partly balanced by immigrating species more tolerant of altered conditions. Within the Cape Floristic Region, most species of Proteaceae are likely to experience geographic range contractions and even a shift to higher elevations (Midgley et al. 2003). The evidence clearly points to
the necessity of maintaining landscape linkages to ensure propagule migration. The challenge however, is that 30% of the currently remaining natural vegetation could be transformed within the next 20 years, with increased agriculture, urbanization and invasion by alien woody plants (Rouget et al. 2003). Midgley et al. (2002) go on to point out that the biome-level approach appears to underestimate the risk of species diversity loss from the impacts of climate change because many narrow range endemics will experience range dislocation throughout the biome and not necessarily just in areas identified as biome contractions. Midgley et al. (2002) recommend that targeted vulnerable plant species be monitored both for early warning signs of enhanced climate change and as empirical tests of predictions. Williams et al. (2005) then add that the sensitive and vulnerable species may not necessarily be able to make use of linkages unless particular and suitable habitat conditions are available for stepping stone events. Indeed, many Proteaceae species will not even disperse across gaps of unsuitable habitat of only 100 m.

**Marginality and the South African odonate fauna**

South Africa has a proportionately high number of endemic and globally threatened odonate taxa compared with neighbouring areas (Samways 1992). These globally threatened taxa have small and restricted geographical ranges mostly in ecosystems sensitive to human impact. In contrast, most of the nationally threatened taxa are marginal, and the threats are largely natural, driven by ENSO events (Samways 2006a). This has an important bearing on practical national Red Listing, because the issue is intrinsically bound to marginal rarity and associated risks of natural local extinction. Such local extinctions of even common insects are not unusual (Dempster 1989). Typically, marginal populations are small, sparse and isolated from each other (Lawton 1993) with considerable variation between the populations in genotype and phenotype (Shreeve et al. 1996). Little evidence is available on how these odonate species respond to climatic variations in the core of their geographical range. However, evidence from East Africa (Clausnitzer 2005) and Seychelles (Samways 2003b) suggests that in general the forest species are restricted to that particular habitat, and only following forest corridors, while many of the open habitat species are more vagile and opportunistic.

Evidence for loss of marginal South African odonate populations is strong. Besides the well-known migrants such as *Anax ephippiger*, *Pantala flavescens*, *Symptemtrum fonscolombii* and *Tramea* spp. (the ‘sweepstake’ species), which readily colonize temporary pools, there are many species (the ‘stepping stone’ species) which rapidly locate and colonize newly-created artificial water bodies (Osborn and Samways 1996). Among this group of species is *Anax tristis*, with its remarkable flight ability. Most of the species in this last category are geographically widespread generalists, although not necessarily strong fliers (e.g. *Africallagma* spp. and *Agriocnemis* spp.), although *Agriocnemis falcifera* (Fig. 1) is a localized species and national endemic which readily colonizes artificial
water bodies so long as they have a constant water level and a wide and shallow margin with an abundance of grasses and sedges.

These ‘stepping stone’ species are highly elevationally tolerant and may move according to prevailing weather conditions (Samways 1989a; Niba and Samways 2006). Species such as *Diplacodes luminans* (Fig. 2), *Urothemis edwardsii* and *Rhyothemis semihyalina* occasionally colonize high-elevation pools when weather conditions are suitably warm. These ‘stepping stone’ species are highly vagile and habitat-tolerant, responding to ENSO events with remarkable speed. Even the localized *Orthetrum robustum* (Fig. 3) behaves in this way. In wet years, it is common in temporary pools in iSimangaliso Wetland Park, retreating to permanent lakes such as Lake Bhangazi North, during dry years.

Most of these ‘stepping stone’ species are inhabitants of still water, which includes pools (‘kuile’) left behind in dropping rivers as the dry season advances. In the Western Cape, species in this category include the very rare and threatened *Metacnemis angusta* (Fig. 4) and *Proischnura polychromatica*, which despite their extremely limited geographical distribution, are highly responsive and rapidly locate their preferred habitat (Samways et al. 2005). Furthermore, the riverine ‘stepping stone’ species recover within one year after an extreme flood event (Samways 1989b).

There is a further category, the ‘range shifting’ species, which change the southern limits of their geographical range margins in accordance with ENSO events. During the extreme floods in February 2000, two taxa *Pseudagrion coeleste coeleste* and *P. sjoestedti* became nationally extinct, as their habitat was changed from tree-lined river channels to early succession vegetation in the south-eastern corner of the
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Figure 2. *Diplacodes luminans*, a ‘stepping stone’ species which moves to new pools up elevational gradients during warm years.

Figure 3. *Orthetrum robustum* populations expand to new pools in wet years, retreating to permanent ones in dry years.

Kruger National Park. While *P. coeleste* has recovered by colonizing another location, *P. sjostedti* has not yet reappeared. These were not the only species that were affected. Others, such as *Lestinogomphus angustus* (Fig. 5) and *Pseudagrion sudanicum*, suffered severe population crashes but nevertheless survived on a reduced source population.
Figure 4. *Metacnemis angusta* is an extremely rare species which readily colonizes suitable habitat when, for example, it is restored by removing invasive alien woody plants.

In contrast, some others benefited from these weather-induced habitat changes. The locally rare *Trithemis werneri*, which prefers savanna rivers with wide riparian zones, responded by becoming abundant the following year. Similarly, *Crocothemis erythraea* readily colonizes quiet river zones where the natural tree canopy has been thinned or largely removed.

Figure 5. *Lestinogomphus angustus* populations dropped substantially during the huge floods of February 2000.
The most extreme geographical range shift was by *Aciagrion dondoense* (Fig. 6), which prior to the floods of 2000, was not known in South Africa. By 2001, it was present in large numbers breeding in the iSimangaliso Wetland Park. It appears that the extensive flooding in southern Mozambique pushed it southwards where it then established, possibly with the benefit of warm conditions in recent years. This was not an isolated case, with other species, such as *Lestes dissimulans* and *L. uncifer* apparently also moving south. Both these species appear to oscillate their southern range margins, as indicated by records over the last few decades. In 1956, *L. uncifer* was even recorded as far south as Durban (Pinhey 1984).

Evidence (from the ongoing South African dragonfly database) is accumulating that these huge shifts in southern range margins may be a relatively common phenomenon in species with a wide African distribution. This cautions mapping exercises, and emphasizes that a distribution map for many of these species can be spurious depending on the timing of the original data records in the ENSO cycle.

**The case for narrow-range endemics**

All except two (*P. coeleste umsingaziense* and *Agriocnemis ruberrima ruberrima*) of the 14 globally Red Listed South African odonate taxa inhabit running water or pools in river systems. The two species which inhabit still water are subject to both anthropogenic pressure, such as overgrazing and loss of habitat to urbanization, and extreme natural events such as drought. This combination of anthropogenic impact and
adverse natural conditions appears to be particularly synergistic, causing permanent local extinction at many sites, without recolonization, as seen in *O. robustum*. There seems to be another twist in the case of *A. ruberrima*, which went rapidly extinct when *Aciagrion dondoense* invaded its stronghold, Mfábeni Swamp in the iSimangaliso Wetland Park. It appears that *A. dondoense* became an intense competitor and possibly predator, as it became very abundant in the same swamp microhabitats as *A. ruberrima* when it disappeared.

Impacts on all the remaining globally Red Listed South African odonates are distinctly anthropogenic, although of course, adverse weather cannot be ruled out as a future synergistic threat. The major impact for most of these taxa is from invasive alien trees (IATs) which shade out the microhabitats and stress the local populations (Samways and Taylor 2004; Samways 2006b). The reverse also occurs. When the IATs are removed there is remarkable recovery of populations, and for three species possibly even extinction reprieve (Samways et al. 2005; Samways and Sharratt 2010). The recovery effect is largely through re-establishment of suitable sunny habitats, although in some cases there is also recovery of populations through improvement in the water table when the IATs are removed.

Evidence points to many of the endemic species having climatic relictual distributions. Certain outlier populations show this very distinctly. There is an isolated population of *Chlorolestes tessellatus* in Sevenweekspoort, apparently at least a hundred kilometers from the nearest population, with arid and unsuitable habitat in between. It is a similar situation for *Chlorolestes fasciatus* (Fig. 7) which is represented by an isolated population in the mountains of the Mountain Zebra National Park, surrounded by a particularly arid and unsuitable matrix.

**Synthesis of findings to date**

Although there has been a claim that recent human-induced climate change has induced range shifts in certain herbivorous insect species in South Africa (Giliomee 1997), the range expansions can be more parsimoniously explained by a switch in host plant (Geertsema 2000). Nevertheless, there is the potential for major geographical range shifts, and even local extinctions of insects with climate elevation of only 2°C (Erasmus et al. 2002). However, empirical evidence from insects suggests that simple climate envelope models overlook the nuances of biology of a species, making future predictions of geographical range change extremely tenuous (Samways et al. 1999).

Evidence from dragonflies in the region clearly suggests that they have already been through substantial climatic bottlenecks, with vicariance being common among many of the narrow endemics, and great elevational tolerance and vagility being a feature of the more widespread species. This situation parallels that in plants, where certain species are at risk of extinction from lack of responsive mobility to climatic change (Williams et al. 2005), which could also be the case with dragonflies (Samways 2008). However, there are two mitigating factors. Firstly, evidence from highly threatened species’ responsiveness to invasive alien plant removal shows that they are remarkably
resilient, rapidly colonizing and populating re-instated habitats where the invasives have been removed. Secondly, many of the narrow-range endemic species still have the opportunity to shift elevation and move up the streams. This assumes of course that the streams still would have sufficient flow at the higher elevations. This is indeed a problem in Mayotte (Samways 2003a), while in the Seychelles, the high elevation endemic species are to some extent tolerant of droughting conditions and minimal flow in the upland streams (Samways 2003b). Behavioural flexibility to elevation is thus already built into the genotype of many dragonfly species in this ENSO-prone region.

Probably the greatest threat to South African dragonflies in the current changing climate scenario is from the synergistic effects of anthropogenic disturbance, particularly from alien plants. This sort of synergism between climate change and habitat disturbance has been described by Travis (2003) as “a deadly anthropogenic cocktail”. For South African dragonflies, like British butterflies (Warren et al. 2001), this may well be the case, with the mountains possibly being their saviour, as has been the case during the Quaternary of Europe (Hewitt 2003). Clearing of the invasive alien woody plants not only improves the maintenance of biodiversity on site but also opens up riparian pathways along the elevational gradient. This has long-term evolutionary value as well as short-term ecological benefit. Bearing this in mind, there does appear to be something concrete that we can do to lessen the blow of further climate change. The first results on South African Odonata species suggest that rehabilitating riparian corridors might well benefit a whole range of aquatic species (Smith et al. 2007; Samways and Sharratt 2010; Magoba and Samways in press).
References


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