

Facilitating adaptation of biodiversity to climate change: a conceptual framework applied to the world's largest Mediterranean-climate woodland

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Abstract The importance of ecological management for reducing the vulnerability of biodiversity to climate change is increasingly recognized, yet frameworks to facilitate a structured approach to climate adaptation management are lacking. We developed a conceptual framework that can guide identification of climate change impacts and adaptive management options in a given region or biome. The framework focuses on potential points of early climate change impact, and organizes these along two main

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axes. First, it recognizes that climate change can act at a range of ecological scales. Secondly, it emphasizes that outcomes are dependent on two potentially interacting and countervailing forces: (1) changes to environmental parameters and ecological processes brought about by climate change, and (2) responses of component systems as determined by attributes of resistance and resilience. Through this structure, the framework draws together a broad range of ecological concepts, with a novel emphasis on attributes of resistance and resilience that can temper the response of species, ecosystems and landscapes to climate change. We applied the framework to the world's largest remaining Mediterranean-climate woodland, the 'Great Western Woodlands' of south-western Australia. In this relatively intact region, maintaining inherent resistance and resilience by preventing anthropogenic degradation is of highest priority and lowest risk. Limited, higher risk options such as fire management, protection of refugia and translocation of adaptive genes may be justifiable under more extreme change, hence our capacity to predict the extent of change strongly impinges on such management decisions. These conclusions may contrast with similar analyses in degraded landscapes, where natural integrity is already compromised, and existing investment in restoration may facilitate experimentation with higher risk options.

1 Introduction

Climate change associated with the enhanced greenhouse effect is one of the greatest incipient threats to the Earth's social and ecological systems (Fischlin et al. 2007; Parry et al. 2007). Irrespective of mitigation efforts, past emissions will contribute to unavoidable climate change for the foreseeable future (Archer 2005; Fischlin et al. 2007; Dunlop and Brown 2008). Indeed, changes in the phenology, distribution and abundance of species and a host of ecosystem level responses to climate change have already been observed and are consistent with the directions expected under global warming (e.g. Parmesan 2005; Steffen et al. 2009).

Climate change science is increasingly recognizing the importance of actions conservation managers can take to reduce the vulnerability of natural systems to climate change (Heller and Zavaleta 2009; Lawler et al. 2010; Hagerman et al. 2010). Earlier studies have identified the importance of scale (Dunlop and Brown 2008) and uncertainty (Lawler et al. 2010; Hagerman et al. 2010) in evaluation of climate change impacts or adaptation options. However, despite many recommendations for biodiversity management responses in the scientific literature, broader conceptual

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Fig. 1 Long-unburnt *Eucalyptus salmonophloia* (salmon gum) woodlands of the Great Western Woodlands. Chenopod shrubs dominate the understorey at this site



frameworks to facilitate a systematic approach to identification and evaluation of on-ground management responses are lacking (Hannah et al. 2002; Williams et al. 2008; Heller and Zavaleta 2009). Heller and Zavaleta (2009) emphasize that such frameworks, in combination with well-documented case studies, are needed to organize the current ‘sea of adaptation ideas’ into a structure to guide adaptation planning.

We developed a conceptual framework for identifying and evaluating climate change impacts and adaptive management options in target biomes or regions. Our goal was to develop and apply a framework that facilitates inference from existing knowledge, reflecting the reality faced by most land managers.

To illustrate the concepts underlying our framework, we applied it to the ‘Great Western Woodlands’ of south-western Australia (GWW, Figs. 1, 2), arguably the largest and most intact area of Mediterranean-climate woodland remaining on Earth (Judd et al. 2008; Underwood et al. 2009). In mosaic with mallee and shrubland, these eucalypt-dominated woodlands cover some 160,000 km² (Watson et al. 2008), greater in area than England. In contrast with other Mediterranean-climate woodlands (Underwood et al. 2009), the region has escaped widespread livestock grazing and clearing for agriculture due to historical circumstances, low and variable rainfall, and lack of accessible groundwater (Yates et al. 2000a; Judd et al. 2008; Watson et al. 2008). The GWW thus provide an ideal model for assessing how naturally functioning, relatively intact ecosystems can adapt to climate change and offer a unique opportunity for developing management approaches that will promote the conservation and adaptation of an important Mediterranean-climate ecosystem. The GWW also provide a stark contrast with the adjacent ecologically similar, but extensively cleared landscapes of the Western Australian wheatbelt (Fig. 2).

2 Methods

Our analysis was undertaken in association with a 3-day workshop involving >40 biological scientists and managers with known experience in the GWW. With climate change expected to occur rapidly over the coming decades, established goals of conservation management need to be reassessed with particular regard to the balance

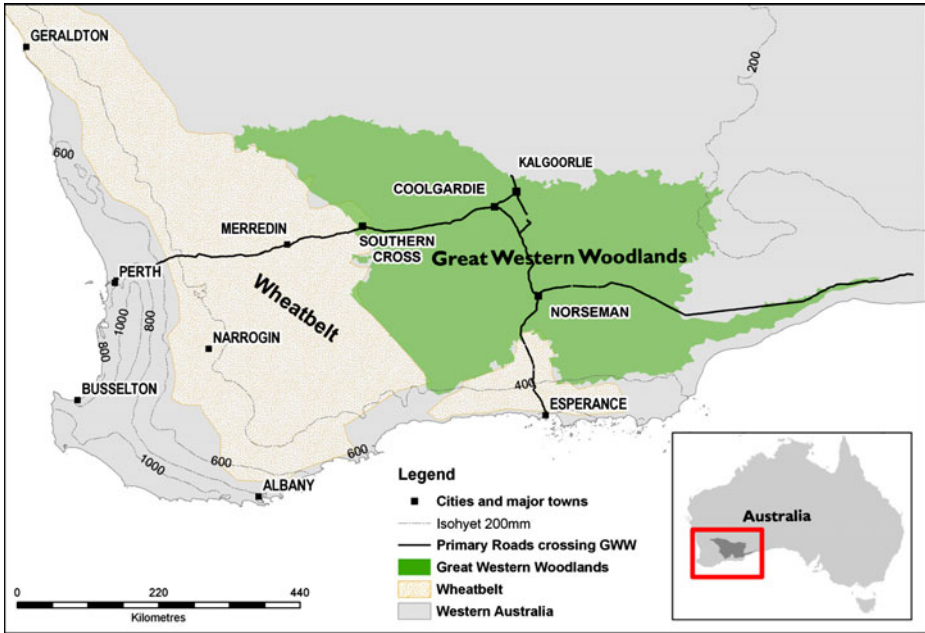


Fig. 2 Area referred to as the Great Western Woodlands (based on Judd et al. 2008). Approximately 56% of the 160,000 km² region supports temperate eucalypt woodland, in mosaic with shrubland, mallee and other vegetation. The adjacent WA wheatbelt is comparable in this regard but 93% has been cleared

between resisting and facilitating change (Dunlop and Brown 2008; Heller and Zavaleta 2009). To develop and apply our framework, we identified three qualitative goals that permit flexibility in this balance: (1) to optimize ecological function, in particular the capture of limiting resources, while maintaining the evolutionary potential of the indigenous biota; (2) to maximize the probability of persistence of species indigenous to the region; and (3), given the diverse functional roles associated with structural dominants, to maintain key characteristics of vegetation structure. The relative emphasis given to each of these goals was expected to vary depending on the extent of climate change.

To develop the framework, we drew on local and general ecological knowledge to characterize likely key points of early climate change impact in the GWW and in ecological systems more broadly; and to identify attributes of these systems that drive their response. This was achieved through iterative consideration (pre-, during and post-workshop) of the following questions at general and local (GWW) levels: (1) What are the key ecological processes that support target ecosystems, and how are these likely to be impacted by climate change? (2) What attributes of the target systems dictate their response to altered environments and processes? Our emphasis was on biophysical change rather than social dimensions of change (see Dunlop and Brown 2008; Richardson et al. 2009).

Errors in representing real climate systems in global climate models and uncertainty about future greenhouse gas emissions contribute to high levels of uncertainty

in future climate projections worldwide. Consequently, realistic climate adaptation management must occur in an uncertain environment (Lawler et al. 2010; Richardson et al. 2009; Hagerman et al. 2010). Thus, to explore climate change impacts in the GWW using the developing framework, we considered the range of regional climate projections published by Australia's leading climate science organization (CSIRO 2007), derived from ensembles of global climate models using low to high greenhouse gas emission scenarios. These suggest an uncertain future to 2070 in the GWW of warming in all seasons (+2° to +5°C) and probable drying (+10% to –40% of current mean annual rainfall). Predictions for change in summer rainfall are the most variable (+40% to –60%) although with current mean summer rainfall ranging from 50–70 mm, this amounts to relatively small absolute changes. Modelling of biotic environments (undertaken using 2030–2070 climate scenarios at national and regional scales after our workshop; Fig. 3; Hilbert and Fletcher 2010) re-inforces this uncertainty, suggesting shifts in the GWW ecological environments by 2070 could vary from minimal to near complete loss under standard low to high warming scenarios.

From the results of the above analysis, workshop participants derived a suite of potential management interventions that might address identified strengths and vulnerabilities in the GWW. To evaluate these with regard to practical utility and uncertainty (Heller and Zavaleta 2009; Lawler et al. 2010), 14 participants subsequently scored potential adaptation options on a scale of 1–10 for each of (1) perceived risk (defined as dependence on the nature and extent of climate change and the likelihood of negative impacts), (2) perceived feasibility (physical difficulty and cost of effective implementation, excluding income forgone), and (3) perceived likely benefits of success (for each goal defined above).

3 A 'change-resilience' framework for addressing climate change

The framework we developed (Fig. 4) focuses on identifying critical points of early climate change impact as the most important potential points for management intervention. These are organized along two main axes. First, the framework recognizes that climate change can act at a range of ecological scales, from individuals and species to ecosystems and landscapes. Secondly, it emphasizes that outcomes of climate change are dependent on two potentially interacting and countervailing forces operating at and among all scales: (1) the effects of altered climate on environmental conditions and ecological processes, and (2) attributes of individuals, populations, species, ecosystems and landscapes that govern their responses to these environmental changes (Fig. 4).

The former (altered conditions and processes) include direct effects of greenhouse gas emissions and climate change on temperature, moisture, light and CO₂ regimes. Beyond these direct effects, they include cascading impacts on processes such as photosynthesis and evapotranspiration at the individual level, demographic processes at population or species scales, biogeochemical cycling and biotic interactions at ecosystem scales, and hydrology and fire regimes at landscape scales (Fig. 4). The latter (attributes of response) can be represented by the overarching concepts of ecological resistance (capacity to maintain integrity under stress) and resilience (capacity to re-establish structure and function after disturbance), sometimes collectively termed

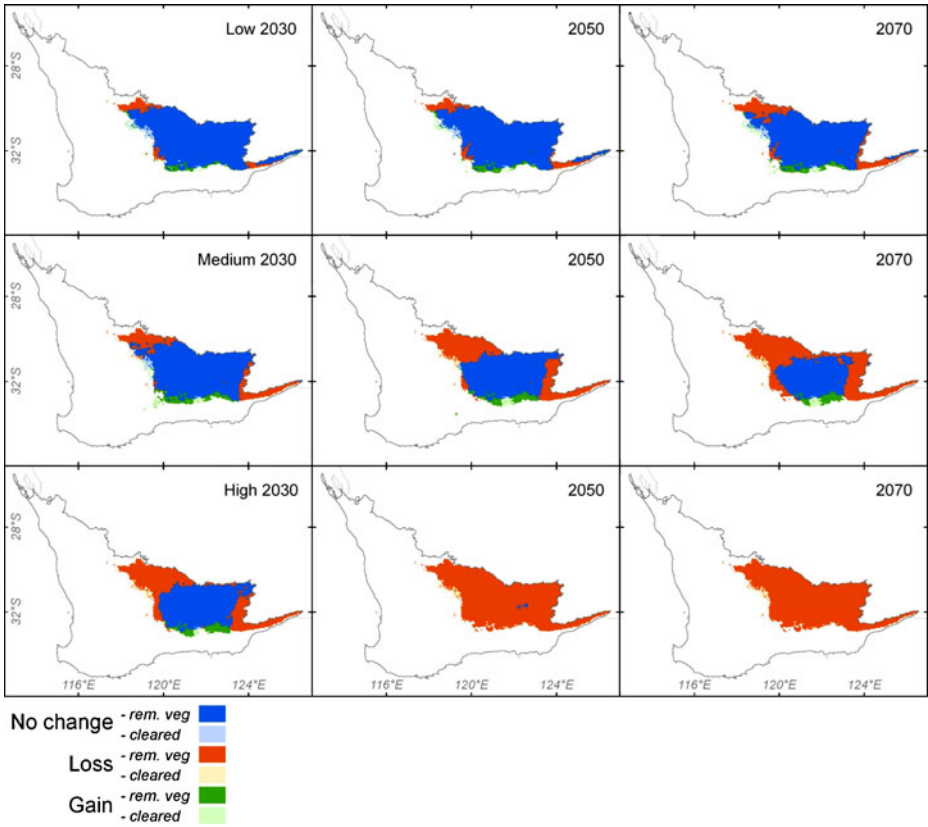


Fig. 3 Predicted shifts in the climate envelope for the Coolgardie (GWW) bioregion under 2070 climate scenarios. Produced using the bioclimatic modelling software MaxEnt (V 3.2.2., Phillips et al. 2006) by (1) modelling the climate envelope for the Coolgardie bioregion (which has the same spatial extent as the GWW), then (2) projecting its potential distribution in south-western Australia (delimited by grey boundaries) for historical (1961–1990) and future climates (2030, 2050, 2070) under three climate change severity scenarios (low, medium, high, see Yates et al. 2010 for detail of scenarios). Models used historical averages (1961–1990) for six biologically important climate variables (mean temperature of the wettest quarter, mean maximum temperature of the warmest quarter, annual precipitation, precipitation seasonality, precipitation of the warmest quarter and evapotranspiration), at 0.025° resolution. Step 1 used fivefold cross-validation to estimate errors around fitted functions and predictive performance on held out distribution data. The model had good predictive ability (AUC = 0.831); precipitation seasonality and annual precipitation made the largest contributions. Modeled results were imported into ArcGIS v.9 (ESRI, Redlands, CA, USA), where the logistic suitability values (0–1) from MaxEnt were converted to presence–absence grids (1/0) using the threshold that maximized training sensitivity plus specificity under current climate (Liu et al. 2005). Predicted distributions for the climate change scenarios were intersected with the projected historical distribution to examine patterns of range loss and gain in the biome

‘resilience’ (Walker et al. 2004). Hence, we refer to the framework as the *change-resilience* framework.

Ecological resistance and resilience to climate change are mediated by a suite of disparate attributes at a range of scales, as identified in Fig. 4. Responses of individuals are dependent on attributes such as physiological tolerance to temperature

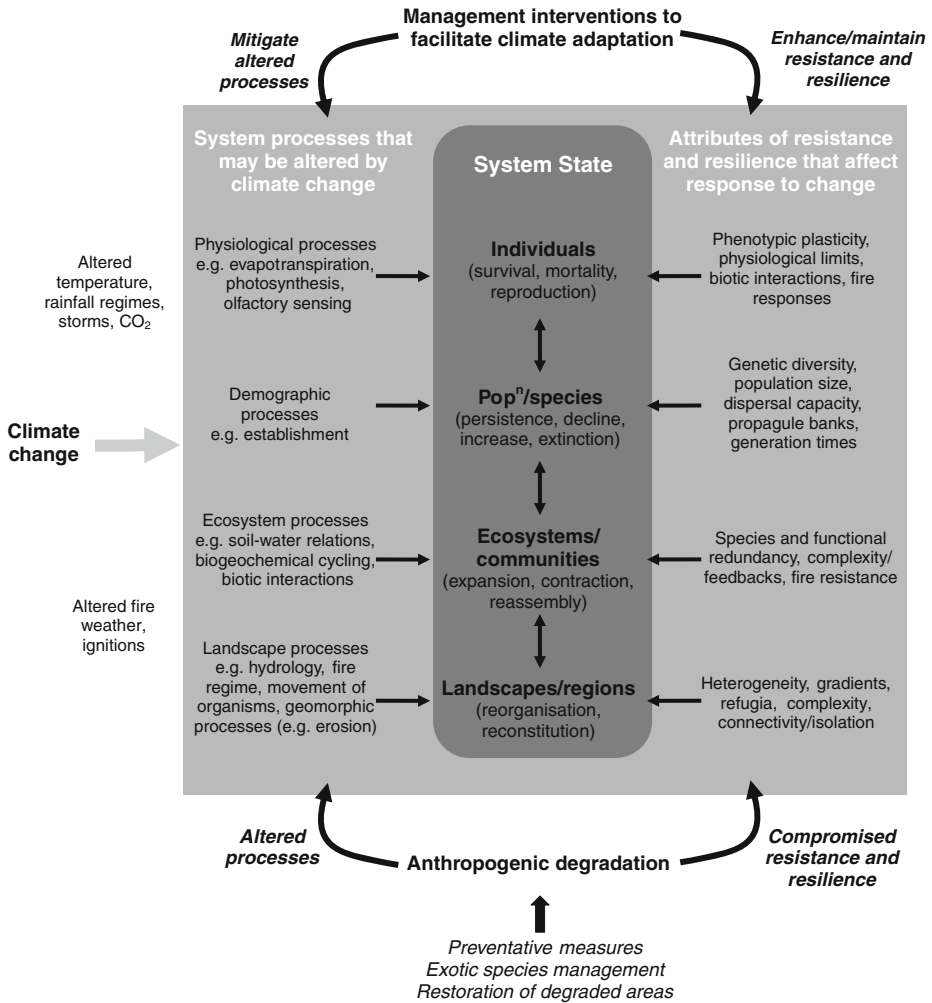


Fig. 4 Change-resilience framework for appraising climate change impacts and adaptation interventions in a given biome or region. Any such system comprises interacting elements at different levels of organisation, from individuals through populations and species to ecosystems and landscapes. Climate change may shift the system’s state through its effects on a number of potentially system-changing processes (*left*); these are ranked alongside the organisation level at which they principally act. Countervailing such forces, resistance and resilience to change act through other attributes (*right*); again, these principally act at different scales. Climate change interventions (*top*) may target either mitigation of the forces that act to change the system, or enhancement of the processes that confer resistance and resilience. Similarly, anthropogenic degradation (*bottom*) may act principally by altering system-changing processes or by compromising processes that confer resilience and resistance. Note that many of the processes in the framework interact in complex ways and may act at multiple levels in the system; for simplicity, these interactions are not shown

extremes and drought, CO₂ and fire responses, and phenotypic plasticity. At the species level, genetic diversity in these characteristics, population size, capacity to recolonise through dispersal and the availability of propagule banks (Grubb and Hopkins 1986) contribute to persistence or recovery of populations or species even if

loss of individuals occurs (Fig. 4). At the ecosystem and landscape scales, resilience is mediated through attributes such as the availability of replacement species capable of maintaining or restoring ecological functions (diversity and redundancy), availability of alternative environments (heterogeneity), potential for negative feedbacks that dampen the impacts of change (ecosystem complexity), and capacity for movement of organisms between suitable environments (connectivity) (Fig. 4, Hobbs and Cramer 2003; Soulé et al. 2004; Walker et al. 2004; Dunlop and Brown 2008).

Importantly, biological outcomes of environmental change at different scales interact. We propose that high resistance and resilience of individual organisms and species confers resilience at higher (ecosystem/landscape) scales; conversely lack of resistance and resilience at lower (individual/species) scales requires change ('adaptation', e.g. through altered species composition) if resilience at higher scales is to be maintained. Hence, we argue that adaptability is a special case of resilience whereby low resilience at one scale results in adaptive change at that scale to permit maintenance (resilience) of higher-order functions (cf. Walker et al. 2004). Examples include high genetic diversity that permits selection of drought tolerant individuals and hence adaptation of populations and species to declining rainfall despite mortality of more susceptible individuals; and species extinctions followed by functional replacement by more tolerant species, leading to the assembly of new, better-adapted communities. This hierarchical view of resistance, resilience and adaptation contributes a useful perspective towards achieving a management balance between resisting and adapting to change (Heller and Zavaleta 2009).

The change-resilience framework offers a starting point for exploring potential adaptation options in a particular region, structured on the basis of scale, driving ecological processes and key response attributes. Our diagram (Fig. 4) provides a generic view, and can be tailored to emphasize the most significant elements of specific regions or biomes, as we illustrate in our GWW example (Fig. 5). Once key potential impacts and response attributes have been determined, potential adaptation options that target these can be more easily identified, including interventions either to mitigate predicted or observed changes to key ecological processes, or to enhance attributes identified as effective for conferring resistance and resilience. While targeted climate adaptation management aims to have a positive influence on outcomes for biodiversity, other human activities can result in degradation along these same paths, i.e. by exacerbating climate-driven changes or by compromising resistance and resilience. Hence the framework indicates that in landscapes influenced by human intervention, measures to restore or prevent this degradation are also important options for facilitating climate adaptation (Figs. 4, 5).

4 Mediterranean-climate ecosystems and the Great Western Woodlands

The five Mediterranean-climate regions of the world, including south-western Australia, are globally significant biodiversity hotspots (Myers et al. 2000). Collectively, these regions occupy just over 2% of the world's land area but support *c.* 20% of the global vascular plant flora. However, they are second only to temperate grasslands in the proportion of their area that has been converted for human land use (Cowling et al. 1996), with less than 3% of Mediterranean-climate woodlands formally protected worldwide (Underwood et al. 2009). Of all of the Mediterranean-

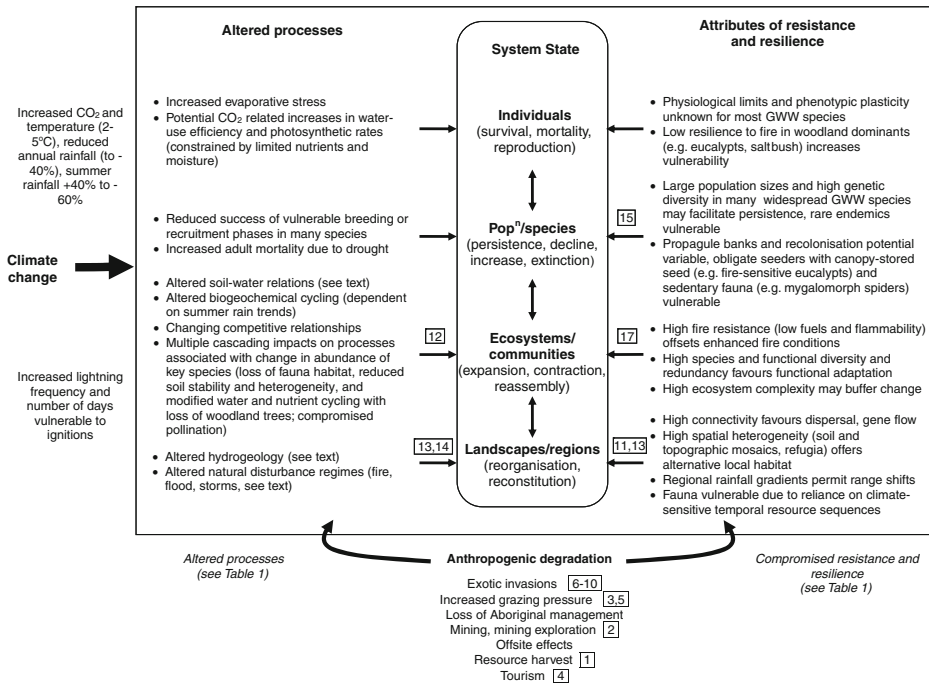


Fig. 5 Annotated change-resilience framework illustrating application to the Great Western Woodlands. *Boxed numbers* refer to adaptation management opportunities (Fig. 7). See text for further detail

climate regions, Klausmeyer and Shaw (2009) predict that the Mediterranean-climate zone of south-western Australia is most vulnerable to contraction under climate change, emphasizing the significance of the GWW as a priority region for investment in climate-adaptation strategies.

Few ecological studies have been undertaken specifically in the GWW (Judd et al. 2008), hence we draw on comparisons with related eucalypt woodlands of the adjacent Western Australian wheatbelt (Fig. 2) and other Mediterranean-climate woodlands to augment our understanding of ecological processes underpinning patterns of biodiversity in the GWW. Mediterranean-climate regions are characterised by mild, rainy winters and hot, dry summers. In the GWW, mean maximum temperatures for January range from c. 29–35°C, and mean July minima range from 4–7°C. Mean annual rainfall ranges from c. 400 mm in the south-west to 200 mm in the north-east, with the strong winter dominance characteristic of the Mediterranean climate declining to the north-east (Bureau of Meteorology 2008, Fig. 2). Rainfall is highly variable, and recent rainfall reconstructions in the southern GWW identified a regular rainfall periodicity, with alternating 20–30 year below-average and 15-year above-average rainfall periods over the last 350 years (Cullen and Grierson 2009).

Woodlands of the GWW share several features with other Mediterranean-climate woodlands, including dominance by evergreen trees, the importance of disturbance (fire, floods, drought and windstorms) for shaping vegetation patterns (Yates et al. 1994), and the presence of woodlands in a mosaic with shrublands that reflects strong

topographic and/or edaphic control of community dominance and structure (Beard 1990). In the GWW, shrublands typically occur on sandplains, while woodlands predominate on heavier soils in lower parts of the very subdued landscape, with dominant eucalypts varying according to more subtle soil and topographic mosaics (Dirnböck et al. 2002). In addition, the strong floristic break between Mediterranean- and arid-climate ecosystems apparent in California, Chile and the Mediterranean Basin, is paralleled at the northern boundary of the GWW by an abrupt change from eucalypt to *Acacia aneura* Benth. (mulga) woodlands (the ‘Menzies Line’, potentially determined by climatic parameters, Beard 1990). Eucalypts in Australian woodlands have similar water-use efficiencies to oaks in Mediterranean-climate woodlands of the Northern Hemisphere, although they use different mechanisms to conserve water. Eucalypts typically have amphistomatal leaves with vertical orientation and low conductance, while oaks have hypostomatous leaves with relatively high photosynthetic capacity and strong stomatal control during drought (P. Rundel unpublished data).

Two features of the GWW distinguish them from other Mediterranean-climate woodlands. First, Mediterranean-climate regions that receive less than 300 mm annual rainfall tend to be dominated by shrublands (Fig. 6). Extensive tracts of woodland with trees 10–25 m in height within the GWW are somewhat surprising; groundwater quality is often saline and acidic, hence reliance on groundwater cannot be assumed (Farrington et al. 1994; Costelloe et al. 2008). Secondly, the GWW have a remarkably high level of diversity and regional endemism among woody plants (Hopper and Gioia 2004), supporting for example, *c.* 30% of Australia’s eucalypt species in <2% of the Australian continent. They also support >200 species of vertebrate (Judd et al. 2008; Watson et al. 2008), and comprise a significant refuge for

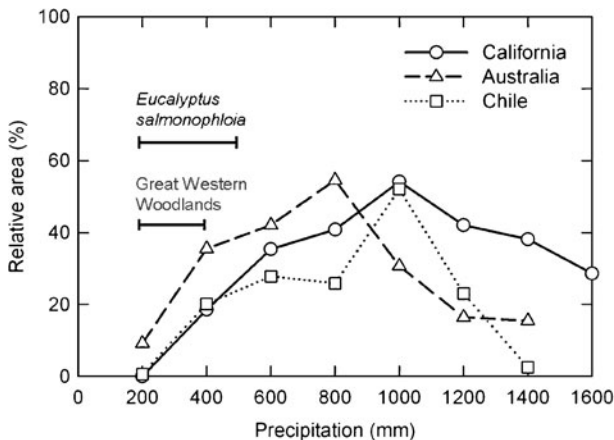


Fig. 6 Relative area of woodland among all vegetation types by rainfall zone within three Mediterranean-climate regions. Data are based on WWF Bioregions categorized as Mediterranean forest, woodland, and shrub biome (Olson et al. 2001) with potential vegetation type mapping following Underwood et al. (2009). Vegetation occurrence within each rainfall zone was categorized as forest, woodland, shrubland, scrub, or grassland. Mean annual rainfall range for the GWW, and a prominent woodland type of the GWW (*Eucalyptus salmonophloia*) is also shown

bird species that have become endangered owing to extensive clearing in the adjacent Western Australian wheatbelt (Recher et al. 2007). Mammal communities have fared less well, with 11 species regionally extinct, probably due to feral predators (Recher and Lim 1990; Watson et al. 2008).

5 Application of the framework to the Great Western Woodlands

We applied the generalized framework of Fig. 4 to the GWW by systematic consideration of ecological processes listed on the ‘change’ side of the framework, and identifying the strengths and weaknesses of response attributes listed on the ‘response’ side of the framework. Of the likely direct impacts of climate change (Fig. 5), declining rainfall, changes in rainfall distribution throughout the year, and extended droughts were considered to have the greatest potential for threatening the persistence of woodland species, given the low rainfall of the region compared with other Mediterranean woodlands (Fig. 6). While few data regarding physiological limits of GWW dominants are available, increased mortality of eucalypts following extended drought has been recorded (Yates et al. 1994). First principles thus suggest that in conjunction with increasing temperatures, community dominance could shift away from eucalypt woodlands to communities more like the *Acacia aneura* and other woodlands currently occurring to the drier and warmer north and east. Such shifts are consistent with predictions of Hilbert and Fletcher (2010) under medium to high emissions scenarios, especially in the northern GWW. On the other hand, our analysis (Fig. 5) emphasized that the extensive, unbroken nature of the GWW coupled with the high integrity and diversity of its ecosystems (Judd et al. 2008) endows the GWW with a wide range of features conferring resistance and resilience to climate change. These attributes, as well as interactions among ecological processes such as fire and fuel accumulation, are likely to result in more complex outcomes than predicted by broadscale shifts in ecological environments (Fig. 3, Hilbert and Fletcher 2010). To illustrate these concepts, the following sections explore potential interactions among environmental changes and attributes of resilience in more detail, focusing on three factors that we considered most likely to drive biological change: fire regimes, soil moisture availability, and the potential exacerbating effects of anthropogenic degradation (Fig. 5, Table 1).

5.1 Fire regimes

Fire fundamentally influences community structure and composition in the GWW (Hopkins and Robinson 1981; O’Donnell et al. 2011). Climate change projections suggest a likely increase in weather conditions promoting fire (impacting on the ‘change’ side of our framework, Fig. 5). In particular, the number of days of extreme fire danger and the frequency of lightning are likely to increase, which in turn would promote an increase in fire intensity and frequency of ignition (Bradstock 2010).

However, impacts of enhanced fire conditions may be tempered by the resistance and resilience of woodlands to fire, as reflected on the ‘resilience’ side of the framework (Fig. 5). Attributes relevant to the response of the GWW to altered fire conditions include (1) the dynamics of fuel availability (here viewed as an attribute of resistance), (2) landscape heterogeneity and (3) fire responses of component

Table 1 Interactions identified among anthropogenic degradation, key ecological processes and response attributes relevant to climate change in the Great Western Woodlands

Threat	Altered processes	Altered resistance and resilience
Exotic invasions	Altered competitive relationships, predation, herbivory Changed nutrient cycling and soil–water relations	Reduced population sizes of native competitors or prey (local extinction of small mammals) Altered fire resistance (e.g. increasing fire fuels)
Increased grazing pressure (livestock, natives and ferals)	Efficiency of soil–water infiltration reduced by compaction and loss of protective cover Exotic invasions Erosion	Loss of diversity and redundancy Ecosystem simplification Reduced population sizes in grazing sensitive species
Loss of Aboriginal management	Altered seed dispersal processes Altered competitive relationships, predation, herbivory due to lack of resource harvests	Greater vulnerability to large intense fires owing to lack of Aboriginal burning
Mining and mining exploration	Altered hydrology Potential fire ignitions Exotic invasions Increased grazing pressure associated with water points	Reduced population sizes in areas of direct impact Increased fragmentation Loss of refugia (e.g. banded ironstones)
Off-site effects (widespread clearing in WA wheatbelt)	Potential amelioration of declining rainfall	Decreased resilience of nomadic, migratory or dispersive species owing to altered temporal and special resource availability
Resource harvesting (e.g. logging, sandalwood)	Altered processes due to loss of keystone species or structural dominants Soil compaction and erosion	Fragmentation Altered heterogeneity
Tourism	Increased fire ignitions Exotic invasions Soil disturbance and compaction	Fragmentation due to roads and infrastructure

See text for further detail and references

taxa. Woodlands comprising single-stemmed trees such as salmon gum (*Eucalyptus salmonophloia*, Fig. 1) have historically burnt infrequently (return intervals of *c.* 400 years), despite much more frequent fires (*c.* 50 years) in adjacent shrubland

(O'Donnell et al. 2011). This indicates an inherent low flammability, or high 'resistance' to fire in woodlands, that is at least partly governed by discontinuous litter and understorey fuels (O'Donnell et al. 2011). Declining rainfall is likely to suppress plant productivity and associated fuel loads even further (Bradstock 2010), potentially increasing this resistance to fire. It is possible that increasing summer rainfall or rising CO₂ (Hovenden 2008) could counter this prediction, although significant productivity increases in response to rising CO₂ are likely to be constrained by nutrient and moisture limitations (Grünzweig and Körner 2003; Bradstock 2010).

Landscape heterogeneity in the GWW confers resistance to extensive fires through the occurrence of fire-breaking features such as fire-resistant patches of vegetation, recently burnt areas, granite outcrops and salt lakes (O'Donnell et al. 2011). This limits fire spread, and results in fire-shadows that allow persistence of species and communities that are vulnerable to fire. Some of these features may become compromised under climate change, while others are likely to continue to provide refuge from fire.

Although resistance to fire in woodlands is high and could increase, resilience to short fire-return intervals, should they occur, is likely to be low. Many woodland eucalypts of the GWW are killed by intense fire and lack long-lived soil seed banks (Yates et al. 1994). Hence, they are vulnerable to local extinction through repeated high intensity fires or interactions between fire and drought. Even where woodland eucalypts persist, structure and composition may be permanently altered should fire frequency increase (Hopkins and Robinson 1981), affecting fauna dependent on mature trees.

The net outcomes of increased fire-inducing weather and altered resistance to fire are difficult to predict. If the increase in the number of fire days and lightning ignitions due to climate change is sufficient to decouple the extent and intensity of fires across the landscape from fuel loads, or if fuel loads increase, fires burning in adjacent shrublands and mallee could more frequently carry through eucalypt woodlands (Boer et al. 2008; Bradstock 2010). At the extreme, this could lead to widespread loss of the mature woodland ecosystem. Landscape and ecosystem resilience may then be maintained through transformation to pyric-successional ecosystems derived from fire resilient taxa; however, such transformation would have dramatic implications for many GWW species.

5.2 Water availability, infiltration and hydrology

Water availability, probably more than any other factor, determines the productivity and distribution of vegetation types in the GWW (Dirnböck et al. 2002; Cullen and Grierson 2009). Climate change will directly impact on the amount of water available for persistence and growth of GWW organisms through changes in the timing, amount and intensity of rainfall, exacerbated or mitigated by changing evaporative demands and potential increases in water-use efficiency associated with increasing atmospheric CO₂ (Berry and Roderick 2004; Hovenden 2008). These direct effects on the hydrological cycle, reflected on the 'change' side of the change-resilience framework (Fig. 5), are likely to be further modified through interactions with site and landscape-scale hydrological processes.

At site scales, capture of limited rainfall in semi-arid ecosystems is dependent on soil–water infiltration. The GWW has low levels of soil compaction, patchy

vegetation and litter cover, an abundant ant and termite fauna, and a high surface micro-relief. These features typically promote water infiltration in semi-arid ecosystems (Ludwig et al. 1997), contributing to short-term water availability and to a longer-term water supply through storage in or at the surface of clay subsoils (Farrington et al. 1994). Under future climate scenarios, increasing summer storms, reduced ground cover due to greater aridity, and/or increased fire frequencies, have the potential to increase water repellence of soils (DeBano 2000) and reduce soil–water infiltration (Casenave and Valentin 1992). In turn, lateral hydrological flows (typically surficial in subdued GWW landscapes) would redistribute water within the landscape to areas of high infiltration capacity or topographic depression (Grayson et al. 2006), with likely greater losses to saline drainage basins. This redistribution of water may buffer soil moisture regimes in run-on zones, while exacerbating soil moisture decline in higher parts of the landscape.

The ecological outcomes of these climate-mediated changes in hydrological processes will depend on attributes of GWW individuals, species, ecosystems and landscapes as highlighted on the resilience side of our framework (Fig. 5). The direct response of individuals and species to declining available moisture will depend on unknown physiological tolerances at different life-stages, and genetic diversity (potentially high in widespread, outcrossing trees and shrubs typical of the GWW, Hamrick and Godt 1989) in these characteristics. Other species-level attributes such as long-lived propagule banks or short generation times in woodland ephemerals could further facilitate persistence or adaptation, while at the ecosystem scale, species redundancy could promote adaptation and buffer ecosystems from further hydrological change.

At the landscape scale, several features of the GWW are likely to confer resilience to declining moisture availability. Regional scale climate gradients and local-scale heterogeneity in soil moisture associated with topographic and soil texture mosaics could allow for local- and regional-scale shifts of many woodland species and ecosystems. This is supported under moderate emissions scenarios by national-scale community-level modelling (Ferrier et al. 2010), and by vegetation distribution models for the adjacent Western Australian wheatbelt (Dirnböck et al. 2002) that show the relationship between vegetation type and the topographic mosaic varies according to mean annual rainfall. Similarly, water-gaining refugia (areas reflecting past environmental regimes and supporting high numbers of endemic species; Morton et al. 1995) at the base of scattered granite outcrops will continue to provide refuge to moisture-limited species, albeit a different suite of species to those supported today. Such shifts of genes, species and communities across soil mosaics or rainfall gradients would be facilitated by the broad scale continuity and connectivity of the intact GWW landscapes (e.g. Hewitt and Nichols 2005).

Given interactions among these processes, the net outcomes of altered quantity and seasonality of rainfall on biota of the GWW remain uncertain. Most likely, increased runoff and an overall decline of rainfall will lead to decreased moisture availability and reduced plant productivity across extensive areas, with consequent effects on plant and animal composition. At lesser extremes of drying, the landscape should prove highly adaptable, with local shifts across soil mosaics or rainfall gradients conferring resilience for many species and communities. At greater extremes, widespread transformation from the current woodland to novel assemblages is likely, especially along lower rainfall margins.

5.3 Anthropogenic degradation

Although human activity in the GWW is not intensive compared with adjacent agricultural landscapes, mineral exploration, mining and tourism are increasing. Live-stock grazing, feral animals and timber harvesting have also affected substantial parts of the region for over a century (Kealley 1991). As illustrated on the ‘change’ side of the change-resilience framework (Fig. 5, Table 1), these impacts increase in significance under climate change, as they can exacerbate potentially unfavourable changes to ecological processes. For example, soil compaction resulting from increased grazing and vehicular pressures reduces soil–water infiltration; and tourism can increase fire ignitions (Table 1, Yates et al. 2000b). Indeed, recent decades have seen substantial increases in woodland area burnt (Watson et al. 2008; Parsons and Gosper 2011), which may be attributable to a combination of human ignitions and climate change. On the response side of the framework (Fig. 5, Table 1), human activities can compromise attributes of the GWW that confer resistance or resilience to climate change, as already widely evident in the adjacent, highly degraded Western Australian wheatbelt (Prober and Smith 2009). Ecosystem complexity, species redundancy, and population sizes are typically reduced by high grazing pressures and clearing (Yates et al. 2000b; Hobbs and Cramer 2003), and as populations of some species contract with climate change, clearing, logging and road building could exacerbate their increasing isolation (Fig. 5, Table 1).

Human activities also facilitate invasions by exotic species, which in turn have flow-on effects on ecological processes and resilience to climate change (Table 1). Currently, few exotic plants occur in the GWW (c. 5% of the total flora compared with 15% Australia-wide, Keighery and Longman 2004), but a number of potentially serious weeds are already present and likely to spread under combinations of human disturbance and climate change. For example, the invasive C4 grass *Cenchrus ciliaris* L. (buffel grass) is more likely to spread through the GWW with increasing winter temperatures and summer rain (Martin et al. 2010). *Cenchrus ciliaris* impacts negatively on native biota, and by increasing connectivity of fire fuels could act synergistically with climate change to increase fire ignition and spread, potentially transforming the structure and composition of landscapes (Martin et al. 2010).

Exotic animals, particularly rabbits, foxes and cats, are widespread in the GWW (Watson et al. 2008) and may already have altered woodland ecosystem processes relevant to climate change. For example, ground-dwelling fauna such as *Bettongia penicillata* (woylies) played an important role in soil turnover, and their widespread decline through predation has undoubtedly affected the capture of moisture and nutrients in woodland ecosystems (although the directions of these changes are uncertain, Garkaklis et al. 2000; Martin 2003). An impending threat is increasing invasion by camels under predicted drying environments (Edwards et al. 2008).

Unplanned outcomes of human activity are not always negative. For example, altered meteorological processes associated with widespread clearing in the adjacent Western Australian wheatbelt may have contributed to increases in rainfall in the GWW since the 1970s (Pitman et al. 2004; Kala et al. 2011), providing some mitigation against general climate change trends. On the other hand, clearing outside the GWW is likely to have decreased the resilience of nomadic, widely dispersive or migratory species that depend on both regions for persistence (Soulé et al. 2004, Table 1).

6 Adaptation options

Structured analysis of key ecological processes and response attributes in the GWW using the change-resilience framework highlighted likely drivers and directions of change in a warming and drying climate. Although this analysis is speculative, we argue that systematic identification of processes likely to drive change and response nonetheless provides a strong basis for identifying potential interventions to manage

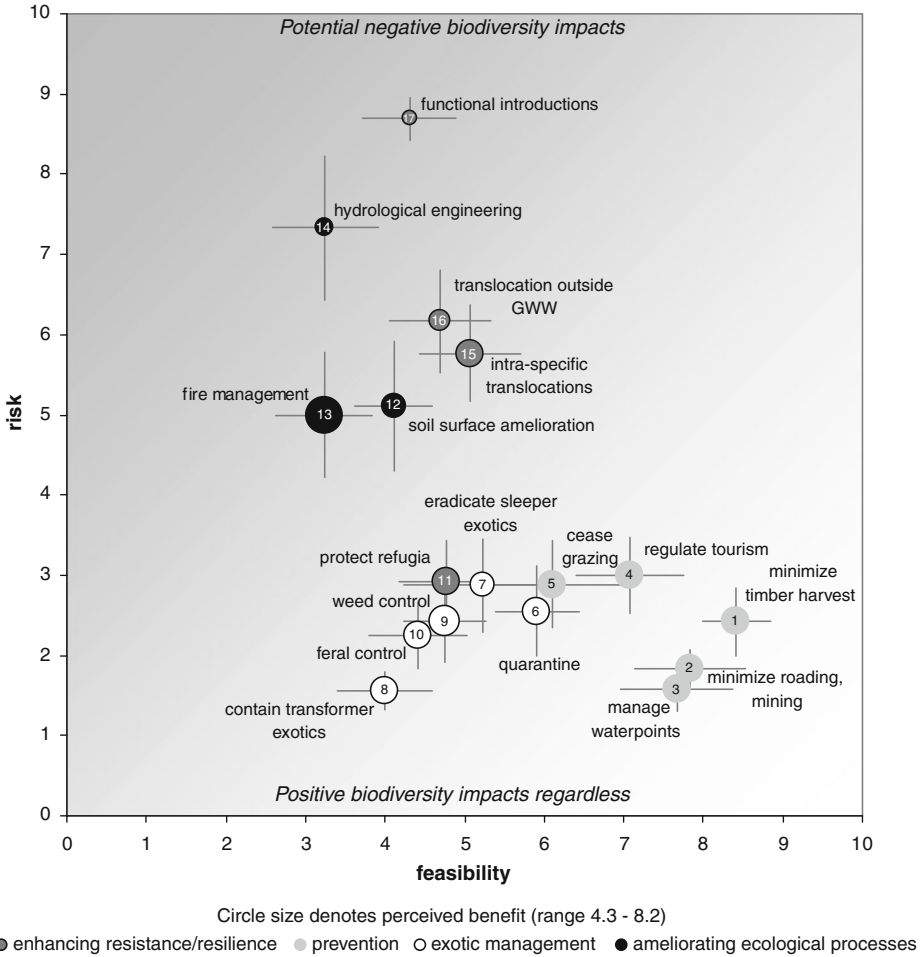


Fig. 7 Adaptive management opportunities in intact landscapes relevant to the Great Western Woodlands. Options were subjectively scored on a scale of 1–10 (low–high) by 14 of the authors (mean and 1 × SE) for each of perceived risk, feasibility and benefit (see Section 2). *Circle size* represents perceived benefits of the intervention if successfully implemented, averaged across separate scores for three biological goals: optimizing ecological function, maximizing biodiversity persistence, and maintaining woodland structure. An intervention typically achieved comparable scores for each goal, with the exception of refugia (6.4, 8.4, 6.4 respectively) and functional translocations (6.1, 2.5, 4.3 respectively). *Numbers* cross-reference to intervention points on Fig. 5

change (Figs. 5 and 7). In turn, explicit consideration of the risks, feasibility and benefits of identified adaptation options suggested clear priorities for intervention (Fig. 7). We acknowledge though that the latter analysis might be improved through wider stakeholder participation and potentially, evaluation of other factors such as timescales to effectiveness.

Consistent with other analyses of climate adaptation options (e.g. Heller and Zavaleta 2009), many interventions identified for the GWW involved prevention or restoration of human-induced degradation, despite the relative intactness of our target region. These formed the set of lowest-risk options, with likely benefits for biodiversity independent of the extent and direction of climate change (Fig. 7). Preventative options associated with mining, grazing and tourism were seen as some of the most feasible from a practical perspective, although a high level of income forgone was recognized. Options associated with managing exotic invasions were considered more difficult to implement, but nevertheless include manageable, low risk options with likely significant benefits. For example, identification and eradication of potentially invasive ‘sleeper’ exotics is likely to be feasible for species with long invasion lag times (e.g. the cacti *Cylindropuntia* and *Opuntia* spp.).

Only three potential interventions to manage climate-driven changes to ecological processes were identified, and these were scored as more challenging and risky than preventative interventions. Engineering of physical soil structures and amelioration of compacted soil surfaces to increase soil water recharge (Sanders 1986) were both considered costly and likely to have significant adverse impacts. Fire management to reduce the incidence of extensive, high intensity woodland fires was considered difficult in this remote region, and of significant risk due to potential ecological degradation (e.g. dissection by large fire breaks). However, fire management (if successfully implemented) was considered to have the highest potential benefit of any intervention for maintaining woodland structure and function, and to maximizing biodiversity persistence (Fig. 7).

Opportunities to enhance resistance and resilience to climate change in undisturbed areas of the GWW are similarly limited, because resistance and resilience attributes in these diverse, intact landscapes have not been substantially compromised. This positive feature promotes natural adaptation, but limits options for human intervention. Fire management that targets not only fire suppression but also optimization of landscape heterogeneity could maintain or enhance landscape resilience (but see Parr and Andersen 2006). Biological refugia are a specific aspect of landscape heterogeneity that is important to identify and protect. Fire management or hydrological engineering could be affordable management tools for creating or maintaining refugia to conserve ecological communities of high conservation priority. At these constrained scales, these activities were seen as lower risk options, with potentially high benefits for biodiversity persistence (Fig. 7).

Translocation is usually viewed as a ‘last resort’ conservation option for at-risk, often iconic taxa, through facilitated dispersal to areas considered likely to offer suitable habitat in the future (Hoegh-Guldberg et al. 2008; Richardson et al. 2009). This approach is relevant to GWW taxa, but here we also considered translocation options for enhancing in situ resilience of species, ecosystems and landscapes to altered climates. Within species, genetic material could be introduced from populations predicted to be better adapted to future climates. At ecosystem and landscape scales, introducing non-local species to the GWW could enhance the diversity of

species available for adaptation and maintenance of ecosystem functions (functional introductions).

We ranked all translocation options as relatively high risk owing to potential for introducing invasive species or genes, and to cascading uncertainty associated with predicting suitable habitat (see also Ricciardi and Simberloff 2009). Intra-specific translocations were considered of lower risk and higher benefit than functional introductions (Fig. 7). The latter were ranked the highest risk and lowest benefit of all interventions, although they were rated more highly for their potential contribution to restoring ecosystem function (average score 6.1). Such interventions may thus be justifiable only under transformational change scenarios. In such cases, assembly of new ecological communities from proximate native sources rather than exotic or distant sources would help conserve the evolutionary character of the south-western Australian biota.

7 Conclusions

The change-resilience framework emphasizes that outcomes of climate change for individuals, species, ecosystems and landscapes are dependent on two potentially countervailing forces operating at and among these scales. As is well-recognized by most studies of climate change impacts (e.g. Fischlin et al. 2007; Steffen et al. 2009), climate change will act directly and indirectly through altered ecological environments and processes. The importance of response attributes has been less well characterized (but see Williams et al. 2008; Heller and Zavaleta 2009; Steffen et al. 2009, perhaps because concepts of resistance, resilience and adaptability are often confusing and hence can be difficult to analyse and apply (Walker et al. 2004). We suggest that identifying their individual components at relevant scales offers a novel approach to climate adaptation planning that explicitly highlights the strengths and weaknesses of natural systems to temper the effects of change. This approach emphasizes where low risk adaptation measures can be applied, even where relatively limited specific ecological information is available.

Through application of the framework we concluded that intact landscapes such as the GWW are well-placed to adapt naturally to climate change, owing both to largely uncompromised ecological functioning and to high natural levels of resistance and resilience. Consequently, the simplest and lowest risk interventions to facilitate climate adaptation in these landscapes are preventative and aim to maintain these characteristics. Such options are likely to be beneficial regardless of future climate scenarios, but will not necessarily prevent transformational ecosystem change.

By contrast, our conclusions regarding management options to manipulate ecological processes and attributes of ecological resilience of the intact system are sobering. The range of options available is limited and all were considered of moderate to high risk. Notionally, high risk options would only be implemented where more severe climate scenarios are expected and transformational ecosystem change and species extinctions are likely. Such decisions are constrained by high uncertainty, and a better understanding of non-linear relationships and thresholds, coupled with improved climate prediction, is needed. In the meantime, some moderate-risk, high value options could be given early priority in the GWW, particularly low-impact fire management to limit the extent and frequency of woodland fires, and smaller scale

activities such as protection of refugia. These conclusions also emphasize the ongoing importance of mitigating climate change by reducing greenhouse gas emissions.

Finally, we applied the change-resilience framework to a relatively intact Mediterranean-climate landscape, but we emphasize that it is equally relevant to degraded landscapes such as those more typical of Mediterranean-climate woodland ecosystems. A parallel analysis of degraded Mediterranean-woodland landscapes such as the WA wheatbelt may suggest similar options to those in intact landscapes, but with significantly different emphases and opportunities. Restoration of degraded processes or attributes of resistance and resilience are likely to offer the highest priority, lowest risk adaptation options, consistent with potential interventions put forward for facilitating climate adaptation in degraded landscapes of Madagascar (Hannah et al. 2008). Notably, considerable existing investment in restoration coupled with lower risks associated with interventions in degraded sites, may provide greater opportunity to experiment with higher risk options (Prober and Smith 2009).

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