Understanding ecosystem dynamics in South Australia's arid lands: a framework to assist biodiversity conservation

Allen P. McIlwee[A,B,E], *Daniel Rogers*[B,D], *Phil Pisanu*[B], *Robert Brandle*[C] *and John McDonald*[B]

[A]Australian Wildlife Research and Monitoring Services, SA 5163, Australia.

[B]Landscapes Team, Science Monitoring and Knowledge, South Australian Department of Environment, Water and Natural Resources, SA 5001, Australia.

[C]Sustainable Landscapes, South Australian Arid Lands Region, South Australian Department of Environment, Water and Natural Resources, SA 5700, Australia.

[D]School of Earth and Environmental Sciences, University of Adelaide, Adelaide, SA 5005, Australia.

[E]Corresponding author. Email: mcil0024@flinders.edu.au

Abstract. Determining what level of investment is required, and where and how it is used, to maintain biodiversity across vast areas is difficult. In response to this challenge, the South Australian Department of Environment, Water and Natural Resources has developed an information framework known as the 'Aridlands Landscape Assessment Framework' (ALAF) to provide a systematic basis for identifying landscape-specific, coarse-filter priorities for conservation investment across the arid zone. The ALAF is an analytical and conceptual framework that seeks to define ecosystem components and ecological processes operating at a landscape level, and understand where these processes are not meeting the requirements of extant biodiversity. This requires a systematic process to identify plant communities that occur in distinct biophysical settings. The next step is to document the dynamic processes that drive change within these communities in space and time. When coupled with knowledge of the requirements of indicator flora and fauna, this understanding will allow identification of those components that are at greatest risk, where, and for what reasons. This paper provides an overview of each step in the ALAF process and outlines how the framework has been used thus far to inform conservation planning across Witjira National Park.

Introduction

In many regions across the globe, the extent of conservation issues requiring attention far exceeds our current capacity to address them (Gilbert 2010; Chandra and Idrisova 2011). There is a need, therefore, to prioritise conservation activity to ensure that limited resources are used effectively. Ideally, such planning should be iterative and fit within an adaptive management framework that effectively links design, implementation, and evaluation in such a way that each phase informs the next (Hobbs 2007; Lindenmayer *et al.* 2008). A key requirement of such planning is the establishment of clearly articulated goals that form the basis of conservation activity (Wilson *et al.* 2006; Bottrill *et al.* 2008). Goals should be specific, measurable, achievable, realistic, and time-bound (Possingham 2001; Mace *et al.* 2006). In addition, there is widespread acknowledgement that conservation goals also need to be specific to a particular context, such that the goals are designed to address the conservation requirements of a particular landscape in terms of its socio-ecological setting (Failing and Gregory 2003; Hobbs 2007; Miller and Hobbs 2007). In particular, intervention should focus on modifying

ecological processes that are operating in such a way that the requirements of dependent biota are not being met. In the absence of clearly articulated, context-specific goals, there is a significant risk that our capacity to implement nature conservation activity will be inappropriately targeted, and fail to address the issues associated with ongoing biodiversity decline.

Identifying the ecological processes associated with decline is particularly problematic in arid ecosystems, due to the inherently dynamic spatial and temporal nature of these ecosystems. Many of the management issues in rangelands are complex by their nature (Boyd and Svejcar 2009), which influences how we approach them. Management and science often interact on a problem-by-problem basis. This relationship can provide tangible answers to simple problems, but does not lend itself to addressing complex problems, the nature of which varies in both space and time. To address complex problems, Boyd and Svejcar (2009) argue that science and management need to interact on a more continuous basis to iteratively refine both our knowledge of the ecology of the problem and the results of 'on the ground' application of that

knowledge (Holling 1978). Many studies that attempt to understand the processes underlying complex problems do not translate into 'on the ground' solutions, and even where they do, the spatial/temporal applicability of such solutions is likely to be limited to specific areas and/or conditions, and cannot be applied generically across the whole system.

The dynamics of rangelands are complex due to the temporal and spatial variation in soils, vegetation, climate, and history. They also cover large areas, so the extrapolation of insights gained from the analysis of a few sites can be misleading. It is also difficult to identify cause and effects because climate is the major driver of change, and often masks the direct impacts of prevailing land uses, such as livestock grazing, and other management practices.

This paper attempts to bring some rigour to the question of how to target investment in natural resource management, and at what level, in order to maintain biodiversity across large areas of the arid zone. Here we have developed a framework for the management of biodiversity in arid rangelands that is designed to answer the question: Is this landscape operating within a safe operating space that ensures the persistence of dependent biota? The framework has been developed to meet the requirements of conservation planning in the South Australian rangelands, but has the potential to be applied beyond South Australia, depending on need and data availability. We also present a working case study for the Witjira sub-region of the Interim Biogeographic Regionalisation for Australia (IBRA; Thackway and Creswell 1995) in the north of southern Australia.

The Aridlands Landscape Assessment Framework

As suggested above, nature conservation programs require an understanding of where intervention is required to prevent the loss of native biota. The primary purpose of the Aridlands Landscape Assessment Framework (ALAF) is to provide a framework that, when populated, provides this understanding for arid landscapes of interest.

Figure 1 outlines the information components that comprise an aridlands landscape assessment, and how they interact to support nature conservation planning. The ALAF essentially comprises four analytical components:

(i) Patch-scale description of geophysical settings and ecosystem dynamics;

(ii) Spatial extrapolation of these patch-scale descriptions, to describe the extent and configuration of physical settings and alternate system dynamics (alternate states);

(iii) Analysis of dependent species' requirements, and nesting of these to determine systemic conservation requirements of a landscape's biota;

(iv) Synthesis of (*i*)–(*iii*) to determine where a landscape is operating within acceptable limits (from the perspective of dependent biota), and where a landscape appears to be approaching critical thresholds at which intervention is required.

The patch-scale descriptions require an understanding of both the relationship between biota and the physical (soil, topography, and geology) environment, and how environmental history determines the ecological dynamics of these different biophysical environments. Here, we have presumed that the
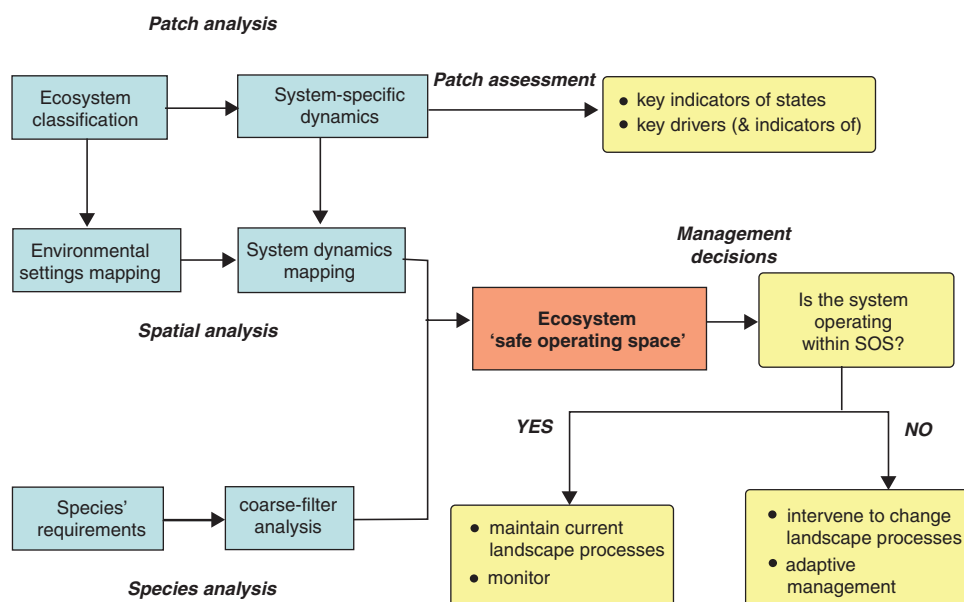

Fig. 1. Schematic diagram describing the steps involved in the Arid Landscape Assessment Framework. Blue boxes describe information components of the framework. The orange box synthesises this information to describe the limits of acceptable change ('safe operating space') for an ecosystem, in terms of the distribution of different ecosystem states (i.e. the area and configuration of alternate states) under conditions where the requirements of dependent biota are being met. Yellow boxes refer to questions that are asked by comparing this information to the current distribution of alternate ecosystem states, either to guide management response or to identify indicators for patch-scale assessment.

nature of these dynamics is at least partly nested within the bounds of the geophysical settings within which they occur (forming a hierarchy); that is, the ecological response to disturbance and land use will at least partly depend upon the physical environment within which this disturbance occurs.

From the perspective of understanding the ecological requirements of dependent biota, however, we need to understand not only the dynamics of ecosystems at the scale of individual patches, but also the spatial extent and configuration over which different biotic expressions of these dynamics occur. Viable populations almost invariably require a minimum area (Connor *et al*. 2000) and a particular configuration of important habitat types such that adequate resources are available. The patch-scale dynamics described in (*i*) above thus need to be extrapolated spatially, using spatial analyses of remotely sensed datasets.

The third component focuses on developing conceptual models of species' ecological requirements within landscapes of interest. A key step here is to translate these conceptual models in such a way that the requirements of different species can be interpreted in the context of the ecosystem dynamics models described in (*i*), and the spatial extent and configuration of patches described in (*ii*). Species for which adequate information are available can be grouped together based on their common association with ecosystems or groups of ecosystems. This is akin to grouping species on the basis of shared habitat requirements, with "habitat" being described in such a way that it meets the 'coarse-filter' requirements of a landscape's biota; Noss 1987).

The steps described in this framework lead to an understanding of where in a landscape ecological processes are operating to support dependent biota (i.e. high resilience) versus where processes have been modified in such a way that the dynamics of ecosystems will not continue to support dependent biota (i.e. low resilience) and, therefore, where conservation intervention is required. Obtaining this understanding for a landscape of interest will be critical for guiding conservation investment, as it will improve our ability to invest in components of the landscape that are both at highest risk of potentially irreversible, deleterious change, and where we can most expect a beneficial response to intervention.

The ALAF has been developed by applying a range of well-established ecological concepts, particularly hierarchy theory and threshold dynamics. Some of these concepts have been applied to the management of rangeland ecosystems with some success. However, to our knowledge, linking system dynamic models (such as state-and-transition models) to the requirements of dependent biota in particular rangeland landscapes has not been explicit. The ALAF provides such an approach that attempts to make these links explicit for particular landscapes.

The framework rests on the assumption that, within a given landscape, biodiversity is organised hierarchically, where the ecological responses to dynamic processes are nested within the physical environmental variation (e.g. soil, topography, and geology). These physical and dynamic processes can be described at a 'patch' (contiguous areas that are homogenous with regard to their physical environment and environmental history) scale and, where adequate spatial data are available, extrapolated to understand the spatial extent and distribution of ecosystems and ecosystem states. Once the dynamics of different ecosystems

within a landscape are described (and mapped to as fine a resolution possible, depending on the available data), then it is possible to describe the relationship between these processes, and the ecological requirements of dependent biota, such that decisions can be made regarding where intervention is required to prevent undesirable state-change.

The ALAF recognises scale as fundamental to the challenge of assessing biodiversity and refers to both spatial and temporal components of ecosystems, widely recognised as important for defining the extent and dynamics of biological features in landscapes (Wiens 1989; Ludwig *et al*. 2000; Wiens and Bachelet 2010). In practice, the scale used to map spatial entities at different levels of the hierarchy is limited by the base data available. For example, the IBRA mapping for South Australia is relatively coarse, at a scale of 1 : 500 000, but finer levels of mapping can be achieved for environmental settings (see below) (e.g. scales of between 1 : 50 000 and 1 : 100 000) and vegetation features mapped using Landsat imagery (scale of 1 : 50 000). Temporal analysis is difficult at fine spatial scales, but archived time-series of satellite data are potentially useful for analysing changes in ecosystem state and trajectory (see case study below).

Overall, it is only possible to produce mapping at relatively coarse scales over the large areas of management interest typical of rangelands, so there can be a mismatch between the mapped information and the actual scale at which ecosystem processes occur and/or at which organisms use landscapes (*sensu* Ludwig *et al*. 2000). The ALAF attempts to address this in a practical way by using state-and-transition models at the level of ecosystem type/subtype (see below), and patch-scale analysis to provide descriptions of fundamental ecological features recognisable in the field. The objective is to apply a framework that is flexible enough to accommodate different types of biophysical data at different levels of the hierarchy, and to allow updating as new data become available, such as would be expected from implementation of an adaptive management approach (Holling 1978).

Conceptual background to the ALAF

Characteristic features of arid lands

Dynamic drivers affect ecosystems over short and long time-frames and include climate, herbivores, competitors, and landscape manipulation by humans. The most important dynamic driver in the arid zone is climate, as soil moisture is the single most important limiting factor determining the structural form and productivity of ecosystem types (Stafford Smith and Morton 1993; Morton *et al*. 1995; Morton *et al*. 2011). As with rangelands worldwide, South Australia's rangelands are characterised by episodic wet and dry cycles where prolonged dry periods are broken by relatively short periods of high rainfall. Rainfall triggers biological, physical, and chemical activities that result in pulses of increased primary productivity which directly influence biological activity at all trophic levels (Letnic and Dickman 2010). Vegetation pattern and change are driven primarily by climate variability, but are also strongly influenced by soil nutrients, fire, and grazing (Morton *et al*. 1995). Some of the major issues affecting biodiversity include alterations to the availability of water and nutrients within a landscape (Ludwig *et al*. 2002; Pringle and Tinley 2003), alterations to the structure

and composition of plant communities (Landsberg *et al.* 2003), and changes in the distribution and spread of pest plants and animals and the associated impacts on native biota (Newsome 1994).

At the simplest level, the dynamics of rangeland plant communities are driven by annual cycles of growth and senescence, while more complex changes are associated with climatic extremes. For example, exceptionally large rainfall events can trigger widespread germination and growth of ephemeral and perennial plants and germination of perennial trees and shrubs (Letnic and Dickman 2010). Such extremes can cause ephemeral plants to differ in species composition from one year to the next, and perennial plants to undergo infrequent but widespread recruitment (or mortality) (Stafford Smith and McAllister 2008).

The need to understand complex, dynamic ecosystems has stimulated a wealth of ecological theory. Two highly influential themes are hierarchy theory, which proposes that scale-dependent levels of organisation exist in nature (Allen and Starr 1982; O'Neill *et al.* 1989), and literature centred on concepts of resilience and ecological thresholds (Suding and Hobbs 2009).

Ecological hierarchies

One way of organising the complexity of biodiversity is by considering it to be hierarchical, where the ecological requirements of lower levels in a hierarchy (e.g. species) can be nested within the ecological requirements of higher levels in the hierarchy (e.g. ecosystems). Using these concepts, an attempt to capture the conservation requirements of the different levels in this hierarchy has been made, using the metaphor of coarse and fine filters (Noss 1987; Hunter *et al.* 1988; Hunter 1991; Hunter 2005).

Based on these hierarchical concepts (Allen and Starr 1982; O'Neill *et al.* 1989), this model proposes that the conservation requirements of higher levels of biodiversity (the 'coarse filter') are considered to encompass those at lower levels. For example, key hydrological processes that support the structure and function of a river ecosystem are likely also to support species that depend on that ecosystem. This coarse filter is often described in terms of ecological communities or ecosystems, although the relatively transient nature of ecological communities (Hunter *et al.* 1988) suggests that the abiotic elements, or the 'enduring features' of a system with which these biotic assemblages interact, should also be incorporated into coarse-filter definitions—hence an increasing focus on ecosystems. More broadly, the coarse-filter approach to nature conservation should aim to identify and address those systemic processes that have been modified in a way that results in the common decline of biodiversity dependent on those processes.

Addressing a landscape's conservation requirements at the ecosystem (coarse-filter) level alone, however, is unlikely to capture the conservation requirements of all biodiversity in a landscape, as some species are likely to have requirements that are not met by meeting the requirements of ecosystems. To continue the metaphor, some species or populations would fall through the pores of the coarse filter, and require conservation activity that is directed at meeting these species-specific requirements (the 'fine filter'). This becomes particularly apparent for very small populations, for which secondary threats associated with small population sizes need to be addressed (Gilpin and Soule 1986) in addition to the systemic issues associated with the coarse filter.

Critically, nature conservation requires goals to be set at multiple levels in the biological hierarchy (Margules and Pressey 2000; Groves *et al.* 2002; Mac Nally *et al.* 2002). Neither the coarse filter nor the fine filter alone will result in a successful nature conservation strategy. While fine-filter conservation issues are often clearly articulated and (in some cases) addressed, e.g. through recovery programs for threatened species, less emphasis has been placed on clearly identifying and addressing coarse-filter issues that are ultimately responsible for the decline of much of the biodiversity at risk. This is a critical gap, not least because the majority of native biodiversity in South Australia falls in the declining (rather than threatened) category, where the most appropriate response is to address those conservation issues associated with coarse-filter elements (Rogers *et al.* 2012).

The 'coarse-filter/fine-filter' approach to conservation planning has received criticism, primarily due to the fact that the spatial distribution of the coarse-filter surrogate (ecosystem) does not necessarily reflect the spatial distribution of lower levels of biodiversity (Januchowski-Hartley *et al.* 2011). These criticisms, however, are based on assumptions that we are only interested in patterns of biodiversity, and not the processes that underpin these patterns. If our aim when using the coarse-filter/fine-filter approach is instead to identify ecological processes associated with declining ecosystems, we assume that addressing these processes will meet the requirements of biota that depend on these systems.

Hierarchy theory provides a theoretical base for the ALAF because it supports the idea that it is important for conservation to understand how rangeland biota respond to changes in the distribution of ecosystem states. The foundation of the hierarchy is based on the distribution of the key physical (geomorphological) features that underpin spatial variation across landscapes. At a finer scale, heterogeneous landscapes can be described in the hierarchy by identifying 'patches' that represent spatially discrete entities, whose internal structure and/or function are significantly different from that of their surroundings, while recognising that adjacent 'patches' do not function independently but are instead connected by ecological flows and linkages, including the movement of water, nutrients, and animals (O'Neill *et al.* 1989).

Biodiversity can be defined in terms of both scale and level of organisation (King 2005), and the ALAF attempts to address aspects of both in rangelands. The organisation of biodiversity can be treated as hierarchical (e.g. landscape, ecosystem, and species; Allen and Starr 1982), and the ALAF starts with the assumption that existing bioregional descriptors such as IBRA (Thackway and Creswell 1995) and land systems (Christian 1958) provide a high-level, coarse-scale representation of landscapes that attempts to represent the hierarchical structure of regions with respect to processes that affect ecosystem function and resilience (Bestelmeyer *et al.* 2009).

The essential premise of these biogeographic classifications is that physical processes drive ecological processes, which in turn are responsible for patterns of biological activity and

associated biodiversity (Thackway and Creswell 1995). In South Australia, biogeographic boundaries used for IBRA are largely based on mapping of environmental associations (Laut *et al.* 1977), and land system mapping from the South Australia Pastoral Lease Assessment Program. Although the current classification is important for the ALAF in terms of broadly characterising important landscape features, we note there is a lack of consistency in the way systems are described, particularly in terms of a hierarchal structure.

The ALAF builds on this existing framework by attempting to describe more fully, and to map, the landscapes, ecosystems, and habitats that occur within broader units such as IBRA sub-regions. The term 'environmental setting' is used to describe a nested group of physical environmental attributes that are regularly repeated in a landscape, although they are not necessarily exclusive to a particular landscape. The descriptions used for landforms in the framework are consistent with McDonald *et al.* (2009). Ecosystem types are the floristic communities that occur within distinctive geomorphic and hydrological settings. The finest level of the hierarchy described by the ALAF is the ecosystem subtype. The subtype is a recognisable unit within an ecosystem type that exists due to a combination of natural drivers and land-use history and could be referred to as an alternate state (Suding *et al.* 2004) of an ecosystem.

For practical purposes, once the dynamics of different ecosystems within a landscape are described (and mapped to as fine a resolution possible, depending on the available data), it is then possible to describe the relationship between these processes, and the ecological requirements of dependent biota, such that decisions can be made regarding where intervention is required to prevent undesirable state-change.

Resilience, thresholds, and state models

The concepts of alternative states, thresholds, and resilience are particularly influential in rangeland ecology (Gillson and Hoffman 2007), where classical successional approaches appear to be inadequate for describing system dynamics for rangeland assessments (Suding and Hobbs 2009). These concepts provide an important basis for addressing the key question for land managers of whether a given system is likely to recover from a disturbance event unaided, or if some form of active management and intervention is needed (Bestelmeyer 2006).

The resilience of a system has been defined as its capacity to persist in the face of disturbances. For rangelands subjected to disturbance, this means having the capacity to maintain and reorganise key attributes, including essential landscape structure (e.g. vegetation patchiness), processes (e.g. nutrient cycling), and functions (e.g. productivity) (Ludwig and Smith 2005). Additionally, ecological thresholds describe abrupt changes in ecological properties in time and space, and the threshold concept has been important for advancing thinking about rangeland management (Bestelmeyer 2006).

King and Hobbs (2006) provide a conceptual model (Fig. 2) that incorporates the concept of abiotic and biotic thresholds. The model shows three stages of degradation, with thresholds between them that represent barriers to ecosystem recovery. In the first stage, biotic function is degraded but the system still has the capacity for autogenic recovery if the cause of degradation is removed. If degradation continues, the first threshold of recovery potential is crossed. This results in damage to biotic function. If the ecosystem has crossed over this threshold and is in the second stage, some manipulation of biotic components beyond removal of disturbance will be required for autogenic recovery to take place. Although abiotic functions may have been degraded in the second stage they still maintain some resilience in terms of their capacity to recover without direct manipulation. However, beyond the second threshold, biotic processes are severely dysfunctional and abiotic function has been degraded beyond its resilience. In this final stage of degradation, abiotic components require manipulation in order to make autogenic recovery possible.
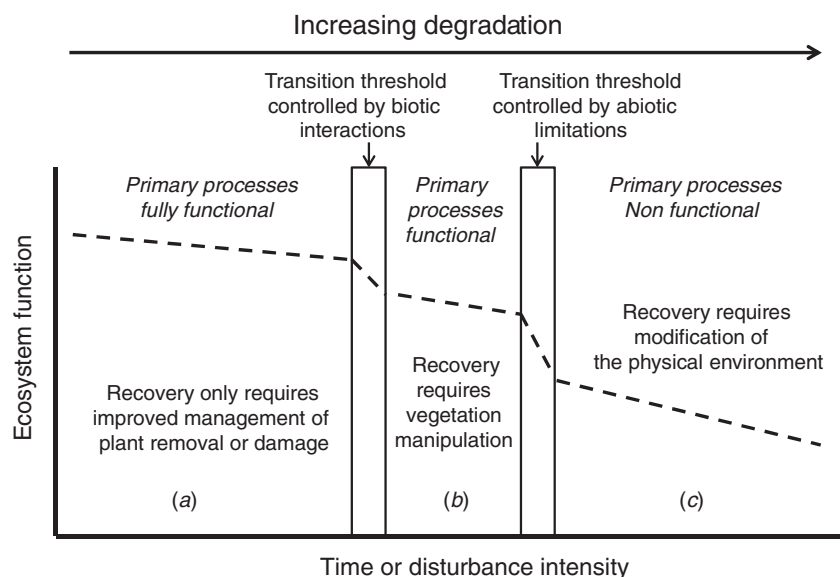

Fig. 2. Concept of biotic and abiotic thresholds indicating break points in ecosystem redevelopment from a degraded state (from King and Hobbs 2006).

In order to restore an ecosystem, we need to understand how it worked before it was modified or degraded, and then use this understanding to reassemble it and reinstate essential processes (Miller and Hobbs 2007). At a fundamental level, it is assumed that climate, geology, and geomorphology have interacted over long time-frames to produce a range of characteristic vegetation communities that are associated with particular physical environments, and whose internal organisation suggests they are likely to respond in a similar way to dynamic changes, driven by either climate or management. However, ecosystems can also exist in several alternative states (Westoby *et al.* 1989), which are contingent on their history of disturbance (Beisner *et al.* 2003; Suding *et al.* 2004), and these states may respond to disturbance and management interventions in different ways.

A commonly used management model is the state-and-transition model (STM) (Westoby *et al.* 1989; Stringham *et al.* 2003; Suding *et al.* 2004), which catalogues the directional changes an ecological community is likely to undergo in response to a sequence of events. One of the first applications of the STM concept in Australia was the classic work in rangelands by Westoby *et al.* (1989). This study challenged the assumptions made by traditional approaches to grazing management, which were underpinned by the objective of maintaining vegetation in a single equilibrium state. The paper introduced rangeland managers to the concept of a range of alternative vegetation states and demonstrated the potential to catalogue these states and the conditions leading to transitions between them, including a range of climatic and management factors such as fire, grazing, and removal of grazing (Westoby *et al.* 1989). As such, STMs provide simple representations of how complex ecosystems respond to 'slow drivers' (e.g. geology, topography, and soils), which limit what plants can grow where, and 'dynamic drivers' (e.g. rainfall and disturbance agents), which largely govern what and how much can grow at any point in time. Importantly, the models attempt to capture information on the types and rates of change in ecosystems that are useful in a management context.

The state-and-transition concept is underpinned by three categories of information about ecosystems that relate to their structure, how they function, and the changes that occur over time (Hobbs 1995). Briske *et al.* (2008) have recommended that STMs incorporate triggers, at-risk community phases, feedback mechanisms, and restoration pathways for each threshold separating individual states. Our approach has been to develop a conceptual model for each ecosystem type that attempts to account for variations in ecosystem expression related to various micro-topographic, soil, and surface-strew characteristics, and incorporates a dynamic component that predicts changes to the system under different types of disturbance, e.g. reduced rainfall, altered flood regimes, weed invasion, and over-grazing, or in response to other processes such as loss of topsoil due to erosion or changes in vegetation–groundwater interactions.

Case study. Witjira sub-region

Development and implementation of the ALAF is an ongoing process. This case study demonstrates primarily the means by which a hierarchical ecosystem classification can be developed that delineates different 'systems' based on an understanding of spatial and temporal variation. This is essential to the development and understanding of alternative states and transitions—steps (*i*) and (*ii*) in the framework described above. The goal has been to bring together information that can be shared and discussed with interested pastoralists and park managers, since only by integrating local knowledge with information provided through the ALAF process can ecosystems that have undergone irreversible change, or are at greatest risk, be identified together with the associated biota that may be at risk of extinction.

Study area

Figure 3 shows the location of the Witjira study area. The Witjira National Park is in the far north of South Australia, ~100 km north of Oodnadatta. Rainfall is extremely low, unreliable, and seasonally unpredictable, averaging 150 mm annually. Most of the land across the Park comprises stony tablelands and plains. This land system generally has a cracking clay soil that develops gilgai and is covered by coarse stones. Sandy plains and dunefields of the Simpson Desert occur east of the Finke River floodplain.

Relationships between biophysical settings and ecological communities (ecosystem types)

The first step in constructing an expert-based ecosystem classification was to undertake a vegetation survey across the Park and, as part of this, construct a range of simple geomorphic models that attempted to explain why the vegetation component of an ecosystem type might exist as a variety of subtypes. Micro-topographic features, including soil and surface-strew characteristics, can have a major impact on the expression of ecosystem types through their role in local soil moisture retention and nutrient accumulation. These are slow drivers because they are generally stable in short-term management time-frames (0–20 years).

Figure 4*a* provides just one example of a 'natural' response model for an ecosystem type, *Atriplex* low shrubs with perennial tussock grasses on stony plains. The model describes the relationships between subtypes 1a–d and their environmental setting. A diagrammatic representation of each of the subtypes is provided in Fig. 4*b*. This highlights the major biotic components along a generalised cross-section of the system. This information is useful when attempting to tease out the potential importance of the impacts of disturbance versus natural variations in micro-topography and soil moisture retention in shaping the species composition and overall productivity of different subtypes. While undertaking the field survey, we also sought to describe the range of dynamic drivers that affect ecosystems over short and long time-frames. These included signs of loss of topsoil, past grazing pressure, introduced weeds, and other forms of landscape modification (e.g. road works and dams).

The next step was to construct an expert-based hierarchical ecosystem classification, with four levels of ecological organisation. Figure 5 illustrates these levels and how they are connected. Geomorphology and soils create the environmental settings for the ecosystem types, which define the mid-level of the hierarchy. Above this, ecosystem types and environmental
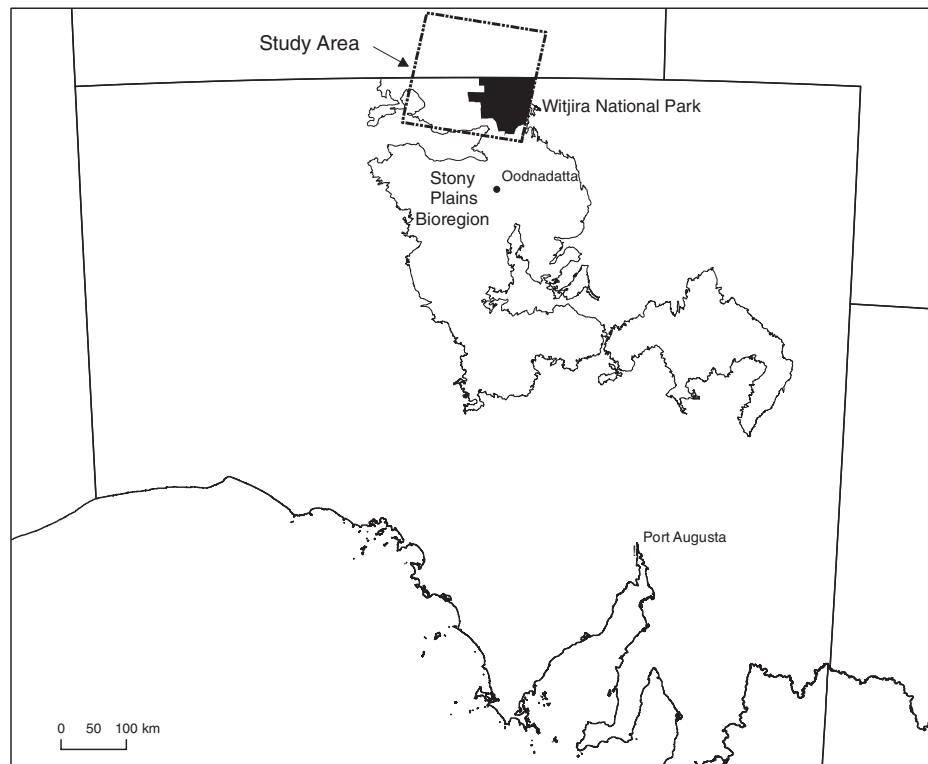
Fig. 3.   Location of Witjira study area.

settings are aggregated into functionally similar geomorphic and hydrological settings. Ecosystem types are defined by a description of the floristic community that 'typically' occurs on a given environmental setting (acknowledging that floristic composition can vary depending on the environmental history of a particular site). The term 'environmental setting' is used to encompass a nested group of physical environmental attributes that are regularly repeated within a landscape, although they are not necessarily exclusive to the landscape.

At the finest level in the hierarchy, ecosystem types are divided into subtypes, which are intended to reflect the number of different functional and compositional states in which the ecosystem can exist. These may be a product of the land-use history and disturbance dynamics and/or long-term (natural) community assembly processes. As such, they can represent finer scale variations in the physical environment or alternate states. Note, however, that the same ecological outcome may result from different mechanisms, with a degraded state in one setting looking much the same as a more typical state in another setting. A description of all 42 ecosystem types and subtypes across Witjira National Park is provided separately (see Supplementary Materials Appendix 1 as available on the journal's website).

Mapping the distribution of ecosystem types and subtypes

There are many challenges associated with producing a thematically consistent ecological hierarchy. In nature, boundaries between different systems are often not sharp, nor are they easily separable, e.g. where stony plains grade into gentle slopes on hills and breakaways. In the expert model, subjective decisions were necessary to determine the distribution of two or more systems across environmental gradients and transition zones. Further difficulty was experienced in assessing the likely temporal dynamics of a system based on a single visit.

Vegetation can be mapped and described at a range of scales, and the methodologies used to capture and disseminate vegetation information vary depending on the intended audience. Across South Australia, vegetation mapping has typically involved the delineation of vegetation communities through a visual interpretation of aerial photography and satellite imagery in conjunction with ground-based assessments. In most cases, the digitising was performed manually using GIS, which is a labour-intensive process.

This case study provides an example of the use of time-series analysis of remotely sensed data as an alternative or complementary method to traditional vegetation mapping, with the advantage that such data sample vegetation in a consistent manner and at scales that are not feasible for the collection of field data (Sparrow and Foulkes 2002; Tueller 1987). Semi-automated image analysis methods can also be used to update maps regularly to reflect the dynamic nature of ecosystems.

The analytical process outlined in Fig. 6 seeks to classify, map, and describe the dynamic nature of different vegetation 'patches' using spectral information from a dry-period, multi-spectral image, and a multi-temporal sequence of images that captures the dynamics of seasonal variation. The dry-period image is critical to ensure that dynamic information can be related to features that are identifiable on the ground.

(*a*)

(i) Oodnadatta Bush +/- Mitchell Grass. Stony plains and rises with significant micro-relief (gilgais) areas with self-mulching clays which temporarily pond water

(iii) Perennial tussock grasses, ephemeral Saltbush and bindyi spp. Stony plains with minimal micro-relief and some gaps between gibbers. Poorly drained clay soils

decreasing | **soil salinity** | increasing

surface sand &/or drainage
decreasing | | increasing

(ii) Bladder Saltbush, Grey Samphire, perennial tussock grasses. Stony plains and rises with significant micro-relief (gilgais) areas with self-mulching saline clays which temporarily pond water

(iv) Bladder Saltbush & perennial tussock grasses. Stony plains, often sloping or with sand thinly overlaying gibber pavement areas or non-sealing better drained gibber soils

← **increasing micro-relief (gilgais), soil moisture and nutrient retention** →

(*b*)

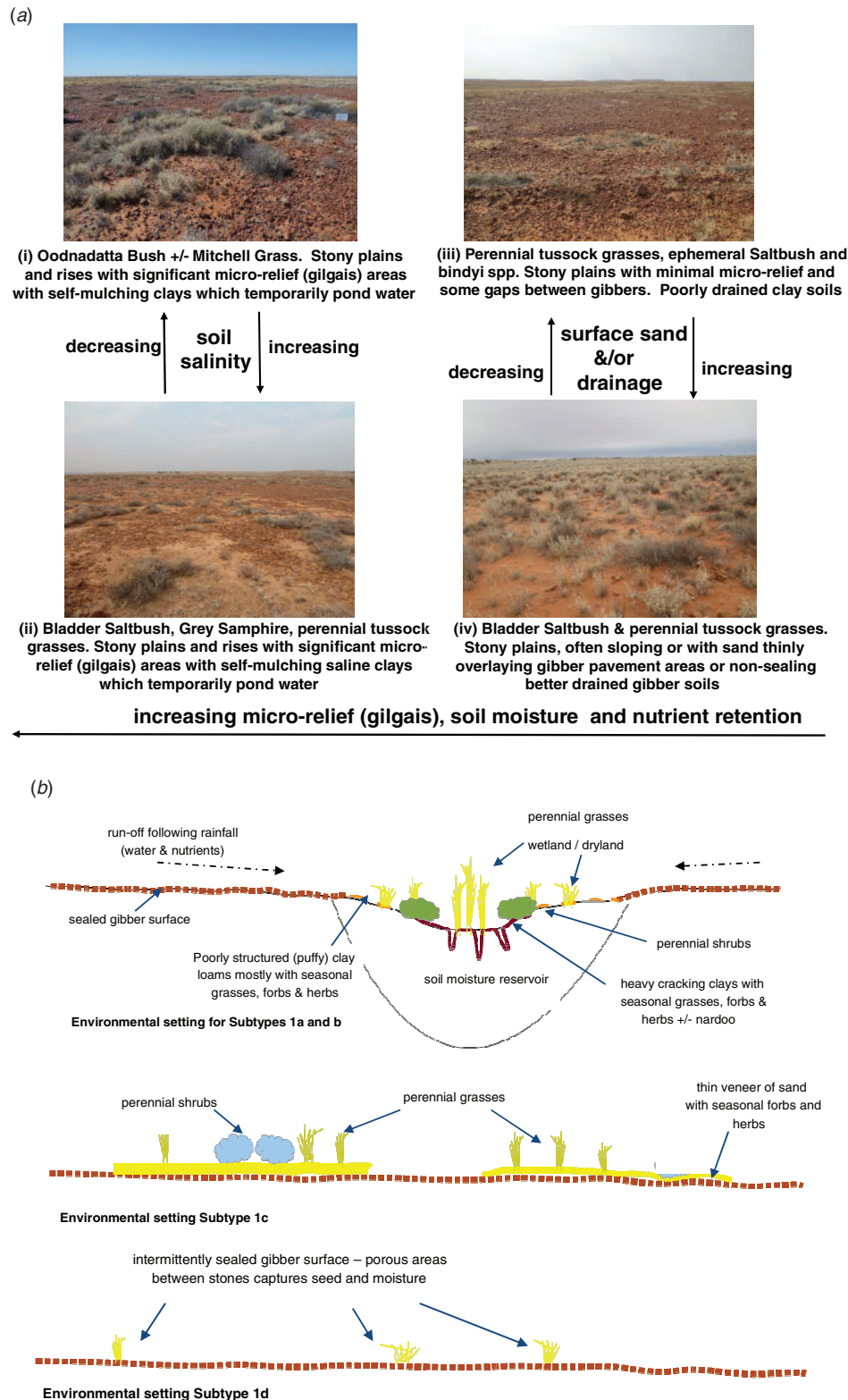**Fig. 4.**   (*a*) Ecosystem type 1 (*Atriplex* low shrubs with perennial tussock grasses on stony plains) in four states (i–iv) as determined by differences in environmental setting which influences the capacity for plants to absorb moisture and nutrients from soil, (*b*) illustrates how micro-topographic differences influence moisture and nutrient retention and how it influences vegetation.

Group landform elements into functionally similar geomorphic and hydrological settings

| Sandplains & Dunefields | Saline Flood Flats | Mound Springs & Tails | Swamps & Claypans | Floodplains | Major Drainage Lines | Minor Drainage Lines | Stony Slopes (Hills & Breakaways) | Stony Plains |

Environmental settings encompass a nested group of physical environmental attributes that are regularly repeated within a landscape

Sand dunes	saline flood flats	mound springs and tails	clay soil drainage depressions and swamps	Floodplains of major drainage lines	sandy river channels	Drainage lines in stony plains/hills	undulating stony plains	Gibber pavement +/- gilgais
sand plains				loamy floodplains in major rivers	moister river channels or waterholes	minor drainage lines in gibber tablelands	stony hills, edges of tablelands and minor drainage lines	gibber plains +/- gilgais with saline soil
deeper sand plains				floodplains and large gilgais on stony plains	larger drainage lines in stony plains with waterholes	drainage lines in stony plains/hills with saline soils	Sandstone /shale low hills & rises	gibber plains with sand veneer over clay soils
saline sand plains in low lying areas				drainage depression	larger drainage lines and associated wetter floodplains with waterholes		Sandstone/ shale low hills & rises	sand to clay loam over clay plains +/- gibber
sandy areas in gibber plains							Escarpments/ breakaways	Gypseous rise
stony interdune corridors in dunefields								
interdune corridors on sand plains								

Ecosystem Types are defined by the vegetation (e.g. Saltbush over perennial tussock grass), and dominant environmental setting (e.g. gibber pavement and gilgais)

Ecosystem Type 1

Subtypes provide the finest level of community description (i.e. dominant perennial plants). Examples: 1a = Oodnadatta Bush +/- Mitchell Grass, 1b = Bladder Saltbush and Grey Samphire over perennial grasses, 1c = Bladder Saltbush +/- Mitchell Grass

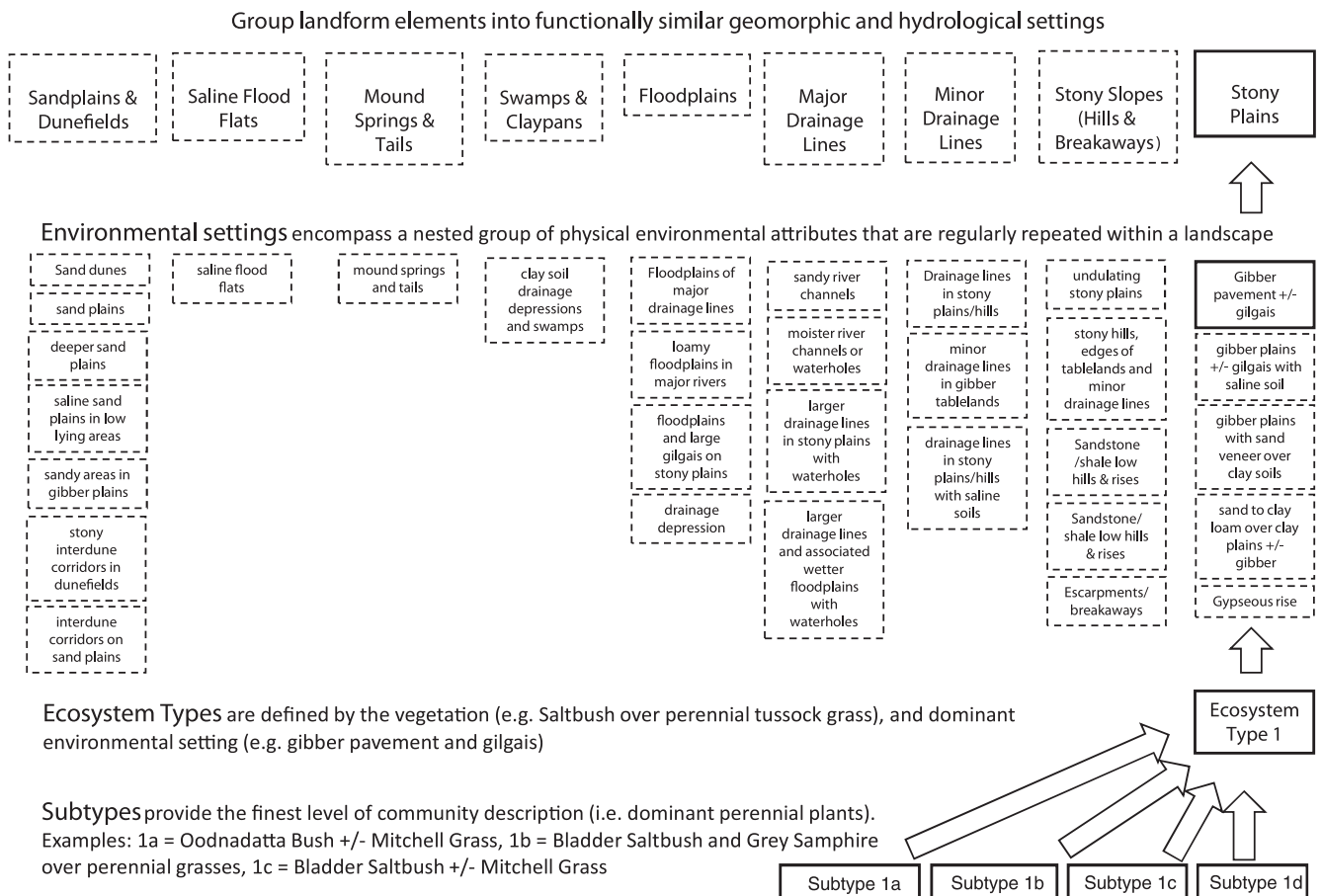| Subtype 1a | Subtype 1b | Subtype 1c | Subtype 1d |

Fig. 5. Proposed ecological hierarchy for Witjira National Park. The full conceptual model linking landform elements, environmental settings, and ecosystem types and subtypes is provided in Supplementary Materials Appendix 1.

The modelling process begins with the acquisition of a set of images for a given Landsat TM scene that cover multiple wet–dry cycles (in this case 18 cloud-free images covering the period June 2003–March 2011). All images are radiometrically calibrated using the Chavez COS$_{(Theta)}$ image-based correction procedure (Chavez 1988, 1996) to ensure that all changes in apparent reflectance between images are attributable to real changes on the ground, and are not a result of variations in atmospheric conditions.

In step three, a vegetation index is calculated for each image, which represents a measure of the per pixel relative change in green (photosynthetically active) vegetation cover through time. While indices such as the normalised difference vegetation index (NDVI) are known to correlate well with ground measurements of green biomass and chlorophyll content in certain environments (Tucker *et al.* 1985), in arid and semi-arid regions, NDVI and other slope-based indices tend not to separate sparse vegetation from a bright soil background. Better separation is usually achieved using a 'tasselled cap' transformation (TCT); this produces a 'green vegetation index' (GVI) which is largely free of soil background effects, since almost all soil characteristics are ascribed to another band called 'brightness' (Kauth and Thomas 1976).

Principal components analysis (PCA) can be used to extract ecologically meaningful information about the dynamics of vegetation from a stack of GVI images. The PCA is used to transform the original set of inter-correlated GVI images into a new set of images (components) that are uncorrelated and are ordered by the percentage of the variability within the original dataset that they explain (Avena *et al.* 1999). Because each of the components is uncorrelated, it essentially carries 'new information' that describes some aspect of the dynamics of vegetation not captured by previous components. For example, one would expect one or more principal components to separate vegetation on a gibber plain from that in an adjacent creek line, since they are likely to have very different growth and decay responses to the same sequence of rainfall events.

In step four, temporal statistics are calculated on a pixel-by-pixel basis across the stack of GVI images. These statistics include the minimum, maximum, mean, and median GVI values, together with their standard deviation and sum. These images reflect, for each pixel, the magnitude of spectral variability in space and time, which is useful in interpreting the results of the unsupervised classification described below.

In step five, unstandardised T-mode and S-mode PCA are performed on the GVI image stack. Here, the image time-
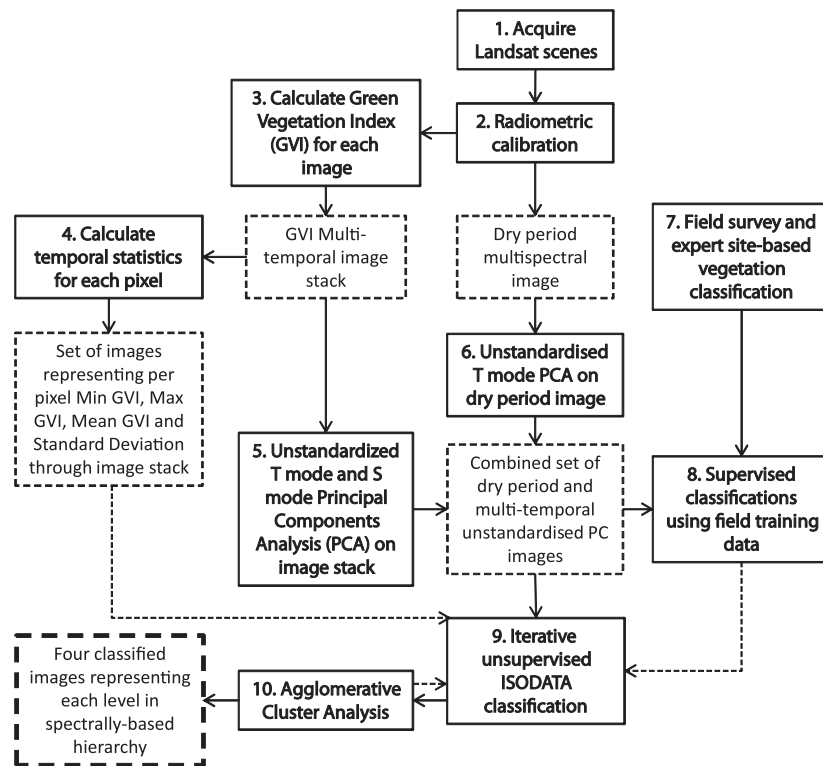
Fig. 6. Steps in a process designed to map the distribution of ecosystem types, environmental settings, and landform elements.

series is viewed from two separate perspectives, one as a set of images in which each represents a slice of time (T-mode), and the other as a temporal profile for each pixel (S-mode). The two orientations provide complementary insights into the nature of variability within the time-series, and regardless of which mode is used, the first few principal components typically explain 90–99% of the total variance in the original dataset (Compagnucci and Richman 2008). Results of PCA can be provided in either a standardised or unstandardised form. In the former, all of the original variables carry equal weight in the analysis since their variances are equalised by the standardisation, whereas in the latter, variables are weighted in the analysis in proportion to their variance. Use of the unstandardised form is important for modelling vegetation dynamics, because any principal components, fed into a subsequent unsupervised classification process, will reflect the dominance of the most variable spectral attributes. In contrast to supervised classification techniques, unsupervised classifications require no prior information about the classes of interest. Instead, each pixel is allocated to the most relevant spectral grouping (cluster), and the analyst is required to identify what each cluster represents, using a combination of field data and the spectral statistics from within the imagery itself.

Steps eight to 10 outline an iterative modelling process in which (*1*) all available field data were used to produce an expert, site-based ecological classification; and (*2*) several supervised classifications were performed, using algorithms incorporating parallelepiped and maximum likelihood

decision rules, using the survey data to create a set of training polygons (signature files) representing each ecosystem type. However, because the majority of pixels across the National Park fell outside the spectral bounds of the existing training signatures, a 128-class, unsupervised ISODATA classification was run, in an attempt to capture the full range of ecosystem types that exist across the landscape, noting that any given ecosystem type could be represented by two or more ISODATA classes. By iteratively altering the number of ISODATA output classes and the number and type of unstandardised principal component input images, a spectral classification was finally produced in which the grouping of ISODATA classes was interpretable at multiple levels in a dendrogram, produced by an agglomerative cluster analysis (see Supplementary Materials Appendix 2). Not surprisingly, at the higher levels, the classification appeared to be determined by the effects of water availability on ecosystem productivity across each the four major land-form types: Saline Flats in and around the Dalhousie mound springs; Gibber Country (stony tablelands and plains); Sandy Country (sand plains and dunefields); and Drainage Country (creeks, river channels, floodplains, and their associated terminal floodouts).

The different levels of the spectral-based classification (representing different cut-off points in the dendrogram) are presented in Supplementary Materials Appendix 3. While every effort was made to label each of the ISODATA classes according to the ecosystem subtype descriptors available, further field work will be required to verify the existing
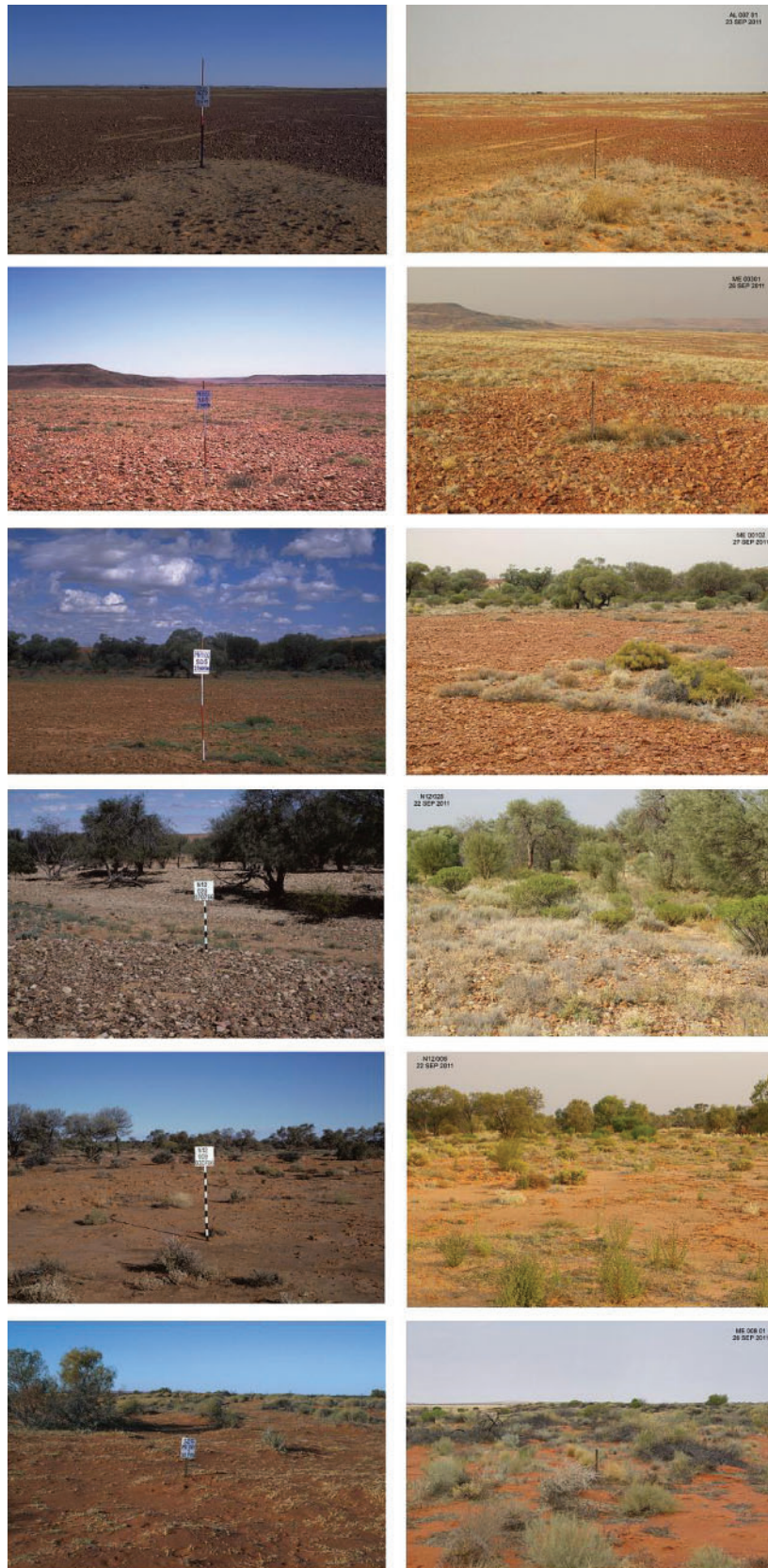
Fig. 7. Observed changes in the landscape across Witjira National Park between 1995 (left) and 2011 (right).

descriptors, as part of an iterative mapping process, and to re-label those classes not represented in any of the training data.

Use of repeat photo-points to infer change

The ability to understand dynamic processes in natural systems is central to the effective management of biodiversity. However, the information described above cannot be used to set conservation priorities without an understanding of how the dynamics relate to the conservation requirements of native biota, and what systems appear to be approaching, or to have crossed, landscape-scale thresholds and are no longer capable of meeting these requirements—components (*iii*) and (*iv*) of the ALAF described previously. The detection of management-related trends in the presence of inter-annual climatic variability is extremely challenging. One approach is to investigate species compositional patterns and trends evident in serial photographs of fixed photo-points; another is to look at broad-scale landscape changes evident from a comparison of recent and historical aerial photographs.

Witjira National Park was proclaimed in 1985. Prior to this, the area, known as Mount Dare Pastoral Lease, was grazed by domestic stock (sheep then cattle) for more than 100 years. Although grazing by cattle has officially ceased, fence maintenance is an issue and cattle regularly move into the Park from neighbouring leases. Donkeys and camels are also regular inhabitants. A collection of historic photographs and photo-points from 1956, 1979, 1986, and 1993–95 was used to assess changes in the perennial cover/abundance of vegetation at 45 locations across the park. A further eight off-park locations were similarly assessed.

The comparison of photo-points highlighted the dynamic nature of perennial vegetation across a range of ecosystem types within the Park. Data, derived from an indexing method similar to that developed by Noble (1977) for Koonamore Station in South Australia, showed that in 55 individual cases, plant species increased in density across alluvial floodplains and drainage channels (*n* = 13 sites). In contrast, individual plant species increased in density in only 36 instances (*n* = 20 sites) on the stony plains. This was an unexpected contrast, since the most obvious trends on the stony plains were the increases in density of *Astrebla pectinata* attributable to recent above-average summer rainfall. Across the plains, *Atriplex nummularia* ssp. *omissa* showed little change in density, whereas *Atriplex vesicaria* increased at eight sites where it was noted and declined at three sites.

Creek lines registered the most substantial changes in terms of species diversity and abundance, particularly the development of a shrub understorey where previously absent, as well as a substantial increase in cover-abundance of canopy species. The re-appearance of species such as *Chenopodium auricomum*, *Atriplex nummularia* ssp. *nummularia*, and *Maireana aphylla* suggested a wide-spread relaxation of grazing pressure. There was also a slight trend for establishment of trees on flood and alluvial plains.

This investigation of vegetation trends has informed the conceptual modelling of disturbance and recovery post disturbance, particularly where state changes are evident. Figure 7

shows examples of changes observed across several ecosystem types between 1995 (Brandle 1998) and 2011. Overall, the photos suggest that vegetation cover has been maintained across most of the stony plains and that perennial cover and species diversity have increased in creek lines and along flood-plains.

Synthesis of knowledge

Implementation of the ALAF across Witjira National Park is ongoing, and current work is focussed on providing an integrated synthesis that is useful to Park managers. Maintaining the long-term needs of a broad range of species is likely to require a set of conservation strategies aimed at conserving the most vulnerable components of a landscape at times when they are under greatest threat (i.e. critical dry periods). Several factors determine the amount and quality of resources available to plant and animal species during such periods. The most productive areas are generally found in water and nutrient-rich pockets such as run-on areas, river systems and their flood-plains, and areas where raised watertables give plants more reliable access to water. These fertile patches are also the main source of herbage production, particularly during dry periods, and are often a focus for feral animals and weeds.

Across Witjira National Park, all ecosystems with the exception of mound springs are assumed to be water-limited during long dry periods and are, therefore, sensitive to changes in the hydrological regime. The most resilient ecosystem types are likely to be those with physical attributes that limit soil erosion, retain water, and support woody shrubs during dry periods. This is due to the ability of these systems to accumulate and retain soil moisture, nutrients, and biological propagules. Future work will evaluate the persistence across the landscape of a range of plant and animal species with different ecological requirements. This will include identifying the location and importance of local refugia for those species whose populations contract during harsh times and expand to recolonise former habitats when conditions improve.

Conclusions

Setting meaningful conservation priorities in the rangelands is difficult without an understanding of which systems appear to be approaching thresholds that, if crossed, would render them incapable of meeting the needs of dependent biota versus systems that appear to be operating within the limits of acceptable change. Identifying these conditions is difficult in the data-poor and extremely dynamic environment of the rangelands. This paper has highlighted some of the foundational information requirements of evidence-based conservation planning in the rangelands, but has also raised questions about how natural resource management agencies can overcome existing knowledge gaps and be proactively engaged in the long-term protection and preservation of biodiversity at a landscape scale.

The outcomes of an initial Aridlands Landscape Assessment should be treated as working hypotheses, which are intended to test and challenge the current understanding of ecosystem dynamics as knowledge improves through time. Ongoing testing of the landscape-scale assessments through the implementation of landscape-scale monitoring programs will

help to determine whether the initial conclusions remain valid, and whether the sum of on-ground conservation activity is reducing the risk of irreversible, deleterious change in those components of the landscape that have been identified as being at risk.

Acknowledgements

References

Allen, T. F. H., and Starr, T. B. (1982). 'Hierarchy, Perspectives for Ecological Complexity.' (University of Chicago Press: Chicago, IL.)

Avena, G. C., Ricotta, C., and Volpe, F. (1999). The influence of principal component analysis on the spatial structure of a multispectral dataset. *International Journal of Remote Sensing* **20**, 3367–3376. doi:10.1080/014311699211381

Beisner, B. E., Haydon, D. T., and Cuddington, K. (2003). Alternative stable states in ecology. *Frontiers in Ecology and the Environment* **1**, 376–382. doi:10.1890/1540-9295(2003)001[0376:ASSIE]2.0.CO;2

Bestelmeyer, B. T. (2006). Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. *Restoration Ecology* **14**, 325–329. doi:10.1111/j.1526-100X.2006.00140.x

Bestelmeyer, B. T., Havstad, K. M., Damindsuren, B., Han, G., Brown, J. R., Herrick, J. E., Steele, C. M., and Peters, D. P. C. (2009). Resilience theory in models of rangeland ecology and restoration: the evolution and application of a paradigm. *In*: 'New Models for Ecosystem Dynamics and Restoration'. (Eds R. J. Hobbs and K. N. Suding.) (Island Press: Washington, DC.)

Bottrill, M. C., Joseph, L. N., Carwardine, J., Bode, M., Cook, C., Game, E. T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., Pressey, R. L., Walker, S., Wilson, K. A., and Possingham, H. P. (2008). Is conservation triage just smart decision making? *Trends in Ecology & Evolution* **23**, 649–654. doi:10.1016/j.tree.2008.07.007

Boyd, C. S., and Svejcar, T. J. (2009). Managing complex problems in rangeland ecosystems. *Rangeland Ecology and Management* **62**, 491–499. doi:10.2111/08-194.1

Brandle, R. (1998). 'A Biological Survey of the Stony Deserts, South Australia, 1994–1997.' (Department for Environment and Heritage South Australia: Adelaide, SA.)

Briske, D. D., Bestelmeyer, B. T., Stringham, T. K., and Shaver, P. L. (2008). Recommendations for development of resilience-based state-and-transition models. *Rangeland Ecology and Management* **61**, 359–367. doi:10.2111/07-051.1

Chandra, A., and Idrisova, A. (2011). Convention on biological diversity: a review of national challenges and opportunities for implementation. *Biodiversity and Conservation* **20**, 3295–3316. doi:10.1007/s10531-011-0141-x

Chavez, P. S. (1988). An improved dark-object subtraction technique for atmospheric scattering correction of multi-spectral data. *Remote Sensing of Environment* **24**, 459–479. doi:10.1016/0034-4257(88)90019-3

Chavez, P. S. (1996). Image-based atmospheric corrections revisited and improved. *Photogrammetric Engineering and Remote Sensing* **62**, 1025–1036.

Christian, C. S. (1958). The concept of land units and landsystems. *Proceedings of the Ninth Pacific Science Congress* **20**, 74–81.

Compagnucci, R. H., and Richman, M. B. (2008). Can principal component analysis provide atmospheric circulation or teleconnection patterns? *International Journal of Climatology* **28**, 703–726. doi:10.1002/joc.1574

Connor, E. F., Courtney, A. C., and Yoder, J. M. (2000). Individuals-area relationships: the relationship between animal population density and area. *Ecology* **81**, 734–748.

Failing, L., and Gregory, R. (2003). Ten common mistakes in designing biodiversity indicators for forest policy. *Journal of Environmental Management* **68**, 121–132. doi:10.1016/S0301-4797(03)00014-8

Gilbert, N. (2010). Conservation biodiversity hope faces extinction. *Nature* **467**, 764. doi:10.1038/467764a

Gillson, L., and Hoffman, M. T. (2007). Rangeland ecology in a changing world. *Science* **315**, 53–54. doi:10.1126/science.1136577

Gilpin, M. E., and Soule, M. E. (1986) Minimum viable populations: processes of species extinction. *In*: 'Conservation Biology. The Science of Scarcity and Diversity'. (Ed. M. E. Soule.) pp. 19–34. (Sinauer Associates: Massachusetts, MA.)

Groves, C. R., Jensen, D. B., Valutis, L. L., Redford, K. H., Shaffer, M. L., Scott, J. M., Baumgartner, J. V., Higgins, J. V., Beck, M. W., and Anderson, M. G. (2002). Planning for biodiversity conservation: putting conservation science into practice. *BioScience* **52**, 499–512. doi:10.1641/0006-3568(2002)052[0499:PFBCPC]2.0.CO;2

Hobbs, R. J. (1995). Landscape ecology. *In*: 'Landscape Ecology'. (Ed. W. A. Nierenberg.) pp. 417–428. (Academic Press: San Diego, CA.)

Hobbs, R. J. (2007). Goals, targets and priorities for landscape-scale restoration. *In*: 'Managing and Designing Landscapes for Conservation.' (Eds D. B. Lindenmayer and R. J. Hobbs.) pp. 511–526. (Blackwell Publishing: Oxford, UK.)

Holling, C. S. (Ed.) (1978). 'Adaptive Environmental Assessment and Management.' (Wiley: Chichester, UK.)

Hunter, M. L. (1991). Coping with ignorance: the coarse-filter strategy for maintaining biodiversity. *In*: 'Balancing on the Brink of Extinction. The Endangered Species Act and Lessons for the Future'. (Ed. K. A. Kohm.) pp. 266–281. (Island Press: Washington, DC.)

Hunter, M. L. (2005). A mesofilter conservation strategy to complement fine and coarse filters. *Conservation Biology* **19**, 1025–1029. doi:10.1111/j.1523-1739.2005.00172.x

Hunter, M. L., Jacobson, G. L., and Webb, T. (1988). Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conservation Biology* **2**, 375–385. doi:10.1111/j.1523-1739.1988.tb00202.x

Januchowski-Hartley, S. R., Hermoso, V., Pressey, R. L., Linke, S., Kool, J., Pearson, R. G., Pusey, B. J., and Van Der Wal, J. (2011). Coarse-filter surrogates do not represent freshwater fish diversity at a regional scale in Queensland, Australia. *Biological Conservation* **144**, 2499–2511. doi:10.1016/j.biocon.2011.07.004

Kauth, R. J., and Thomas, G. (1976). The Tasselled cap – A Graphic Description of the Spectral-Temporal Development of Agricultural Crops as seen by LANDSAT. LARS Symposia Paper 159. Available at: http://docs.lib.purdue.edu/lars_symp/159.

King, A. W. (2005). Hierarchy theory and the landscape...level? or, words do matter. *In*: 'Issues and Perspectives in Landscape Ecology'. (Eds J. A. Wiens and M. A. Moss.) pp. 29–35. (Cambridge University Press: Cambridge, UK.)

King, E. G., and Hobbs, R. J. (2006). Identifying linkages among conceptual models of ecosystem degradation and restoration: towards an integrative framework. *Restoration Ecology* **14**, 369–378. doi:10.1111/j.1526-100X.2006.00145.x

Landsberg, J., James, C. D., Morton, S. R., Muller, W. J., and Stol, J. (2003). Abundance and composition of plant species along grazing gradients in Australian rangelands. *Journal of Applied Ecology* **40**, 1008–1024. doi:10.1111/j.1365-2664.2003.00862.x

Laut, P., Heylingers, P. C., Keig, G., Löffler, E., Margules, C., and Scott, R. M. (1977). 'Environments of South Australia Handbook.' (Division of Land Use Research, CSIRO: Canberra, ACT.)

Letnic, M., and Dickman, C. R. (2010). Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews of the Cambridge Philosophical Society* **85**, 501–521.

Lindenmayer, D., Hobbs, R. J., Montague-Drake, R., Alexandra, J., Bennett, A., Burgman, M., Cale, P., Calhoun, A., Cramer, V., Cullen, P., Driscoll, D., Fahrig, L., Fischer, J., Franklin, J., Haila, Y., Hunter, M., Gibbons, P., Lake, S., Luck, G., MacGregor, C., McIntyre, S., MacNally, R., Manning, A., Miller, J., Mooney, H., Noss, R., Possingham, H., Saunders, D., Schmiegelow, F., Scott, M., Simberloff, D., Sisk, T., Tabor, G., Walker, B., Wiens, J., Woinarski, J., and Zavaleta, E. (2008). A checklist for ecological management of landscapes for conservation. *Ecology Letters* **11**, 78–91.

Ludwig, J. A., and Smith, M. D. S. (2005). Interpreting and correcting cross-scale mismatches in resilience analysis: a procedure and examples from Australia's rangelands. *Ecology and Society* **10**, 20–27.

Ludwig, J. A., Wiens, J. A., and Tongway, D. J. (2000). A scaling rule for landscape patches and how it applies to conserving soil resources in savannas. *Ecosystems* **3**, 84–97. doi:10.1007/s100210000012

Ludwig, J. A., Eager, R. W., Bastin, G. N., Chewings, V. H., and Liedloff, A. C. (2002). A leakiness index for assessing landscape function using remote sensing. *Landscape Ecology* **17**, 157–171. doi:10.1023/A:1016579010499

Mac Nally, R., Bennett, A. F., Brown, G. W., Lumsden, L. F., Yen, A., Hinkley, S., Lillywhite, P., and Ward, D. A. (2002). How well do ecosystem-based planning units represent different components of biodiversity? *Ecological Applications* **12**, 900–912. doi:10.1890/1051-0761(2002)012[0900:HWDEBP]2.0.CO;2

Mace, G. M., Possingham, H., and Leader-Williams, N. (2006). Prioritizing choices in conservation. *In*: 'Key Topics in Conservation Biology'. (Eds D. MacDonald and K. Service.) pp. 17–34. (Blackwell Publishers: Oxford, UK.)

Margules, C. R., and Pressey, R. L. (2000). Systematic conservation planning. *Nature* **405**, 243–253. doi:10.1038/35012251

McDonald, R. C., Isbell, R. F., Speight, J. G., Walker, J., and Hopkins, M. S. (2009). 'Australian Soil and Land Survey: Field Handbook.' (Department of Primary Industries and Energy and CSIRO: Canberra, ACT.)

Miller, J. R., and Hobbs, R. J. (2007). Habitat restoration – do we know what we're doing? *Restoration Ecology* **15**, 382–390. doi:10.1111/j.1526-100X.2007.00234.x

Morton, S. R., Stafford Smith, D. M., Friedel, M. H., Griffin, G. F., and Pickup, G. (1995). The stewardship of arid Australia – ecology and landscape management. *Journal of Environmental Management* **43**, 195–217. doi:10.1016/S0301-4797(95)90402-6

Morton, S. R., Smith, D. M. S., Dickman, C. R., Dunkerley, D. L., Friedel, M. H., McAllister, R. R. J., Reid, J. R. W., Roshier, D. A., Smith, M. A., Walsh, F. J., Wardle, G. M., Watson, I. W., and Westoby, M. (2011). A fresh framework for the ecology of arid Australia. *Journal of Arid Environments* **75**, 313–329. doi:10.1016/j.jaridenv.2010.11.001

Newsome, A. E. (1994). Vertebrate pests versus wildlife conservation in semi-arid New South Wales: a profound imbalance. *In*: 'Future of the Fauna of Western New South Wales'. (Eds D. Lunney, S. Hand, P. Reed and D. Butcher.) pp. 43–51. (Royal Zoological Society of New South Wales: Sydney.)

Noble, I. (1977). Long-term biomass dynamics in an arid chenopod shrub community at Koonamore, South Australia. *Australian Journal of Botany* **25**, 639–653. doi:10.1071/BT9770639

Noss, R. F. (1987). From plant communities to landscapes in conservation inventories: a look at the nature conservancy (USA). *Biological Conservation* **41**, 11–37. doi:10.1016/0006-3207(87)90045-0

O'Neill, R. V., Johnson, A. R., and King, A. W. (1989). A hierarchical framework for the analysis of scale. *Landscape Ecology* **3**, 193–205. doi:10.1007/BF00131538

Possingham, H. (Ed.) (2001). 'The Business of Biodiversity: Applying Decision Theory Principles to Nature Conservation.' (Australian Conservation Foundation: Melbourne.)

Pringle, H., and Tinley, K. (2003). Are we overlooking critical geomorphic determinants of landscape change in Australian rangelands? *Ecological Management & Restoration* **4**, 180–186. doi:10.1046/j.1442-8903.2003.00154.x

Rogers, D. J., Willoughby, N., Pisanu, P., McIlwee, A. P., and Gates, J. A. (2012) 'Landscape Assessment: A Process for Identifying Ecosystem Priorities for Nature Conservation.' (Department for Environment and Natural Resources South Australia: Adelaide, SA.)

Sparrow, B., and Foulkes, J. (2002). Evaluating a method for combining ecological and remote sensing data for structural vegetation mapping. *In*: 'Proceedings of the 11th Australian Remote Sensing and Photogrammetry Conference'. Brisbane, 2–6 September 2002. pp. 209–221.

Stafford Smith, M., and McAllister, R. R. J. (2008). Managing arid zone natural resources in Australia for spatial and temporal variability – an approach from first principles. *Rangeland Journal* **30**, 15–27. doi:10.1071/RJ07052

Stafford-Smith, D. M., and Morton, S. (1993). Hierarchical design for conservation of biodiversity. *In*: 'Australian rangelands in a changing environment. Seventh Biennial Conference of the Australian Rangeland Society'. (Australian Rangeland Society: Cobar, NSW.)

Stringham, T. K., Krueger, W. C., and Shaver, P. L. (2003). State and transition modeling: an ecological process approach. *Journal of Range Management* **56**, 106–113. doi:10.2307/4003893

Suding, K. N., and Hobbs, R. J. (2009). Models of ecosystem dynamics as frameworks for restoration ecology. *In*: 'Models of Ecosystem Dynamics as Frameworks for Restoration Ecology'. (Eds R. J. Hobbs and K. N. Suding.) pp. 3–21. (Island Press: Washington, DC.)

Suding, K. N., Gross, K. L., and Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology & Evolution* **19**, 46–53. doi:10.1016/j.tree.2003.10.005

Thackway, R., and Creswell, I. (1995). 'An Interim Bioregionalisation for Australia: A Framework for Establishing the National System of Reserves.' (Australian Nature Conservation Agency: Canberra, ACT.)

Tucker, C. J., Vanpraet, C. L., Sharman, M. J., and Vanittersum, G. (1985). Satellite remote sensing of total herbaceous biomass production in the Senegalese Sahel 1980–1984. *Remote Sensing of Environment* **17**, 233–249. doi:10.1016/0034-4257(85)90097-5

Tueller, P. T. (1987). Remote-sensing science applications in arid environments. *Remote Sensing of Environment* **23**, 143–154. doi:10.1016/0034-4257(87)90034-4

Westoby, M., Walker, B. H., and Noy-Meir, I. (1989). Oportunistic management for rangelands not at equilibrium. *Journal of Range Management* **42**, 266–273. doi:10.2307/3899492

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology* **3**, 385–397. doi:10.2307/2389612

Wiens, J. A., and Bachelet, D. (2010). Matching the multiple scales of conservation with the multiplesScales of climate change. *Conservation Biology* **24**, 51–62. doi:10.1111/j.1523-1739.2009.01409.x

Wilson, K. A., McBride, M. F., Bode, M., and Possingham, H. P. (2006). Prioritizing global conservation efforts. *Nature* **440**, 337–340. doi:10.1038/nature04366