Understanding and predicting the combined effects of climate change and land-use change on freshwater macroinvertebrates and fish

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Summary

1. Climate change and land-use change are having substantial impacts on biodiversity worldwide, but few studies have considered the impact of these factors together. If the combined effects of climate and land-use change are greater than the effects of each threat individually, current conservation management strategies may be inefficient and/or ineffective. This is particularly important with respect to freshwater ecosystems because freshwater biodiversity has declined faster than either terrestrial or marine biodiversity over the last three decades.

2. This is the first study to model the independent and combined effects of climate change and land-use change on freshwater macroinvertebrates and fish. Using a case study in southeast Queensland, Australia, we built a Bayesian belief network populated with a combination of field data, simulations, existing models and expert judgment. Different land-use and climate scenarios were used to make predictions on how the richness of freshwater macroinvertebrates and fish is likely to respond in future.

3. We discovered little change in richness averaged across the region, but identified important impacts and effects at finer scales. High nutrients and high runoff as a result of urbanization combined with high nutrients and high water temperature as a result of climate change and were the leading drivers of potential declines in macroinvertebrates and fish at fine scales.

4. *Synthesis and applications.* This is the first study to separate out the constituent drivers of impacts on biodiversity that result from climate change and land-use change. Mitigation requires management actions that reduce in-stream nutrients, slows terrestrial runoff and provides shade, to improve the resilience of biodiversity in streams. Encouragingly, the restoration of riparian habitats is identified as an important buffering tool that can mitigate the negative effects of climate change and land-use change.

Key-words: Bayesian belief network, freshwater biodiversity, interactions, land-cover change, management, multiple stressors, restoration, riparian vegetation, urbanization, water quality

Introduction

Climate change and land-use change are two of the greatest threats to terrestrial, marine and freshwater biodiversity globally (Sala *et al*. 2000). Yet, most studies reporting past or future impacts of climate change (e.g.

Miles, Grainger & Phillips 2004; Parmesan 2006) or land-use change on biodiversity (e.g. Fahrig 2003; Nacoulma *et al*. 2011) have typically studied each stressor in isolation. However, in recent years, it has become increasingly clear that a single-stressor perspective is inadequate when ecosystems and species are threatened by multiple, co-occurring stressors (e.g. Brook, Sodhi & Bradshaw 2008; Ormerod *et al*. 2010; Mantyka-Pringle, Martin & Rhodes 2012).

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Freshwater ecosystems occupy less than one per cent of the Earth's surface, yet they contribute disproportionately to global biodiversity (Strayer & Dudgeon 2010). Despite their importance, freshwaters are experiencing declines in biodiversity far greater than those in the most affected terrestrial and marine ecosystems due to widespread habitat degradation, overexploitation, exotic invasions, water extraction and flow regulation (Ormerod *et al.* 2010; Strayer & Dudgeon 2010). The process of urbanization, for example, has resulted in the conversion of terrestrial vegetation to expanses of impervious surfaces. Increases in impervious surfaces influence the amount of runoff and nutrients entering streams; decrease bank stability and sediment trapping; reduce shading; and influence natural flow regimes (e.g. Allan 2004). Changes triggered by urbanization and other forms of land-use change have important consequences for river ecosystems, causing declines in freshwater productivity, biodiversity and overall abundances of freshwater organisms, as well as impacting the composition of in-stream community assemblages (e.g. Roy *et al.* 2003; Morgan & Cushman 2005).

Freshwater biodiversity is also vulnerable to climate change (e.g. Abell 2002; Dudgeon *et al.* 2006). With climate warming, freshwater ecosystems will experience increases in water temperature; evaporation is likely to increase during dry seasons; and flood intensity and frequency are also expected to increase due to more frequent heavy rain events (Lake *et al.* 2000). Climate change effects are expected to differ among and within broadly defined freshwater taxonomic groups (Heino, Virkkala & Toivonen 2009). Fish are the most studied freshwater taxa in this respect, with documented and predicted changes in species' distributions, stocks and productivity, upstream migrations, diversity and recruitment (e.g. Tedesco *et al.* 2013). Some declines and shifts in amphibians and invertebrate communities have also been recorded (Pounds *et al.* 2006; Thomson *et al.* 2011). Overall, those species that are highly restricted in their geographical distribution, or that have a very specialized ecological niche, seem to be most vulnerable.

There is growing evidence to suggest that when climate change and land-use change occur together, they will synergistically contribute to the degradation of biological diversity at the genetic, species and/or habitat level (e.g. Opdam & Wascher 2004; Nelson *et al.* 2009; Mantyka-Pringle, Martin & Rhodes 2012). In freshwater ecosystems, the consequences of interactions between landscape change and climate change have the potential to be quite significant (Dudgeon *et al.* 2006; Heino, Virkkala & Toivonen 2009), yet rarely are both climate and land-use change considered together (Sala *et al.* 2000; Moss 2010; Ormerod *et al.* 2010; Piggott *et al.* 2012; Porter *et al.* 2012). For example, nitrogen deposition and its interactions with climate change and land-use have been reported to be relatively large (e.g. Sala *et al.* 2000; Moss 2010). However, large uncertainties remain regarding which processes (e.g. biophysical processes such as water temperature or nitrogen enrichment) will have the greatest impact on biodiversity in freshwater ecosystems and whether the sum of the individual stressor effects is greater than either stressor alone (i.e. a synergistic interaction).

To tease out the drivers of climate change and land-use change impacts on freshwater biodiversity, we modelled the independent and combined effects of these two stressors on freshwater macroinvertebrates and fish using south-east Queensland, Australia, as a case study. We used a Bayesian belief network (BBN) parameterized under current land-use and climatic conditions to predict the effect of future land-use and climate change on the richness of macroinvertebrates and fish at two different spatial extents, a broad regional spatial resolution and a finer site-specific spatial resolution (hereafter referred to as 'regional scale' and 'site scale'). We compared the combined and individual effects of climate change and land-use change at both scales. Then, at the site scale, we examined which environmental factors are likely to be responsible for variation in macroinvertebrate or fish losses and/or gains as a result of both climate and land-use change.

Materials and methods

STUDY REGION

South-east Queensland (SEQ) contains 14 major river catchments and numerous subcatchments (Fig. 1). SEQ has the highest level of richness and/or endemism of freshwater lungfishes, gobies, catfishes, rainbowfishes, eels, basses, snails, damselflies, limpets, dragonflies, water striders, water beetles and backswimmers in Australia (Australian Government 2011). Loss of 75% of the native vegetation in SEQ has caused significant changes in catchment hydrology and sediment delivery, resulting in declining water quality and loss of aquatic biodiversity (Bunn *et al.* 2007). SEQ is also Australia's fastest growing metropolitan region, and from 2006 to 2031, its population is expected to grow from 2·8 to 4·4 million people and 754 000 additional dwellings will be required (OUM 2009). Predicted population increases in the region are likely to further impact on the ecological health of its waterways. Projected changes in climate will therefore act on freshwater ecosystems that are already under considerable stress and have reduced adaptive capacity. For these reasons, SEQ provides an excellent case study for understanding the consequences of global change on freshwater biodiversity and how we might conserve it.

CONCEPTUAL MODEL

A conceptual model was constructed to identify the major causal links between land-use (i.e. the amount of hard impervious surfaces and the amount of riparian vegetation) and climate (i.e. air temperature, precipitation and rainfall variability) on freshwater biodiversity (i.e. macroinvertebrate taxa richness and fish species richness) (Fig. 2; see Appendix S1 in Supporting Information for a review). Nitrogen, phosphorus, runoff and water temperature are among the most important drivers of freshwater biodiversity
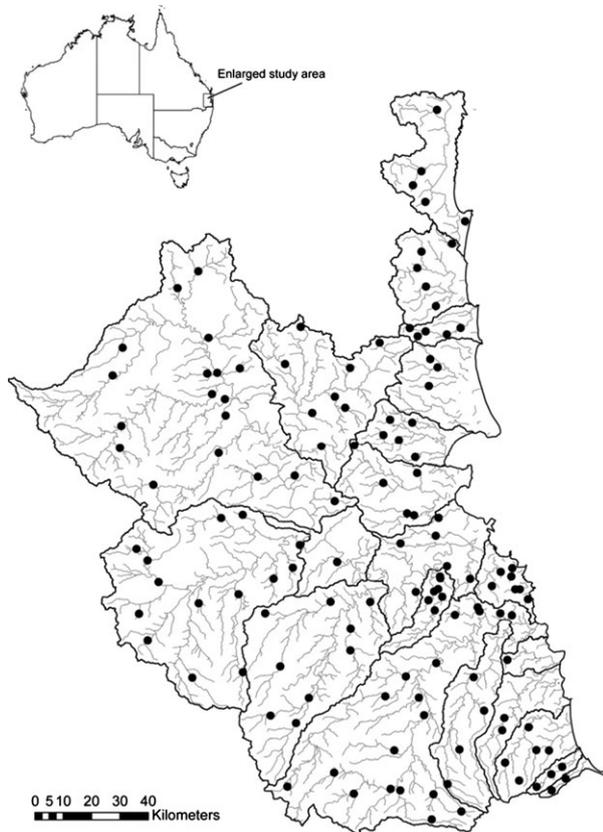
Fig. 1. Map of south-east Queensland, Australia, showing boundaries of the 14 river catchments, subcatchments and distribution of the 135 Ecosystem Health Monitoring Program survey sites (black dots).

loss identified in the literature and were included as variables in the conceptual model (e.g. Allan 2004; Nyenje *et al.* 2010). A 'nutrient' variable was included to represent the effect between higher nitrogen, phosphorus, runoff and rainfall variability caused by climate and land-use change (i.e. nutrient load). Elevation was also included because it as an important natural determinant for predicting macroinvertebrate and fish distributions (e.g. Pusey, Kennard & Arthington 2000).

BAYESIAN BELIEF NETWORK STRUCTURAL DEVELOPMENT

To build a predictive model for the impacts of climate and land-use change on macroinvertebrate and fish richness, the conceptual model was converted into a BBN using Netica software (Norsys Software Corporation 2008). The BBN consists of independent and dependent variables (nodes), and the links (arrows) represent how the variables are related. Underlying each dependent variable is a conditional probability table (CPT) that specifies the probability of each state conditional on other variables (Marcot 2006). A BBN framework was chosen to model this system because of its ability to model interactions within the CPTs, and integrate empirical data with expert knowledge (Martin *et al.* 2012).

DATA SOURCES

An Ecosystem Health Monitoring Program (EHMP) was established in SEQ in 2002 to assess the effectiveness of management and planning activities aimed at improving SEQ's waterways (Bunn *et al.* 2010). The EHMP currently involves the assessment of 135 freshwater sites, twice per year, and reports on five ecological indicators encompassing sixteen separate indices (EHMP 2012). The EHMP provided us with data on pollutants (total nitrogen and phosphorus) for the period 2007–2010, and water temperature (mean maximum annual water temperature), macroinvertebrates (mean total taxa richness; excluding cladocerans, ostracods, copepods and spiders) and fish data (mean total species richness; excluding exotics and any translocated species) for the period 2002–2010 from each of their 135 survey sites (see Fig. 1 for the distribution of these sites). Macroinvertebrate taxa richness and fish species richness were chosen as indices based on their statistically strong association with the disturbance gradient in this study region (Bunn *et al.* 2010) and because they are generally sensitive to multiple stressors (e.g. Statzner & Bêche 2010; Stendera *et al.* 2012).

To calculate runoff and impervious cover, we used GIS layers (1 : 250 000) provided by the National Environmental Stream Database version 1.1.5 (Stein 2011) and averaged the mean annual accumulated soil water surplus (1970–2008) and the mean proportion of areas that is urban or a road (2009) within a 500 m (for runoff) and 5 km (for impervious cover) radius of every EHMP
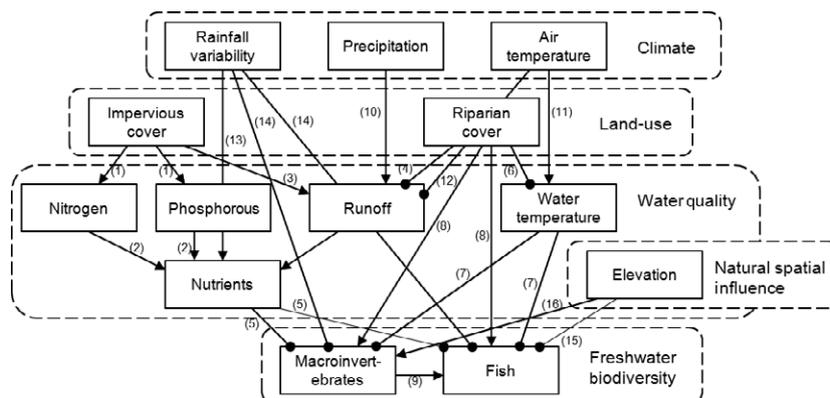
Fig. 2. A conceptual model of the key climate, land-use and water quality variables that interact and impact macroinvertebrate and fish richness (see Appendix S1 for a full review of the conceptual model). A solid arrow indicates a positive effect or link, whereas a closed circle indicates a negative effect or link. Each link is numbered based on the relationships as explained in Appendix S1.

survey site. Elevation was calculated at the centre of each EHMP point using a $30 \times 30 \text{ m}^2$ resolution digital elevation model (DEM; Gallant 2010). To calculate riparian cover, we edited a stream network (1 : 25 000) by buffering a fixed width either side of each stream: eighth-order streams by 70 m, seventh-order by 60 m, sixth-order by 50 m, fifth-order by 40 m, fourth-order by 30 m, third-order by 20 m, second-order by 10 m. First-order streams were removed because they represented only dry gullies in SEQ. The reduced buffer widths were chosen to approximate the size of the streams throughout the catchments. A woody vegetation cover map produced by the Queensland Statewide Landcover and Trees Study (2007; 25 m resolution) (SLATS; https://data.qld. gov.au/dataset/, accessed October 2010) was then clipped to the buffered stream network map. A 500 m radius was buffered around each EHMP site, and the proportion of foliage cover in the riparian zones was calculated within this buffer.

For climate data, we used a previously published spatial data set (5 km^2; Jeffrey *et al.* 2001) to calculate air temperature (mean maximum annual air temperature), precipitation (mean total annual rainfall) and rainfall variability (coefficient of variation of annual total rainfall) at each site for the period 2000–2010. All GIS processing was undertaken using ARCGIS version 10.0 (Environmental Systems Research Institute, Redlands, CA, USA).

POPULATING CONDITIONAL PROBABILITY TABLES AND CALCULATING MODEL ACCURACY

Bayesian learning in Netica was used to update the CPTs of our BBN with a random selection of 75% of the 135 EHMP sites. We set the BBN to learn from the data with 1 000 000 iterations. The remaining 25% of the 135 sites were then used to validate the CPTs using the test-with-cases function in Netica. Prior to parameterization, all variables in the BBN were categorized into states (classes) using the 33rd and 66th percentile values of each data set and/or via consultation with freshwater scientists and managers who were familiar with the study region (Table 1). This is a common approach and best practice when observed data thresholds are absent (e.g. Bashari, Smith & Bosch 2008; Choy, O'Leary & Mengersen 2009) and expert judgment is a credible source of information for ecological applications and conservation management (e.g. Choy, O'Leary & Mengersen 2009; Martin *et al.* 2012). Experts were also approached to take part in a survey to assist in estimating values within CPTs (see Appendix S1). The CPTs based on empirical data using 75% of the sites ($n = 100$) were averaged with the CPTs based on the experts' elicited probabilities. To assess the model fit of the populated BBN, we performed a sensitivity analysis using the remaining 35 sites and visually inspected the actual vs. predicted number of macroinvertebrate taxa and fish species while allocating different weights to the empirical and expert CPTs. The best-fit model was produced when we gave the empirical CPTs 75% weighting and the expert CPTs 25% (see Appendix S2).

SCENARIOS

Current conditions and ten alternative scenarios were run through the model to examine the future susceptibility of macroinvertebrates and fish to climate and land-use change. The scenarios consisted of two climate impact scenarios (moderate and high climate), two urban growth scenarios (moderate and high growth) and two combination scenarios (moderate climate + moderate growth; high climate + high growth) (see Appendix S1 for details

on how these scenarios were simulated). We also simulated four adaptation scenarios by taking the two combination scenarios and altering the riparian vegetation cover at each EHMP site by −25% or +25% to represent two non-adaptation strategies (climate + growth + riparian loss) and two potential management strategies (climate + growth + riparian restoration).

STATISTICAL ANALYSES

Prior to running the BBN, Pearson's correlation coefficient was used to test for collinearity among all environmental variables (see Table 1). To detect differences in the mean magnitude of change of macroinvertebrates and fish (averaged across all EHMP sites = regional scale) between current climate and land-use conditions and the modelled future conditions for different scenarios, we used Friedman tests followed by Friedman *a posteriori* multiple comparison tests (Conover 1999). Entropy reduction was used to determine which variables were the most influential in terms of their impact on macroinvertebrates and fish at the regional scale. Entropy reduction measures the sensitivity of changes in probabilities of response variables (i.e. macroinvertebrate taxa richness and fish species richness) when parameters and inputs were changed within the BBN (Marcot 2006). For each scenario output, sites were divided into five groups based on their magnitude of change in macroinvertebrate taxa richness or fish species richness (see Fig. 3). Mean change in variables was calculated for each macroinvertebrate and fish group across sites. Principal components analysis (PCA, based on a covariance matrix) of the standardized variables (y-mean/SD) was then used to examine which variables at the site scale were most highly associated with specific macroinvertebrate and fish responses for each scenario. Only those environmental variables directly linked to each climate change, urban growth or climate change + urban growth scenario were included in each PCA. For example, under a climate change scenario, the variables rainfall variability, precipitation, air temperature, runoff, water temperature and nutrients were included in the PCA, whereas all other variables remained constants and were therefore excluded. In contrast, under an urban growth scenario, the variables impervious cover, nitrogen, phosphorus, runoff and nutrients were included in the PCA, whereas all other variables were excluded as constants.

Results

We identified correlations between the variables riparian cover and precipitation, phosphorus and nitrogen, nutrients and phosphorus, and nutrients and nitrogen ($r > 0.5$, $P > 0.05$). However, because these correlations were all small ($r < 0.65$), we decided to keep the variables in the model.

At the regional scale, there were no significant differences detected in the mean magnitude of change in macroinvertebrate taxa richness or fish species richness between the two climate impact scenarios, between the two urban growth scenarios, between the two combination scenarios, between the two non-adaptation scenarios or between the two potential management scenarios (Friedman test; Appendix S3). All subsequent analyses were therefore based on only the five moderate impact scenarios:

Table 1. Description of the variables used in the Bayesian belief network, the methodology used to categorize them, and the states (i.e. classes) of these variables

Variable	Description; categorization methodology	States
Air temperature	Max annual temperature at the site; classes calculated using the current climates 33rd & 66th percentile values	Low ≤ 16 °C Moderate = 16–25·2 °C High ≥ 25·2 °C
Precipitation	Total annual rainfall at the site; classes calculated using the current climates 33rd & 66th percentile values	Low ≤ 776·6 mm Moderate = 776·6–1143·5 mm High ≥ 1143·5 mm
Rainfall variability	Coefficient of variation of annual total rainfall at the site; classes calculated using the current climates 33rd & 66th percentile values	Low ≤ 0·28 CV Moderate = 0·28–0·32 CV High ≥ 0·32 CV
Impervious cover	Mean % of urban land + roads within a 5 km radius of a site; classes calculated using expert knowledge	Protected (<10%) Impacted (10–30%) Degraded (>30%)
Riparian cover	% of riparian zone covered in vegetation, within a 500 m radius of a site; classes calculated using expert knowledge	Degraded (<30%) Impacted (30–60%) Protected (>60%)
Water temperature	Max annual water temp at the site; classes calculated using the EHMPs 33rd & 66th percentile values*	Low ≤ 19·6 °C Moderate = 19·6–22·2 °C High ≥ 22·2 °C
Runoff	Mean annual accumulated soil water surplus within a 500 m radius of a site; classes calculated using current 33rd & 66th percentile values	Low ≤ 4620 ML Moderate = 4620–13 072 ML High ≥ 13 072 ML
Nitrogen	Total water-column nitrogen at the site; classes calculated using the EHMPs 33rd & 66th percentile values*	Low ≤ 0·31 mg L^{-1} Medium = 0·31–0·6 mg L^{-1} High ≥ 0·6 mg L^{-1}
Phosphorus	Total water-column phosphorus at the site; classes calculated using the EHMPs 33rd & 66th percentile values*	Low ≤ 0·038 mg L^{-1} Medium = 0·038–0·077 mg L^{-1} High ≥ 0·077 mg L^{-1}
Nutrients	Risk of biodiversity loss at a site caused by runoff, nitrogen, phosphorus & rainfall variability interactions; classes calculated using expert knowledge	Low = Low risk Med = Medium risk High = High risk
Elevation	Height above sea level at the site; classes calculated using expert knowledge	Low ≤ 150 m Medium = 150–250 m High > 250 m
Macroinvertebrates	Total number of macroinvertebrate taxa at the site; classes calculated using the EHMPs 33rd & 66th percentile values*	Low ≤ 18 taxa Medium = 18–24 taxa High ≥ 24 taxa
Fish	Total number of fish species at the site; classes calculated using the EHMPs 33rd & 66th percentile values*	Low ≤ 4 species Medium = 4–6 species High ≥ 6 species

*EHMP, South-east Queensland's Ecosystem Health Monitoring Program.
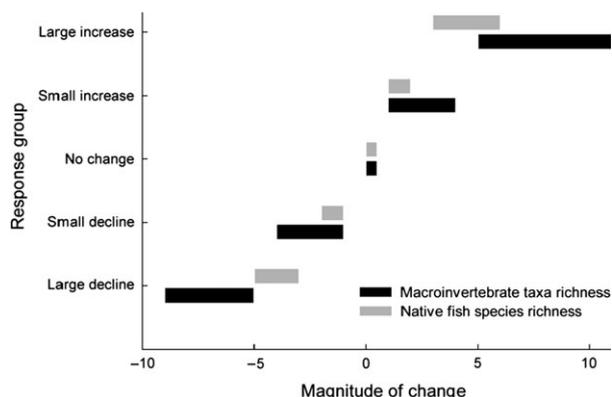
Fig. 3. The five response groups chosen to represent the range of changes in macroinvertebrate taxa richness and fish species richness at each Ecosystem Health Monitoring Program site in response to future climate and land-use change conditions.

1. Moderate Climate.
2. Moderate Urban Growth.
3. Moderate Climate + Moderate Growth.
4. Moderate Climate + Moderate Growth + Riparian Loss.
5. Moderate Climate + Moderate Growth + Riparian Restoration.

MACROINVERTEBRATES AND FISH RESPONSE TO FUTURE CLIMATE AND LAND-USE CHANGE

Our model predicted only a small change in the richness of macroinvertebrates or fish in response to climate change, urban growth or climate and urban growth together when differences were aggregated across sites (i.e. the regional scale) (Friedman tests; Fig. 4). Sensitivity analysis revealed that riparian cover and nutrients

followed by water temperature were the most influential variables for macroinvertebrate richness across sites (Table 2). Elevation and nutrients were the most influential variables for fish richness, followed by macroinvertebrate richness and riparian cover.

In contrast, there was substantial variation among sites; approximately two-thirds of the sites either increased in richness of both macroinvertebrates and fishes or showed no change, whereas the remaining third declined (Fig. 3). PCA revealed that, on average, the first two principal components for each scenario accounted for more than 90% of overall variance in macroinvertebrate and fish responses (see Appendix S4). Under the climate scenario, higher water temperature played a leading role and lower runoff a secondary role in predicting the responses of both macroinvertebrates and fish (Table 3; Appendix S4a,d). Sites that had the highest increases in water temperature were associated with the largest increases in macroinvertebrate taxa

Table 2. Sensitivity of macroinvertebrate taxa richness and fish species richness to key climate, land-use and water quality variables at the site scale expressed using entropy reduction (see Marcot 2006 for details)*

Variable	Macroinvertebrate entropy reduction	Fish entropy reduction
Macroinvertebrates		0·4943[†]
Riparian cover	1·8340[†]	0·4618
Nutrients	0·6906[†]	0·5105[†]
Water temperature	0·3874[†]	0·4450
Nitrogen	0·1393	0·0819
Phosphorus	0·0747	0·0426
Air temperature	0·0289	0·0082
Impervious cover	0·0127	0·0061
Runoff	0·0032	0·0006
Rainfall variability	0·0022	0·2385
Elevation	0·0008	0·8683[†]
Precipitation	0·0003	0·0000

*Entropy reduction is a measure of how much findings at one variable can influence the beliefs in another.
[†]The three most influential variables for macroinvertebrate taxa richness and fish species richness.

richness, and the largest increases and declines in fish species richness. In contrast, sites that had the smallest increases in water temperature were associated with declines or the smallest increases in macroinvertebrates, and the smallest declines or no changes in fish. Sites that had the highest increases in water temperature as well as the lowest runoff were associated with no change in macroinvertebrates, and the largest declines in fish.

Under the urban growth scenario, variations in macroinvertebrate and fish responses were linked with higher nutrients, nitrogen and phosphorus (Table 3; Appendix S4b,e). Sites that had the highest increases in nutrients, phosphorus and nitrogen loads were associated with declines in the richness of both macroinvertebrates and fish, whereas sites that had the smallest increases in those three variables were associated with increases in macroinvertebrates and the largest increases in fish.

Under the climate + growth scenario, a similar pattern arose from the PCA in that sites that had higher nutrients, phosphorus and nitrogen were strongly linked with declines in the richness of macroinvertebrates and fish (Table 3; Appendix S4c,f). In contrast, sites that had lower disturbance levels were strongly associated with increases in macroinvertebrates and fish. A second pattern arose between declines in macroinvertebrates based on runoff; sites that had the highest increases in nutrients, phosphorus, nitrogen and runoff were associated with the largest declines in macroinvertebrates. However, sites that had higher levels of nutrients, phosphorus and nitrogen, but had the smallest increase in runoff were associated with the smallest declines in macroinvertebrates. For fish, a similar trend was found with water temperature; sites that had the highest increases in nutrients, phosphorus, nitrogen and water temperature were associated with the largest declines in fish, whereas sites that had higher levels of nutrients,

Fig. 4. Mean magnitude of change between current and future projected (a) macroinvertebrate taxa richness and (b) fish species richness to five climate change and land-use change scenarios at the regional scale. Bars represent means ± 1 SE. Analysis is by Friedman test followed by Friedman multiple comparisons test. Letters indicate homogenous subgroups, $n = 134$ sites for each scenario.

Table 3. The main variables associated with each macroinvertebrate and fish response group at the site scale for three future scenarios based on principal components analysis (see Appendix S4 for ordination plots)*

Response group	Climate change	Urban growth	Climate change + Urban growth
Macroinvertebrates			
Large decline	−water temp, +runoff	+nutrients, +P, +N, +runoff	+nutrients, +P, +N, +runoff
Small decline	−water temp, −runoff	+nutrients, +P, +N	+nutrients, +P, +N, −runoff
No change	+water temp, −runoff	+nutrients, +P, +N, −runoff	+nutrients, +P, +N, −runoff
Small increase	−water temp	−nutrients, −P, −N	−nutrients, −P, −N, +runoff
Large increase	+water temp	−nutrients, −P, −N	−nutrients, −P, −N, −runoff
Fish			
Large decline	+water temp, −runoff, +nutrients	+nutrients, +P, +N, +runoff	+nutrients, +P, +N, +water temp
Small decline	−water temp	+nutrients, +P, +N	+nutrients, +P, +N, −water temp
No change	−water temp	+nutrients, +P, +N, −runoff	−nutrients, −P, −N
Small increase	+runoff, −nutrients	−runoff	−nutrients, −P, −N
Large increase	+water temp, +runoff, −nutrients	−nutrients, −P, −N	−nutrients, −P, −N

*water temp, water temperature; P, phosphorus; N, nitrogen; a positive sign (+) indicates a high level of that variable, whereas a negative sign (−) indicates a low level; see Table 1 for descriptions of variables. Variables are listed in order of importance from left to right based on their principal component analysis loadings (Appendix S4).

phosphorus and nitrogen, but the smallest increase in water temperature were associated with the smallest declines.

INFLUENCE OF RIPARIAN VEGETATION

Although we did not run a riparian vegetation scenario without climate change or urban growth, our model showed a strong effect of riparian vegetation that was independent of climate change and urban growth. This is based on the difference between the climate and growth scenarios with no change in riparian cover and the climate and growth scenarios with riparian loss or with riparian restoration (Friedman tests; Fig. 4). At the regional scale, riparian loss occurring simultaneously with climate change + urban growth would result in significant declines in both macroinvertebrates ($\chi^2 = 219.34$, $P < 0.001$; Fig. 4a) and fish richness ($\chi^2 = 82.41$, $P < 0.001$; Fig. 4b). In contrast, riparian restoration occurring simultaneously with climate change + urban growth would result in significant increases in richness, especially for macroinvertebrates (by 2–3 taxa).

Discussion

When multiple ecological stressors act simultaneously, the consequences for biodiversity have the potential to be significant (Dudgeon *et al.* 2006; Heino, Virkkala & Toivonen 2009). However, it is often difficult to tease apart and identify the processes, effects and/or interactions that are the key drivers of change (like the loss of native biodiversity). Consequently, there is also still a great deal of uncertainty in projecting species and freshwater ecosystem-specific responses for the future (Downes 2010). This study reveals the combined effects of climate change and land-use change on freshwater macroinvertebrates and fish, which can lead to dramatic declines in biodiversity.

We found only small effects of climate and/or land-use change on macroinvertebrates and fish averaged across the region. The combined effects of climate change and land-use change had a similar impact on the richness of both macroinvertebrates and fish in comparison with either stressor alone. However, at the site scale, there were considerable effects and variation in macroinvertebrate and fish responses to climate and land-use change, and clear patterns in what drives these. For example, higher water temperature caused by higher air temperature was a major driver of macroinvertebrate and fish responses under climate change conditions alone. Our results indicate that higher temperatures may cause substantial increases or decreases in the richness of fish depending on the site. Previous studies have shown that direct effects of elevated water temperature will likely force contractions or extinctions of cold-adapted fish species and those with very localized ranges or narrow tolerances, whereas those species that can tolerate a wider thermal range are likely to expand (e.g. Kopp *et al.* 2012). The effect of water temperature on macroinvertebrates can also vary (e.g. Feio *et al.* 2010; Lawrence *et al.* 2010), but according to our model, sites that had the highest increases in water temperature had the largest increases in macroinvertebrate richness. Thus, it is possible that warmer water temperatures as a result of climate change may increase the richness of macroinvertebrates in some areas. With climatic warming, water temperature could shift 1–2 degrees higher and make it similar to a more northerly region, such as north Queensland's Wet Tropics bioregion, for example, where the diversity of some freshwater invertebrates appears higher than in comparable areas of SEQ (EHMP, unpublished data). Thus, differences in the apparent response of freshwater fish and macroinvertebrates to climate change will largely reflect the species' biological attributes and life histories.

Higher nutrient loads (including correlated phosphorus and nitrogen) caused by an increase in the amount of impervious surfaces were the main driver of macroinvertebrate and fish responses under urban growth alone, and when urban growth and climate change were impacting

simultaneously. Our study supports findings suggesting human land-use and land-cover change represents the most important component of global change now and in future for freshwater biodiversity (e.g. Piggott *et al.* 2012; Martinuzzi *et al.* 2013). In SEQ, macroinvertebrate richness was projected to decline most at sites with highest increases in nutrients. The negative effect of higher nutrients on macroinvertebrate richness is a common trend reported by other investigators (e.g. Chadwick *et al.* 2006). The combined effect of high nutrients and high runoff, however, appears to have both negative and positive effects, depending on the stream condition (e.g. Chadwick *et al.* 2006; Thomson *et al.* 2011). Nevertheless, our results imply that the effect of higher nutrients and higher runoff, led by increased urbanization and higher rainfall variability, as a result of climate change may lead to significant declines in macroinvertebrate richness. A similar effect was also found for nutrients and water temperature for fish. The response of freshwater fish to higher water temperatures (e.g. Kopp *et al.* 2012) or higher nutrient loads (Nyenje *et al.* 2010) is well-established, but the response of freshwater fish richness to the combined effect of higher water temperatures and higher nutrients is poorly documented. This is the first study to separate out the constituent drivers of impacts on biodiversity that result from climate change and land-use change. Thus, we urge future studies to consider changes in nutrients in addition to those of water temperature when projecting the effect of climate change and/or land-use change on freshwater biodiversity.

MODEL LIMITATIONS

Logically, the next step would be to analyse different species and/or functional groups of macroinvertebrates and fish based on known tolerances, as richness as a metric potentially cancels out negative and positive effects on different species. This was not possible for SEQ because this level of data does not exist, as is also true for many regions, and would require extensive laboratory experiments and/or expert knowledge to obtain. Importantly, however, richness indicators are being used for decision-making in freshwater systems (e.g. Bunn *et al.* 2010; EHMP 2012) and to answer important research questions (e.g. Heino & Soininen 2007; Jacobsen *et al.* 2012; Piggott *et al.* 2012). Therefore, we believe that it is an important measure.

Another limitation of our model is that it lacks a suspended sediment variable and a variable representing the quality of riparian vegetation (i.e. native vs. exotic vegetation). Both variables have been found to influence freshwater biodiversity (e.g. Burkhead & Jelks 2001; Death & Collier 2010), but due to the absence of this data for SEQ, these variables were excluded from our model. Future work can be done to develop empirical thresholds to improve the BBN. We also decided to focus on only two consequences of land-use change: the amount of impervious surface and the amount of riparian vegetation

cover. Although there were other measures of land-use change (i.e. the amount of agricultural and grazing land) and other variables (e.g. flow regulation and thermal modification caused by water extraction or dams) that could potentially be impacting on these waterways (e.g. Dudgeon 2000; Geist 2011), urbanization is the major anthropogenic activity impacting SEQ now and in future (OUM 2009). Over-complicating the network structure by including too many measures is a common BBN shortcoming which we tried to avoid (Barton *et al.* 2008).

IMPLICATIONS FOR MANAGEMENT AND CONSERVATION

Given the multiplicity of environmental stressors associated with global change, there is an urgent need to develop a better understanding of the combined and interactive effects of multiple stressors on biodiversity to better predict their responses to change. Accelerated climate change and the destruction of natural habitats through direct human activities are two of the greatest threats to biodiversity (Sala *et al.* 2000). Interactions between climate and land-use change will therefore be the key drivers of biodiversity responses and have important implications for the design of climate adaptation strategies. For example, management strategies that reduce the amount of in-stream nutrients and high water temperatures or slow the quantity and velocity of runoff flowing into storm drains may serve as important adaptation measures that buffer the impact of climate change and land-use change effects on freshwater biota. The construction or restoration of riparian habitats is one common management strategy that can directly reduce terrestrial runoff, indirectly filter nutrients and provide shade, therefore reducing solar radiation absorbed by the water (e.g. Kreiling *et al.* 2013). Given that we found a strong riparian vegetation restoration effect in the presence of climate change and urban growth, our study supports the use of riparian restoration as an important buffering tool for reducing the negative effects of climate change and land-use change. In contrast, we also found that streams with low riparian cover and/or high riparian loss are likely to be more vulnerable to the effects of climate change and land-use change. This is good news, because unlike some other climate adaptation strategies (e.g. restoration genetics: increasing genetic variability in preparation of unexpected conditions), we already have a good understanding of how to restore damaged riparian vegetation ecosystems, as well as the knowledge in how to measure its success (e.g. Seavy *et al.* 2009; Piggott *et al.* 2012). In Australia and other countries of European descent, riparian restoration management has been transformed over the last few decades from engineer-based to ecosystem-based approaches (Fryirs, Chessman & Rutherfurd 2013). As a result, planting of native riparian buffers has become a priority for restoration projects as it improves ecological conditions within streams without negatively impacting riparian soils (e.g. Collins *et al.* 2013; Laub *et al.* 2013). Riparian buffer

widths of between 30 and 200 m are generally recommended, dependent on stream size, land-use intensity and management objective (Hansen *et al.* 2010; Richardson, Naiman & Bisson 2012). Closed canopy revegetation is also recommended for introducing microclimatic changes to increase native species richness while decreasing exotic species numbers (Harris *et al.* 2012; Lee *et al.* 2012). In a more urbanized and warmer world, however, alternative best management practices for riparian restoration may be necessary as these guidelines may be insufficient for mitigating future climate and land-use change impacts. Future studies should therefore include alternative riparian widths and canopy cover into their scenarios for strategic freshwater conservation planning under climate and land-use change.

Comparisons of our regional- and site-scale analyses clearly illustrate the need for freshwater biodiversity impact studies to focus at multiple spatial scales. Although the catchment scale is most relevant to management, we suggest that the impacts of climate and land-use change can be mistakenly missed at this scale. For instance, at large regional spatial extents, some freshwater fish species and macroinvertebrate taxa may dramatically decline while others increase, but overall diversity may be relatively unchanged. If management were, therefore, to use only one indicator (e.g. richness) and focus only on large regional patterns due to limited resources, they could miss out on important species declines and even extinctions. Thus, it is imperative that future research and monitoring use a multiscalar approach and appropriate indicators to ensure resource managers do not overlook important on-the-ground changes (Nielsen *et al.* 2009).

Acknowledgements

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Supporting Information

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

Appendix S1. Conceptual model, expert elicitation survey and scenarios.

Appendix S2. Visual representation of the best-fit model.

Appendix S3. Comparisons among scenarios.

Appendix S4. Principal components analysis.