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OPINION

# Ecological mechanisms underpinning climate adaptation services

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## Abstract

Ecosystem services are typically valued for their immediate material or cultural benefits to human wellbeing, supported by regulating and supporting services. Under climate change, with more frequent stresses and novel shocks, 'climate adaptation services', are defined as the benefits to people from increased social ability to respond to change, provided by the capability of ecosystems to moderate and adapt to climate change and variability. They broaden the ecosystem services framework to assist decision makers in planning for an uncertain future with new choices and options. We present a generic framework for operationalising the adaptation services concept. Four steps guide the identification of intrinsic ecological mechanisms that facilitate the maintenance and emergence of ecosystem services during periods of change, and so materialise as adaptation services. We applied this framework for four contrasted Australian ecosystems. Comparative analyses enabled by the operational framework suggest that adaptation services that emerge during trajectories of ecological change are supported by common mechanisms: vegetation structural diversity, the role of keystone species or functional groups, response diversity and landscape connectivity, which underpin the persistence of function and the reassembly of ecological communities under severe climate change and variability. Such understanding should guide ecosystem management towards adaptation planning.

*Keywords:* climate change adaptation, ecosystem service, fire, functional diversity, functional traits, landscape configuration, littoral rainforest, livestock grazing, Murray-Darling Basin, resilience

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## Introduction

Ecosystem services (ES) are defined as the benefits that humans derive from ecosystems. They have become prominent in informing natural resource management and policy (Perrings *et al*., 2011; Crossman *et al*., 2013). Practice of ecosystem service valuation commonly focuses on supply of immediate, direct benefits for human wellbeing - provisioning and cultural services (Millennium Ecosystem Assessment, 2005) - often without considering underpinning regulating and supporting services (Abson & Termansen, 2011). However, shifts towards maintaining regulating and supporting services are increasingly advocated given the threats posed by climate change to the continued supply of provisioning and cultural services. Such shifts are exemplified by the development of adaptation responses to climate change (Prober *et al*., 2012), including increased investment in ecosystem-based adaptation (EBA) (World Bank, 2010).

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Ecosystem-based adaptation approaches 'harness the capacity of nature to buffer human communities against the adverse impacts of climate change through the sustainable delivery of ecosystem services' and include 'the potential for natural infrastructure to provide... disaster risk reduction, food security, sustainable water management and livelihood diversification' (Jones *et al*., 2012). Examples include local economic benefits from supply of nontimber products from tropical forests, regulation of local and regional climate and hydrology, mitigation of riparian erosion and coastal protection from storms (Jones *et al*., 2012; Pramova *et al*., 2012; Arkema *et al*., 2013). In most cases, the benefits are incremental, focused on proximate causes of vulnerability, and assessments are based on assumptions that ecosystem characteristics and services, and societal preferences for these, will remain largely unchanged. However, empirical data and modelled projections indicate ecosystems and landscapes will undergo fundamental, unpredictable changes in structure, composition and functions in response to novel, global-scale warming of >+3 °C (Schellnhuber *et al.*, 2012). Therefore, applications of the ES concept that assume stationarity of current bundles of ES that support livelihoods and economies, and societal preferences for these, will likely lead to maladaptive future actions (Stafford Smith *et al.*, 2011).

The concept of climate adaptation services (hereafter 'adaptation services') can be proposed to complement the ecosystem services approach and help people develop choices for adaptation to climate change. This concept highlights the prospect of substantial ecosystem change and stresses the importance of option and insurance values of services not currently considered important for human wellbeing, but which may prove critical in the future. Societal responses to climate change will vary from short-term incremental management aimed at maintaining existing ecosystem characteristics, through to transformational change in values, rules and knowledge that promote resilience and resistance of novel ecosystems. In this context, adaptation services are defined as the *benefits to people from increased social ability to respond to change, provided by the capacity of ecosystems to moderate and adapt to climate change and variability*. Adaptation services include the buffering capacity of ecosystems against change and incorporate some currently valued ecosystem services such as coastal protection or crop diversification for food security. Also, the capacity of ecosystems to transform in composition, structure and function in response to climate change or new management regimes will result in new provisioning services such as firewood supply after grassland has transitioned to woodland. Such new services form the basis for choices and options to support social climate adaptation.

To operationalize the adaptation services concept we need to explore its applicability and usefulness across a range of social-ecological systems. Here, considering the ecological dimensions of this endeavour, we propose a methodological framework to reveal testable hypotheses on biological traits and ecological mechanisms that underpin adaptation services, and to facilitate comparison and synthesis. To illustrate this capability, we present one case study in detail and three in summary for Australian ecosystems that are vulnerable to climate change. We synthesize common features of these case studies that relate to the main types of adaptation services and their trait-based mechanisms. We identify knowledge and research gaps in the operational framework and conclude by identifying the implications for management.

## The operational framework

The operational framework involves the identification of adaptation services under different scenarios of climate and management change, based on our understanding of the ecological mechanisms that underpin the supply of ecosystem services (Bennett *et al.*, 2009; Luck *et al.*, 2009) (Fig. 1). Climate, other abiotic factors and management are proximate drivers that determine the ecosystem state at a particular time and place. Each state has specific characteristics of biodiversity and functioning that contribute to the supply of ecosystem services.

Scenarios may involve change of ecosystem state due to direct climate impacts, including increased temperatures, droughts and storms, and indirect impacts via management responses such as changed grazing regimes or water flows in regulated rivers. Adaptation services can then be identified that support human well-being under these new conditions. Finally, ecosystem properties that underpin adaptation services need to be managed for, including, where possible, the conservation of existing biodiversity and ecosystem services. The four steps in the operational framework are outlined below.

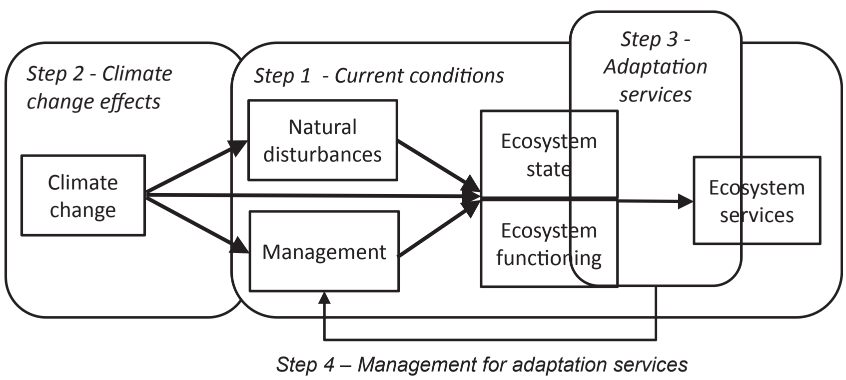



**Fig. 1** The operational framework for the identification and quantification of adaptation services. Four steps are identified: (1) characterization of the system and its bundles of ecosystem services, (2) describing climate change direct and indirect impacts, (3) identifying adaptation services and (4) proposing management for adaptation services.

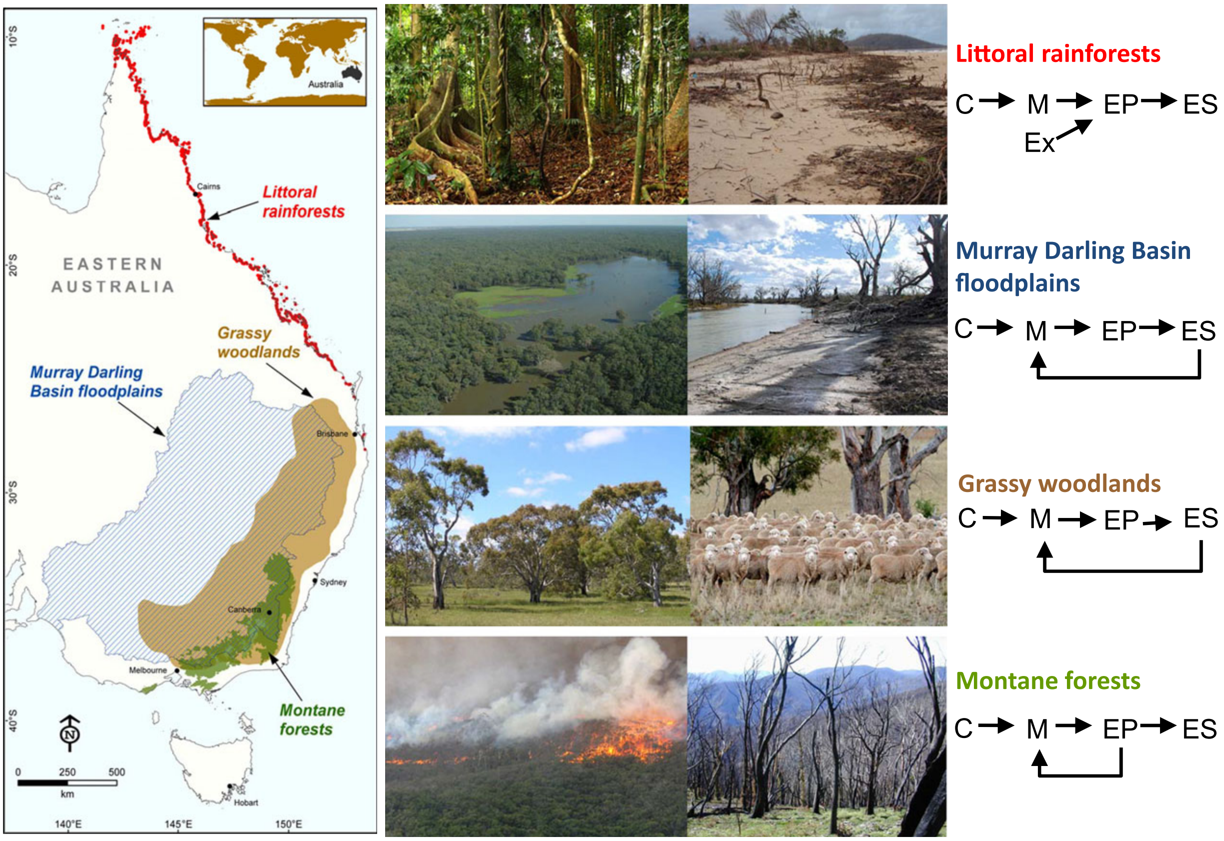



**Fig. 2** The four case studies: distribution ranges and typical landscapes for littoral rainforests, the inland floodplains and wetlands, grassy woodlands and montane forests. Inset diagrams for each case study picture the most important drivers and feedbacks for each case study: climate (C), management (M), exotic species (Ex), ecosystem properties (EP) and ecosystem services (ES). Drivers are common for inland floodplains and grassy woodlands.

### *Step 1: Initial system characterization*

*1a*: Characterization of ecosystem dynamics under historical and current climate allows projections of future states and properties. Appropriate models may be conceptual or quantitative (Scheffer, 2009), state-and-transition (McIntyre & Lavorel, 2007; Zweig & Kitchens, 2009), or succession-based (Noble & Slatyer, 1980; Dickie *et al.*, 2011). Alternative states may be represented by vegetation composition and associated biodiversity, biomass pools, ecosystem functions and disturbance regimes.

*1b*: For each ecosystem state, identification of bundles of ecosystem services supplied under current climate helps define benefits desirable for the long-term. We emphasize bundles of services (Bennett *et al.*, 2009; Crossman *et al.*, 2013), rather than single services, because bundles covary though space and time, dependent on shared ecosystem properties, processes and environmental drivers. Thus, management approaches need to consider functional linkages between all adaptation services.

### *Step 2: Climate change effects*

To identify adaptation services (Step 3), it is necessary to describe and, where possible, quantify biodiversity and ecosystem responses to climate change scenarios, including recent empirical or modelled trends, like changed frequency and magnitude of extreme events. Scenarios integrate direct climate impacts and indirect effects of land use and management (Fig. 2, inset diagrams).

Ecosystem responses involve changes affecting supply of current ecosystem services and autonomous ecological adaptation: community structure, composition, functional groups and traits, plus landscape changes that affect ecosystem responses and persistence. Methods for characterization include the assessment of altered supply of ecosystem services under climate- and land-use change by building on state-and-transition models as done for rangelands (Havstad *et al.*, 2007), or alpine grasslands (Lamarque *et al.*, 2014). In the latter, vegetation states-and-transitions (Quétier *et al.*, 2007) were linked to plant and microbial functional traits-based models (Lavorel *et al*., 2011; Grigulis *et al*., 2013) to project effects of climate and management change on ecosystem service bundles.

*Step 3. Adaptation services*

*Identification of adaptation services.* Ecosystem properties that facilitate societal climate adaptation by supporting current ecosystem service bundles, supplying novel services and moderating or enabling ecological transformation are identified as adaptation services. These different functions contribute to the different facets of social adaptation: providing time for societies to change, slowing down ecological responses to climate change, or providing novel livelihoods. In contrast with authors who determined adaptation services *a priori*, subsequently relating them to ecosystem characteristics (Jones *et al*., 2012; Pramova *et al*., 2012), we take a bottom-up approach by identifying intrinsic ecological mechanisms required to support future bundles of ecosystem services.

*Identification of mechanisms underlying adaptation services.* Ecological mechanisms and processes that support adaptation services and their management include traits of organisms, biodiversity effects on biogeochemical cycling and biotic moderation of resource availability, and landscape properties. Assessment of functional diversity and redundancy of relevant traits is required to anticipate ecosystem service responses to climate change, and how species range shifts may affect service supply.

*Step 4. Management of adaptation services*

Changes in ecosystem properties and supply of adaptation services are likely to be emergent, requiring an adaptive management approach. Management may target abiotic drivers such as water flows and disturbance regimes, or biotic components including keystone taxa and functional groups, through conservation, restoration and translocation. Intervention objectives should be to retain the ecosystem properties that supply those ecosystem services that support societal adaptation to climate change.

## Four case studies

In this section, we apply the operational framework to four case studies from climate-sensitive Australian social-ecological systems representing different climate-management interactions related to ecosystem service supply (Fig. 2). We provide a detailed account for grassy woodlands and summaries for littoral rainforests, temperate montane forests and floodplain ecosystems.

*Grassy eucalypt woodlands in south-eastern Australia*

*Step 1a: Ecosystem description.* Temperate grassy woodlands occupying subhumid regions of eastern Australia, are associated with soils of inherently low fertility (McIntyre, 2011), and since European settlement have been modified by livestock grazing, tree clearing and cropping. Transformation to exotic plant dominance was hastened in the mid-20th century though the use of phosphorus fertilizers and introduced annual legumes, encouraging the replacement of perennial native species with annual exotics (Dorrough *et al*., 2006, 2011). Crops and fertilized pastures have reduced the regenerative capacity of remaining trees. Soils are prone to erosion, acidification and salinization (Hobbs & Yates, 2000).

Grassy woodlands have characteristics that make them resistant to warming and drying, owing to the highly perennial, stress-tolerant nature of their native plants. Some climatic adaptability may be found in the flora as the geographical range of many species spans large rainfall and temperature gradients (McIntyre, 2011). The flora is also stress-tolerant and slow-growing as an adaptation to naturally low soil fertility, while low pH and poor soil structure make large areas vulnerable to erosion. These features of the ecosystem make it vulnerable to agricultural impacts that lead to losses of perennial native vegetation and displacement by ruderal species under conditions of disturbance and enrichment.

Five major ground-layer vegetation states are recognized (McIntyre & Lavorel, 2007; McIntyre, 2008; Fig. 3; Box 1). Reference and native pasture states have high resistance to grazing and fire, which maintain diversity, but low resistance to fertilization. Transformation from native to exotic dominance occurs when fertilization raises soil phosphorus above ~20 mg kg$^{-1}$ (Dorrough *et al*., 2006; McIntyre, 2008). Established trees persist, but are vulnerable to insect attack, root damage and disrupted regeneration. Decline of trees and shrubs is associated with decline in fauna (Lindenmayer, 2011).

Dominant perennial tussocks are the keystone plant functional group in the ground layer, with the greatest influence on ecosystem properties and processes (Mokany *et al*., 2008). Fertilization disrupts the tussock matrix and diverse forbs are replaced with exotics. Available phosphorus declines over decades following cessation of fertilization (Sharpley, 1995), but nitrate pools remain seasonally elevated when annuals dominate, thus reinforcing the prevalence of exotic species (Prober & Lunt, 2009).

*Step 1b: Current ecosystem services.* Grassy woodlands are valuable production systems, with a trade-off

**Box 1** Five alternative states identified by the state-and-transition model for grassy woodlands of south-eastern Australia (based on McIntyre & Lavorel, 2007; McIntyre, 2008)

*Reference*: Our understanding of pre-European vegetation relies on historical accounts depicting well-spaced trees, tall thick grass with abundant forbs and variable, but often low, shrub densities (Gammage 2011). Available water, hunting and dingoes would have regulated marsupial grazing.
*Native pasture*: Permanent settlement and introduced domestic livestock (sheep and cattle) increased grazing pressures and transformed the composition of the grassland to shorter, more-grazing tolerant native grasses and forbs. While still perennial-dominated, the annual component of the vegetation (native and exotic) is higher owing to the presence of livestock. Native plant diversity (of grazing-tolerant species) is high, and trees and shrubs generally persist, with some impacts of browsing.
*Fertilized pasture:* The addition of nutrients through fertilizers and legume N-fixation, elevates nitrogen and phosphorus and allows higher grazing pressures than in native pastures. Exotic and native perennial grasses can be maintained with grazing management, but annual grasses and forbs are abundant and often dominate. Native plant diversity is low, and conditions for tree regeneration are poor.
*Sown pasture and crops*: Cultivation and fertilization, with the addition of legumes and sown grasses or crop species result in almost complete loss of native diversity and perennial species.
*Enriched grassland*: Any fertilized or otherwise nutrient enriched grassland that is not grazed. Common situations are roadsides or pastures fenced for tree establishment. Large perennial grasses dominate, accumulating thick litter with a very low diversity of forbs.

between intensifying or extending production and overall sustainability in terms of preserving vegetation, soils and biodiversity (Smith *et al*., 2013). We undertook a literature review to identify ecosystem attributes that underpin ecosystem services supplied by grassy woodlands (Tables S1 and S2, Supporting Information). We quantified each ecosystem service using a 5-level rating (Table S3, Supporting Information). Star diagrams summarize the varying provision of ecosystem services between states (Fig. 3). A principal component analysis of Table S3 (not shown) revealed three distinct bundles of services, i.e. services co-occuring in given grassland states.

Reference and native pasture states share high multifunctionality with high values for regulating and cultural services and biodiversity indicators. The incorporation of production, albeit low, in native pastures comes at a small cost to these other services (Fig. 3). In contrast, the fertilized pasture, sown pasture and cropping states show radical shifts towards provisioning services at the expense of all others (except aesthetics) due to loss of perenniality and native plant diversity, tree decline and ultimately loss. Ceasing or reducing production in fertilized pastures restores some regulating services by allowing recovery of a largely exotic perennial ground layer, but not of biodiversity or cultural services specific to reference and native pastures.

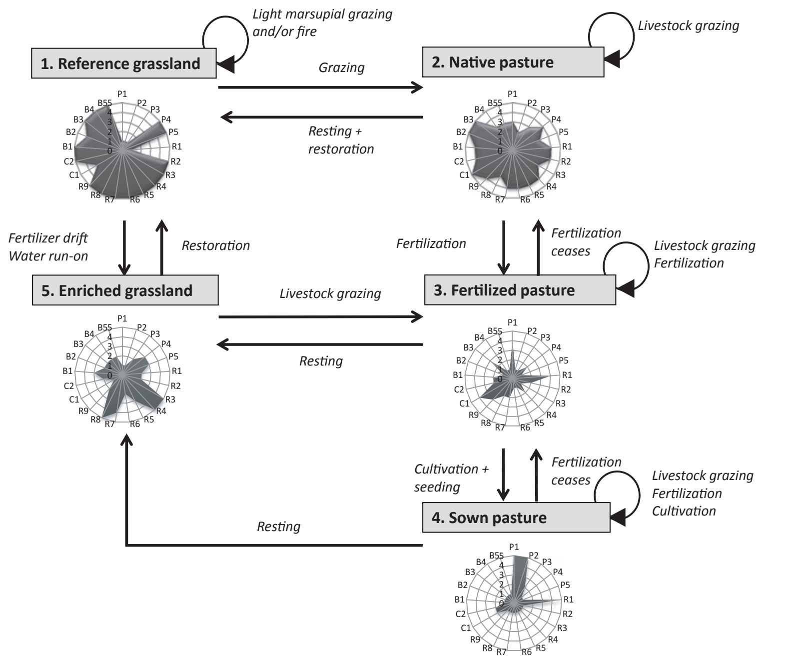
*Step 2: Climate change effects.* Climate change projections indicate a trend of high temperature, reduced or warm rather than cool-season precipitation precipitation, and more extreme rainfall and drought events (CSIRO & Bureau of Meteorology 2012). These changes are depicted under four scenarios of increasingly severe climate change and predicted land use responses (Table 1).

Reduced capacity for cropping is predicted, and cropping is likely to become more marginal (scenario 3) or be replaced by extensive grazing (scenario 4; Nidumolu *et al*., 2012). A history of extensive cropping in a landscape may limit the development of native perennial vegetation suitable for rangeland grazing, and decrease its ability to retain soil and sustain biomass. Abandoned cropland is likely to become annual grassland, with extensive areas of exposed soil in summer, vulnerable to water and wind erosion.

In reference and native pastures there is potential to support assembly of novel perennial diverse semi-arid rangelands combining some original grassy woodland, exotic and semi-arid species. We consider that the plant diversity currently available in these states provides a sufficient array of ecological strategies in order to support responses to scenario 3, and to a lesser extent scenario 4. The latter may require some assisted dispersal of semi-arid native species.

*Step 3: Adaptation services.* We assume that, similar to current use in semi-arid and arid Australia, livestock grazing will remain a primary future land use. Other objectives may be biodiversity conservation and maintenance of vegetation cover as appropriate for natural resource conservation under more severe scenarios.

We identified a bundle of adaptation services that are essential to support viable medium-term livestock production (Fig. 4), including soil regulation services




| **Provisioning services** | **Label** | **Regulation services** | **Label** |
|---|---|---|---|
| Forage & fodder | P1 | Fire hazard | R1 |
| Quality of fodder | P2 | C sequestration | R2 |
| Surface water quantity | P3 | Alleviation of GHG emissions | R3 |
| Production stability | P4 | Erosion protection + maintenance of soil fertility | R4 |
| Rural microclimatic regulation | P5 | Salinity control | R5 |
| **Biodiversity component** | **Label** | Potential for P level decrease | R6 |
| Eucalypt health | B1 | Control of soil acidification | R7 |
| Native ground layer regen | B2 | Surface water quality | R8 |
| Genetic resources | B3 | Po | R9 |
| Restoration potential | B4 | **Cultural services** | **Label** |
| Resistance to new weed invasions | B5 | Woodland aesthetics | C1 |
| | | Wildlife | C2 |

**Fig. 3** Summary of Step 1 for grassy woodlands: initial system characterization of system dynamics by a state-and-transition model and ecosystem service characterization. The states are described in Box 1.

underpinning stable plant production, microclimate regulation for welfare of livestock and the provision of water for livestock and people. During the transformation of the flora towards novel semi-arid communities (Step 2), several ecosystem attributes will increasingly support these adaptation services (Fig. 4). Perennial grasses, the keystone functional group supporting current landscape multifunctionality, will have increasing importance in soil protection and primary productivity. Additional ecosystem attributes supporting adaptation services for continued livestock production (Table 1) include structural and life form diversity, and large plant functional diversity of natives and exotics in the ground layer. These have a large response diversity to climate variability, to management interventions, and disturbance from drought and fire. The proportion of stress-tolerant species, already a major component of these ecosystems, is also expected to increase. The persistence of all these attributes under changing climate requires landscape scale biodiversity and connectivity to support interactions and trophic complexity.

As climate changes, many species will not persist. Their contribution to response diversity will decline and be replaced by species from less intensively managed states, with wide geographic distributions (Figure S1, Supporting Information). We assume gradual community re-assembly with immigration of semi-arid species under more severe scenarios 3 and 4, but translocation may be required to maintain the matrix structure of perennial grasses and enable the adaptation service of response diversity. For this, landscape connectivity will be an essential attribute. Climate regulation is expected to emerge as a novel adaptation service as climate change becomes more severe.

Importantly, the ecosystem properties that are likely to contribute to future adaptation services currently

**Table 1** Description of the grassy woodlands system under climate and management scenarios, impacts on ecosystem state and processes, adaptation services and their supporting attributes and mechanisms, and management needs for each of the four change types of increasing severity. Arrows indicate increasing importance of specific attributes across scenarios

| | **Scenario 1 - Moderate effects over regional scale and longer timeframe** | **Scenario 2 - Moderate effects over regional scale and shorter timeframe** | **Scenario 3 - Severe, widespread effects over longer timeframe** | **Scenario 4 - Severe, widespread effects over shorter timeframe** |
|---|---|---|---|---|
| **Scenario description** | Periods of severe dryness<br>Mixed cropping, fertilized pastures, native pastures and conserved woodlands.<br>Fertilization in wet periods.<br>Rotational grazing (recent) | Record drought<br>Increasing periods of extremely high grazing pressure.<br>Reduction in fertilizer use due to diminishing returns. | Declining rainfall averages.<br>Transition to opportunistic cropping. Greater grazing pressure on diminishing average forage production.<br>Continued reduction in fertilizer use; lag effects of past use. | Declining rainfall averages.<br>Threshold of dryness and temperature, transforming to semi-arid climate.<br>Transformation to rangeland use - dryness prohibits cropping. |
| **Species, ecosystem and landscape effects** | **Scenario 1** | **Scenario 2** | **Scenario 3** | **Scenario 4** |
| ***Landscape pattern*** | Fragmentation processes continuing due to increasing grazing pressure | | More diversified landscape mosaic | A mosaic of exotic-dominated vegetation and re-assembling native vegetation. |
| ***Trees and shrub*** | Negative effects of intensification and grazing | Eucalypt mortality increasing, recruitment of a few semi-arid tree and shrub species → | | |
| ***Ground layer - native*** | Negative effects on grazing-sensitive and nutrient-sensitive spp., | Local extinctions of some species, increase in native grazing-tolerant species. | Climate and increasing grazing pressure causes turnover in dominants. | Reduced plant diversity. |
| | Perennial grass dominance varies with grazing and fertilization | | | |
| | Annual dominance varies with grazing and fertilization | Opportunities for annual flushes, including infrequent species. | Increasing native ephemerals → | |
| ***Groundlayer- exotic*** | Exotics increasing | Some exotic species vulnerable | Stress tolerant ruderal exotics increasing → | |
| | Annual exotics increasing → | | | |
| ***Soil*** | Negative effects of intensification and grazing | Bare ground and erosion increasing → | | |
| ***Landscape-scale processes*** | | Local climate effects leading to positive feedback reinforcing more arid local climate → | | |
| **Ecosystem properties supporting adaptation** | **Scenario 1** | **Scenario 2** | **Scenario 3** | **Scenario 4** |
| ***Original flora of grassy woodlands (exotics and natives)*** | Presence of trees and shrubs and perennial grasses, current diversity of plant and animals, (native and some exotic). Many hemicryptophytes and stress-tolerant spp.<br>Diversity of strategies and species associated with states with relatively less intensification; and/or with diversified exotic flora in un-fertilized states<br>Species with wide geographical ranges. | | | |

**Table 1** (Continued)

| | Scenario 1 - Moderate effects over regional scale and longer timeframe | Scenario 2 - Moderate effects over regional scale and shorter timeframe | Scenario 3 - Severe, widespread effects over longer timeframe | Scenario 4 - Severe, widespread effects over shorter timeframe |
|---|---|---|---|---|
| *Responses of original flora to climate change and management adaptation* | Increasing importance of stress-tolerant plant species | | | |
| | | | Decreasing contribution of original species pool to response diversity | |
| | | | Greater contribution of flora from reference and native pasture states to re-assembly | |
| *Desirable for adaptation* | | | | Immigrating or translocated species from semi-arid regions |
| | Increasing importance of stability of production under increasing inter-annual climate variability, maintenance of soil structure, erosion protection, rural microclimatic regulation, amount of abstracted surface water | | | |
| | | | Increasing importance of: global climate regulation, local and regional climate regulation, response diversity to climate change and variability, landscape connectivity. | |
| **Relevant traits and mechanisms** | **Scenario 1** | **Scenario 2** | **Scenario 3** | **Scenario 4** |
| *Functional composition and diversity* | Increasing importance of perenniality, presence of trees and shrubs, diversity of life forms, diversity of species within life forms providing response diversity | | | |
| *Landscape* | | | Increasing importance of amount and connectivity of the above | |
| **Management response to support adaptation** | **Scenario 1** | **Scenario 2** | **Scenario 3** | **Scenario 4** |
| | Landscape planning to create a matrix of native dominated pastures and native vegetation | | | |
| | | | Increasing value of assisted dispersal of semi-arid native plant species. | |
| | | | Transfer of arid grazing knowledge to the east. | |
| | | | Extension on improved grazing and soil management practices. | Up-skilling with respect to agronomic practices, extension and 'ecologically acceptable' technology development. |
| | | | Increase in farm sizes | |
| | | | Support the transition economic base from grain production to livestock. | |

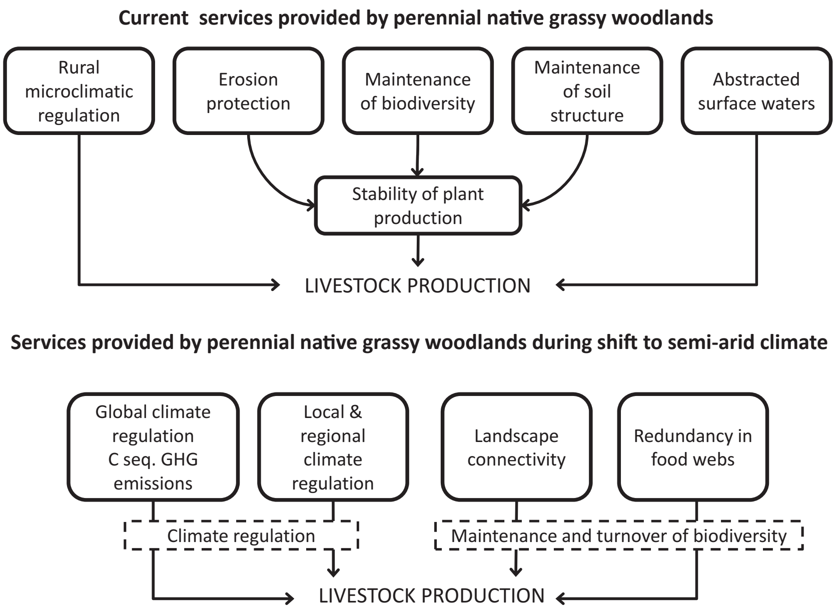



**Fig. 4** Ecosystem services provided by unfertilized perennial tussock grasslands in grassy eucalypt woodlands under current variability and trends in climate (above). The adaptation services provided by the same vegetation under a more severe transition to a semi-arid climate (below) differ, and contribute to climate regulation and biotic adaptation. In both cases conservative livestock production is possible within the restrictions of soil moisture availability.

support ecosystem services from conservatively grazed native pastures (Fig. 3). They comprise many of the attributes that maintain viable livestock production as part of the bundle of services provided by reference grasslands and native pastures.

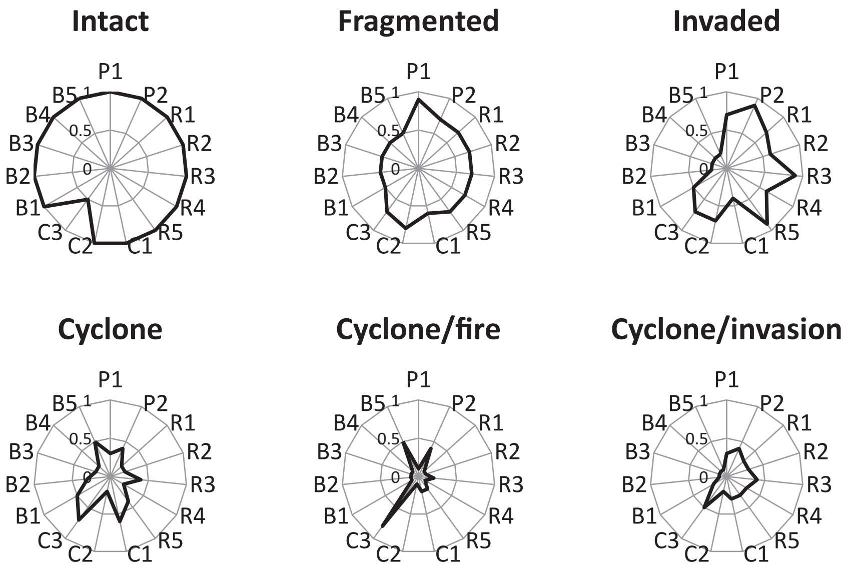
*Step 4: Management implications.* Currently, the highest priority is maintaining perennial vegetation to reduce the risk of future desertification. While short-term returns from the expansion of annual cropping may be attractive, the long-term functionality and productivity of the landscape will be at risk from erosion and declining soil health. Expanding cropping will further reduce plant and animal diversity, thus risking loss of species tolerant of environmental stress, with potentially important, yet presently unrealized, adaptation service roles. As aridity increases, management will need to be fundamentally different in type and operation. Errors in over-harvesting and intensification are likely as new climate extremes are experienced. It will become increasingly important that agricultural extension incorporates perspectives from semi-arid areas and implements landscape-integrated management.

### *Littoral rainforest*

*Step 1a: Ecosystem description.* Consistent with global patterns, and exacerbated by the scarcity of inland resources, Australian coasts have been, and are increasingly, the focus of human settlement and urbanization. The Littoral Rainforest and Coastal Vine Thickets of eastern Australia (henceforth littoral rainforest) represent a complex of rainforests and coastal vine thickets structured by processes including effects of salt spray and on-shore winds, tidal inundation and storms, saltwater intrusion of groundwater and unstable, dynamic substrates. In the Wet Tropics, due to the protection provided by the fringing reefs, these communities only exist within 2 km of the coast and <10 m above sea level (Metcalfe *et al*., 2013). Littoral rainforest is naturally distributed as a series of disjunct, localized stands which provide important stepping stones for migratory shorebirds.

Littoral rainforests are highly dynamic ecosystems, often in a state of regeneration following repeated storm disturbance. Structure is typically a closed canopy of trees which may include emergents. Patches regularly exposed to disturbance may have many canopy gaps. Whilst canopy species are well adapted to coastal exposure, the canopy protects less tolerant species and propagules in the understorey.

Because of their coastal location, littoral rainforests are highly vulnerable to interacting effects of climate change and sea-level rise, along with existing threats such as invasion by transformer weeds, which alter structure and function, and fragmentation due to coastal development.




| Provisioning Services | Label | Regulating services | Label |
|---|---|---|---|
| Shade | P1 | Wind buffer | R1 |
| Filter sediments/pollutants | P2 | Wave dissipation | R2 |
| **Biodiversity and habitat services** | **Label** | Dune stability | R3 |
| Connectivity - migration | B1 | Storm surge mitigation | R4 |
| Invasion resistance | B2 | Erosion prevention | R5 |
| Nesting sites | B3 | **Cultural services** | **Label** |
| Food/fruit resources | B4 | Cultural sites/significance | C1 |
| Regeneration potential | B5 | Tourism, recreation | C2 |
| | | Views | C3 |

**Fig. 5** Characterization of the ecosystem services, and semi-quantitative assessment of their relative importance, for littoral rainforests, comparing intact forest with the effects of alternative drivers in scenarios.

*Step 1b: Current ecosystem services.* Littoral rainforest occurs at the interface between terrestrial and aquatic systems, where it protects land from erosion, filters sediments, nutrients and pollutants, mitigates the effects of flooding and wind during storms and provides habitat for biodiversity (Fig. 5). Foreshore vegetation and natural dunes also provide protection to coastal communities, beaches and infrastructure including roads, marinas, agricultural (e.g. sugarcane, fruit and nut production) and aquacultural industries. Tree height, vegetation structure, stem density and ground cover all influence the ability of littoral rainforest to stabilize soils, attenuate waves and act as wind breaks. Other ecosystem services include the provision of shade, nesting sites and food resources for fauna, migration capacity for endemic and iconic species, and cultural and aesthetic services.

*Step 2: Climate change effects.* Four scenarios of increasing severity, and outcomes for species, ecosystems, landscapes and adaptation services, are summarized in Table S4 (Supporting Information). Climate change predictions for the tropical rainforest habitats of Queensland (Suppiah *et al.*, 2010) indicate air temperature increases and declining rainfall particularly during the 'dry season', resulting in seasonal drought (Williams *et al.*, 2012), increase in extreme rainfall events across the coastal high rainfall zone, and more intense cyclones (Suppiah *et al.*, 2010). Projections of sea level rise are of particular significance for littoral rainforest.

Under less severe scenarios, minor changes in community composition and diversity can be expected as some native species reach their tolerances to heat and low water availability. Rising sea levels and greater storm intensity will increase exposure to inundation and disturbance, which will gradually increase fragmentation and create opportunities for invasion by exotic species.

As climate change increases in rate and severity across scenarios, a simplification of community structure is expected. Loss of emergent trees and physical canopy damage from more intense storms effects will reduce vegetation height and create canopy gaps (Kellner & Asner, 2009). Increasing internal and external fragmentation of littoral rainforest patches will continue to facilitate exotic species invasions and place further stress on native species, resulting in losses of biodiversity.

Transformative changes in ecosystem structure, function and composition are likely with increased sea level rise, storm surges, floods and cyclone intensity, or with co-incident extreme events like fire during the dry season. Littoral rainforests may be lost or transform to mangroves, depending on location and level of inundation. In many coastal margins, natural features and urban development prevent shoreward migration. Sea-level rise will result in narrower distributions (intensifying the effect of coastal squeeze), smaller patch size and increasing fragmentation. These effects may result in littoral rainforest patches being lost or dominated by transformer weeds, highly invasive taxa with the potential themselves to significantly alter the structure and function of the community.

*Step 3: Adaptation services.* Littoral rainforests confer adaptation services by (i) mitigating storm surge, inundation and wind impacts on infrastructure and people by providing a barrier to wind, salt spray and debris mobilized by cyclones (Wamsley *et al*., 2010; Shepard *et al*., 2011; Arkema *et al*., 2013); and (ii) buffering impacts, enabling continued ecosystem function after extreme events (Fig. 5). High diversity of response-traits in the community allows important functions to be maintained, including provision of food, shade, and habitat for endemic and iconic fauna targeted by conservation and tourism. Littoral rainforest provides a barrier to wind and salt spray.

The adaptation service of erosion regulation will be important in mitigating the impact of sea level rise on nearby settlements and ecosystems. Eroded coastal dune systems and saltwater intrusion into freshwater wetlands will negatively affect public uses such as tourism and recreation (Environment Planning, 2011), including the loss of public assets like beaches. Critical ecological mechanisms supporting these adaptation services are an intact vegetation structure and a diversity of plant life forms including emergent canopy trees, sub-canopy and understorey layers, a diversity of disturbance and regeneration response traits, and the extent and connectivity of littoral rainforest patches.

*Step 4: Management implications.* Maintenance of intact, diverse, connected forest stands of good quality is the key management requirement to support adaptation services. Assisted regeneration to maintain size and quality may be required in vulnerable, small, isolated patches following major disturbance. Under more severe climate change scenarios, assisted regeneration and restoration may be necessary if autonomous regeneration is compromised. Landscape and development planning that facilitates the inland movement of dunes and littoral rainforest will become increasingly important with rising sea levels combined with greater intensity of storm surges and inundation events.

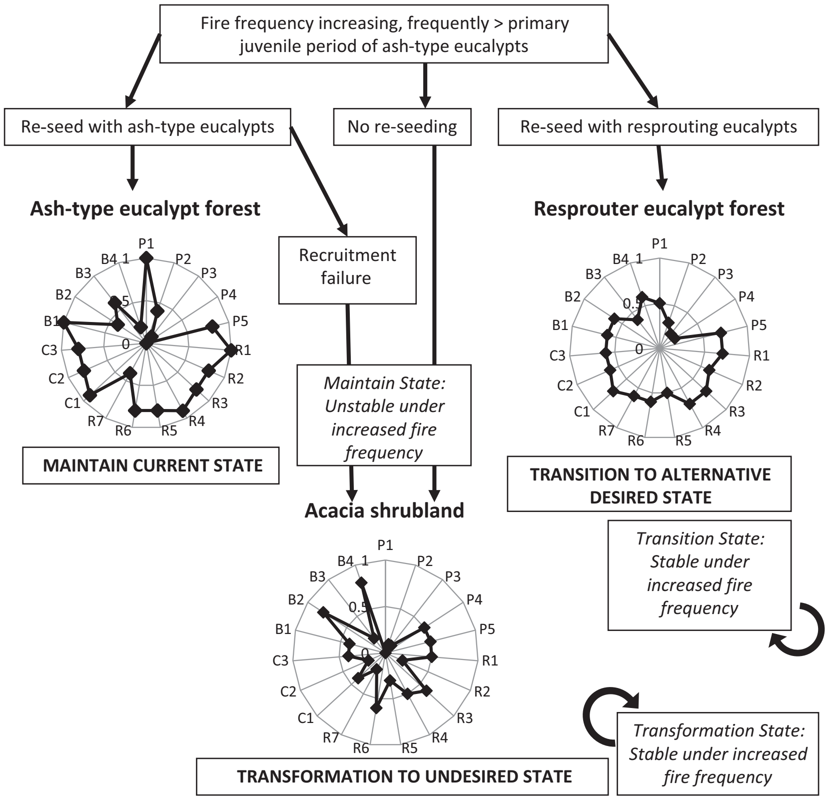
Engineering solutions may substitute for some services, but are usually not as cost-effective as natural foreshore vegetation at protecting coastal infrastructure (Jones *et al*., 2012). Infrastructure engineering approaches may also impair recreation and aesthetic values, enhance seaward erosion of littoral habitats, degrade water quality and impair aquatic system function (Arkema *et al*., 2013).

### *Temperate montane forest*

*Step 1a: Ecosystem description.* The Australian Alps and Southeastern Highlands Bioregions in south-eastern Australia include large areas of montane forest (Thackway & Cresswell, 1995) (Fig. 2). The dynamics of sclerophyllous montane forests are driven by infrequent high-intensity fire. Continuing supply of ecosystem services, such as erosion protection and water quality hinges upon the ability of these forests to recover from periodic severe disturbances. Montane forest communities broadly comprise two disturbance-response types: (i) forests dominated by fire-killed eucalypt 'ash' species (*Eucalyptus delegatensis* and *E. regnans*) which as obligate seeders are sensitive to inter-fire intervals shorter than the ~20-years required to reach maturity; and (ii) forest dominated by resprouting eucalypts (*E. dalrympleana*, *E. robertsonii*, *E. fastigata and E. obliqua*) which recover within a few years from even high intensity fire.

*Step 1b: Current ecosystem services.* The major land uses associated with montane forests are catchment protection (to provide water to towns), forestry and nature conservation with diverse forested vegetation types supporting bundles of ecosystem services including soil conservation, water supply, carbon sequestration, nutrient cycling, timber provision, genetic diversity, biomass production, fauna habitat, landscape aesthetics and recreation (Fig. 6).

Because most of the forested areas are public lands, management of timber harvests, fuel-reduction burns to protect adjacent or nearby property, stock grazing and the mix of production and conservation uses are




| Provisioning Services | Label | Regulating Services | Label |
|---|---|---|---|
| Sawlog Production | P1 | Groundwater Storage | R1 |
| Other Tree Products | P2 | Carbon Sequestration | R2 |
| Other Forest Products | P3 | Erosion Prevention | R3 |
| Grazing | P4 | Nutrient Regulation; Sequestration | R4 |
| Water Supply | P5 | Microclimate Regulation | R5 |
| **Biodiversity Services** | **Label** | Water Quality; Infiltration | R6 |
| Habitat | B1 | Pollination | R7 |
| Understorey Health; Regeneration | B2 | **Cultural Services** | **Label** |
| Genetic Resources | B3 | Cultural & Heritage Significance | C1 |
| Biotic Persistence; Resilience | B4 | Tourism; Recreation; Wildlife Appreciation | C2 |
| | | Spiritual; Sense of Place | C3 |

**Fig. 6** Characterization of the ecosystem services, and semi-quantitative assessment of their relative importance, for montane forests comparing current values of ash-type eucalypt forests with values under transition (scenario 3) and transformation (scenario 4) scenarios with greatly increased fire frequency.

hotly contested (Lindenmayer, 1995). For example, after extensive fire events in *E. regnans* forests, streamflow and water yields reach a maximum reduction 20–25 years after fire, only reaching their prefire levels after 100–150 years in the absence of further disturbance (Kuczera, 1987). After large fire events, salvage logging has occurred within prescriptions designed to protect water catchment values (O'Shaughnessy & Jayasuriya, 1991). These prescriptions do not account for multiple values of standing timber, including provision of breeding and roosting hollows, and carbon storage (Mackey *et al*., 2008).

*Step 2: Climate change effects.* Under climate change, the number of extreme fire weather days is expected to increase in south-eastern Australia (Hennessy *et al*., 2005; Lucas *et al*., 2007) with potential for greater number, extent and return time of large fires. There is a direct feedback between fire as a driver, the ensuing ecosystem state and maintenance of ecosystem services. Increased frequency and extent of high intensity fires may lead to a change in forest structure (scenario 2), the loss of mature forests (scenario 3), or the loss of forest and substitution with shrubby vegetation (scenario 4; Fig. 6), with alternative state-and-transition pathways dependent on the dominant eucalypt species (Table S5).

Resprouting forests are likely to maintain composition but may change structure, forming coppiced low woodlands (Stephens *et al*., 2013). Ultimately, resprouters may be replaced by seedlings, but only over hundreds of years, with a mixture of age cohorts present at any time point. In contrast, Ash-type eucalypt forests may be buffered from short-term climate and fire regime change because of their mesic understorey and low background fire frequency. However, under more severe change scenarios, with increased recurrence of catastrophic fire, a transformation is expected due to the local extirpation of these obligate seeders. The beginnings of transformation have occurred in the southern Alps (Bowman *et al.*, 2014). Ash-type eucalypt forests lack endogenous capacity to adapt locally under these fire regime scenarios.

*Step 3: Adaptation services.* Resprouting is a key functional trait supporting autonomous adaptation, enabling persistence with an increase in fire frequency, recovery after high intensity fire (Burrows, 2013; Clarke *et al.*, 2013) and underpinning the supply of ecosystem services. Species lacking this trait are far more sensitive to a shortened inter-fire interval and, where they dominate, landscapes are vulnerable to losses of ecosystem services under a future drier, hotter climate. Conversely, the ecosystem services from ash-type eucalypt forests are vulnerable to changing climate and fire regimes. These forests could become the focus of expensive, maladaptive management if there is a mismatch between the type of forest that is currently desired and the type of forest that can persist under a range of future climate and fire regime scenarios.

*Step 4: Management implications.* The risk to ecosystem services is severe because montane forests occur in upper catchments that supply water to cities and regional centres. High intensity fire in *E. regnans* forests reduces water yield, timber and biodiversity habitat. In *E. delegatensis* forests, fires in 2003, 2007, 2009, and 2013 have created patches with no regeneration (Bowman *et al.*, 2014). These areas have been aerially reseeded at a cost of ~A\$ 3000 $ha^{-1}$, but if anticipated fire regime change converts larger tracts to this denuded state, the cost of re-seeding with ash species may become prohibitive. The inherent adaptation service provided by resprouting eucalypt forests requires no active management. This means in the short-term a greater management focus on fire-sensitive Ash-type eucalypt forests, including fire suppression, fuel reduction and reseeding. However, novel approaches to management may need to be considered in the future, such as translocating seed from resprouting montane species rather than fire-sensitive ash species. The management of these systems need to be formulated within the context of multiple scenarios and competing or conflicting ecosystem service values, particularly between water yield, timber harvests and wildlife habitat (Lindenmayer & Likens, 2009).

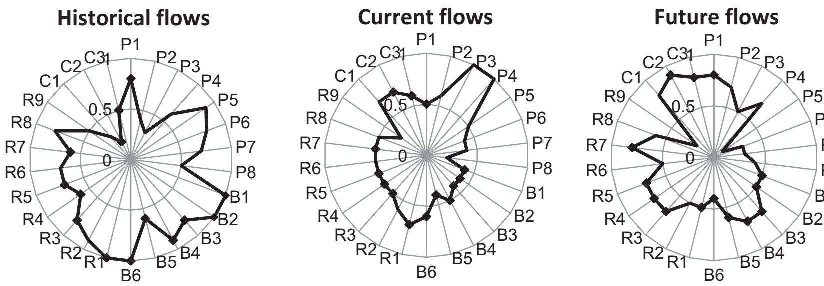
### *Inland floodplains and wetlands*

*Step 1a: Ecosystem description.* The Murray-Darling Basin covers 14% of Australia and generates 45% of the irrigated agricultural production, worth ~\$5.5 bn p.a. (MDBA, 2010). Westerly flowing rivers receive runoff from high rainfall regions to the east, undergoing irrigation diversions and high evaporative losses over long traverses across semi-arid floodplains before terminating in extensive wetlands that drain into the Darling and Murray rivers. Floodplain woodlands and forests, consisting of few flood- and drought-tolerant *Eucalyptus* and *Acacia* species (river red gum *Eucalyptus camaldulensis*, black box *E. largiflorens*, coolibah *E. coolabah*, river cooba *Acacia stenophylla*), give way to riparian woodland corridors hemmed by chenopod shrubland and grassland in more arid regions. Historically, river flows were highly variable, driven by inter-decadal ENSO cycles, with prolonged drought preceding extensive floods (Chiew *et al.*, 2008). The biota has adapted accordingly, and dry periods are needed for key ecosystem processes (Baldwin *et al.*, 2013). Due to 50–100 years of river regulation and water resource development, floods are now of lower volume, duration, extent and frequency (Sims *et al.*, 2012) and many wetlands are in poor and declining condition (Davies *et al.*, 2012).

*Step 1b: Current ecosystem services.* Floodplains supply grazing and cropping. Wetlands supply critical habitat for vegetation, waterbirds and fish, and are important for tourism, recreation, cultural and spiritual values. Rivers supply water for irrigated agriculture and domestic use and wetlands buffer the impact of floods on surrounding land and regulate nutrients, sediments and microclimate. Supply of ecosystem services from wetlands dependent on regulated river flows is via natural floods and managed releases of 'environmental flows' from dams. The impact of historical water diversions has been increased provisioning services from irrigated agriculture at the expense of biodiversity/habitat and regulating services (Fig. 7).

*Step 2: Climate change effects.* Climate change adds to stressors from water diversions. Four scenarios of climate change are considered, that represent increasing levels of rainfall reduction and aridity, frequency of extreme floods, and their consequences for cropping and grazing, all the way to a shift to rangeland grazing under the most severe scenario. Detailed information on their climate impacts and adaptation services is




| Provisioning services | Label | Regulation services | Label |
|---|---|---|---|
| Floodplain grazing | P1 | Groundwater recharge | R1 |
| Stock and domestic water supply | P2 | Carbon sequestration | R2 |
| Irrigation water supply | P3 | Mitigation of flood events | R3 |
| Food and fibre crop production | P4 | Erosion prevention and soil fertility | R4 |
| Timber production | P5 | Salinity control | R5 |
| Fishing | P6 | Nutrient regulation and sequestration | R6 |
| Wildfowl hunting | P7 | Microclimate regulation | R7 |
| Bush foods and medicines | P8 | Water quality and filtration | R8 |
| **Biodiversity and habitat services** | **Label** | Pollination | R9 |
| Tree health and regeneration | B1 | **Cultural services** | **Label** |
| Understorey health and regeneration | B2 | Cultural and heritage significance | C1 |
| Genetic/biodiversity resources | B3 | Tourism, recreation, wildlife appreciation | C3 |
| Biotic persistence and resilience | B4 | Spiritual and sense of place | C2 |
| Invasion resistance and buffering | B5 | | |
| Wetland habitat for biodiversity | B6 | | |

**Fig. 7** Characterization of the ecosystem services, and semi-quantitative assessment of their relative importance, for inland floodplains under three scenarios of river flow regimes: historical, without river regulation and water resource development; under current regulation and development and future, under climate change including Basin Plan water. Black diamonds = adaptation services.

presented in Table S6 (Supporting Information). Floodplain vegetation is structured by flood frequency and duration, with the most flood-requiring species located on the lower floodplain. Responses to climate change include contraction and compositional shifts in plant communities, fewer flood-induced breeding and regeneration events and loss of habitat for biodiversity. There will be fewer, smaller, saltier wetlands, filled less often (Nielsen & Brock, 2009). Water-demanding plants will be replaced with water-conserving ones. Areas of *E. camaldulensis* forest will thin to open woodland and be partly replaced by slower-growing, drought-tolerant *E. largiflorens* and *E. coolabah*. Floodplain extent is likely to contract, with upper zones transitioning to terrestrial grassy woodland and chenopod shrubland. Impacts on ecosystem services include declining irrigated agriculture and some increases in regulating, habitat/biodiversity and cultural services (Fig. 7).

*Step 3: Adaptation services.* Floodplain ecosystems are likely to persist under climate change, though with reduced extent and altered vegetation structure, due to the following attributes: (i) high response diversity of trees and understorey to flood and drought; (ii) drought-resistant life-cycle stages, with long-lived propagule banks; (iii) rapid growth and regeneration after rainfall and flooding (Colloff & Baldwin, 2010); (iv) resources produced during floods are sequestered to provision dry-phase biotic activity (Baldwin *et al.*, 2013); (v) high connectivity via riparia for recolonization and propagule transport. These adaptation services underpin bundles of regulating services, including flood mitigation and erosion prevention from rare, extreme rainfall events, salinity control and provision of shade and shelter. The fewer, smaller wetlands that can be maintained with environmental flows are likely to be of high biodiversity conservation value and increasingly important for bundled cultural services of tourism, recreation, heritage and spiritual values. Some wetlands will persist in a low-diversity state, with rare floods driving regeneration from propagule banks, but capable of rapid, high-productivity responses to rainfall and floods. Fodder for livestock grazing is an adaptation service likely to become increasingly important from upper floodplains that transition to drought- and salt-tolerant grassy woodland and chenopod shrubland.

*Step 4: Management implications.* To counter ecological decline, limits on water diversions and an objective of 2750 gigalitres of water restored to the environment is planned (MDBA, 2010). For scenarios 3 and 4 of an increasingly arid climate associated with much reduced river flows, along with rare, intense floods (Table S6, Supporting Information), prioritising wetlands by their likelihood of autonomous adaptation or capacity to shift to alternate stable states will be needed. Future environmental flow management will include cessation of delivery to wetlands unlikely to persist long-term and inclusive, adaptive community and governance arrangements. As less irrigation water is available, dryland agriculture, grazing and mixed income approaches will emerge and their impacts be managed. Lake Eyre, west of the Murrray-Darling Basin, is a dry salt lake most of the time. It filled in 2010–2011, stimulating high-value tourism and recreation (Lockyer, 2012), providing an example of how wetlands enhance cultural values, even in arid landscapes.

## Discussion

The four case studies illustrate the operational application of the adaptation services concept (Fig. 1) to contrasting ecosystems and climatic regions. They highlight the versatility of the framework across bioclimatic conditions, land use types, ecosystem service bundles, and likely ecological response pathways to anticipated climate change. Beyond their diversity, they illustrate common functional mechanisms that we hypothesize are generic to adaptation services. Below we synthesize these mechanisms before considering their implications for the selection of methods to quantify adaptation services. Lastly, we discuss how the new concept of adaptation services and knowledge about intrinsic biophysical mechanisms can inform management and decision-making in adapting to a variable and uncertain future.

### *Trajectories of ecosystem change under worsening climate change and types of adaptation services*

The four case studies illustrate trajectories for ecosystems with different initial resistance and disturbance regimes (Fig. 2). Grassy woodlands, inland floodplains and fire-driven montane forests have already been modified during historical and recent times (e.g. the 1997–2010 Millennium Drought). Grassy woodlands are expected to gradually transform under climate changes and ultimately reach critically dry conditions, with vegetation only suitable for rangeland grazing. Floodplains are expected to reach a tipping point where water availability no longer meets environmental requirements, so that wetlands contract in area and upper floodplains transform to terrestrial ecosystems. Resprouting montane forests may gradually change structurally while maintaining their characteristic species, but the probability and timing of transformation to a complex mosaic comprising native trees and shrubs, and even exotic grass-dominated vegetation need to be considered as core uncertainties. In contrast, pathways for stands dominated by fire-killed Ash are highly sensitive to management. If regenerating stands in surrounding forests are protected then gradual change would be possible, but if fire recurs within the 20-year maturation period then an abrupt transformation to shrubland would be inevitable.

Contrasting with these cases of initial gradual dynamics, littoral rainforest can readily shift to an alternative community state with a highly simplified structure and low diversity, particularly in the presence of exotic transformer weeds, as soon as an unprecedented combination of disturbance events occurs, such as a series of cyclones in rapid succession or cyclone followed by fire. These alternative states may provide dune stabilization and erosion prevention, but at the expense of biodiversity/habitat services and cultural and aesthetic services.

The four case studies highlight three types of adaptation services, i.e. *benefits to people from increased social ability to respond to change, provided by the capacity of ecosystems to moderate and adapt to climate change and variability*: attributes that (i) allow ecosystems to resist or cope in the face of direct and indirect impacts of climate change; or (ii) transform autonomously to a state that supports social adaptation, especially by being responsive to management that fosters new bundles of ecosystem services and (iii) support new valuable ecosystem services, including ones currently supplied but less-valued or in demand. The first type prevails across all case studies and is expected to be an important feature of climate change adaptation across many ecosystems. As detailed in the next section, it is underpinned by mechanisms relating to ecological resilience (Holling, 1973). Examples for the second type are provided by resprouting trees replacing Ash-type eucalypt stands in montane forest, and the role of other keystone functional groups such as perennial tussocks in grassy woodlands. Landscape connectivity also recurs as a critical process for this second type. Here, adaptation services rely on ecological transformability rather than resilience mechanisms (Walker *et al*., 2004). Instances of the third type include climate regulation in grassy woodlands, coastal buffering by littoral rainforest and the increasing importance of regulating services and novel cultural values and grazing resources on floodplains. More generally, and as noted in previous ecosystem-based adaptation literature (Jones *et al*., 2012; Pramova *et al*., 2012) the value of regulating services will increase and new food, fibre and fuel sources will

**Table 2** Synthesis of functional mechanisms underpinning adaptation services

| Case study | Grassy woodlands | Floodplains | Montane forests | Littoral rainforests |
|---|---|---|---|---|
| Structural/life form diversity | Yes | No | Yes | Yes |
| Keystone species/ functional groups | Perennial tussock grasses | Keystone acacia, eucalypt species | Resprouter/seeder | Canopy-forming Lauraceae, Myrtaceae |
| Climate response diversity within: | All life forms and especially perennial grasses | Keystone acacia, eucalypt and understorey spp. | Resprouting species | All life forms |
| Disturbance response diversity | Diversity of regeneration responses | Diversity of survival and persistence responses | Resprouters: Diversity of regeneration responses Seeders: No | Diversity of responses to wind and inundation and regeneration responses |
| Landscape connectivity | Propagule flow | Biogeochemical flow | No | Propagule flow |

become available to societies in various ecosystems undergoing climate-driven transformation. In this last case, not only are ecological resilience and transformability necessary, but also social adaptation (Adger *et al.*, 2005) enabling new values for existing or emerging ecosystem attributes.

### *Functional mechanisms underpinning adaptation services*

Table 2 summarizes five recurring functional mechanisms across the four case studies. Vegetation structure, its complexity and structural diversity appeared critical in all case studies, except floodplains, for the future maintenance of current ecosystem services by buffering climate change effects.

The dynamics of all systems hinge on the persistence of keystone species or functional groups carrying a syndrome of traits which shape the ecosystem across trophic levels and have strong effects on nearly all current ecosystem services. Examples include perennial tussocks in grassy woodlands, eucalypt resprouters in montane forests as well as canopy-forming species in littoral rainforest and floodplains. We assume that they would be critical to adaptation by supporting ecological resilience, while their local extinction would readily lead to transformation. Thus, a high risk is associated with their climate responses and possible range shifts, especially in the case of one or a few keystone species such as the drought-, flood- and salinity-tolerant trees on floodplains. Conversely, their response diversity to climate through range shifts among species or replacement by more arid-adapted species could be a strong component of coping and transition. Overall, we hypothesize that in all systems, response diversity to climate, combined with functional redundancy for ecosystem services results in greater ecological resilience (Walker *et al.*, 1999), and thereby supports the realization of adaptation services. This hypothesis could be tested across a greater number of case studies, and by analyzing responses to recent increased climate variability or to historical extremes.

We noted that disturbance response diversity, i.e. the presence of species with diverse survival and regeneration responses, was involved in acclimation or coping. Relevant traits include high diversity of germination cues (all systems), varying fire tolerance and resprouting abilities (all systems), response diversity to cyclones in littoral rainforest, or to management and drought in grassy woodlands and floodplains. Response diversity can mediate ecological transformation in several ways: (i) through shifting contributions of different species groups (Table 1, Figure S1 for grassy woodlands; see also Tables S4 for littoral rainforests and S6 for floodplains); (ii) through response diversity within keystone functional groups of grassy woodlands, montane forests and floodplains and (iii) through generic response diversity in the absence of keystone functional groups (littoral rainforests).

Landscape connectivity is already adaptive currently and sustains multiple ecosystem services (Mitchell *et al.*, 2013). It is expected to play a key role in ecological transformation of fragmented systems like grassy woodlands and littoral rainforests through its effects on propagule flows that are necessary for disturbance responses and for migration of climatically suitable species. Connectivity is critical for floodplains whereby carbon, nutrients and propagules are distributed via water flows (Baldwin *et al.*, 2013). Alternatively, increased connectivity in relation to fire in montane forests would result in greater rather than lesser impacts where obligate-seeders dominate.

### *Functional assembly mechanisms supporting adaptation services*

Assembly of future communities remains problematic for prediction of future biodiversity and ecosystem functioning (Boulangeat *et al.*, 2012). Elucidating assembly mechanisms will be critical for understanding and quantifying adaptation services. New communities will assemble following species range shifts, first within response groups like resprouters in fire-driven systems or gradual integration of semi-arid species into grassy woodland communities. In these cases, functional redundancy within these response groups will support adaptation services. Next, in contrast with gradual increase or decrease of specific life forms or functional groups (e.g. transition to fire-tolerant species in rainforest or montane forests under changed fire regimes), transformation will require immigration by, or dominance of, species with novel traits where previously dominant traits have been lost. Novel ecosystems containing exotic species, following extinction of dominant native species, are likely to become commonplace (Hobbs *et al.*, 2006). Also, ecosystems may be engineered for adaptation using dominant species with traits that support desired ecosystem services, for example using a species framework approach (Tucker & Murphy, 1997) as done for restoration of littoral rainforests (Goosem & Tucker, 2013).

### *Quantifying adaptation services*

Quantifying adaptation services will be required for scenario predictions and adaptive management. Knowledge of ecological mechanisms and functional traits is likely to facilitate this challenging task. Below we identify three avenues for the development of quantitative approaches.

Step 1 in the operational framework highlights the importance of historical context. Its analysis identifies whether adaptation services are present or have been compromised by past management or recent climate change (e.g. a mean 0.9 °C increase for Australia since 1910; CSIRO & Bureau of Meteorology 2012) or, in the case of floodplains, major water diversions for irrigation. Consideration of history informs which adaptation services should be maintained or restored under climate change. For instance, for grassy woodlands, adaptation services are supported by relatively intact perennial-dominated communities, but these have largely been lost through historical management (Fig. 3).

Once adaptation services have been identified (Step 3), they can be quantified by transfer of values depending on ecosystem state, or by modelling supporting services and processes like net primary productivity and nutrient cycling (Crossman *et al.*, 2013). Considering the covarying nature of ecosystem services, and their linkages to supporting services (Bennett *et al.*, 2009), we recommend systemic approaches to quantify bundles of ecosystem services that include adaptation services. An intermediate level of modelling sophistication could be achieved by predictive mapping of landscape 'hot spots' that are critical for adaptation services (see e.g. Qiu & Turner, 2013 for relevant methodology), for example when linked to particular functional groups such as Ash eucalypt species in montane forests.

Lastly, landscape configuration effects will need to be considered. These can be implicit through the proportions of different vegetation states, which can be linked to connectivity and the functional quality of the landscape [Smith *et al.* (2013) for grassy woodlands; Fahrig *et al.* (2011) for agricultural landscapes], or the presence of refugia. Spatially explicit modelling will be required to account for adaptation services linked to processes like fire propagation, river flows, storm energy interception or species migration.

### *Management of adaptation services*

Implicit to increasing severity of climate change is the shifting nature of risk profiles which will be increasingly characterized by extreme events, unpredictability and coincident novel events. The unpredictable, changing nature of risks will necessitate that approaches to planning, development and management change focus from optimising returns to managing those risks, including management of ecosystems for their adaptation services. Since many changes in ecosystem properties and adaptation services will be emergent, an adaptive learning and management approach is necessary, as suggested for managing future ecosystem services (Cowling *et al.*, 2008). With our four case studies we identified three types of management for adaptation services.

As the first priority, management should identify and protect existing adaptation services such as those that occur in ecosystems in good condition. Secondly, degraded but existing adaptation services can be restored by supporting establishment of key functional groups of the vegetation matrix and restoring drivers and regimes. The former will serve biodiversity conservation objectives (McIntyre, 2008) and adaptation needs simultaneously. The latter applies to the management of environmental flows, as outlined by the Murray-Darling Basin Plan (MDBA, 2010) or altered fire regimes (Bradstock *et al.*, 2012). Lastly, novel management will be needed for emergent adaptation services, e.g. adaptive management of environmental water to high-priority wetlands likely to persist under climate change. Beyond this sequence, the novel context of climate change will require prioritization in adaptation service management, for instance managing fire in dry forest to protect humid, sensitive Ash-type eucalypt forest patches. For adaptation service management to be successful, social adaptation is required including specific actions for managers, new knowledge and technology and transformation of whole industries.

Adaptation service management may be incorporated into biodiversity conservation strategies when it has benefits for nonutilitarian biodiversity values (e.g. response diversity within non-iconic species groups), or when managing for iconic biodiversity (e.g. vertebrates in montane forests, birds and bats in littoral rainforest) and promotes ecosystem states commensurate with adaptation services.

Finally, the focus on adaptation services should help avoid maladaptive management trajectories, for example the use of environmental water allocations for floodplains that cannot be sustained in the long-term because of likely transition to terrestrial ecosystems, or the reseeding of fire-killed eucalypt Ash stands when risk from recurring fire increases. In montane forests, a hierarchy of strategies may be required such as prioritizing controlled fire management in areas from timber production to water production, managing dryer forest types more intensively than wet types, or potentially reseeding resprouting species with desirable adaptive properties into some fire killed Ash stands.

## Conclusion

The broadened concept of adaptation services we present moves beyond that currently proposed in the literature under Ecosystem Based Adaptation (EBA) by focusing on the understanding of key ecological mechanisms and traits supporting the intrinsic capacity of ecosystems to adapt to change. While EBA highlighted how ecosystems can support new valuable ecosystem services under climate change, we have demonstrated the additional value of ecosystems in good condition for: (i) allowing ecosystems to resist or cope in the face of climate change direct and indirect impacts or (ii) transforming autonomously to a state that supports social adaptation. This novel perspective provides direction and focus for climate change research and ecosystem modelling relevant for the exploration of social adaptation pathways. While this article provides a deliberate focus on biophysical knowledge, next steps will also need to consider economic, institutional and social mechanisms for adaptation services.

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## References


Abson DJ, Termansen M (2011) Valuing ecosystem services in terms of ecological risks and returns. *Conservation Biology*, **25**, 250–258.

Adger NW, Arnell NW, Tompkins EL (2005) Successful adaptation to climate change across scales. *Global Environmental Change*, **15**, 77–86.

Arkema KK, Guannel G, Verutes G *et al*. (2013) Coastal habitats shield people and property from sea-level rise and storms. *Nature Climate Change*, **3**, 913–918.

Baldwin D, Rees G, Wilson J, Colloff M, Whitworth K, Pitman T, Wallace T (2013) Provisioning of bioavailable carbon between the wet and dry phases in a semi-arid floodplain. *Oecologia*, **172**, 539–550.

Bennett EM, Peterson GD, Gordon LJ (2009) Understanding relationships among multiple ecosystem services. *Ecology Letters*, **12**, 1394–1404.

Boulangeat I, Gravel D, Thuiller W (2012) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, **15**, 584–593.

Bowman DMJS, Murphy BP, Neyland DLJ, Williamson GJ, Prior LD (2014) Abrupt fire regime change may cause landscape-wide loss of mature obligate seeder forests. *Global Change Biology*, **20**, 1008–1015.

Bradstock RA, Williams RJ, Gill AM (2012) *Flammable Australia: Fire Regimes, Biodiversity and Ecosystems in a Changing World*. CSIRO Publishing, Melbourne.

Burrows GE (2013) Buds, bushfires and resprouting in the eucalypts. *Australian Journal of Botany*, **61**, 331–349.

Chiew FHS, Teng J, Kirono D *et al*. (2008) Climate data for hydrologic scenario modelling across the Murray-Darling Basin. A report to the Australian government from the CSIRO Murray-Darling Basin sustainable yields project. CSIRO, Canberra. Available at: http://www.csiro.au/science/MDBSY.html (accessed 22 March 2014).

Clarke PJ, Lawes MJ, Midgley JJ *et al*. (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist*, **197**, 19–35.

Colloff MJ, Baldwin DS (2010) Resilience of floodplain ecosystems in a semi-arid environment. *The Rangeland Journal*, **32**, 305–314.

Cowling RM, Egoh B, Knight AT *et al*. (2008) An operational model for mainstreaming ecosystem services for implementation. *Proceedings of the National Academy of Sciences*, **105**, 9483–9488.

Crossman ND, Burkhard B, Nedkov S *et al*. (2013) A blueprint for mapping and modelling ecosystem services. *Ecosystem Services*, **4**, 4–14.

CSIRO, Bureau of Meteorology (2012) *State of the Climate - 2012*. CSIRO, Canberra.

Davies PE, Stewardson MJ, Hillman TJ, Roberts JR, Thoms MC (2012) *Sustainable Rivers Audit 2: The Ecological Health of Rivers in the Murray-Darling Basin at the End of the Millennium Drought (2008–2010)*. Vols. 1 & 2. MDBA Publication No. 72/12, Murray-Darling Basin Commission, Canberra.

Dickie IA, Yeates GW, St. John MG *et al*. (2011) Ecosystem service and biodiversity trade-offs in two woody successions. *Journal of Applied Ecology*, **48**, 926–934.

Dorrough J, Moxham C, Turner V, Sutter G (2006) Soil phosphorus and tree cover modify the effects of livestock grazing on plant species richness in Australian grassy woodland. *Biological Conservation*, **130**, 394–405.

Dorrough J, McIntyre S, Scroggie MP (2011) Individual plant species responses to phosphorus and livestock grazing. *Australian Journal of Botany*, **59**, 669–680.

Environment Planning (2011) *Queensland Coastal Plan*. Department of Environment and Resource Management, Queensland Government, Brisbane.

Fahrig L, Baudry J, Brotons L *et al*. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, **14**, 101–112.

Gammage B (2011) *The Biggest Estate on Earth: how Aborigines Made Australia*. Allen and Unwin, Sydney.

Goosem S, Tucker NIJ (2013) *Repairing the Rainforest*. Wet Tropics Management Authority, Cairns.

Grigulis K, Lavorel S, Krainer U *et al*. (2013) Combined influence of plant and microbial functional traits on ecosystem processes in mountain grasslands. *Journal of Ecology*, **101**, 47–57.

Havstad KM, Peters DPC, Skaggs R *et al*. (2007) Ecological services to and from rangelands of the United States. *Ecological Economics*, **64**, 261–268.

Hennessy K, Lucas C, Nicholls N, Bathols J, Suppiah R, Ricketts J (2005). *Climate Change Impacts on Fire-Weather in South-East Australia*. CSIRO Marine and Atmospheric Research/Bushfire CRC/Australian Bureau of Meteorology, Melbourne.

Hobbs RJ, Yates CJ (2000) *Temperate Eucalypt Woodlands in Australia: Biology, Conservation*. Management and Restoration. Surrey Beatty & Sons, Sydney.

Hobbs RJ, Arico S, Aronson J *et al.* (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.

Holling CS (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, **4**, 1–23.

Jones HP, Hole DG, Zavaleta ES (2012) Harnessing nature to help people adapt to climate change. *Nature Climate Change*, **2**, 504–509.

Kellner JR, Asner GP (2009) Convergent structural responses of tropical forests to diverse disturbance regimes. *Ecology Letters*, **12**, 887–897.

Kuczera GA (1987) Prediction of water yield reductions following a bushfire in ash-mixed species eucalypt forest. *Journal of Hydrology*, **94**, 215–236.

Lamarque P, Lavorel S, Mouchet M, Quétier F (2014) Plant trait-based models identify direct and indirect effects of climate change on bundles of grassland ecosystem services. *Proceedings of the National Academy of Sciences*, in press.

Lavorel S, Grigulis K, Lamarque P *et al.* (2011) Using plant functional traits to understand the landscape-scale distribution of multiple ecosystem services. *Journal of Ecology*, **99**, 135–147.

Lindenmayer DB (1995) Forest disturbance, forest wildlife conservation and the conservative basis for forest management in the mountain ash forests of Victoria—comment. *Forest Ecology and Management*, **74**, 223–231.

Lindenmayer DB (2011) *What Makes a Good Farm for Wildlife?* CSIRO Publishing, Melbourne.

Lindenmayer DB, Likens GE (2009) Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends in Ecology & Evolution*, **24**, 482–486.

Lockyer P (2012) *Lake Eyre: A Journey Through the Heart of the Continent*. Harper Collins, Sydney.

Lucas C, Hennessy K, Mills G, Bathols J (2007) *Bushfire Weather in Southeast Australia: Recent Trends and Projected Climate Change Impacts*. Consultancy Report Prepared for the Climate Institute of Australia. Bushfire CRC/Australian Bureau of Meteorology, Melbourne.

Luck GW, Harrington R, Harrison PA *et al.* (2009) Quantifying the contribution of organisms to the provision of ecosystem services. *BioScience*, **59**, 223–236.

Mackey BG, Keith H, Berry SL, Lindenmayer DB (2008) *Green Carbon: The Role of Natural Forests in Carbon Storage. Part 1, a Green Carbon Account of Australia's South-Eastern Eucalypt Forests and Policy Implications*. ANU E Press, Canberra.

McIntyre S (2008) The role of plant leaf attributes in linking land use to ecosystem function in temperate grassy vegetation. *Agriculture, Ecosystems and Environment*, **128**, 251–258.

McIntyre S (2011) Ecological and anthropomorphic factors permitting low-risk assisted colonization in temperate grassy woodlands. *Biological Conservation*, **144**, 1781–1789.

McIntyre S, Lavorel S (2007) A conceptual model of land use effects on the structure and function of herbaceous vegetation. *Agriculture, Ecosystems and Environment*, **119**, 11–21.

MDBA (2010) *Guide to the Proposed Basin Plan. Volume 1: Overview*. MDBA Publication No. 60/10. Murray-Darling Basin Authority, Canberra.

Metcalfe DJ, O'Malley T, Lawson TJ, Ford AJ (2013) Mapping littoral rainforest & coastal vine thickets of eastern Australia in the wet tropics: Mission Beach pilot study. Report to the National Environmental Research Program. Reef and Rainforest Research Centre Ltd, Cairns. Available at: http://www.nerptropical.edu.au/research (accessed 22 March 2014).

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington.

Mitchell MGE, Bennett EM, Gonzalez A (2013) Linking landscape connectivity and ecosystem service provision: current knowledge and research gaps. *Ecosystems*, **16**, 894–908.

Mokany K, Ash J, Roxburgh S (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, **96**, 884–893.

Nidumolu UB, Hayman PT, Howden SM, Alexander BM (2012) Re-evaluating the margin of the south Australian grain belt in a changing climate. *Climate Research*, **51**, 249–260.

Nielsen DL, Brock MA (2009) Modified water regime and salinity as a consequence of climate change: prospects for wetlands of southern Australia. *Climatic Change*, **95**, 523–533.

Noble IR, Slatyer RO (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, **43**, 5–21.

O'Shaughnessy PJ, Jayasuriya MDA (1991) Managing the ash type forests for water production in Victoria. In: *Forest Management in Australia* (eds McKinnell FH, Hopkins ER, Fox JED), pp. 341–363. Institute of Foresters Australia/Surrey Beatty & Sons, Sydney.

Perrings C, Duraiappah AK, Larigauderie A, Mooney HA (2011) The biodiversity and ecosystem services science-policy interface. *Science*, **331**, 1139–1140.

Pramova E, Locatelli B, Djoudi H, Somorin OA (2012) Forests and trees for social adaptation to climate variability and change. *Wiley Interdisciplinary Reviews: Climate Change*, **3**, 581–596.

Prober SM, Lunt ID (2009) Restoration of *Themeda australis* swards suppresses soil nitrate and enhances ecological resistance to invasion by exotic annuals. *Biological Invasions*, **11**, 171–181.

Prober SM, Thiele KR, Rundel PW *et al*. (2012) Facilitating adaptation of biodiversity to climate change: a conceptual framework applied to the world's largest Mediterranean-climate woodland. *Climatic Change*, **110**, 227–248.

Qiu J, Turner MG (2013) Spatial interactions among ecosystem services in an urbanizing agricultural watershed. *Proceedings of the National Academy of Sciences*, **110**, 12149–12154.

Quétier F, Thébault A, Lavorel S (2007) Linking vegetation and ecosystem response to complex past and present land use changes using plant traits and a multiple stable state framework. *Ecological Monographs*, **77**, 33–52.

Scheffer M (2009) *Critical Transitions in Nature and Society*. Princeton University Press, Princeton, NJ.

Schellnhuber HJ, Hare W, Serdeczny O *et al*. (2012) *Turn down the heat: why a 4°C warmer world must be avoided*. A Report for the World Bank by the Potsdam Institute for Climate Impact Research and Climate Analytics. The World Bank, Washington, DC.

Sharpley AN (1995) Soil phosphorus dynamics: agronomic and environmental impacts. *Ecological Engineering*, **5**, 261–279.

Shepard CC, Crain CM, Beck MW (2011) The protective role of coastal marshes: a systematic review and meta-analysis. *PLoS ONE*, **6**, e27374.

Sims NC, Chariton A, Jin H, Colloff MJ (2012) A classification of floodplain ecosystems in the Murray-Darling Basin based on changes in flooding between pre-regulation and current conditions. *Wetlands*, **32**, 239–248.

Smith FP, Prober SM, House APN, McIntyre S (2013) Maximizing retention of native biodiversity in Australian agricultural landscapes - the 10:20:40:30 guidelines. *Agriculture, Ecosystems and Environment*, **16**, 35–45.

Stephens SL, Agee JK, Fule PZ, North MP, Romme WH, Swetnam TW (2013) Managing forests and fire in changing climates. *Science*, **342**, 41–42.

Stafford Smith M, Horrocks L, Harvey A, Hamilton C (2011) Rethinking adaptation for a 4 °C world. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **369**, 196–216.

Suppiah R, Watterson IG, Macadam I, Collier MA, Bathols J (2010) Climate change projections for the tropical rainforest region of north Queensland. Final report on MTSRF activities, 2006–2010. Report prepared for the Marine and Tropical Sciences Research Facility (MTSRF) Research Report Series. Reef and Rainforest Research Centre Ltd, Cairns. Available at: http://www.rrrc.org.au/publications/research_reports.html (accessed 22 March 2014).

Thackway R, Cresswell ID (eds.) (1995) *An Interim Biogeographic Regionalisation for Australia: A Framework for Setting Priorities in the National Reserve System Cooperative Program. Version 4.0*. Australian Nature Conservation Agency, Canberra.

Tucker NIJ, Murphy TM (1997) The effects of ecological rehabilitation on vegetation recruitment: some observations from the wet tropics of Queensland. *Forest Ecology and Management*, **99**, 133–152.

Walker B, Kinzig A, Langridge J (1999) Plant attribute diversity, resilience and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, **2**, 95–113.

Walker B, Holling CS, Carpenter SR, Kinzig A (2004) Resilience, adaptability and transformability in social–ecological systems. *Ecology and Society*, **9**, 5.

Wamsley TV, Cialone MA, Smith JM, Atkinson JH, Rosati JD (2010) The potential of wetlands in reducing storm surge. *Ocean Engineering*, **37**, 59–68.

Williams KJ, Dunlop M, Bustamante RH *et al*. (2012) *Queensland's biodiversity under climate change: impacts and adaptation - synthesis report*. A Report Prepared for the Queensland Government, Brisbane. CSIRO Climate Adaptation Flagship, Canberra.

World Bank (2010) *Convenient Solutions to an Inconvenient Truth - Ecosystem-Based Approaches to Climate Change*. The World Bank, Washington, DC.

Zweig CL, Kitchens WM (2009) Multi-state succession in wetlands: a novel use of state and transition models. *Ecology*, **90**, 1900–1909.

## Supporting Information

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

**Appendix S1.** Ecosystem attributes, functions and services associated with different vegetation states in the temperate eucalypt grassy woodlands of southeastern Australia.
**Table S1.** Summary of ecosystem functions and attributes. References relevant to more than two states are listed under the function name.
**Table S2.** Summary of ecosystem services that may be associated with five major land uses in the temperate grassy eucalypt ecosystems. Values are those associated with the functional state of the ground layer vegetation. References relevant to more than two states are listed under the value name.
**Table S3.** Semi-quantitative translation of data from Table S2 using a categorical scale of increasing provision (1–5).
**Figure S1.** Hypothetical response of plant groups to increasing aridity in the eucalypt grassy woodland biome. Native species are predicted to increase initially with increasing drought stress, while more mesic adapted exotics may decline. At a critical level of heat and dryness, locally adapted species could potentially be replaced by semi-arid species in adjoining regions assuming dispersal is not limiting.
**Appendix S2.** Data for the adaptation service assessment in littoral rainforests, montane forests and the Murray-Darling Basin floodplains
**Table S4.** Description for the littoral rainforest system of climate and management scenarios, impacts on ecosystem state and processes, adaptation services and their supporting attributes and mechanisms, and management needs for each of the four change types of increasing severity. Arrows indicate increasing importance of specific attributes across scenarios.
**Table S5.** Description for the montane forests system of climate and management scenarios, impacts on ecosystem state and processes, adaptation services and their supporting attributes and mechanisms, and management needs for each of the four change types of increasing severity. Arrows indicate increasing importance of specific attributes across scenarios.
**Table S6.** Description for the inland floodplains and wetlands of climate and management scenarios, impacts on ecosystem state and processes, adaptation services and their supporting attributes and mechanisms, and management needs for each of the four change types of increasing severity. Arrows indicate increasing importance of specific attributes across scenarios.