

Predicting Novel Riparian Ecosystems in a Changing Climate

Jane A. Catford,^{1*} Robert J. Naiman,^{2,3} Lynda E. Chambers,⁴ Jane Roberts,^{5,6} Michael Douglas,⁷ and Peter Davies³

¹*School of Botany, The University of Melbourne, Melbourne, Victoria 3010, Australia;* ²*School of Aquatic and Fishery Sciences, University of Washington, 355020, Seattle, Washington 98195, USA;* ³*Centre of Excellence in Natural Resource Management, University of Western Australia, Albany, Western Australia 6330, Australia;* ⁴*Centre for Australian Weather and Climate Research, Bureau of Meteorology, GPO Box 1289, Melbourne, Victoria 3001, Australia;* ⁵*Institute of Land, Water and Society, Charles Sturt University, Albury-Wodonga, New South Wales 2640, Australia;* ⁶*PO Box 6191, O'Connor, Australian Capital Territory 2602, Australia;* ⁷*Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory 0909, Australia*

ABSTRACT

Rapid changes in global climate are likely to alter species assemblages and environmental characteristics resulting in novel ecosystems. The ability to predict characteristics of future ecosystems is crucial for environmental planning and the development of effective climate change adaptation strategies. This paper presents an approach for envisioning novel ecosystems in future climates. Focusing on riparian ecosystems, we use qualitative process models to predict likely abiotic and biotic changes in four case study systems: tropical coastal floodplains, temperate streams, high mountain streams and urban riparian zones. We concentrate on functional groups rather than individual species and consider dispersal constraints and the capacity for genetic adaptation. Our scenarios suggest that climatic changes will reduce indigenous diversity, facilitate non-indigenous invasion (especially C4 graminoids), increase fragmentation and result in simplified and less distinctive riparian ecosystems. Compared to models based on biota-environment correlations, process models built

on mechanistic understanding (like Bayesian belief networks) are more likely to remain valid under novel climatic conditions. We posit that predictions based on species' functional traits will facilitate regional comparisons and can highlight effects of climate change on ecosystem structure and function. Ecosystems that have experienced similar modification to that expected under climate change (for example, altered flow regimes of regulated rivers) can be used to help inform and evaluate predictions. By manipulating attributes of these system models (for example, magnitude of climatic changes or adaptation strategies used), implications of various scenarios can be assessed and optimal management strategies identified.

Key words: non-indigenous species invasions; community composition; environmental planning; functional traits; emerging ecosystems; process models.

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*Corresponding author; e-mail: catfordj@unimelb.edu.au

INTRODUCTION

Novel (or emerging) ecosystems are characterized by new species assemblages that result from human-induced changes to the environment and biota (Hobbs and others 2006; Walther and others 2009). Species occur in combinations and abun-

dances that have not occurred previously, which can prompt changes in ecosystem structure and function (Hobbs and others 2006). Humans intentionally and unintentionally facilitate the development of novel ecosystems through the extinction of indigenous taxa or depletion of their propagule pool, introduction of non-indigenous taxa, creation of dispersal barriers (for example, cities, roads, dams) and environmental modifications (for example, agriculture, fire suppression, river regulation, overgrazing; Hobbs and others 2006). Hybrid ecosystems have a combination of original and novel components that are outside the historical range of ecological variability (Hobbs and others 2009). There are no definitive boundaries between hybrid and novel ecosystems, so—for simplicity—we refer to both as novel ecosystems in this paper.

Biological invasions and climate change are among the most widespread and dominant causes of ecological change in all types of environments (Pressey and others 2007); their global reach and increasing rates of change suggest that many of the world's ecosystems will transition to novel states, including riparian zones. Human-induced climate change and the associated increase in greenhouse gas concentrations are predicted to affect precipitation, temperature, storminess and precipitate a rise in sea level (Hulme 2005). The type, extent, and intensity of these changes will vary among ecosystems and their geographic location, so myriad scenarios may unfold. Being the interface between terrestrial and freshwater ecosystems (Naiman and Décamps 1997; Naiman and others 2005), riparian ecosystems are affected by changes that occur to watercourses, catchments and riparian zones themselves (Davies 2010). Of particular concern are global alterations in river discharge; in future climates, many river basins will experience water stress either from extended periods of waterlogging or from drought (Palmer and others 2008; Vörösmarty and others 2010). Rapid changes in climate may reduce or eliminate habitable space for many species (Pressey and others 2007), alter species distributions, prompt changes in biotic interactions (Morin and Thuiller 2009) and will potentially alter ecosystem processes and services (S. J. Capon, S. Williams, L. Chambers and others, unpublished).

In addition to changes prompted by various types of environmental modification (Catford and others 2011), human-mediated introduction of non-indigenous (non-native, alien, exotic) species is altering community composition at an ever-increasing rate (Hulme and others 2009). Predictions suggest that, under climate change, non-indigenous species will

expand and reproduce in previously inhospitable areas (Walther and others 2009) and that higher temperatures will favor traits that are usually possessed by non-indigenous species, facilitating their dominance (Sandel and Dangremond 2012). Growth rates of invasive plant species may increase more than their indigenous counterparts from CO₂ enrichment (Dukes and others 2011). Combined with their greater plasticity (Davidson and others 2011) and broader environmental ranges (Canning-Clode and others 2011; Davey and others 2012), CO₂ enrichment may facilitate the dominance of invasive species. Dispersal will become more important as environmental conditions shift geographically thus giving a further advantage to non-indigenous species, which are likely to experience greater dispersal opportunities than indigenous species because of their close association with humans (Catford and others 2012). Unlike indigenous species that are adapted to historical conditions, non-indigenous species may also be pre-adapted (or adapt rapidly) to new environmental conditions (Catford and others 2012). Riparian ecosystems are among the most invaded types of ecosystem (Richardson and others 2007) and it is likely that they will continue to have a high non-indigenous component in the future.

Natural resource management, maintenance of ecosystem services and conservation of biodiversity require information about patterns of biodiversity and ecosystem processes and condition (Pressey and others 2007). The ability to predict the ecological character and function of future ecosystems is therefore crucial for environmental planning, like reserve design, and the development of effective mitigation and adaptation strategies (Morin and Thuiller 2009). Because, by definition, novel ecosystems have not previously existed, it is very difficult to predict their characteristics and few attempts have been made to do so. Controlled experiments cannot be carried out at appropriate spatial or temporal scales, so modeling approaches are required.

In this paper, we propose a qualitative approach for envisioning future riparian ecosystems. Based around four recommendations, we present the approach in the first part of the paper. We then use four case studies from contrasting environments to illustrate the approach and to determine:

Whether certain characteristics make some ecosystems more susceptible to climate-induced shifts in community structure than others; and
Which aspect of climate change seems to have the greatest effect on community structure and therefore should be a research priority.

Focusing on changes in community structure, we investigate likely consequences of climate change for tropical floodplains, temperate streams, high mountain streams and urban riparian zones. The paper centers on Australian riparian zones experiencing climate change, but we note that the approach can be applied to ecosystems in other biomes that are subject to environmental change. Although human adaptations to climate change can lead to novel ecosystems, we do not address these changes. Instead we concentrate on unintentional physical and biogeochemical changes that, although the result of human activities, are outside of direct and immediate human control and manipulation.

WAYS TO PREDICT NOVEL ECOSYSTEMS: LAYING OUT AN APPROACH

Recommendation 1: Use Process Models to Predict Characteristics of Future Ecosystems, but Integrate Their Predictions with Those from Other Models

We advocate the use of process (or mechanistic or causal) models, rather than correlative models, when envisioning characteristics of novel ecosystems. Process models are based on ecological mechanisms, dynamics and feedbacks; they consider the various factors that influence ecosystem characteristics and indicate how a change in one factor can lead to changes in others (Pearl 2009). Using forecasts about environmental change combined with current understanding of ecological relationships and processes, process models can be used to predict ecological responses. Because they are based on mechanistic understanding, such predictions are more general than those based purely on correlative relationships and are more likely to remain valid under novel climatic conditions (Koca and others 2006). However, like any predictive models, process models assume that current knowledge can predict future relationships (Hulme 2005). However, if relationships are non-linear and move to a level and type not witnessed before, the capacity to predict cause-effect relationships will diminish. Updating cause-effect relationships as new information becomes available is crucial for the efficacy of process models.

There are a number of forms that predictive models can take (Ferrier and Guisan 2006; Koca and others 2006; Morin and Thuiller 2009; Kearney and others 2010). To help counter deficiencies in individual modeling approaches, it is important

to develop several different types of models and compare their predictions (Morin and Thuiller 2009; Kearney and others 2010). Accordingly, a number of existing modeling approaches could be adapted to help predict novel ecosystems, for example, models based on responses of specific species (Morin and Thuiller 2009), vegetation types (Koca and others 2006) and communities (Ferrier and Guisan 2006).

Here we devise qualitative process models based on expert knowledge. A pre-requisite of quantitative models, qualitative models enable rapid appraisal of the type of ecological changes that can be expected under climate change. Qualitative models can be used to gauge the relative importance of different drivers, though the magnitude of changes cannot be accurately assessed.

Recommendation 2: Use Functional Groups, as well as Species, to Predict the Types of Communities that will Develop in the Future

We recommend that predictions based on functional groups be used to complement predictions about individual species and vegetation types. Functional groups are collections of taxa grouped according to shared traits, life history characteristics or ways they interact with the environment (Keith and others 2007). Classifications can be based on species' morphological, physiological, phenological, and behavioral characteristics. Functional traits affect growth, reproduction and survival of organisms (Violle and others 2007) and can indicate early responses to environmental change (Merritt and others 2010), including climate. In this article, we are specifically interested in shifts in community structure that relate to climate change so we concentrate on the biological form of animal and plant taxa and, when germane, use these descriptions in combination with the environmental preferences of the taxa (Table 1). However, for illustrative purposes, we occasionally refer to culturally significant and species that may be considered "key-stone" or "umbrella" species.

To date, most predictions about community composition under future climates have relied upon species-based forecasts (Hijmans and Graham 2006). Correlative species distribution models and mechanistic niche models can indicate the likely future distribution and abundance of individual species (Elith and others 2010), and these approaches have merit when interested in the fate of particular species (especially when used in combination; Morin and Thuiller 2009). However, the

Table 1. Details of the Functional Classification Scheme Used in the Paper.

Descriptors	Definition
<i>Response to climate change</i>	
Temperature	
Stenothermic	Organisms that can only function in a narrow range of temperatures
Eurythermic	Organisms that can function over a broad range of temperatures
Hydrology	
Aquatic	Organisms that live, grow and reproduce underwater
Semi-aquatic	Organisms that inhabit wet-dry ecotone
Terrestrial	Organisms that inhabit dry land. Includes organisms that live on saturated soil or where the water table is below soil surface
Fire	
Fire adapted	Organisms that are able to withstand fire through physiological adaptation (resistance or tolerance in plants) or behavioral responses (avoidance in animals)
Fire sensitive	Organisms that are killed by fire
Salinity	
Salt-tolerant	Organisms that can function in saline and brackish (and potentially freshwater) conditions
Salt-intolerant	Organisms that can only function in freshwater and are very sensitive to increases in salinity
Carbon dioxide	
CO ₂ sensitive	Organisms whose growth rate and physiological processes are sensitive to CO ₂ concentrations
CO ₂ insensitive	Organisms whose growth rate and physiological processes vary little with changes in CO ₂ concentrations
<i>Origin of biota</i>	
Indigenous	Species that are locally native to the region of interest
Non-indigenous	Species that are not locally native; includes alien/exotic/non-native species and species that are native to Australia but have not historically occurred in the region of interest
<i>Structural form of biota</i>	
Plants	
Trees	Perennial woody plants that usually have many secondary branches that are clear of the ground and are on a single main stem or trunk with strong apical dominance
Shrubs	A woody plant that branches below or near the ground into several main stems, so has no clear trunk. Includes scramblers (for example, <i>Rubus</i> species) and subshrubs (for example, <i>Erica</i> species)
Climbers	Plants that have trailing or scandent stems or runners. Includes vines
Forbs ¹	Herbaceous flowering plants that are not graminoids
Graminoids ¹	Graminoids are monocotyledonous plants with narrow leaves growing from the base. They include grasses, sedges, rushes.
C3	C3 graminoids use a C3 pathway to capture carbon from photosynthesis and produce a 3-carbon molecule; C3 plants are adapted to cool season establishment and growth in either wet or dry environments
C4	C4 graminoids use their additional C4 pathway to produce a 4-carbon molecule; C4 plants are better adapted to warm or hot seasonal conditions under moist or dry environments; compared to C3 plants, C4 plants have higher light requirements, higher productivity, lower moisture requirements and are more sensitive to frost
Algae	Eukaryotic, typically autotrophic, organisms that lack many of the distinct organs found in land plants (for example, roots, stems, leaves)
Animals	
Invertebrates	
Microinvertebrates	Organisms without a backbone that are generally less than 1–5 mm in size
Macroinvertebrates	Organisms without a backbone that are generally 5 mm or larger in size; macroinvertebrates are typically more tolerant of environmental fluctuations and are longer lived than microinvertebrates
Vertebrates	
Mammals	Air-breathing endothermic organisms characterized by the possession of hair, three middle ear bones and mammary glands that are functional in mothers with young

Table 1. continued

Descriptors	Definition
Birds	Air-breathing endothermic organisms that lay eggs, are feathered, winged and bipedal
Reptiles	Air-breathing, ectothermic tetrapods characterized by skin covered in scales and/or scutes
Amphibians	Air-breathing ectothermic tetrapods with eggs that are not surrounded by membranes
Fish	Gill-bearing aquatic craniate organisms that lack limbs with digits

¹With some exceptions (for example, *Bambusa* species), forbs and graminoids are collectively referred to as herbs; herbs lack woody stems.

large number of species (including those in Australia's biodiverse riparian zones) makes broad-scale application of these approaches untenable; there are insufficient data and resources to model the distributions of thousands of species. Plus, individual species respond differently in different places making it hard to generalize from one region to the next. Even in mechanistic niche models that incorporate species' ecophysiological requirements, community interactions cannot be accurately predicted. Although lack of information about community dynamics limits the ability of any method (including those based on functional groups) to accurately predict the composition of future biological communities (compare Ferrier and Guisan 2006), more general approaches may be less sensitive to this uncertainty. For instance, individual species from one functional group may buffer the response of others.

Use of functional groups overcomes some of the disadvantages of using a species-based approach (Neilson and others 2005). Based on traits rather than the identity of individual taxa, functional groups enable findings to be generalized and compared across ecosystems and biomes (Westoby 1998). Depending on the type of functional classification used, they enable implications of climate change for ecosystem structure and function to be more apparent (Violle and others 2007) and often can integrate information about constituent taxa.

The influence of history on community composition may be less important when considering functional groups as opposed to individual species. Variation in the order of species immigration results in diverse and often unpredictable community assemblages, but community assembly based on trait-based functional groups may be less stochastic and more deterministic (Fukami and others 2005; though evidence for this remains mixed: Trowbridge 2007). It should, however, be acknowledged that not all species will follow the trends of their group (Keith and others 2007), and it can be harder to evaluate model predictions when using groups of taxa (Neilson and others 2005).

Recommendation 3: Use of Analogue Systems to Help Envisage the Sorts of Ecosystems that Might Develop in the Future

Although novel ecosystems are—by definition—"new", it may be possible to use ecosystems with similar attributes (or those that have experienced similar conditions at some point in time) to help inform predictions. Flow regulation and diversion of water from rivers may result in similar effects as the reduction in precipitation associated with climate change. Similarly, urbanization and an increase in the proportion of impervious surfaces may be similar to an increase in extreme flow events: both result in a "flashy" hydrograph with increased river discharge over a short period of time. In this sense, information about ecological changes in regulated and urban rivers could be used to inform predictions about climate change effects in unregulated and rural rivers. As well as modified systems, ecosystems in different biogeographic regions may serve as suitable comparisons. For example, many lowland rivers in Australia's temperate south-east may become more like dryland rivers in arid and semi-arid Australia. At a broader level, these systems could even start to resemble those in southern states of the US, like Arizona and Nevada.

The use of functional groups will facilitate comparisons across biogeographic regions. Further, the world's biota is becoming increasingly similar (Stohlgren and others 2011) as the rate of species transfer and biological invasions continues to rise (Hulme and others 2009), so regional differences in biota are declining (Villéger and others 2011). Knowledge of similar ecosystems could be used to help inform the development of process-based models for predicting novel ecosystems, but care must be taken as differences may still be great.

Recommendation 4: Incorporate Information About Taxon Migration Rates, Dispersal Patterns and Genetic Adaptation

The majority of models that predict biological responses to climate change do not explicitly consider

species migration or dispersal (Neilson and others 2005; but refer to work on invasive species, for example, Elith and others 2010). However, it cannot be assumed that, just because a species can tolerate the environmental conditions of a site, it will occur there now or in the future. Whether based on individual species or functional groups, modeling approaches need to include information about migration and succession processes (Neilson and others 2005), dispersal pathways (including the role of humans as dispersal vectors) and proximity of source populations.

Similarly, the ability of a species or population to adapt to altered conditions must be considered. It is likely that species with higher phenotypic or genotypic plasticity will tolerate changes in climate better than species with low genetic diversity or plasticity. This is thought to be one reason why the abundance of invasive non-indigenous species will increase under climate change (Davidson and others 2011).

SCENARIOS OF CHANGE

Using the four recommendations presented above, we develop process models to examine the potential consequences of climate change in four riparian ecosystems in Australia. The patterns and consequences of climate change for riparian zones will vary according to local conditions. These conditions include not only the rate and magnitude of climate alterations but also how they interact with topography, land use, human legacies (for example, past land uses), flow regimes for water and sediment, and indigenous and non-indigenous species. We illustrate this complexity by examining expected changes for riparian zones in contrasting environmental settings and with different histories of human activities. The sites represent a broad range in environmental characteristics and thus have the potential to indicate general trends as well as regional differences. They are also ecosystems with which we are most familiar. We consider climate change impacts on temperature, precipitation, sea level rise and carbon dioxide concentrations. Addressing the aims of the paper, we use the models to assess whether some ecosystems are more vulnerable to change than others, and which aspect of climate change is likely to have the greatest effect on community structure. We first provide an overview of climate change impacts predicted in Australia.

CLIMATE CHANGE IMPACTS

As global climate change escalates, it is expected that average temperatures in Australia will rise by

0.6–1.5°C above 1990 temperatures by 2030 and 2.2–5°C by 2070 (Cleugh and others 2011). Rainfall projections are less certain than temperature projections, but most models suggest that rainfall will decline in southern Australia, particularly during winter (Davies 2010), and spring rainfall will markedly decline in southern and eastern Australia (Cleugh and others 2011). The magnitude of extreme rainfall events is expected to increase throughout the country (Cleugh and others 2011). In south-eastern Australia, reductions in snow depth and season length and an earlier timing of maximum snow depth are predicted (CSIRO and Bureau of Meteorology 2007). The El Niño-Southern Oscillation, a major driver of climate variability in eastern Australia, will become more extreme and droughts more severe (DECCW 2010). Changes in the seasonality and amount of precipitation will have important implications for stream flow and soil moisture. Warmer and drier conditions in southern Australia are likely to result in an increased fire-weather risk and a lengthening of the fire season (Lucas and others 2007). There is some uncertainty as to the magnitude of future sea level rise, but it is anticipated that sea level rise will increase the frequency of coastal flooding. For instance, coastal flooding events that used to occur once in every 100 years may occur more than once a year by 2100 (Cleugh and others 2011). CO₂ levels are expected to continue to rise until at least 2040 (Nakicenovic and others 2000), and further increases in CO₂ levels are likely to amplify long-term average warming (Pachauri and Reisinger 2007).

TROPICAL FLOODPLAINS IN NORTHERN AUSTRALIA

Coastal floodplain wetlands that flank macro-tidal river systems are conspicuous riparian habitats in northern Australia (Bayliss and Yeomans 1990). Having formed only 1,500–6,000 years ago, these seasonally inundated floodplains are recent landscape features yet they are highly productive and rich in biodiversity (Finlayson and others 2006). Internationally recognized for significant natural and cultural values they include, among others, the Ramsar and World Heritage listed wetlands of Kakadu National Park (Finlayson and others 2006). Environmental alterations caused by climate change will be large and complex in these tropical floodplain ecosystems.

The floodplains are still largely vegetated by indigenous species, but they are currently being modified by non-indigenous plants and animals and by altered

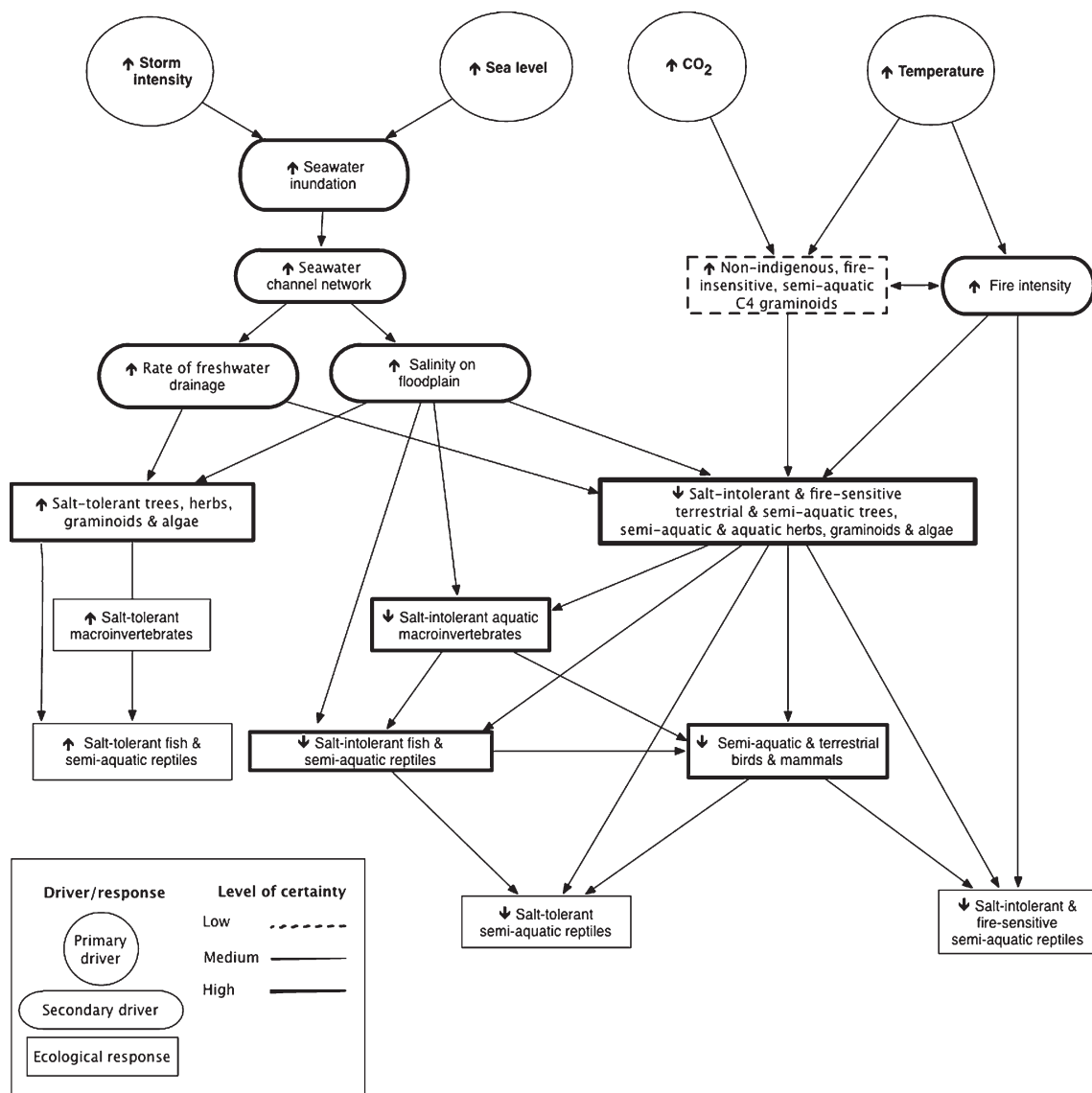


Figure 1. Conceptual model of ecological responses to projected changes in sea level, storm intensity, and carbon dioxide levels in tropical coastal floodplains in northern Australia.

fire regimes (Pusey and others 2011). They are also susceptible to rising sea levels (Bartolo and others 2008) because of their low elevation (most are <2 m above sea level). The landward margins of the floodplains are topographically constrained, so the floodplains cannot migrate inland as sea levels rise. Projections for sea level rise during the next century range from 0.4 to 1.0 m (Horton and others 2008). Although it is difficult to reliably quantify the extent of seawater intrusion in northern Australia due to a lack of high resolution elevation models, it is likely that more than half of the floodplain wetlands will be inundated with seawater over the next 50 years (Bartolo and others 2008) and nearly all within 300-400 years (Traill and others 2010).

The likely effects of seawater intrusion are based on previous experiences of seawater intrusion in the Northern Territory, on recent modeling of the potential impacts on key fauna and on recent research into the ecological role of tropical floodplains (Figure 1). Seawater intrusion has already occurred in some areas due to human activity, extreme weather events and the effects of non-indigenous water buffalo (*Bubalus bubalis*). These provide a valuable analogue for the likely effects of climate-induced changes. Elevated sea levels will alter floodplain hydrology and water quality. Seawater intrusion will dramatically change the pattern of floodplain inundation as it will be driven by tidal movement and storm surge rather than rain-

fall alone. Saline water makes floodplain soils more dispersive, which will in turn extend seawater channels, facilitate the ingress of seawater (Winn and others 2006) and increase the drainage of freshwater from floodplains (Petty and others 2007). Increased salinity can kill salt-intolerant vegetation and facilitate a transition to salt-tolerant trees, forbs and graminoids, such as mangroves. For example, the East Alligator River has already experienced tidal intrusion up to 4 km inland, resulting in a nine-fold increase in the area of saline mudflats and a loss of salt-intolerant semi-aquatic vegetation, including 64% of the original *Melaleuca* forest (Winn and others 2006). Seawater intrusion has also prompted upstream colonization by mangroves in the Wildman and South Alligator Rivers (Cobb and others 2007). The most dramatic example of seawater intrusion in northern Australia is on the Mary River. Since tidal creeks began extending into Mary River wetlands in the 1930s and 1940s, more than 17,000 ha of freshwater floodplain have been affected by seawater, which has resulted in vast areas of salt-intolerant vegetation being replaced by a saline swamp and a transition to salt-tolerant vegetation (Mulrennan and Woodroffe 1998).

The loss of salt-intolerant vegetation has serious consequences for floodplain fauna including semi-aquatic birds such as magpie geese (*Anseranas semipalmata*, Figure 1), which rely on freshwater vegetation for forage and nesting. Magpie geese, once widespread across Australia but now restricted to the north, have a population of less than 3 million (Delaney and others 2009). They are a tourist icon, a popular species for recreational hunting, an important food source for Aboriginal people and are ecologically important because of their abundance (Delaney and others 2009). Modeling has shown that a loss of just 5% of the wetland habitat currently available to magpie geese could reduce populations to just a few thousand individuals and possibly initiate an ecological bottleneck or “point-of-no-return” (Traill and others 2010). Other waterbirds, reptiles, such as the saltwater crocodile (*Crocodylus porosus*), and mammals that use the floodplains in the dry season will also be affected by reductions in the availability of suitable food and habitat (Figure 1; BMT WBM 2010). For other animals though, effects will be more direct: it will simply be impossible for some to persist in the saline water, for example, salt-intolerant fish and reptiles such as freshwater turtles.

Saline water and the loss of freshwater floodplain vegetation will likely alter the food supply for many species through a reduction in freshwater epiphytic

algae, which grows on plants and is a primary carbon source on these floodplains (Figure 1; Douglas and others 2005). Change in salinity and primary productivity may affect other aquatic habitats as many fish species feed, grow and reproduce on the floodplains and transport this energy to upstream riverine or downstream estuarine and coastal ecosystems (Jardine and others 2012). The floodplains are critical to the life history of many species including economically important fish species such as barramundi (*Lates calcarifer*).

Floodplains unaffected by seawater intrusion are also likely to be altered by direct climatic changes (Figure 1). Elevated CO₂ (Williams and Baruch 2000) and temperature (Hamilton 2010) favor non-indigenous, fire-tolerant semi-aquatic C4 graminoids (Williams and Baruch 2000) such as para grass (*Brachiaria mutica*), which could replace the diverse indigenous vegetation with a non-indigenous monoculture (Douglas and O'Connor 2003) and increase dry season fuel loads (Douglas and O'Connor 2004) and fire intensities. Increased temperatures are also expected to result in more frequent and intense dry season fires, which could further reduce the abundance of salt-intolerant semi-aquatic trees (for example, *Melaleuca* sp.) as well as fire-intolerant terrestrial trees in riparian vine forests. It is also highly likely that non-indigenous pigs (*Sus scrofa*), which disturb the soil, alter local hydrology and compete with indigenous fauna for plants and invertebrates, will concentrate in the remaining floodplain areas putting further pressure on these refugial habitats.

RIPARIAN ZONES IN TEMPERATE SOUTH-WESTERN AUSTRALIA

South-western Australia is a global biodiversity hotspot and the only one located on the Australian continent (Myers and others 2000). The Gondwanic origin of the biota, combined with a long period of geographic isolation, has resulted in distinctive riparian habitats and a high level of endemism in both freshwater and terrestrial species (Bunn and Davies 1990). Streams and rivers are characterized by low rates of primary production and aquatic food webs rely heavily on the input of riparian carbon (Davies 2010).

Riparian zones in this region are highly degraded as a result of flow regulation, intensive agriculture (Horwitz and others 2008) and uncontrolled livestock access (Bunn and others 1999). The clearing of indigenous vegetation commenced with European settlers in 1829 and escalated in the early part

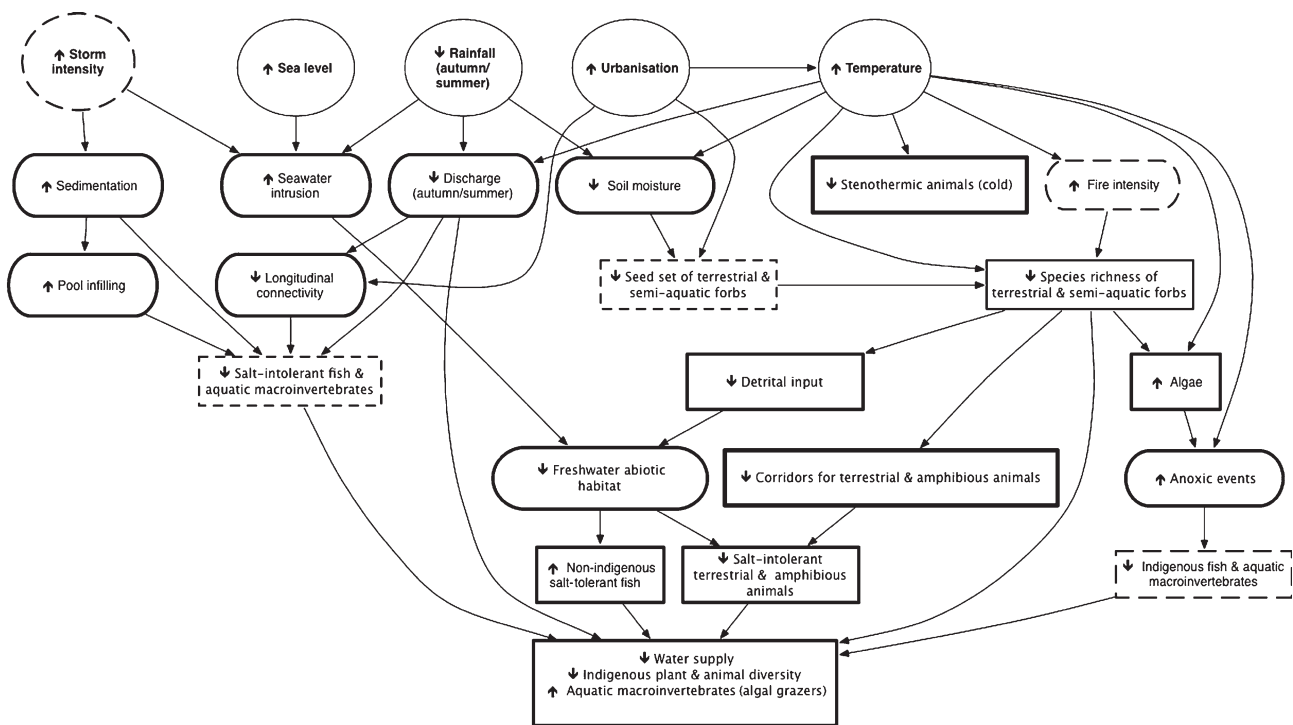


Figure 2. Conceptual model of ecological responses to projected changes in sea level, storm intensity, temperature and rainfall on riparian ecosystems in temperate south-western Australia. Based on evidence from Davies (2010), CSIRO and Bureau of Meteorology (2007) and Nakicenovic and others (2000). Legend as in Figure 1.

of the twentieth century (Bolton 1972) resulting in a fragmented distribution of remnant vegetation. Riparian restoration efforts have been patchy and success limited. Increasingly harsh climatic conditions (typically warming and drying) will interact with the already fragmented landscape of south-western Australia (Horwitz and others 2008) leading to further degradation and the creation of novel riparian ecosystems.

Many ecological processes in river and riparian habitats are regulated by the magnitude, frequency and seasonality of flows (Poff and others 1997). As a consequence, substantial and complex changes are expected in riparian areas from climate change (Figure 2). Altering the timing of rainfall will affect seed-set and the subsequent recruitment of riparian plants, particularly indigenous trees, which may in turn disrupt host-pollinator relationships (for example, a mismatch between insects emerging and plants flowering: Davies 2010). A reduction in the magnitude of winter flows will limit overbank flows and riparian inundation. Flow regulation in rivers in south-western Australia narrows the riparian zone and reduces overall plant species richness (Pettit and others 2001). Such effects will likely be compounded under climate change, though an increase in invasive non-indigenous species in this region may partially

compensate for declines in indigenous plant richness (O'Donnell and others 2012).

Drying and warming of the riparian zone will also lead to the removal of stenothermic animals and may indirectly facilitate the establishment of invasive animal species, which often tolerate a broader thermal range (in marine systems at least; Canning-Clode and others 2011). The predicted increase in the severity of fires will open the riparian canopy increasing light into the understorey, thus providing more suitable conditions for non-indigenous plant species (Davies 2010). In lower river reaches, sea level rise will increase the extent of floodplain inundation and will inhibit salt-intolerant species. Many river and riparian systems in south-western Australia have undergone secondary salinization as a consequence of overclearing (Horwitz and others 2008). The community structure of macroinvertebrates in these rivers has shifted from insect forms to a dominance of crustaceans, common in nearby still-water habitats (Bunn and Davies 1992). Increased sea levels and intrusion into lower river floodplains is expected to result in a similar response with a shift in community structure favoring crustaceans.

Overall, we foresee climate change leading to increased fragmentation, narrowing of riparian

zones and simplification (and homogenization) of the biota due to the loss of stenothermic species and increased abundance of non-indigenous flora that are dispersed widely by humans (Figure 2). In particular, an increase in non-indigenous plants in these novel ecosystems, particularly C4 graminoids, will reduce the current strong subsidy between the riparian zone and in-stream food webs (Bunn and others 1997). A more open canopy will encourage algal growth potentially leading to a shift from heterotrophy to autotrophy in streams. Increased autotrophy in association with low water levels is expected to increase the likelihood of anoxia. This could hasten the decline of indigenous species, especially fish and macroinvertebrates, and lead to an increase in more tolerant non-indigenous species.

Many riverine plant and animal species in south-western Australia are endemic with small range sizes and restricted geographic distributions (Bunn and Davies 1990). A result of range compression about 18,000 years ago, these endemic species have little genetic diversity (De Deckker 1986) and many are now restricted to national parks and nature reserves in the cool, wet south coast of south-western Australia. As conditions become warmer and drier, these species are not be able to move southward nor is it likely that they can genetically adapt to the changes.

RIPIARIAN ZONES IN THE HIGH COUNTRY

In south-eastern Australia, land over 1,000 m in elevation occurs as topographic islands with rounded tops and steep flanks, the largest and highest being the northern part of the Snowy Mountains. The high country is significant for its glacial landscapes, endemic plant and animal alpine species, and as the water source for economically important rivers such as the Snowy, Murray and Murrumbidgee. Although now largely reserved in national parks, the high country has a history of human use. Alluvial gold mining and timber harvesting have ceased, but tourism and hydro-electricity generation continues. Plant communities are mostly intact except where disturbed by roads and engineering structures, or by the 100-year legacy of cattle grazing, particularly in bogs and fens. Non-indigenous plant species are relatively few, with low cover (McDougall and others 2005), though some highly invasive species have established recently and are spreading rapidly (for example, *Hieracium aurantiacum*, Orange hawkweed, Williams and others 2008). Non-indigenous animals (for example, horses, deer and pigs) damage vegetation,

especially along stream edges and in wetlands (McDougall and Walsh 2002).

The riparian plant communities of the high country are few, small in area and are floristically and structurally distinct from each other. They form a discontinuous riparian zone, arranged in altitudinal sequence from short alpine herbfields (forbs and graminoids) above the tree-line, to bogs in the alpine and subalpine zones (typically a mix of semi-aquatic mosses, namely *Sphagnum cristatum*, forbs, graminoids and shrubs), then a fringe of medium-tall semi-aquatic and terrestrial shrubs at lower forested elevations (Costin 1954).

A prolonged drought (2001–2010) and the 2003 wildfires indicate some of the potential effects of a warmer, drier climate in the high country. Observations from this period thus serve as a suitable analogue for climate change. After a few years of reduced rainfall and higher temperatures, bogs and terrestrial herb communities will become drier (Good and others 2010) resulting in mortality and areal contraction and the development of bare patches (Figure 3). These bare patches may be colonized by regenerating terrestrial graminoids and shrubs, invaded by indigenous and non-indigenous species, or eroded by summer storms or frost-heave (McDougall and others 2005). Once dry, bogs are more susceptible to wildfires, further shifting the balance from semi-aquatic herbs to terrestrial plants better adapted to fire (McDougall 2007). Compounding this trend, the forbs and graminoids (including endemic species) dependent on snow patches may be replaced by other plants as the cover and persistence of snow declines (Green and Pickering 2009).

If the exposed patches of soils are eroded, the material is likely to accumulate in headwater streams, especially if perennial streams become intermittent because of reduced rainfall. Like the desiccated and burnt bogs, in-stream accumulations of sediment and organic materials may be colonized by non-indigenous, as well as indigenous, species (McDougall and others 2011). Most non-indigenous species are expected to be eurythermic generalists from lower altitudes that can move to higher elevations via wind dispersal, non-indigenous herbivores and humans (McDougall and others 2011). The variety of sites and the type of invasion pathways available suggest that species establishing in stream channels could include semi-aquatic herbs, shrubs and trees such as willow (*Salix* spp.), recognized as a serious environmental weed in Australia and one that would dramatically alter the vegetation structure and in-stream functioning. The combined effects of sedimentation and

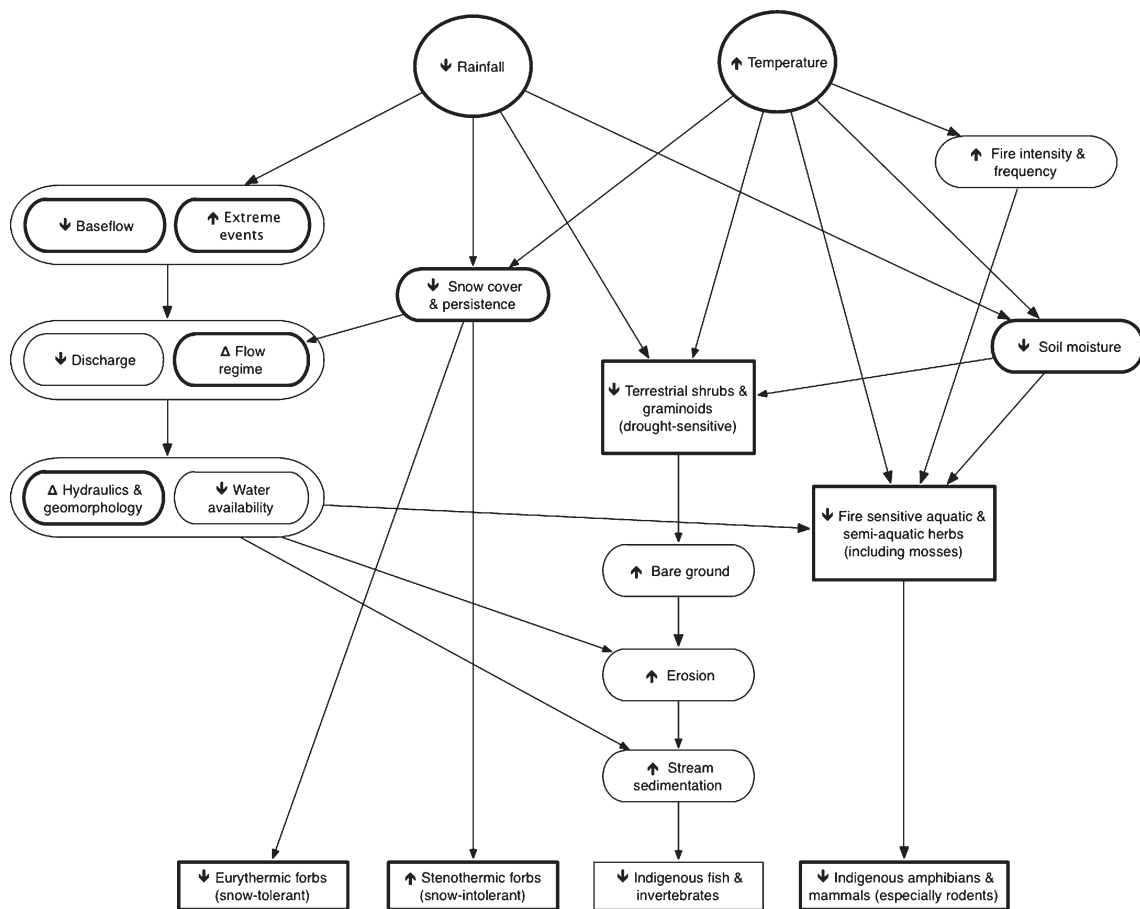


Figure 3. Conceptual model of ecological responses to projected changes in temperature and rainfall in high country riparian systems. Climate change projections for the high country include warmer temperatures, less annual rainfall (but with an increase in summer), less precipitation as snow, reduced streamflow, loss of spring snowmelt signal, increased drought intensity and increased fire intensity (DECCW 2010). The levels of uncertainty assume that no mitigation is in place. Legend as in Figure 1.

vegetation change on high country fauna are potentially dramatic: a shift from perennial to intermittent streams and loss of bogs will cause localized and possibly even total extinctions of endemic fish, amphibians, and small mammals, such as galaxids, the northern corroboree frog *Pseudophryne pengilleyi* and the broad-toothed rat *Mastacomys fuscus*; in-stream sedimentation is likely to change invertebrate abundance and composition (Figure 3; Harrison and others 2008).

Under climate change, these riparian systems are likely to comprise three elements with respect to vegetation: fragments of the current riparian vegetation; replacement of semi-aquatic moss and shrub communities by terrestrial graminoids and shrubs; and the presence of opportunistic semi-aquatic herbs, shrubs and possibly even trees in patches of in-stream sediment, analogous to those that develop on fine and coarse sediments of reg-

ulated rivers at lower altitudes. Although smaller in extent and more species-rich than contemporary systems, future riparian ecosystems are likely to become more variable in structure, less distinct and their altitudinal sequence more diffuse.

RIPARIAN ZONES IN URBAN MELBOURNE

Urban areas represent one of the most dramatic ways humans can alter ecosystems, especially riparian zones (Groffman and others 2003; Meyer and others 2005). Urbanization impacts on riparian zones may exceed those associated with climate change, but it is likely that ecosystem alterations are compounded when they occur simultaneously.

Over half of the world's human population lives in urban areas (United Nations 2010) and this proportion will increase in coming decades (Meyer and others 2005). Australia is one of the more

urbanized countries in the world, with about 90% of its population residing in cities (United Nations 2010). In south-eastern Australia, over four million people currently reside in Melbourne (Australian Bureau of Statistics 2011). Over the period 2001–2011, this city has seen the largest annual growth of all Australian capital cities with an average increase of over 1,300 people per week (Australian Bureau of Statistics 2011).

Founded in the 1830s, Melbourne experienced rapid growth following the discovery of gold in 1851. This led to wholesale ecosystem changes. River hydrology, hydraulics and geomorphology were altered through a number of processes, including: clearance of streamside vegetation, flattening of hills, draining of wetlands, diversion of streams and rivers (sometimes underground), dam construction and water extraction, conversion of retentive small upland drainage lines into a vast network of hydraulically efficient stormwater pipes, and an increase in impervious (non-porous) surfaces (Leahy and others 2005; Otto 2005). Although many measures were put in place to reduce flood risk, they actually increased it: removal of vegetation and an increase in hard surfaces accelerated runoff leading to increased flooding (Otto 2005; Lake 2008). Melbourne's metropolitan area is now almost entirely served by stormwater drains that bypass riparian zones and thus does not make use of the capacity of riparian zones to ameliorate diffuse runoff pollution (Walsh and others 2001). The hyperconnection of impervious surfaces throughout the catchment to the stream by pipes, the disconnection of rivers from floodplains and alteration of riparian vegetation has severely reduced the ecological quality of Melbourne's streams and rivers (Walsh and others 2001).

Most indigenous riparian plant communities in Melbourne have been eliminated, degraded or reduced to small remnants (though there are exceptions; Walsh and others 2007). Together with the loss of many wetlands and direct urban impacts, this has resulted in significant faunal changes (Leahy and others 2005). Substantial changes in riparian flora and fauna also occurred through planned (including willow *Salix* spp., blackberry *Rubus* spp., rabbit *Oryctolagus cuniculus* and fox *Vulpes vulpes*) and accidental introductions of non-indigenous species (Otto 2005). Collectively, these changes have resulted in novel riparian ecosystems that are expected to be further modified by climate change.

In many ways, potential effects of climate change on riparian systems have a number of similarities with effects of urbanization (Table 2; Figure 4): channel form can be altered through engineering

works or channel incision, which may limit over-bank flows and isolate floodplains for long periods; floodplains are fragmented in ways that impede dispersal of terrestrial species along the river corridor; the balance of erosion and sedimentation is outside historic experiences; non-indigenous species can dominate; efficiency of nutrient cycling on floodplains and in channels is low with urban riparian zones acting as sources rather than sinks for nitrate; populations of indigenous plants and animals fail to recruit sufficiently to maintain numbers across the range of age classes; and the diversity of ecological components and processes declines. With a growing human population size, it is likely that Melbourne's urban riparian zones will continue to experience high levels of disturbance and there will be increased demand for water interception and extraction, particularly in response to the drying effects of climate change (Seavy and others 2009). Although reductions in rainfall in pervious catchments will lead to disproportionately greater reductions in runoff, reductions in rainfall and runoff in impervious catchments will be of a similar proportion. As a consequence, by re-engineering stormwater drainage systems to artificially maintain more natural wetting and drying cycles of riparian soils, there is a greater opportunity to buffer some effects of climate change in urban areas (Walsh and others 2005).

Climate change and urbanization act together to amplify system decline. However, provided suitable remnant vegetation occurs and riparian soils experience wetting events, it is likely that urban riparian zones will continue to act as local micro-climate refugia from the warmer, higher density urban areas. As such, riparian ecosystems in urban Melbourne, novel as they may be, have the potential to act as local biodiversity hotspots and wildlife corridors and offer some relief from climate change if managed "creatively" (Seavy and others 2009).

DISCUSSION

The four scenarios highlight the complexity and potential magnitude of climate change impacts on riparian ecosystems in Australia. Each suggests an increase in non-indigenous species, especially C4 graminoids, and a reduction in indigenous diversity. Even if overall diversity changes little, loss of specialization through the decline of specialist species and range expansion of generalist species will lead to homogenization and loss of ecological distinctiveness, as observed elsewhere (Davey and others 2012). The models suggest that changes in precipitation (that is, stream discharge) are likely to

Table 2. Comparison of the Effects of Urbanization and Climate Change on Riparian Systems

Issue	Urbanization effect	Climate change effect
Disconnection of river from floodplain ecosystems (reduced lateral connectivity)	Reduced frequency of connection in urban environments through building over streams, elevated river banks and walls, incised river channels and construction of stormwater drains	Reduction in rainfall and runoff reduces frequency, duration and magnitude of overbank flow
Water quality	Degradation of water quality; for example, increased pollution and contaminant concentrations from reduced base flows and from rubbish and runoff from roads, industrial land and stormwater	Reduction in runoff and discharge reduces dilution effect
Hydrology changes—altered frequency, duration, seasonality, and magnitude of river flow	Increased proportion of impervious surfaces in a catchment increases the volume of surface runoff and the rate at which it is transferred to streams after a rainfall event (“flashy” hydrograph) Stormwater drains that bypass riparian zones increase the speed at which surface runoff reaches streams High runoff volumes over short periods of time (that is, from rainfall events) can incise urban stream channels which, together with impervious uplands, can lead to lower groundwater levels in riparian zone	Reduced rainfall and increased evaporation reduces magnitude and alters seasonality of runoff Increased frequency and severity of extreme weather events, including severe flooding Altered surface flows Increased frequency and magnitude of extreme rainfall events results in increased channel erosion and altered ecosystem processes
Drought	Land clearance and subsequent drying, reductions in soil carbon, increased surface albedo and compaction of soils may give rise to catchments that have increased surface runoff, but less groundwater recharge, reducing the capacity of groundwater to maintain streams during drought	More frequent and intense droughts
Species composition and habitat connectivity	Increased fragmentation of remnant vegetation reduces connectivity and impedes dispersal of terrestrial species along river corridors Increased proportion of exotic species Habitat degradation or simplification (for example, altered patterns of nutrient and energy cycling, altered production: respiration ratio)	Altered habitat connectivity, for example, faster drying of ponds due to warmer and drier summers reduces connectivity among wetland systems Prolonged dry periods inhibits biota requiring wetter conditions Smaller patch sizes leads to loss of species richness Disturbances, including climate, beyond an ecosystem’s natural range likely to lead to proliferation of disturbance-adapted invasive non-indigenous species
Warming	Loss of vegetation (shading and evapotranspiration) and heat storage capacity of concrete/brick (heat island effect) leads to warmer local temperatures, including in-stream	Increased air and surface water temperatures

Table 2. continued

Issue	Urbanization effect	Climate change effect
Phenology and distribution	Urbanization can facilitate an increase in the distribution and abundance of disturbance-tolerant species Heat island effect can influence phenology, typically by advancing spring events (Lu and others 2006)	Warmer and drier conditions, together with altered rainfall seasonality, influences reproductive timing and species distributions – the direction of the effect depends on the species (Chambers and others 2005; Pachauri and Reisinger 2007)

Information sourced from: Groffman and others (2003); Walsh and others (2005); Lake (2008); Seavy and others (2009); Davies (2010); Verdonschot and others 2010; also see Figure 4.

have the largest direct influence on riparian ecosystems overall, with the exception of coastal floodplains that will be affected by sea level rise. We suggest that improving predictions about future rainfall patterns and rainfall-discharge relationships is a key research priority for predicting the magnitude of ecological change in riparian zones. Currently, predictions about rainfall in Australia are generally less certain than temperature projections (Cleugh and others 2011). For coastal floodplains, improved digital elevation models are needed to underpin hydrodynamic models so that more accurate predictions can be made about the extent of seawater intrusion.

Changes in flow and increases in temperature were predicted to affect all four ecosystems, but community structures were not predicted to change in the same way or to the same extent. Because they are geographically restricted, riparian ecosystems in the high country and in south-western Australia will be especially susceptible to species extinctions from increases in temperature. Changes in these ecosystems will likely be compounded by their geographic isolation and high levels of endemism as well: without dispersal of similar taxa from similar types of ecosystems and with limited capacity for genetic adaptation, the loss of endemic species will likely herald a marked shift in community structure. In contrast, the recent age of tropical floodplains and the highly dynamic hydrology means that there are few endemic species and much of the fauna undertakes seasonal migration and is highly adapted to dispersal. However, their uniformly low elevation means that massive losses of freshwater habitat will occur rapidly once sea levels exceed a certain threshold. Although human-mediated dispersal of non-indigenous species may partially compensate for loss of indigenous species in the high country and south-western Australia when focusing on total

species richness, it is likely that the “new arrivals” will be functionally different. In contrast to the other ecosystems, riparian zones in Melbourne have already experienced a high degree of modification through urbanization, so changes resulting from climate change may be relatively negligible.

Although riparian zones, as an ecosystem type, will persist under climate change, we expect that their structure, processes, and ecosystem services will change, at least in part. For instance, fragmentation in southern temperate ecosystems will reduce the role of riparian zones as dispersal corridors, and loss of freshwater wetlands in northern Australia will reduce recreational and economic opportunities associated with hunting and fishing. These changes create complex challenges for management especially if fundamental ecosystem properties vary significantly among the types of novel riparian zones. Anticipating the type of changes likely to occur in the future is essential for the efficacy of long-term environmental management and planning. Knowledge of the key factors that shape ecosystem characteristics—and the extent to which those factors will change in the future—will be instructive in predicting the properties of emerging ecosystems.

VALUE AND EXTENSION OF APPROACH

Despite encompassing considerable uncertainty (for example, nature of climate change impacts and ecological responses to these impacts; Hulme 2005; Koca and others 2006), our predictions illustrate that altering several key abiotic factors may lead to the development of a range of novel ecosystems. By using process models and functional groups, we were able to envisage the potential implications of climate change on the abiotic characteristics and community structure of these riparian ecosystems. Considering the dispersal and genetic constraints of

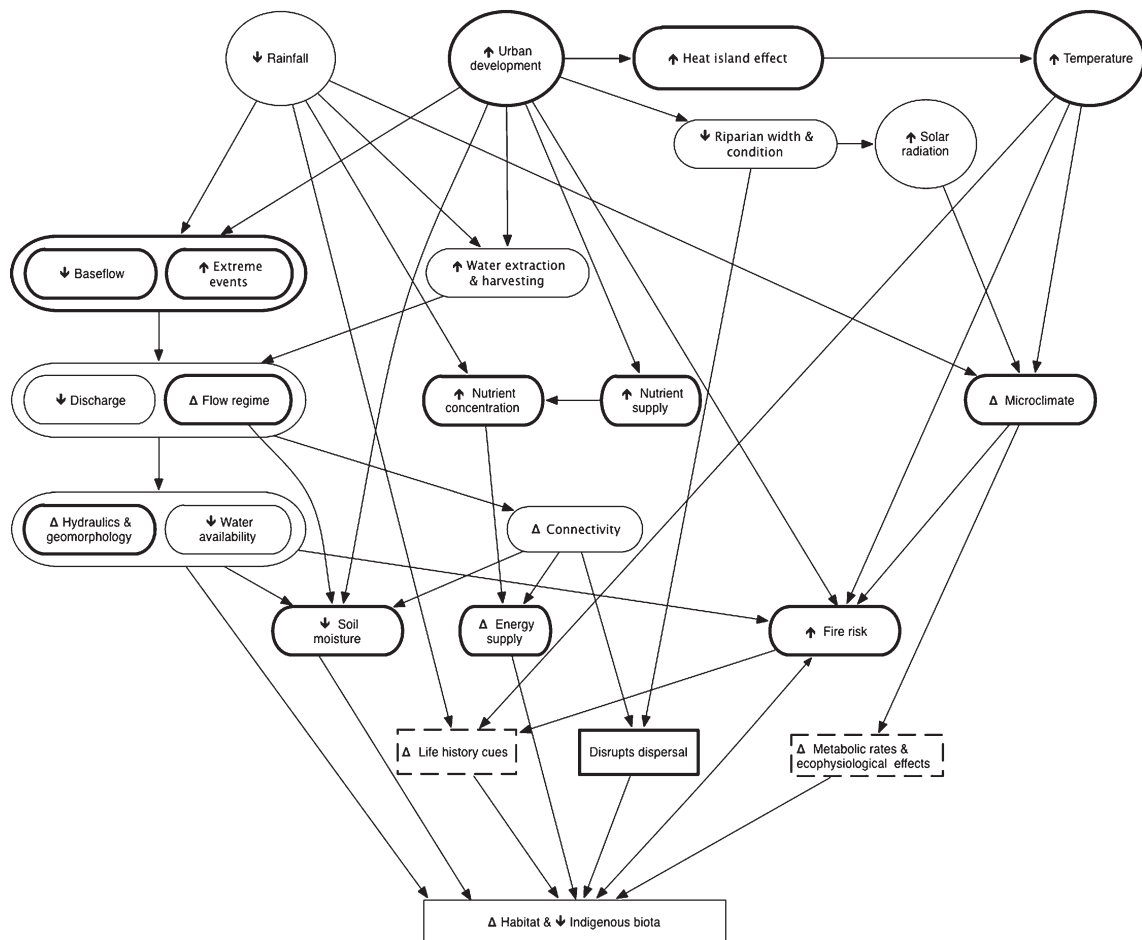


Figure 4. Conceptual model of ecological responses to projected changes in temperature and rainfall in urban (Melbourne) riparian systems. Climate change projections for Melbourne include warmer temperatures (particularly in summer), decreased annual rainfall (with the strongest signal in winter and spring), reduced streamflow, decreased relative humidity, and increased potential evaporation and solar radiation (CSIRO and Bureau of Meteorology 2007). The levels of uncertainty assume that no additional mitigation strategies are used, that is, system management follows the *status quo*. Legend as in Figure 1.

taxa was fundamental to this goal. Comparison with systems that have similar conditions or have experienced similar changes enabled us to assess the likelihood of our predictions. Such comparisons will become more important if quantitative predictions are desired.

To gauge the magnitude of predicted changes and the effectiveness of different management approaches, the models presented here could be further refined by including quantitative relationships. This would facilitate the development of quantitative predictions. Based on analyses of similar issues (Murray and others 2012; Rumpff and others 2011), Bayesian belief networks appear to be particularly suitable for including both qualitative and quantitative understanding (Figures 1, 2, 3, 4). Bayesian networks are a type of process

model that are increasingly being used to predict ecological responses to environmental change and management actions (Rumpff and others 2011). They take the form of flow charts where the relationships among, and values of, factors are specified. They can include uncertainty about both the understanding and variability of ecosystem responses, which is instructive when making management decisions (McCann and others 2006). Data from previous studies can be used to parameterize the models, as can information elicited from experts. By manipulating the value of variables included in the models (for example, altering the magnitude of climate change impacts or altering the adaptation strategies used), the implications of a number of different scenarios on ecosystem structure and function can be rapidly assessed. The

models can be updated as more information becomes available and understanding increases, and the way they operate can be easily communicated to non-experts (McCann and others 2006). These attributes make Bayesian networks particularly attractive for use in adaptive management (Rumpff and others 2011), which would be a suitable approach for climate change adaptation.

Most conservation activities have focused on conserving particular suites of species in particular locations (Pressey and others 2007; Hobbs and others 2009). Such a goal, however, may be unrealistic as ecosystems and their species assemblages change. Instead, it may be more pragmatic to focus on maximizing genetic, species and functional diversity, maintaining the biogeochemical configuration of a system (Seastedt and others 2008) or increasing habitat complexity. The ability to accurately predict the characteristics of future ecosystems is crucial for setting realistic management objectives and represents an exciting area of research.

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