

Impacts of Climate Change on Freshwater Macroinvertebrates and Conservation Prioritisation

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This thesis represents a major part of the prescribed program of study.

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SUMMARY

My thesis focuses on issues of monitoring and conserving aquatic macroinvertebrate biodiversity under climate change within Australia. Initially the research examines how existing bio-monitoring datasets from New South Wales could be analysed to draw conclusions about broad-scale trends in diversity and how these trends may affect vulnerability of assemblages in the future. The focus is then directed towards dragonflies and whether they have potential as biological indicators of climate change and surrogacy among macroinvertebrate families. The results show climatically sensitive habitats can be identified from biological trends using relatively coarse biomonitoring data, that turnover of dragonflies is highly sensitive to climatic factors, but that they also relatively poor surrogates for other macroinvertebrates. The distribution of suitable habitat for most dragonflies in Australia was then modelled under current and future climate conditions. The likely vulnerability of each species was assessed according to criteria of exposure, sensitivity and the importance of dispersal capacity. The distribution of dragonfly diversity was then analysed for Australia as a whole, including evolutionary as well as species diversity. A large number of species were found to be potentially vulnerable to the effects of climate change and the associated shifts in distribution could significantly modify the patterns of diversity in Australia. Finally, the modelled distribution of dragonflies was used to test the performance of proactive approaches to systematic conservation in eastern Australian rivers, and the effect of emphasising connectivity in reserve selection. Anticipating the effects of climate change can offer significant gains in efficiency, and connectivity that allows movement across catchment boundaries improves representation of dragonflies within reserve systems under climate change. Overall, the predicted impacts of climate change are likely to be conservative estimates and emphasise the urgent need for action to improve adaptation to climate change in freshwater ecosystems.

STATEMENT OF CANDIDATE

I certify that the work in this thesis entitled 'Impacts of Climate Change on Freshwater Macroinvertebrates and Conservation Prioritisation' has not previously been submitted for a degree, nor has it been submitted as part of the requirements for a degree, to any other university or institution other than Macquarie University. This thesis is an original piece of work, and any help and assistance that I have received in my research, and in the preparation of the thesis itself, have been appropriately acknowledged. I estimate my contribution to each thesis chapter has been:

- Chapter 1 - Writing (95%)
- Chapter 2 - Study design (70%), Data collection (50%), Data analysis (90%), Writing (90%)
- Chapter 3 - Study design (100%), Data collection (50%), Data analysis (90%), Writing (90%)
- Chapter 4 - Study design (90%), Data collection (100%), Modelling (75%), Data analysis (90%), Writing (95%)
- Chapter 5 - Study design (50%), Data collection (100%), Data analysis (90%), Writing (95%)
- Chapter 6 - Study design (80%), Data collection (100%), Data analysis (80%), Writing (95%)
- Chapter 7 - Writing (95%)

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CHAPTER 1

INTRODUCTION

Status of freshwater biodiversity

Rivers, lakes and wetlands are some of the most species rich environments on the planet (Balian et al., 2007). Over 126,000 species occur in freshwater systems, almost 10% of all described species. The enormous value and high species richness of freshwater habitats is disproportionate to their area as they only cover about 0.01% of the Earth's surface (Carpenter et al., 1992). A broad variety of goods and services are provided by freshwater biodiversity for human society which are often irreplaceable (Covich et al., 2004). They have a direct productive economic value (e.g. fisheries); they act as 'insurance' for unexpected events; have value as a store of genetic information; and support ecosystem service provision (e.g. cleaning water) (Brauman et al., 2007). This has been underappreciated and it is hoped that improving understanding of biodiversity's importance for terrestrial ecosystem functioning will lead to a re-evaluation of the importance of freshwater biodiversity (Holland et al., 2011).

Freshwater systems face unprecedented and growing threats from human activities, and although the nature of threats was identified long ago, there has been little success in mitigating or alleviating them (Dudgeon et al., 2006). Over half of available run-off is being diverted for human use, almost as much again is stored in reservoirs and withdrawal is predicted to increase significantly as global population rises (Jackson et al., 2001). Physical alteration, habitat loss, water withdrawal, pollution (including thermal pollution, heavy metals, acidification and eutrophication), sedimentation, overexploitation and the introduction of non-native species, have all contributed to the decline in freshwater species (Ormerod et al., 2010; Vörösmarty et al., 2010). As a result, extinction risk among freshwater species is significantly higher than in terrestrial or marine ecosystems (WWF, 2012; Collen et al., 2013). By the end of the century, the rate of extinction for freshwater fauna is projected to be five times greater than in terrestrial systems, and comparable to the rate of loss observed in tropical rainforest (Ricciardi & Rasmussen, 1999; Revenga et al., 2005). As in other natural

systems, the observed extinction rate is likely to be a significant underestimate because knowledge about the status and trends of freshwater species is still very poor, with many species likely to go extinct before they are even taxonomically classified (Balian et al., 2007; Heino et al., 2009; Cardoso et al., 2011). The Living Planet Index has shown a continual decline of global biodiversity health of around 30% since 1970, but is greatest for freshwater at 37%, and increases to 70% for tropical freshwaters compared to 60% across all tropical systems (WWF 2012).

Freshwater systems are highly sensitive to changes in climate (Carpenter et al., 1992; Meyer et al., 1999; Dudgeon et al., 2006), and climate change is also likely to exacerbate many of the negative impacts of other anthropogenic stressors (Wrona et al., 2006). Although there is some evidence that decades of investment to improve environmental health and water quality in Europe have partially offset changes due to climate (Durance & Ormerod, 2009), such action is rare in other regions and will need to be continued to reduce the stress on freshwater ecosystems from climate change (Palmer et al., 2008; Palmer et al., 2009)).

Climate Change

Greenhouse gas emissions continue to rise and the global climate is rapidly changing in response (Le Quéré et al., 2013; Peters et al., 2013). The global hydrological cycle is accelerating and the frequency of heavy precipitation events (or proportion of total rainfall from heavy falls) will increase over most areas during the 21st century, with an increased risk of rain-generated floods (Durack et al., 2012). Changes to air temperatures, rainfall and the intensity of extreme events (tropical cyclones and storms) means droughts and floods are likely to be increasingly common in the future (IPCC, 2012). Droughts are expected to increase in severity and frequency in some regions, and by the 2090s the current proportion of

the globe in extreme drought at any given time is predicted to have increased ten-fold (Bates et al., 2008; Kundzewicz et al., 2008; Mishra & Singh, 2011).

The temperature trend for Australia mirrors the global one and annual average daily mean temperatures have increased in Australia by 0.9 °C since 1910, with most warming occurring since 1970. Higher temperatures are also resulting in more temperature extremes that match model expectations (Alexander & Arblaster, 2009; Perkins et al., 2012). The frequency of hot days and warm nights has increased, and the frequency of cold weather and cold nights has decreased across Australia (Hennessy et al., 2008; Donat & Alexander, 2012). The difference between observed warming in Australia and climate model simulations shows that the changes are very unlikely to have occurred as a result of natural variations alone and are the result of human greenhouse gas emissions (Karoly & Braganza, 2005; Lewis & Karoly, 2013).

Just as temperatures have been rising rapidly since the 1970's, there is now more evidence of trends in Australian rainfall and runoff (BoM, 2013). In particular, south-western Western Australia, the far southeast, and Tasmania, have become drier, with more moderate drying along the east coast and centre of the continent. The effect of droughts on river ecosystems is exaggerated by human interventions that reduce flows and extend low flow periods (e.g. Bond et al., 2008). Pressure on water resources and issues ensuring water security are likely to increase across most of southern and eastern Australia (Chiew et al., 2003; Jones & Durack, 2005; Chiew et al., 2010; Crosbie et al., 2010). Extreme low and high flows in particular are likely to lead to changes in the management of flow regimes and associated infrastructure that could both benefit or hinder species adaptation (Palmer et al., 2008; Pittock & Hartmann, 2011). Higher water temperatures and hydrological extremes may also lead to a number of secondary changes that affect water quality, including sedimentation, nutrient loading,

dissolved organic carbon, pathogens, pesticides and salinization, with negative impacts on ecosystems, human health, water system reliability and operating costs (Nielsen et al., 2003; Jeppesen et al., 2009; Aldous et al., 2011).

Lastly, global sea level has risen by approximately 20 cm since 1870 (IPCC AR4) and recent data suggests sea level rise is occurring faster than previously predicted (Rahmstorf et al., 2007; Church et al., 2011). The most recent estimates show sea-level rise is likely to be double those made in the IPCC 2007 projections and highlight the fact that unchecked global warming is likely to raise sea level by several metres in coming centuries, leading to the loss of many major coastal cities and entire island states (Allison et al., 2009; Hunter et al., 2013). The incremental and short-term impact of sea-level rise on freshwater systems will depend on geology and topography and therefore will vary among locations (Tiruneh & Motz, 2004; Sánchez-Arcilla et al., 2008). Even so, a small rise in sea-level can dramatically extend the influence of saline water inland through freshwater channels, low-lying coastal wetlands and groundwater (Mulrennan & Woodroffe, 1998; Ross et al., 2000; Bowman et al., 2010). Saline intrusion of aquifers due to sea level rise is also exacerbated by water withdrawals for human consumption and further reduces the natural availability of freshwater (Kundzewicz et al., 2008; Kundzewicz & Döll, 2009; Abd-Elhamid & Javadi, 2011).

Climatic Control in Freshwater Ecosystems

There is extensive evidence to show that temperature has a major influence on freshwater species' ecology, including primary productivity, metabolism and growth rates (Markarian, 1980; Dallas, 2008; Haidekker & Hering, 2008). Consequently, temperature also heavily influences species phenology (Donnelly et al., 2011), life cycles, and distribution (Vannote, 1980; Hawkins et al., 1997). Higher temperatures allow greater primary production, and metabolic rates approximately double for a 10°C increase in water temperature (Caissie,

2006), in turn supporting faster growth and earlier emergence in a wide range of species (e.g. Wagner, 2002; Wagner, 2005; Li et al., 2009; Thompson et al., 2013). However, higher temperatures also lead to higher respiratory and maintenance costs and in many invertebrates there is a reduction in body size within populations at earlier emergence and consequently lower female fecundity (Daufresne et al., 2009; Thompson et al., 2013). The impact of increases in temperature may also vary spatially and temporally. At the landscape scale changes in the richness of macroinvertebrates and fish occur along latitudinal temperature gradients (Jacobsen et al., 1997; Heino, 2002; Heino, 2011). Although temperatures are increasing more rapidly at high latitudes (Wrona et al., 2006), the ability of species to tolerate changes in temperature is proportional to the variation they experience and as a consequence, tropical species may be more vulnerable to small changes (Deutsch et al., 2008). A subtle additional effect is that warm water holds less dissolved oxygen, although this reduction is rarely critical by itself. However, if high water temperatures persist, particularly overnight, oxygen concentrations can be severely depleted by the elevated metabolism of the freshwater fauna and kill fish and other sensitive macroinvertebrates (Davies et al., 2004; Caissie, 2006).

Hydrology is system-specific because it depends on the climate, geology, channel morphology and source of its base flow (i.e. groundwater, rainfall, snow melt) (Pusey et al., 2010). As regional patterns of precipitation and temperature change, the natural flow regimes will be altered. In rivers and streams, temporal and spatial variability of river flow is a fundamental control on in-stream habitat structure and availability (Richter et al., 2003; Dudgeon et al., 2006). Stream assemblages respond to variation in the flow regime and magnitude, frequency, timing and duration of high, low and intermediate flow events (Jowett & Duncan, 1990; Lytle & Poff, 2004; Monk et al., 2006). As climates change, the changing seasonality of rainfall could shift the peak runoff into a different season (Wagner & Schmidt, 2004). Alternatively, decreases in precipitation and increased evaporation can result in

drought and temporary fragmentation of the stream or river that leads to a series of substantial changes in community structure (Boulton, 2003; Hamilton, 2010). While dams have had a considerable influence on river ecosystems, climate change is expected to result in more significant changes to flow in all but the most modified global rivers, which in Australia includes the Murray Darling (Döll & Zhang, 2010). Conserving free flowing rivers, sustaining environmental flows and removing barriers to adaptive range shifts will be key actions for improving conservation of rivers under climate change (Pittock & Finlayson, 2011).

Ecological changes in response to climatic cycles such as the North Atlantic Oscillation (NAO), or the El Niño Southern Oscillation (ENSO) also demonstrate the strong link between climate and freshwater species (e.g. Garcia et al., 2004). For example, positive phases of the NAO have milder winters and increase discharge by approximately 15-18%. In headwater streams in Wales, positive phases of the NAO have been linked to a decline in macroinvertebrate species persistence or assemblage stability based on the pattern of ranked abundances through time (Bradley & Ormerod, 2001). Furthermore, the development period of mayfly nymphs was reduced during positive winter phases of the NAO, advancing emergence by up to 2 months compared with negative phases (Briers et al., 2004). In the case of ENSO, a succession of La Niña phases are connected to more flooding that can improve recruitment of fish (Puckridge et al., 2000) and likewise droughts during El Niño phases will extend the low and no-flow period to the extent that fish fail to spawn (Mol et al., 2000).

Observed and Predicted Effects of Climate Change on Freshwater Ecosystems

Phenology

Synchronised phenological responses between interacting species can be disrupted if individual species respond differently to changes in the environment (Thackeray et al., 2010).

In lake systems the onset of spring is associated with increasing temperatures, day length, nutrient and light levels, which in turn drive seasonal changes in planktonic species (Donnelly et al., 2011). Using data spanning 20 years, Adrian et al. (2006) found spring plankton species (both phytoplankton and zooplankton) had remained synchronised, but summer plankton species had slower growth, and more complicated life cycles, and not all were able to advance their phenology with warming. The emergence of British dragonflies has also advanced consistently over a 44 year period at approximately 1.5 days per decade, consistent with rising temperatures (Hassall et al., 2007). Experimental warming has also demonstrated that temperature can reduce the age and size of species at emergence, and therefore fecundity, and lead to asynchronous emergence of male and females (Li et al., 2011; Thompson et al., 2013).

Community Composition and Structure

Estimates of population size, growth rates or sex ratios are rarely recorded, particularly over long periods of time, and more often shifts are observed as changes in distribution or in assemblage composition across many species (e.g. Hickling et al., 2005; Hickling et al., 2006). More recently there has been an increasing interest in changes to species traits such as body size within a community. Species, or populations within a species, tend to be smaller in warmer environments, and there is now evidence of significant shifts among aquatic ectotherms in response to climate change that has resulted in an observable decrease in the size structure of species and individuals (Daufresne et al., 2009). This is thought to be driven more strongly in aquatic than terrestrial systems due to the added impact of lower dissolved oxygen (Forster et al., 2012). These shifts in the distribution of body sizes at the community level, and across multiple trophic levels, are likely to have significant implications for the stability of food webs and maintenance of ecosystem function (Perkins et al., 2010).

Shifts in Species Distributions

One of the key mechanisms by which species can respond to climate change is to track the movement of climatic isotherms in space, just as phenological change follows a seasonal shift (Burrows et al., 2011). A broad range of species from all ecosystems have been observed moving on average to higher latitudes or altitudes as temperatures increase (e.g. Parmesan & Yohe, 2003). Although the majority of this evidence has come from well-recorded terrestrial groups like birds and butterflies, there have also been significant observed changes in the distribution of freshwater taxa (Hickling et al., 2006). The most rapid responses have been recorded among dragonflies, with many studies now reporting shifting ranges across the globe (Aoki, 1997; Ott, 2001; Hickling et al., 2005; Ott, 2007; Flenner & Sahlén, 2008; Ott, 2010). Although the movement of fish can be constrained by natural barriers (Dudgeon, 2007), the network of canals in the UK allows relatively high landscape connectivity and over approximately 25 years 15 species have moved on average 51 km further north and 32.7m higher (Hickling et al., 2006). Decline in brown trout (*Salmo trutta*) at its southern limits has also been attributed to loss of its thermal habitat (Almodóvar et al., 2012), and the same species has moved 130 m higher on average in Switzerland (Hari et al., 2006). Most aquatic species are likely to shift their distribution along thermal gradients upstream as opposed to following suitable climates to higher latitudes because dispersal is generally limited by the river network (Meyer et al., 2007; Clarke et al., 2008). However the capacity of headwaters in low gradient lowlands to provide thermal refugia is limited (Palmer et al., 2009) and just as terrestrial species may become isolated in climatic *cul-de-sacs* on mountain ranges, movement to cooler refugia in headwaters could still isolate or fragment freshwater populations within the same basin (Ponniah & Hughes, 2004; Hughes et al., 2009; Sauer et al., 2011).

Long-term Datasets

Long-term datasets available for some regions have also made it possible to distinguish the impacts of changing climate in freshwater from those of natural variation. As mentioned, monitoring of headwaters in Wales, has shown macroinvertebrate communities remain stable during cooler drier winters in negative phases of the NAO, but that they become unstable during positive phases of warm wet winters (Bradley & Ormerod, 2001). Over 25 years (1981-2005), there has been an additional 1.4-1.7 °C rise in water temperature beyond the effect of the NAO, and this has led to detectable reduction in the abundance of 5-12% of the taxa present (Durance & Ormerod, 2007). In the Upper Rhône River in France, a survey of macroinvertebrate and fish communities over a 20 year period (1979-1999) showed that water temperatures have also risen by 1.5 °C, and favoured replacement of the “northern” cold-water species by thermophilic “southern” species from downstream (Daufresne et al., 2003; Daufresne & Boët, 2007). In addition, gastropods and bivalves along the same river were severely impacted by the 2003 heat wave and macroinvertebrate composition showed very little recovery in the following years. This is believed to be a sign that the cumulative pressure of climate change, in addition to other anthropogenic impacts, has lowered the ecosystem’s resilience to disturbance (Mouthon & Daufresne, 2006; Daufresne et al., 2007).

Changes are beginning to be observed over shorter time periods as well. Biological monitoring of Swedish lakes showed evidence of changes in species composition consistent with rising temperatures in a period of just 10 years (Burgmer et al. 2007). This was despite high variation in lake type and associated species communities. Likewise, in New South Wales, Australia, significant changes to macroinvertebrate assemblages were evident within just 13 years (Chessman, 2009). However, although the changes are consistent with those of climate change, in a climate as variable as that in Australia, much longer term monitoring will

be required to confidently separate the direct effect of anthropogenic climate change from cyclical variability such as ENSO (Jackson & Füreder, 2006).

Biological Monitoring

‘Ecosystem health’ is not a property that can be measured directly. Instead it requires the measurement of surrogates that indicate the system’s functional processes (e.g. carbon exchange, nutrient cycling and sediment transport) and the structural components (e.g. communities, populations) (Davies et al., 2010). Assessing whether water use, or disturbances from human activities are having an effect on ecosystem health is based on features such as stability, integrity, resilience and function, but without a universal definition, human judgement plays a significant role (e.g. Bunn et al., 2010).

The preferred approach to monitoring freshwater systems in Australia uses the deviation of an observed assemblage from a notionally undisturbed reference state to reflect the effects of various stressors such as eutrophication or hydrological degradation (Turak et al., 1999; Turak et al., 2004). The approach relies on predictions of observed/expected (O/E) taxa scores based on a set of environmental predictor variables and macroinvertebrate data collected from numerous reference sites (Wright et al., 1993). In the future, the reference condition will also change and so to remain up to date the models will need to be re-calibrated through time with new reference-site data. While it is believed the updated reference condition approach will remain suitable under climate change (Nichols et al., 2010), without long-term data collection it is more difficult to interpret whether a response is due to climate change (Jackson & Füreder, 2006). In addition, to reduce the costs of doing environmental assessments, most surveys reduce the resolution of sampling and taxonomy (Marshall et al., 2006; Jones, 2008). This has proven satisfactory for detecting changes to water quality but could be ineffective for identifying the nature of complex shifts due to climate change (Hering et al., 2010).

Thesis Structure

Although there is clear evidence that climate change presents a major threat to freshwater biodiversity, comparatively few studies have made quantitative predictions about which species, ecosystems or regions will change in the future, and which are most at risk. In this thesis I investigate the potential impacts of climate change on freshwater macroinvertebrate fauna in eastern Australia, and in particular the effect climate change will have on dragonflies.

1. *Does the degree of assemblage turnover explained by climatic factors vary between habitats and regions?*

Identifying recent effects of climate change on biodiversity is difficult because we very rarely have data collected over a long enough duration to detect temporal trends (Jackson and Füreder 2006). Chapter 2 presents an alternative approach using data from biological monitoring of river health to infer relative vulnerability of habitats under climate change. Although data collected for monitoring ecosystem health has not been designed for this purpose, a standard sampling methodology applied over large number of sites across natural environmental gradients can overcome this challenge by substituting space for time. Chapter 2 focuses on the underlying patterns of macroinvertebrate assemblage turnover along a latitudinal gradient. Vulnerability of habitats under climate change was considered higher where the proportion of turnover explained by climatic factors increased. If turnover among habitats was not explained by changes in climate then habitats would be considered at lower risk.

This chapter was published in *Freshwater Biology* in June 2012 (see Appendix, Bush et al., 2012).

2. *Can identification of dragonflies improve the ability of standard biomonitoring to detect the effects of climate change?*

Assemblage turnover driven by climatic change could also reflect a bias in the sensitivity of a particular taxonomic group. Chapter 3 compares the degree of turnover explained by climatic change for varying macroinvertebrate groups. One of the reasons the influence of climate on turnover may vary is that taxa are identified to family level and not species (Jones, 2008). To determine whether taxonomic resolution was important the turnover of dragonflies was compared at family, genus and species level. Dragonflies are potentially suitable candidates to detect the effects of climate change because their development is known to be strongly temperature dependent; they are generalist predators and not dependent on host species; and most importantly they have strong dispersal capacity, allowing them to quickly colonise new habitats (Córdoba-Aguilar, 2008). We also ask whether shifts in dragonfly composition could be used as a surrogate for shifts among other macroinvertebrate taxa?

This chapter was published in *Diversity and Distributions* in January 2013 (see Appendix, Bush et al., 2013).

3. *Which dragonflies are vulnerable to climate change?*

A common first step in assessing the vulnerability of species to future climate change is the use of species distribution modelling (SDM) which describes the statistical relationship between species occurrences and the environmental characteristics of those sites. This relationship is then used to predict current or future suitability across the landscape or through time (Elith & Leathwick, 2009). Until recently, few studies had applied SDMs to freshwater taxa, typically because suitable environmental proxies were not available as digital layers, and because records of species distributions have rarely been suitably collated. Dragonflies are particularly well suited to SDM studies because there is evidence for climatic control of larval

development and they disperse well, thereby occupying the majority of suitable habitat available to them (e.g. Hickling et al., 2006). In Chapter 4 SDMs were used to predict the distribution of dragonflies under current and future climate conditions at a fine spatial scale for the whole of continental Australia. This formed the basis of a comprehensive vulnerability assessment that accounted for each species exposure to environmental change across its current range, its predicted sensitivity to climate change, and the future risk to the species if their dispersal capacity does match the shifts in suitable habitat. Finally, the conservation value of each subcatchment can be identified and the locations of the streams and rivers most important for the conservation of those species most vulnerable to climate change.

This chapter has been submitted for publication in *Global Change Biology*.

4. *How will climate change affect the distribution of dragonfly diversity?*

Though individual species may require urgent conservation action, it is impractical to approach the management of each individually. There are limited resources for conservation and we must therefore identify where our actions will have the greatest impact. Common approaches focus on the richest and most diverse areas, often referred to as biodiversity hotspots (Myers et al., 2000). However, under climate change the distribution of species' suitable habitat is likely to change, or worse disappear altogether, and this undermines the focus on current species richness hotspots. Another basis for prioritising conservation effort is to protect evolutionary diversity by selecting assemblages that are composed of distantly related, rather than closely related species (Tucker et al., 2012). Taxonomically diverse assemblages are considered more likely to support a breadth of ecosystem functions than the same number of species within a single genus or family (Cadotte et al., 2012; Mouillot et al., 2013). Chapter 5 describes the distribution and predicted changes to Australian dragonfly

diversity, and tests whether a taxonomic bias is expected that would suggest a significantly greater loss of functionality than simply the number of species would suggest.

This chapter is likely to be submitted for publication in either *Global Ecology and Biogeography*, or *Diversity and Distributions*.

5. *Does anticipating climate change in conservation planning significantly reduce the loss of species from reserve systems in the future?*

Conservation planning tools now exist to identify near-optimum solutions for the problem of reserve selection when prioritising multiple species over large areas (Linke et al., 2011).

However, climate change is rarely considered in conservation planning studies despite the obvious implications of spatially shifting habitat for static reserves (Hannah et al., 2007).

Rather than allow climatic shifts to occur and add additional reserves to compensate for lost representation with the reserve system (reactive approach), anticipating change in the planning of reserves from the outset is likely to result in significantly different priorities (proactive approach). Furthermore, connectivity is a crucial aspect of any freshwater conservation plan but a particular emphasis could also change the likelihood of species loss or retention in reserves under climate change. Chapter 6 demonstrates the use of modelled dragonfly distributions in conservation planning for rivers along the east coast of Australia.

This chapter is likely to be submitted for publication in either *Global Change Biology*, or *Journal of Applied Ecology*.

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CHAPTER 2

DERTERMINING VULNERABILITY OF STREAM COMMUNITIES TO CLIMATE CHANGE AT THE LANDSCAPE SCALE

Alex Bush, David Nipperess, Eren Turak and Lesley Hughes

ABSTRACT

As the climate changes, species are expected to shift to higher latitudes and altitudes where suitable habitat is available if dispersal is not constrained by geographic barriers. We analyse patterns of turnover in freshwater macroinvertebrate assemblages to identify which communities are most likely to be at risk from climate change, and the location of geographic barriers that could impede such adaptive range shifts.

We analysed macroinvertebrate data from standard biological assessments at the family-level, from surveys of all coastal basins of New South Wales, Australia, covering a latitudinal gradient of more than 1000km. We used variance partitioning to separate the variation in composition explained by climate, among-site distance, human disturbance and other stream factors.

Montane stream assemblages showed high turnover in response to climatic variation.

Turnover in coastal-fringe streams was least affected by climate but strongly correlated with distance and stream variables. Significant shifts in assemblage composition occurred between habitats within catchments and across catchment boundaries.

Montane stream assemblages are most vulnerable to climate change because their distribution is most responsive to climatic factors, and elevated sites are isolated from one another, reducing the scope for altitudinal migration. Dispersal limitations in coastal-fringe assemblages will also increase their vulnerability to habitat loss from sea-level rise. For all stream-classes, the separation of many neighbouring catchment assemblages, either due to limited dispersal or the lack of suitable habitat, are likely to constrain adaptive range shifts. This would lead to an overall reduction in beta diversity among reaches, and subsequently to a reduction in landscape-level gamma diversity.

INTRODUCTION

Global climate change is already affecting many aspects of the natural environment (Parmesan and Yohe, 2003) and will continue to do so for the foreseeable future (Solomon et al., 2009). While a great deal of progress has been made towards understanding the variety and levels of responses to climate change in marine and terrestrial systems, freshwater systems have received relatively little attention. Available evidence suggests freshwater taxa are highly sensitive to climatic changes (Durance and Ormerod, 2007) and that climate change will interact with existing threats that already challenge conservation efforts (Palmer et al., 2009, Turak et al., 2011).

Understanding the spatial distribution of taxa in relation to environmental gradients such as temperature and rainfall is critical for predicting how species and communities will be affected as the climate changes. Monitoring of the effects of climate change is best done over a long period of time (e.g. 50 years) at locations where human disturbance remains otherwise constant (Burgmer et al., 2007). Such long-term monitoring is rare, but by substituting space-for-time, the distribution of biodiversity across environmental gradients can be used to analyse the potential consequences of climate change (Hering et al., 2009). Fortunately, the increasing use of macroinvertebrates as bio-monitoring tools in some freshwater systems has meant that extensive and well-planned surveys have been made in a standard fashion in many regions (e.g. Wright et al., 1993, Turak et al., 2004). To achieve the objectives of water quality monitoring while meeting cost constraints, such surveys typically have low sampling intensity and coarse taxonomic resolution, reducing the likelihood that changes in distribution will be detected (Marshall et al., 2006, Jones, 2008). Nonetheless it has been shown that family-level data can be as effective as species data for describing assemblage variation across ecological gradients (Heino, 2008). In this study we focus on the underlying patterns of assemblage turnover (beta-diversity) (Whittaker, 1972) along a latitudinal gradient to

investigate how adaptive range-shifts may be constrained by the landscape, and where climate change is likely to have most impact (Boyero et al., 2011). If either dispersal or habitat availability limits the ability of macroinvertebrate taxa to shift in response to changing climate, the risk of local extinction increases. Where assemblages exhibit a high degree of turnover along climatic gradients, rapid climate change is expected to lead to an overall reduction in all levels of diversity, with individual streams becoming increasingly dominated by similar sets of species with broad climatic tolerances (*sensu* Leprieur et al., 2011).

Assemblage turnover is predominantly dictated by the degree of dispersal limitation and by species specialisation along environmental gradients (Mouquet and Loreau, 2003, Buckley and Jetz, 2008). Regions that support a diversity of habitats, incorporating either heterogeneity in climate, physical topography or availability of water and nutrients, typically show the greatest turnover in assemblage composition (Buckley and Jetz, 2008, Davidson et al., 2012). We examined latitudinal gradients across all sites, and again for headwater streams that had been subdivided according to altitudinal classes. Small, headwater streams may contribute more than three-quarters of the total channel length in drainage basins (Clarke et al., 2008). They are critical for maintaining the ecological health of downstream river sections through organic matter processing (Wallace and Webster, 1996), and nutrient cycling (Gomi et al., 2002), and provide habitat for a significant component of regional biodiversity (Meyer et al., 2007, Clarke et al., 2008).

Our study focused on the coastal catchments of New South Wales (NSW), Australia, along a latitudinal gradient spanning 8° from sub-tropical to temperate regions (>1000km). Climate change threatens to exacerbate the significant declines of freshwater biodiversity that have already occurred in Australia primarily due to intensive and growing demand for water resources (Kingsford, 2011). Average annual temperatures in Australia have warmed by

0.7°C since 1960, and rainfall has declined in some regions, including NSW (Lough and Hobday, 2011). Temperatures are projected to increase 1.8 to 5°C by 2070 and further declines in run-off are expected in NSW, although the magnitude and direction of precipitation and run-off changes are uncertain (Hobday and Lough, 2011). The vulnerability of freshwater species to climate change is expected to be exacerbated by significant habitat degradation, fragmentation and regulation of watercourses that together reduce the connectivity required for species to adapt via range shifts (Hein et al., 2011, Pittock and Finlayson, 2011). There is particular concern about climate change in this region because the rivers flow eastwards, restricting the potential latitudinal movement of species unable to cross catchment boundaries (Turak et al., 2011).

In this study we asked three questions about landscape scale patterns in freshwater biodiversity: (1) Is assemblage turnover of freshwater macroinvertebrate families correlated with the degree of environmental heterogeneity within catchments? (2) Over what distance do freshwater assemblages become significantly different along a latitudinal gradient? (3) What environmental factors are associated with assemblage turnover among stream classes and catchments, and how can this association be used to indicate vulnerability under climate change?

METHODS

Study area

The study region covers 139,360 km² in eastern New South Wales (Fig. 1). It includes the catchments of 19 of Australia’s 456 river basins (basins 201-219, Australian Government, Bureau of Meteorology, 2009) and parts of three others (basins 220, 221 and 222).

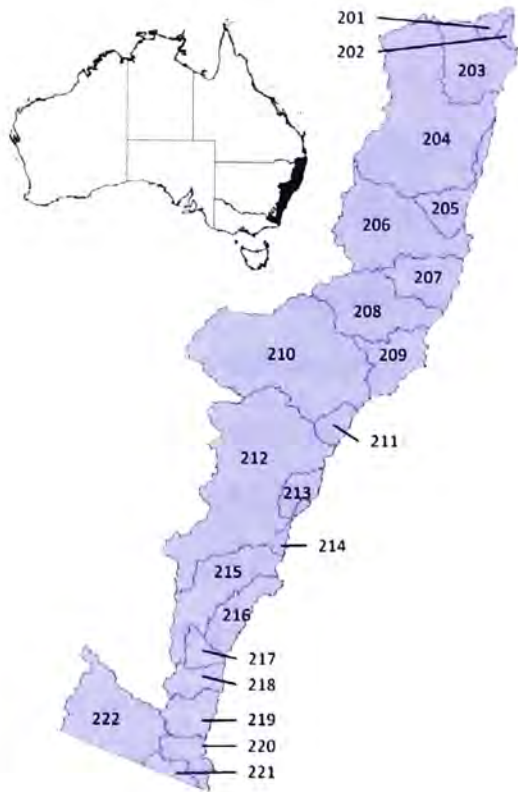


Fig. 1 Study area in eastern New South Wales (inset). Catchments are referenced by their Australian River Basin Numbers (Australian Government, Bureau of Meteorology, 2009).

Macroinvertebrate data

Samples of macroinvertebrates were collected from more than 800 sites between October 2006 and May 2010 by the NSW Department for Environment, Climate Change and Water (now NSW Office of Environment and Heritage) as part of state-wide assessments of river

health (Muschal et al., 2010). The collection of macroinvertebrate samples followed sampling protocols for the Australian state of NSW (Turak et al., 2004), as part of a national river bio-assessment system (AUSRIVAS) in Australia (Davies, 2000). The sampling unit was a river reach with a length of 10 x the modal width of the river, or 100 metres, whichever was greater. Macroinvertebrate samples were collected from edge habitats at every site and, when present, samples were also collected from riffles. Edge habitats are areas along the riverbank with little or no flow and riffle habitats are areas of broken water with rapid current. All major sub-habitats within an edge or riffle habitat were identified and sampling effort was divided amongst habitats in proportion to their occurrence. Examples of edge sub-habitats included tree roots, overhanging banks, sand, gravel, pebble, cobble or boulder beaches, and emergent macrophytes. Riffle sub-habitats included cobble, boulder or bedrock sections of fast/slow and shallow/deep riffles. Macroinvertebrate samples were collected with a 0.25mm mesh net by sweeping towards the banks at edge habitats and, for riffles, by kicking the substratum while holding the net vertically while standing on the bed downstream. Macroinvertebrates were live-sorted from the sample for a minimum of 40 minutes; the period was extended to 50 or 60 minutes if new taxa were still being recorded, or fewer than 20 individuals of the family Chironomidae had been collected, or if fewer than 200 animals in total had been collected. More than 135,000 specimens were collected in total and were classified into more than 130 taxa. Assemblage composition was assessed at the family level for all taxa with the exception of Chironomidae (identified to sub-family). Taxa only identified to Class (e.g. Oligochaeta and Ostracoda) or Order (e.g. Acarina) were removed from the analysis.

The majority of the sites were selected randomly using a stratified design, with the aim of representing all major river types in eastern NSW. Five elevation classes and three river size classes (maximum distance from source) were used as strata (Muschal et al., 2010). Data from four basins (201, 202, 217 and 221) were excluded from the analysis because fewer than 10 samples had been taken.

Environmental Data

Assemblage turnover was analysed in relation to four broad categories of environmental factors: climatic, spatial, anthropogenic disturbance and water variables.

Climate variables: Monthly climate data for minimum and maximum temperature and total rainfall were sourced from the Australian Bureau of Meteorology at 3 arc minute resolution (data points distributed on a regular raster grid, approximately 5 km apart) for the period 1911-2007. Climate data on monthly minimum and maximum temperature, and precipitation, were combined to produce 19 bioclimatic variables following the criteria described in Worldclim (www.worldclim.org/bioclim-aml). Based on multiple regression (DistLM), a smaller proportion of assemblage variation could be explained by more recent climate series (2000-2007) than when the full record was used. Therefore, averages based on the entire climate record available were used in the analysis to describe the effect of climatic factors.

Spatial variables: Spatial autocorrelation between sites was addressed by calculating straight-line distance vectors using GPS measurements.

Disturbance variables: We used the Stein et al. (2002) River Disturbance Index, designed specifically to provide an estimate of ecological health based on data available on human-induced disturbances in the catchment. The index is based on a stream network derived within a GIS and scores for disturbance were weighted by their distance from the channel. Because the index is organised according to stream hierarchy, it allows disturbance activities to be combined at successive scales from reach to catchment. We used factors affecting water quality (land-use factor, settlement factor, infrastructure factor) and hydrology (flow-diversion factor, impoundment factor) of a stream-reach, and then combinations of these at the sub-catchment and catchment scale (sub-catchment disturbance index, sub-catchment flow regime disturbance index, catchment disturbance index, flow regime disturbance index and river disturbance index) (Stein et al., 2002).

Water variables: Six standard water quality measurements were taken during each survey: alkalinity, pH, conductivity, turbidity, dissolved oxygen (DO) and water temperature.

Channel width and the percentage of the channel substratum composed of cobble, boulder and bedrock were also recorded. Maximum distance from source (DFSM) and the slope of each site were remotely calculated based on a Digital Elevation Model (DEM) as described by Turak et al. (2004).

Analysis

Trends in assemblage turnover were analysed in three ways: turnover within catchments, turnover between catchments and the relationship between turnover and environmental variables.

Although a sub-set of sites were surveyed repeatedly as part of long-term monitoring, the majority of sites in the monitoring program were only sampled once. For those sites where replicate samples were taken ($n=163$), increasing the number of samples increased both the overall family richness recorded from a site and the potential variation that could be explained using multiple regression (DistLM) (Fig. 2). This shows that replicate samples could reduce observed variation between sites and increase the potential variation explained by environmental variables by approximately 6%. We considered this a relatively minor increase and unlikely to substantially alter the results. Nonetheless, because lack of replication could increase variation and dissimilarity between sites, the more conservative alpha-level of 0.01 was used when testing for differences in the degree of turnover and assemblage composition. We also repeated the analysis after removing infrequently sampled taxa (encountered less than 5, 10, 15 and 30 times, and 50 times among edge samples) to ensure the patterns of assemblage dissimilarity were not biased by rarity. The analyses presented include all surveyed sites (total $n=865$ edge, 256 riffle) and are broadly representative of NSW coastal catchments.

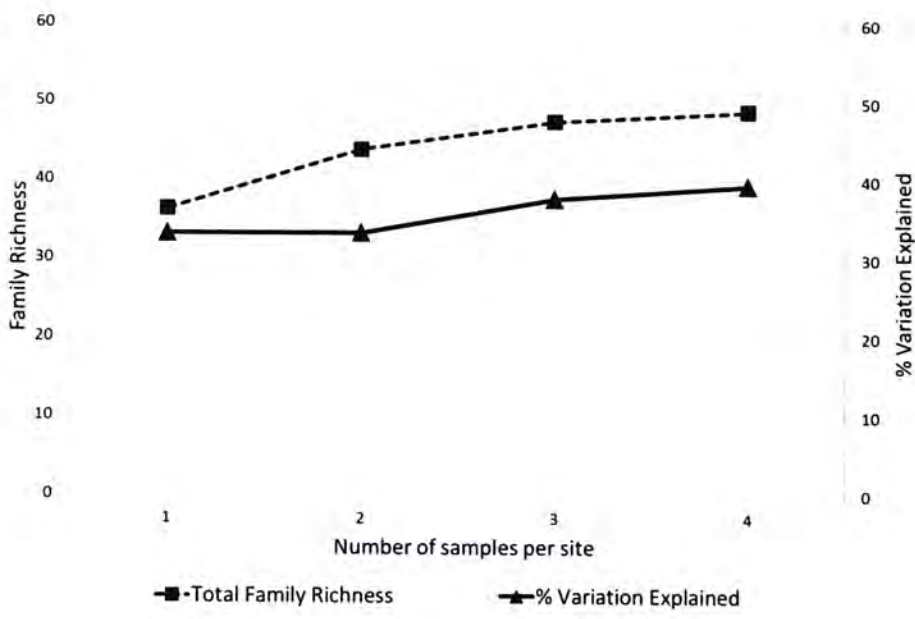


Fig. 2 Impact of increasing numbers of replicate edge samples on the total number of macroinvertebrate families recorded at a site, and the amount of variation that could be explained by multivariate multiple regression (DistLM) (n=163).

Assemblage composition was analysed separately for edge and riffle samples. We investigated the relationship of catchment assemblage dissimilarity with latitude, catchment area, altitudinal range (standard deviation), precipitation and the RDI. River disturbance was included to test whether the observed turnover would appear exaggerated among sites due to comparisons between degraded and reference condition sites. To remove the influence of human disturbance, tests were also performed using only reference-condition sites (n=485). Reference condition was defined as sites with Observed/Expected scores using presence/absence data of over 0.82 and 0.85 for edges and riffles respectively (Turak and Waddell, 2002).

Variation in assemblage composition was also investigated for specific stream classes. Headwater streams (less than 10 km from their source) were split into five elevation classes: coastal fringe <30m, lowland 31-200m, mid-elevation 201-600m, upland 601-1000m and

montane >1000m. These classes follow those of previous studies (Turak and Koop, 2008, Muschal et al., 2010, Turak et al., 2011) while maintaining adequate numbers of samples per class ($n > 50$). With these restrictions of sample size, edge assemblages could only be compared between catchments (minimum $n = 10$) for three of the stream classes (coastal, mid-elevation and montane streams). Riffle assemblages were only comparable among catchments for lowland, mid-elevation and montane streams ($n > 10$).

Statistical analyses were performed in R (R Development Core Team, 2010) and using PRIMER6: PERMANOVA+ (Clarke and Gorley, 2006). Turnover (i.e. beta diversity) was measured using the Bray-Curtis dissimilarity index. Turnover within and between catchments was analysed using PERMDISP (Permutation of Dispersion). Differences in assemblage composition between catchments were tested using ANOSIM (Analysis of Similarity) and PERMANOVA (permutational multivariate ANOVA). PERMDISP (Anderson, 2006) identifies whether certain groups of sites are more variable in their composition than others by comparing the mean dissimilarity distance of sites to their group centroid, with that of other groups. Similarly, ANOSIM (Clarke, 1993) tests whether groups of samples are the same in terms of composition, by comparing the average rank-transformed dissimilarity of samples from different groups with the average dissimilarity of samples from the same group. ANOSIM is considered by some a weaker test, so analysis between catchments was repeated with PERMANOVA which performs an ANOVA within dissimilarity matrices (Anderson, 2001).

We used variance partitioning to determine the relative importance of climate, compared to other environmental variables, in explaining assemblage turnover. Variance partitioning is a multiple regression analysis in which independent variables are grouped, in this case to represent four broad types of factors (Climate, Spatial, Disturbance and Water) (Anderson and Gribble, 1998). In this approach, the total percentage of variation explained by the model

($r^2 \times 100$) is partitioned into unique and common contributions of the sets of predictors (Fig. 4A). To account for the number of environmental variables used, the percentage of variation explained was measured with an adjusted r^2 (adj. r^2) (Peres-Neto et al., 2006). Variation partitioning was performed in PRIMER using DistLM to conduct a systematic combination of multiple regression analyses according to the format outlined by Anderson and Gribble (1998). The number of variables within each group was initially reduced by removing strongly co-correlated variables and then through forward selection on AIC (Akaike Information Criterion) in PRIMER. This was necessary to remove strongly correlated predictors and “suppressor variables” that can lead to negative shared variation among groups (Legendre and Legendre, 1998, Gilbert and Bennett, 2010). The variation explained by a single group of factors, without accounting for co-variation of other groups, is hereafter referred to as “Group-only”. Variation is referred to as “shared” if it can be explained by multiple groups. Those components of Group-only variation not shared, are hereafter referred to as the “pure”-components.

The Spatial variables (Principal Coordinates of Neighbour Matrices) were calculated using great-circle-distances in the SpacemakerR package of the R Statistical Environment (Dray, 2010). Forward selection on Spatial variables within DistLM was limited to the first 25 vectors because larger combinations could not be considered without exceeding the available processing capacity of PRIMER. To avoid over-fitting when partitioning data among stream classes, a maximum of 10 spatial vectors was considered. Forcing the inclusion of altitude as a spatial variable improved the proportion of variation explained by only 0.5%. As we considered the effect of altitude to be a combined consequence of climate and water factors it was not included in further analyses. Variation was also comparable between samples of different years and seasons, and their inclusion only improved the proportion of variation explained by less than 1% each. Although populations of species naturally fluctuate, the small effects of season or year on assemblage variability could have resulted from either the coarse

taxonomic resolution, use of presence-absence data or large sample size (Metzeling et al., 2002). To help present analysis of turnover consistently, we did not include seasons or years as factors. To improve normality, the Water factors (channel width, slope and DFSM) were each log-transformed before analysis.

RESULTS

Assemblage turnover

Among stream-edge samples, average dissimilarity in assemblage composition was typically greater than 30% (Table 1). Although the difference in the average turnover of sites within catchments was often significant (PERMDISP $F_{17/808} = 9.585$ $p < 0.001$), differences were small and showed no relationship to latitude or catchment characteristics. This result was not affected if only reference-quality sites were used because turnover within most catchments did not change significantly. The exception was basin 213 (effectively greater Sydney) where turnover was more than 10% higher when degraded sites were included. Turnover in riffle-habitat samples was not related to catchment area, altitudinal range, precipitation or the River Disturbance Index, but was negatively related to latitude (multiple-regression $F(1,13) = 7.526$, $p = < 0.001$), falling by 15% from north to south. The higher turnover among northern NSW catchments was also reflected in a greater richness of families ($F(1,13) = 14.55$, $p = 0.003$).

Comparison of turnover among stream classes revealed that assemblages were most similar at mid-elevations, and that turnover was highest among coastal-fringe and montane streams (>40%). A small number ($n=10$) of sub-alpine sites that occurred at particularly high elevations (>1500m) could have biased such a finding but their removal did not affect the results. Although turnover varied inconsistently among catchments for coastal and mid-elevation streams, among montane stream-edges it increased with latitude by 10% from north to south ($F(5,76) = 7.526$, $p = 0.001$). The increase in turnover was accompanied by a decrease in the average family richness per site, meaning that family richness of montane streams remained similar across latitudes within NSW.

Table 1 Family richness and average turnover (Bray-Curtis dissimilarity) for the river basins analysed in eastern New South Wales. Variation was compared for all basins with at least 10 samples (NA - not analysed).

Catchment	Basin No.	Edge Assemblages		Riffle Assemblages	
		Average Turnover - %	Family Richness	Average Turnover - %	Family Richness
Richmond	203	38.5	94	45	66
Clarence	204	33.8	108	43	90
Bellinger	205	36.3	78	40	56
Macleay	206	37.2	98	46	87
Hastings	207	35.6	90	41	64
Manning	208	36.3	91	29.7	60
Port Stephens	209	32.6	77	27	44
Hunter	210	36.5	104	32	62
Lake Macquarie	211	29.1	65	NA	NA
Hawkesbury	212	42.5	111	36.1	70
Port Jackson	213	30.4	63	NA	NA
Lake Illawarra	214	29.6	54	NA	NA
Shoalhaven	215	34.9	92	30.4	64
Clyde	216	39.4	92	23.6	40
Tuross	218	31.1	77	NA	NA
Bega	219	27.6	82	27.4	60
Towamba	220	32.1	86	23.1	42
Snowy	221	38.5	97	29.6	61

Assemblage composition

Increasing separation of catchments increases the likelihood that catchments will have significantly different assemblages of families (ANOSIM global $r=0.267$, $p<0.001$, PERMANOVA $F(829,21) = 7.47$, $p = <0.001$) and although spatial autocorrelation plays a part in this, there was a stronger clustering of sites based on distance in climatic-space (ANOSIM global $r=0.427$, $p<0.001$). Of greater interest are those differences that occur between neighbouring catchments (Fig. 3), for example between basins 204 and 206 ($r=$

0.236, $p = <0.001$). Although the same analysis of stream riffle assemblages found fewer significant differences between neighbouring catchments, composition was distinct across the same divides as for edge samples (global $r=0.193$, $p=<0.001$). Despite the accumulation of significant shifts in assemblage composition along the latitudinal gradient, we could not identify any consistent trends whereby families were progressively lost or gained. Families could reappear further along the latitudinal gradient and at this taxonomic resolution we cannot determine if these consisted of the same or closely related species.



Fig. 3 Study area with river catchment boundaries shown. Arrows indicate significant differences in the composition of stream-edge macroinvertebrates among adjacent river catchments (ANOSIM global- $r=0.123$, $p=<0.001$).

The assemblages of each stream class were significantly different from one another (ANOSIM global- $r=0.106$, $p=<0.001$) except for those of lowland and mid-elevation streams ($p=0.054$). Within stream classes, montane streams in particular showed distinct differences

among catchments ($F(5,76) = 1.53$, $p = <0.001$), and clear consistent shifts were evident in family-level composition. Typical families of montane streams common in the south included the Notonemouridae, Gripopterygidae, Hydrobiosidae, Philorheithridae and Conoesucidae. These were completely replaced in the north by families such as Coenagrionidae, Notonectidae and Atyidae (Turak et al., 1999). Assemblages with many “southern” taxa extended as far north as basin 208, but further north (206) there was a sharp shift to the “northern” taxa ($r=0.829$, $p=<0.001$).

Partitioning of variance explained by environmental drivers

When all environmental variables describing climate (Climate), spatial distribution (Spatial), human disturbance (Disturbance) and stream characteristics (Water) were included in the analysis, the total proportion of variation that could be explained across all sites varied from 30% in edge samples to 35% in riffles (Table 2, Fig. 4), and increased to as high as 60% when partitioning within headwater stream classes. Removing rarely sampled taxa at increasing thresholds of occurrence had little effect on the variation that could be explained, despite greatly simplifying assemblage composition (see Table S1 in supplementary information). The increase from edges to riffles reflected the greater explanatory power of factors characterising water quality and channel type.

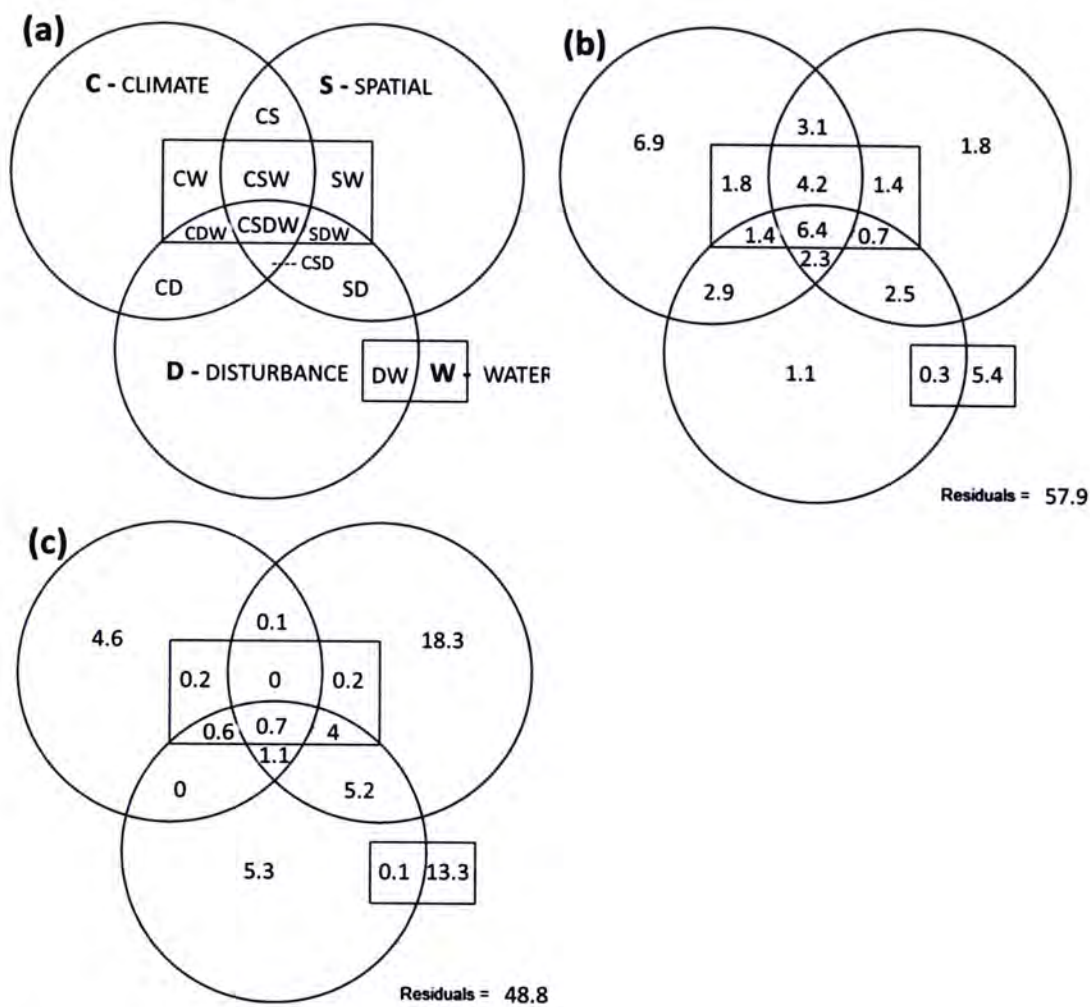


Fig. 4 Diagram A illustrates the partitioning of variance between four groups of factors: Climate (C), Spatial (S), Disturbance (D) and Water (W). The total variation explained by each group is portrayed by a circle, although Water is divided into two rectangles because four-way partitioning cannot be easily viewed in two dimensions (Oksanen et al., 2011). Where variation can be explained by factors from multiple groups, the shapes overlap, and sections that have no overlap are referred to as pure-components. For example, the section CS is the variance explained by Climate variables overlapping with variance explained by Spatial variables. The values from partitioning of variation among edge samples in montane (B) and coastal-fringe (C) streams are percentages of the variation explained.

Table 2 Partitioning of variance analysis, between edge (A) and riffle (B) samples. Values represent estimated percentage variance explained (adj. $r^2 \times 100$) by groups of environmental variables. Group “only” components use only factors from that group and combining the groups together as “All Factors” represents the maximum variation that could be explained using all factors simultaneously. “Pure” components show the variance explained by that group of factors, but none of the others, once covariance had been accounted for. There were too few riffle samples to analyse coastal-fringe and upland streams (NA – not analysed).

A.

Partitioning Section	All Edge Sites	Coastal-fringe Streams	Lowland Streams	Mid-elevation Streams	Upland Streams	Montane Streams
Climate only	15.3	11.2	22.4	20.0	21.8	28.0
Spatial only	14.8	29.2	22.2	24.7	24.3	24.3
Disturbance only	8.2	15.8	18.4	11.1	11.0	12.6
Water only	11.9	20.3	18.3	14.4	22.0	21.5
All Factors	30.1	60.4	51.1	47.4	53.2	51.3
Pure Climate	5.1	4.2	5.7	5.8	6.9	7.6
Pure Spatial	4.2	23.5	8.3	11.3	7.0	6.3
Pure Disturbance	1.2	9.3	7.6	4.2	2.0	2.6
Pure Water	4.5	14.8	8.3	9.5	10.0	8.1

B.

Partitioning Section	All Riffle Sites	Coastal-fringe Streams	Lowland Streams	Mid-elevation Streams	Upland Streams	Montane Streams
Climate only	16.8	NA	10.9	18.4	NA	32.4
Spatial only	20.1	NA	29.1	22.2	NA	25.8
Disturbance only	5.0	NA	14.6	3.5	NA	16.1
Water only	20.4	NA	16.6	15.3	NA	27.8
All Factors	35.4	NA	38.2	42.9	NA	44.8
Pure Climate	1.5	NA	1.4	6.4	NA	6.6
Pure Spatial	4.1	NA	15.0	10.3	NA	6.1
Pure Disturbance	1.2	NA	2.5	3.4	NA	0.1
Pure Water	10.7	NA	6.8	12.1	NA	4.5

Over a quarter of the variation in montane stream assemblages (edge and riffle) could be explained by Climate factors only. However, in most stream classes there was a large amount of overlap in the variation explained by Climate and Spatial variables (e.g. 9% of the explained variation is co-correlated between Climate and Spatial groups in montane streams) (Fig. 4B). Among both edge and riffle samples, the pure-Climate fraction of variation increased marginally, but steadily, with the altitude of the stream class. Conversely, the pure-Spatial component of variation decreased with altitude and was four times higher in coastal-fringe edges compared to montane streams (Fig. 4C). Disturbance explained the least variation of the four groups overall, but notably in the low-altitude stream classes the pure-Disturbance fraction exceeded that of Climate. The response to Water-factors was mixed; the highest amount of variation explained by Water-only was in montane riffles, whereas the highest pure-Water fraction was in stream-edge assemblages in the coastal fringe.

The power to explain turnover among stream-edge macroinvertebrate assemblages using Climate factors (Climate-only) was also compared across catchments. The most variation explained by Climate was among assemblages in the Snowy (basin 221 - 35.6%), Clyde (basin 216 - 27.4%) and Manning (basin 208 - 26.6%) catchments. Despite assemblages having high levels of turnover in the Hawkesbury, dissimilarity in this catchment was not strongly explained by Climate factors (Fig. 5). There were too few samples to repeat the same analysis with riffles and although mid-elevation stream-riffles had a high pure-Climate fraction of variance, their level of turnover and overall response to climate was comparable to that of their equivalent edge samples.

The climate factors that explained most variation among sites were annual mean temperature and precipitation. Temperature range or seasonality was also important, as was precipitation of either the warmest or driest quarter. Riffle assemblage dissimilarity was better explained by

factors such as precipitation of the wettest month. Maximum and minimum temperatures were not important in explaining differences among edge or riffle assemblages, presumably because the study focused above the species level, blurring the potential existence of tolerance thresholds for individual species. Disturbance factors had a minor impact, but those factors relating to sub-catchment land use, and in particular the proximity of roads, were more influential than those affecting flow. Among the Water-variables, DFSM was consistently important but many combinations of factors were retained, indicating turnover in macroinvertebrate assemblages is associated with a complex combination of these factors. Other Water factors that had greater explanatory power were stream slope, conductivity, pH and proportion of cobbles.

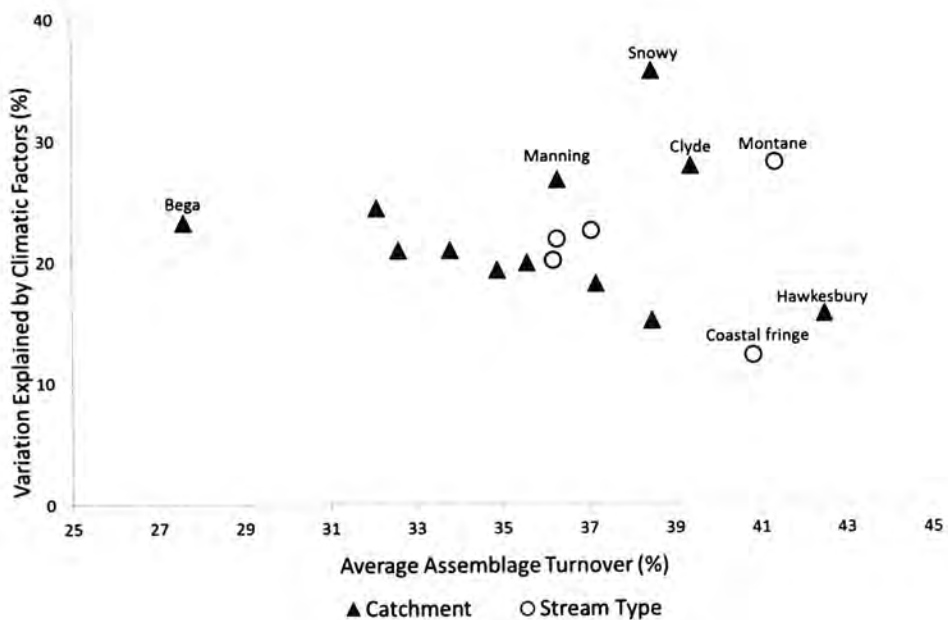


Fig. 5 Percentage variation explained by climatic factors using DistLM ($\text{adj.}r^2 \times 100$) against the average percentage turnover among assemblages within catchments (\blacktriangle), and stream classes (\circ). Vulnerability to climate change is expected to increase where higher assemblage turnover is combined with high climate-sensitivity.

DISCUSSION

Freshwater ecosystems are a priority for conservation, and understanding how climate and other factors are associated with trends in community composition will help improve management strategies with regard to climate change (Heino et al., 2009). This study shows climatic factors explain a greater portion of the variation among higher elevation stream assemblages, indicating that montane communities may be most vulnerable to climate change. Our results also provide evidence that adaptation of stream macroinvertebrates via range shifts will, in general, be constrained by catchment boundaries.

Between 30 and 60% of the variation in macroinvertebrate assemblages could be explained by the factors tested, from which vulnerability under climate change could be estimated based on the power of climate factors. However, as annual average temperature in NSW decreases approximately 0.5°C for every degree of latitude to the south, the climatic variation among sites across a latitudinal gradient was inevitably co-correlated with the distance separating them (Peres-Neto et al., 2006). By partitioning variation we found that climate could explain an increasing proportion of turnover at higher elevations, with or without the inclusion of subalpine sites, indicating the greater potential for vulnerability to climate change in high-elevation streams. Stream types showed significant differences across the elevation gradient and were consistent with the climate sensitivity observed in other upland and alpine freshwater communities (e.g. Brown et al., 2007). This supports the widely held view that montane regions are vulnerable to climate change because they contain species with low thermal tolerances and have limited adaptive capacity through vertical migration (Brown et al., 2007, Hering et al., 2009).

In addition to turnover along the altitudinal gradient, assemblage composition showed significant latitudinal turnover, even between adjacent catchments. These sharp changes in composition even at the family level show that distributions do not vary smoothly with such

gradients, but are much more fragmented. Differences in composition were particularly marked between basins 204, 206 and 208 and their neighbours in the north east of New South Wales. In particular basin 206 appeared to mark the northern extent of the southerly montane assemblages, although members of many families occurred north and south of this. Even with variance partitioning, removing the effect of spatial auto-correlation is difficult (Gilbert and Bennett, 2010), yet it seems unlikely that sharp transitions in climate or eco-hydrology could account for the differences we found between many adjacent catchments (Marchant et al., 1999, Turak and Koop, 2008). Most families do still occur in each catchment, so discerning whether there are two separate or one continuous species distribution is not possible.

Nevertheless, where highly significant differences occur between adjacent catchments at the family level, then differences at species level are likely to be even greater (Heino, 2008). The existence of significant barriers to dispersal between catchments is likely to be part of the explanation for these patterns (Thompson and Townsend, 2006, Hughes et al., 2009). Lack of connectivity between catchments could severely hinder the adaptive response of species unable to shift their distribution across catchment divides (Alexander et al., 2011, Keller et al., 2012).

Coastal-fringe streams may also be vulnerable to climate change due to limited adaptive movement. Recent modelling suggests that global sea level rise may exceed IPCC AR4 predictions (18-79cm increase over 1990 by 2095) (Church et al., 2011). Sea levels along the coast of New South Wales are projected to rise 90cm above 1990 levels by 2100 (DECCW NSW, 2009). Rising sea levels will eventually inundate many coastal watercourses and dramatically extend the influence of saline water inland through freshwater channels and aquifers (Tiruneh and Motz, 2004). Turnover among coastal-fringe assemblages is strongly explained by Spatial-factors, indicating dispersal limitations, and Water-factors, highlighting more specialised requirements of coastal-stream communities. Dispersal may be limited because many coastal-fringe streams drain directly into the sea without freshwater

connections to other comparable streams, and specialised habitat requirements will further reduce capacity for adaptation via range shifts (Turak et al., 2011). Sea level has fluctuated 100m in the last 16,000 years, submerging previous coastlines and lowland river connections of modern catchments (Jansen et al., 2007). Coastal stream assemblages may have been able to migrate and establish themselves upstream in the past, but their ability to respond to future rises may be compromised by the rapidity of change and the lack of similar habitats further inland. The significant modification of lowlands by urban and agricultural development limits the opportunity for natural replacement of lost habitat unless more proactive strategies are incorporated into coastal management. This includes connectivity and the creation or restoration of wetlands.

The landscape trends in assemblage turnover and family-level richness against environmental gradients found in this study are difficult to interpret. Catchment turnover varied between 30-40% and was not strongly related to broad indicators of heterogeneity or gradients such as latitude. This level of turnover is also not easily comparable with other studies, because family-level beta diversity is naturally lower than analyses based on species-level data (e.g. Leprieur et al., 2011). Family richness and turnover in riffle samples suggests that a latitudinal gradient in diversity could exist (e.g. Boulton et al., 2005). However, we did not find the same pattern among edge samples, particularly in montane streams, and based on the coarse taxonomic resolution and history of opposing findings we cannot infer the strength of local and regional mechanisms in controlling assemblage patterns at a landscape level (Heino, 2011).

Despite the broad scale and large sample size, the partitioning of variance was still limited by the spatial and taxonomic resolution of the samples. The fact that reaches were represented by single samples means the recorded assemblages were incomplete and, although we found infrequently sampled taxa had little influence on the analysis, a further 6% of the variation

could have been explained with additional sampling (Hose et al., 2004). More differences in assemblage composition could have been explained by increasing the taxonomic resolution (Jones, 2008, Koperski, 2011), and/or by using alternative factors better suited to describing distribution of freshwater macroinvertebrates (Thompson and Townsend, 2006, Landeiro et al., 2011). These include descriptors of riparian condition (Warfe and Barmuta, 2006), the presence of macrophytes (Humphries, 1996), the diversity and abundance of fish (Nicola et al., 2010), better measures of hydrology (Davidson et al., 2012), and by using distance between sites along watercourses (e.g. Landeiro et al., 2011). Overall, considering this dataset had only presence/absence data at family level and single samples for most sites, the conclusions should be regarded as conservative because the true strength of underlying trends at species level are likely to be greater (Jones, 2008). Increasing taxonomic resolution in particular, would significantly improve the application of monitoring data to climate change vulnerability assessments (Koperski, 2011).

Although bio-monitoring data for water quality assessment has generally not been collected with the aim of assessing the vulnerability of particular taxa to climate change, we have demonstrated that it can provide useful information for this purpose. There is promise that the multitude of monitoring datasets globally could greatly improve our understanding of freshwater biogeographic patterns. Furthermore, these datasets can help identify potential biogeographic barriers to range shifts, although confirmation will require species-level surveys (e.g. Keller et al., 2012). The greatest strength of such datasets is their broad-scale which, when combined with environmental data, allows us to highlight specific regions where assemblages may change markedly as the climate changes. Turnover across the landscape could decline in the future if species are unable to track shifting climate zones and overcome other anthropogenic threats, with local extinctions rapidly accumulating to reduce overall landscape (gamma) diversity in eastern New South Wales (Maloney et al., 2011). Inclusion of high altitude streams within protected areas along the Great Dividing Range is relatively high,

but future conservation strategies may need to include more interventionist actions such as assisted colonisation if natural dispersal among sites is limited (Heller and Zavaleta, 2009). Improving connectivity within areas of high turnover, and high sensitivity to climate, will improve landscape resilience to climate change, particularly if this can be linked to suitable climatic refugia (Palmer et al., 2009). Catchment management in heavily developed lowland landscapes is a major challenge but if we consider the effects of sea-level rise early, opportunities could be found to conserve vulnerable coastal habitats (Maloney et al., 2011, Turak et al., 2011).

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Supplementary Information

Table S1 Results from partitioning of variance analysis between edge (A) and riffle (B) samples. Values represent estimated percentage variance explained (adj. $r^2 \times 100$) by groups of environmental variables for datasets including taxa that were sampled at least once, 5, 10, 15 , 30 or 50 times.

A.

Edge Partitioning Section	All Taxa Sampled	Taxa sampled 5+	Taxa sampled 10+	Taxa sampled 15+	Taxa sampled 30+	Taxa sampled 50+
All Factors	30.122	30.183	30.367	30.459	30.731	31.026
Climate only	15.308	15.316	15.413	15.464	15.601	15.65
Spatial only	14.816	14.846	14.953	14.996	15.172	15.307
Disturbance only	8.20	8.209	8.271	8.300	8.441	8.603
Water only	11.905	11.912	11.994	12.041	12.215	12.43

B.

Riffle Partitioning Section	All Taxa Sampled	Taxa sampled 5+	Taxa sampled 10+	Taxa sampled 15+	Taxa sampled 30+	Taxa sampled 50+
All Factors	35.372	35.832	36.227	36.704	36.904	38.446
Climate only	16.761	17.025	17.316	17.659	18.387	18.376
Spatial only	20.072	20.385	20.689	20.942	21.48	21.708
Disturbance only	5.031	5.11	5.151	5.246	5.363	5.70
Water only	20.371	20.581	20.733	21.025	21.697	21.925

CHAPTER 3

DRAGONFLIES: CLIMATE CANARIES FOR RIVER MANAGEMENT

**Alex Bush, Gunther Theischinger, David Nipperess, Eren Turak, and
Lesley Hughes**

ABSTRACT

Freshwater ecosystems are highly vulnerable to the effects of climate change. Where long-term datasets are available, shifts in species phenology, species distributions and community structure consistent with a climate change signal have already been observed. Identifying trends across the wider landscape, to guide management in response to this threat, is limited by the resolution of sampling. Standard biomonitoring of macroinvertebrates for water-quality purposes is currently not well suited to the detection of climate change effects, and there are risks that substantial changes will occur before a management response can be made. This study investigated whether dragonflies, frequently recommended as general indicators of ecological health, are also suitable as indicators of climate change.

Data were analysed from standard bio-assessment monitoring at over 850 sites spanning a 9° latitudinal gradient in eastern Australia. Using variation partitioning, we analysed the proportion of assemblage turnover in dragonflies and other macroinvertebrate assemblages that can be explained by climate and other environmental drivers. We also tested whether the utility of dragonflies as indicators improved at higher taxonomic resolution, and if the turnover of dragonfly assemblages was congruent with that of other groups.

Climate explained three-times as much variation in turnover of dragonfly species, than dragonfly and other macroinvertebrate assemblages at family-level. The dissimilarity of dragonflies and varying turnover in each macroinvertebrate assemblage meant surrogacy among groups was low. Based on the influence of climate on turnover of macroinvertebrate assemblages, dragonfly species distribution appears highly sensitive to climatic factors, making this taxon a potential useful indicator of climate change responses. However, the low surrogacy among assemblages also suggests that a shift in the focus of conservation management from specific taxa to the functional composition of assemblages across a diverse range of habitats is needed.

INTRODUCTION

There are major challenges to improving the ecological integrity of freshwater ecosystems across the globe, and climate change will potentially exacerbate many existing problems (Dudgeon et al., 2006; Rosenzweig et al., 2008; Pittock & Finlayson, 2011). Changes in species phenology (Hassall et al., 2007), distribution (Daufresne et al., 2004; Hickling et al., 2005) and assemblage structure (Flenner & Sahlén, 2008; Chessman, 2009; Daufresne et al., 2009) of freshwater species have already been recorded, consistent with being responses to recent climatic change. To meet the challenge of improving or maintaining the ecological integrity of rivers we must consider climate change effects (Palmer et al., 2009; Turak et al., 2011). Acting before significant ecological change occurs will increase the likelihood of success and reduce the risk of inefficient resource allocation (Heller & Zavaleta, 2009). To provide an informed basis for adaptive management action (e.g. revegetation (Davies, 2010; Thomson et al., 2012), ecologically relevant indicators are required that improve prediction of species responses (e.g. range shifts) and provide rapid feedback of observed changes (Hering et al., 2010).

The state of freshwater ecosystems is frequently assessed by monitoring the diversity and/or structure of freshwater communities (e.g. Bunn et al., 2010; Davies et al., 2010). Many biological monitoring programmes in freshwater use the deviation of an observed assemblage from a notionally undisturbed reference state to reflect the effects of various stressors such as eutrophication or hydrological degradation (Hering et al., 2010). The effects of climate change are more difficult to interpret because without historic reference conditions and long-term data collection, there is no baseline with which to reference ecological response (Jackson & Füreder, 2006). The resolution of sampling and taxonomy that has proven satisfactory for previous monitoring to detect changes in water quality may also be insufficient to recognise the potentially complex network of effects predicted due to climate change (Hering et al.,

2010). Given the significant additional impact climate change is expected to have on freshwater ecosystems (Daufresne & Boët, 2007; Hassall & Thompson, 2008; Daufresne et al., 2009; Woodward et al., 2010), it is urgent we consider specific indicators and establish baseline conditions with which to compare future changes (Morecroft et al., 2009; Lawrence et al., 2010).

The term “indicator” is used here to describe a simple measure that acts as a signal of a more complex process; response to climate change (Fleishman & Murphy, 2009). Ideally, the response of an indicator (such as a single species) will be congruent with the wider system of interest (such as multiple, co-occurring species within a community) and its sensitivity to climate should not only be sufficient to observe a measurable response, but also exceed its sensitivity to other environmental conditions such as changing land-use and pollution. In addition, an indicator will be more useful if it represents a single functional group (e.g. predators) because inferring the likely relationships with other species is more straightforward (Hughes, 2003). Finally the choice of an indicator in a monitoring program depends largely on costs, so one that is readily and consistently observed, measured and identified will be more useful (Marshall et al., 2006; Jones, 2008).

Freshwater biomonitoring programs are typically designed to identify specimens only to family-level, as part of a trade-off between cost and information requirements (Beattie & Oliver, 1994; Lenat & Resh, 2001). Low-resolution taxonomy assumes that species within higher levels, especially within genera and families, have similar ecological preferences (Marshall et al., 2006). However, in cases where ecological similarity of species does not correspond closely to their phylogenetic relatedness, the overall response of those species grouped at family-level may be misleading (Lenat & Resh, 2001; Heino & Soininen, 2007; Bevilacqua et al., 2012). Further, when species are combined into families, potentially valuable information for discriminating between samples may be lost. Deciding if the loss of

information by aggregating species at family-level is acceptable depends on the data required and the level of discrimination needed. Whether families are taxonomically sufficient to discern the important environmental drivers of assemblage change is largely dependent on scale, as well as region and amount of species radiation within a group (Hewlett, 2000; Marshall et al., 2006; Heino et al., 2007). Therefore, in selecting indicators to monitor climate effects, it is important to consider taxonomic resolution (Lawrence et al., 2010).

Amongst freshwater invertebrates, the dragonflies (Order: Odonata) receive the same “flagship” recognition that butterflies offer for terrestrial ecosystems (Hawking & New, 2002; Fleishman & Murphy, 2009). In comparison to other freshwater invertebrates, dragonflies have a long history of research that provides a solid basis for understanding the implications of climate change (Corbet, 1999; Córdoba-Aguilar, 2008; Hassall & Thompson, 2008). Dragonflies originated and spread from the tropics and display a multitude of thermodynamic adaptations in both adult and larval stages that have allowed them to colonise temperate and sub-arctic environments (Hassall & Thompson, 2008). In the absence of fish, dragonfly larvae are often the top aquatic predators and may be key to maintaining diverse communities (Fox, 1977). Their development rate is strongly correlated with temperature, including the ability to complete multiple life-cycles per year at lower latitudes (higher voltinism) (Corbet, 1999; Braune et al., 2008; Hassall & Thompson, 2008; Flenner et al., 2009). Where long-term records exist, phenological changes have been observed that are consistent with climate change predictions, showing an advance in the timing of emergence (Hassall et al., 2007). Most importantly, dragonflies are mobile and have the potential to disperse widely, readily colonizing new habitats (e.g. Suhling et al., 2004). As a result, a number of studies have demonstrated range shifts among dragonflies, consistent with being an adaptive response to climate change (Aoki, 1997; Hickling et al., 2005; Hickling et al., 2006; Ott, 2007; Flenner & Sahlén, 2008). Dragonflies have been proposed as indicators of environmental quality in many circumstances (Chovanec & Waringer, 2001; Sahlén & Ekestubbe, 2001; Foote & Rice

Hornung, 2005; Smith et al., 2007; Simaika & Samways, 2009, 2010). Given the interest in using dragonflies, we empirically tested whether they could be extended to representing climate change effects (Fleishman & Murphy, 2009).

This study investigated the potential for dragonflies to be used as indicators of climate change effects in freshwater environments, and as surrogates for the responses of other stream macroinvertebrates. Initially, we asked whether spatial turnover of dragonfly assemblages is related to climate, and whether this group shows a higher degree of turnover in response to climate than other macroinvertebrate assemblages. Based on the results of these analyses, we asked whether the utility of dragonflies as indicators can be improved by increasing the taxonomic resolution at which they are identified. Finally, we asked whether changes to dragonfly assemblages are congruent with shifts in other aquatic macroinvertebrate assemblages. This investigation used data collected as part of an extensive monitoring program of rivers and streams from sub-tropical to temperate climates, across 9.1° of latitude in eastern Australia. The region is well suited for studying the effects of climate change on range shifts in freshwater taxa because it contains multiple large catchments, all draining west-east, that potentially constrain migration across the latitudinal gradient.

METHODS

Study area

The study area covers 139,360 km², extending over 1000 km along the east coast of New South Wales (NSW), Australia (Fig. 1), and includes the entire catchments of 19 of Australia's 456 river basins and parts of three others.



Fig. 1 Study area with catchment boundaries in eastern New South Wales (inset).

Macroinvertebrate data

Macroinvertebrates were collected from more than 850 river and stream sites, sampled between October 2006 and May 2010 by the NSW Department for Environment, Climate Change and Water (now the NSW Office of Environment and Heritage) as part of state-wide assessments of river health (Muschal et al., 2010). Most of the sites were selected randomly using a stratified design with the aim of representing all major river types in eastern NSW. Five elevation classes and three river size classes (maximum distance from source) were used

as strata in the design (Muschal et al., 2010). Data from the four smallest basins were excluded from the analysis because their sample size was small ($n < 10$). Macroinvertebrates were collected from river edge habitats and live-sorted in the field in accordance with the AUSRIVAS Sampling and Sample Processing Manual for NSW (Turak et al., 2004). The survey period covered a severe drought in eastern Australia and it is likely to have favoured the occurrence of more tolerant taxa (Chessman, 2009; Thomson et al., 2012). Consequently the dataset could be considered reflective of assemblage patterns during drought and is the reason why riffle samples were not included in the analysis.

We compared the congruence in turnover between macroinvertebrates at family-level taxonomic resolution, grouped either by phylum (Mollusca and Crustacea) or order (Table 1). Each group included a minimum of 10 families that had been recorded at least 10 times. Assemblage variation due to sampling intensity was minimal due to the removal of rare species, large sample size and coarse taxonomic resolution. The Diptera group of families included four subfamilies of Chironomidae. In addition to having Trichoptera as a single group, Ephemeroptera, Plecoptera and Trichoptera were combined as a collective group (EPT). EPT is a commonly used aggregate of families typically regarded as sensitive to disturbances such as changes to hydrology and oxygen depletion (Wallace & Webster, 1996).

The Australian dragonfly fauna comprises 325 species nationally, of which 137 are believed to occur in NSW. Importantly their taxonomy, particularly as larvae, is among the best known of the Australian macroinvertebrate fauna (Theischinger & Endersby, 2009). Dragonfly larvae were identified to the highest taxonomic resolution possible although species within some genera cannot yet be determined with confidence (e.g. *Eusynthemis* or *Dipblebia*). If a family or genus could not be identified to species because the larvae were immature, the site from which they were sampled was removed from the dataset.

Table 1 – Groups of macroinvertebrate families compared in this study. Trichoptera were tested separately (T), and as part of the EPT (Ephemeroptera, Plecoptera and Trichoptera).

Dragonflies	EPT	Coleoptera	Hemiptera	Diptera	Crustacea	Mollusca
Aeshnidae	Ameletopsidae	Curculionidae	Belostomatidae	Athericidae	Atyidae	Ancylidae
Corduliidae	Baetidae	Dytiscidae	Corixidae	Ceratopogonidae	Palaemonidae	Hydrobiidae
Gomphidae	Caenidae	Elmidae	Gerridae	Culicidae	Parastacidae	Lymnaeidae
Libellulidae	Leptophlebiidae	Gyrinidae	Gelastocoridae	Dixidae	Chiltoniidae	Physidae
Amphipterygidae	Oniscigastridae	Haliplidae	Hebridae	Ephydriidae	Eusiridae	Planorbidae
Coenagrionidae	Gripopterygidae	Hydraenidae	Hydrometridae	Simuliidae	Paramelitidae	Thiaridae
Isostictidae	Notonemouridae	Hydrochidae	Mesoveliidae	Stratiomyidae	Talitridae	Corbiculidae
Lestidae	Atriplectididae (T)	Hydrophilidae	Naucoridae	Tabanidae	Corallanidae	Hyriidae
Megapodagrionidae	Calamoceratidae (T)	Psephenidae	Nepidae	Tipulidae	Oniscidae	Sphaeriidae
Protoneturidae	Calocidae (T)	Ptilodactylidae	Notonectidae	Chironominae		Bithyniidae
Synlestidae	Ecnomidae (T)	Scirtidae	Pleidae	Orthocladinae	Phreatoicoidea	
	Helicophidae (T)	Staphylinidae	Veliidae	Podonominae	(Phreatoicidae)	
	Helicopsychidae (T)			Tanypodinae	Sphaeromatidae	
	Hydrobiosidae (T)					
	Hydropsychidae (T)					
	Hydroptilidae (T)					
	Leptoceridae (T)					
	Odontoceridae (T)					
	Philopotamidae (T)					
	Philorheithridae (T)					
	Polycentropodidae(T)					
	Tasimiidae (T)					

Environmental Data

The association of assemblage turnover with climate and other environmental factors was analysed using variation partitioning (Anderson & Gribble, 1998; Peres-Neto et al., 2006). The factors used were grouped into four categories; climate, spatial, disturbance and water.

Climate data: Monthly climate data for minimum and maximum temperature and total rainfall were obtained from the Australian Bureau of Meteorology (BoM) at 3 arc minute resolution (data points distributed on a regular raster grid, approximately 5 km apart) for the period 1911-2007. Climate data were averaged to produce 19 biologically meaningful bioclimatic variables (using Matlab (www.mathworks.com)) following the criteria described in Worldclim (www.worldclim.org/bioclim-aml). Multivariate regression (DistLM) based on a shorter climate series (2000-2007) found that explained variation in assemblage turnover was reduced by 2-4% depending on taxonomic group. Therefore, the results presented use the longer climate dataset to describe the long-term climatic processes important in determining landscape patterns in turnover.

Spatial factors: Similarity between sites because a result of spatial autocorrelation was addressed by calculating distance vectors called Principal Coordinates of Neighbour Matrices (PCNMs)(Dray et al., 2006). PCNMs were calculated using great-circle-distances in the SpacemakeR package of the R Statistical Environment (Dray, 2010) and limited to 25 vectors

because higher combinations could not be considered without exceeding the available processing capacity.

Disturbance factors: Addressing disturbance in this analysis was vital because the surveys included a range of affected sites and the tolerance of species to environmental degradation could potentially confound their sensitivity to climate. We used the Stein et al. (2002) River Disturbance Index, designed specifically to provide an estimate of ecological health based on data available on human-induced disturbances in the catchment. The index is based on a stream network derived within a GIS and scores for disturbance are weighted by their distance from the channel according to expert opinion. Further, because the index is organised according to stream hierarchy, it allows disturbance activities to be combined at successive scales from reach to catchment. We used factors affecting water quality (land-use, settlement, infrastructure) and hydrology (flow-diversion, impoundment) of a stream-reach, and then combinations of these at the sub-catchment and catchment scale (sub-catchment disturbance index, sub-catchment flow regime disturbance index, catchment disturbance index, flow regime disturbance index and river disturbance index) (Stein et al., 2002).

Water factors: This group includes variables that define water and stream type. Six standard water quality measurements were taken during each survey: alkalinity, pH, conductivity, turbidity, dissolved oxygen, and water temperature. Channel width and the percentage of the channel substrate composed of cobble, boulder and bedrock, were also recorded. Maximum distance from source (DFSM) and slope of each site was calculated as described by Turak et al. (2004) using a GIS. To improve normality, channel width, slope and DFSM were each log-transformed before analysis.

Analysis

Statistical analyses were performed in R and using PRIMER6: Permanova+ (Clarke & Gorley, 2006). To determine the relative importance of climate on assemblage turnover we used variation partitioning to identify its common and unique contributions, relative to other groups of environmental variables. Variation partitioning is a multiple regression analysis, where independent variables are grouped to represent broad groups of factors (i.e. Climate, Spatial, Disturbance and Water) (Anderson & Gribble, 1998). In this approach, the total percentage of variation explained by the model ($r^2 \times 100$) is partitioned into unique and common contributions of the sets of predictors (Fig. 2). To account for the number of environmental variables used, the percentage of variation explained was measured with an adjusted r^2 (adj. r^2) (Peres-Neto et al., 2006). Variation partitioning was performed in

PRIMER using DistLM to perform a systematic combination of multiple regression analyses as outlined by Peres-Neto et al. (2006). Strongly correlated variables within each group were initially removed, retaining those with the strongest marginal scores, and then reduced through forward selection on AIC (Akaike Information Criterion) in PRIMER. A variety of selection methods available in PRIMER were trialled and found to have minimal effect on overall explained variation, but caution should be exercised in interpreting the relative importance of variables. This process was necessary to remove strongly correlated predictors and “suppressor variables” that can lead to negative shared variation among groups (Chevan & Sutherland, 1991). The variation explained by a single group of factors, without accounting for co-variation of other groups is hereafter referred to as “Group-only”. Variation is referred to as shared if it can be explained by multiple groups, and thus those components of Group-only variation not shared, are hereafter referred to as the pure-components.

Forcing the inclusion of altitude as a spatial variable improved the proportion of variation explained by 0.5%. As we considered the effect of altitude to be a combined consequence of climate and water factors, it was not included in further analyses. Variation was also comparable between samples of different years and seasons, and their inclusion only improved the proportion of variation explained by <1% each. As a result, to present analysis of turnover consistently we did not include seasons or years as factors.

Congruence between assemblage dissimilarity among different taxonomic assemblages was compared at both local and regional levels. Analysis of Similarity (ANOSIM, Clarke, 1993) was used to compare the degree of clustering in assemblage composition among catchments, and Mantel tests used to compare both the site dissimilarity values (local-scale) and ANOSIM pairwise-*r* values (regional-scale). Tests between macroinvertebrate assemblages were conducted only between locations that contained at least one family from each group. This restriction meant that sample size was variable among comparisons, but was unlikely to have affected the ANOSIM results as all tests were conducted with over 600 sites.

RESULTS

Over 92,000 specimens from 91 families were collected, and 3754 dragonflies identified (Table 1). From family through to species level, climate and water factors were the most important for explaining turnover, both as group-only and pure-components (Table 2 and Fig. 2). Much less variation could be explained by distance between sites or the degree of disturbance.

The largest amount of variation that could be explained in family-level assemblage turnover was among the dragonflies and the Crustacea (Table 2). The influence of climate-only was also greatest among dragonflies and Crustacea, and even after partitioning other variation, their pure-climate fraction was similar (6-6.4%). Spatial separation was also influential for Crustacea assemblages, with a greater proportion confounded with climate than when partitioning dragonfly assemblages. In contrast, spatial factors were not important for assemblage turnover of either Trichoptera or Diptera families. Disturbance could potentially be highly influential for the distribution of Mollusca, but the variation explained was again largely co-correlated with other groups of factors. Dragonfly families showed equal sensitivity to stream and water factors as the EPT, although based on pure-fractions, Trichoptera were the most sensitive taxon. For each taxonomic group the potential explained variation for each factor, and the explanatory variables ranked most important are included in Tables S1 and S2.

From the 10 dragonfly families, we identified 46 genera and 97 species across a total of 791 sites. Although at family-level the variation in dragonfly assemblages that could be explained was comparable to other taxonomic groups, this increased significantly at higher taxonomic resolution (Figure 2). Almost half the variation in dragonfly-species assemblage composition could be explained by the tested factors and the Climate-only component rose to 27%, comparable with the total variation-explained by all factors among any taxonomic group at family-level. Most importantly, the pure-climate fraction of this variation tripled from family to species-level resolution, due largely to a separation of previously co-correlated spatial factors. Although selection priority could not determine the importance for some variables, those associated with summer extremes such as precipitation of the warmest quarter, and the temperature of the hottest month were consistently influential. The distribution of some dragonflies clearly demonstrates the importance of climate. *Dendroaeschna conspersa*, *Cordulephya pygmaea*, *Nannophlebia risi*, *Pseudagrion ignifer* and *Rhadinosticta simplex* appear to be warm-adapted and experience strong declines with increasing latitude or altitude,

whereas *Synthemis eustalacta* and *Austrolestes cingulatus* appear cool-adapted and become increasingly common at higher altitudes.

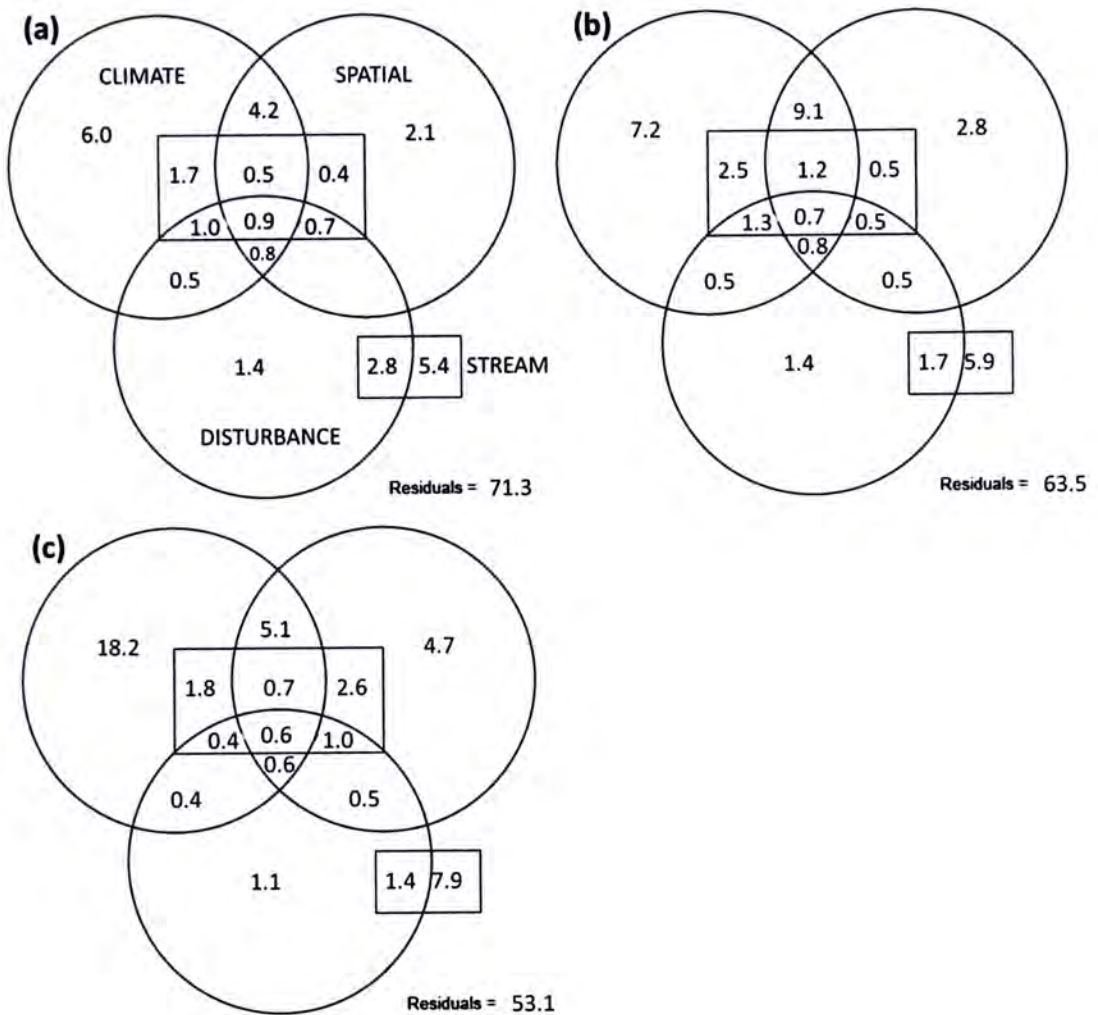


Fig. 2 Venn diagram illustrating the variation partitioning between four groups of factors: Climatic, Spatial, Disturbance and Water. The values are percentages from partitioning of variation among dragonfly assemblages at (A) family, (B) genus and (C) species-level. The total potential variation explained by each group is portrayed by a circle, and because four-way partitioning cannot be easily viewed in two dimensions, Water is divided into two rectangles (Oksanen et al., 2011). Where variation can be explained by factors from multiple groups the shapes overlap, and sections that have no overlap are referred to as pure-components.

Table 2 Proportion of variation (%) explained in macroinvertebrate groups by partitioning four groups of environmental factors; climate, spatial distance, disturbance and water. EPT are Ephemeroptera, Plecoptera and Trichoptera.

	Dragonflies	EPT	Trichoptera	Coleoptera	Hemiptera	Diptera	Crustacea	Mollusca
Climate-only	15.6	12.8	9.8	11.6	11.1	6.8	17.8	10.3
Spatial-only	9.5	7.7	5.2	7.3	9.1	4.1	15.0	8.9
Disturbance-only	8.1	6.4	3.2	3.9	4.6	4.1	4.2	13.8
Water-only	13.4	13.2	9.9	6.9	7.4	8.6	7.5	7.7
Total explained	28.7	24.4	18.9	18.9	21.7	15.5	28.5	19.6
Climate-pure	6.0	4.1	4.1	4.5	4.9	2.9	6.4	3.7
Spatial-pure	2.1	1.4	1.1	0.9	3.7	0.8	2.9	4.2
Disturbance-pure	1.4	1.5	0.8	1.0	1.6	1.6	1.0	0.3
Water-pure	5.4	5.8	6.4	2.9	3.8	4.2	3.2	3.2

When comparing congruence across all samples, dissimilarity among assemblages of dragonflies was significantly correlated with that in all the other taxa ($p < 0.001$) (Table 3). However, the strength of the relationship was weak across all groups ($r^2 = < 0.25$), including comparisons among non-dragonfly assemblages. The congruence between assemblages was stronger when comparing among catchments, although still not sufficient for prediction (ANOSIM $r = 0.4-0.5$). The use of dragonflies at genus or species-level did not improve their performance as surrogates for assemblage turnover in families from other taxonomic groups.

Table 3 Mantel test of correlation in dissimilarity of dragonfly families, genera and species with other taxa. Local (L) correlation compares assemblage dissimilarity directly between sites and regional (R) correlation is based on the congruence in dissimilarity of different taxa across catchments (using pair-wise ANOSIM). Values expressed are r-values. EPT are the Ephemeroptera, Plecoptera and Trichoptera.

Taxon	Scale	Dragonfly Families	Dragonfly Genera	Dragonfly Species
Dragonfly Families	L	n/a		
	R			
Dragonfly Genera	L	0.6625 ***	n/a	
	R	0.8748 ***		
Dragonfly Species	L	0.6834 ***	0.8801 ***	n/a
	R	0.8259 ***	0.9618 ***	
EPT	L	0.1275 ***	0.1918 ***	0.1779 ***
	R	0.3571 ***	0.3807 ***	0.403 ***
Trichoptera	L	0.1148 ***	0.1661 ***	0.1543 ***
	R	0.1879 *	0.2186 **	0.1898 ***
Coleoptera	L	0.1122 ***	0.1256 ***	0.1239 ***
	R	0.4093 ***	0.3563 ***	0.3332 ***
Hemiptera	L	0.06964 ***	0.09709 ***	0.09412 ***
	R	0.3209 **	0.3612 ***	0.3909 ***
Diptera	L	0.09168 ***	0.09988 ***	0.09013 ***
	R	0.02053	0.02647	0.08707
Crustacea	L	0.1542 ***	0.2193 ***	0.2132 ***
	R	0.2385 **	0.3051 ***	0.3719 ***
Mollusca	L	0.1372 ***	0.2032 ***	0.1989 ***
	R	0.2106 **	0.2523 ***	0.2458
All Other Taxa	L	0.2022 ***	0.2644 ***	0.2478 ***
	R	0.2873 ***	0.3255 ***	0.3422 ***

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

DISCUSSION

Influence of Climate on Dragonflies

Climate factors explained three times as much assemblage variation among dragonflies species than dragonflies, or other macroinvertebrate assemblages, at family-level. This result suggests that dragonflies may have potential to provide advanced warning of climate change effects in freshwater environments provided that they can be identified to species. The implication is not that other macroinvertebrate taxa are less sensitive to climate change, but that the distribution of dragonfly assemblages can be most strongly associated with climatic factors at the species level. Ideally the strength of an indicator would be measured against multiple taxa but due to the same taxonomic constraints that limit biomonitoring surveys this was not feasible. By identifying dragonflies to species, a large proportion of variation in turnover that could not be distinguished between climate and distance factors at family-level in this study, could then be separated, and climate typically explained the majority of turnover. Even among generalist predators such as dragonflies, there were habitat-specific preferences and their response to human disturbance appeared to be as strong as other macroinvertebrate taxa (Hofmann & Mason, 2005). The interaction between climate and environmental factors that determine the availability of suitable habitat is complex but could further enhance the shifts resulting from climate change. For example, a consequence of climate change could be the increasing frequency of droughts that favour dominant vagrant species (r-strategists) who swiftly re-colonise habitats, while disadvantaging species with bivoltine or semivoltine life-cycles that cannot complete their larval stages as surface water becomes increasingly intermittent (Hering et al., 2010). The strong relationships we found between dragonfly assemblages and summer temperature and rainfall are likely to reflect both their inherent ecological requirements as well as recent extremes during preceding years of drought (Chessman, 2009). Further study could focus on the link between modelled climate variables and larval development (Hassall & Thompson, 2008).

This study supports previous observations that dragonfly ranges are related to climate factors (Ott, 2010). The high dispersal ability of dragonflies means that distance between sites is not necessarily a barrier, and as the climate changes they are able to colonise widespread habitats (Conrad et al., 1999; Angelibert & Giani, 2003; Suhling et al., 2004). Long-term monitoring studies have already shown shifts in range boundaries of dragonflies in response to climate change (Aoki, 1997; Ott, 2001; Hickling et al., 2006; Ott, 2007; Hassall & Thompson, 2008; Winterbourn et al., 2011). Based on the 37 non-migratory dragonflies in the UK, Hickling et

al. (2005) found northern range boundaries advanced on average 74 km between 1960-70 and 1985-95. Even greater rates of expansion have been recorded in Sweden of up to 88 km/year in *Anax imperator*. However the rapid range expansion is not limited to the largest species and includes *Zygoptera* such as *Sympecma fusca* (15 km/year in Sweden)(Flenner & Sahlén, 2008) and *Erythromma viridulum* (28km/year in the UK)(Watts et al., 2010). Range shifts can also occur within river catchments along the stream network as downstream warm-adapted species move towards the headwaters (Hering et al., 2010; Domisch et al., 2011).

Surrogacy across macroinvertebrate assemblages

This study could not determine whether dragonfly species are more sensitive to climate than other macroinvertebrates because obtaining species level data from these other groups for comparison was not possible. Consequently we were interested in the surrogacy among family level groups, and dragonfly assemblages. Although the results suggest that common processes underlie shifts in assemblage composition, particularly at the regional scale, the high variability meant congruence among all macroinvertebrate assemblages was low (Heino, 2010). Biodiversity across such a wide range of groups is unlikely to be captured by a single surrogate, but other measures could be used in combination with dragonflies (Noss, 1990; Heino, 2010; Hering et al., 2010; Lawrence et al., 2010). The lack of congruence among taxa means management plans will require a broader approach to protect entire freshwater assemblages encompassing a functionally diverse range of habitats. We also found that climate plays a relatively major role in the distribution of Crustacea as well as dragonflies at the family level. This is likely to be a reflection of the range boundaries of Crustacea within the study region, because several Crustacea have either northern (e.g. *Eusiridae*), or southern (e.g. *Palaemonidae*) range extents in New South Wales. While paleoecological evidence shows some Crustacea have responded to climate change in the past (Eggermont & Martens, 2011), observed shifts in the distribution of dragonflies with current climate change may not be reflected in Crustacea if the availability of suitable habitat is restrictive, particularly if their dispersal ability is poor (Coughran, 2007; Hughes et al., 2009).

Application to conservation management

Dragonflies are recorded as part of standard freshwater biomonitoring surveys in many parts of the world (e.g. Norris & Hawkins, 2000) meaning no modification to sampling is required to use them as climate change indicators (Hering et al., 2010). Identification of all macroinvertebrates to species would be prohibitive (Marshall et al., 2006) but because dragonflies generally represent only a small proportion of the entire macroinvertebrate

sample, the additional costs are minimised. Where larvae cannot be separated morphologically, genetic bar-coding is a possibility (Curry et al., 2012), or else some species could be aggregated to genera as in this study (Hewlett, 2000; Bevilacqua et al., 2012). More targeted sampling of dragonflies could also be introduced, but while sampling adults can aid identification, larvae and exuviae are more reliable in determining the actual breeding range of a species (Raebel et al., 2010; Bried et al., 2012). Although we found that assemblage turnover could not be entirely explained by environmental factors, further reductions to the unexplained residual variation in future studies could be achieved by repeat sampling of sites (Hose et al., 2004), and the selection of other ecologically-relevant variables (e.g. hydrological characteristics) (Thompson & Townsend, 2006; Hawkins et al., 2007). Additional abiotic factors such as the reduction in ice cover, change from permanent to intermittent flow regimes, or changes in water chemistry (higher temperatures and lower dissolved oxygen) could complement information from dragonflies to understand climate change effects (e.g. Hamilton, 2010).

Changes in dragonfly assemblages can inform us about the magnitude and direction of movement of species in response to climate change provided suitable reference conditions can be established. The same reference condition approach used to record human disturbance in biomonitoring surveys could be used for dragonflies whereby dissimilarity of observed assemblages is compared to the “expected” baseline-climate assemblage. Furthermore, assemblage shifts due to disturbance factors independent of climate can be included based on the survey of the entire macroinvertebrate community. As with existing biomonitoring, separating trends due to climate change from those due to inherent population and sampling variability will be most successful at regional scales. The sensitivity of monitoring could be improved by incorporating data on species dispersal ability, and thermal or flow regime preferences of larvae. For example we would expect those species responsible for most observed changes in assemblage dissimilarity to have the highest ranked mobility, or for flow dependant species to decline fastest (e.g. Chessman, 2009; but see Angert et al., 2011).

Predictive modelling using climate-sensitive taxa such as dragonflies could also inform adaptive management plans, which could then be updated on the basis of the observed assemblages shifts from baseline conditions. By selecting appropriate targets, the requirements of other less mobile species could still be covered by those same actions (e.g. Bond et al., 2011). For regions and types of habitat that are identified as vulnerable to climate change dragonflies can be used to determine where to replicate or restore those conditions at other locations. In the case of montane streams, the lack of refugia means translocation to

locations predicted to be suitable by modelling should be considered proactively as an option to save those communities (Heller & Zavaleta, 2009). More broadly, based on the low congruence of turnover between macroinvertebrate assemblages we recommend conservation priorities shift from the narrow perspective of species identity and focus more on higher-order or functional composition of freshwater habitats. However, abiotic classifications of regional habitat diversity are unlikely to be ecologically representative and should be complemented by classifications of biological data (Turak & Koop, 2008; Melles et al., 2011). It is by linking movement of dragonflies and other indicators to management objectives at the landscape scale that they will be most effective at improving adaptive management of freshwater biodiversity to climate change (Turak et al., 2011).

The potential for rapid and dramatic changes to the species composition of freshwater ecosystems means the management of ecosystem functionality and biodiversity must take climate change into consideration. The practicality and potential for dragonflies as indicators within an existing monitoring framework is supported by this study. By including species identification of dragonflies into biomonitoring schemes early, baseline data will be available to inform an adaptive management strategy on the pace of ongoing ecological responses to climate change.

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Supplementary Information

Table S1 For each taxonomic group the potential variation in assemblage composition explained by a single factor from climatic, disturbance and water groups represented as a percentage (adj. r^2 x 100).

Factor	Dragonfly F	Dragonfly G	Dragonfly Sp	EPT	Trichoptera	Coleoptera	Hemiptera	Diptera	Mollusca	Crustacea
CLIMATE *										
Bio1	6.12	6.6	7.23	4	2.45	2.94	4.57	2.36	10.42	2.19
Bio2	4.95	3.54	3.35	3.65	1.87	2.73	2.35	0.83	0.25	4
Bio3	5.52	4.73	6.9	3.32	2.68	4.01	2.66	0.76	7.53	1.84
Bio4	2.37	3.94	4.95	3.77	2.13	1.51	4.31	1.77	4.79	3.34
Bio5	8	7.28	9.89	4.32	2.15	3.33	2.03	1.63	5.71	3.55
Bio6	3.47	4.97	4.25	3.63	2.2	1.91	4.83	2.29	9.2	2.02
Bio7	3.61	3.48	3.53	3.64	1.84	1.99	3.48	1.18	2.02	3.85
Bio8	5.91	4.79	3.75	4.23	2.16	3.4	2.87	1.52	7.15	2.51
Bio9	4.03	5.62	5.05	2.01	1.7	2.53	4.13	2.48	7.2	2.34
Bio10	7.83	8.28	10.88	4.25	2.13	3.31	2.18	1.65	6.07	3.42
Bio11	3.7	5.18	4.37	3.74	2.27	1.91	4.88	2.39	9.27	2.04
Bio12	3.11	6.07	5.85	2.59	2.47	3.41	5.67	2.22	7.51	4.06
Bio13	2.67	6.16	5.96	2.14	2.89	4.06	5.29	2.47	8.46	3.07
Bio14	5.58	3.97	3.61	3.58	2.06	2.45	2.81	1.06	0.99	3.16
Bio15	4	5.28	4.97	2.29	2.9	4.52	2.92	1.68	5.59	1.64
Bio16	2.85	6.41	6.14	2.14	2.87	4	5.33	2.48	8.67	3.05
Bio17	5.51	4.34	3.96	3.7	2.06	2.83	3.14	1.09	2.15	4.05
Bio18	4.3	6.63	8.28	2.32	3.31	4.49	5.71	2.63	10.39	2.49
Bio19	4.1	3.85	3.67	3.23	1.84	3.22	2.81	1.06	2.5	3.86
DISTURBANCE **										
SFRDI	1.18	1.06	1.09	1.56	1.33	0.92	0.48	0.93	1.09	4.55
IMF	1.19	1.01	1.06	1.45	1.23	0.98	0.5	0.41	0.59	1.53
FDF	0.24	0.21	0.21	0.38	0.6	0.64	0.17	0.67	0.56	0.59
SCDI	5.13	3.89	3.01	3.27	1.56	1.97	2.07	3.36	0.06	5.73
IF	1.64	1.31	1.06	1.59	0.77	1.34	0.82	1.58	0.93	2.37
SF	2.69	2.25	1.8	2.47	0.92	1.63	1.52	2.57	1.58	1.76

LUF	4.87	3.68	2.97	2.38	1.3	2.09	2.05	2.54	1.57	6.43
CDI	3.86	4.04	3.2	2.59	1.92	1.75	1.75	3.32	2.8	3.59
FRDI	3.49	2.46	2.43	2.91	2.01	1.23	2.5	0.9	1.19	3.55
RDI	5.81	4.43	3.92	4.58	3.36	1.68	3.24	2.8	2.18	7.8
WATER ***										
Alkalinity	2.06	2.52	2.29	1.92	1.53	1.44	1.61	1.77	1.72	3.19
Conductivity	3.32	4.29	3.53	2.46	1.78	1.33	0.97	2.42	1.52	2.18
DO	0.78	0.55	0.44	0.18	0.15	0.12	0.09	0.56	0.34	0.21
pH	0.93	0.73	0.3	1.47	0.76	1.23	0.96	1.1	0.08	1.63
Temperature	2.06	3.17	2.89	2.56	2.38	2.33	1.44	2.32	2.13	1.85
Turbidity	1.19	1.22	1.05	1.09	1.37	0.86	0.83	0.74	1.38	0.57
Bedrock	1.42	1.08	0.94	1.68	2.24	0.86	0.92	1.11	0.68	0.17
Boulder	0.94	1.43	0.6	2.2	2.44	1.86	0.98	0.77	0.36	1.39
Cobble	2.48	3.12	2.61	2.7	3.29	2.2	1.71	1.24	2.39	0.99
DFSM	7.97	5.03	3.88	5.15	2.43	2.89	4.15	2.02	3.6	3.14
Slope	5.93	4.37	3.37	3.26	1.45	2.19	3.64	3.48	2.57	1.74
Mode width	4.65	3.67	2.94	3.01	1.34	2.61	3.19	2.23	3.19	1.85

* Climate factors; Bio1 = Annual Mean Temperature, Bio2 = Mean Diurnal Range, Bio3 = Isothermality, Bio4 = Temperature Seasonality, Bio5 = Max Temperature of Warmest Month, Bio6 = Min Temperature of Coldest Month, Bio7 = Temperature Annual Range, Bio8 = Mean Temperature of Wettest Quarter, Bio9 = Mean Temperature of Driest Quarter, Bio10 = Mean Temperature of Warmest Quarter, Bio11 = Mean Temperature of Coldest Quarter, Bio12 = Annual Precipitation, Bio13 = Precipitation of Wettest Month, Bio14 = Precipitation of Driest Month, Bio15 = Precipitation Seasonality, Bio16 = Precipitation of Wettest Quarter, Bio17 = Precipitation of Driest Quarter, Bio18 = Precipitation of Warmest Quarter, Bio19 = Precipitation of Coldest Quarter (www.worldclim.org/bioclim).

** Disturbance factors; LF = land-use factor, SF = settlement factor, IF = infrastructure factor, FDF = flow-diversion factor, IF = impoundment factor, SCDI = sub-catchment disturbance index, SFRDI = sub-catchment flow regime disturbance index, CDI = catchment disturbance index, FRDI = flow regime disturbance index and RDI = river disturbance index (Stein et al., 2002).

*** Water factors; DO = Dissolved Oxygen, DFSM = maximum distance from source

Table S2 List of the most influential climate, disturbance and water factors for each macroinvertebrate assemblage tested. Only one set of factors is provided for dragonflies across taxonomic levels because although the order of importance between factors changed, their identity was quite consistent. n/a indicates where less than five factors were selected.

	Dragonflies	EPT	Trichoptera	Coleoptera	Hemiptera	Diptera	Crustacea	Mollusca
CLIMATE FACTORS *								
1	18	5	18	15	18	18	1	12
2	5	4	1	19	14	1	13	5
3	4	18	14	3	5	12	3	17
4	10	2	3	9	8	19	4	15
5	3	14	4	4	6	4	2	3
DISTURBANCE FACTORS **								
1	RDI	RDI	RDI	LUF	RDI	SCDI	CDI	RDI
2	LUF	SCDI	SCDI	CDI	LUF	FRDI	FRDI	LUF
3	CDI	SF	IF	SF	SFRDI	CDI	IF	SCDI
4	IF	CDI	CDI	RDI	SF	SF	LUF	SFRDI
5	n/a	SFRDI	n/a	n/a	n/a	n/a	SF	n/a
WATER FACTORS ***								
1	DFSM	DFSM	Cobble	DFSM	DFSM	Slope	DFSM	Alkalinity
2	Conductivity	Slope	Bedrock	Cobble	Slope	Conductivity	Cobble	DFSM
3	Slope	Alkalinity	Water Temperature	Water Temperature	Alkalinity	Water Temperature	Water Temperature	Water Temperature
4	Cobble	Water Temperature	DFSM	Mode Width	Cobble	DFSM	Alkalinity	pH
5	Water Temperature	Cobble	Alkalinity	Alkalinity	Mode Width	Alkalinity	Slope	Slope

* BioClim variables. 1 = Annual Mean Temperature, 2 = Mean Diurnal Range, 3 = Isothermality, 4 = Temperature Seasonality, 5 = Max Temperature of Warmest Month, 6 = Min Temperature of Coldest Month, 8 = Mean Temperature of Wettest Quarter, 10 = Mean Temperature of Warmest Quarter, 12 = Annual Precipitation, 13 = Precipitation of Wettest Month, 14 = Precipitation of Driest Month, 15 = Precipitation Seasonality, 17 = Precipitation of Driest Quarter, 18 = Precipitation of Warmest Quarter, 19 = Precipitation of Coldest Quarter (www.worldclim.org/bioclim).

** Disturbance factors as per Stein et al. (2002). Land-use factor (LUF), settlement factor (SF), infrastructure factor (IF), sub-catchment disturbance index (SCDI), sub-catchment flow regime disturbance index (SFRDI), catchment disturbance index (CDI), flow regime disturbance index (FRDI) and river disturbance index (RDI).

*** DFSM = Maximum distance from source.

CHAPTER 4

CONTINENTAL-SCALE ASSESSMENT OF RISK TO THE AUSTRALIAN DRAGONFLY FAUNA FROM CLIMATE CHANGE

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ABSTRACT

Climate change is expected to have substantial impacts on the composition of freshwater communities, and many species are threatened by the loss of climatically suitable habitat. In this study we identify Australian Odonata (dragonflies and damselflies) vulnerable to the effects of climate change on the basis of exposure, sensitivity and pressure to disperse in the future. We used an ensemble of species distribution models to predict the distribution of 270 (85%) species of Australian Odonata, continent-wide at the subcatchment scale, and for both current and future climates using two emissions scenarios each for 2055 and 2085. Exposure was scored according to the departure of temperature, precipitation and hydrology from current conditions. Sensitivity accounted for change in the area and suitability of projected climatic habitat, and pressure to disperse combined measurements of average habitat shifts and the loss experienced with lower dispersal rates. Streams and rivers important to future conservation efforts were identified based on the sensitivity-weighted sum of habitat suitability for the most vulnerable species. The overall extent of suitable habitat declined for 56-69% of the species modelled by 2085 depending on emissions scenario. The proportion of species at risk across all components (exposure, sensitivity, pressure to disperse) varied between 7 and 17% from 2055 to 2085 and a further 3-17% of species were also projected to be at high risk due to declines that did not require range shifts. If dispersal to Tasmania was limited, many south-eastern species are at significantly increased risk. Conservation efforts will need to focus on creating and preserving freshwater refugia as part of a broader conservation strategy that improves connectivity and promotes adaptive range shifts. The significant predicted shifts in suitable habitat could potentially exceed the dispersal capacity of Odonata and highlights the challenge faced by other freshwater species.

INTRODUCTION

Climate change is a major challenge for biodiversity within all ecosystems e.g. (Vörösmarty et al., 2010). River and stream ecosystems appear to be particularly sensitive (Ricciardi & Rasmussen, 1999; Durance & Ormerod, 2007) and face numerous challenges including the direct impacts of warming temperatures (Flenner et al., 2009; Floury et al., 2012), altered hydrology (Döll & Zhang, 2010), the increased frequency of floods and drought (Lough & Hobday, 2011), sea-level rise (Winn et al., 2006) and multiple other anthropogenic stressors (Nelson et al., 2009; Ormerod et al., 2010; Maloney & Weller, 2011). Climate change is projected to have impacts across all scales of organisation in freshwater ecosystems, from effects on genetic diversity (Taubmann et al., 2011) to community composition (Woodward et al., 2010). Observations of climate change impacts are increasing rapidly, including shifts in phenology (Hassall et al., 2007), shifts in distribution (Hickling et al., 2006; Domisch et al., 2012) and shifts in community composition and structure e.g. (Chessman, 2009; Comte et al., 2012).

Understanding how best to conserve biodiversity under climate change is a major challenge, in part due to a poor understanding of species distribution i.e. the Wallacean shortfall (Cardoso et al., 2011). Freshwater diversity in particular has often been overlooked within the wider terrestrial landscape (Abell et al., 2007) and conservation focus is biased to vertebrates, despite invertebrates contributing the bulk of biodiversity (Cardoso et al., 2011). To overcome the shortfall in data, Species Distribution Models (SDMs) have become popular tools because they can maximise the use of the limited records we have to predict the suitability of habitat in the wider landscape e.g. (Elith & Leathwick, 2009). By extending projections through time they can be used to predict the threat posed by climate change (Heikkinen et al., 2006; Sinclair et al., 2010; Araújo & Peterson, 2012). If the area of suitable habitat is predicted to be dramatically reduced by climate change then that species may face significant risk of

extinction in the future as conditions become increasingly marginal. The resolution and complexity of geographic data for river systems is continuously improving and as a result the number of studies applying SDMs to freshwater taxa has increased rapidly in recent years, with applications to fish (Bond et al., 2011; Buisson et al., 2012), platypus (Klamt et al., 2011), and aquatic invertebrates (Cordellier & Pfenninger, 2009; Balint et al., 2011).

In this study we described the distribution of Australian Odonata (dragonflies and damselflies). Air temperature has increased 0.9°C in Australia since 1910, with most warming occurring since 1970, and includes more temperature extremes that match model expectations (Alexander & Arblaster, 2009; Perkins et al., 2012). Predicted changes to rainfall and hydrology will mean some regions experience significant deficits and others increased variability in coming decades (Hobday & Lough, 2011). Previous studies have shown that Odonata appear to be suited to assessing the impacts of climate change because their development is strongly temperature dependent (Flenner et al., 2009), their distribution is not dependent on other species (Araújo & Luoto, 2007), and they are sensitive to climatic factors e.g. (Rosset & Oertli, 2011; Bush et al., 2013), a key assumption when using SDMs for climate change assessments. Odonata have been successfully modelled for conservation purposes (Simaika et al., 2013), and within studies of climate change effects on macroinvertebrates (Domisch et al., 2012). There have also been many reported changes in odonate ranges consistent with a response to recent climate change e.g. (Ott, 2010). In addition, Odonata were selected because, among the major orders of aquatic invertebrates, they occur in all Australian surface waters, their taxonomy is relatively well known, and comprehensive occurrence data are available (Theischinger & Endersby, 2009).

We assessed threats to species based on a combination of their likely exposure to climatic change, their sensitivity to climatic factors, and the relative importance of dispersal capability (Williams et al., 2008; Foden et al., 2013). This study assesses the threat to Odonata, an invertebrate group widespread across the Australian continent and models changes in

suitability at a spatial scale appropriate for conservation management of freshwater systems. In the absence of measured trait-data to characterise species' adaptive capacity, typical for invertebrate taxa (but see (Arribas et al., 2012)), we used the distance habitats are predicted to shift in the future to describe the pressure on species to disperse and track suitable conditions. This approach does not therefore describe species' adaptive capacity per se, but identifies the species that would face significantly greater risk if they were not able to disperse as fast as their suitable habitats shift. Of the species included in the models, we identified those Australian Odonata most vulnerable to climate change across multiple criteria, and identified the specific locations most important for conservation of the most vulnerable species.

MATERIALS AND METHODS

Species Data

Records of odonate distributions were collated from a diverse range of sources including all state and museum collections, government survey records, local catchment authorities, scientific literature and private collectors. For several collections these records were entered into digital format for the first time, significantly increasing the overall number of records available (Table S1). Locality records and taxonomic identification were verified for accuracy as much as possible using habitat descriptions within metadata and expert advice of collectors and museums (Langhammer et al., 2007; Kennard, 2010). Although outlying records can influence model fitting, where doubt existed over observation validity the records were removed. Decisions on record validity incorporated factors such as date recorded, life stage (favouring larvae over adults) and gender (females over males). For example, some species had adult males recorded far beyond their usual range (300 km+) in highly arid environments, presumably following an unusually heavy period of rainfall. Populations in these areas are

unlikely to be self-sustaining for even a few generations and the records were removed from the dataset.

The completed dataset included over 32,000 occurrence records from approximately 12,100 localities. Of the 324 Australian Odonata, modelling included 197 species recorded from 30 or more subcatchments, and a further 76 species that were treated as “Uncommon” (15-30 subcatchments)(Wisz et al., 2008). The majority of records were collected within the last 20 years (95%), but records as far back as 1950 were also used in the case of some uncommon species where native vegetation was still intact, and they had not been recorded in more than 14 subcatchments more recently. A number of species distribution modelling studies have used low numbers of records to successfully predict distributions e.g. (James et al., 2013; Reside et al., 2013), and by adjusting parameters so models were not over-fitted we were able to include uncommon species e.g. (Pearson et al., 2007; Domisch et al., 2012). Nonetheless, approximately 51 species were recorded from fewer than 15 subcatchments and were not included in this study.

Environmental Data

Climate change projections were based on Representative Concentration Pathways (RCPs), being the standardised warming trajectories due to be used in the Intergovernmental Panel on Climate Change’s Fifth Assessment Report in 2013 (Moss et al., 2010; van Vuuren et al., 2011). The RCPs used in this study describe a range of stabilisation, mitigation and non-mitigation pathways that under medium or high emissions scenarios result in radiative forcing reaching 6 and 8.5 W/m² respectively by 2100, equivalent to global average temperatures increasing 3.0 and 4.9°C (Rogelj et al., 2012). Coarse resolution climate data were provided by the Tyndall Centre, University of East Anglia, UK (available at <http://climascope.wwfus.org>). Based on the study by Fordham et al. (2012) we selected an ensemble of the seven global climate models (GCMs) most successful at reproducing the

recent global and regional precipitation patterns of Australia (specifically CCSR-MIROC32MED, CSIRO-MK30, GFDL-CM20, MPI-ECHAM5, MRI-CGCM232A, UKMO-HADCM3 and UKMO-HADGEM1). The data were 10-year averages centered around 2055, and 2085, for RCP6 (medium emissions scenario) and RCP8.5 (high emissions scenario). Lower emissions scenarios were omitted in this study as all indications suggest achieving the necessary reductions are unlikely (Peters et al., 2013). Research has shown that climate ensembles perform better than any single GCM in simulating observed conditions (Fordham et al., 2011), and multiple scenarios are useful to span the range of uncertainty in predicting future climates (Beaumont et al., 2008). Monthly RCP data were statistically downscaled to a 1 km² resolution, independent of elevation, using a cubic spline of the anomalies (deviance from modelled current and modelled future) and these anomalies were applied to a current climate baseline of 1950 to 2000. The current climate data were sourced from Worldclim (www.worldclim.org) and the data were created as defined in Hijmans et al. (2005). The same method was used to create bioclimatic variables from the downscaled future climate data. All downscaling and bioclimatic variable generation was performed using the 'climates' package (VanDerWal et al., 2012) in R v.2.15 (R Development Core Team, 2013).

Rather than using gridded data, models were based on the stream network from the National Catchment and Stream Environment Database V.1.1.3, part of the Australian Hydrological Geospatial Fabric (GEOFABRIC, 2011). When predicting habitat suitability in river networks, organising the modelling environment and predictor variables to reflect the structure of a freshwater system is important because it can influence the accuracy of freshwater SDMs without necessarily affecting performance metrics (Domisch et al., 2013). Catchment boundaries were coded hierarchically using the Pfafstetter classification system that defines 1.4 million stream subcatchments at the continental scale. Climate data were aggregated to the same stream subcatchments. Mean annual runoff was generated by James et al. (2013) for the same stream network and same future climate scenarios using a bucket

model outlined by Donohue et al. (2012). Local differences in precipitation can be poor proxies for changes to runoff (Chiew & McMahon, 2002), and hydrological forecasts can therefore greatly improve projections of habitat suitability for freshwater species.

We used ENMTools (Warren & Seifert, 2010) and Maxent (Elith et al., 2011) to calculate model AIC (Akaike Information Criterion (Akaike, 1973)) and to rank variables for approximately 20% of the species. We did not observe a significant difference in variable selection among major taxonomic families or between species that could be associated with still or flowing waters, but variable selection did differ among species assigned to different geographic regions (see S2). By selecting models with the lowest AIC the array of climatic, hydrological and topographic variables was reduced to eight. The predictor variables used included three temperature variables (annual mean, seasonality, and minimum of the coldest month), three precipitation variables (precipitation of the wettest and driest quarters, and seasonality), one hydrological (mean accumulated flow) and one topographical (valley confinement). Valley confinement is a useful proxy for the sedimentation characteristics of a subcatchment and particularly useful for upland catchments (Gallant & Dowling, 2003). Most species were best modelled using seven variables, although uncommon species in each region were modelled using five. Selection only varied geographically among groups based on the use of precipitation in either dry or wet quarters. Australia has very few Odonata exclusively associated with standing water and this may be why presence of standing water bodies such as lakes did not rank highly (Theischinger & Endersby, 2009). In the case of two dune lake specialists, the density of lakes and extent of sandy soils were included in models, although this did not significantly improve model scores.

Habitat Suitability Modelling

Odonata distributions were modelled using an ensemble of five commonly used algorithms within the package BIOMOD 2 in R (Thuiller et al., 2009). Algorithms included generalised

linear models (GLM), generalised boosted models (GBM), generalised additive models (GAM), multivariate adaptive regression splines (MARS), and Maxent (Elith et al., 2006). All models were run with 10 replicates, using a standard 70/30 split for training and testing data. Algorithms were run using their default settings and adjusted as follows: GLM, polynomial terms were ranked by AIC; GBM, fourfold cross-validation and a maximum of 2,000 trees; GAM, a spline function with a degree of smoothing of four and 10,000 pseudo-absences.

Model evaluation was conducted using the standard measure of area under the receiver operating characteristic curve (AUC), and the True Skills Statistic (TSS). The sole use of AUC in SDM studies has received some criticism, particularly when models are fitted across large areas (Lobo et al., 2008; Smith, 2013), and so TSS was used in weighting model importance for ensemble projection (Thuiller et al., 2009), and maximised when selecting a suitable threshold to perform binary transformations (Cao et al., 2013; Liu et al., 2013). AUC scores range from 0 to 1; values of 0.5 indicate a performance no better than random, whereas 1 reflects perfect model accuracy. TSS scores range from -1 to 1, with 0 indicating no skill and 1 a perfect ability to distinguish positive and false scores.

The majority of Odonata records in Australia were distributed through the more mesic coastal regions, and there was a bias in their proximity to urban settlements, some major rivers and highways. As the ranges of most species are regionally restricted, the use of pseudo-absences from the entire study area would have led to exaggerated discrimination statistics (Lobo et al., 2008; Smith, 2013), and less informative models (Acevedo et al., 2012). Pseudo-absences were selected from background points where other species had been collected within a 300 km radius of a species' presence record (Barbet-Massin et al., 2012), the maximum range we considered available to dispersing Odonata under current conditions. Pseudo-absences were supplemented where necessary by random selection to standardise the total across species. By reducing the overall extent of pseudo-absences, the model projections are more likely to

extrapolate beyond the known species-environment relationships, potentially overestimating suitability in distant locations (VanDerWal et al., 2009a). To counter extrapolation we constrained projections using environmental clamping that reduced the suitability of a subcatchment when more than one environmental factor was outside the limits used in model construction (Elith et al., 2011). The clamping allowed some reasonable extrapolation of distributions to fill gaps in current habitat, but constrained suitability under future projections to reflect similar environmental conditions to the present.

Model performance based on TSS (0.827 ± 0.124) and AUC was typically high (0.946 ± 0.06), although TSS scores were more variable (see S2 and S3). TSS scores were lowest among several common continental species, but they were retained after closer examination showed that their poor scores were the result of misclassification only in the arid zone where the patchy nature of waterholes made assessment difficult. However, three species with highly restricted current distributions were subsequently removed from the analysis because of high variation in projections from different models, particularly for future climate change scenarios. For the 270 remaining species modelled, the treatment of species as uncommon did not significantly influence the predicted overall change in habitat extent ($t_{(89)} = -0.09$, $p = 0.926$), but there was an increase in model performance commonly observed for narrow range species (Lobo et al., 2008). All projections of individual species presented in this study are freely available on request from the corresponding author.

Vulnerability Assessment

We determined species vulnerability to climate change based on three components; exposure (the extent to which a species' currently occupied physical environment will change), sensitivity (the extent to which suitable habitat is lost) and dispersal pressure (the reliance on dispersal to avoid further negative impacts); Fig.1 and (Foden et al., 2013). Species at risk across all components were classified as highly vulnerable (Category 1). Species that are not

required to disperse long distances but are still exposed and sensitive to change are considered vulnerable (Category 2). If a species is exposed to climate change and alternative suitable habitats are available but require significant dispersal, it was classified as having the potential to persist (Category 3). It is also possible, though unlikely in a modelled environment, for a species to experience a significant decline and distributional shift before becoming significantly exposed to environmental change (Category 4). A detailed example of the assessment process is available in the supplementary S4.

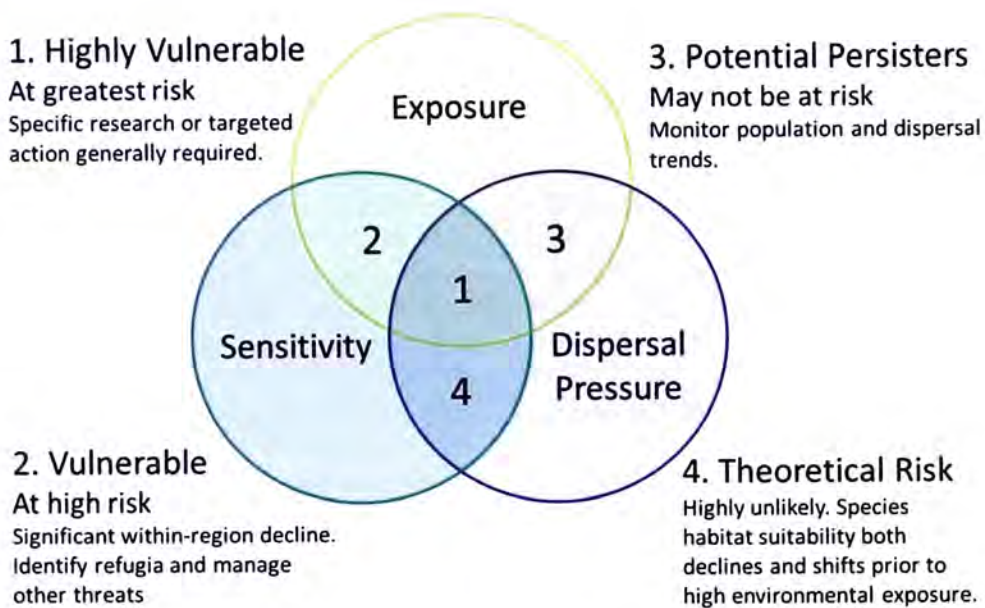


Fig. 1 Categories of vulnerability to climate change. The effects of climate change on a species were based on three components: exposure, sensitivity and dispersal pressure. Possible adaptation options are given for species at risk under multiple components (adapted from (Foden et al., 2013)).

For each climate scenario and time period, exposure was calculated as the average number of standard deviations (SD) that conditions are projected to shift in the future across a species' current modelled habitat. A change of one to two SDs in exposure meant 67-97.5% of a species habitat would be outside the current environmental extent. We assumed that species

have evolved to cope with the inter-annual variation within their current environment. A change of two SDs was therefore considered a reasonable limit, beyond which the likelihood that a species would adapt in situ was very low (Palmer & Raisanen, 2002; Beaumont et al., 2011). The mean and seasonality of annual temperature and precipitation, mean annual flow, and sea level rise were used as measures of exposure. A species was considered vulnerable if its exposure was above two SDs for any climate or hydrological factor, or if it was exposed above one SD for multiple factors. Exposure of a species' suitable habitat to sea-level rise was also considered important if 10% of the habitat was within 1m of sea level (Radić et al., 2013).

Species' sensitivity was calculated using the methods described in Crossman et al. (2011) as the ratio between the change in habitat suitability, and the future scenario total suitability. Change in a species' distribution was based on the sum of habitat suitability over all streams in the future, subtracted from the sum of suitability for streams under current climate. Suitability scores below the species TSS-threshold were not included. Species with negative sensitivity values are likely to expand their range or have higher overall suitability in the future, whereas higher values occur when the species' habitat either contracts in area, or becomes less suitable. Species with sensitivity ratios above one were considered highly vulnerable.

Dispersal

In addition to exposure and sensitivity, the adaptive capacity of a species can also affect vulnerability. Dispersal is a key aspect of adaptive capacity because it affects the proportion of environmentally suitable habitat that a species can occupy, both now and in the future. Dispersal constraints were initially used to prevent highly unlikely scenarios requiring long-distance movements and improve upon standard no- and full-dispersal comparisons (Reside et al., 2012). As the raw species model was constrained using a relatively high dispersal rate the

estimate of vulnerability was considered conservative. The analysis of the impact of dispersal capacity on species vulnerability was therefore made in relation to this upper rate. Species were considered more vulnerable if suitable habitat in the future was distant from current records, or if the extent of suitable habitat rapidly declined when the dispersal threshold was reduced (see examples in S4).

Measuring dispersal capacity directly is extremely difficult but studies of genetic population structure in aquatic insects suggest regular movement does occur across catchment divisions (Hughes et al., 2013). Migratory dragonflies can move 12 km per day (Wikelski et al., 2006) and as the climate has changed over the past few decades, there have been an increasing number of reports of species dispersing considerable distances to colonise new regions; e.g. *Anax imperator* (Leach, 1815) 88 km per year (Flenner & Sahlén, 2008).

Nonetheless, most species are likely to disperse much shorter distances. Six European species studied by Jaeschke et al. (2012) disperse between 0.5 and 14 km per year and the 37 non-migratory British species studied by Hickling et al. (2005) expanded north by an average 6.8 km per year.

We restricted the area of suitable habitat available to a species based on a cost-weighted distance, and a dispersal kernel. The cost-weighted distance calculates a least-cost path across a 1 km grid that determines the cost of movement (done in ArcMap 10.1). Distance from recorded observations of a species to the centroid of other streams could be modified by altering the cost of movement across surfaces such as open water (Sawyer et al., 2011). We then used a dispersal kernel based on a four-parameter logistic curve to model declining dispersal probability in an ecologically relevant way (Fig. 2). The dispersal kernel converted the cost-weighted distances to a value between 0 and 1 that indicates the probability of dispersal to that stream from known presences (Crossman et al., 2011; Meier et al., 2012). The threshold distance and decay rate of the dispersal curve were varied so that weighting

suitability scores by dispersal probability are reduced at distant locations beyond the threshold.

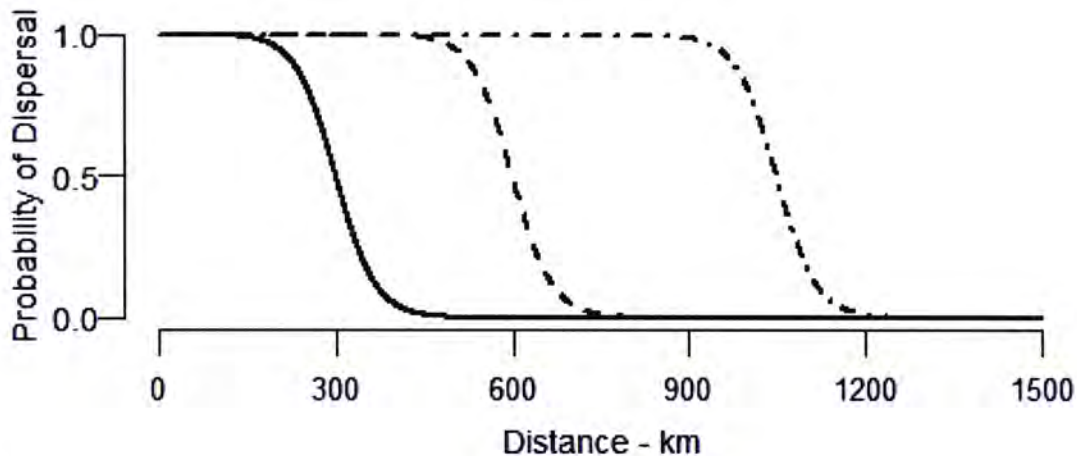


Fig. 2 Modelled probability of species dispersal with distance from known records. Under current conditions (solid line) suitability is reduced around 300 km, and extended to 630 km (2055) and 1080 km (2085) under future climate change scenarios.

The choice of appropriate threshold and dispersal cost was based on the initial observation that many Odonata in Victoria have not been recorded in Tasmania, about 200 km away across the Bass Strait. However, a 200 km threshold would have prevented continuous distribution of some species in northern and central Australia where gaps are most likely a reflection of low sampling. As a result, we doubled the cost of crossing open water, but increased the threshold to 300 km, thereby allowing continuous mainland distributions and still constraining species occurrence in Tasmania if they currently only occur on the mainland. Under future projections, potential range shifts were allowed to occur by increasing the threshold distances to 630 and 1080 km for 2055 and 2085 respectively. These distances were equivalent to an expansion of 15 km year⁻¹ from their current recorded position; a rate observed in the damselfly *Sympecma fusca*, that has responded rapidly to climate change in Sweden (Flenner & Sahlén, 2008). Interestingly the observed rate of expansion in the study

by Hickling et al. (2005) was not related to body size, indicating Anisoptera may not disperse more rapidly than Zygoptera (Angert et al., 2011). In the absence of data for Australian species, this seemed an appropriate upper limit for this analysis (Jaeschke et al., 2012).

To assess vulnerability based on the predicted pressure on a species to disperse, we split the assessment into two parts: the mean distance of habitat shifts, and the dependence of the sensitivity weighting on dispersal thresholds. First, we compared the mean distance from recorded observations of each species to all suitable habitat in their current and future modelled ranges using a Wilcoxon rank sum test. Species scored 0 if suitable habitat was not significantly further away from observed records in the future than the present, 1 if the difference was significant ($p=0.05 \sim 2$ SDs), and 2 if the difference was over three SDs, indicating decreasing overlap of habitats, or potentially greater fragmentation. The second approach identified the importance of rapid dispersal for a species by estimating at what point a reduction in dispersal ability from the conservative estimate of 15 km year⁻¹ would significantly reduce the habitat available based on the sensitivity weight. The dispersal thresholds were split into 30 levels with 10 high, medium and low thresholds between the current habitat limit (300 km) and future threshold (630 or 1050 km depending on the scenario) (see examples in S4). Sensitivity weights increased as suitable habitat was successively removed and we estimated the rate of change from the slope of a regression between threshold distance (log transformed) and the sensitivity weight. A species was given a score of 3, 2 or 1 if the slope was less than one for high, medium or low thresholds respectively, and zero if it was not. Thus species whose future suitable habitats are concentrated in distant regions are considered more vulnerable because small reductions (0.5–5 km year⁻¹) in dispersal capacity would significantly reduce the availability of suitable habitat. Thus combined with the habitat shift score, a maximum of 5 points was available, and species that scored three or more were considered vulnerable.

Finally, separate to the two measurements of dispersal ability above, we also considered the possibility that the Bass Strait could remain a barrier to species shifting their distributions to Tasmania under climate change. This time the dispersal kernel was kept constant, but by increasing the cost of movement across the sea to 100 times that of land the dispersal kernel then acts to remove all potentially suitable habitat from Tasmania for species not already recorded there. Although some Odonata occur either side of the Bass Strait (e.g. the damselfly *Hemiphysalis mirabilis*), most do not, and we compared the sensitivity and vulnerability scores of species affected by this change.

Conservation Priorities

The importance of all subcatchments to the conservation of vulnerable species was calculated for both highly vulnerable (Category 1) and vulnerable (Category 2) species for each time and emissions scenario. The score for all streams was the sum of habitat suitability weighted by the sensitivity weighting for that species in each scenario (Crossman et al., 2011). Thus, subcatchments scored highly if they contained suitable habitat for many vulnerable species, or for species that had experienced major declines in habitat suitability elsewhere.

RESULTS

Between 56 and 69% of species are predicted to experience an overall decline in habitat extent by 2085 depending on emissions scenario. Using the RCP 8.5 scenario, 17% of species were classified as vulnerable by 2085 (Category 2) due to high exposure to climatic change and significant declines in habitat suitability. A further 17% were classified as highly vulnerable (Category1) because to occupy suitable habitats they also need to disperse long distances (Fig. 3 and Fig. 4).

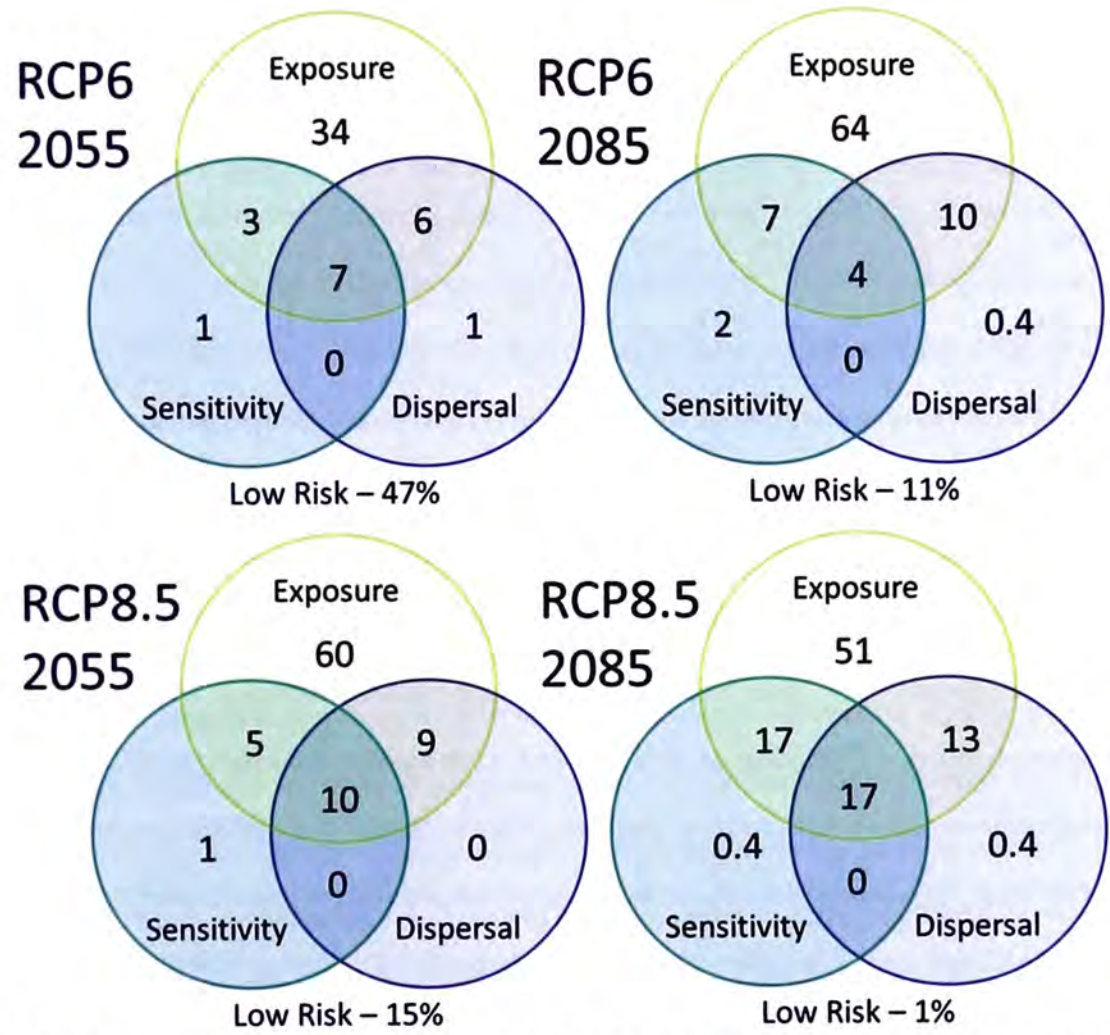


Fig. 3 Percentage of species ($n=270$) found to be vulnerable to climate change according to their exposure, sensitivity and predicted pressure to disperse. Species are most vulnerable if they are at risk in all components (Category 1).

Exposure

Environmental conditions shifted beyond the range experienced by 50-95% of species in their current suitable range under future climate change. By 2085 the current distribution of 30-61% of species was two SDs outside their current mean annual temperature range and two SDs outside the current range of annual flow in 59-71% of species. In all, 39-65% of species were exposed over multiple factors, and the number of factors to which a species was exposed was higher among uncommon species ($t_{93}=-7.62$, $p<0.001$). The species with the greatest exposure to potential change was *Archiargiolestes parvulus* (Watson, 1977), exposed across four factors as well as sea level rise. A 1m rise in sea level was influential (loss>10%) for 44 species that on average lost 17% (SD 7.8, max 37%) of their suitable habitat due to this factor alone.

Sensitivity

Species whose habitat was predicted to either contract substantially or to become significantly less suitable had a higher sensitivity weight. The predicted range of sensitivity scores reflects a broad range of potential responses from considerable expansion (e.g. $S=-0.84$, +500% for *Camacinia othello* Tillyard 1908) to near extinction (e.g. $S=30.5$, -97% for *Lathrocordulia metallica* Tillyard 1911). Under both RCP6 and RCP8.5 emissions scenarios, six species (*Austroaeschna ingrid* Theischinger 2008, *Austroaeschna muelleri* Theischinger 1982, *Hemigomphus cooloola* Watson 1991, *Indolestes obiri* Watson 1979, *Lestoidea lewisiana* Theischinger 1996, *Nososticta pilbara* Watson 1969) are predicted to lose all suitable habitat by 2055. Fifteen species (including the six above) are predicted to have no suitable habitat remaining by 2085. Sensitivity weight was not correlated with overall habitat extent ($r^2=0.313$) because there could be significant losses or gains in suitability as well. It was also

not highly correlated with loss of current suitable habitat ($r^2 < 0.2$) because many species were assumed to be able to colonise new suitable habitats.

Dispersal Pressure

When relatively rapid movement (15 km year⁻¹) using the dispersal kernel was assumed, most species were projected to be able to shift to higher latitudes (68% >1° by 2085-RCP8.5) or altitudes (46 Wet Tropics species move 245 m higher on average by 2085-RCP8.5), consistent with the exposure to rising temperatures. For example under the RCP8.5 scenario, 85 species were projected to potentially shift their distributions an average of 370 km by 2085 (max. species average = 862 km). Successful transitions to these new habitats are less likely with increasing distance and we scored species vulnerability based on both distance travelled, and the impact of distance threshold on the species overall sensitivity. Of the 85 species above, 31 were projected to experience significant declines if the dispersal rate was reduced by just 0.5 to 5 km year⁻¹. Manipulation of the dispersal kernel also showed that some species could be more vulnerable in the mid-term (2055) than under long-term projections (2085) because they needed to disperse long distances by 2055 to reach suitable habitat. This is partly the reason why the proportion of species in Category 1 is higher under scenario RCP6 in 2055 than 2085.

This assessment chose to rank each of the three components of vulnerability equally, and therefore only species at risk in all components were classified as highly vulnerable (i.e. Category 1 Fig. 4a). However, Category 2 species from the far south-west of the continent and from Tasmania do not have the option of shifting to habitats further south, and likewise suitable habitat conditions for species in the Wet Tropics are not predicted to become available elsewhere, meaning the species are inherently dispersal limited by the landscape (Foden et al., 2013). Despite being highly exposed and sensitive to change, the lack of opportunity for movement meant habitats declined in situ, and dispersal capacity may be

unlikely to contribute to greater vulnerability (Fig. 4b). In some cases, the overall decline (and sensitivity score) in suitable habitat was greater than for Category 1 species and therefore species in Category 2 are still considered at high risk (Fig. 1 and Fig. 3). Although a high proportion of species are predicted to be exposed to climate change, sensitivity was low for many species if suitable habitat was still available or even increased overall (Category 3, Fig. 4c).

Dispersal Barriers

By assuming an increased cost of dispersal across the open sea, predicted suitable habitat in Tasmania was removed for species currently found only on the mainland. Potentially suitable habitat could be available in Tasmania for up to 73 new species by 2085 under the RCP8.5 scenario (Fig. 4a and c). In many cases losing this potential dispersal option was not significant, but for 24 species the increase in the sensitivity weighting was sufficient to alter their overall score and switch the category of vulnerability from Category 3 to Category 1 or 2 (see Fig. 1). Changing the nature of the Bass Strait to a dispersal barrier is particularly significant for the projections for three upland specialists found on the mainland (*Cordulephya montana* Tillyard 1911, *Austroaeschna subapicalis* Theischinger 1982, *A. flavomaculata* Tillyard 1916), reducing the availability of their potential new habitat by 36-90%.

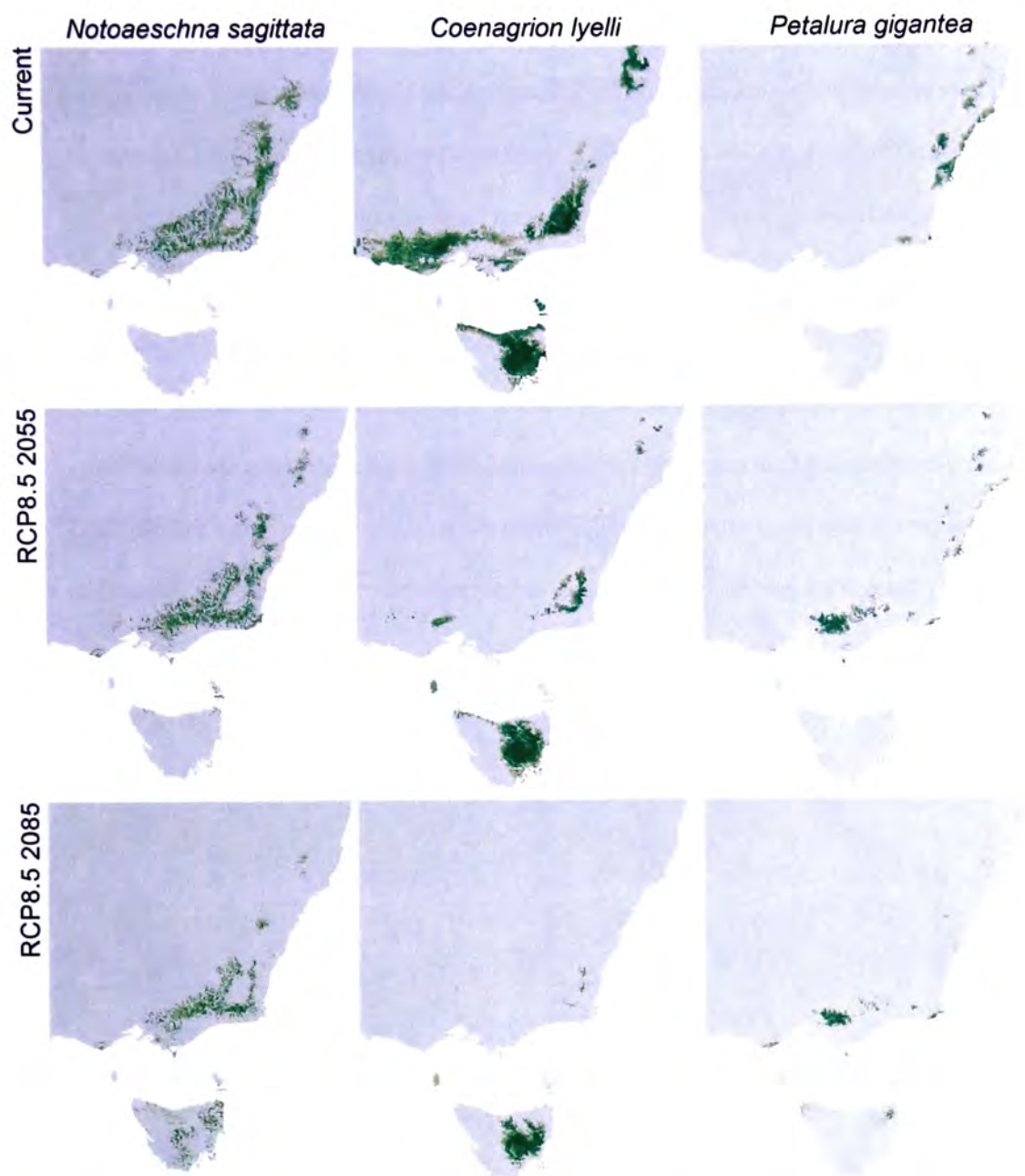


Fig. 4 Predicted suitable habitat in south-eastern Australia under current climate and 2055 and 2085 using emissions scenario RCP8.5 for *Notoaeschna sagittata*, *Coenagrion lyelli* and *Petalura gigantea*. High suitability is in dark green.

Conservation Priorities for Vulnerable Species

Priority streams and rivers important for conserving the highly vulnerable Category 1 and high risk Category 2 species varied for different time periods and emissions scenarios modelled, but were largely nested within the same core regions (Fig. 5). For the most vulnerable Category 1 species, pockets of permanent water in the Pilbara and north-west of Australia are critical, in particular the Gascoyne and Ashburton rivers. By 2085, there is also a strong emphasis on coastal New South Wales and high altitude areas extending south to the Australian Alps. Without assuming high dispersal limitations to crossing the Bass Strait, Tasmania will also be an important conservation focus. Although not under pressure to disperse, Category 2 species would become increasingly restricted to pockets of suitable habitat within the Wet Tropics and east Cape York peninsula in northern Queensland, the far south-west of Western Australia, Tasmania and small areas within the Kimberley in the north.

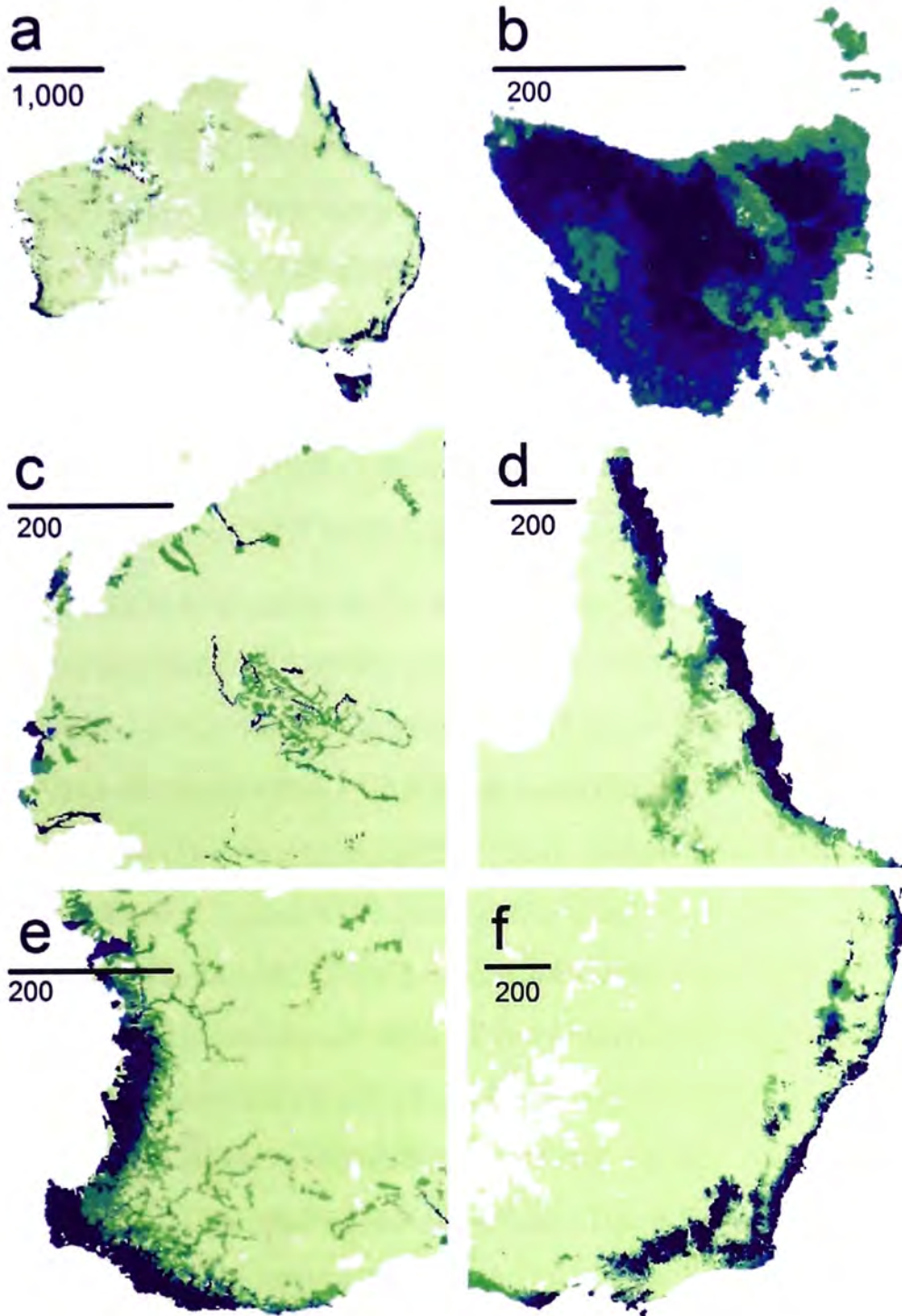


Fig. 5 Map of conservation priorities for Odonata vulnerable to climate change in Categories 1 and 2. The panels show priorities in dark blue for (a) Australia, and regional views of (b) Tasmania, (c) the north-west, (d) Cape York peninsula, (e) the south-west and (f) the south-east.

DISCUSSION

This study predicts that 56-69% (153-187 species) of the Australian Odonata modelled will experience a decline in habitat extent by 2085 as a result of climate change, including a number of potential extinctions in the medium and long term. A third of modelled species were considered highly vulnerable or vulnerable by 2085-RCP8.5 (Category 1 and 2) and though species vulnerability was reduced under a more moderate emissions scenario (RCP6) they remain highly dependent on their ability to rapidly track shifting habitats. Priorities for the conservation of vulnerable species are highest in the south-west and south east of the continent, the Wet Tropics region, and in the rivers in the north-west.

Species classified as uncommon prior to modelling were more likely to be vulnerable to the effects of climate change because of their higher exposure. This seems reasonable given stochastic fluctuations from climatic disturbances represent a greater risk to small populations (Williams et al., 2008). Australian Odonata appear to face a similar degree of threat as European aquatic macroinvertebrates where 57% of species are predicted to decline by 2080 (Domisch et al., 2012). Several recent modelling studies have assessed climate change effects on a variety of taxa across continental Australia (Garnett et al., 2013; James et al., 2013; Reside et al., 2013) and Odonata appear to be among the less threatened taxa, although the rarest taxa were not modelled. Although there is some congruence between the distribution of the most vulnerable Odonata and species of birds and crayfish, differences in the distribution of threatened terrestrial and freshwater taxa demonstrates the importance of combining datasets to avoid taxonomic biases when setting conservation priorities (Darwall et al., 2011).

Modelling limitations

All models could be improved with greater availability of occurrence records (Comte et al., 2012), or more detailed environmental data (Storlie et al., 2013). However, the main cause of uncertainty stems from the fact that modelling techniques that make projections based on

environmental predictors and presence-only data are at risk of over-estimating suitable habitat extent and including errors of commission because the models assume that all suitable climate space is occupied (Pineda & Lobo, 2012). Although we account for a number of issues including testing and incorporating a number of non-climatic variables, targeting selection of background points and limiting the degree of extrapolation to novel environments (Heikkinen et al., 2006), other factors including local habitat conditions, dispersal and species interactions could limit species occurrence within regions of environmental suitability.

While climate and historical factors account for the distribution of freshwater biota at regional spatial scales (Pace et al., 2013), and the high spatial resolution of the study increased the potential for microclimatic refugia to be identified (Gillingham et al., 2012; Pineda & Lobo, 2012), species occurrence within stream segments is often determined by additional factors such as water volume, habitat heterogeneity, water chemistry, temperature, disturbance and predation e.g. (Warfe & Barmuta, 2006; Nicola et al., 2010). If these conditions are not suitable within a climatically suitable region (Heino, 2011), then by default a species will be absent from the entire region. For example, the extent of stream habitat available to species specialising in riffles (e.g. *Lestoideidae* spp.), bogs (e.g. *Petalura* spp.) or waterfalls (e.g. *Austropetalia* spp.) will only be a fraction of the subcatchment. In addition, an important factor affecting habitat suitability is human disturbance, with large areas of the landscape already modified (Stein et al., 2002). Highly disturbed sites could have been excluded in this analysis, except that our understanding of how rapidly habitat suitability changes, and at what point this could exclude a species, is poor. One method for improving our understanding would be to examine the assembly rules that determine local composition from a species pool generated by SDMs (Pellissier et al., 2013).

Although we include changes in stream hydrology within our models, climate change could alter the intensity of cease-to-flow events, floods, droughts and increase evaporation of pool

habitats, modifying the true nature of habitat availability within a subcatchment from year to year (Lake, 2003; Hobday & Lough, 2011). A switch from perennial to intermittent streams and ponds reduces the time available for larvae to complete development, but may well suit some taxa such as Lestidae (Theischinger & Endersby, 2009). The threat of saltwater intrusion as a result of sea-level rise is also potentially under-appreciated, as many species were projected to lose habitat along the east coast, including some dune system specialists (Arthington & Watson, 1982; Bush et al., 2012). Finally, it is worth noting that a species may persist in a region modelled as climatically unsuitable. *Nososticta pilbara* was predicted to lose all climatically suitable habitat, but because it primarily occurs in a few groundwater-fed streams, it may persist in these refuge habitats in the future, resilient to the broader changes in climate (Davis et al., 2013).

For suitable habitat to support a particular species it must also be within dispersal range. Odonata are among the strongest of flying insects, but dispersal ability can still limit their ability to colonise suitable habitat e.g. (Keller et al., 2010). Estimates of dispersal ability could be improved through more intensive monitoring of range shifts or by mark-recapture studies (Conrad et al., 1999), but even then it can be difficult to relate species' traits and landscape suitability to the distances travelled in response to climate change (Angert et al., 2011).

Our assessment of the contribution dispersal could have to vulnerability is more thorough than previous studies that have simply assumed either full- and no-dispersal (Bateman et al., 2013). Some species modelled in this study will not disperse as quickly as 15 km year⁻¹, perhaps because they have multi-year development as larvae (Jaeschke et al., 2012), or due to preferences for lentic or lotic habitats (Grewe et al., 2013). The Bass Strait is likely to present a dispersal barrier to at least some of the 24 species we predict will be affected, and exacerbate the decline in available habitat. Furthermore, while many species classified in

Category 3 are not considered at risk because their sensitivity is low, this will only be the case if they can colonise new habitats, and their progress should be monitored.

Although Odonata are generalist predators, and therefore not reliant on particular prey species, competition amongst ecologically similar species or with other macroinvertebrates could also modify their future distributions. For example, the competitive balance between two coexisting dragonfly species in Germany is predicted to become skewed as temperature increases because one will grow faster, and is subsequently more likely to prey on the smaller conspecific larvae (Suhling & Suhling, 2013). Changes in the structure of fish assemblages (Buisson et al., 2012) could also result in changes to predation pressure (McPeck, 1998).

Based on the range of limitations that could potentially reduce the realised distribution of species from the modelled extent, the suitability scores are best viewed as a species' maximum potential abundance in an area (VanDerWal et al., 2009b). Therefore, although some species may adapt or have the flexibility to occupy novel climates, the risk of local and potentially global extinction is likely to be significantly higher than we can currently identify due to our limited knowledge of species ecology (Cardoso et al., 2011). Furthermore, insufficient records for 51 Odonata meant SDMs could not be applied to the species potentially at greatest risk under climate change.

Implications for Management and Conservation

Australia's low relief offers little capacity for altitudinal movement, meaning most species must undergo latitudinal shifts to stay within their current environmental envelopes. All species determined to be vulnerable or highly vulnerable are endemic to Australia, and given Australia's history of isolation from neighbouring countries such as Papua New Guinea (Kalkman & Orr, 2012), it is unlikely species would be able to reach suitable habitats outside

Australia (but see (Winterbourn et al., 2011)). Our modelling indicated that suitable odonate habitats retreated to higher elevations in the Wet Tropics, where changes in precipitation and cloud cover that threaten rainforest vertebrates could also affect these invertebrates (Hagger et al., 2013). Several high elevation species in New South Wales are also highly isolated, and these regions will also become priorities for other species as climate change intensifies.

Within cooler region such as Tasmania, regional endemics may persist unless other environmental changes alter habitat suitability e.g. fire (Barmuta et al., 2013), and if they are not competitively displaced by immigrant species (Suhling & Suhling, 2013). Many species endemic to the Pilbara or south-west Australia will be reliant on the availability of permanent freshwater to avoid extinction (Pinder et al., 2010; Davis et al., 2013).

Preventing the loss of species in the face of multiple stressors, many of which are synergistic with the effects of climate change, is a virtually impossible task (Rohr & Palmer, 2013).

Nonetheless, climate change presents a clear danger to Odonata and other freshwater species and we can improve conservation efficiency by incorporating these projections into decision-making (Hannah et al., 2007), identifying suitable strategies before declines become severe (Shoo et al., 2013). Habitat restoration can be effective at local scales and insect populations including Odonata can be quick to respond (Simaika & Samways, 2009; Morimoto et al., 2010), although problems may persist if restoration does not account for upstream influences or when sites are isolated (Armin et al., 2013). Freshwater refugia will be crucial to species persistence in regions like the Wet Tropics (James et al., 2013) and the Australian alpine region, but also more generally during droughts, as the climate continues to change (Chester & Robson, 2011).

Although the predicted risks to Australian Odonata from climate change outlined in this study are significant, they are probably quite conservative. Other threats such as habitat modification and water extraction would also need to be included to avoid underestimating the true extinction risk (Brook et al., 2009). Shifts in suitable habitat predicted by this analysis

could soon become observed range shifts and the current and future value of streams should be considered in conservation planning.

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Supplementary Information

Table S1 Sources of Australian Odonata Occurrence Data

Source	Approximate # Records
Museums	29,400
Australian Museum	1600
Australian National Insect Collection	16100
National Museum of Victoria	650
Northern Territory Museum	850
Queensland Museum	8600
Queen Victoria Museum and Art Gallery	350
South Australian Museum	1000
Tasmanian Museum and Art Gallery	150
Western Australian Museum	100
Government	15,450
Australian Plant Pest Database	1500
Bush Blitz (see http://www.bushblitz.org.au/)	100
Georges River Catchment Authority	200
Sydney Catchment Authority	100
New South Wales Office of Environment and Heritage	7450
Queensland Department of Environment and Resource Management	200
Department of Environment and Primary Industries	3100
Western Australia Department of Environment and Conservation	2800
Private	13,300
Dennis Paulson	1450
Ian Endersby	450
Roger Garrison	350
Vincent Kalkman	400
Karen Sutcliffe (PhD thesis)	1500
Nick Donnely	450
Fons Peels	450
Reiner Richter	3100
Gunther Theischinger	5150

S2 Predictor variables and model validation summary

Table S2 Environmental factors used to predict species distributions and their mean predictive importance (r^2). Variables were assigned to species on the basis of broad geographic regions and number of locality records (common on the left side, uncommon on the right).

Variable	Continental	North	North East	East	South	West
Mean Annual Temperature	0.53	0.41	0.31	0.41	0.45	0.36 0.38
Temperature Seasonality	0.38	0.38 0.35	0.33 0.38	0.40 0.50	0.35 0.39	0.44
Min. Temp. Coldest Month	0.38	0.33 0.36	0.31 0.42	0.33 0.50	0.28 0.50	0.43 0.33
Precipitation Seasonality	0.32	0.39 0.45	0.47 0.53	0.35 0.52	0.35 0.49	0.39 0.30
Precipitation of Wettest Qtr.	0.41	0.61 0.56	0.66 0.83			0.76 0.54
Precipitation of Driest Qtr.				0.41 0.41	0.44 0.59	
Mean Annual Flow	0.37	0.41 0.50	0.47 0.37	0.48 0.50	0.40 0.30	0.46 0.57
Valley Confinement	0.45	0.43	0.40	0.39	0.46	0.39

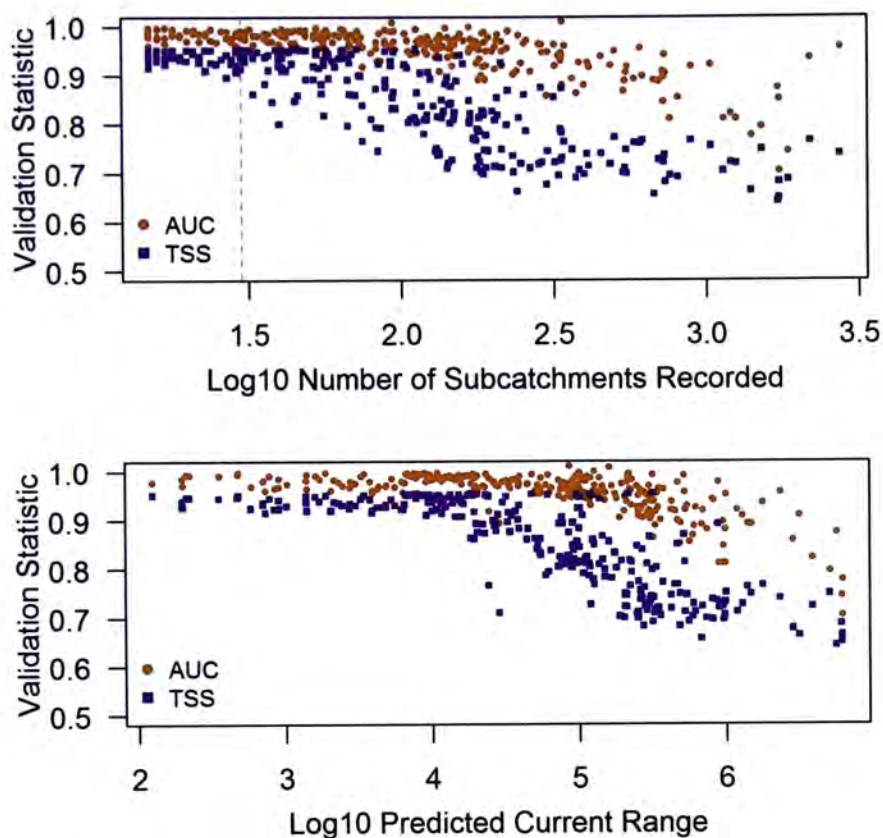


Figure S2.2 The ensemble model score for each species ($n=270$) based on either the area under the receiver operating characteristic curve (AUC), or the True Skill Statistic (TSS). The dashed line indicates species with occurrences in 30 subcatchments below which species were modeled as "Uncommon".

Table S3. Model predictions for all species under emissions scenario RCP8.5. The region code and record group dictate which group of variables were used to predict species habitat suitability (C=continental, N=north, NE=north-east, E=east, S=south and W=west). Model scores are for the True Skills Statistic (TSS) and Area under the Operating Curve (AUC). Current range is the current extent of suitable habitat in km2.

For projections in 2055 and 2085 values indicate the percentage loss (Loss) and percentage (gain) in suitable habitat extent, the sum of the climate exposure score (C), whether the sensitivity score was above one and considered vulnerable (S), the sum of dispersal score measurements (D), and the overall vulnerability class (V). Vulnerability classes; vulnerable across all categories(1), combination of exposure and sensitivity (2), exposure and dispersal (3), dispersal and sensitivity(4), exposure only (5), sensitivity only (6), dispersal only (7) and not vulnerable for any category (0)

Species	Region	Record Group	Model Score		Current Range	RCP85_2055					RCP85_2085					
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D
<i>Acanthaeschna victoria</i>	E	U	0.952	0.993	15129	40	176	0.5	1	0	57	170	3	5	3	
<i>Aciagrion fragile</i>	NE	C	0.768	0.924	109898	38	19	1.5	1	5	70	4	1.5	Y	1	2
<i>Adversaeschna brevistyla</i>	C	C	0.67	0.795	891865	33	3	0.5	1	0	45	5	1.5	1	5	
<i>Aethriamanta circumsignata</i>	NE	C	0.801	0.944	178981	27	90	1	1	5	44	41	1.5	1	5	
<i>Aethriamanta nymphaea</i>	NE	U	0.883	0.975	38953	36	166	1	1	5	51	160	2.5	1	5	
<i>Agriocnemis argentea</i>	N	C	0.81	0.951	287560	66	32	1.5	1	5	78	41	2	1	5	
<i>Agriocnemis dobsoni</i>	NE	U	0.952	0.999	212	100	41	1	Y	4	100	8	2.5	Y	4	1
<i>Agriocnemis kunjina</i>	W	U	0.952	0.995	5291	100	41	1	Y	5	100	41	1.5	Y	5	1
<i>Agriocnemis pygmaea</i>	NE	C	0.64	0.847	316948	36	140	1	1	5	52	35	1	1	5	
<i>Agriocnemis rubricauda</i>	NE	C	0.794	0.956	62119	67	17	1.5	0	5	93	14	3	Y	3	1
<i>Agrioptera insignis allogenes</i>	NE	C	0.782	0.938	99676	32	22	1	1	5	43	16	2.5	1	5	
<i>Agrioptera longitudinalis biserialis</i>	NE	C	0.953	0.992	5571	34	79	1	1	5	65	71	1.5	1	5	
<i>Anaciaeschna jaspidea</i>	N	U	0.951	0.995	18778	27	125	1	1	5	50	104	3	1	5	
<i>Anax gibbosulus</i>	NE	C	0.859	0.958	123661	21	149	1.5	1	5	38	53	2.5	1	5	
<i>Anax guttatus</i>	N	C	0.764	0.949	159657	12	136	1.5	1	5	24	128	3	1	5	
<i>Anax papuensis</i>	C	C	0.598	0.735	6137882	1	0	1	1	5	3	1	1	0	5	
<i>Antipodogomphus acolythus</i>	E	C	0.846	0.969	246243	31	102	1	1	5	30	110	2	1	5	
<i>Antipodogomphus hodgkini</i>	W	U	0.952	0.998	1711	100	34	2	4	3	100	55	2	3	3	
<i>Antipodogomphus proselythus</i>	NE	U	0.952	0.988	13345	64	160	1.5	1	5	84	185	2.5	2	5	
<i>Antipodophlebia asthenes</i>	E	U	0.91	0.983	34641	54	65	1.5	1	5	80	37	2.5	Y	5	1
<i>Apocordulia macrops</i>	S	C	0.953	0.991	95762	40	51	1.5	1	5	60	46	2	1	5	

Species	Region	Record Group	Model Score		Current Range	RCP85_2055						RCP85_2085					
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D	V
<i>Archaeophya adamsi</i>	E	U	0.952	0.997	4338	98	144	2.5	3	3	3	100	45	3	Y	5	1
<i>Archaeophya magnifica</i>	NE	U	0.945	0.987	7772	40	60	1	1	5	5	64	41	2	0	5	
<i>Archaeosynthemis leachii</i>	W	C	0.899	0.979	25874	42	1	1	1	5	5	61	3	2	Y	1	2
<i>Archaeosynthemis occidentalis</i>	W	C	0.905	0.976	75771	16	4	1	0	5	5	27	7	2	Y	1	2
<i>Archaeosynthemis orientalis</i>	S	C	0.811	0.944	111703	42	22	0	1	0	0	65	24	1.5	1	5	
<i>Archaeosynthemis spiniger</i>	W	U	0.949	0.986	24167	62	38	2	Y	0	2	86	14	2	Y	0	2
<i>Archargiolestes parvulus</i>	W	U	0.952	0.999	3274	98	91	2.5	1	5	5	100	41	4.5	2	5	
<i>Archargiolestes pusillissimus</i>	W	U	0.953	0.992	20201	69	8	1.5	Y	1	2	72	16	1.5	1	5	
<i>Archargiolestes pusillus</i>	W	C	0.856	0.963	96223	31	8	0.5	1	0	0	42	10	1.5	Y	1	2
<i>Archibasis mimetes</i>	NE	C	0.938	0.986	15753	42	32	1	0	5	5	65	25	2	0	5	
<i>Archipetalia auriculata</i>	S	U	0.925	0.983	6212	94	4	2	Y	3	1	100	0	3	Y	5	1
<i>Argiocnemis rubescens</i>	C	C	0.645	0.842	590293	37	169	1	1	5	5	60	161	1.5	2	5	
<i>Armigomphus armiger</i>	W	U	0.952	0.993	6818	100	0	2	Y	5	1	100	0	2	Y	5	1
<i>Austroaeschna anacantha</i>	W	C	0.861	0.966	19345	50	0	2	Y	0	2	69	0	2	Y	1	2
<i>Austroaeschna obscura</i>	S	C	0.876	0.966	33824	84	110	2.5	4	3	3	94	122	2.5	4	3	
<i>Austroaeschna parvistigma</i>	S	C	0.636	0.886	342452	41	0	0	0	0	0	61	0	1.5	Y	0	2
<i>Austroaeschna pinheyi</i>	E	C	0.953	0.999	1886	100	351	3	Y	5	1	100	187	3	5	3	
<i>Austroaeschna pulchra</i>	S	C	0.608	0.875	271809	17	22	1	1	5	5	32	23	2	2	5	
<i>Austroaeschna sigma</i>	E	C	0.767	0.928	118725	26	123	1	1	5	43	131	2.5	2	5		
<i>Austroaeschna speciosa</i>	NE	U	0.951	0.996	6797	73	1	1	Y	0	2	93	0	1.5	Y	0	2
<i>Austroaeschna subapicalis</i>	S	C	0.715	0.917	59114	47	67	1	5	3	69	72	1.5	4	3		

Species	Region	Record Group	Model Score		Current Range	RCP85_2055					RCP85_2085						
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D	V
<i>Austroaeschna tasmanica</i>	S	C	0.781	0.94	18344	35	28	0	1	0	64	33	1.5	1	5		
<i>Austroaeschna unicornis</i>	S	C	0.687	0.869	447473	28	5	0.5	1	0	43	4	1.5	0	5		
<i>Austroagrion cyane</i>	W	C	0.769	0.933	513930	39	77	0	1	0	43	85	0.5	1	0		
<i>Austroagrion exclamationis</i>	NE	C	0.646	0.902	204037	43	65	1.5	1	5	86	14	2	Y	1	2	
<i>Austroagrion pindrina</i>	W	C	0.867	0.969	143842	89	3	2	3	3	89	3	2	Y	2	2	
<i>Austroagrion watsoni</i>	C	C	0.662	0.791	979482	42	15	0.5	1	0	51	15	1	0	5		
<i>Austroargiolestes alpinus</i>	S	U	0.952	0.999	473	8	67	2.5	1	5	100	0	2.5	Y	0	2	
<i>Austroargiolestes amabilis</i>	E	C	0.832	0.955	54161	52	48	1	1	5	90	23	2.5	Y	5	1	
<i>Austroargiolestes aureus</i>	NE	C	0.936	0.983	9857	46	15	1	1	5	66	2	2	Y	0	2	
<i>Austroargiolestes brookhousei</i>	S	U	0.952	0.995	2046	73	258	1.5	5	3	87	105	2.5	5	3		
<i>Austroargiolestes calcaris</i>	S	C	0.826	0.96	84490	46	43	0.5	1	0	66	49	1.5	4	3		
<i>Austroargiolestes christine</i>	E	C	0.954	0.996	3897	47	335	2	1	5	90	18	2	Y	5	1	
<i>Austroargiolestes chrysoides</i>	E	C	0.953	0.995	3915	87	254	2.5	5	3	98	224	3	4	3		
<i>Austroargiolestes icteromelas</i>	E	C	0.604	0.816	481535	25	15	1	1	5	38	17	1.5	2	5		
<i>Austroargiolestes isabellae</i>	E	C	0.944	0.984	15575	81	153	2.5	4	3	98	179	2.5	3	3		
<i>Austrocnemis maccullochi</i>	N	C	0.915	0.972	33091	39	516	2	1	5	66	142	3	2	5		
<i>Austrocnemis splendida</i>	E	C	0.648	0.887	421876	35	44	1	1	5	46	50	1.5	1	5		
<i>Austrocordulia leonardi</i>	E	U	0.951	0.999	707	100	152	3	Y	4	1	100	318	3	5	3	
<i>Austrocordulia refracta</i>	E	C	0.632	0.882	298017	32	32	1	1	5	46	36	1.5	1	5		
<i>Austroepigomphus gordonii</i>	W	C	0.813	0.957	520849	70	20	1.5	Y	4	1	74	26	2	Y	3	1
<i>Austroepigomphus praeurptus</i>	E	C	0.699	0.918	370755	49	37	2	1	5	66	49	2	1	5		

Species	Region	Record Group	Model Score		Current Range	RCP85_2055					RCP85_2085					
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D
<i>Austroepigomphus turneri</i>	NE	C	0.839	0.959	267132	44	66	1.5	1	5	79	24	1.5	Y	3	1
<i>Austrogomphus amphilictus</i>	E	C	0.615	0.882	247376	39	52	1	1	5	56	67	2		2	5
<i>Austrogomphus arbustorum</i>	NE	U	0.952	0.998	8941	61	229	2.5	1	5	75	269	2.5		1	5
<i>Austrogomphus australis</i>	C	C	0.659	0.909	814103	63	20	1.5	1	5	68	22	2.5		1	5
<i>Austrogomphus bifurcatus</i>	NE	U	0.937	0.984	9998	40	21	1	1	5	68	13	2	Y	0	2
<i>Austrogomphus collaris</i>	W	C	0.855	0.972	52315	37	24	0.5	1	0	59	11	1.5		0	5
<i>Austrogomphus cornutus</i>	E	C	0.659	0.864	690334	35	15	1	0	5	51	17	2		1	5
<i>Austrogomphus divaricatus</i>	NE	C	0.917	0.986	19346	51	17	0.5	1	0	76	6	1.5	Y	1	2
<i>Austrogomphus guerini</i>	S	C	0.665	0.857	262475	47	6	1	0	5	69	8	1.5	Y	1	2
<i>Austrogomphus mjobergi</i>	N	C	0.924	0.986	101458	61	724	2	1	5	85	538	2		4	3
<i>Austrogomphus ochraceus</i>	E	C	0.661	0.851	325917	27	32	1	1	5	43	33	2		2	5
<i>Austrogomphus prosinus</i>	NE	C	0.893	0.969	19830	64	15	0.5	0	0	89	17	1.5	Y	0	2
<i>Austrogynacantha heterogena</i>	C	C	0.682	0.863	1471593	29	63	1	1	5	34	57	1.5		1	5
<i>Austrolestes aleison</i>	W	C	0.918	0.984	36915	27	40	0.5	1	0	70	45	1.5		1	5
<i>Austrolestes analis</i>	C	C	0.673	0.807	958274	34	8	0	1	0	44	8	1.5		1	5
<i>Austrolestes annulosus</i>	C	C	0.684	0.901	804125	31	3	0	0	0	40	3	0.5		0	0
<i>Austrolestes aridus</i>	C	C	0.571	0.865	3139891	68	5	1	Y	2	72	7	1.5	Y	0	2
<i>Austrolestes cingulatus</i>	S	C	0.671	0.894	321128	38	3	0.5	Y	0	62	5	1.5	Y	1	2
<i>Austrolestes insularis</i>	N	C	0.793	0.93	225815	41	36	1.5	1	5	78	17	2	Y	1	2
<i>Austrolestes io</i>	C	C	0.776	0.947	463180	25	26	0	1	0	34	25	0.5		1	0
<i>Austrolestes leda</i>	C	C	0.611	0.774	958761	38	12	0.5	1	0	48	12	2		1	5

Species	Region	Record Group	Model Score		Current Range	RCP85_2055					RCP85_2085						
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D	V
<i>Austrolestes minjerriba</i>	E	C	0.953	0.997	4832	95	56	1	4	3	100	39	2.5	Y	4	1	
<i>Austrolestes psyche</i>	S	C	0.649	0.843	485223	34	2	0.5	0	0	52	3	2	Y	0	2	
<i>Austropetalia patricia</i>	S	U	0.952	0.999	585	100	533	2.5	5	3	100	300	3		4	3	
<i>Austropetalia tonyana</i>	S	U	0.862	0.964	54273	55	36	1	0	5	69	26	2	Y	4	1	
<i>Austrophlebia costalis</i>	E	C	0.777	0.942	73920	29	88	1.5	1	5	57	109	2		2	5	
<i>Austrophlebia subcostalis</i>	NE	U	0.952	0.994	2449	80	31	1	0	5	100	0	2	Y	5	1	
<i>Austrophya mystica</i>	NE	U	0.907	0.983	14427	73	42	1	4	3	82	7	1.5	Y	1	2	
<i>Austrosticta fieldi</i>	N	U	0.952	0.993	60927	71	80	2	3	3	94	56	2		5	3	
<i>Austrosticta frater</i>	N	U	0.952	0.995	23119	64	284	2	1	5	98	186	3		3	3	
<i>Austrosynthemis cyanitincta</i>	W	C	0.897	0.978	26641	53	0	2	Y	2	76	1	2	Y	1	2	
<i>Austrothemis nigrescens</i>	C	C	0.802	0.955	335342	24	60	0	1	0	27	66	1		1	5	
<i>Brachydiplax denticauda</i>	NE	C	0.74	0.931	124617	26	155	1	1	5	49	47	2.5		1	5	
<i>Brachydiplax duivenbodei</i>	NE	U	0.951	0.995	8583	19	178	1.5	1	5	24	318	3		2	5	
<i>Callagrion billinghursti</i>	S	C	0.892	0.977	77444	63	98	2	1	5	76	146	2.5		2	5	
<i>Camacinia othello</i>	NE	U	0.951	0.998	2993	21	301	1	1	5	47	555	3		1	5	
<i>Ceragrion aeruginosum</i>	NE	C	0.662	0.908	345650	14	56	1	1	5	35	21	1.5		1	5	
<i>Charismagrion risi</i>	NE	C	0.954	0.991	6335	54	74	1	2	5	81	39	2		1	5	
<i>Charisthemis flavoterminata</i>	E	C	0.63	0.872	329891	30	48	0.5	1	0	43	57	1.5		2	5	
<i>Coenagrion lyelli</i>	S	C	0.818	0.962	144651	74	1	0.5	Y	0	6	87	1	1	Y	0	2
<i>Cordulephya montana</i>	S	U	0.936	0.979	30014	78	55	1	Y	3	1	90	43	2	Y	5	1
<i>Cordulephya pygmaea</i>	E	C	0.616	0.883	252285	30	33	1	0	5	47	34	2		1	5	

Species	Region	Record Group	Model Score		Current Range	RCP85_2055					RCP85_2085						
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D	V
<i>Crocothemis nigrifrons</i>	C	C	0.643	0.848	983366	25	92	1	1	1	5	24	89	1.5	1	5	
<i>Dendroaeschna conspersa</i>	E	C	0.756	0.938	54787	44	80	1.5	1	5	66	96	2.5	2	5		
<i>Dipblebia coerulescens</i>	E	C	0.878	0.972	27169	46	93	1.5	1	5	82	109	2.5	3	3		
<i>Dipblebia euphoeoides</i>	NE	C	0.875	0.964	20331	54	9	0.5	1	0	77	4	1.5	Y	1	2	
<i>Dipblebia hybridoides</i>	NE	U	0.952	0.994	4869	70	26	1	1	5	84	11	2	Y	1	2	
<i>Dipblebia lestoides</i>	S	C	0.636	0.889	252136	31	40	1	1	5	52	44	2	2	5		
<i>Dipblebia nymphoides</i>	S	C	0.664	0.888	288748	34	34	1	0	5	48	32	2	1	5		
<i>Diplacodes bipunctata</i>	C	C	0.596	0.684	6134082	1	1	1	1	5	3	1	1	1	1	5	
<i>Diplacodes haematodes</i>	C	C	0.685	0.758	5041586	3	10	1	1	5	4	14	1.5	1	5		
<i>Diplacodes melanopsis</i>	E	C	0.66	0.889	280866	31	36	0.5	1	0	48	40	2	1	5		
<i>Diplacodes nebulosa</i>	N	C	0.811	0.946	96726	16	125	1.5	1	5	29	41	2	1	5		
<i>Diplacodes trivialis</i>	NE	C	0.639	0.901	189245	21	186	1	1	5	59	38	2.5	1	5		
<i>Dromaeschna forcipata</i>	NE	C	0.907	0.974	15888	33	16	0.5	0	0	60	4	1.5	Y	1	2	
<i>Dromaeschna weiskei</i>	NE	C	0.919	0.985	10057	41	9	1	0	5	74	1	2	Y	0	2	
<i>Episynlestes albicauda</i>	E	C	0.759	0.924	80800	79	38	1.5	4	3	95	26	2.5	Y	4	1	
<i>Episynlestes cristatus</i>	NE	U	0.952	0.999	1402	92	71	1	1	5	100	1	2	Y	3	1	
<i>Eurysticta coolawanyah</i>	W	C	0.865	0.969	298177	83	33	2	Y	5	1	84	40	2	Y	4	1
<i>Eusynthemis aurolineata</i>	E	C	0.809	0.944	78530	34	146	1.5	1	5	64	116	2.5	4	3		
<i>Eusynthemis brevistyla</i>	S	C	0.715	0.917	223119	35	32	1	1	5	53	32	1.5	2	5		
<i>Eusynthemis guttata</i>	S	C	0.785	0.952	116988	46	51	0.5	2	0	68	49	1.5	4	3		
<i>Eusynthemis nigra</i>	E	C	0.79	0.947	107382	22	86	0	1	0	41	109	1.5	1	5		

Species	Region	Record Group	Model Score		Current Range	RCP85_2055					RCP85_2085						
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D	V
<i>Eusynthemis rentziana</i>	E	U	0.896	0.977	32567	74	34	1.5	Y	4	1	94	16	2.5	Y	5	1
<i>Eusynthemis tillyardi</i>	S	C	0.814	0.949	102556	52	29	1.5		1	5	62	26	2		1	5
<i>Eusynthemis ursula</i>	S	U	0.952	0.999	223	77	70	2		1	5	100	0	3	Y	5	1
<i>Eusynthemis virgula</i>	S	C	0.689	0.923	211123	40	27	1		1	5	63	22	2		4	3
<i>Griseargiolestes albescens</i>	E	C	0.954	0.995	7875	95	43	2		5	3	100	38	3	Y	4	1
<i>Griseargiolestes bucki</i>	E	U	0.952	0.996	2744	88	290	1.5	Y	3	1	93	131	2.5		5	3
<i>Griseargiolestes eboracus</i>	E	C	0.844	0.965	100286	53	46	1		1	5	83	36	1.5	Y	5	1
<i>Griseargiolestes fontanus</i>	E	U	0.952	0.989	9302	97	9	2	Y	4	1	100	4	2.5	Y	5	1
<i>Griseargiolestes griseus</i>	S	C	0.761	0.948	126301	46	35	1		1	5	60	33	2		2	5
<i>Griseargiolestes intermedius</i>	S	C	0.911	0.97	28031	37	56	1		0	5	56	37	2		5	3
<i>Griseargiolestes metallicus</i>	NE	U	0.952	0.997	845	100	9	2	Y	3	1	100	0	2	Y	5	1
<i>Gynacantha dobsoni</i>	N	C	0.804	0.946	88543	38	282	1.5		1	5	61	71	1.5		1	5
<i>Gynacantha mocsaryi</i>	NE	C	0.935	0.988	13843	22	53	1		1	5	51	36	3.5		0	5
<i>Gynacantha nauriangie</i>	N	C	0.73	0.937	166293	41	120	2		1	5	91	28	2	Y	3	1
<i>Gynacantha rosenbergi</i>	NE	C	0.927	0.989	12310	34	43	1		1	5	60	45	1.5		1	5
<i>Hemicordulia australiae</i>	C	C	0.635	0.838	557063	32	26	1		1	5	37	29	1.5		1	5
<i>Hemicordulia continentalis</i>	E	C	0.838	0.966	64490	39	28	0.5		1	0	54	22	2.5		1	5
<i>Hemicordulia intermedia</i>	C	C	0.69	0.861	861310	38	66	1		1	5	65	55	1.5		1	5
<i>Hemicordulia kooina</i>	W	U	0.952	0.986	119416	97	3	2	Y	4	1	99	5	2	Y	4	1
<i>Hemicordulia superba</i>	E	C	0.947	0.991	101316	50	97	2		1	5	76	119	3		1	5
<i>Hemicordulia tau</i>	C	C	0.655	0.895	1768259	30	66	1		1	5	40	115	1.5		1	5

Species	Region	Record Group	Model Score		Current Range	RCP85_2055					RCP85_2085						
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D	V
<i>Hemigomphus comitatus</i>	NE	C	0.901	0.969	38306	45	31	0.5	0	0	0	78	14	2	Y	5	1
<i>Hemigomphus cooloola</i>	E	U	0.972	0.999	125	100	0	2.5	Y	5	1	100	0	4	Y	5	1
<i>Hemigomphus gouldii</i>	E	C	0.688	0.871	304650	26	17	1	1	1	5	44	18	2	2	2	5
<i>Hemigomphus heteroclytus</i>	E	C	0.608	0.863	188130	37	39	1.5	1	5	58	52	2	2	1	5	
<i>Hemigomphus magela</i>	N	U	0.952	0.996	2316	97	52	1.5	Y	3	1	100	66	2	Y	2	2
<i>Hemigomphus theischingeri</i>	NE	U	0.952	0.998	2147	87	66	1.5	1	5	97	32	2	Y	0	2	
<i>Hemiphebia mirabilis</i>	S	C	0.93	0.99	39071	97	50	1	1	5	100	54	1	1	1	5	
<i>Hesperocordulia berthoudi</i>	W	C	0.91	0.979	9110	86	1	2	Y	2	2	100	0	2	Y	5	1
<i>Hydrobasileus brevistylus</i>	NE	C	0.753	0.932	105908	46	129	1	1	5	66	36	1.5	1	5		
<i>Ictinogomphus australis</i>	NE	C	0.645	0.888	523418	22	183	1	1	5	23	185	1.5	1	5		
<i>Ictinogomphus dobsoni</i>	W	C	0.943	0.986	137401	88	13	1.5	Y	4	1	91	14	2	Y	3	1
<i>Indolestes alleni</i>	N	U	0.952	0.987	13344	27	60	1.5	1	5	39	73	3	1	5		
<i>Indolestes obiri</i>	N	U	0.951	0.997	2766	100	0	1	Y	5	1	100	0	2	Y	5	1
<i>Indolestes tenuissimus</i>	NE	C	0.942	0.988	14448	51	34	1.5	1	5	72	33	3	0	5		
<i>Ischnura aurora</i>	C	C	0.586	0.854	5582244	8	9	1	0	5	8	10	1	1	5		
<i>Ischnura heterosticta</i>	C	C	0.69	0.914	2321650	25	56	1	1	5	34	75	1	1	5		
<i>Ischnura pruinescens</i>	NE	C	0.71	0.924	126613	57	82	1	1	5	79	13	1.5	Y	1	2	
<i>Labidiosticta vallisii</i>	E	C	0.892	0.982	72550	28	64	1	1	5	44	93	1.5	2	5		
<i>Lathrecista asiatica festa</i>	NE	C	0.741	0.932	84211	34	121	1.5	1	5	65	24	3	1	5		
<i>Lathrocordulia metallica</i>	W	C	0.936	0.987	11524	97	0	2	Y	2	2	100	0	2	Y	5	1
<i>Lestes concinnus</i>	N	C	0.676	0.871	309099	35	172	1.5	1	5	74	51	2	1	5		

Species	Region	Record Group	Model Score		Current Range	RCP85_2055						RCP85_2085					
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D	V
<i>Letoidea brevicauda</i>	NE	U	0.952	0.999	734	80	72	2	1	5	90	101	3	1	5		
<i>Letoidea conjuncta</i>	NE	C	0.922	0.986	10835	49	28	1	1	5	73	13	2	Y	0	2	
<i>Letoidea lewisiana</i>	NE	U	0.952	0.999	354	100	0	3.5	Y	5	1	100	0	4	Y	5	1
<i>Macrodiplox cora</i>	C	C	0.682	0.915	260085	41	321	1.5	1	5	73	189	1.5	2	5		
<i>Macromia tilyardi</i>	NE	C	0.909	0.982	104862	63	82	1.5	1	5	77	75	1.5	1	5		
<i>Micromidia atrifrons</i>	E	C	0.848	0.967	90250	29	39	0.5	1	0	52	45	1.5	1	5		
<i>Micromidia convergens</i>	E	U	0.952	0.999	783	100	503	2.5	4	3	99	369	3	3	3		
<i>Miniargiolestes minimus</i>	W	C	0.889	0.975	26576	45	6	1	Y	1	2	58	1	2	Y	1	2
<i>Nannodiplox rubra</i>	C	C	0.621	0.88	420494	15	37	1	1	5	39	12	1.5	1	5		
<i>Nannophlebia eludens</i>	NE	C	0.81	0.942	116902	18	40	1	1	5	42	12	1.5	1	5		
<i>Nannophlebia injibandi</i>	N	C	0.954	0.993	314512	53	140	2	3	3	94	105	2	4	3		
<i>Nannophlebia mudginberri</i>	N	U	0.953	0.99	19412	67	108	2	1	5	85	37	3	1	5		
<i>Nannophlebia risi</i>	E	C	0.619	0.896	202605	27	41	1	1	5	45	44	2	1	5		
<i>Nannophya australis</i>	E	C	0.74	0.936	226849	72	47	1	Y	1	2	86	43	1	Y	5	1
<i>Nannophya dalei</i>	S	C	0.745	0.928	194220	47	10	0	1	0	60	8	1	Y	1	2	
<i>Nannophya occidentalis</i>	W	U	0.953	0.99	19107	42	40	0.5	1	0	52	50	1.5	1	5		
<i>Neosticta canescens</i>	E	C	0.838	0.959	91359	19	104	1	1	5	35	129	2	2	5		
<i>Neosticta fraseri</i>	NE	C	0.936	0.989	9483	29	49	1	2	5	52	17	1.5	1	5		
<i>Neurothemis oligoneura</i>	NE	U	0.952	0.994	8363	66	29	2	4	3	82	39	3	3	3		
<i>Neurothemis stigmatizans</i>	N	C	0.675	0.901	277758	5	140	1.5	1	5	10	150	2	1	5		
<i>Nososticta baroalba</i>	N	C	0.953	0.994	47516	42	58	1	1	5	44	16	1.5	Y	1	2	

Species	Region	Record Group	Model Score		Current Range	RCP85_2055					RCP85_2085						
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D	V
<i>Nososticta coelestina</i>	N	C	0.827	0.95	83749	46	24	1.5	1	5	59	15	1.5	1	5		
<i>Nososticta fraterna</i>	N	C	0.746	0.929	92210	76	65	2	4	3	100	18	2	Y	5	1	
<i>Nososticta kalumburu</i>	N	U	0.951	0.992	17434	83	5	2	Y	4	1	90	4	2	Y	3	1
<i>Nososticta koalpinyah</i>	N	U	0.952	0.995	1605	100	28	2	Y	4	1	100	0	3	Y	5	1
<i>Nososticta koongarra</i>	N	U	0.952	0.998	1028	100	176	1	3	3	100	50	1	Y	3	1	
<i>Nososticta liveringa</i>	N	C	0.924	0.972	97573	70	107	2	4	3	92	18	2	Y	5	1	
<i>Nososticta pilbara</i>	N	U	0.952	0.999	199	100	0	2.5	Y	5	1	100	0	2.5	Y	5	1
<i>Nososticta solida</i>	E	C	0.667	0.856	599998	34	32	1	1	5	49	38	1.5	1	5	1	5
<i>Nososticta solitaria</i>	E	C	0.783	0.94	149277	18	39	1.5	1	5	27	45	1.5	1	5	1	5
<i>Nososticta taracumbi</i>	N	U	0.952	0.998	1392	98	31	1.5	Y	4	1	98	2	3	Y	2	2
<i>Notoaeschna geminata</i>	E	C	0.84	0.955	51743	20	105	1.5	1	5	41	87	2.5	2	5	2	5
<i>Notoaeschna sagittata</i>	S	C	0.782	0.953	85029	54	34	1.5	1	5	75	25	2	Y	4	1	
<i>Notalbellula bicolor</i>	N	U	0.951	0.997	10868	88	182	2	1	5	94	208	2	3	3	3	3
<i>Oristicta filicicola</i>	NE	C	0.944	0.985	12059	35	52	0.5	1	0	61	41	1.5	1	5	1	5
<i>Orthetrum bourniera</i>	E	U	0.953	0.998	906	84	84	2	1	5	100	81	4	5	3		
<i>Orthetrum caledonicum</i>	C	C	0.634	0.728	6065482	1	1	1	0	5	3	1	1.5	0	5		
<i>Orthetrum migratum</i>	C	C	0.613	0.871	616573	35	67	1.5	1	5	70	51	2	2	5		
<i>Orthetrum sabina</i>	C	C	0.655	0.893	204114	10	157	1	1	5	25	61	2.5	1	5		
<i>Orthetrum serapia</i>	NE	C	0.882	0.974	44700	35	89	1.5	1	5	69	97	3	1	5		
<i>Orthetrum villosovitatum</i>	C	C	0.694	0.852	465265	39	26	1	1	5	55	24	1.5	1	5		
<i>Pantala flavescens</i>	C	C	0.612	0.836	2833165	6	38	1.5	1	5	7	64	2	1	5		

Species	Region	Record Group	Model Score		Current Range	RCP85_2055					RCP85_2085						
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D	V
<i>Parasynthemis regina</i>	E	C	0.65	0.874	539172	38	29	1	1	1	5	53	33	2	1	5	
<i>Pentathemis membranulata</i>	N	C	0.894	0.982	90251	14	331	1.5	1	5	34	202	3	1	5		
<i>Petalura gigantea</i>	S	C	0.891	0.971	22059	80	79	1.5	3	3	97	45	2.5	5	3		
<i>Petalura hesperia</i>	W	U	0.952	0.994	9622	26	18	2.5	1	5	44	16	3	1	5		
<i>Petalura ingentissima</i>	NE	C	0.913	0.986	11616	18	102	1	2	5	56	81	1.5	2	5		
<i>Petalura litorea</i>	E	U	0.952	0.995	6620	39	62	2	1	5	60	66	4	2	5		
<i>Podopteryx selysi</i>	NE	U	0.952	0.996	7570	72	39	1	1	5	96	19	2	Y	1	2	
<i>Potamarcha congener</i>	N	C	0.797	0.938	312330	9	250	1.5	1	5	13	248	2	1	5		
<i>Procardulia affinis</i>	W	C	0.891	0.978	882546	64	1	0.5	Y	2	6	69	1	1.5	Y	0	2
<i>Procardulia jacksoniensis</i>	S	C	0.647	0.903	209815	54	4	0	0	0	0	68	3	0.5	Y	0	6
<i>Pseudagrion aureofrons</i>	C	C	0.684	0.876	1288735	30	121	1	1	5	43	127	1.5	1	5		
<i>Pseudagrion cingillum</i>	N	C	0.953	0.989	212429	50	466	1.5	1	5	74	323	3	2	5		
<i>Pseudagrion ignifer</i>	E	C	0.699	0.909	252537	28	48	1	1	5	42	53	1.5	1	5		
<i>Pseudagrion jedda</i>	N	C	0.817	0.964	219876	39	132	2	1	5	80	46	2	4	3		
<i>Pseudagrion lucifer</i>	N	C	0.832	0.954	174071	16	141	2	1	5	43	38	2	1	5		
<i>Pseudagrion microcephalum</i>	C	C	0.664	0.856	949461	14	136	1	1	5	33	157	1.5	1	5		
<i>Pseudocordulia circularis</i>	NE	U	0.952	0.999	710	99	61	2	Y	3	1	99	62	2	Y	2	2
<i>Pseudocordulia elliptica</i>	NE	U	0.952	0.995	7631	47	34	1	1	5	70	8	2	Y	1	2	
<i>Rhadinosticta banksi</i>	N	C	0.953	0.995	216370	42	227	1	1	5	68	90	1.5	2	5		
<i>Rhadinosticta simplex</i>	E	C	0.604	0.87	675694	40	32	1	1	5	53	36	2	1	5		
<i>Rhodothemis lieftincki</i>	C	C	0.643	0.882	355893	25	146	1	1	5	32	93	1.5	1	5		

Species	Region	Record Group	Model Score		Current Range	RCP85_2055					RCP85_2085						
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D	V
<i>Rhyothemis braganza</i>	N	C	0.68	0.902	303520	18	60	1.5	1	5	35	32	1.5	1	5	1	5
<i>Rhyothemis graphiptera</i>	C	C	0.634	0.838	737526	10	88	1	1	5	10	58	1.5	1	5	1	5
<i>Rhyothemis phyllis</i>	NE	C	0.729	0.923	149396	9	79	1	1	5	20	123	2.5	1	5	1	5
<i>Rhyothemis princeps</i>	NE	C	0.873	0.968	22721	32	58	1	1	5	65	25	2.5	1	5	1	5
<i>Rhyothemis resplendens</i>	NE	C	0.935	0.98	11576	35	32	1.5	0	5	52	32	3.5	0	5	0	5
<i>Spinaeschna tripunctata</i>	S	C	0.814	0.964	76305	31	72	1	1	5	52	64	2	1	5	1	5
<i>Spinaeschna watsoni</i>	NE	U	0.942	0.985	10299	66	4	1	Y	0	95	0	2	Y	2	2	2
<i>Synlestes selysi</i>	E	C	0.748	0.929	89716	44	84	0.5	1	0	68	89	1.5	5	3	5	3
<i>Synlestes tropicus</i>	NE	C	0.953	0.993	4248	77	36	1.5	1	5	97	12	2	Y	0	2	2
<i>Synlestes weyersii</i>	S	C	0.688	0.868	261308	28	21	1	2	5	48	23	2	2	5	2	5
<i>Synthemiopsis gomphomacromioides</i>	S	U	0.952	0.989	3784	94	17	1.5	Y	1	99	8	2.5	Y	1	2	2
<i>Synthemis eustalacta</i>	S	C	0.656	0.899	266770	43	25	0.5	1	0	67	24	1.5	Y	4	1	1
<i>Synthemis tasmanica</i>	S	C	0.71	0.901	24177	58	20	0.5	1	0	76	8	2	Y	1	2	2
<i>Teinobasis rufithorax</i>	NE	C	0.954	0.999	3435	41	122	1.5	1	5	65	162	3	1	5	1	5
<i>Telephlebia brevicauda</i>	S	C	0.804	0.95	72187	47	50	0.5	1	0	63	46	1	4	3	4	3
<i>Telephlebia cyclops</i>	E	C	0.862	0.961	50277	44	44	1.5	1	5	72	41	2.5	2	5	2	5
<i>Telephlebia godeffroyi</i>	E	C	0.768	0.939	110546	50	58	2	1	5	71	55	2	3	3	3	3
<i>Telephlebia tillyardi</i>	NE	U	0.942	0.99	9652	78	39	1	1	5	96	19	2	Y	1	2	2
<i>Telephlebia tryoni</i>	E	U	0.953	0.99	7294	97	49	2	Y	5	100	39	3	Y	5	1	1
<i>Tetrathemis irregularis cladophila</i>	NE	C	0.937	0.986	9666	67	11	0.5	Y	0	91	7	2	Y	1	2	2
<i>Tholymis tillarga</i>	N	C	0.744	0.929	113138	11	348	1.5	1	5	23	172	3	1	5	1	5

Species	Region	Record Group	Model Score		Current Range	RCP85_2055						RCP85_2085					
			TSS	AUC		Loss	Gain	C	S	D	V	Loss	Gain	C	S	D	V
<i>Tonyosynthemis claviculata</i>	NE	U	0.938	0.983	6486	59	18	1	0	5	81	2	2	Y	0	2	
<i>Tonyosynthemis ofarrelli</i>	E	U	0.934	0.991	16394	60	236	2.5	1	5	96	207	3		2	5	
<i>Tramea eurybia</i>	E	U	0.953	0.998	1396	81	181	3	5	3	83	233	4		5	3	
<i>Tramea laewii</i>	C	C	0.646	0.847	1394206	3	153	1	1	5	3	197	1.5		1	5	
<i>Tramea stenoloba</i>	C	C	0.686	0.91	993288	52	62	1.5	3	3	62	70	2		2	5	
<i>Urothemis aliena</i>	NE	U	0.948	0.982	31745	41	52	1.5	3	3	58	62	3		1	5	
<i>Xanthagrion erythroneurum</i>	C	C	0.663	0.803	3840167	29	12	1	0	5	29	18	1.5		1	5	
<i>Zephyrogomphus lateralis</i>	W	C	0.954	0.992	18110	45	2	2	Y	0	2	69	1	2	Y	0	2
<i>Zyxomma elgneri</i>	C	C	0.645	0.903	1184788	37	78	1	1	5	40	70	1.5		1	5	
<i>Zyxomma petiolatum</i>	NE	U	0.95	0.989	11191	22	61	1.5	1	5	45	40	3.5		1	5	

Supplementary S4. Demonstration of Species Vulnerability Assessment

This supplement provides a detailed description of the information used to assess vulnerability for three of the dragonfly species modelled. We chose species that displayed differing responses to climate change and resulted in different threat categories in the RCP8.5 2085 scenario. These species are: *Notoaeschna sagittata* classified as Highly Vulnerable in Category 1, *Tetrathemis irregularis cladophila* (Vulnerable, Category 2), and *Austrosticta frater* (possible persistence, Category 3). First, Figure S4.1 shows the distribution of available records for model building after the dataset had been reviewed and outliers removed. An ensemble of modelling algorithms was then used to predict habitat suitability under current and future climate scenarios, and shows *N. sagittata* is likely to lose suitable habitat in the north of its range and could occupy new habitats in Tasmania in 2085 (Fig. S4.2). The decline in the current suitable habitat of *T. irregularis cladophila* is proportionally much greater and this species is not predicted to shift to higher latitudes (Fig. S4.3). Despite some loss of suitability in the current range, the extent of suitable habitat for *Austrosticta frater* is predicted to increase in all scenarios (Fig. S4.4).



Figure S4.1 Distribution of occurrence records for *Notoaeschna sagittata* (green, $n=336$), *Tetrathemis irregularis cladophila* (red, $n=57$) and *Austrosticta frater* (blue, $n=24$).

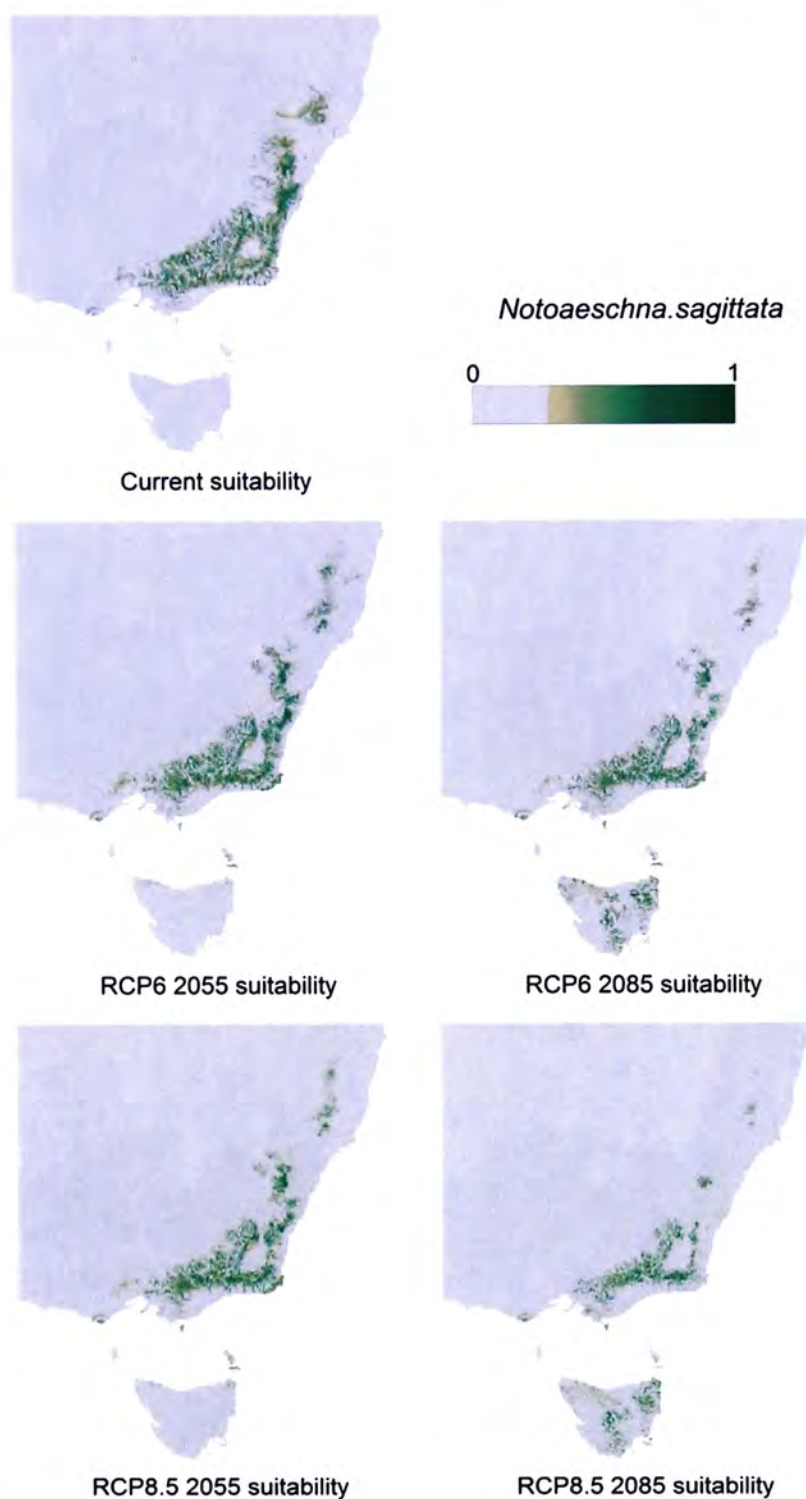


Figure S4.2 Predicted habitat suitability for *Notoaeschna sagittata* under current and future climatic conditions.

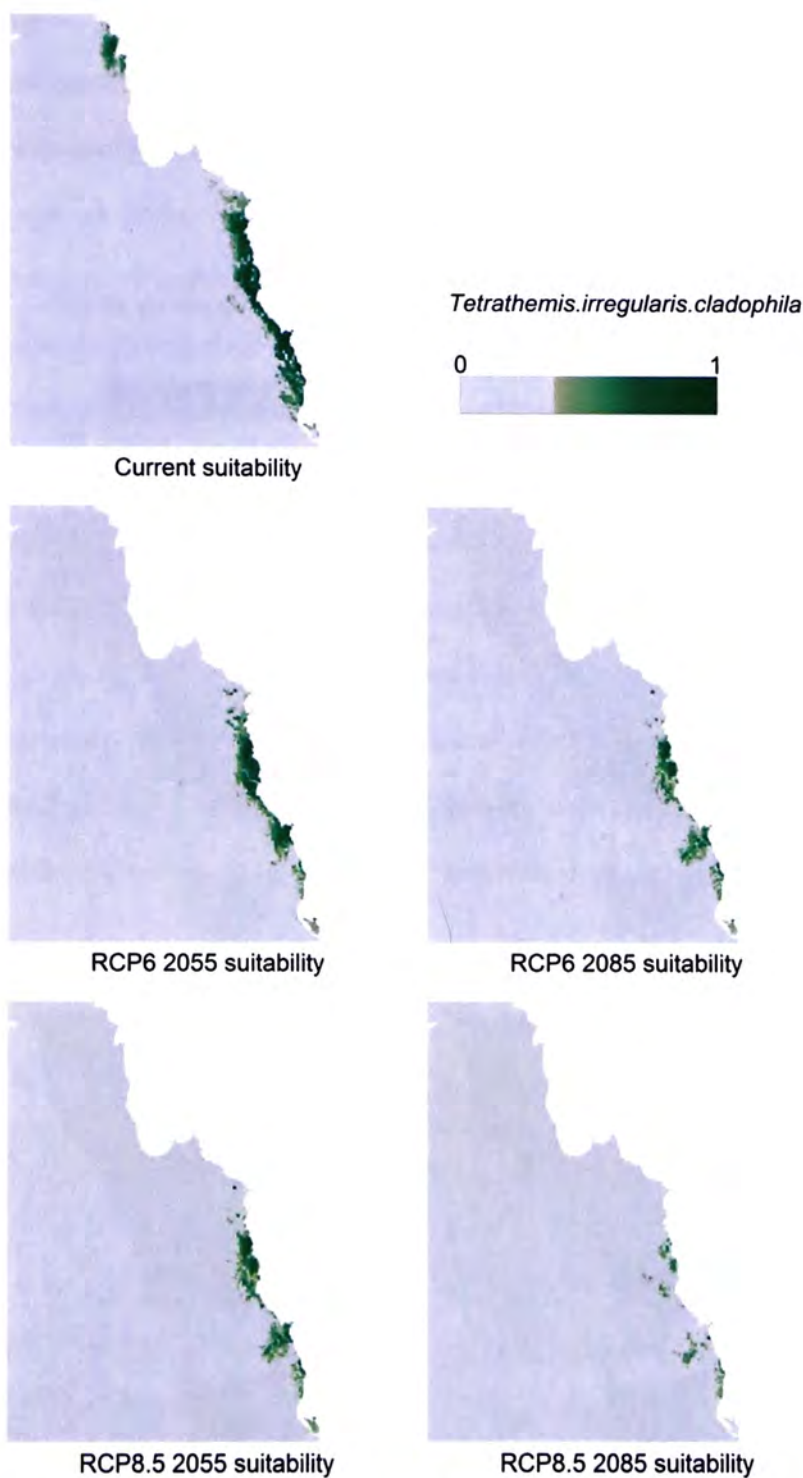


Figure S4.3 Predicted habitat suitability for *Tetrathemis irregularis cladophila* under current and future climatic conditions.

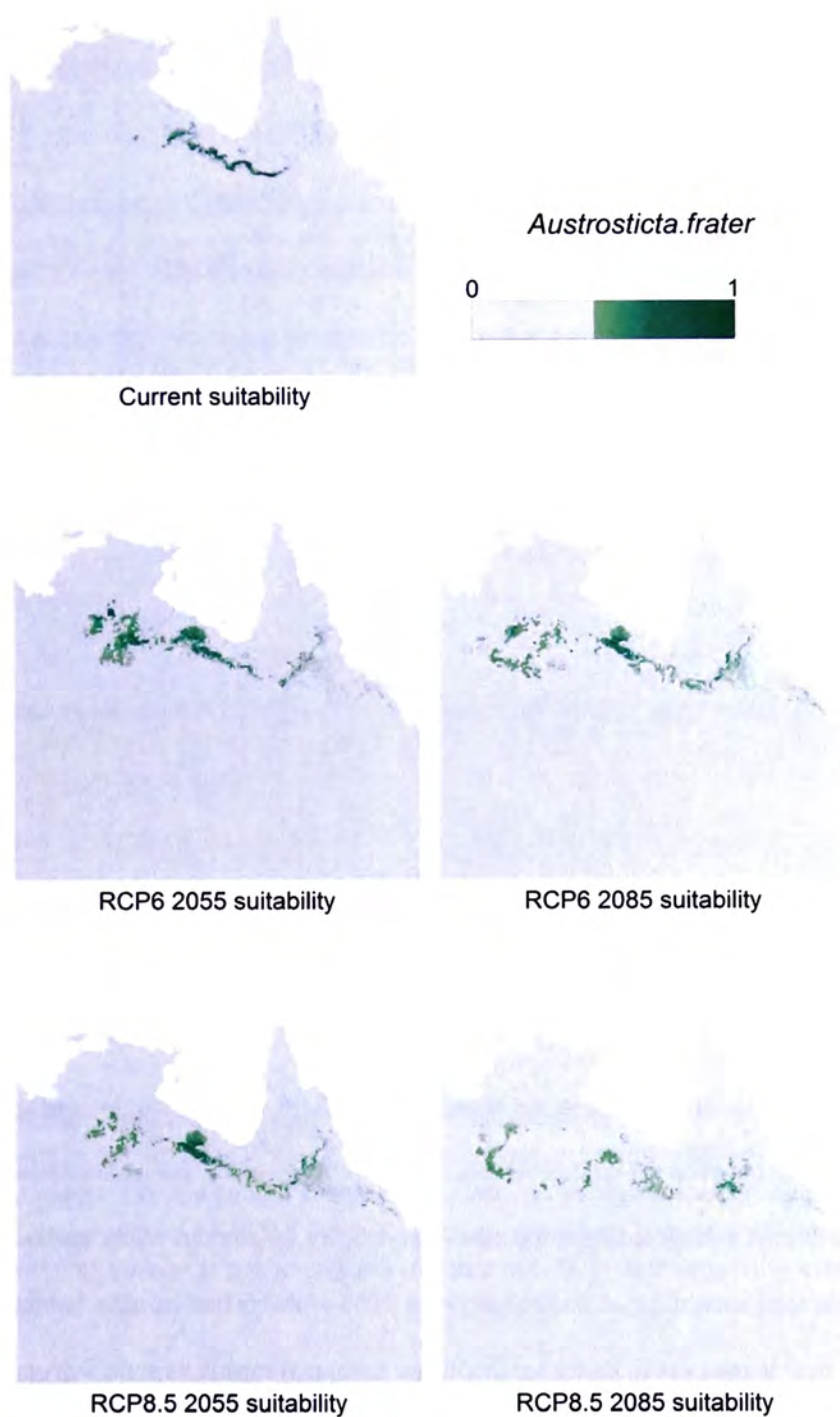


Figure S4.4 Predicted habitat suitability for *Austrosticta frater* under current and future climatic conditions.

Table S4.5 Predicted change in suitable habitat for two emissions scenarios for 2055 and 2085. Values are the percentage loss, percentage gain, overall change and sensitivity weighting.

Scenario		<i>Notoaeschna sagittata</i>	<i>T. irregularis cladophila</i>	<i>Austrosticta frater</i>
RCP6_2055	% Loss	39	50	56
	% Gain	24	7	286
	% Change	-15	-43	230
	Sensitivity	0.1598	0.9111	-0.4439
RCP85_2055	% Loss	51	64	61
	% Gain	20	11	227
	% Change	-31	-53	166
	Sensitivity	0.3569	1.8425	-0.5664
RCP85_2055	% Loss	54	67	64
	% Gain	34	11	284
	% Change	-20	-56	220
	Sensitivity	0.4725	1.6474	-0.5058
RCP85_2085	% Loss	75	91	98
	% Gain	25	7	186
	% Change	-50	-84	88
	Sensitivity	1.3499	8.2038	-0.1267

The vulnerability assessment includes three components: sensitivity (the extent to which a suitable habitat is lost), exposure (the extent to which a species' currently occupied physical environment will change), and dispersal pressure (the reliance on dispersal to avoid further negative impacts) (Fig.1 main document).

SENSITIVITY

Changes to species distribution are summarized in Table S4.5 and include the sensitivity weights which are the ratio between the change in habitat suitability (sum of habitat suitability over all streams in the future, subtracted from the sum of suitability for streams under current climate), and the current total suitability. *A. frater* loses over 50% of its current suitable habitat but the expansion of new habitats even under harsh climate scenarios means its sensitivity weights are low. Declines in *T. irregularis cladophila* are more severe than for *N. sagittata*, and so its sensitivity weights are higher. For *T. irregularis cladophila*, its extent declines slightly more in

RCP8.5 2055 than RCP6 2085 and yet the sensitivity weight is lower. This is because the weighting is based on summed suitability, not the overall change in extent, and in this case although habitat may qualify as sufficiently suitable to support the species, its range overall contains fewer areas with high suitability (Fig. S4.6). Species with negative sensitivity values are likely to expand their range or have higher overall suitability in the future, whereas higher values occur when the species' habitat either contracts in area, or becomes less suitable. We considered species with a sensitivity score above one to be highly vulnerable.

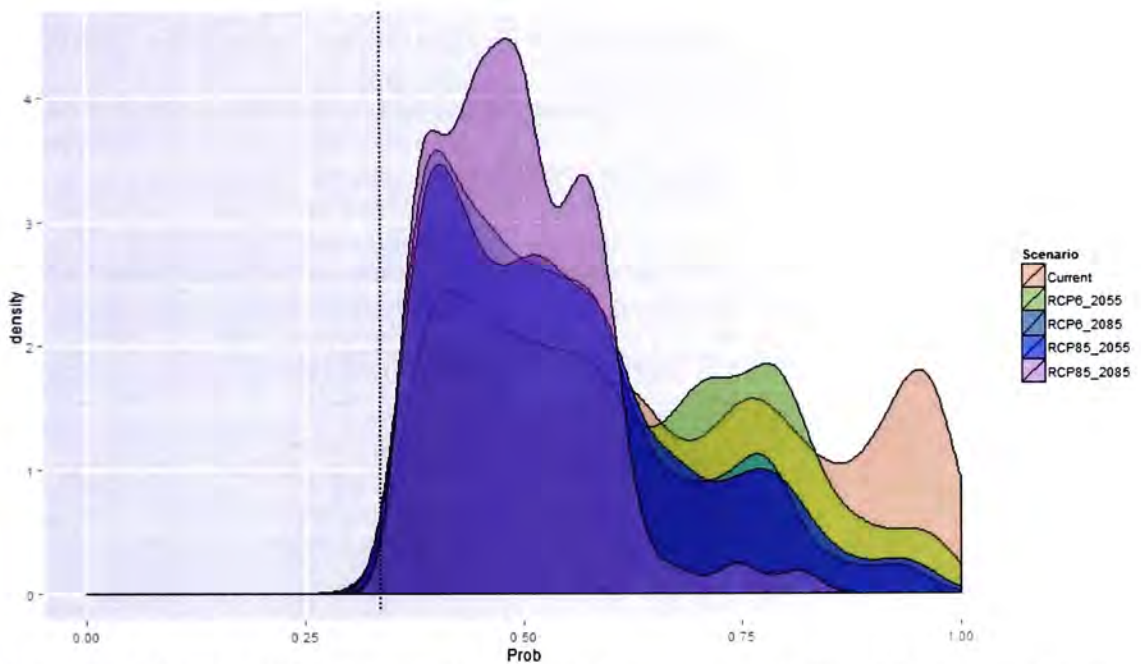


Figure S4.6 Density plot showing the frequency of habitat suitability scores within the current and future range of *Tetrathemis irregularis cladophila*. Note density is proportional and does not reflect habitat extent. Current habitat suitability includes more high suitability sites than future scenarios and under scenario RCP8.5 2085 the species' remaining habitat is dominated by lower suitability sites. The species is not considered to occur in habitat with suitability values below 0.3 (dashed line).

EXPOSURE

The exposure component of vulnerability was based on the degree to which the physical environment is predicted to change within the current extent of suitable habitat. An average shift of two standard deviations would be equivalent to 97.5% of habitat changing beyond the species current environmental limits. Exposure was based on four climatic factors, one hydrological, and sea level rise (Table S4.7). Species were considered vulnerable to climatic exposure if the change in one environmental factor was greater than two SDs, or greater than one SD for multiple factors. Sea level rise was considered important if more than 10% of current habitat was below 2m above sea level. In the case of the three example species, none were significantly at risk due to changes in temperature seasonality, mean annual precipitation or sea level rise, but all three were exposed to other environmental factors (Table S4.8).

Table S4.7 Summary of scoring system for environmental exposure. A species that scored 1 or more was considered vulnerable for that component.

Change in Environment	1SD	2SD+
Mean Temperature	0.5	1
Temperature Seasonality	0.5	1
Mean Precipitation	0.5	1
Precipitation Seasonality	0.5	1
Man Annual Flow	0.5	1
Sea Level Rise	<10%	>10%
Current range below 2m	0	0.5

Table S4.8 Environmental exposure scores for *Notoaeschna sagittata*, *Tetrathemis irregularis cladophila* and *Austrosticta frater*. Values represent the number of standard deviations future environment will shift from the current habitat average across the species current suitable habitat area. For sea level rise, values are the percentage of current habitat affected by a 1 m rise in sea level.

Species	Factor	RCP6 2055	RCP6 2085	RCP8.5 2055	RCP8.5 2085
<i>N. sagittata</i>	Mean annual temperature	0.67	1.12	1.04	1.82
	Temperature Seasonality	0.32	0.47	0.44	0.71
	Mean annual precipitation	0.05	0.15	0.13	0.28
	Precipitation Seasonality	0.69	1.00	0.95	1.62
	Mean Annual Flow	2.12	4.91	4.22	6.43
	Sea Level Rise	0.36	0.36	0.36	0.36
<i>T. irregularis cladophila</i>	Mean annual temperature	1.17	1.95	1.81	3.19
	Temperature Seasonality	-0.01	0.00	0.00	0.04
	Mean annual precipitation	-0.16	-0.11	-0.12	-0.06
	Precipitation Seasonality	0.48	0.77	0.72	1.24
	Mean Annual Flow	0.51	0.61	0.59	1.02
	Sea Level Rise	6.98	6.98	6.98	6.98
<i>A. frater</i>	Mean annual temperature	1.58	2.57	2.40	4.14
	Temperature Seasonality	0.28	0.23	0.24	0.16
	Mean annual precipitation	-0.50	-0.55	-0.54	-0.65
	Precipitation Seasonality	-0.22	0.75	0.60	2.26
	Mean Annual Flow	1.67	3.30	2.81	8.81
	Sea Level Rise	0.06	0.06	0.06	0.06

DISPERSAL

The third component of the vulnerability assessment is the pressure on a particular species to disperse rapidly in order to occupy suitable habitat in the future. Predicted habitat suitability (Table 4.5) was modelled under the assumption species would be able to disperse at an average rate of 15 km year⁻¹. Faster expansion consistent with climate change has already been observed in some dragonfly species (e.g. Flenner & Sahlén, 2008). Nonetheless, predicting the success of range shifts over such large distances is highly uncertain (Astorga *et al.*, 2011), and species are potentially at greater risk if their predicted future persistence relies on the assumption of rapid dispersal (Crossman *et al.*, 2011). We therefore split the assessment of dispersal into two parts: distance of habitat shifts, and the dependence of the sensitivity weighting to dispersal thresholds.

The significance of range shifts was assessed using a Wilcoxon rank sum test to determine whether future suitable habitats were significantly further away from point records of that species than the predicted distribution of current suitable habitats. Distances from records were calculated as least cost paths to account for the lower probability that species would cross open seas (Fig. S4.9). Species scored 0 if suitable habitat shifts were not significant, 1 if the difference was significant ($p=0.05 \sim 2$ SDs), and 2 if the difference was over three SDs indicating decreasing habitat overlap. In the case of the three example species, the shift south by *N. sagittata* was significant, but did not cover a significant distance (Table S4.10). By 2085, new suitable habitats in Tasmania are much further away. The distribution of *T. irregularis cladophila* shrinks but does not show a significant shift. The current range of *A. frater* was predicted to be quite dispersed, and as such although range expansion by 2055 was projected to be extensive, it was only above three SDs in 2085.

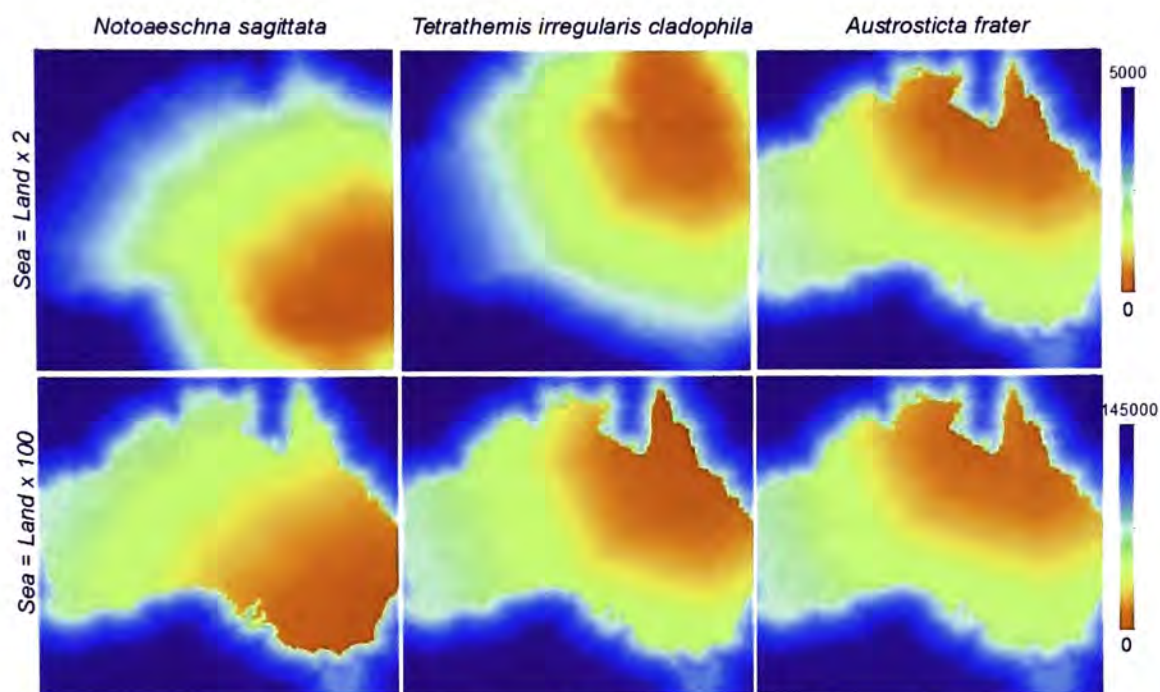


Figure S4.9 Distance (km) from existing records of a species to all other sites. In the top row, the costs of crossing open water are double that of land used for standard modelling. In the second row, the costs are 100 times greater, making the Bass Strait a dispersal barrier for mainland species shifting to Tasmania.

Table S4.10 Average habitat shifts (km) under climate change scenarios. Distances marked with a * were significantly further than the current habitat distribution, and ** if the change was over three standard deviations further.

Species	Current	RCP6 2055	RCP6 2085	RCP8.5 2055	RCP8.5 2085
<i>Notoaeschna sagittata</i>	34	60 *	170 *	53 *	222 **
<i>Tetrathemis irregularis cladophila</i>	16	14	14	14	16
<i>Austrosticta frater</i>	92	249 *	293 **	210 *	363 **

To account for the uncertainty in a species ability to disperse, we considered the effect on a species overall habitat suitability, using the sensitivity weighting, when dispersal rates were gradually reduced. Suitable habitat was constrained by dispersal using the distances from observed records (Fig. S4.9) and a dispersal kernel (see Fig. 2, main document). The dispersal kernel is a four-parameter logistic curve that converts all distances to a value between 0 and 1, interpreted as the estimated probability a species could disperse to that site. The dispersal kernel can be modified depending on a threshold distance, and the rate of decay (Fig. S4.11).

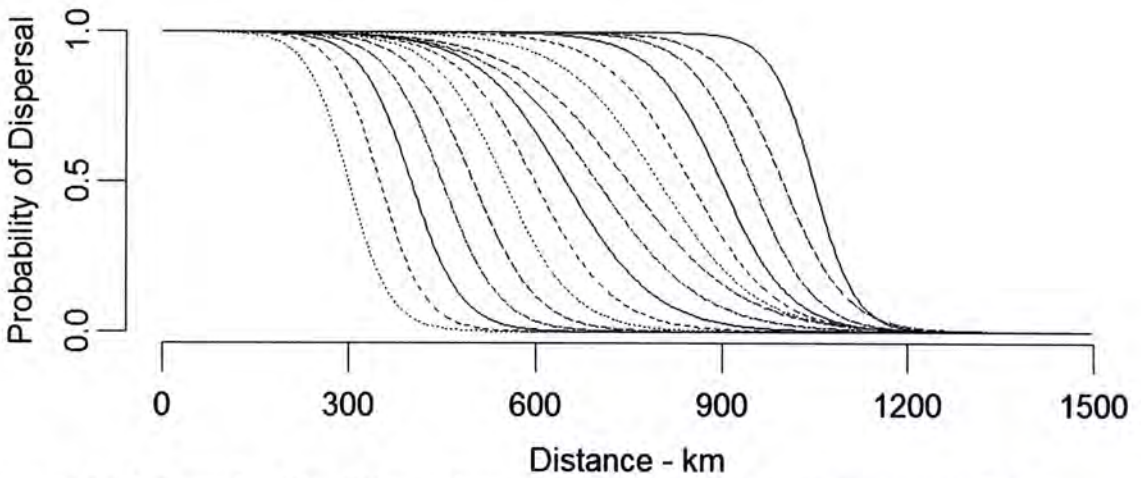


Figure S4.11 The probability of dispersal according to distance from occurrence records. By iteratively reducing the threshold or rate of decay, the dispersal constraint increasingly restricts the suitable habitat within dispersal (note not all levels are shown).

As the overall limit of dispersal is reduced, habitat suitability is reduced at distant locations from species current records, and as a consequence, the suitability weighting increases. Reducing the rate of dispersal by increments of 0.5 km year^{-1} provides 30 dispersal thresholds, which we divided into three groups ($10.5\text{-}15 \text{ km year}^{-1}$ = High dispersal, $5.5\text{-}10 \text{ km year}^{-1}$ = Medium dispersal, and $0.5\text{-}5 \text{ km year}^{-1}$ = Low dispersal). The rate at which sensitivity weight increased was determined from the slope of a linear model between the threshold distance and the sensitivity weighting (note distances were different for 2055 and 2085) (Fig. S4.12). The effect of

a reduction in dispersal capacity on a species suitable habitat is relative to its overall sensitivity weighting for each emission scenario, but was considered significant if the slope was less than -1. A species was given a score of 3, 2 or 1 if the slope was less than one for high, medium or low thresholds respectively, and zero if it was not.

In the case of the three example species, the extent and suitability of habitat for *T. irregularis cladophila* would not be at greater risk if its dispersal ability was constrained. A small reduction in the dispersal capacity may not greatly affect *N. sagittata* either, but if dispersal rates were reduced below $\sim 11 \text{ km year}^{-1}$, the overall quantity of suitable habitat available quickly decreases, observed here as a rapid increase in sensitivity weighting (Fig. S4.12a, green line, score =2). A rapid increase in the sensitivity weighting only occurred for *A. frater* if the dispersal rate was heavily reduced (Fig. S4.12c, blue line, score=1) and so there is only a small risk it will not be able to occupy the majority of suitable habitats available.

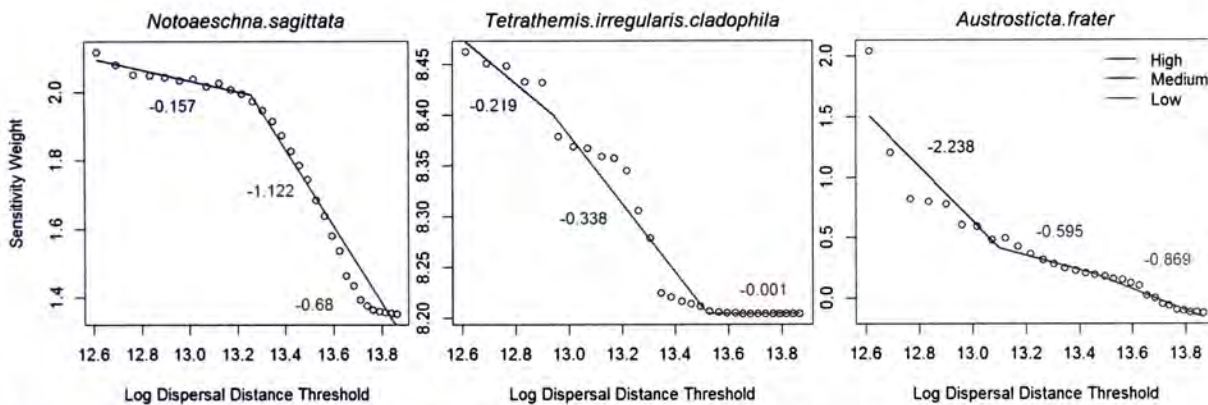


Figure S4.12 Sensitivity weighting for RCP8.5 2085 plotted against dispersal threshold (distance in metres log transformed). Values are the slope of a linear regressions fitted to scores for high (blue), medium (green) and low (red) rates of dispersal ($n=10$).

The scores allocated for the distance of habitat shifts (0-2) and reliance on dispersal (0-3) provide a maximum of 5 points and species that scored three or more in a particular climate scenario were considered as vulnerable for this component of the assessment (Table S4.13). Thus, all species whose sensitivity would increase rapidly from minor reductions in the dispersal threshold are considered vulnerable. For example in 2085 RCP8.5, *N. sagittata* was considered vulnerable based on dispersal because it is predicted to both shift a significant distance from its current distribution (Table S4.10), and the majority of its suitable habitat will be at risk if it cannot maintain at least moderately high rates of dispersal (Fig. 4.12, Table S4.13).

Table S4.13 Scoring for the dispersal component of the vulnerability assessment. Species that score three or more in any climate scenario (shaded) are considered at risk.

		Sensitivity to Dispersal Threshold			
		0	1	2	3
Score for Habitat Shift	0	0	1	2	3
	1	1	2	3	4
	2	2	3	4	5

Thus we have three components that address vulnerability under climate change. Species at risk across all components are most vulnerable (Category 1) but species under less pressure to disperse are still considered vulnerable (Category 2) (Fig. S4.14). If a species is exposed to climate change and alternative suitable habitats require significant dispersal, they are considered potential persisters (Category 3). Theoretically habitat suitability could decline and shift without high environmental exposure, but this is highly unlikely using modeled predictions (Category 4).

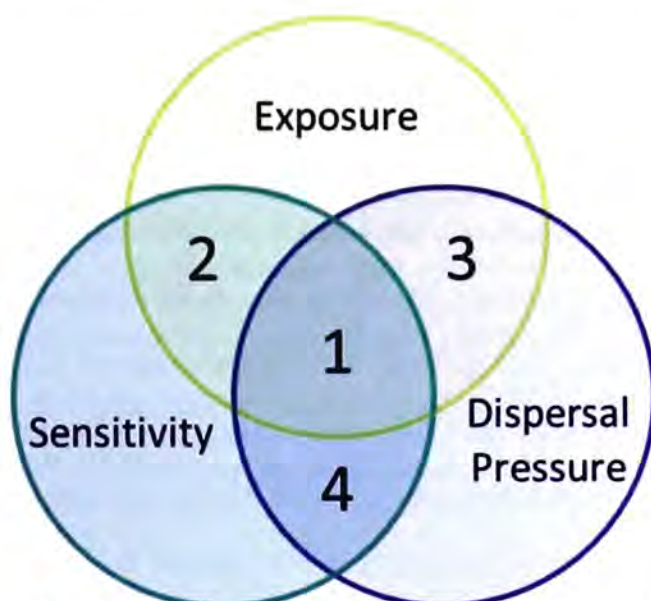


Figure S4.14 - Categories of vulnerability to climate change effects for species based on three components; exposure, sensitivity and dispersal pressure.

In summary;

- *Notoaeschna sagittata* was exposed in all future climate scenarios, as was *Austrosticta frater* (Table S4.7). *Tetrathemis irregularis cladophila* was only significantly exposed in the RCP8.5 2085 scenario, although note mean annual temperature was close to two SDs in RCP6 2085, and RCP8.5 2055.
- None of the three species had a high sensitivity weighting under RCP6 2055, but *T.irregularis cladophila* was considered sensitive in all three remaining scenarios. The sensitivity weighting was only high for *N. sagittata* under RCP8.5 2085; *A. frater* did not decline and so was not considered “sensitive” (Table S4.5).
- For the dispersal component, *N. sagittata* was only significantly at risk under the RCP8.5 2085. The range of *T. irregularis cladophila* is predicted to contract *in-situ* and so it would not rely on high rates of dispersal. *A. frater* is predicted to avoid overall loss of suitable habitat by expanding its range into new areas. Consequently, suitable habitat

shifts in all scenarios (Table S4.10), and in the RCP8.5 2085 scenario there is a risk it will experience significant declines if it fails to sustain at least low rates of dispersal (Fig. S4.12).

- In most scenarios *N. sagittata* is only considered exposed, but under the RCP8.5 2085 scenario it is projected to be at risk for all components and is classed as “Highly Vulnerable” (Category 1, Fig. S4.14). *T. irregularis cladophila* is not considered threatened at all in RCP6 2055, and only sensitive in RCP6 2085 and RCP8.5 2055. However under RCP8.5 2055 it is both highly sensitive and highly exposed and considered “Vulnerable” (Category 2). Like *N. sagittata*, *A. frater* is only threatened by its exposure for most scenarios, but in 2085 additional distances shifted by its habitat and the implications for dispersal capacity means it is assigned to Category 3 for lower risk species that have potential to persist.

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CHAPTER 5

TESTING FOR TAXONOMIC BIAS IN THE FUTURE DIVERSITY OF AUSTRALIAN ODONATA

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Hughes**

ABSTRACT

Invertebrates are often overlooked in assessments of climate change impacts. Odonata (dragonflies and damselflies) are a significant component of freshwater macroinvertebrate diversity and are likely to be highly responsive to a changing climate. We investigate whether climate change could lead to significant alteration of continental patterns of diversity and if vulnerable species are taxonomically clustered. Habitat suitability of 270 odonate species was modeled and a simplified phylogeny was developed based on taxonomic relationships and expert opinion. These maps were then combined to compare species richness, endemism, taxonomic diversity and taxonomic endemism under climate change scenarios, and estimate turnover in species composition. Based on the concentration of vulnerable species in regions associated with Gondwanan relicts, we tested the possibility that a focus on species loss would underestimate loss of evolutionary diversity. Species richness of Australian Odonata is concentrated in the Wet Tropics, central-north Australia and south-east Queensland. Several additional regions support endemic assemblages, including the Victorian alpine region, the Pilbara and far south-western Australia. Major shifts in composition are expected across most of the east coast in response to climate change and Tasmania has the potential to become a major refuge for mainland species. For many regions, the loss of taxonomic diversity is greater than expected based on the changes in species richness, and the loss of suitable habitat was unevenly distributed among families. However, the potential loss of evolutionary diversity among vulnerable species was not significantly different from random. The major shifts in the distribution of Australian odonate diversity predicted to occur under climate change imply major challenges for conservation of freshwater biodiversity overall. Although major evolutionary losses may be avoided, climate change is still a serious threat to Australia's Odonata, and could pose an even greater threat to Australian freshwater biodiversity as a whole.

INTRODUCTION

Freshwater ecosystems have become increasingly altered by human activities and the decline in freshwater biodiversity over recent decades has been faster than in either terrestrial or marine ecosystems (Jenkins, 2003; WWF, 2012). The effects of extensive human modification of biodiversity will be exacerbated in the future by climate change (Palmer et al., 2008; Palmer et al., 2009) and significantly increases the prospect of major biodiversity loss (Xenopoulos et al., 2005; Bellard et al., 2012). Across multiple species the combination of shifting habitat suitability and novel interactions are predicted to significantly alter the composition of regional freshwater assemblages (e.g. Durance & Ormerod, 2007; Chessman, 2009) and, where the opportunity to move to higher latitudes or altitudes is not available, the risk to species is likely to be high (Sauer et al., 2011). If climate change results in local or regional loss of sensitive (Hering et al., 2009) or dispersal-limited species (Kappes & Haase, 2012), the potential for a reduction in ecosystem stability and function increases (Cadotte et al., 2012; Mouillot et al., 2013).

Despite the dominance of invertebrates in aquatic communities, few studies of climate change impacts have been able to include invertebrate taxa due to taxonomic difficulties, the low availability of records, and poor overall understanding of species ecology (Cardoso et al., 2011). A powerful first step in assessing vulnerability is to model the relationship between species occurrence and the environment using species distribution models (SDM, e.g. Diniz-Filho et al., 2009; Elith et al., 2010). Although several studies have shown SDMs can be applied to freshwater invertebrates (e.g. Domisch et al., 2012; Simaika et al., 2013), spatial assessments of climate change impacts are uncommon for these taxa and this shortfall could bias the balance of recommendations for adaptation and protection (Darwall et al., 2011). There is also increasing pressure to consider genetically distinct species in conservation

prioritisation in addition to rarity and threats (Moritz, 2002; Isaac et al., 2007). Phylogenetic diversity captures the evolutionary relations of species based on the sum of branch lengths, and this is also likely to reflect phenotypic and ecological similarities (Erwin, 1991; Hartmann & André, 2013). By accounting for the evolutionary distinctiveness among species, we are more likely to conserve multiple unknown, and hard to measure, ecological traits (Crozier et al., 2005; Tucker et al., 2012).

In Australia, climate change is a major threat to freshwater biodiversity. Temperatures continue to rise, and there have been regional declines in rainfall and discharge (Lough & Hobday, 2011; Hughes et al., 2012). Further declines in rainfall are projected in western and south-eastern Australia by 2055, with more variable projections in the north (Petheram et al., 2012; James et al., 2013). Australia's Odonata (dragonflies and damselflies) includes many ancient lineages of Gondwanan origin, and most are thought to have become restricted to cooler climates and perennial freshwater habitats following periods of aridification that started approximately 20 Mya (Martin, 2006). Asian-origin odonates did subsequently colonise Australia and are now a large part of the fauna, including many of the vagrant and arid-zone adapted species (Watson et al., 1991). Under climate change, the vulnerability of Australian Odonata (Bush et al., 2014) is strongly associated with regions containing Gondwanan refugia (Moritz, 2002; Krosch et al., 2009). Endemics of these regions are at greater risk of climate change impacts because they have evolved within narrower climatic boundaries (Hering et al., 2009; Calosi et al., 2010; Botts et al., 2013). We therefore suggest that a focus on the number of species vulnerable to climate change could underestimate the proportion of evolutionary diversity at risk if those species are predominantly from distinct Gondwanan lineages, and in some cases families endemic to Australia (e.g. Hemiphlebiidae).

This study uses the modelled distribution of habitat for Australian Odonata to identify continental trends in diversity and how these patterns could change in the future as a result of climate change. We also specifically aimed to identify where the greatest overall change in odonate assemblages may occur, and whether those species at higher risk represent a taxonomically-biased portion of the community, the loss of which could result in a significantly increased reduction in taxonomic diversity.

METHODS

Species Data and Species Distribution Modelling

Records of Australian odonates were compiled from the collections of all Australian museums, environmental agencies in four States (Queensland, New South Wales, Victoria and Western Australia), and all known private collectors. There were insufficient data available to model 37 species, and we also did not consider any species from countries outside Australia. We believe the likelihood of many species colonising Australia under changing climates is low because the monsoon system appears to inhibit movement across the Coral Sea, evident in the low numbers of species shared between Australia and Papua New Guinea (Kalkman & Orr, 2012).

An ensemble forecasting approach was used to account for uncertainty in modelling method (Jones-Farrand et al., 2011) based on five statistical algorithms: (1) Generalized Linear Models, (2) Generalized Additive Models, (3) Boosted Regression Trees, (4) Multivariate Adaptive Regression Splines and (5) Maxent (Elith et al., 2006; Beaumont et al., in review). Analyses were implemented with the BIOMOD2 package (Thuiller et al., 2009) for the R statistical and programming environment (R Development Core Team, 2013). Pseudo-absences for the models were selected from localities within a 300 km radius of observed occurrences at localities where other Odonata had also been recorded. The True Skill Statistic (TSS; Doswell et al., 1990) was used to weight models in the ensemble, and used to calculate a minimum threshold for species habitat suitability (Liu et al., 2013). Habitat suitability was projected onto maps of stream sub-catchments across Australia derived from 250 m square digital elevation models (GEOFABRIC, 2011). Projections included climatic, topographic and hydrological factors and suitability was reduced when more than one predictive factor was outside the limits of the training data (Elith et al., 2011). Projections under current conditions were constrained to a 300 km radius from observed records, and extended under

future climates based on a maximum dispersal rate of 15 km year⁻¹ (Bush et al., 2014). Future climate scenarios were based on relative concentration pathways (RCPs) that describe emissions pathways in the forthcoming Fifth Assessment Report of the Intergovernmental Panel on Climate Change. We chose to use the higher scenarios (RCP6 and RCP8.5) because at present these capture the most likely trajectories of emissions (Peters et al., 2013). Climate predictions for 2055 and 2085 were based on ensembles of seven global climate models that perform well in predicting Australian patterns of precipitation (Fordham et al., 2012). At the continental scale, the downscaled climate data available is independent of elevation and so projections in topographically complex terrain may suffer (Corney et al., 2010). Overall, the final data set contained the modelled distribution of suitable habitat for 270 Odonata in all Australian sub-catchments under current and future climates. These sub-catchment layers were split into 250 m square blocks and re-aggregated as 1 km² grids matching the resolution of the climate data so that the equal area assumptions of the analysis could be met.

Richness and Turnover

The composition of local assemblages was inferred by aggregating species-level projections for all species (the “predict first, assemble later” method of Ferrier & Guisan, 2006). Stacked species distribution models (S-SDMs) based on binary projections are likely to overestimate the number of species present in a community and so we used the suitability scores as weights to estimate richness (Calabrese et al., 2013; Rosauer & Moritz, 2013). Richness was thus equivalent to the sum of suitable habitat scores for all species in a cell. Suitability scores from marginal habitats where that were below the TSS based threshold were set to zero. Weighted endemism counts the same species weighted by the inverse of their range (e.g. Slatyer et al., 2007), calculated here as the sum of their habitat suitability scores (see also Rosauer & Moritz, 2013). Turnover in this study was simply defined as the sum of species suitability

scores lost and gained by a site from the present to a future climate scenario. This is the equivalent of defining turnover as $b + c$, where b and c are matching components commonly used in beta-diversity indices (Koleff et al., 2003), and are the quantities unique to the present and future scenarios respectively. We chose not to use indices such as a Jaccard or Bray-Curtis to compare turnover because they are proportional to richness (e.g. Carvalho et al., 2010), and this merely highlighted complete replacement in species-poor regions at the expense of much greater absolute change in diverse communities.

Taxonomic Diversity

A molecular-based phylogeny was not available for Australian Odonata but taxonomic hierarchies are considered reasonable surrogates of the information present in dated phylogenies (Crozier et al., 2005; Ricotta et al., 2012). We therefore constructed a phylogeny for Australian Odonata largely based on taxonomic divisions following the familial arrangement in Dijkstra et al. (2013) (see Appendix S1 and S2 in Supporting Information). Additional taxonomic groups for Australian Odonata that have not yet been resolved within the global literature, including subfamilies, tribes or lower level units, were included from relevant literature (Theischinger & Watson, 1984; Watson & Theischinger, 1984; Watson et al., 1991; Peters & Theischinger, 2007; Theischinger & Endersby, 2009; Theischinger, 2012) and several unpublished phylogenetic studies (Gunther Theischinger, pers. comm.). The purpose of this phylogeny is not to advance the systematic debate over relationships among Odonata (Ballare & Ware, 2011), but to provide a basis for analytical comparison using the best available current knowledge. The tree was built in Treemaker v1.3 (Crozier et al., 2005) with branch lengths scaled as one for each change in taxonomic rank.

To complement the analysis of richness, endemism and turnover for species diversity, phylogenetic diversity (Faith, 1992), phylogenetic endemism (Rosauer et al., 2009) and

phylogenetic-turnover (Nipperess et al., 2010) were calculated based on the same principle, but using branch-lengths as units of diversity, as opposed to species, and weighting presences according to suitability scores. We hereafter refer to these indices as taxonomic diversity (TD) and taxonomic endemism (TE). TD counts the branches linking a set of taxa as a surrogate for unique or shared features represented by the taxa in the tree (Faith, 1992). TE is used to identify areas where substantial components of taxonomic diversity are restricted (Rosauer et al., 2009). The value of TE for taxa in a given area requires calculating the range size of each branch of the taxonomic tree (rather than the range of each taxon). TE is then the sum of branch lengths, each divided by the total range of its descendent species. TD-turnover is calculated in an analogous way to that for species turnover where total branch length lost and gained is summed, and without standardising according to overall diversity. This uses the same definition of absolute turnover ($b + c$), with the phylogenetic equivalents defined by Nipperess et al. (2010), and substituting suitability score for abundance as the weighting.

Analysis of taxonomic diversity was performed in R using the ape package (Paradis et al., 2004) and the phylo.div and phylo.endemism functions (available from David Nipperess: <http://davidnipperess.blogspot.com.au/>). We tested whether families or genera explained a significant amount of change to a species' range (sum of their habitat suitability scores) using a mixed model in the lme4 package (Bates et al., 2012). We then tested for differences in the relative amount of TD in different groups of species assessed as being threatened by climate change (Bush et al., 2014, see Appendix S3). These included: (1) species predicted to lose all environmentally suitable habitat in 2085 using scenario RCP8.5 ($n=14$); (2) highly vulnerable ($n=46$); (3) and vulnerable species for the same scenario ($n=47$); and (4) species poorly known and too rare to model ($n=37$). The TD of n vulnerable species was compared against a null model, which calculated the expected TD for n randomly selected species drawn a thousand times from the total pool. The probability of the observed TD for a vulnerable species subset occurring by chance was calculated as the proportion of times the null model

had an equal or higher TD than that observed. Finally, we compared whether differences in TD were approximately greater or less than might be expected for the given change in species richness by plotting the residuals of a linear regression between differences in TD (dependent variable) and richness (independent variable).

RESULTS

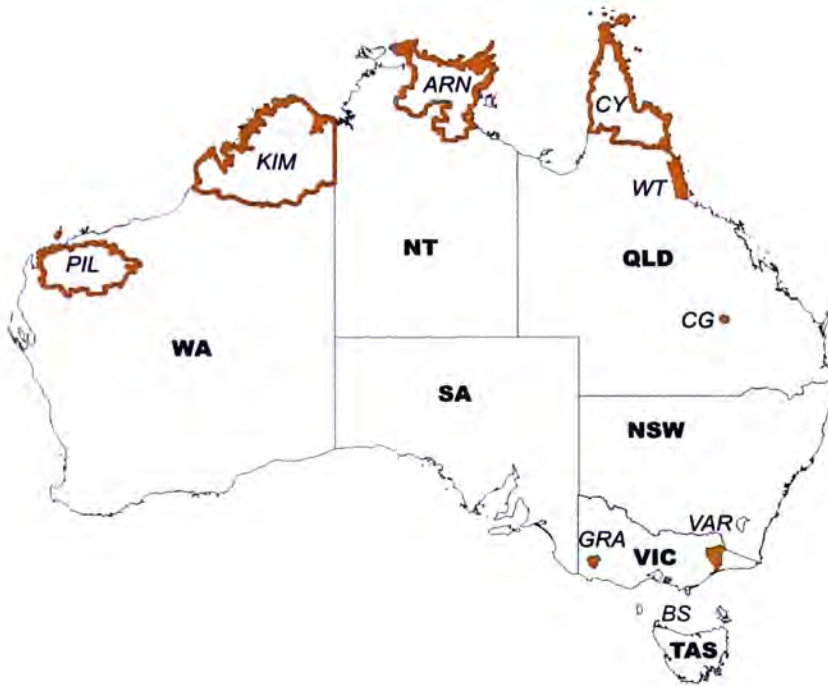


Figure 1 Australian states (bold): WA – Western Australia, NT – Northern Territory, SA – South Australia, QLD - Queensland, NSW – New South Wales, VIC - Victoria, TAS - Tasmania, and regions referred to in the main text (*italics*): PIL - Pilbara, KIM - Kimberly, ARN – Arnhem Land, CY – Cape York peninsula, WT – Wet Tropics, CG – Carnarvon Gorge, GRA - Grampians, VAR – Victorian Alpine Region, BS – Bass Strait.

Diversity

Current species richness of Australian Odonata is predicted to be greatest in the north Queensland Wet Tropics, with potentially up to 92 species found in the region. Lesser “hotspots” also occur in the far north of the Northern Territory, the tip of Cape York, south-east Queensland, and north-east New South Wales (NSW) although there is reasonably high richness along most of the east coast (Fig. 1 and 2). The richness hotspots also contain a high degree of endemism because each region has a distinct suite of species, but differences occur in some less diverse regions that contain their own restricted endemics such as small areas in

the Pilbara and Kimberley in northern-Western Australia, Carnarvon Gorge in central Queensland, the Grampians in western Victoria, western Tasmania and south-west Western Australia. The predicted distribution of taxonomic diversity (TD) is similar to that of species richness, but TD in Victoria and far south-western Australia is proportionally greater than expected for the number of species and the hotspot in south-east Queensland extends well into coastal NSW. High taxonomic endemism (TE) indicates that a site contains a large proportion of the range of those evolutionary lineages present. The current predicted distribution of TE was closely related to that of weighted endemism with a slightly greater concentration in southern regions like the Victorian alpine region and Tasmania.

Species richness is expected to decline in each of richness hotspots under current conditions, with nearly all species potentially lost from the far tropical northwest of the Northern Territory by 2085. Many of these species could significantly expand their current range under climate change, but the gains are partially lost again under the RCP8.5 scenario by 2085. Species richness is predicted to increase along the east of the Cape York Peninsula, and along the coasts and highlands of NSW, Victoria and South Australia. Assuming species are able to track suitable habitat and cross the Bass Strait, the richness of Tasmania could also double in the future. Potential loss of endemic species in the Pilbara, north Northern Territory and Carnarvon Gorge are projected. Changes in TD resemble the change in species richness but the balance of TD gains and losses varies among regions. Gain in TD along the east of the Cape York Peninsula, NSW coast and Tasmania is lower than expected for the given gains in species richness, and in the Pilbara, Wet Tropics, and south-east Queensland in particular, the loss of TD is significantly higher than expected for the decline in species richness (Fig. 3). Changes to TE are more difficult to interpret because it is affected by both the number of species predicted to be present, and by the extent of their suitable habitat, but overall the trends follow changes in endemism. The magnitude of change increased from RCP6 to RCP8.5 emissions scenarios projections but the patterns of changes were very similar.

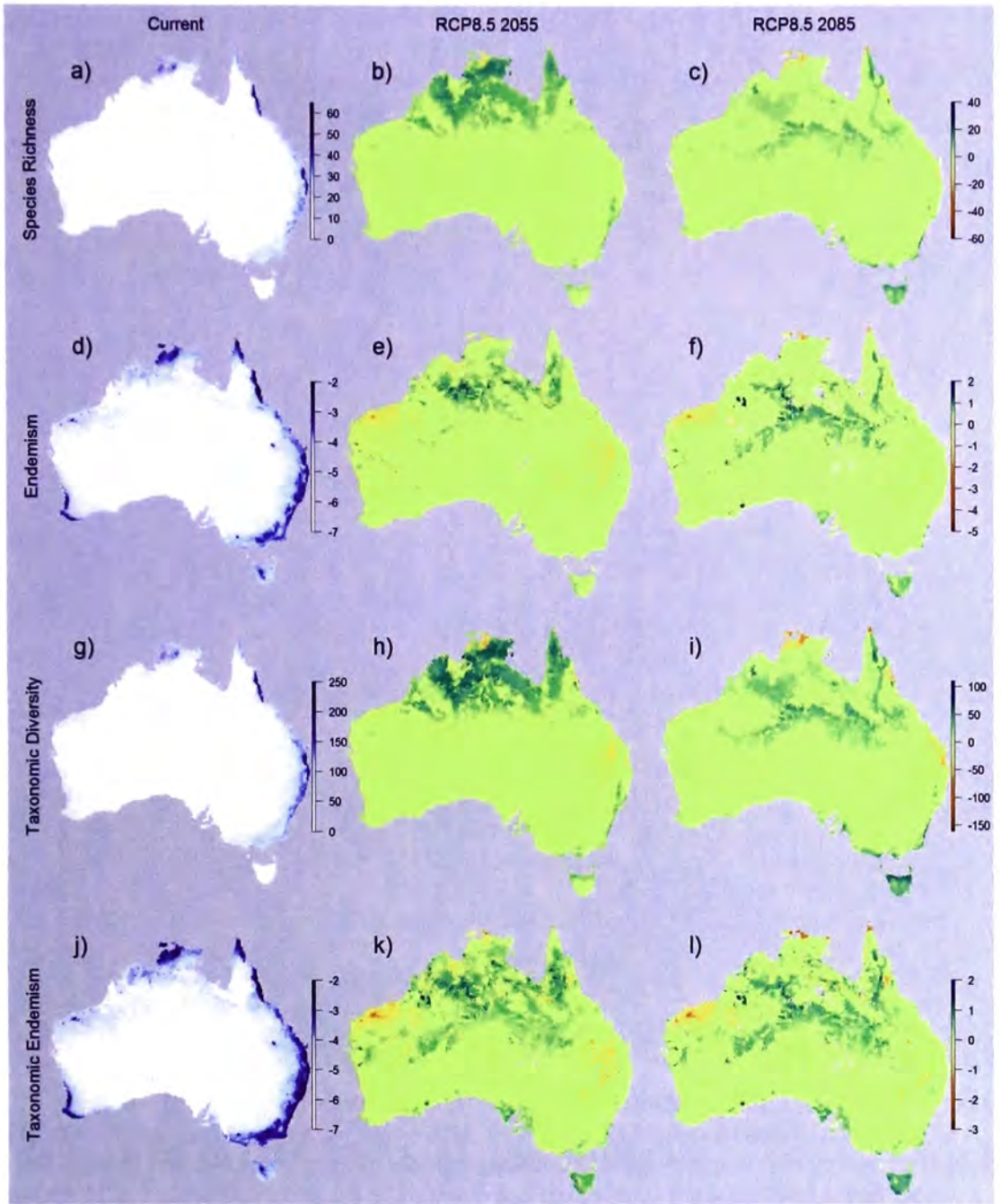


Figure 2 Australian Odonata richness, endemism, taxonomic diversity (TD) and taxonomic endemism (TE), under current climatic conditions (high values in blue), and the predicted change by 2055 and 2085 under emissions scenario RCP8.5 (increases in green, and decreases in red). Richness and TD represent the sum of suitability values across all species or taxonomic branches. Endemism and TE are displayed on a log scale, and represent the local suitability for a species or taxonomic branch divided by the total of their habitat suitability scores, summed across all species.

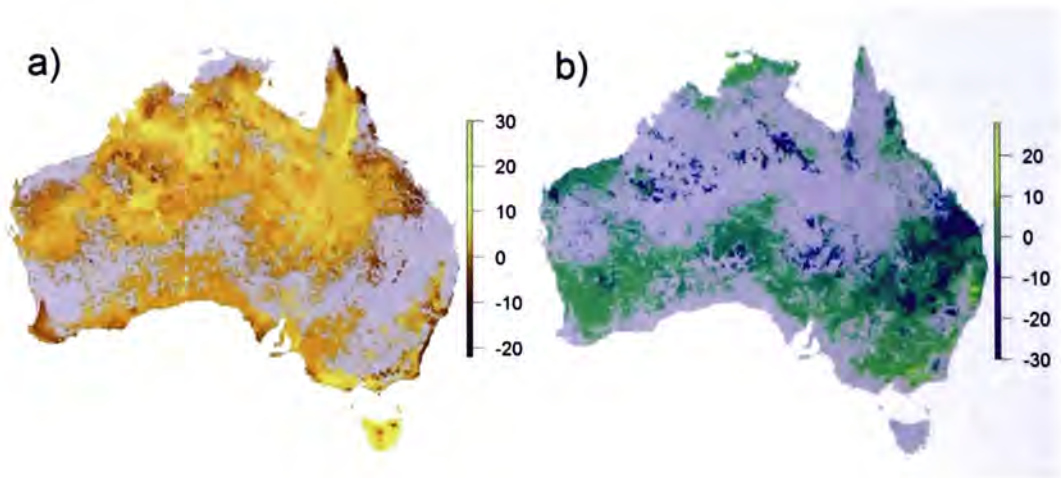


Fig. 3 Changes in odonate taxonomic diversity (TD) relative to changes in species richness (SR) from the current to the RCP8.5 2085 scenario, where richness is predicted to a) increase and b) decrease. Dark red and blue regions would have less TD than expected based on the change in SR, whereas yellow regions have higher TD given the change in SR.

Turnover

Under both RCP6 and RCP8.5 emissions scenarios, shifts in assemblage composition by 2055 are confined to small areas of the north and east coast, but by 2085 suitable habitat shifts south for large numbers of species along the east coast of Australia (Fig. 4 a-b). A few small regions of the north in the Kimberley and Arnhem Land are also predicted to see significant changes, mostly as result of species immigration from the hotspots on the north coast.

Turnover is primarily driven by local extinction in the far north of Australia and gains in the south such as in Tasmania. In southern coastal NSW the high turnover is a combination of local extinction and immigration that is equivalent to the current regional species richness. The absolute turnover of taxonomic diversity (Fig. 4 c-d), based on the combined gains and losses of branches over time, is always higher than species turnover because changes in a single species can affect multiple branches. High TD turnover extends from south-east

Queensland to south-east NSW and is also proportionally higher than expected by from species turnover in northern Tasmania and south-western Australia.

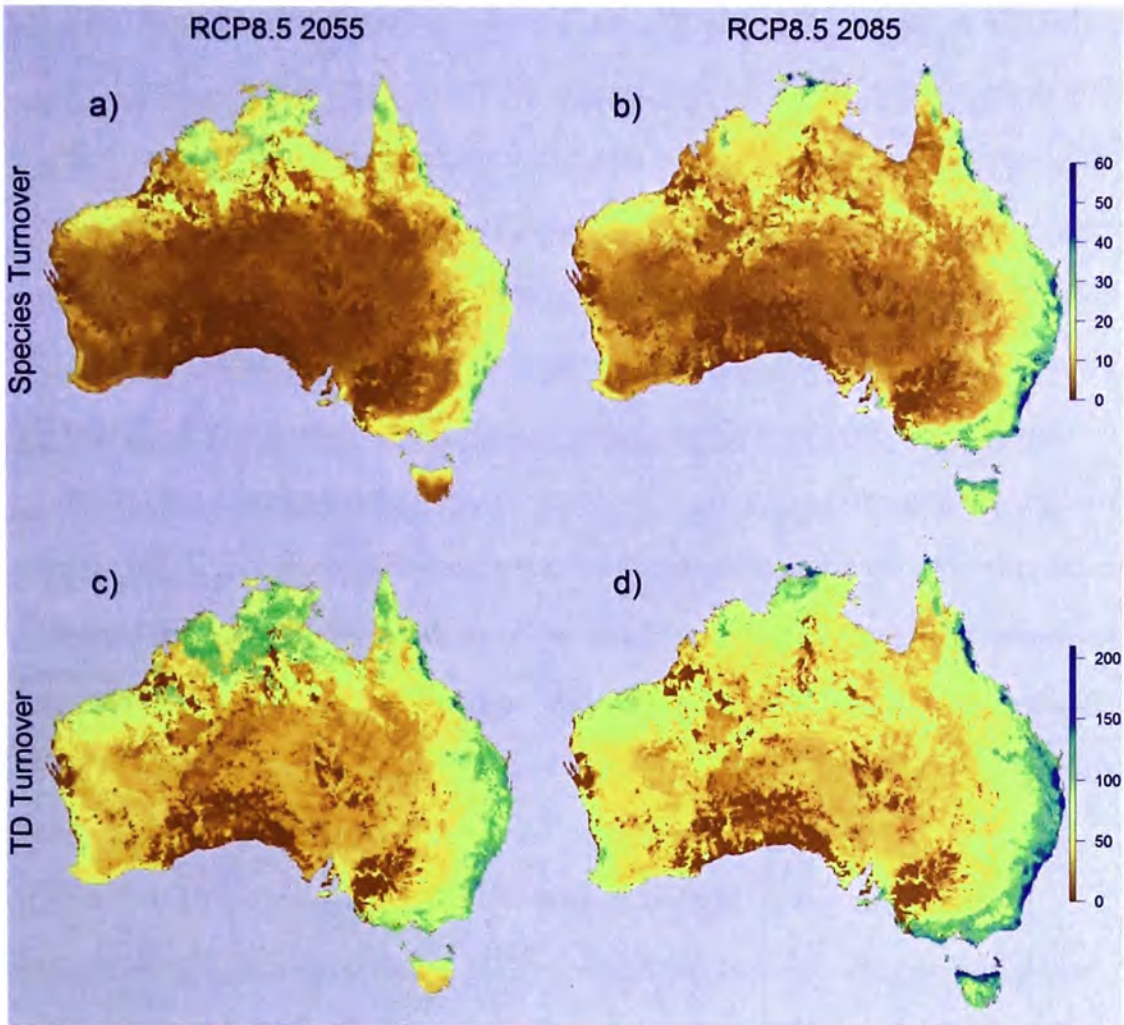


Fig. 4 Predicted turnover defined as the combined gains and losses in habitat suitability of species (a and b), or of taxonomic branches (c and d) for Australian odonate assemblages between the current climate and the future climate in 2055 and 2085 (scenario RCP 8.5). The greatest turnover is in blue.

Evolutionary bias among threatened Odonata

In addition to spatial variation in the distribution of diversity shifts, there was significant variation in the overall range shifts of species depending on their family and genus ($\Delta AIC = 3.0$). Genus explained 14% of the variation in range size (total suitability), and family explained 6%. Families such as Libellulidae, Aeshnidae, and Corduliidae increased their range on average whereas others like Lestoideidae, Synlestidae and Gondwanan Aeshnidae declined. Platycnemidae was the most adversely affected with 10 of 11 species predicted to decline. Despite the variation in overall outcomes for families and genera, the taxonomic diversity of species threatened with extinction ($p=0.25$), highly vulnerable ($p=0.67$), or at high risk due to climate change ($p=0.37$), or too rare to be modelled using species distribution models ($p=0.78$), was not significantly greater than a random selection (Fig. 5). Therefore the species lost and threatened by climate change are not predicted to be biased towards more distinct evolutionary lineages and are unlikely to result in an exaggerated loss of evolutionary diversity.

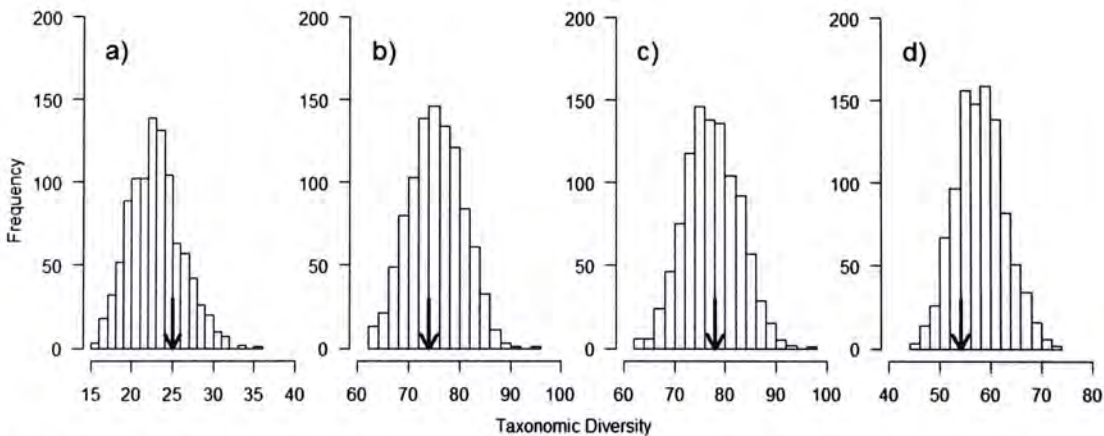


Fig. 5 Distribution of taxonomic diversity (TD) for 1000 random subsets of n Australian Odonata, equivalent to species threatened with (a) extinction ($p=0.25$), or (b) highly vulnerable ($p=0.67$), or (c) at high risk to climate change ($p=0.37$), and (d) rare species whose distribution has not been modelled ($p=0.78$). Arrows indicate the TD for the threatened species.

DISCUSSION

This study indicates that dramatic changes in the distribution of suitable habitats for Australian Odonata may occur this century, particularly in present day “hotspots” of species richness. In addition, significant turnover may extend across almost the entire east coast. Vulnerable assemblages in the Pilbara, south-western Australia and Tasmania contain a high proportion of endemic species. If species are able to track suitable habitats and cross Bass Strait, Tasmania could become an important refuge for mainland species. Although there is a coarse taxonomic bias in threat from climate change, and a spatial mismatch between the change in taxonomic diversity and species richness, we did not find evidence that species most vulnerable in the future represent a greater than average proportion of evolutionary diversity at the continental scale.

Richness

Odonata have been the focus of several large-scale modeling studies, either to help prioritise continental conservation targets (Simaika et al., 2013) or estimate gaps in sampling effort (Hassall, 2011). Odonates are well suited to SDM studies because they are particularly responsive to climatic factors (Hassall & Thompson, 2008), and have strong aerial dispersal which means spatial changes in assemblage composition and richness are predominantly driven by environmental changes (Bush et al., 2013; Heino, 2013). Australian Odonata have previously been identified as showing a strong latitudinal gradient in species richness (Boulton et al., 2005; Pearson & Boyero, 2009) but given the high richness of south-east Queensland (subtropical), and New South Wales (temperate) our study does not support this. We did not attempt to associate patterns of diversity of species with environmental factors because these factors would not have been independent of the variables used to model individual species distributions. However, it does seem likely that the richness of Odonata in Australia is driven by a water-energy balance in the environment (Keil et al., 2008), with

particularly rich assemblages found in regions that support rainforest (Clausnitzer et al., 2009).

It is important to understand that the SDM outputs assume a species is present throughout all suitable habitats and overlaying them to estimate richness and composition is predisposed to include errors of commission and overestimate richness (Guisan & Rahbek, 2011; Pineda & Lobo, 2012). Species could be absent or uncommon at sites that are predicted to be environmentally suitable due to dispersal constraints, biotic interactions, unsuitable micro-habitats, and stochastic effects (Heikkinen et al., 2006) or human habitat modification (Mangiacotti et al., 2013). For example, SDMs predicted 26 species could occur at Middle Creek in Victoria where Hawking and New (2002) sampled odonates (larvae and adults) intensively on 20 visits over three years. They found fine-scale patterns in sediment composition affected species composition, allowing 18 species to occur in the creek, four more in the nearby river, and at least nine more in the surrounding area (Hawking & New, 1999), including all those species predicted by the models. The relationship between local and regional species richness could have been used to modify estimates, but there were few locations in Australia with the required intensity of sampling to model richness directly (Gotelli et al., 2009).

Endemism and Taxonomic Diversity

Understanding the relationship of threatened species within communities has become increasingly important as the need to prioritize conservation effort seeks to emphasize the most evolutionarily distinct species (Isaac et al., 2007; Tucker et al., 2012). Furthermore, high regional endemism indicates the overlap of species with restricted ranges that are more likely to have narrower environmental tolerances, and be threatened by climate change (Calosi et al., 2010). Distinct regional assemblages are evident in Tasmania, and in the Pilbara which is increasingly recognised as a centre of invertebrate endemism (Pinder et al., 2010). Many

endemic Odonata are found in south-western Australia, a similar pattern to that in the flora (Davies & Stewart, 2013). These species represent proportionally more taxonomic diversity than just species richness would suggest (Sander & Wardell-Johnson, 2011). The rainforests of the Wet Tropics are both species rich and taxonomically diverse, but the region is highly threatened by climate change (Hughes, 2011; James et al., 2013) and the mismatch between loss of species and decrease in taxonomic diversity demonstrates that the more evolutionarily distinct species are under threat in this region.

Although there were broad biases among odonate families, the groups of species considered vulnerable were not a significantly diverse evolutionary subset of Australian Odonata (Thuiller et al., 2011). Naturally this depends on whether the taxonomic hierarchy is congruent with a molecular phylogeny that can resolve both the many polytomies, and improve the estimation of branch lengths. For example, some of the basal polytomies among odonate families could mean TD is more likely to be underestimated (Swenson, 2009). Ricotta et al. (2012) found a strong correlation between dated phylogenies and taxonomic hierarchy suggesting that at least the relative distribution of TD/TE is likely to remain similar. Whether the diversity of vulnerable species was in fact higher is difficult to judge, but given the results were not marginal and species from monotypic families were not threatened, a fully resolved phylogeny would have to significantly alter perceived relationships to reverse this result. Nonetheless, we should be aware the loss of taxonomic diversity associated with species vulnerable to climate change would be a significant loss from a conservation perspective and there are also likely to be further losses of genetic diversity within species, with unknown consequences for population resilience (Balint et al., 2011).

Turnover

Although loss of species in distinct and endemic regional faunas is a major concern, the implications of high turnover in response to climate change are an even more serious challenge for many other freshwater taxa (Heino, 2011; Turak et al., 2011). We assume Odonata will be able to track at least some of the predicted shift in habitat suitability to higher latitudes because they are relatively strong flyers (e.g. Hickling et al., 2006). Those species unable to fly, however, will face dispersal difficulties because most river basins along the Australian east coast are oriented from west to east (Turak et al., 2011; Bush et al., 2012). Even among Odonata, some species can be dispersal limited (Hassall & Thompson, 2012), and may not be able to reach all suitable habitats under changing climates (Jaeschke et al., 2012). For example, aside from the Bass Strait, there are several gaps along the Great Dividing Range that suggest odonate species diverged according to breaks in the terrain (Watson & Theischinger, 1984). Even if species can disperse to climatically suitable regions, it may not ensure successful establishment (Angert et al., 2011), resident species could competitively exclude new arrivals, or alternatively, climate change may provide immigrant species with a competitive advantage, displacing resident species (Suhling & Suhling, 2013). However, research in Victoria has shown the relationship between local and regional richness of macroinvertebrates appears to be linear, suggesting communities are not necessarily saturated, and could accept immigrant species (Marchant et al., 2006). Overall we might therefore expect most Odonata to follow predicted range shifts, the more significant projected increases in richness should be interpreted with caution, for regions such as Tasmania which is 220 km from the mainland.

The capacity for altitudinal migration is limited in most catchments (Sauer et al., 2011), and headwaters are also less likely to sustain flows during droughts (Robson et al., 2011). Many species are already isolated on mountain ranges, in climatic *cul de sacs* from which they

cannot disperse across lowlands to other refugia (Hughes et al., 2009). Regions that retain suitable habitat for the greatest number of species under climate change could be conservation targets for freshwater focal areas (Abell et al., 2007), but this also requires critical management zones to safeguard these habitats in the long term by managing the riparian corridor and landscape upstream (Davies, 2010). Promoting connectivity with focal refugia is essential, and those with high turnover could act as useful transition areas for multiple species over time (e.g. Phillips et al., 2008). Habitat connections can serve multiple species and connectivity is best viewed in conjunction with terrestrial conservation as part of a single holistic strategy. In the case of truly aquatic and dispersal-limited species, managed translocation may have to be considered (Morrongiello et al., 2011). Rugged terrain could provide sufficient resilience to safeguard vulnerable species in regions like the Wet Tropics (Luoto & Heikkinen, 2008), but as elsewhere, this depends on the capacity of species to reach suitable habitats (Krosch et al., 2009).

In contrast to many other macroinvertebrate orders, odonates are typically thermophilic, strong dispersers and generalist predators, traits that improve their adaptive capacity under climate change (Hassall & Thompson, 2008; Williams et al., 2008). Conversely a large number of other aquatic macroinvertebrates are sensitive to temperature increases, or are slow to recover following reductions in flow, and are potentially more susceptible to the effects of climate change than Odonata (Hering et al., 2009; Belmar et al., 2012). Other freshwater taxa such as fish, molluscs and crustaceans may be at even greater risk if they are sensitive to change but cannot disperse to climatically suitable habitats (Buisson et al., 2012; Kappes & Haase, 2012; James et al., 2013). Previous research on whole community studies suggest that climate change will result in dramatic changes to macroinvertebrate assemblage structure and ecosystem dynamics (Daufresne et al., 2007; Thompson et al., 2013), and this will have consequences for primary productivity and organic matter processing, that in turn support diversity and abundance of higher consumers (e.g. Mulholland et al., 2001). Therefore where

possible, trait data should guide conservation priorities to sustain ecosystem function under climate change (e.g. Bonada et al., 2007; Mouillot et al., 2013), and in their absence, taxonomic diversity is likely to provide the most practical criterion for preserving functional diversity.

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Supplementary Information

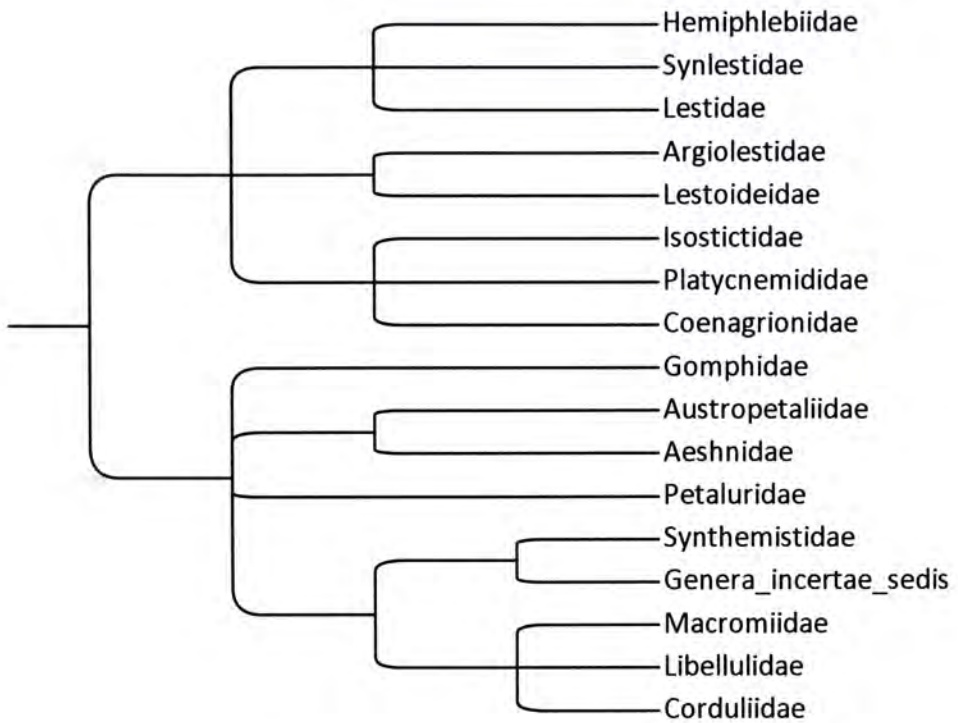
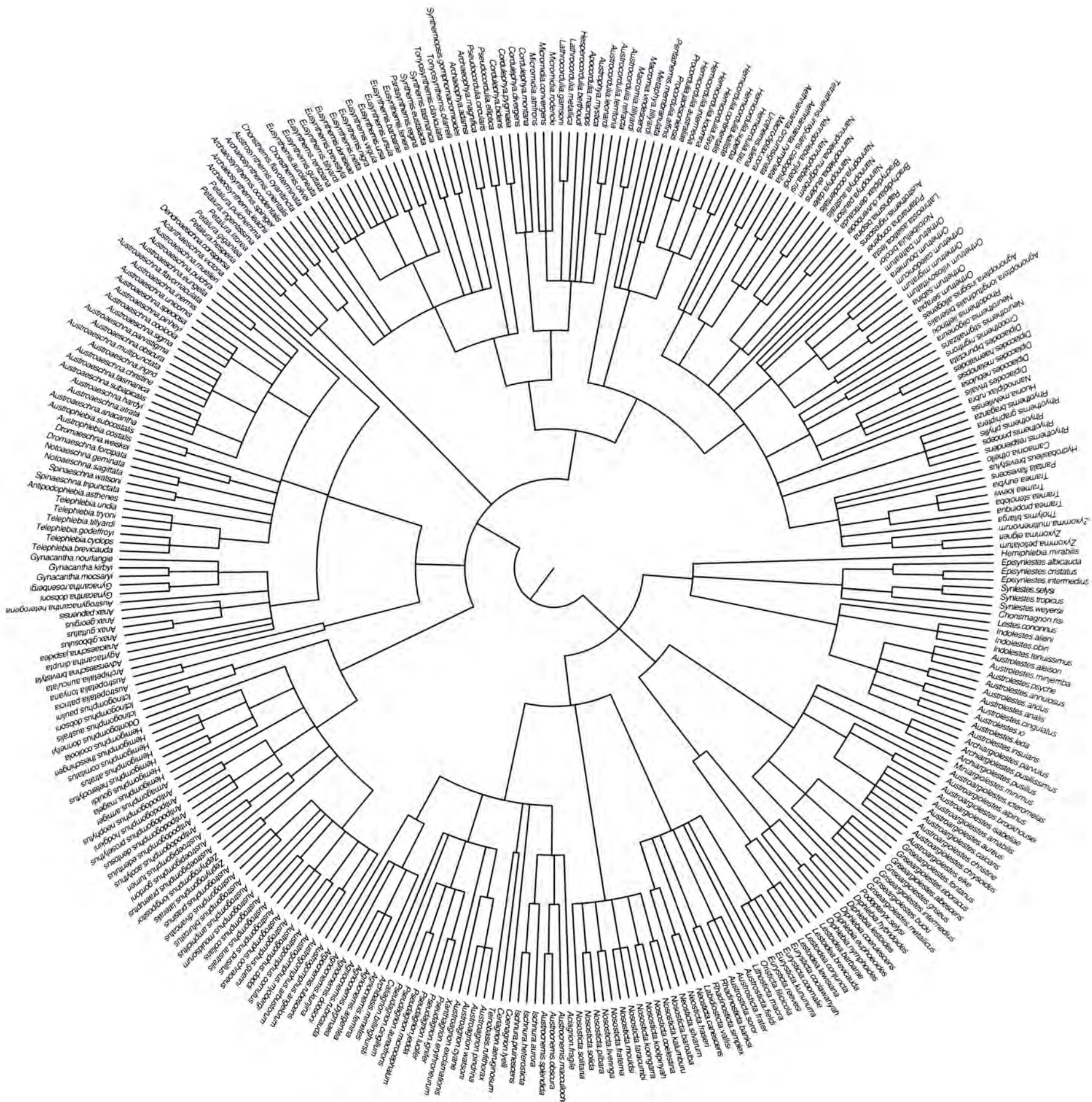


Fig. S1 Basal taxonomic phylogeny of Australian dragonflies.

Fig. S2 Full taxonomic phylogeny of Australian dragonflies



CHAPTER 6

FRESHWATER CONSERVATION PLANNING UNDER CLIMATE CHANGE: DEMONSTRATING PROACTIVE APPROACHES FOR AUSTRALIAN ODONATA

**Alex Bush, Virgilio Hermoso, Simon Linke, David Nipperess, Eren Turak
and Lesley Hughes**

ABSTRACT

Climate change represents a major challenge for conservation in the future, and undermines protection within reserve boundaries. Freshwater biodiversity is still under-represented within reserves worldwide, and connectivity among reserves will become increasingly crucial if species are to persist under climate change. We tested the likely benefits of including predicted species distributions in systematic reserve design for rivers under climate change, and the impact of varying connectivity requirements on future representation. Here we used the modelled distribution of 126 east Australian Odonata to identify reserve networks using data for current, 2055 or 2085 distributions either by filling gaps additively, or as separate targets in a single solution. Second, we assessed the potential improvements to species representation in the future by using different types of connectivity penalties that emphasised either longitudinal riverine connections or connections to all neighbouring sub-catchments. Solutions that did not include future distributions in the planning stages were 16 to 30% less likely to protect the same species by 2055 and 2085 respectively. Including species' future distributions in the design phase leads to short term increases in cost, but in the longer term, fewer additional areas are required to meet targets and this strategy is likely to be significantly more efficient than implementing systematic design in stages. In addition, solely targeting riverine connectivity was significantly less likely to protect current species in the future than if cross-catchment connections were included. Where protected areas can be expanded to assist species adaptation to climate change, significant gains in efficiency are possible if longer-term goals are considered when selecting sites. Furthermore, to improve the representation of species under future climates, reserve selection should consider inter-catchment connectivity, although the nature of optimal solutions will depend heavily on the range of taxa included, their dispersal capacity, and the availability of climatic refugia.

INTRODUCTION

Significant climatic changes are predicted to occur before the end of the century and freshwater biodiversity is likely to be particularly sensitive (Woodward, Perkins & Brown 2010). Relatively small increases in temperature have led to shifts in species phenology (Hassall et al. 2007), expansion of species' ranges to higher elevations and latitudes (e.g. Hickling et al. 2006), and significant shifts in community composition and size structure (Daufresne, Lengfellner & Sommer 2009). Other threats to freshwater biodiversity such as the modification of flows and withdrawal of water could be exacerbated by drying climates (Pittock & Finlayson 2011) and could reverse the ecological gains that have been achieved through improved landscape management in recent decades (Floury et al. 2012). There is an urgent need to identify effective conservation strategies that will conserve freshwater biodiversity under a changing climate before species losses accumulate to affect ecosystem function (Mouillot et al. 2013).

Globally, conservation of freshwater ecosystems has been poor (Collen et al. 2014), and rivers in particular are often regarded as boundaries of protected areas rather than as habitats requiring protection (Abell, Allan & Lehner 2007). Reserves often fail to consider catchment boundaries or headwaters in their design, or the allocation of freshwater downstream (Dudgeon et al. 2006). With little information on the broad-scale distribution of freshwater species, systematic prioritisation has focused on priorities for terrestrial ecosystems that are not necessarily effective for freshwater conservation (Darwall et al. 2011). Under climate change, existing reserves are likely to become increasingly unsuitable for many of the species they were intended to protect (e.g. Araújo et al. 2004). To address long-term conservation goals, the Convention on Biological Diversity committed member nations to increase protection from 10 to 17% of their territory, including freshwater systems (CBD 2010a), and

to implicitly target adaptation under climate change (CBD 2010b). To improve long-term protection and adaptive capacity in a cost effective manner we must explicitly consider what effect climate change is likely to have on species distributions, and integrate these projections into the conservation planning process. Model projections have been used to evaluate the adequacy of terrestrial (Araújo et al. 2004) and marine (e.g. Game et al. 2008) reserves under climate change, but there has been little research on the implications of climate change for conservation planning in freshwater.

In Australia, significant temperature increases, and reductions in rainfall (Hobday & Lough 2011) are likely to alter habitat suitability for many species (James et al. 2013) and are expected to lead to significant shifts in assemblage composition (Chessman 2009; Bush et al. 2012). . We chose to focus on Odonata (dragonflies and damselflies) because they are a diverse component of Australian freshwater biodiversity with a high proportion of endemic species (78%) (Theischinger & Endersby 2009) and they are likely to be highly responsive to climate change (Bush et al. 2013). Odonata also present an interesting context for studying how reserves can be clustered to improve connectivity (Hermoso, Kennard & Linke 2012). For a mobile group such as odonates, we can ask whether a strict emphasis on riverine connectivity hinders conservation under climate change?

This study evaluates the ability of reserve systems to protect Odonata in eastern Australia under current and future climate conditions in two stages. First, we compare the representation of species under different climate scenarios in priority areas identified using contrasting reactive and proactive reserve planning approaches. The reactive approach responds to gaps in the representation of species following climate change, whereas proactive selection anticipates change by combining future scenarios as separate targets in the same

solution (Palmer et al. 2009). In the second part of the study we compare the representation of Odonata in the future within reserves that consider connectivity either along river channels or across catchment boundaries.

METHODS

Odonata Data and Species Distribution Models

The study area comprised the Eastern Coastal Australia (ECA) freshwater ecoregion under the Freshwater Ecoregions of The World (Abell et al. 2008). The region extends from the Haughton and Burdekin rivers on the edge of the Wet Tropics in northern Queensland, south to Wilsons Promontory in Victoria, and includes 51 river basins.

Records of Australian Odonata were compiled from all Australian museums, private collectors, and the state environmental monitoring agencies. The complete database included over 35,000 separate records for 324 species and in 12,100 sub-catchments nationwide, from which the distributions of 273 species that occurred in at least 15 sub-catchments were modelled (Bush et al. 2014). The majority of records were collected within the last 20 years (95%), but records as far back as 1950 were also used for some uncommon species (Bush et al. 2014). Rather than using species occurrence records directly, it is increasingly common for conservation planning to use the predicted distribution of species and communities as inputs for prioritisation, thereby reducing the bias due to incomplete sampling (Linke et al. 2007).

Habitat suitability was predicted using a subset of three temperature variables (annual mean, seasonality and the minimum of the coldest month), three precipitation variables (seasonality, wettest quarter, driest quarter), one hydrological (mean annual flow) and one topographic (valley confinement). Given that the current trajectory of global emissions continues to track the high end of emissions scenarios (Peters et al. 2013), we used a high emissions scenario (Relative Concentration Pathway 8.5: RCP8.5) to model climate effects (van Vuuren et al. 2011). The climate projections were themselves an ensemble of seven global climate models (CCSR-MIROC32MED, CSIRO-MK30, GFDL-CM20, MPI-ECHAM5, MRI-CGCM232A, UKMO-HADCM3 and UKMO-HADGEM1) that perform well when predicting Australian patterns of precipitation (Fordham et al. 2012).

Species distributions were predicted using an ensemble forecasting approach in the BIOMOD2 package (Thuiller et al. 2009) in R (R Development Core Team 2013). This included five modelling techniques: Generalised Linear Models, Generalised Additive Models, Boosted Regression Trees, Multivariate Adaptive Regression Splines and Maxent (Elith et al. 2006). These models predict higher suitability in areas where environmental conditions were most “typical” of species occurrence records, and were evaluated for their ability to distinguish between these occurrences and the environment of pseudo-absences. To moderate the extent of environmental predictors and control for spatial collection bias, pseudo-absence points were selected from previously sampled sub-catchments within a 300 km radius of species’ occurrences (Elith, Kearney & Phillips 2010).

To weight the contribution of each model in the ensemble projection we used the True Skill Statistic, and also used it to calculate the minimum habitat suitability threshold (Liu, White & Newell 2013). Habitat suitability of the ensemble model was constrained using environmental clamping (Elith, Kearney & Phillips 2010) and a dispersal constraint that assumed species ranges could shift up to 15 km year⁻¹ (Jaeschke et al. 2012). Habitat suitability was projected onto 166,900 sub-catchments within the ECA (GEOFABRIC 2011), defined using a 250 x 250 m digital elevation model. To reduce processing time while still retaining enough detail for the purposes of this study we used the same elevation-grid to define 45,963 new larger sub-catchments units within the ECA as the planning units, and averaged suitability scores from the previous sub-catchments based on the area of overlapping grid cells. The new sub-catchments were defined using the same digital elevation model (Geoscience Australia 2009) within the ArcHydro package in ArcMap 10.1 (ESRI 2011).

Systematic Selection of Reserves

Conservation planning using continuous suitability scores rather than binary range predictions is more robust because it helps direct effort from marginal populations towards species core

habitats (Araújo & Williams 2000). To identify near-optimal reserve systems we used a modified version of the software Marxan (Ball, Possingham & Watts 2009) that has been developed to incorporate probabilities (hereafter referred to as Marprob, Fig. 1; Game et al. 2008; Carvalho et al. 2011). Marprob aims to minimise the sum of planning unit costs and connectivity costs in a reserve network, while still protecting the targeted amount of each species and at the desired probability. In this study we treated the predicted habitat suitability for Odonata species as equivalent to probability of occurrence (see equivalent use of MarProb in Carvalho et al. 2011). Marprob uses a probability weighting factor to penalise solutions that do not meet target probabilities of capture, in addition to the species penalty factor for not meeting areal targets. These weightings were calibrated separately for each solution so that solutions were required to meet all their targets while still being subject to costs.

In this study, existing protected areas were included as fixed features in all solutions, meaning additional protected areas would complement the current system (CAPAD 2010). High-level protection for freshwater taxa requires the landscape to be in favourable condition and so we only considered a catchment to be protected if over 75% of the sub-catchment area was within an existing reserve (e.g. Nel et al. 2011). The cost of additional sub-catchments was weighted according to the River Disturbance Index, which estimates the potential human disturbance of rivers based on accumulated upstream impacts of human landscape modification and flow regulation (RDI; Stein, Stein & Nix 2002). We used area rather than length of watercourse to scale costs because protection of freshwater habitats must also consider the impact of upstream land uses on water quality (Linke et al. 2007). We weighted the most disturbed sites ($RDI=1$) at double the cost of pristine locations ($RDI=0$) to reflect the additional management costs required for restoring and protecting disturbed sites (Linke et al. 2012). Although pressure on water resources is expected to increase in the future (Nelson et al. 2009), quantitative and spatially explicit predictions are lacking for most factors needed to estimate the RDI in the future, and consequently the value of the RDI for each period is the same.

However, not using the RDI would have allowed costly sub-catchments to be included and increased the potential likelihood that reserve selection procedures differed by chance, rather than being due to differences in selection procedure.

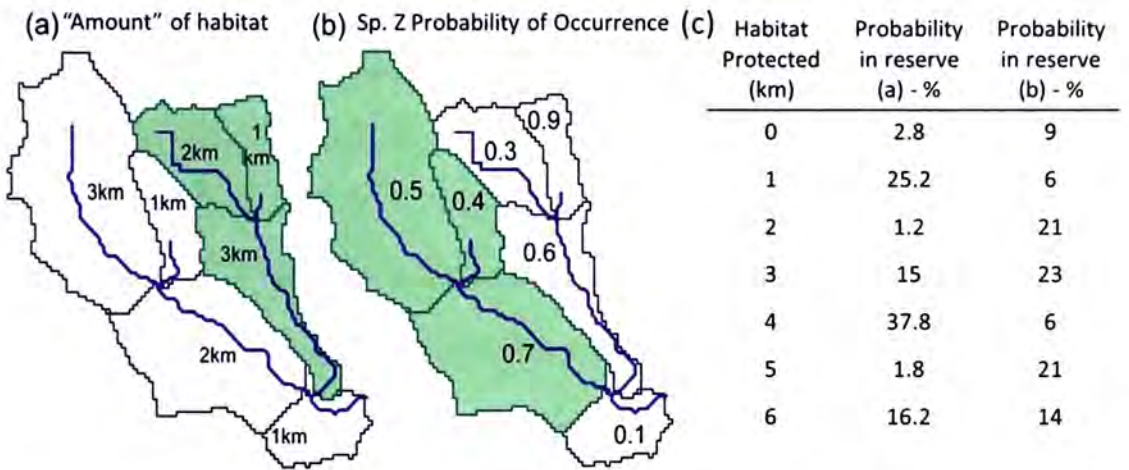


Figure 1. Consider two possible reserve systems in the shaded sub-catchments; (a) and (b), for which we know the amount of habitat (river length; a), and the probability of occurrence for a single species Z (b). As input to Marxan we could differentiate between sub-catchments by weighting distances or areas by the probability of occurrence. In this case both possible reserve systems would have the same summed score; $(3 \times 0.6) + (2 \times 0.3) + (1 \times 0.9)$ or $(3 \times 0.5) + (2 \times 0.7) + (1 \times 0.4) = 3.3$ units of sp. Z protected. However, it is possible species Z has been protected in none, or in up to 6km (c), and using Marprob we can see the probability of protecting at least 4km for species Z is greater in (a) $(37.8 + 1.8 + 16.2 = 55.8\%)$ than in (b) $(6 + 21 + 14 = 41\%)$. However, if 2km of habitat for species Z is considered adequate then the likelihood of meeting this target is higher in (b) (85%), than it is in (a) (72%). To calculate the probability of every potential solution would be very time consuming and so Marprob estimates the feature capture based on the summed score above, its variance and the desired level of certainty.

Analysis

We evaluated the representation of reserve systems i.e. the level of protection that was achieved across all species, by summing the probability of each species meeting its conservation target (see Carvalho et al. 2011) under each scenario (current, 2055 and 2085). We also compared the efficiency of reserve solutions by dividing this sum by the estimated cost (number of species protected per unit cost). All solutions in this study were set to reach a conservation target of a 75% probability of protecting a species across 250 km of river system. Therefore, unless 250km of habitat is available with full certainty of species' presence, the shortfall must be made up by additional areas that could increase the overall likelihood of protection for that species across 250 km above 75%. It is likely that populations of Odonata would persist in streams and rivers less than 250 km altogether, but the targets were increased for this study to investigate the effects of reserve selection at a scale appropriate to the study region and national targets (i.e. close to 17% of the ECA region). Where the 250 km target was greater than all available habitats for the species within the ECA, we reduced targets for those species to 75% of the maximum achievable river length, while still achieving a 75% certainty of protection. Targets for each species were kept consistent across time by using the lowest target achievable in the three scenarios. We did not increase the desired certainty of protection further because reducing uncertainty means solutions becomes disproportionately more expensive (Williams & Araújo 2002).

To avoid targets from being met by the selection of large numbers of sub-optimal sites with low suitability scores, values below the minimum habitat suitability threshold were set to zero (Liu, White & Newell 2013). To be comprehensive, conservation planning usually includes all species, but comparisons between scenarios could have been inconsistent if species were included that in the future (2055 or 2085) were either lost from the ECA entirely, or immigrated into the region. Consequently for the purposes of the study, species not present in

all three time periods were excluded. Furthermore, we found species with suitable habitat in more than 20% of sub-catchments were not influencing the reserve selection process and so to reduce computation time we removed them from the dataset. Conversely, species predicted to occur in less than 0.1% of streams were so rare that suitable sub-catchments effectively became fixed in all solutions, biasing solutions to include those species. To allow flexible selection of all species targets these rare species ($n=26$) were also removed. Out of approximately 189 Odonata predicted to occur in the ECA during current or future climate scenarios, the final dataset contained 126 species that met all criteria.

Reactive vs. Proactive

We considered two basic approaches to reserve design in the future under different climate scenarios; Reactive and Proactive (Palmer et al. 2009). The Reactive option would be equivalent to adding new reserves after observing the distribution of species shifting beyond the borders of existing protected areas. The Reactive solution was thus initially based on reserve selection for the current distribution of species, which are then fixed within solutions together with the existing protected areas. Additional reserves are then added to protect the distribution of species in 2055, and the process is repeated for 2085. In the alternative Proactive approach, complementary sub-catchments are selected by treating the distribution of species from all three scenarios (Current, 2055 and 2085) as separate targets in the same solution.

Initially we established whether a Proactive approach would improve the representation of species in the future in comparison to the optimal current solution (first stage in the rReactive approach). To get a subset of the Proactive solution equivalent to the current optimum, we ran Marprob for current species distributions only, and using only those sub-catchments selected in the Proactive solution (based on all three scenarios). Solutions in Marprob were based on the means of 1000 runs, with 1,000,000 iterations per run. It is difficult to make sure

the BLM has the same effect across scenarios and therefore, for the sake of comparability between Reactive and Proactive approaches, the boundary length modifier (connectivity penalty) was set to zero at this stage of the analysis and meant there was no penalty for fragmented solutions.

Connectivity

In the second part of the study we introduced connectivity to the selection process. The ability to account for connectivity has improved significantly and has been critical for advances in systematic conservation of rivers (Hermoso et al. 2011; Hermoso, Kennard & Linke 2012). In the case of Marxan/Marprob, solutions are penalised for all connections not included in the final reserve network. Hierarchical riverine (longitudinal) connectivity was included following the methods of Hermoso et al. (2011) which weights distances among stream segments so that solutions that omit connections with closer upstream or downstream planning units receive a higher penalty than if they miss distant connections. However, Odonata are not restricted to longitudinal dispersal along a river corridor and can disperse across basin boundaries, and consequently lateral connections to neighbouring sub-catchments may be more appropriate to improve connectivity efficiently (Hermoso, Kennard & Linke 2012). Cross-catchment (lateral) connectivity was calculated using the *gdistance* package in R (van Etten 2012; R Development Core Team 2013) and included connections to all sub-catchments based on Euclidean distances among sub-catchment nodes, and applying the same weighting system used in the longitudinal connectivity file. To reduce the computation time we limited lateral connections to 25 km or less, and when longitudinal and lateral connectivity files were combined duplicate lateral connections of the longitudinal file were removed.

Marprob was run using only the current distribution of species and five combinations of the connectivity files: (1) longitudinal connections only, (2) lateral connections only, (3) an equal

combination of the two, (4) & (5) combinations where the longitudinal or lateral connection penalties were doubled. We evaluated the summed probability that reserves would meet their conservation targets across a range of connectivity penalties. Scores at equivalent connectivity penalties cannot be compared directly because the balance of connections in the five connectivity files changes the overall costs included in the Marprob optimization. As a result, summed probability in connectivity types was compared based on the number of planning units in that solution, and log transformed to compare linear models (Huitema 2011).

Summed probability within protected areas (response variable) would increase naturally as the number of planning units is increased (covariate), and so an analysis of covariance (ANCOVA) was used to test for the interaction effect of connectivity type (factor). A significant interaction shows that the effect of increasing the connectivity penalty, and by extension the number of planning units, on reserve representation, depends on the type of connectivity used.

Given conservation of rare species is a critical element for implementing complementary reserve design, we also evaluated whether 26 rare species omitted from the main analysis were indirectly protected by the distributions of the 126 species used, or if additional reserves to promote their protection altered the outcomes of the analysis (supplement S1).

RESULTS

Reactive vs. Proactive

On average, 11% of ECA planning units were chosen to protect current distributions, and both Reactive and Proactive solutions included 12-13% in the long term. As 8.4% of planning units were existing protected areas, the alternative approaches only influenced selection of the additional complementary areas, and yet approximately 35% of the new planning units selected by the Proactive scenario were not chosen in the Reactive solutions (Fig. 2).

Proactive and Reactive solutions were each calibrated to meet 100% of the targets for the current distribution of species (Fig. 3a), but by 2055 and 2085 there were significant declines in the likelihood species would meet their targets ($F(2,299)=35198$ and 11500 respectively, $p < 0.0001$). The summed probability of the Reactive solution fell by 16% and 30% respectively, compared to a reduction of 9 and 15% for the Proactive solution. Though the certainty of meeting the conservation targets set in this study were much lower in the existing protected areas to begin with, the summed probability actually recovered slightly in 2085 showing that some species distributions were predicted to shift to protected areas where they do not currently occur.

Naturally, the subset of the Proactive solution for current species distributions was not as efficient as the near-optimum Reactive solution designed to suit that particular climate period (Fig. 3b, $F(1,198)=46$, $p < 0.0001$). Efficiency declines in both solutions over time because in each case some areas required for conservation under the current climate become redundant in the future and new areas are added to fill gaps. The Reactive solution required more additional reserves under future climates than the Proactive solution. Consequently the efficiency of the final reserve solution in 2085 is lower than the Proactive solution and in the long term across all three scenarios, the Proactive approach is approximately 6.8% more efficient ($F(2,594)=475$, $p < 0.0001$). Accounting for rare species in the selection of

reserves did not alter the pattern of results between Reactive and Proactive approaches (see supplement S1).

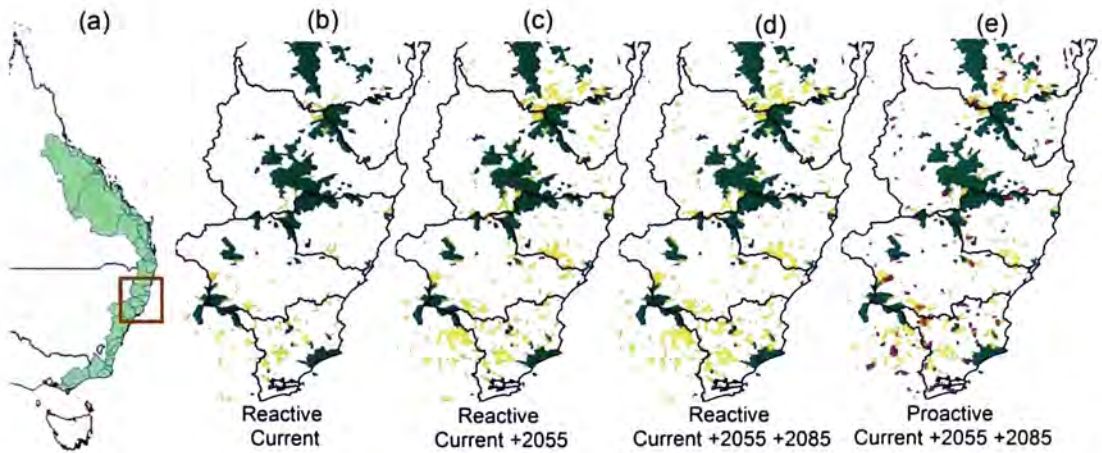


Figure 2. (a) Study area in the Eastern Coastal Australia eco-region (green; Abell et al. 2008). (b-e) Regional view of study catchments showing existing protected areas (dark green) and the least costly reserve solution (orange). The Proactive solution (e) includes sub-catchments in pink where the solution differs to that of the complete Reactive approach in (d).

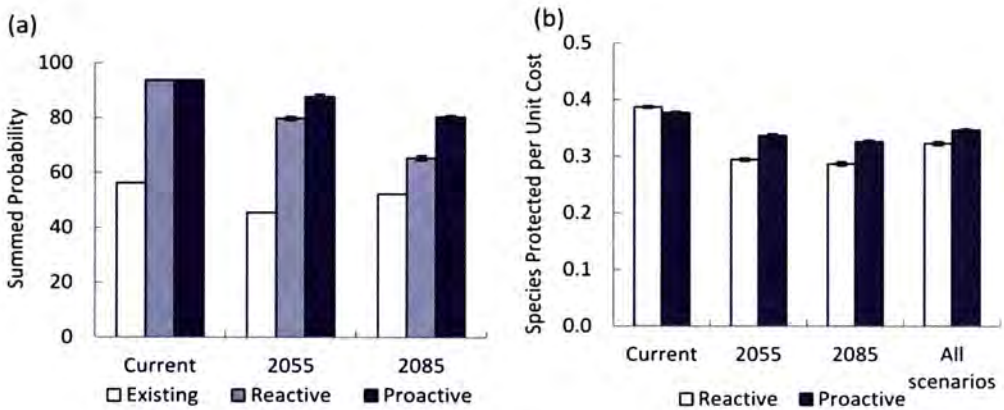


Figure 3. (a) Summed probability of Odonata meeting their conservation targets (\pm SD, $n=126$, $\max=93.7$) based on distributions under current, 2055 and 2085 climate scenarios, using reserve networks from existing protected areas, the current optimal solution (Reactive) and the current Proactive solution. (b) Efficiency of Reactive and Proactive reserve networks for Odonata under current, 2055 and 2085 climates, and averaged for all three scenarios.

Improving Reserve Adequacy in the Future with Connectivity

Increasing the connectivity penalty for reserve selection always requires more planning units and eventually entire catchments began to be selected, so the analysis was limited to changes in connectivity below 15,000 (~30%) planning units. The type of connectivity used had a significant effect on the summed probability of protection for species projections in 2055 (ANCOVA $r^2=0.97$; Interaction effect: $F(4,3100)=707$, $p<0.001$, Fig. 4a), and 2085 projections (ANCOVA $r^2=0.98$; Interaction effect: $F(4,3100)=1741$, $p<0.001$, Fig. 4b) for a given number of planning units in a reserve network (full results in S2). Specifically the rate at which summed probability increased was lower if prioritisation used only longitudinal connections, and for an equivalent number of planning units, solutions that included lateral connectivity to a greater or lesser degree were more likely to protect species under future climate scenarios. Although increasing connectivity did improve species' representation under climate change, naturally it is relatively inefficient compared to targeted reserve selection. For example, both the Reactive and Proactive solutions were able to protect species in all three time periods using 6000 sub-catchments whereas 2-3 times as many may be required if we simply expand the network through improved connectivity. The lack of focus for reserve selection is likely to be one reason why the differences between connectivity types are difficult to distinguish visually (see S3). These results remained consistent even when additional reserves for rare species protection were incorporated (see S1).

Naturally, the subset of the Proactive solution for current species distributions was not as efficient as the near-optimum Reactive solution designed to suit that particular climate period (Fig. 4b). Efficiency declines in both solutions over time because in each case some areas required for conservation under the current climate become redundant in the future and new areas are added to fill gaps. The Reactive solution required more additional reserves under future climates than the Proactive solution. Consequently the efficiency of the final reserve

solution in 2085 is lower than the Proactive solution and in the long term across all three scenarios, the Proactive approach is approximately 6.8% more efficient.

Increasing Protection in the Future with Connectivity

In the second stage of the analysis we investigated whether improving connectivity would be likely to provide added protection to species in the future. Solutions always require greater numbers of planning units when the connectivity penalty is increased and so efficiency declines. For all types of connectivity, low penalties could be met with little additional area. At higher values of the connectivity strength modifier, particularly using longitudinal connectivity, entire catchments begin to be selected and so analysis was limited to changes in connectivity below 15,000 planning units, approximately one third of the EAC total.

The connectivity type used had a significant effect on the summed probability of protection for species projections in 2055 (ANCOVA $r^2=0.97$; Interaction effect: $F(4,3100)=707$, $p<0.001$, Fig. 5a), and 2085 projections (ANCOVA $r^2=0.98$; Interaction effect: $F(4,3100)=1741$, $p<0.001$, Fig. 5b) for a given number of planning units in a reserve network (full results in Table S1). Specifically the rate at which summed probability increased was different between reserves that used only longitudinal connections, and reserves designed using all other connectivity types, all of which included lateral connections to a greater or lesser degree. For an equivalent number of planning units, solutions that included lateral connectivity were more likely to protect species under future climate scenarios. Although increasing connectivity does improve conservation under climate change, the increasing probability of meeting conservation targets is relatively slow compared to targeted reserve selection. For example, both the Reactive and Proactive solutions in the first section of this study were able to protect species in all three time periods using 6000 sub-catchments whereas 2-3 times as many may be required if we simply expand the network through improved connectivity.

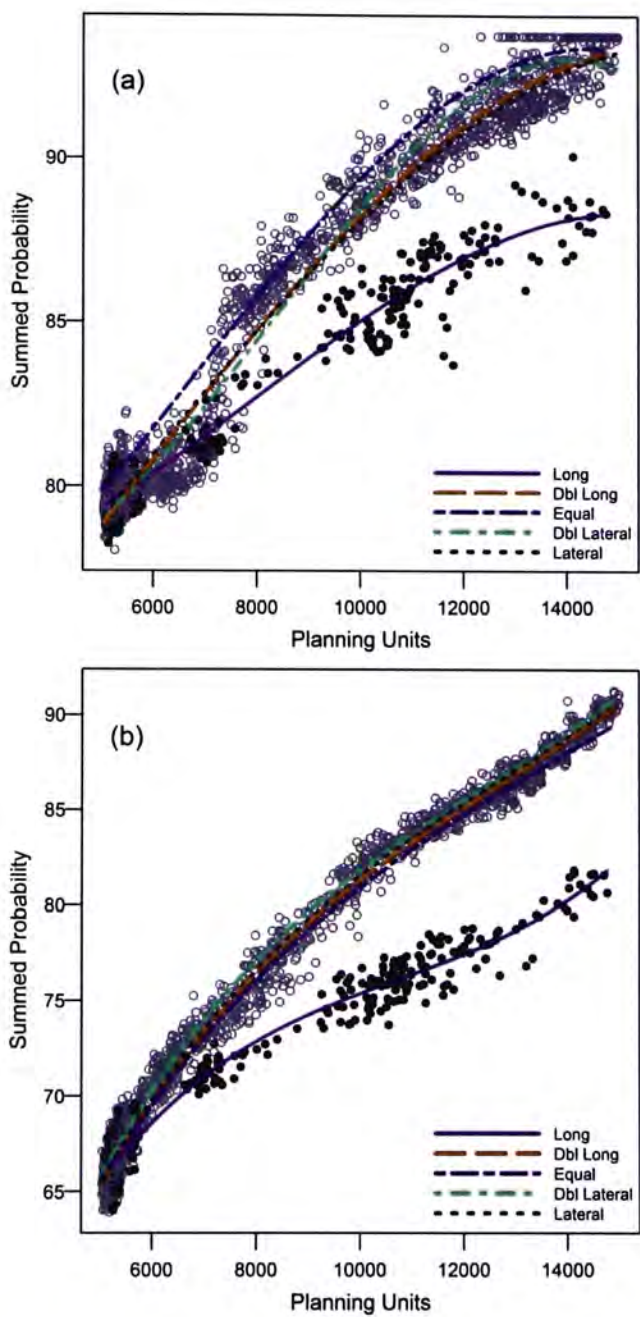


Figure 4. Relationship between summed probability of meeting conservation targets (max sum=93.7) in 2055 (a) and 2085 (b) following an increase in the number of planning units by emphasizing connectivity. The lines indicate differing connectivity types and are divided between the use of just longitudinal connections (closed circles, solid line), and lateral connections or combinations of the two (open circles, dashed lines).

DISCUSSION

The suitability of a reserve system optimised under current climate will inevitably decline if species distributions shift as the climate changes, and either reserves do not encompass the same range of environmental conditions in the future as they do now (Araújo et al., 2004; Pyke & Fischer, 2005; Dunlop et al., 2012), or species are not able to disperse to alternative protected areas (Vos et al., 2008). This study demonstrates that the identity of sub-catchments chosen to protect the current distribution of dragonfly species is different in light of climate change, and in the long term would include many areas not considered by 'optimal' solutions. By planning for future climates simultaneously, solutions effectively anticipate changing distributions by ensuring targets from all periods are met. As a consequence, fewer protected areas become less suitable in the future and lead to long-term gains in efficiency.

Conservation planning is highly unlikely to be successful or efficient in the long term if shifts in suitability as a result of climate change are not considered and our results show that proactive solutions remained more likely to conserve species in the future, and required fewer additional areas to meet gaps in protection. However, proactive conservation strategies inherently carry a degree of risk because decisions are reliant on predictions that carry some uncertainty (Heller & Zavaleta, 2009). Methods are available to include uncertainties due to the modelling technique (e.g. Buisson & Grenouillet, 2010) and climate scenarios (e.g. James et al., 2013), and these should also be incorporated into conservation planning (Carvalho et al., 2011). Many aspects of prediction under climate change are likely to remain uncertain and consequently there is growing interest in how other disciplines incorporate uncertainty into decision making (e.g. financial risk management: Ando & Mallory, 2012). Despite the uncertainty, there are clear benefits for considering climate change in setting conservation priorities (Hannah et al., 2007). Prioritisation of species based on modelled habitat suitability provides a quantitative and spatially explicit method for planning under varying climate

scenarios, and by adopting a probability-based approach towards more suitable habitat we can favour the selection of species' core habitats (Araújo et al., 2004). We would still recommend the proactive solution be implemented in stages, but unlike the reactive solution, new protected areas are more likely to contribute to conservation of species of interest in the future.

Increasing reserve connectivity is essential for conserving rivers because there are a number of ecological processes such as fish migration, and threats such as pollution and flow alteration, that need to be considered (Hermoso et al., 2011). Increasing connectivity has also been one of the most commonly cited measures for improving adaptation to climate change, particularly across environmental gradients (Heller & Zavaleta, 2009; Game et al., 2011). Longitudinal connectivity along rivers follows a number of environmental changes including temperature, and species are predicted to move further upstream in response to climate change (Buisson & Grenouillet, 2009). The results of this analysis would initially suggest that in order to improve the future representation of dragonfly species within protected areas, lateral connectivity should be emphasised, without necessarily including longitudinal connectivity along rivers. This is primarily due to the fact that under severe climate change, environmentally suitable habitats of dragonflies were predicted to shift along latitudinal gradients (Bush et al., Thesis Ch.5). This underlying trend was significant enough for reserve selection to benefit from even minor additional cross catchment connectivity. Although lateral connections did not specifically emphasise latitudinal gradients, this result would support a corridor approach to climate change adaptation such as the Great Eastern Ranges (GER) initiative that has been primarily focused on terrestrial ecosystems (Mackey et al., 2010). As strong dispersers, dragonflies may benefit from such an approach, but for other freshwater-dependent species, the west-east orientation of catchments in eastern Australia is a particular problem (Turak et al., 2011a). Even if protection strategies were to focus on the conservation of tributaries oriented North-South there are terrestrial limitations, and some species will in

fact preferentially move among headwaters rather than disperse through lowland streams (Hughes et al., 2013). Freshwater and terrestrial ecosystems are too often treated independently in terms of conservation strategies, and we suggest one approach that could meet goals for the majority of species would be to prioritise riverine connectivity from lowland habitats to headwaters and connect with the GER that already conserves many potential refugia at high altitudes (Turak et al., 2011a; James et al., 2013).

An important extension of this study will be to expand the range of taxa assessed because dragonflies may not be suitable surrogates for broader freshwater biodiversity (Heino, 2010; Bush et al., 2013), and this can lead to biases in conservation planning (Darwall et al., 2011). The adaptive capacity of dragonflies to climate change is likely to be higher than for many other freshwater taxa such as fish, molluscs and crustaceans that have less capacity to follow shifts in climatically suitable habitats (Buisson et al., 2012; Kappes & Haase, 2012; James et al., 2013). The importance of a proactive approach, and the extent of efficiency gains available, increases with the proportion of species distributions that will become climatically unsuitable in the future. Species expanding north in the UK, including dragonflies, are disproportionately more likely to be within protected areas as they follow shifting habitat suitability and colonise new areas (Thomas et al., 2012). Aquatic insects are also more likely to disperse across catchment boundaries if there is vegetation cover (Alexander et al., 2011). By including species in conservation planning with varying capacity for dispersal we might observe a trade-off between connecting currently suitable habitats in favour of ensuring connectivity to promote persistence under climate change. Features such as wetlands, and connections to them, were also not considered by this study and are often vital for supporting habitat suitability elsewhere (Nel et al., 2011). To better account for connectivity under climate change, particularly in cases where the current and future species distributions do not overlap and dispersal abilities are varied, new methods such as network-flow prioritisation could improve the efficiency of conservation planning (Williams et al., 2005).

Despite the alarming state of river health in Australia (Stein et al., 2002), conservation has typically focused on terrestrial biomes rather than the protection of freshwater systems within them (Abell et al., 2007). Without considering impacts on rivers from upstream sources or even downstream, the length of channel habitats within protected areas overestimates the true extent of protected riverine habitat (Stein & Nevill, 2011). Placing an area under protection can increase the resilience of the ecosystem to climate change effects by alleviating other threatening processes. As demonstrated by the slow decline in performance of existing protected areas in this study, climate change is projected to affect freshwater ecosystems both within and beyond reserve boundaries and so changes to management are required in each (Wilby et al., 2010). Management of protected areas will require specific actions that build resilience, particularly against drought (Hodgson et al., 2009; Thomson et al., 2012). For example, greater channel complexity and deep pools provide refugia for invertebrates during extreme high and low flows (Dunbar et al., 2010) and riparian restoration can significantly reduce stream temperatures (Seavy et al., 2009; Davies, 2010). The greatest challenge for freshwater conservation in eastern Australia will be to ensure suitable connectivity between areas of important lowland habitats, often within a highly modified landscape, and headwaters within protected areas (Pittock & Hartmann, 2011; Turak et al., 2011a).

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Supplementary Information

Supplementary Information S1 - Analysis of Rare Species Representation

Twenty-six species, for which modelled projections were available, were not included in the main analysis for this study because they are extremely rare within the study region for at least one of the climate scenarios. Furthermore, these 26 species were not simply rare because their main distribution is outside that of the study region. The highly limited range predicted for these species meant that to meet representative targets alongside other species meant selecting all available planning units, restricting the ability of Marprob to make a flexible choice among reserve networks. Nonetheless, excluding these species is contrary to the purposes of most actual conservation goals that seek to be comprehensive and representative of all species.

To acknowledge the importance of rare species, we consider their importance in two ways;

1. First, we evaluate the indirect coverage of the rare species within the reserve networks designed for the included species ($n=126$) in the main analysis (hereafter referred to as the “study solutions” and “study species” respectively). We refer to this as indirect representation of rare species because they were not specified as targets in Marprob, and therefore any overlap between species’ ranges and reserves was not by design.
2. Second, we include targeted protection for rare species prior to the main Maprob analysis to see whether added features for protecting rare species modify our conclusions.

1. Indirect Conservation of Rare Species within Reserve Networks

To evaluate the ability of reserve networks to meet a conservation target we set the total for each of the rare species to a 75% probability of protection across just 10 km of stream or river habitat. For five species this target could not be met in all scenarios because they were

predicted to be entirely absent from the EAC study region and as such the summed probability that could be achieved varied slightly between scenarios.

Overall, the 10 km target was met for the majority of rare species within the current protected area network, although it declined sharply in 2085 (Fig S1.1). The probability of rare species protection was higher overall among the Reactive and Proactive networks, but the shortfall indicates several species would not meet the target. The higher probability of protection in Reactive and Proactive solutions could also be due to their larger area and the result of greater overlap purely due to chance. For comparison we introduced a random solution, still keeping existing protected areas fixed, but randomly selecting additional units equivalent to the numbers chosen by the Proactive approach. This random solution did increase the overall probability of protection for rare species, although significantly less so than Reactive and Proactive solutions did in all scenarios ($F_{(2,298)} = 8321, p = <0.0001$). Comparison with a randomised equivalent of the Reactive solutions gave the same result. Finally, there was no significant difference between the summed probability of protection for rare species between Reactive and Proactive approaches.

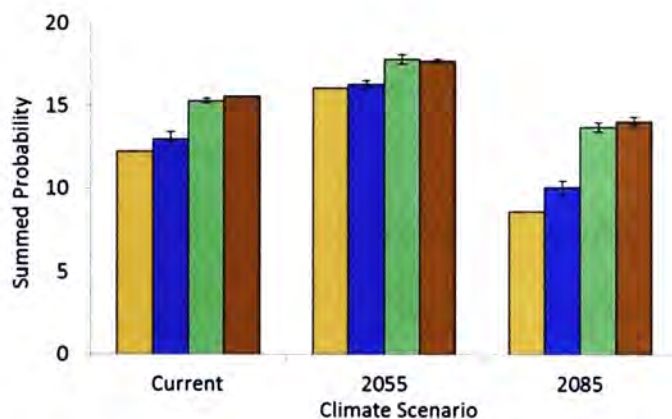


Figure S1.1 - Summed probability of protection for rare Odonata (+/-SD, $n=26$, $\max=19.5$) based on distributions under current, 2055 and 2085 climate scenarios, using reserve networks from existing protected areas (orange), the randomised solution (blue), the current optimal solution (Reactive, green) and the current Proactive solution (red). Targets are based on a 75% probability in 10 of stream or river habitat.

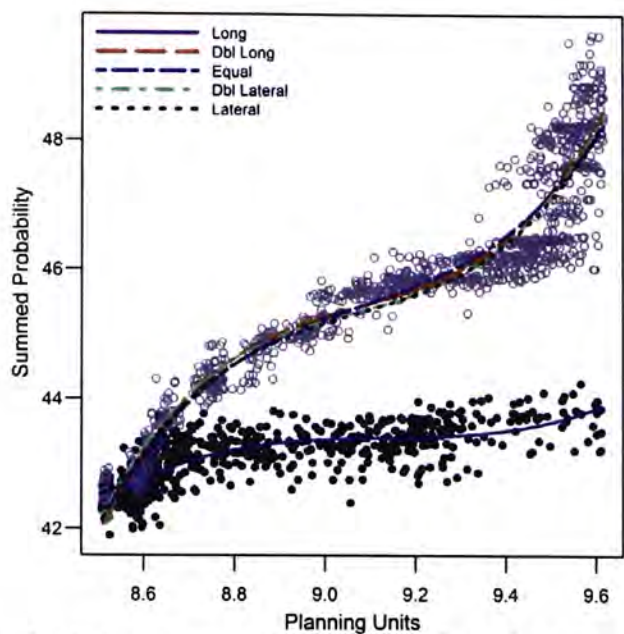


Figure S1.2 Relationship between summed probability of meeting conservation targets across all scenarios (current, 2055 and 2085; max sum=56) following an increase in the number of planning units. Lines indicate connectivity types and are divided between the use of just longitudinal connections (closed circles, solid line), and lateral connections or combinations of the two (open circles, dashed lines).

Indirect representation of rare species through increasing connectivity also supported the results of the main study. There was a significant interaction between the number of planning units selected and the type of connectivity used on the probability of protection for the 26 rare species across all climate scenarios (Fig. S1.2; ANCOVA $r^2=0.92$, $F_{(4,3100)}=22$, $p<0.001$).

2. Including Rare Species Conservation Features in Planning Solutions:

For this approach, the 10 km target for rare species was initially used to select a reserve system just for the rare species, prior to the introduction of the main 126 study species. These subcatchments were then fixed, just as existing protected areas were, in the reserve solutions of all subsequent solutions. As before, targets for some rare species could not be met in all scenarios, but were included where possible. This approach still allows a fair comparison between reactive and proactive approaches but instead of only selecting reserves

complementary to existing protected areas, the choices are also complementary to those subcatchments required for rare species.

Targeting protection of rare species directly, with a 75% certainty in just 10 km of stream habitat, would require an additional 214 subcatchments equal to 850 km of stream habitat.

The high cost is due to the low certainty with which rare species could be considered protected in any single area and Marprob therefore selects additional available planning units to increase certainty to 75%.

Overall, the addition of fixed features for rare species conservation did not alter the pattern of results from that in the main study. Following the addition of the extra fixed reserves for rare species, both Reactive and Proactive approaches to protecting current species' distributions included approximately 140 more planning units than in the main study, showing the conservation of rare species does overlap to some degree, but additional areas are required to protect all rare species. With more planning units it was not surprising that the summed probability of species meeting their conservation targets declined more slowly under future climate scenarios (Fig. S1.3). The summed probability of the Reactive solution fell by 9% and 18% respectively, compared to a 5 and 10% reduction for the Proactive solution. One difference to the main study was that while the solution with the lowest cost was based on a Reactive approach, on average costs were even with Proactive selection. As a result, although there were fewer species needing added protection in the future, the Proactive approach remained approximately 4.9% more efficient ($F_{(2,594)} = 346, p = <0.0001$).

Lastly, the addition of rare species also did not alter the overall conclusions regarding connectivity types under climate change. The type of connectivity used (specifically only longitudinal connectivity as opposed to any that include lateral connectivity) had a significant impact on the representation of species under future climate scenarios ($F_{(4,2880)} = 505$ and 684 for 2055 and 2085 scenarios respectively, $p < 0.001$).

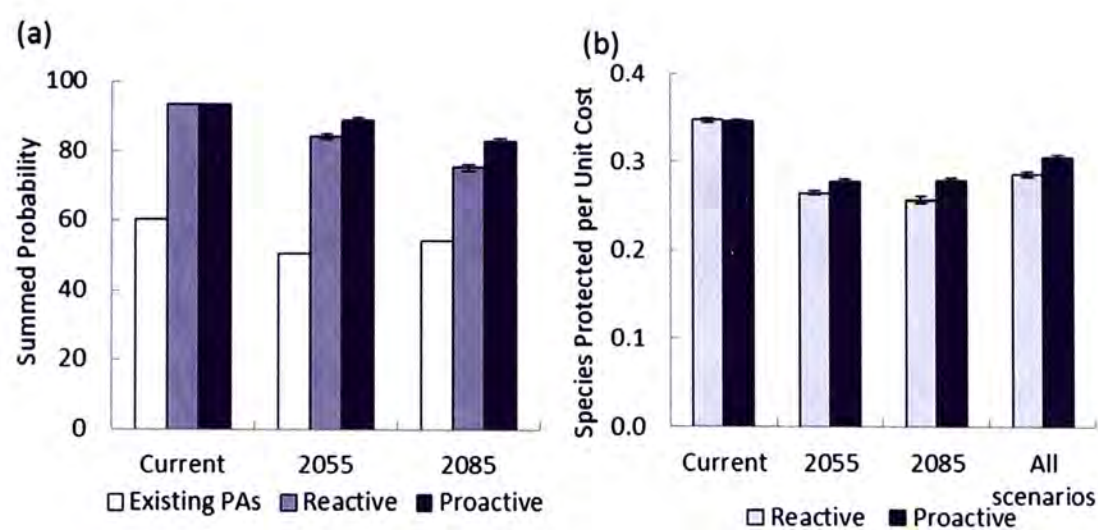


Figure S1.3 - (a) Summed probability of Odonata meeting their conservation targets (\pm SD, $n=126$, $\text{max}=93.7$) based on distributions under current, 2055 and 2085 climate scenarios, using reserve networks from existing protected areas (and subcatchments selected for rare species), the current optimal solution (Reactive) and the current Proactive solution. (b) Efficiency of Reactive and Proactive reserve networks for Odonata under current, 2055 and 2085 climates, and averaged for all three scenarios.

Supplementary Information S2. Results of ANCOVA from the fit of the model based on the number of planning units (PUs) log transformed against the connectivity type with summed probability in 2055 (a) and 2085 (b) as the covariate.

(a) Summed Probability 2055	df	MS	<i>F</i>	<i>P</i>
Connection type	4	3720	7115.04	<0.001
PUs	1	60797	116297.98	<0.001
Connection type * PUs	4	370	707.24	<0.001
Residuals	3100	1		

(b) Summed Probability 2085	df	MS	<i>F</i>	<i>P</i>
Connection type	4	36858	15011.2	<0.001
PUs	1	164448	267903.7	<0.001
Connection type * PUs	4	1069	1741.9	<0.001
Residuals	3100	1		

Supplementary Information S3

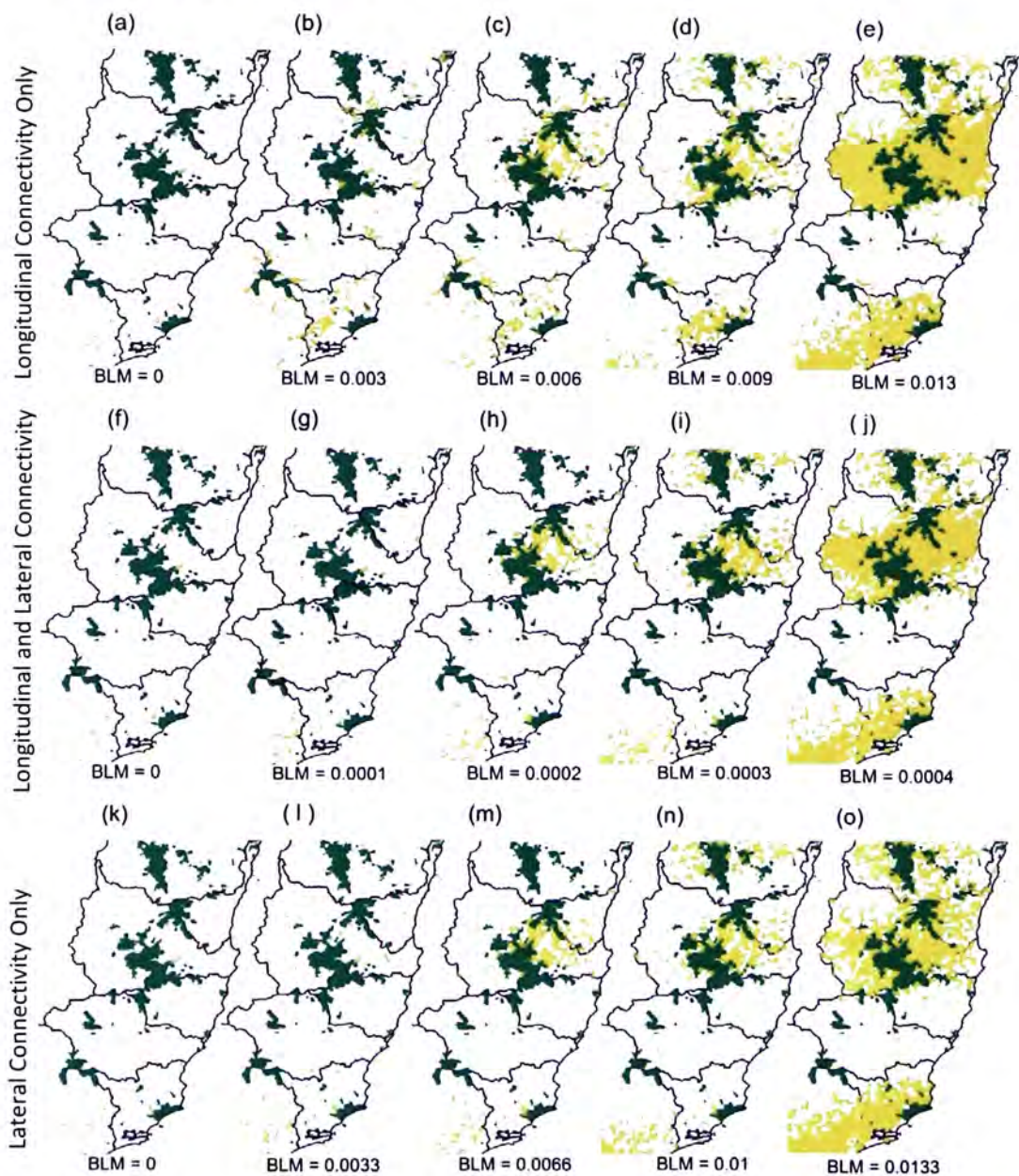


Figure S3 – Reserve selection under increasing connectivity penalties in coastal New South Wales in the middle of the study region. Existing reserves are marked in green, and new planning units within the solution are orange. Planning units were connected along river systems (a-e, longitudinal connectivity), along rivers and across catchment boundaries (f-j, lateral connectivity), or just using lateral connections (k-o). The connectivity penalty was increased using the boundary length modifier (BLM), but to keep the displayed maps comparable, the BLM was used to balance the numbers of planning units protected across the whole eastern coastal Australia study area (approximately 5000, 5300, 6000, 8000 and 10000). The displayed solutions are the “best” (least costly) of 100 runs.

CHAPTER 7

CONCLUSIONS

Water resources are a key global commodity that affects the well-being of billions of people, as well as the health of most ecosystems (Vörösmarty et al., 2010). The impacts of climate change on flow regimes in the next few decades will exacerbate the many threatening processes to which these systems are already subjected (e.g. dams, abstraction and irrigation)(Döll & Zhang, 2010). While paleoecological studies show that Australian insects, including aquatic species, have shifted their distribution in response changes in past climatic conditions (Porch, 2010), the rate and magnitude of projected change is unprecedented (Burrows et al., 2011; Reside et al., 2013). Freshwater species must contend with multiple threats in the short term including changes in land-use, nutrient cycling, eutrophication and invasive species (Ormerod et al., 2010; Rohr & Palmer, 2013) and climate change increases the risk that a substantial proportion of the world's global species will go extinct in the next 50 years (Thomas et al., 2004). Independent of a global effort to reduce the emission of greenhouse gases, there is a need to better understand how we can help biodiversity adapt (Warren et al., 2011). This discussion reviews the outcomes of the preceding chapters describing the vulnerability of freshwater macroinvertebrates and their conservation, identifies some of the strengths and limitations of the approaches taken, and offers some suggestions for the directions of future research.

Summary of Main Findings

Using data from water quality monitoring programs we examined the correlation between climate and turnover of macroinvertebrate communities to provide an indication of potential vulnerability (Chapter 2). Montane streams were identified as most vulnerable to climate change, consistent with the predictions of other studies based on dispersal limitations and thermal tolerances of select taxa (Brown et al., 2007; Hering et al., 2009). This study demonstrated this trend could also be identified from relatively coarse data on assemblage composition and in a way that was comparable to other regions, or streams within the same catchment. Lowland stream turnover was not correlated with climatic factors, but they may still be vulnerable to sea level rise (Mulrennan & Woodroffe, 1998; Bowman et al., 2010). The low exchange of families between similar habitats, suggests a low capacity to colonise new habitats inland, and more specific habitat requirements means those conditions may not be replicated elsewhere (e.g. Arthington & Watson, 1982). The study also identified distinct breaks in community composition between adjacent catchments, indicating a widespread limitation in aquatic macroinvertebrate dispersal across catchment boundaries (Thompson & Townsend, 2006; Hughes et al., 2009). While the distribution of families could not be used to identify a distinct barrier (e.g. Watson & Theischinger, 1984), it does support the view that many species distributions are constrained by dispersal within freshwater habitats. The lack of connectivity between catchments could severely hinder the adaptive response of species unable to shift their distribution across catchment divides (Alexander et al., 2011; Keller et al., 2012).

In addition to greater vulnerability of streams based on spatial distribution, the identity of vulnerable taxa is important for designing appropriate management responses (Domisch et al., 2011). Higher taxonomic resolution increases the proportion of community turnover that can be explained by environmental and spatial variables. Chapter 3 showed climate factors

explained three times as much of the assemblage variation amongst dragonfly species than it did among families of dragonflies, or other macroinvertebrates. This suggests dragonfly species have potential to provide advanced warning of climate change effects in freshwater environments, and a reference condition dataset could be established from just identifying dragonflies within biomonitoring samples. However, because the turnover of other macroinvertebrate family-groups was explained by different combinations of factors, changes in one group were not significantly correlated with others. A single surrogate for such a wide range of taxa is highly unlikely to exist regardless of taxonomic resolution, but the information provided by dragonflies can be enhanced in several key areas (Heino, 2010; Hering et al., 2010; Lawrence et al., 2010). The response of less mobile taxa could be compared using fish, which in New South Wales are already part of the Sustainable Rivers Audit (Davies et al., 2010). Also parameters such as stream temperature or perenniality will become invaluable in determining how regional climatic changes are being translated to local habitat characteristics that drive assemblage turnover (Friberg et al., 2009).

Given that dragonflies are likely to respond relatively rapidly to changes in climate (Hickling et al., 2006; Flenner & Sahlén, 2008), I was then interested in identifying what responses are likely among particular dragonfly species in the future. The application of species distribution modelling to freshwater taxa in Chapter 4 is relatively new (Comte et al., 2012) and invertebrate taxa have only been modelled in a few instances (Domisch et al., 2012; Simaika et al., 2013). By collating large numbers of new records from museum collections, the study described in Chapter 4 was modelled 270 species overall, and determined their relative vulnerability to climate change using a combination of factors. Dispersal capacity is likely to be a key determining factor for many aquatic species and even among dragonflies there are likely to be species whose distribution will be limited in future by dispersal. Although relatively few species were predicted to experience a complete loss of environmentally suitable habitat, a large proportion were predicted to be highly vulnerable. Conservation

priorities for the most vulnerable species were concentrated in permanent rivers in south-western and north-western Australia, montane and upland rivers of coastal New South Wales and north Queensland, and much of Tasmania.

There is rarely the opportunity to validate species distribution model projections, but during the preparation of this thesis, new records for two species (*Apocordulia macrops* and *Austrocordulia leonardi*) were discovered well beyond their known ranges (Theischinger et al. 2013). Interestingly, in both cases the new records were within subcatchments considered suitable by the modelled projections (see Appendix). These new occurrence records were subsequently incorporated to update the models for each species.

Chapter 5 describes how, as the distributions of individual species shift, the distribution of dragonfly diversity is likely to change in response to climate change. Current hotspots of richness and phylogenetic diversity were predicted to be almost completely transformed in the far north, and the changes in phylogenetic diversity were not always consistent with the changes to regional species richness. There are likely to be major changes in the composition of local dragonfly assemblages along the entire east coast, with potentially very large increases in species richness in Tasmania. Species richness is positively correlated with many key ecosystem processes (Cardinale et al., 2006; Cardinale, 2011) but phylogenetic diversity was considered to be a better proxy for functional diversity because groups of closely related species tend to occupy similar niches (Cadotte et al., 2012; Mouillot et al., 2013). The surrogacy of dragonfly assemblages and other macroinvertebrate families was low in chapter 3 but still highly significant and therefore the turnover of dragonflies indicates significant changes to other macroinvertebrates assemblages are likely (Domisch et al., 2012). One avenue of future research will be to estimate whether the predicted changes in composition are actually likely to result in a different combination of traits that affects ecosystem processes (Bonada et al., 2007).

In Chapter 4 important locations for conservation of dragonfly species vulnerable to climate change was highlighted at the continental level. To narrow down the range of possibilities across such a large area, conservation planning uses complementarity-based algorithms to select sites that protect species missed by the existing reserve network (Linke et al., 2011). Climate change is rarely considered in conservation planning studies despite the obvious potential mismatches between static reserves and spatially shifting habitat suitability (Hannah, 2010). Using the predicted distribution of dragonflies to support conservation planning, Chapter 6 demonstrates that instead of allowing shifts to occur and adding new reserves to compensate (reactive approach), anticipating change in reserve planning from the beginning results in significantly different priorities (proactive approach). A difference in the representation of species also occurs in the future depending on the type of connectivity promoted within a reserve system. For aquatic species such as insects that can disperse overland, forest cover can help improve the chances movement across catchment boundaries (Alexander et al., 2011). In eastern Australian, some catchments are separated by just a few hundred meters of flat boggy ground making movement much more likely. By allowing lateral connections across catchment boundaries in reserve selection, the representation of dragonflies in the long term was significantly improved. Naturally these benefits would not apply to species dependent on longitudinal connectivity along river channels, and it may be necessary to consider managed translocation (Morrongiello et al., 2011). For a given budget this then leads to a trade-off between protecting habitat along river channels that support functional processes, aquatic movement and alleviates upstream threats (Turak et al., 2011; Linke et al., 2012; Esselman et al., 2013), and connectivity along climatic gradients that provides protection as species ranges shift (Game et al., 2011). Naturally aquatic species that cannot fly will be more reliant on connectivity to climatic refugia within the catchment (Hermoso et al., 2012).

Strengths and Weaknesses

Chapters 2 and 3 used existing data from biomonitoring programs and then reevaluated that data with the aim of improving risk assessment to climate change. Although the study found significant trends, there are a number of factors that have reduced the scientific potential of freshwater monitoring to be used for scientific analyses. Low taxonomic resolution blurs the effect of environmental changes on assemblage turnover and hinders any interpolation of point based sampling to the wider landscape (Koperski, 2011). Given these data constraints it is even more noteworthy that we were able to detect significant trends. It seems likely that such trends would have been even stronger if the data had allowed analysis at the species level and/or among specific habitat types (Jones, 2008; Bevilacqua et al., 2012). There is therefore, significant potential for biomonitoring approaches to be modified to extend their scientific value, while still being cost-effective (Friberg et al., 2011).

Using dragonflies as indicators is just one possible approach that, for a small investment, could be used to monitor the effect of climate change in freshwater ecosystems. Ideally, the strength of an indicator would have been measured amongst multiple taxa, but this was not feasible because of the same taxonomic constraints that limit biomonitoring surveys in general (Marshall et al., 2006a). The study could not therefore judge whether dragonflies were more sensitive than other macroinvertebrate taxa to climatic change, but did show that turnover of dragonfly-species assemblages is strongly associated with climatic factors compared to other environmental or spatial factors. The importance of climatic factors is fundamental to using species distribution models for predicting the effect of climate change (Elith et al., 2010) and although non-climatic factors were considered prior to modelling, they were consistently ranked below climatic predictor variables. The strong dispersal capacity of dragonflies also meant fewer assumptions for predicting range changes under future climate scenarios. Nevertheless, given the speed of climatic change, dispersal constraints could still

be limiting for some species (Jaeschke et al., 2012a) and this was considered in the vulnerability analysis. Ideally the vulnerability assessment would have included information on the species habitat requirements (Jaeschke et al., 2012b), and some consideration of competitive outcomes (Foden et al., 2013) but in Australia, as with many parts of the world, this information is almost entirely absent for invertebrates (Cardoso et al., 2011).

A major weakness of current research into the effects of climate change on species and ecosystems is the focus on means rather than variability and extremes (Katz & Brown, 1992). Australia's stream flow, is among the most variable in the world (McMahon, 1982) and this creates high temporal variability in aquatic macroinvertebrate assemblages (Marshall et al., 2006b). To what extent will species distributions, particularly at the tail-edge, be driven by the occurrence of extreme events? Many Australian wetlands are in decline as precipitation becomes increasingly periodic (Erwin, 2009; NRC, 2009; Pittock & Finlayson, 2011). These rainfall changes also increase downstream flood risk, the erosion of riparian habitats, and can cause major blackwater events (e.g. King et al., 2012). Streams in less disturbed watersheds are somewhat buffered against dramatic increases in discharge and from drought (Thomson et al., 2012), and specific refugia may be available in parts of the landscape (Sheldon et al., 2010), but whether these can continue to act as "source" populations for recovery following major disturbances is a different matter.

Future Research Priorities

While it is tempting to suggest that understanding the effects of climate change in Australia could be improved by establishing long-term monitoring networks, the confounding effects of the El Niño–Southern Oscillation cycle could take a long time to separate, and the current climate of scientific funding does not support these projects. Furthermore, we cannot afford to wait another 20 years to confirm climate change is an issue for managing freshwater

ecosystems. Although there are many avenues for future research, based on the findings of the research in this thesis I suggest three themes:

1. *Taxonomic resolution*

Management of all natural environments under climate change must recognise that some change is now beyond our control. However, monitoring is still required in the future to record whether changes are conforming to predictions, and whether management actions have desired outcomes (Friberg et al., 2011). One of the main drawbacks of current biomonitoring, both for detecting anthropogenic disturbances on water quality, and for applying the data to other scientific uses, is the lack of taxonomic resolution (Jones, 2008), and to some extent sampling intensity (Hose et al., 2004). Fortunately to meet the demand for more detailed information, there is encouraging evidence that surveying methods combined with DNA sequencing and environmental DNA are likely to revolutionise survey outputs (Baird & Hajibabaei, 2012). This seems the most feasible opportunity to expand our survey capacity to species level with an expected gain in cost efficiency, and the ability to perceive environmental changes much more quickly. The challenge will be to establish reference conditions for comparison, and to compare results from the different methods. Also, can we begin to relate more diverse assemblages of species to functional processes, or to the loss of species to particular human impacts?

2. *Adequacy*

Although modelling species distributions and accounting for shifts under climate change can be used to increase the representation of species within protected areas in the future, setting targets for adequacy is difficult. Adequacy is defined as 'the maintenance of the ecological viability and integrity of populations, species and communities' (Commonwealth of Australia, 1992). However viability is a complicated concept and the number of individuals in a viable population will vary among species and regions. Adequacy does not therefore have a precise

definition (Kukkala & Moilanen, 2013). Other standard concepts such as island biogeography and species-area curves used to determine aerial targets for conservation also produce inconsistent results in freshwater systems as other factors like water volume and stream hierarchy play a role (Linke et al., 2011). Climate change means determining conservation adequacy has become even more complicated because populations that were viable previously may decline if conditions become increasingly suboptimal. Maintaining connectivity is one action that can improve population persistence, particularly if this connects to habitats with potential to be suitable in the future, or to climatic refugia (e.g. Linke et al., 2012). Nonetheless, to improve the debate on what we can afford to protect, and what we value (Prober & Dunlop, 2011), we need to try to answer how many is enough, or how much space is needed to protect a species?

3. *Resistance and resilience*

Considering the potentially serious nature of predictions made in this thesis, once dispersal constraints, population fluctuations due to droughts, floods and heatwaves, and competition are all considered, the risk of extinction is actually likely to be a conservative estimate. What action should be taken to prevent the greatest number of species being pushed to extinction? A large variety of possible actions are available (Heller & Zavaleta, 2009), but what is the most efficient combination? Protection within reserves is likely to continue to form the backbone of most conservation strategies (CBD, 2010) but methods are now being developed to systematically select conservation actions outside reserve boundaries too (e.g. habitat restoration: Maggini et al., 2013). Against competition from other water users, will maintaining “healthy” ecosystems be practical across the entire landscape? The success of protecting freshwater ecosystems in Australia will therefore probably depend most on how well environmental requirements can be integrated into the management of human water use (Pittock et al., 2013).

Conclusions

This thesis provides evidence that there will be significant shifts in the composition of freshwater macroinvertebrate communities as a result of climate change, but the landscape may constrain adaptation. Dragonflies can sometimes have very specific habitat requirements, or long larval development, but on the whole have more flexibility to respond to climate change than most other freshwater taxa (Hassall & Thompson, 2008). There will also be shifts in the dragonfly community itself, and assuming dispersal is not limiting, it will be very interesting to learn how communities reorganise (Thompson & Townsend, 2006), particularly in regions such as Tasmania, where regional richness could double. The position of dragonflies as predators in freshwater ecosystems is perhaps unlikely to change (McPeck, 1998), but new competitive interactions between dragonfly species may lead to either more rapid declines or slower range expansions of some species (Suhling & Suhling, 2013). These impacts are almost impossible to predict and the best hope of conserving the majority of species will be to protect habitats predicted to remain environmentally suitable under climate change.

Looking to the future, current research suggests that the composition of freshwater species will change under future climates and that we are going to have to accept we will lose some or many species. There is also evidence to suggest we must be very cautious about assuming a level of redundancy in the system (Mouillot et al., 2013). If we cannot preserve native ecological communities, are we only interested in function? If so we might as well build new ecosystems from those species of practical utility (Prober & Dunlop, 2011). This may seem a little dramatic but as we move from managing what we know to managing for what might be, it becomes ever more complicated to define the targets for biodiversity conservation. Which principle of conservation: comprehensiveness, adequacy and representativeness, is no longer

achievable? Although I find it distasteful to even consider knowingly allowing a species to go extinct without acting, accepting that some losses are inevitable may free up the resources needed to avoid it elsewhere. A debate on the philosophy behind this turning point is urgently needed, both among scientists, and in wider society. I believe a greater awareness of the looming biodiversity crisis and its consequences will help galvanise action to reduce the worst effects of climate change to a point where we can still allow an adaptive response in most ecosystems.

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APPENDIX

Papers published associated with this thesis

Bush, A., et al. (2012). Determining vulnerability of stream communities to climate change at the landscape scale. *Freshwater Biology* 57(8): 1689-1701.

Bush, A., et al. (2013). Dragonflies: climate canaries for river management. *Diversity and Distributions* 19(1): 86-97

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