

Determining vulnerability of stream communities to climate change at the landscape scale

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SUMMARY

1. 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.

2. 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 1000 km. We used variance partitioning to separate the variation in composition explained by climate, among-site distance, human disturbance and other stream factors.

3. 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.

4. 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, owing to either limited dispersal or the lack of suitable habitat, is 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.

Keywords: assemblage turnover, conservation, dispersal barrier, macroinvertebrate, variation partitioning

Introduction

Global climate change is already affecting many aspects of the natural environment (Parmesan & 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 that freshwater taxa are highly sensitive to climatic changes (Durance &

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 carried out over a long period of time (e.g. 50 years) at locations where human disturbance remains otherwise constant (Burgmer, Hillebrand & Pfenninger, 2007). Such

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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, Furse & Armitage, 1993; Turak, Waddell & Johnstone, 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, Steward & Harch, 2006; Jones, 2008). Nonetheless, it has been shown that family-level data can be as effective as species-level 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 & Loreau, 2003; Buckley & 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 & 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 & Webster, 1996) and nutrient cycling (Gomi, Sidle & Richardson, 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 subtropical to temperate regions (>1000 km). Climate change threatens to exacerbate the significant declines in 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 & Hobday, 2011). Temperatures are projected to increase 1.8–5 °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 & 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, Öhlund & Englund, 2011; Pittock & 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: (i) Is assemblage turnover of freshwater macroinvertebrate families correlated with the degree of environmental heterogeneity within catchments? (ii) Over what distance do freshwater assemblages become significantly different along a latitudinal gradient? (iii) 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).

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

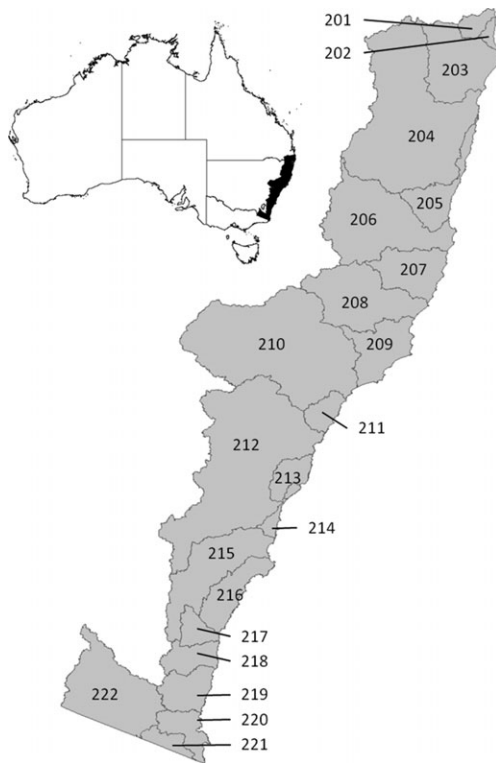


Fig. 1 Study area in eastern New South Wales (inset). Catchments are referenced by their Australian River Basin Numbers (Australian Government, Bureau of Meteorology, 2009).

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× the modal width of the river, or 100 m, 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 among 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 0.25-mm mesh net by sweeping towards the banks at edge habitats and, for riffles, by kicking the substratum while holding the net vertically while stand-

ing on the bed downstream. Macroinvertebrates were live sorted from the sample for a minimum of 40 min; the period was extended to 50 or 60 min if new taxa were still being recorded, if 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, *c.* 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 (<http://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, Stein & Nix (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 programme 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 *c.* 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 <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

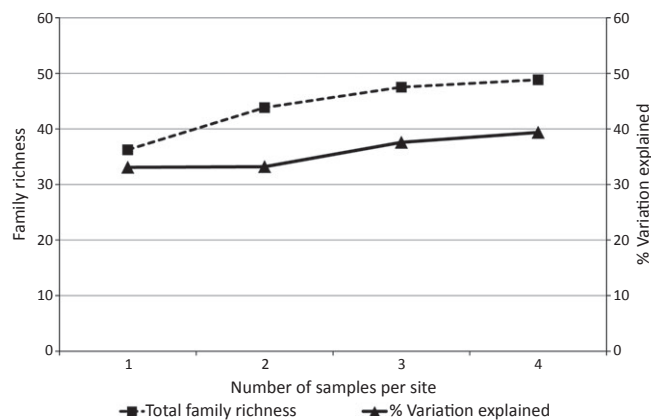


Fig. 2 Impact of increasing numbers of replicate edge samples on the total number of macroinvertebrate families recorded at a site, and the amount of variation that could be explained by multivariate multiple regression (DistLM) ($n = 163$).

surveyed sites (total $n = 865$ edge, 256 riffle) and are broadly representative of NSW coastal catchments.

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 owing 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 & Waddell, 2002).

Variation in assemblage composition was also investigated for specific stream classes. Headwater streams (<10 km from their source) were split into five elevation classes: coastal fringe <30 m, lowland 31–200 m, mid-elevation 201–600 m, upland 601–1000 m and montane >1000 m. These classes follow those of previous studies (Turak & 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: PER-

MANOVA+ (Clarke & Gorley, 2006). Turnover (i.e. beta diversity) was measured using the Bray–Curtis dissimilarity index. Turnover within and between catchments was analysed using permutation of dispersion (PERMDISP). 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 with 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 & 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 & 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 & Legendre, 1998; Gilbert & 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 Spacemaker 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 were 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 <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 >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 with 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 $F_{(1,13)} = 7.526$, $P \leq 0.001$), 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

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

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

NA, not analysed.

montane streams (>40%). A small number ($n = 10$) of sub-alpine sites that occurred at particularly high elevations (>1500 m) 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.

Assemblage composition

Increasing separation of catchments increases the likelihood that catchments will have significantly different assemblages of families (ANOSIM global $r = 0.267$, $P \leq 0.001$, PERMANOVA $F_{(829,21)} = 7.47$, $P \leq 0.001$), and although spatial autocorrelation plays a part in this, there was a stronger clustering of sites based on distance in climatic space (ANOSIM global $r = 0.427$, $P \leq 0.001$). Of greater interest are those differences that occur between neighbouring catchments (Fig. 3), for example between basins 204 and 206 ($r = 0.236$, $P \leq 0.001$). 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 $r = 0.193$, $P \leq 0.001$). Despite the

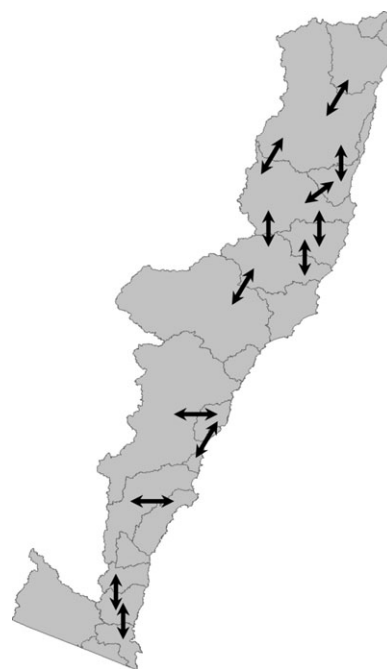


Fig. 3 Study area with river catchment boundaries shown. Arrows indicate significant differences in the composition of stream-edge macroinvertebrates among adjacent river catchments (ANOSIM global $r = 0.123$, $P \leq 0.001$).

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 whether these consisted of the same or closely related species.

The assemblages of each stream class were significantly different from one another (ANOSIM global $r = 0.106$, $P \leq 0.001$) except for those of lowland and mid-elevation streams ($P = 0.054$). Within stream classes, montane streams in particular showed distinct differences among catchments ($F_{(5,76)} = 1.53$, $P \leq 0.001$), 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 ($r = 0.829$, $P \leq 0.001$).

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 Appendix S1 in Supporting Information). The increase from edges to riffles reflected the greater explanatory power of factors characterising water quality and channel type.

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-Climature 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 with montane streams (Fig. 4c). Disturbance explained the least

Table 2 Partitioning of variance analysis between edge (a) and riffle (b) samples

Partitioning section	All edge sites	Coastal-fringe streams	Lowland streams	Mid-elevation streams	Upland streams	Montane streams
(a)						
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)						
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

NA, not analysed.

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.

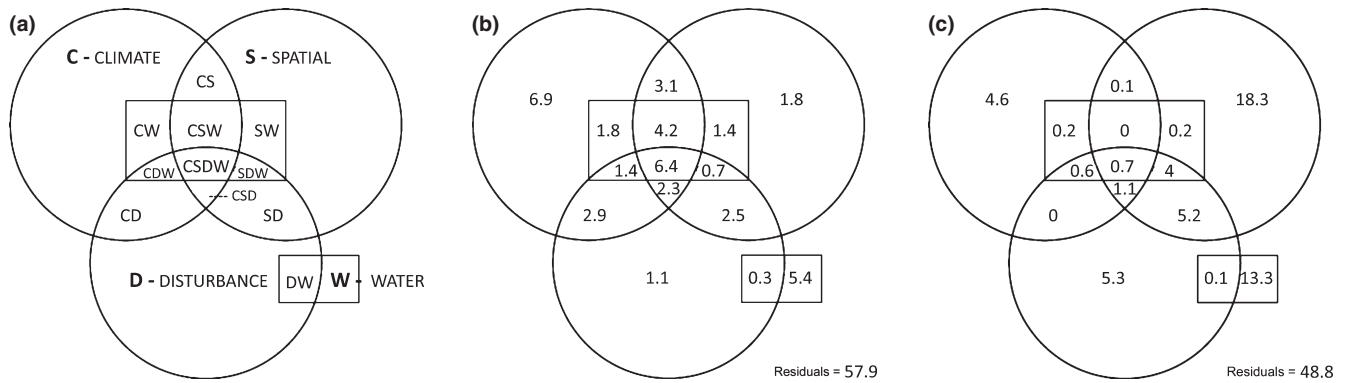


Fig. 4 Diagram A illustrates the partitioning of variance between four groups of factors: Climate (C), Spatial (S), Disturbance (D) and Water (W). The total variation explained by each group is portrayed by a circle, although Water is divided into two rectangles because four-way partitioning cannot be 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.

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-Climatic 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 on 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 that 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.

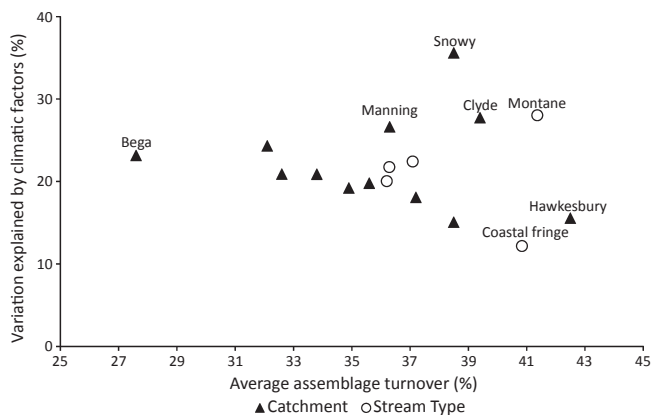


Fig. 5 Percentage variation explained by climatic factors using DistLM (adj. $r^2 \times 100$) against the average percentage turnover among assemblages within (▲) catchments and (○) stream classes. Vulnerability to climate change is expected to increase where higher assemblage turnover is combined with 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, Virkkala & Toivonen, 2009). This study shows that 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 *c.* 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, Hannah & Milner, 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 autocorrelation is difficult (Gilbert & 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 & 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 & Townsend, 2006; Hughes, Schmidt & Finn, 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, Van Strien & Holderegger, 2012).

Coastal-fringe streams may also be vulnerable to climate change because of limited adaptive movement. Recent modelling suggests that global sea-level rise may exceed IPCC AR4 predictions (18–79 cm increase over 1990 by 2095) (Church *et al.*, 2011). Sea levels along the coast of New South Wales are projected to rise 90 cm 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 & 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 100 m 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 and 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 that infrequently sampled taxa had little influence on the analysis, a further 6% of the variation could have been explained with additional sampling (Hose, Turak & Waddell, 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 & Townsend, 2006; Landeiro *et al.*, 2011). These include descriptors of riparian condition (Warfe & Barmuta, 2006), the presence of macrophytes (Humphries, 1996), the diversity and abundance of fish (Nicola, Almodóvar & Elvira, 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 data set 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 data sets globally could greatly improve our understanding of freshwater biogeographic patterns. Furthermore, these

data sets 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 data sets 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, Munguia & Mitchell, 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 & 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).

Acknowledgments

We are grateful to the New South Wales Office of Environment and Heritage, Department of Premier and Cabinet (formerly Department for Environment Climate Change and Water) for providing both biological and environmental data used in this study. In particular, we thank Jan Miller, Gunther Theischinger, Chris Rush, Dan Bickel and Cheryl Tang for their help in collecting and identifying specimens and preparing the data. We also appreciate the constructive suggestions of our anonymous referees.

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Supporting Information

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

Appendix S1. Results from partitioning of variance analysis between edge (a) and riffle (b) samples using taxa at increasing thresholds of occurrence.

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(Manuscript accepted 23 May 2012)