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Dragonflies: climate canaries for river management

A. Bush[1]*, G. Theischinger[2,3], D. Nipperess[1], E. Turak[2,3] and L. Hughes[1]

[1]*Macquarie University, Sydney, NSW, Australia,* [2]*Office of Environment and Heritage New South Wales, Sydney, NSW, Australia,* [3]*Australian Museum, 6 College Street, Sydney, NSW, 2010, Australia*

*Correspondence: Alex Bush, Department of Biological Sciences, Macquarie University, North Ryde, Sydney, NSW 2109, Australia.
E-mail: alex.bush@mq.edu.au

ABSTRACT

Aim 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.

Location Data were analysed from standard bio-assessment monitoring at over 850 sites spanning a 9° latitudinal gradient in eastern Australia.

Methods 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 whether the turnover of dragonfly assemblages was congruent with that of other groups.

Results 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 amongst groups were low.

Main conclusions On the basis of 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 amongst 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.

Keywords

Adaptive management, assemblage turnover, climate change, Odonata, taxonomic resolution.

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

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(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 the 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 recognize the potentially complex network of effects predicted because of climate change (Hering *et al.*, 2010). Given the significant additional impact that 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 that 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 programme 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 programmes 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 whether 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 with 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 colonize temperate and subarctic 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 amongst dragonflies, consistent with being an adaptive response to climate change (Aoki, 1997; Hickling *et al.*, 2005, 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. On the basis of 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 programme of rivers and streams from subtropical 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 km^2, 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.

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 statewide 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 (DFSM)] 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.

Figure 1 Study area with catchment boundaries in eastern New South Wales, Australia (inset).

We compared the congruence in turnover between macroinvertebrates at family-level taxonomic resolution, grouped either by phylum (Mollusca and Crustacea) or by order (Table 1). Each group included a minimum of 10 families that had been recorded at least 10 times. Assemblage variation because of sampling intensity was minimal because of 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 amongst 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 *Diphlebia*). 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.

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

Table 1 Groups of macroinvertebrate families compared in this study.

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	Ephydridae	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
Protoneuridae	Calocidae (T)	Ptilodactylidae	Notonectidae	Chironominae	Phreatoicidea (Phreatoicidae)	Bithyniidae
Synlestidae	Conoesucidae (T)	Scirtidae	Pleidae	Orthocladiinae		
	Ecnomidae (T)	Staphylinidae	Veliidae	Podonominae		
	Helicophidae (T)			Tanypodinae		
	Helicopsychidae (T)					
	Hydrobiosidae (T)					
	Hydropsychidae (T)					
	Hydroptilidae (T)					
	Leptoceridae (T)					
	Odontoceridae (T)					
	Philopotamidae (T)					
	Philorheithridae (T)					
	Polycentropodidae (T)					
	Tasimiidae (T)					

Trichoptera were tested separately (T), and as part of the Ephemeroptera, Plecoptera and Trichoptera (EPT).
Dragonfly nomenclature follows Watson *et al.*, 1991.

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 (2000–07) 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 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 organized 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 subcatchment and catchment scale (subcatchment disturbance index, subcatchment 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. 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 Akaike Information Criterion (AIC) in PRIMER. A variety of selection methods available in PRIMER was 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 amongst groups (Chevan & Sutherland, 1991). The variation explained by a single group of factors, without accounting for covariation 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 amongst 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 amongst catchments, and Mantel tests used to compare both the site dissimilarity values (local scale) and ANOSIM pairwise *r*-values (regional scale). Tests

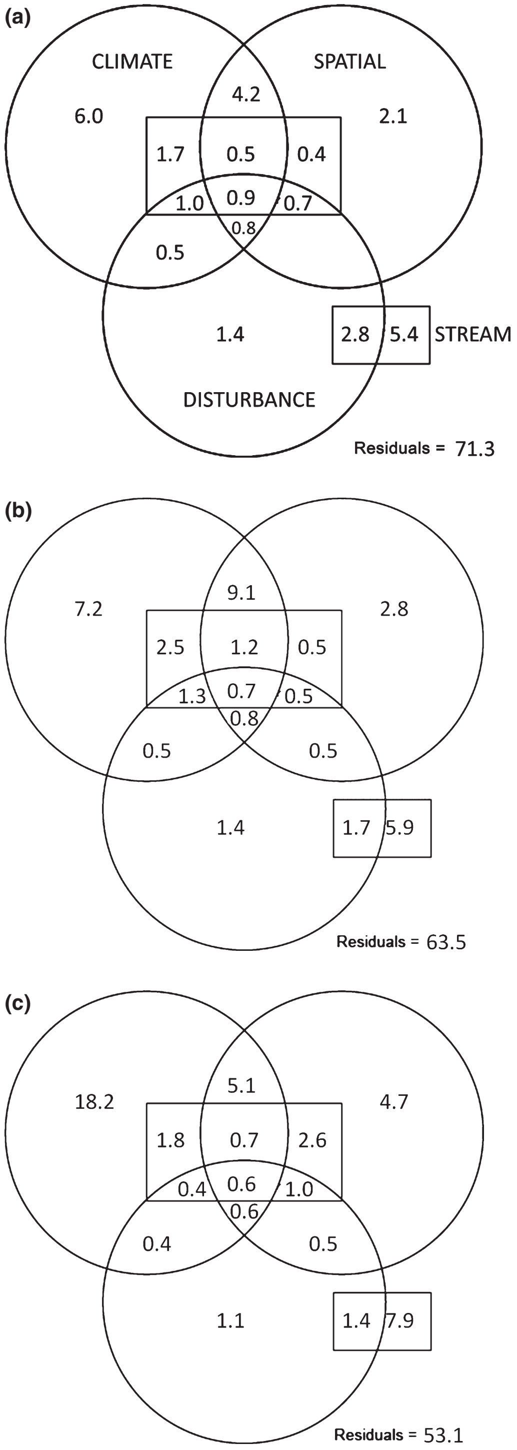

Figure 2 Venn diagram illustrating the variation partitioning between four groups of factors: Climatic, Spatial, Disturbance and Water. The values are percentages from partitioning of variation amongst dragonfly assemblages at (a) family, (b) genus and (c) species level. The total potential variation 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.

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 amongst 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 amongst the dragonflies and the Crustacea (Table 2). The influence of climate-only was also greatest amongst 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 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 in Supporting Information.

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 (Fig. 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 amongst 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 covarying 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.

When comparing congruence across all samples, dissimilarity amongst assemblages of dragonflies was significantly correlated with that in all the other taxa ($P \leq 0.001$) (Table 3). However, the strength of the relationship was weak across all groups ($r^2 \leq 0.25$), including comparisons amongst non-dragonfly assemblages. The congruence between assemblages was stronger when comparing amongst 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.

DISCUSSION

Influence of climate on dragonflies

Climate factors explained three times as much assemblage variation amongst dragonflies species than dragonflies, or other macroinvertebrate assemblages, at family level. This result suggests that dragonflies may have potential to provide

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

	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

EPT are Ephemeroptera, Plecoptera and Trichoptera.

Table 3 Mantel test of correlation in dissimilarity of dragonfly families, genera and species with other taxa.

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***

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.

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

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 because of 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 amongst 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 recolonize habitats, whilst disadvantaging species with bivoltine or semi-voltine 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 colonize 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). On the basis of 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^{-1} 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^{-1} in Sweden)(Flenner & Sahlén, 2008) and *Erythromma viridulum* (28 km year^{-1} 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 amongst 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 amongst 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 amongst 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. Whilst palaeoecological 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 minimized. 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 whilst 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 because of disturbance factors independent of climate can be included based on the survey of the entire macroinvertebrate community. As with existing biomonitoring, separating trends owing to climate change from those owing 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 the 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 are 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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REFERENCES

Anderson, M.J. & Gribble, N.A. (1998) Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Austral Ecology*, **23**, 158–167.

Angelibert, S. & Giani, N. (2003) Dispersal characteristics of three odonate species in a patchy habitat. *Ecography*, **26**, 13–20.

Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J. (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, **14**, 677–689.

Aoki, T. (1997) Northward expansion of *Ictinogomphus pertinax* (selys) in eastern Shikoku and western Kinki Districts, Japan (Anisoptera: Gomphidae). *Odonatologica*, **26**, 121–133.

Beattie, A.J. & Oliver, I. (1994) Taxonomic minimalism. *Trends in Ecology and Evolution*, **9**, 488–490.

Bevilacqua, S., Terlizzi, A., Claudet, J., Fraschetti, S. & Boero, F. (2012) Taxonomic relatedness does not matter for species surrogacy in the assessment of community responses to environmental drivers. *Journal of Applied Ecology*, **49**, 357–366.

Bond, N., Thomson, J., Reich, P. & Stein, J. (2011) Using species distribution models to infer potential climate change-induced range shifts of freshwater fish in south-eastern Australia. *Marine and Freshwater Research*, **62**, 1043–1061.

Braune, E., Richter, O., Söndgerath, D. & Suhling, F. (2008) Voltinism flexibility of a riverine dragonfly along thermal gradients. *Global Change Biology*, **14**, 470–482.

Bried, J.T., D'Amico, F. & Samways, M.J. (2012) A critique of the dragonfly delusion hypothesis: why sampling exuviae does not avoid bias. *Insect Conservation and Diversity*, in press.

Bunn, S.E., Abal, E.G., Smith, M.J., Choy, S.C., Fellows, C.S., Harch, B.D., Kennard, M.J. & Sheldon, F. (2010) Integration of science and monitoring of river ecosystem health to guide investments in catchment protection and rehabilitation. *Freshwater Biology*, **55**, 223–240.

Chessman, B.C. (2009) Climatic changes and 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. *Global Change Biology*, **15**, 2791–2802.

Chevan, A. & Sutherland, M. (1991) Hierarchical partitioning. *The American Statistician*, **45**, 90–96.

Chovanec, A. & Waringer, J. (2001) Ecological integrity of river-floodplain systems – assessment by dragonfly surveys (Insecta: Odonata). *River Research and Applications*, **17**, 493–507.

Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.

Clarke, K.R. & Gorley, R.N. (2006) *PRIMER v6: User Manual. PRIMER-E*, Plymouth, UK.

Conrad, K.F., Willson, K.H., Harvey, I.F., Thomas, C.J. & Sherratt, T.N. (1999) Dispersal characteristics of seven odonate species in an agricultural landscape. *Ecography*, **22**, 524–531.

Corbet, P.S. (1999) *Dragonflies: behaviour and ecology of Odonata*. Harley Books, Essex, UK.

Córdoba-Aguilar, A. (2008) *Dragonflies and damselflies; model organisms for ecological and evolutionary research*. Oxford University Press, Oxford.

Coughran, J. (2007) Distribution, habitat and conservation status of the freshwater crayfishes, *Euastacus dalagarbe*, *E. girurmulayn*, *E. guruhgi*, *E. jagabar* and *E mirangudjin*. *Australian Zoologist*, **34**, 222–227.

Curry, C.J., Zhou, X.I.N. & Baird, D.J. (2012) Congruence of biodiversity measures among larval dragonflies and caddisflies from three Canadian rivers. *Freshwater Biology*, **57**, 628–639.

Daufresne, M. & Boët, P. (2007) Climate change impacts on structure and diversity of fish communities in rivers. *Global Change Biology*, **13**, 2467–2478.

Daufresne, M., Roger, M.C., Capra, H. & Lamouroux, N. (2004) Long-term changes within the invertebrate and fish communities of the Upper Rhône River: effects of climatic factors. *Global Change Biology*, **10**, 124–140.

Daufresne, M., Lengfellner, K. & Sommer, U. (2009) Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences USA*, **106**, 12788–12793.

Davies, P.M. (2010) Climate change implications for river restoration in global biodiversity hotspots. *Restoration Ecology*, **18**, 261–268.

Davies, P.E., Harris, J.H., Hillman, T.J. & Walker, K.F. (2010) The sustainable rivers audit: assessing river ecosystem health in the Murray Darling Basin, Australia. *Marine and Freshwater Research*, **61**, 764–777.

Domisch, S., Jähnig, S.C. & Haase, P. (2011) Climate-change winners and losers: stream macroinvertebrates of a submontane region in Central Europe. *Freshwater Biology*, **56**, 2009–2020.

Dray, S. (2010) spacemakeR: spatial modelling. *R package version 0.0-5/r83. R: a language and environment for statistical computing* (ed. by R Development Core Team), R Foundation for Statistical Computing. http://R-Forge.R-project.org/projects/sedar/.

Dray, S., Legendre, P. & Peres-Neto, P.R. (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, **196**, 483–493.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A. H., Soto, D., Stiassny, M.L.J. & Sullivan, C.A. (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society*, **81**, 163–182.

Eggermont, H. & Martens, K. (2011) Preface: Cladocera crustaceans: sentinels of environmental change. *Hydrobiologia*, **676**, 1–7.

Fleishman, E. & Murphy, D.D. (2009) A realistic assessment of the indicator potential of butterflies and other charismatic taxonomic groups. *Conservation Biology*, **23**, 1109–1116.

Flenner, I.D.A. & Sahlén, G. (2008) Dragonfly community re-organisation in boreal forest lakes: rapid species turnover driven by climate change? *Insect Conservation and Diversity*, **1**, 169–179.

Flenner, I.D.A., Richter, O. & Suhling, F. (2009) Rising temperature and development in dragonfly populations at different latitudes. *Freshwater Biology*, **55**, 397–410.

Foote, A.L. & Rice Hornung, C.L. (2005) Odonates as biological indicators of grazing effects on Canadian prairie wetlands. *Ecological Entomology*, **30**, 273–283.

Fox, L.R. (1977) Species richness in streams – an alternative mechanism. *The American Naturalist*, **111**, 1017–1021.

Hamilton, S.K. (2010) Biogeochemical implications of climate change for tropical rivers and floodplains. *Hydrobiologia*, **657**, 19–35.

Hassall, C. & Thompson, D.J. (2008) The effects of environmental warming on Odonata: a review. *International Journal of Odonatology*, **11**, 131–153.

Hassall, C., Thompson, D.J., French, G.C. & Harvey, I.F. (2007) Historical changes in the phenology of British Odonata are related to climate. *Global Change Biology*, **13**, 933–941.

Hawking, J.H. & New, T.R. (2002) Interpreting dragonfly diversity to aid in conservation assessment: lessons from the Odonata assemblage at Middle Creek, north-eastern Victoria, Australia. *Journal of Insect Conservation*, **6**, 171–178.

Hawkins, B.A., Diniz-Filho, J.A.F., Mauricio Bini, L., De Marco, P. & Blackburn, T.M. (2007) Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. *Ecography*, **30**, 375–384.

Heino, J. (2010) Are indicator groups and cross-taxon congruence useful for predicting biodiversity in aquatic ecosystems? *Ecological Indicators*, **10**, 112–117.

Heino, J. & Soininen, J. (2007) Are higher taxa adequate surrogates for species-level assemblage patterns and species richness in stream organisms? *Biological Conservation*, **137**, 78–89.

Heino, J., Mykrä, H., Hämäläinen, H., Aroviita, J. & Muotka, T. (2007) Responses of taxonomic distinctness and species diversity indices to anthropogenic impacts and natural environmental gradients in stream macroinvertebrates. *Freshwater Biology*, **52**, 1846–1861.

Heller, N.E. & Zavaleta, E.S. (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation*, **142**, 14–32.

Hering, D., Haidekker, A., Schmidt-Kloiber, A., Barker, T., Buisson, L., Graf, W., Grenouillet, G., Lorenz, A., Sandin, L. & Stendera, S. (2010) Monitoring the responses of freshwater ecosystems to climate change. *Climate change impacts on freshwater ecosystems* (ed. by M. Kernan, R.W. Battarbee and B. Moss), pp. 84–118. Wiley-Blackwell Publishing, Oxford, UK.

Hewlett, R. (2000) Implications of taxonomic resolution and sample habitat for stream classification at a broad geographic scale. *Journal of the North American Benthological Society*, **19**, 352–361.

Hickling, R., Roy, D.B., Hill, J.K. & Thomas, C.D. (2005) A northward shift of range margins in British Odonata. *Global Change Biology*, **11**, 502–506.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.

Hofmann, T.A. & Mason, C.F. (2005) Habitat characteristics and the distribution of Odonata in a lowland river catchment in eastern England. *Hydrobiologia*, **539**, 137–147.

Hose, G., Turak, E. & Waddell, N. (2004) Reproducibility of AUSRIVAS rapid bioassessments using macroinvertebrates. *Journal of the North American Benthological Society*, **23**, 126–139.

Hughes, L. (2003) Indicators of climate change. *Climate change impacts on biodiversity in Australia; outcomes of a workshop sponsored by the Biological Diversity Advisory Committee, Oct 2002* (ed. by M. Howden, L. Hughes, M. Dunlop, I. Zethoven, D. Hilbert and C. Chilcott), pp. 58–62. Commonwealth of Australia, Canberra.

Hughes, J.M., Schmidt, D.J. & Finn, D.S. (2009) Genes in streams: using DNA to understand the movement of freshwater fauna and their riverine habitat. *BioScience*, **59**, 573–583.

Jackson, J.K. & Füreder, L. (2006) Long-term studies of freshwater macroinvertebrates: a review of the frequency, duration and ecological significance. *Freshwater Biology*, **51**, 591–603.

Jones, F.C. (2008) Taxonomic sufficiency: the influence of taxonomic resolution on freshwater bioassessments using benthic macroinvertebrates. *Environmental Reviews*, **16**, 45–69.

Lawrence, J.E., Lunde, K.B., Mazor, R.D., Beche, L.A., McElravy, E.P. & Resh, V.H. (2010) Long-term macroinvertebrate responses to climate change: implications for biological assessment in Mediterranean-climate streams. *Journal of the North American Benthological Society*, **29**, 1424–1440.

Lenat, D.R. & Resh, V.H. (2001) Taxonomy and stream ecology – the benefits of genus- and species-level identifications. *Journal of the North American Benthological Society*, **20**, 287–298.

Marshall, J.C., Steward, A.L. & Harch, B.D. (2006) Taxonomic resolution and quantification of freshwater macroinvertebrate samples from an Australian dryland river: the benefits and costs of using species abundance data. *Hydrobiologia*, **572**, 171–194.

Melles, S.J., Jones, N.E. & Schmidt, B. (2011) Review of theoretical developments in stream ecology and their influence on stream classification and conservation planning. *Freshwater Biology*, **57**, 415–434.

Morecroft, M.D., Bealey, C.E., Beaumont, D.A., Benham, S., Brooks, D.R., Burt, T.P., Critchley, C.N.R., Dick, J., Littlewood, N.A., Monteith, D.T., Scott, W.A., Smith, R.I., Walmsley, C. & Watson, H. (2009) The UK Environmental Change Network: emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation*, **142**, 2814–2832.

Muschal, M., Turak, E., Gilligan, D., Sayers, J. & Healey, M. (2010) *Riverine ecosystems; Technical report series of the NSW Monitoring, Evaluation and Reporting Program*. NSW Office of Water, Sydney.

Norris, R.H. & Hawkins, C.P. (2000) Monitoring river health. *Hydrobiologia*, **435**, 5–17.

Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, **4**, 355–364.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H. & Wagner, H. (2011) vegan: Community Ecology Package. R package version 2.0-1. Available at: http://CRAN.R-project.org/package=vegan (accessed 25 July 2012).

Ott, J. (2001) Expansion of Mediterranean Odonata in Germany and Europe – consequences of climatic changes. *'Fingerprints' of climate change: adapted behaviour and shifting species ranges* (ed. by G.R. Walther, C. Buga and P.J. Edwards), pp. 89–112. Kluwer Academic/Plenum Publishers, New York.

Ott, J. (2007) The expansion of *Crocothemis erythraea* (Brulle, 1832) in Germany – an indicator of climate changes. *Biology of dragonflies* (ed. by B.K. Tyagi), pp. 201–222. Scientific Publishers, Jodhpur.

Ott, J. (2010) *Biorisk Vol.5. Monitoring climate change with dragonflies*. Pensoft, Sofia.

Palmer, M.A., Lettenmaier, D.P., Poff, N.L., Postel, S.L., Richter, B. & Warner, R. (2009) Climate change and river ecosystems: protection and adaptation options. *Environmental Management*, **44**, 1053–1068.

Peres-Neto, P.R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, **87**, 2614–2625.

Pittock, J. & Finlayson, C.M. (2011) Australia's Murray Darling Basin: freshwater ecosystem conservation options in an era of climate change. *Marine and Freshwater Research*, **62**, 232–243.

Raebel, E.M., Merckx, T., Riordan, P., Macdonald, D.W. & Thompson, D.J. (2010) The dragonfly delusion: why it is essential to sample exuviae to avoid biased surveys. *Journal of Insect Conservation*, **14**, 523–533.

Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T.L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S. & Imeson, A. (2008) Attributing physical and biological impacts to anthropogenic climate change. *Nature*, **453**, 353–357.

Sahlén, G. & Ekestubbe, K. (2001) Identification of dragonflies (Odonata) as indicators of general species richness in boreal forest lakes. *Biodiversity and Conservation*, **10**, 673–690.

Simaika, J.P. & Samways, M.J. (2009) An easy-to-use index of ecological integrity for prioritizing freshwater sites and for assessing habitat quality. *Biodiversity and Conservation*, **18**, 1171–1185.

Simaika, J.P. & Samways, M.J. (2010) Comparative assessment of indices of freshwater habitat conditions using different invertebrate taxon sets. *Ecological Indicators*, **11**, 370–378.

Smith, J., Samways, M.J. & Taylor, S. (2007) Assessing riparian quality using two complementary sets of bioindicators. *Biodiversity and Conservation*, **16**, 2695–2713.

Stein, J.L., Stein, J.A. & Nix, H.A. (2002) Spatial analysis of anthropogenic river disturbance at regional and continental scales: identifying the wild rivers of Australia. *Landscape and Urban Planning*, **60**, 1–25.

Suhling, F., Schenk, K., Padeffke, T. & Martens, A. (2004) A field study of larval development in a dragonfly assemblage in African desert ponds (Odonata). *Hydrobiologia*, **528**, 75–85.

Theischinger, G. & Endersby, I. (2009) *Identification guide to the Australia Odonata*. Department for Climate Change and Water NSW, Sydney.

Thompson, R. & Townsend, C. (2006) A truce with neutral theory: local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology*, **75**, 476–484.

Thomson, J.R., Bond, N.R., Cunningham, S.C., Metzeling, L., Reich, P., Thompson, R.M. & Nally, R.M. (2012) The influences of climatic variation and vegetation on stream biota: lessons from the Big Dry in southeastern Australia. *Global Change Biology*, **18**, 1582–1596.

Turak, E. & Koop, K. (2008) Multi-attribute ecological river typology for assessing ecological condition and conservation planning. *Hydrobiologia*, **603**, 83–104.

Turak, E., Waddell, N. & Johnstone, G. (2004) *New South Wales Australian River Assessment System (AUSRIVAS) sampling and processing manual*. Commonwealth of Australia and NSW Department of Environment and Conservation, Canberra and Sydney.

Turak, E., Marchant, R., Barmuta, L.A., Davis, J., Choy, S. & Metzeling, L. (2011) River conservation in a changing world: invertebrate diversity and spatial prioritisation in south-eastern coastal Australia. *Marine and Freshwater Research*, **62**, 300–311.

Wallace, J.B. & Webster, J.R. (1996) The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, **41**, 115–139.

Watson, J.A.L., Theischinger, G. & Abbey, H.M. (1991) *The Australian Dragonflies: A Guide to the Identification, Distribution and Habits of Australian Odonata*, CSIRO, Melbourne.

Watts, P.C., Keat, S. & Thompson, D.J. (2010) Patterns of spatial genetic structure and diversity at the onset of a rapid range expansion: colonisation of the UK by the small red-eyed damselfly *Erythromma viridulum*. *Biological Invasions*, **12**, 3887–3903.

Winterbourn, M.J., Pohe, S.R. & Ball, O.J.P. (2011) Establishment of larval populations of the dragonfly *Tramea loewii* Kaup, 1866 (Odonata: Libellulidae) in lakes of northern New Zealand. *New Zealand Journal of Zoology*, **38**, 173–179.

Woodward, G., Perkins, D.M. & Brown, L.E. (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2093–2106.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Variance explained by each variable per taxonomic group.
Table S2 Top five explanatory variables for each taxonomic group.

BIOSKETCH

Alex Bush is a PhD student at Macquarie University, Sydney. He is studying the potential effects of climate change on stream macroinvertebrates and the implications for conservation of freshwater ecosystems. He is a member of the climate change ecology workgroup led by Professor Lesley Hughes.

Author contributions: A.B. and G.T. led data collection and collation. A.B. and D.N. assembled the data and performed the analyses. A.B. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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