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A framework to predict the effects of livestock grazing and grazing exclusion on conservation values in natural ecosystems in Australia

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Abstract. Grazing by domestic livestock has greatly degraded many Australian ecosystems and its legacy will be longlasting in many areas. Although livestock are usually removed from conservation reserves because they are perceived to be incompatible with the conservation of natural ecosystems, they have been retained in several reserves in south-eastern Australia as a management tool to achieve conservation outcomes. These cases highlight the fact that no framework currently exists to address the question, under what circumstances (and in what ecosystems) is livestock grazing—or the removal of grazing-likely to have positive, negative, neutral or uncertain impacts on the diversity and composition of native plants? This paper provides a conceptual framework to predict the effects of livestock grazing and grazing exclusion on the conservation values of native vegetation across natural ecosystems in Australia. It should prove equally relevant to other ecosystems around the world which have evolved without heavy grazing by large herbivores. The framework is based on disturbance- and grazing-ecology literature from Australia and elsewhere, and incorporates the following six main factors: (1) impacts of livestock grazing on soil and ecosystem processes, (2) historical exposure to grazing, (3) site productivity, (4) relative palatability of dominant species, (5) species-specific factors influencing plant recruitment and (6) spatial scale and landscape context. These factors are integrated into a decision tree to describe the potential impacts of livestock on native vegetation in a particular area. Livestock grazing is likely to have detrimental impacts on conservation values in many ecological contexts, especially in relatively intact, uninvaded ecosystems on unproductive soils. By contrast, it may be a useful management tool to achieve conservation objectives where it either (1) controls the biomass of existing potentially dominant, grazing-sensitive plants (native or exotic), (2) prevents encroachment by undesirable, grazing-sensitive, potential dominants, (3) provides disturbance niches required by rare or significant plant species, (4) maintains fauna habitat structure or (5) enhances the diversity of species and vegetation structures across the landscape, especially when most of the landscape is ungrazed. In many cases, other disturbance regimes (especially burning) may achieve similar outcomes; however, other disturbances will not necessarily be more effective than grazing per se, especially in degraded or invaded areas. The framework provides a coarse-level filter to inform management decisions and to allow the findings from individual studies to be placed in a larger ecological context. Although the framework is intended to improve decisions about conservation management, it is clear that much more research is needed to assess the role of grazing exclusion in previously grazed ecosystems, and that modifications to current grazing regimes require testing, perhaps by using adaptive management principles, to ensure optimal outcomes for biodiversity conservation.

Introduction

Grazing by domestic livestock, and associated land-management activities, has created enormous ecological changes in many areas of Australia. Prior to European settlement, Australian ecosystems had not experienced heavy grazing by ungulate herbivores, and the introduction of large herds of cattle and sheep had a catastrophic and often immediate impact on soils, landscape processes, vegetation and fauna, especially in the

mid- to late 1800s (Dixon 1892; Carr and Turner 1959; Moore 1962; Harrington *et al.* 1979; Wimbush and Costin 1979; Noble and Tongway 1983; Wilson 1990; Prober and Thiele 1995; James *et al.* 1999; Kirkpatrick 1999; Young 2000; Gale and Haworth 2005). These impacts are described more fully below.

In many places, this degradation has stabilised over the past century, after the initial depletion in ecological capital. Original soils have been transformed, and grazing-sensitive species

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depleted, to create degraded but potentially stable ecological states under ongoing grazing (Williams 1969; Williams and Oxley 1979; Westoby *et al.* 1989; Lawrence 1999; Gale and Haworth 2005; Witt *et al.* 2006). Furthermore, stocking levels in native vegetation are now lower than those that occurred in the late 1800s in many regions (Williams and Oxley 1979; Noble and Tongway 1983; Lawrence 1999; Lunt and Spooner 2005). Nevertheless, grazing by domestic livestock is still a major degrading activity in many Australian ecosystems (Williams 1990; Tiver and Andrew 1997; James *et al.* 1999; McKeon *et al.* 2004), and livestock are usually removed when new conservation reserves are proclaimed, to promote native species and ecological functions.

However, several recent conservation initiatives in southeastern Australia belie this trend. Livestock grazing has been intentionally retained as an ecological management tool to help achieve conservation outcomes in several reserves in southeastern Australia, including Terrick Terrick National Park in Victoria, Oolambeyan National Park in New South Wales and many reserves in the Australian Capital Territory. These decisions do not reflect compromises between conservation objectives and other socio-economic values, but were made because livestock grazing was believed to be the most effective way to maintain conservation values (Baker-Gabb 1993; Foreman 1999; ACT Government 2004a, 2004b). The recognition that livestock can play a valuable role in maintaining biodiversity is well documented on continents where vegetation evolved under heavy grazing pressure, such as Europe, the Middle East and parts of North America (Bakker 1989; Vavra et al. 1994; Perevolotsky and Seligman 1998; Rook et al. 2004), but is rare in Australia, where livestock grazing is commonly seen as being antithetical to biodiversity conservation (e.g. in alpine landscapes: Wahren et al. 2001).

Currently, there is no holistic framework to interpret why livestock grazing might have positive ecological outcomes in the reserves mentioned above, while having negative impacts in other reserves and ecosystems. Consequently, it would be useful to develop a broad conceptual framework to address the question, under what circumstances (and in what ecosystems) is livestock grazing—or the removal of grazing—likely to have positive, negative, neutral or uncertain impacts on conservation values, particularly to values related to the diversity, structure and composition of native plants? Managers of areas devoted to conservation face two important decisions in relation to livestock grazing. First, whether livestock should be retained or removed from new reserves which historically have been grazed by livestock. And second, if livestock are retained as a management tool to help achieve conservation goals, what are the impacts of different grazing strategies on biodiversity, and can specific grazing strategies be used to maximise conservation outcomes or to restore degraded sites? In this review we address the first of these two questions.

The aim of this paper is to develop a conceptual framework to predict the effects of livestock grazing and grazing exclusion on the conservation values of native vegetation across natural ecosystems in Australia. This paper includes (1) a review of ecological factors that influence responses to grazing and grazing removal and (2) a synthesis of these ecological concepts to provide a decision support framework to help ecologists and land

managers to predict the impacts of grazing and grazing exclusion in any particular ecosystem or area in Australia. Even though we focus on Australian ecosystems, our review and decision support framework are relevant to all global ecosystems that have evolved without heavy grazing by large herbivores.

This paper addresses grazing by introduced livestock and not grazing by native herbivores. Even though Australian ecosystems evolved with grazing pressure from native animals, extremely high grazing pressures by native herbivores (especially kangaroos) can cause serious ecological degradation, leading to moves to manage their numbers (e.g. Cheal 1986; Sluiter *et al.* 1997). Although this issue is not addressed in the paper, our framework should help managers consider and communicate the ecological impacts of abnormally high grazing intensities by native herbivores.

Land-use context

Attitudes to livestock grazing differ between areas devoted to nature conservation (e.g. national parks) and areas dedicated to agricultural production (e.g. commercial grazing properties). The primary objective of commercial grazing businesses is to make a financial return, although property managers' actions are influenced by many non-economic, social and environmental factors. By contrast, in areas devoted solely to nature conservation (on public or private land), the main reason for retaining livestock grazing is to provide a disturbance regime or management tool to help achieve conservation objectives. Consequently, livestock are usually permanently removed from conservation reserves if they have negative or neutral impacts on biodiversity or ecosystem processes, whereas negative impacts may be accepted and neutral impacts welcomed in production areas. This contrast in approaches influences the questions asked by many rangeland ecologists and conservation biologists.

Rangeland ecologists and grazing managers usually address the important question 'how can grazing be managed to minimise adverse environmental outcomes?', assuming that some form of livestock grazing will continue in the area concerned, and that there is an intrinsic trade-off between conservation and production goals (e.g. Dorrough et al. 2004a). By contrast, many conservation biologists and reserve managers wish to know whether livestock grazing is necessary and able to achieve positive conservation outcomes. If not, or if similar outcomes can be achieved by other practical methods (e.g. burning), then livestock are usually removed. Many excellent review papers and extension pamphlets have addressed the first question (e.g. Barlow 1998; Anon. 2000; Eddy 2002; McIvor 2002; Dorrough et al. 2004a), but we know of no national syntheses that have attempted to address the second question.

Global models of grazing impacts

Several models have been developed to explain the variable effects of livestock grazing and other disturbances on small-scale plant diversity and composition. These models underpin the framework that we present in this paper. Early disturbance—diversity models suggested that disturbances such as grazing would have varying effects on diversity, according to the intensity of disturbance (Grime 1973; Connell 1978). Thus, the intermediate-disturbance hypothesis predicted that plant

diversity would be low in undisturbed conditions (owing to competitive exclusion by dominant species), high at moderate grazing levels (owing to reduced biomass of dominant species, and enhanced recruitment and reduced mortality of less competitive species) and low under heavy grazing (owing to the physiological intolerance of many species to frequent defoliation). Although this simple model may predict responses in productive ecosystems (e.g. fertile grasslands), it is less appropriate in unproductive areas where low resource levels prevent dominant species from capturing above-ground space.

By integrating diversity responses across disturbance and productivity gradients, Huston (1979, 2004) suggested that the impacts on diversity of disturbances such as grazing would vary as a result of interactions across disturbance and productivity gradients. At productive sites, moderate grazing intensity was expected to increase diversity, as suggested by the intermediate-disturbance hypothesis. However, at unproductive sites, the opposite outcome was expected, owing to enhanced mortality of slow-growing, stressed species. Huston's model has been supported by modelling studies (e.g. Kondoh 2001) and a meta-analysis of published grazing studies (Proulx and Mazumder 1998), which showed that grazing repeatedly promoted species diversity in productive ecosystems and decreased diversity in unproductive ecosystems.

In addition to disturbance and productivity gradients, ecosystem responses to livestock grazing are influenced by the degree of exposure to large grazing animals over evolutionary periods (Mack and Thompson 1982; Mack 1989). Historically, the introduction of large herds of domestic livestock caused more substantial changes in ecosystems that had not experienced heavy grazing by large indigenous animals over their evolutionary history (e.g. Australian woodlands; see below), compared with ecosystems that evolved with heavy grazing pressure by large indigenous herbivores (e.g. African savannas and North American steppes; Mack and Thompson 1982; Milchunas et al. 1988; Mack 1989). Cingolani et al. (2005) suggested that the degree of exposure to large grazing animals over evolutionary periods might better be considered as the ratio of the estimated long-term grazing intensity before the introduction of European stock, to that after. Regardless of uncertainties about grazing pressure by indigenous herbivores before European colonisation, many Australian ecosystems experienced substantially greater grazing pressures after the introduction of European stock.

In a seminal review, Milchunas *et al.* (1988) argued that grazing impacts on plant diversity were principally driven by interactions between the evolutionary history of grazing by large herbivores and site productivity (as indicated by above-ground net primary productivity, ANPP). Plant-diversity responses to increasing grazing intensities were expected to vary among the four combinations of high v low site productivity, and long v short evolutionary exposure to large herbivores. Thus, in semi-arid (low-productivity) ecosystems with little evolutionary exposure to heavy grazing, plant diversity was predicted to decline under all grazing intensities, whereas in subhumid productive areas with a long exposure to grazing, plant diversity was predicted to increase under moderate grazing and decline under heavy grazing intensities. Intermediate responses were predicted for the other two combinations of

productivity and evolutionary exposure to grazing. This model was supported by a meta-analysis of global grazing studies by Milchunas and Lauenroth (1993), who found that site productivity and evolutionary history of grazing were more important determinants of grazing-induced changes in species composition than the actual intensity of grazing.

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In a refinement to the Milchunas *et al.* (1988) model, Olff and Ritchie (1998) suggested that large and small grazing animals would have different impacts on plant diversity. Large generalist herbivores were predicted to increase diversity in productive areas (through non-selective consumption), whereas small specialist herbivores were predicted to reduce plant diversity because of more selective herbivory. Indeed, in a recent multi-site experiment, Bakker *et al.* (2006) found that grazing by large mammals promoted plant diversity in productive areas and decreased diversity in unproductive areas, although no consistent effects were found for small mammals.

The diversity-disturbance models reviewed above highlight the key processes that influence livestock impacts on smallscale plant diversity across the globe, and provide a valuable framework for predicting the impacts of livestock grazing on plant diversity in Australia. However, notwithstanding their immense value, these models provide a limited perspective on grazing impacts for the purposes of biodiversity conservation. They focus solely on the direct effects of herbivory and do not encompass other ways in which livestock affect natural ecosystems, such as soil compaction, erosion, pugging and nutrient deposition. Additionally, they do not accommodate livestock impacts on larger-scale phenomena, such as landscape processes, nor do they distinguish between native and exotic species. While pastoralists commonly value all palatable forage (native or exotic), conservation managers aim to promote native diversity and to minimise exotic species.

An implicit assumption in many disturbance-diversity models (e.g. intermediate disturbance hypothesis) is that grazing impacts are reversible; thus, if high-intensity grazing leads to a reduction in diversity, then diversity can be increased again by reducing grazing intensity. However, many grazinginduced changes to natural ecosystem are not so reversible. Non-equilibrium models recognise that ecosystem dynamics can be non-linear and irreversible, and that disturbances may create multiple stable states rather than a single, climatically determined 'climax' (Pickett et al. 1992; Wu and Loucks 1995; Briske et al. 2003; Cingolani et al. 2005). Non-equilibrium dynamics are commonly described by using state-and-transition (S&T) models (Westoby et al. 1989; George et al. 1992; Whalley 1994) which incorporate multiple stable states, with transitions between states being triggered by extreme or novel disturbances (such as heavy grazing) or climatic events. In contrast to the diversity-disturbance models reviewed above, S&T models can encompass a range of ecological attributes across multiple scales of organisation, and so can incorporate changes to landscape processes, soils, vegetation structure, composition and small-scale plant diversity. In Australia, S&T models have been used to describe how grazing and other processes can drive ecosystem degradation (Yates and Hobbs 1997), changes to vegetation structure (Westoby et al. 1989), dominant species (Lodge and Whalley 1989), species composition, including invasion and maintenance of exotic

species (Prober *et al.* 2002), and plant traits (McIntyre and Lavorel 2007). A key principle of these models is that livestock grazing can cause a range of ecosystem changes that may be impossible to reverse.

Historical impacts of livestock grazing in Australia

Attitudes to the use of livestock grazing in conservation areas in Australia are likely to be strongly influenced by perceptions of the historical impacts of livestock on Australian ecosystems. Consequently, a brief review of these impacts is warranted. As well as directly eating plants, livestock affect vegetation by altering soils and affecting soil and ecosystem processes at a range of spatial scales from the micro-site and patch level, to the whole catchment. Historically, livestock caused substantial changes to many Australian soils, including loss of biological soil crusts, alteration to soil surface morphology and integrity, changes to soil physical and chemical processes, increases in erosion and ultimately, a reduction in function at the patch and ecosystem scales (Noble and Tongway 1983; Yates et al. 2000; Greenwood and McKenzie 2001; Prober et al. 2002; Holm et al. 2003; Olley and Wasson 2003; Gale and Haworth 2005). The effect of grazing on soils, plants and animals is most pronounced where livestock congregate close to watering points (the 'piosphere' effect sensu Lange 1969) and in stock camps, where high levels of nitrates, declines in species diversity and palatability, and increases in erosion commonly occur (Taylor et al. 1984; Andrew 1988; James et al. 1999; Landsberg et al.

Grazing animals also affect ecosystem processes, particularly water and nutrient flows, across large spatial scales. In many regions, grazing in riparian areas affects streambank vegetation, stream-channel morphology and in-stream water quality, and adversely affects aquatic organisms (Robertson 1997; Robertson and Rowling 2000; Jansen and Robertson 2001; Price and Lovett 2002). In alpine areas of south-eastern Australia, cattle have degraded Sphagnum peatlands by creating incised stream channels. This reduces the water-holding capacity of the peatlands, leading to changes in their structure and vegetation composition and to water flows across the landscape (Wahren et al. 1999, 2001). In semi-arid Australia, groves of mulga (Acacia aneura) function as run-on areas. The upslope side of these groves is bordered by bands of perennial grasses that intercept the flow of water and sediments, allowing the accumulation of resources within the resource-rich mulga groves. Heavy grazing can incise rills, allowing water to flow out of the groves, creating 'leaky', dysfunctional landscapes. This can lead to the death of mulga groves, owing to inadequate resources (Tongway and Ludwig 1990; Ludwig et al. 1997). In all cases, these adverse impacts on soils, streams and landscape processes have substantial off-site impacts, and are usually difficult (if not impossible) to reverse within reasonable time spans.

Livestock grazing has caused significant changes to ecosystem structure in many regions, including the conversion of open, grassy ecosystems to dense shrublands (Hodgkinson and Harrington 1985; Noble 1997; Sharp and Whittaker 2003). Encroachment by native shrubs (or 'woody weeds') involves a suite of interacting processes (Archer 1995). Livestock consume

grasses and create patches of bare soil. Reductions in grass biomass reduce fuel continuity and prevent the spread of fires. Shrub establishment is promoted by reduced grass competition and shrub mortality is diminished by lower fire frequencies. Dense shrubs further reduce grass levels and consequent fire spread, resulting in a positive feedback loop which continues to favour shrub encroachment. In the Victoria River region of the Northern Territory, heavy grazing in the 1970s led to riparian savanna grasslands being replaced by dense forests above a ground layer of non-flammable exotic weeds (Sharp and Whittaker 2003). These major changes to ecosystem structure have substantial impacts on landscape functions and biodiversity patterns, and are often difficult or impossible to reverse across large scales (Archer 1995; Noble 1997; Sharp and Whittaker 2003; Briggs *et al.* 2005).

In stark contrast to examples of shrub encroachment, in other regions, livestock grazing has simplified ecosystem structure as livestock consumed and prevented regeneration of palatable trees and shrubs. In the Riverine Plain of western New South Wales, heavy grazing in the 1800s rapidly transformed large areas of semi-arid shrublands dominated by Atriplex nummularia and Acacia pendula to native grasslands (Moore 1953; Williams 1962; Leigh and Noble 1972). Across large parts of semi-arid Australia, grazing by livestock and feral animals continues to prevent recruitment of native trees and shrubs (Crisp 1978; Chesterfield and Parsons 1985; Tiver and Andrew 1997; Hunt 2001). In more intensively grazed agricultural landscapes, livestock suppress recruitment of native trees and shrubs, creating landscapes dominated by mature and senescent paddock trees (Reid and Landsberg 2000; Saunders et al. 2003; Dorrough and Moxham 2005).

In temperate grasslands and woodlands in southern Australia, livestock grazing has converted understories originally dominated by tall, perennial, summer-growing, native tussock grasses (e.g. Themeda triandra) to dominance by short, wintergrowing, exotic annuals, such as Avena, Bromus, Hordeum and Trifolium species, with losses of associated native forbs (Moore 1967; Pettit et al. 1995; Prober and Thiele 1995; Dorrough et al. 2004a, 2004b). Many of these changes appear difficult, if not impossible, to reverse over large scales, given the absence of soil seed banks of native forbs (Lunt 1997a; Morgan 1998a) and self-reinforcing changes to soil nutrient cycles driven by annual species (Prober et al. 2005). Interestingly, grazing-induced floristic changes appear to have been less substantial in many subtropical and tropical woodlands receiving summer rainfall, where pastures remain dominated by diverse native species, despite changes in their life-form composition (McIntyre and Martin 2001; McIntyre and Lavorel 2001). In a compendium of threatened plant species in Australia, Leigh and Briggs (1992) noted that grazing is a 'presumed cause' of extinction for 34 plant species, has provided a 'past threat' to another 51 endangered plant species, and provides a 'present and future threat' to 55 plant species. Livestock grazing is second only to agriculture in the number of plant species it threatens across Australia.

Separating historical from current grazing impacts

The impacts of livestock grazing described above are well documented and uncontroversial. However, these historical

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impacts are not necessarily directly relevant to decisions about whether to retain or remove livestock from areas devoted to conservation. Ideally, from an ecological perspective, decisions about whether to retain or remove livestock to achieve conservation objectives should be based on the impacts of present (and potential future) grazing regimes on current conditions and future trends. This is far more relevant to current management than the historical impacts of past regimes on original ecosystem conditions. In any particular area, present grazing regimes may have different impacts on ecosystem attributes than do past grazing regimes—because of historical changes in the grazing regimes and the ecosystems being affected (Borman 2005). Thus, current grazing regimes may potentially have positive, neutral or negative effects on biodiversity, in the same places where livestock grazing originally caused substantial damage to ecosystems conditions (Fig. 1).

For example, as noted earlier, livestock grazing in the New South Wales Riverina rapidly transformed semi-arid shrublands to native grasslands in the 1800s (Moore 1953; Williams 1962; Leigh and Noble 1972). However, these disclimax (or derived) native grasslands are now considered to be 'stable' (although temporally variable) under current grazing regimes (Williams 1969; Foreman 1996). In some (but not all) places in the region, the removal of livestock has promoted exotic species and a decline in richness of herbaceous native plants (Margules and Williams 1986). Conservative stock grazing is widely promoted

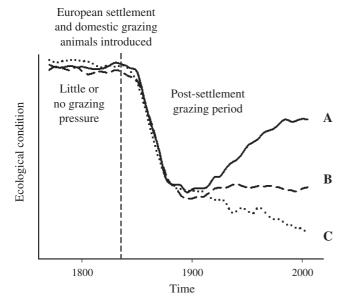


Fig. 1. Three possible trajectories of change in ecological condition under grazed conditions, following an initial decline in ecological condition caused by the historical imposition of heavy livestock grazing. Scenario A represents the recovery of ecological condition after initial degradation, even under current grazing regimes, whereas scenario B suggests that the ecosystem condition is stable, but degraded, with on-going grazing. Scenario C suggests that ecosystem condition continues to degrade in the presence of grazing, even if grazing regimes are more conservative than historical regimes. Not all Australian ecosystems experienced such a dramatic decline in initial ecological conditions.

in the region to retain suitable habitat for endangered fauna such as plains wanderers (Baker-Gabb 1993, 1998). Thus, regardless of initial negative impacts, current grazing regimes are not necessarily always deleterious to biodiversity conservation. In this case, since this system has changed from an original 'shrubland' state to a new and stable (disclimax or secondary) 'grassland' state, the key question for conservation management is how current grazing affects biodiversity patterns in the new stable state, not how past grazing affected the original state.

Unfortunately, much grazing research conducted by Australian ecologists does not adequately distinguish between the impacts of past and current grazing regimes. A common approach is to compare plant composition among land tenures with different assumed, but poorly defined and historically variable, grazing histories (e.g. Moore 1967; Stuwe and Parsons 1977; McIntyre and Lavorel 1994; Prober and Thiele 1995; Lunt 1997b, 2002; Bromham et al. 1999; Fensham et al. 1999; Clarke 2003; Holm et al. 2003; Dorrough et al. 2004b).

Results from cross-tenure studies describe the accumulated impacts of past and present grazing regimes on current vegetation composition, but fail to separate the two. Regardless of whether past grazing has caused degradation, current grazing regimes could potentially be maintaining conservation values in grazed areas (Scenario B in Fig. 1). Undoubtedly, this research approach has contributed greatly to ecological theory (e.g. McIntyre and Lavorel 1994) and to our understanding of the regional impacts of historical grazing regimes on Australian ecosystems (which indeed were the primary objectives of most studies). However, the methodology is not well suited to identifying whether *current* regimes are having positive, neutral or negative impacts within any particular tenure, as historical grazing regimes are likely to have changed considerably in all tenures, and detailed information on past grazing practices is rarely available.

Thus, these studies do not address the following two key issues faced by conservation managers: should livestock be removed from grazed areas and, if not, what grazing strategies should be used? To address these issues, the impacts of current grazing regimes need to be compared against alternative grazing strategies (including grazing exclusion) within *the same* assemblage or degradation state, not among tenures with different grazing histories.

An integrated model to predict grazing impacts

Since livestock grazing affects ecosystems in complex ways across a range of spatial and temporal scales, there is a need to integrate potential grazing impacts in models that can be used by land managers. In Fig. 2, we present a decision tree which describes the potential impacts of livestock on the vegetation of any particular area. From an ecological perspective, the decision tree represents a series of hypotheses based on concepts derived from disturbance and grazing ecology. From a management perspective, it raises a series of questions to inform decisions about whether to retain or exclude livestock from conservation areas. For extension purposes, it provides a framework to communicate why livestock grazing may play a useful role in some conservation areas but not others. Such an integrated framework has not been available previously.

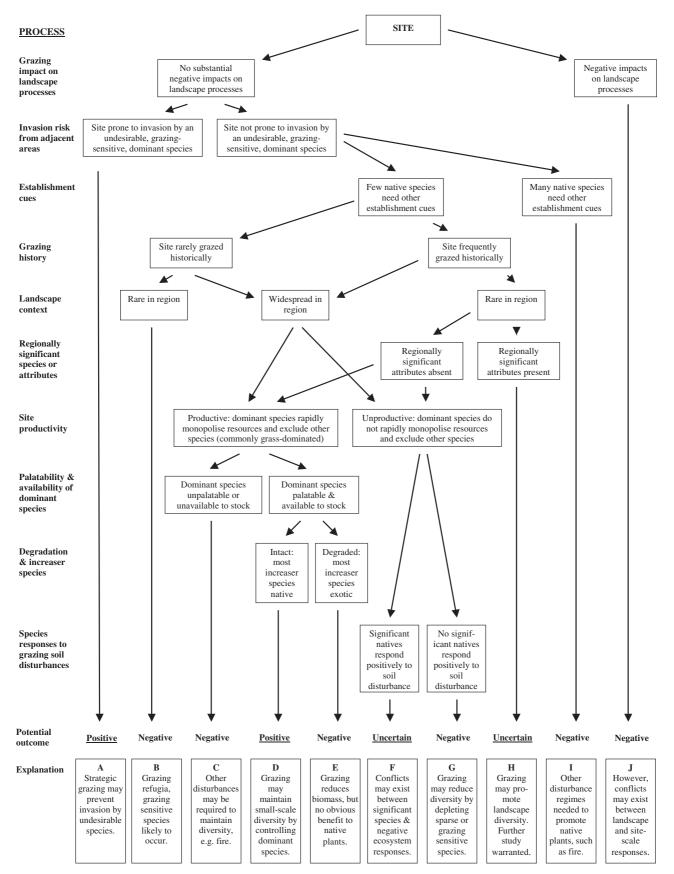


Fig. 2. A decision tree to help predict the effects of livestock grazing and grazing exclusion on conservation values in natural ecosystems in Australia.

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The decision tree is presented in a hierarchical fashion, and generally progresses from issues relating to large spatial and temporal scales, such as impacts on landscape processes, risk of weed invasion from surrounding areas and historical exposure to grazing, to smaller-scale processes, including the relative palatability of dominant species and the degree of degradation or relative abundance of native and exotic species. The decision tree incorporates six major factors that have been identified in the international literature on disturbance ecology and grazing ecology as having a strong influence on how livestock grazing affects vegetation diversity and composition. These factors include (1) impacts of livestock grazing on soil and ecosystem processes, (2) historical exposure to grazing, (3) site productivity, (4) relative palatability of dominant species, (5) species-specific factors influencing plant recruitment and (6) spatial-scale and landscape context. These issues are ordered in slightly different ways in the decision tree and the following text, as the text needs to provide a linear narrative, whereas the decision tree is organised to give the simplest set of options for any particular circumstance.

Impacts of livestock grazing on soil and ecosystem processes

Given the potential for livestock grazing to adversely affect landscape processes across large spatial scales, this issue receives the prime position in the decision tree (Fig. 2) since conservation managers are likely to exclude livestock if they adversely affect landscape processes, regardless of potential positive impacts at smaller scales. While the flowchart demands a binary 'yes/no' response, in reality, the intensity of impacts may grade from the imperceptible to extremely severe, depending (among other things) on stocking levels and grazing patterns. In many cases, the intensity of many impacts may be reduced by lowering stocking rates. In other cases, even low stocking rates may still adversely affect ecosystem processes if stock affect key ecosystem features (e.g. drainage systems; Wahren et al. 1999, 2001; Pringle et al. 2006). Importantly, we know of no contexts in which livestock grazing has positive (rather than negative or neutral) impacts on landscape processes.

Historical exposure to grazing

Australian ecosystems did not experience heavy grazing by ungulate herbivores before European colonisation (Mack and Thompson 1982) and fire, rather than grazing, is thought to be the major landscape-scale disturbance regime that structured Australian ecosystems before European settlement (Bowman 1998, 2000; Bradstock *et al.* 2002). Consequently, the issue of evolutionary exposure to livestock has little discriminatory value within intact Australian ecosystems, since all ecosystems are assumed to have been grazed at relatively low intensities before the introduction of livestock.

However, grazing history is an important issue when intact (ungrazed) and degraded (or long-grazed) patches are compared. Many native ecosystems that have been continually grazed over the past 150 years now contain a mixture of native and exotic grazing-tolerant species and genotypes (e.g. Scott and Whalley 1984). Many of the exotic species evolved under heavy grazing pressure in other continents, especially Mediterranean annuals (Perevolotsky and Seligman 1998; Noy-Meir and Kaplan 2002).

Thus, it is not possible to view these degraded systems as having little evolutionary exposure to heavy grazing, since their current soil and vegetation condition have been produced by livestock.

By contrast, small grazing refugia (such as country cemeteries) exist in many landscapes where grazing has rarely occurred since European settlement. These patches of native vegetation commonly support grazing-sensitive species that have been grossly depleted from other parts of the landscape, especially in southern Australia (Stuwe and Parsons 1977; Prober and Thiele 1995; Lunt 1997b). The introduction of heavy livestock grazing to these sites may be expected to cause more substantial changes to composition than continued grazing in areas that have experienced heavy grazing over the past century.

Historical exposure to livestock grazing may be viewed as a 'filter' which removed grazing-sensitive species and promoted grazing-tolerant species. The 'grazing history' option in the decision tree (Fig. 2) highlights the fact that sites that have rarely been grazed historically may possess grazing-sensitive species which have not previously been 'filtered out' of the system, many of which may be of conservation significance if grazing refugia are rare regionally. Hence, managers should avoid introducing livestock to grazing refugia. If biomass reduction is required to maintain plant diversity in these sites (see below), other disturbance regimes such as burning may be more appropriate. By contrast, in long-grazed sites, species that are highly sensitive to livestock grazing are likely to have been depleted ('filtered out') in the past, leaving a flora (and soil conditions) that are relatively stable under continued grazing.

Site productivity

Site productivity is a key determinant of ecosystem responses to disturbance regimes, including livestock grazing (Grime 1973; Huston 1979, 2004; Milchunas et al. 1988; Milchunas and Lauenroth 1993; Landsberg et al. 1999). In productive systems with high nutrient and water levels, frequent or intense disturbances are commonly required to maintain high plant diversity, as potentially dominant species can rapidly re-establish between disturbance events, causing subordinate species to be out-competed. By contrast, at unproductive sites, plants recover more slowly after disturbances (owing to resource constraints), leading to slower rates of competitive exclusion. In unproductive areas, frequent disturbances can promote plant mortality by exhausting limited carbohydrate reserves (Hodgkinson 1976; O'Connor 1991). Productivity differences can arise from natural (e.g. soils and climate) and human causes (e.g. eutrophication, fertilisation).

The decision tree (Fig. 2) focuses on the competitive outcomes of varying productivity levels, rather than requesting information on soil fertility or water-holding status. Thus, users are asked whether dominant species can rapidly occupy canopy space to exclude other species through competitive dominance. For example, the importance of regular disturbance to remove dense grass has long been recognised in the literature on the conservation management of temperate native grasslands in Australia, where dominance by native perennials such as *Themeda triandra* (kangaroo grass) can lead to reductions in plant populations and species diversity (Stuwe and Parsons 1977; Scarlett and Parsons 1982; Tremont 1994; Lunt and Morgan 2002). In such cases, grazing could play a positive role

for biodiversity conservation by reducing canopy dominance and promoting small-scale plant diversity. By contrast, at unproductive sites, canopy dominance may take very long periods to occur, if ever. In these circumstances, grazing cannot promote small-scale plant diversity by reducing canopy dominance. In general, livestock grazing has the greatest potential to promote small-scale plant diversity at productive sites.

In many Australian ecosystems, site 'productivity', as affected by soil nutrient and water resources, strongly controls the relative dominance of shrubs and grasses, with grasses commonly dominating in fertile well watered soils, and shrubby or heathy ecosystems occurring in less fertile areas (Specht 1981; Groves and Catling 2003). The widespread trend for fertile soils to support grassy vegetation has been demonstrated experimentally (Specht 1963; Heddle and Specht 1975) and explains why graziers add fertilisers and legumes to soils to promote pasture growth. Consequently, as a general rule, livestock grazing is more likely to promote small-scale diversity, through the mechanism of controlling dominant species, in grassy ecosystems than in shrubby ecosystems. However, the same effect could perhaps occur in some shrubby (or ferndominated) ecosystems, provided that dominant shrubs were preferentially grazed by stock (see below).

Palatability of dominant species

Grazing can promote species coexistence only if potentially dominant species suffer the greatest proportional loss of foliage. Grazing cannot promote species diversity if the dominant species are either unpalatable to livestock (and therefore are rarely eaten) or unavailable to livestock (e.g. tall trees and shrubs). If grazing animals preferentially select smaller subordinate species rather than dominant species, then the suggested increase in diversity following grazing of productive sites is unlikely to eventuate; instead, a decline in diversity may occur. This is well illustrated in pastures dominated by unpalatable grasses such as Nassella trichotoma (serrated tussock). In these cases, livestock preferentially graze associated species that are more palatable and nutritious than Nassella, reducing their abundance (Campbell 1998). Reduced competition from other species further promotes seedling recruitment of the unpalatable Nassella, leading to increasing dominance by an unpalatable species in an increasingly species-poor pasture and to a decline in carrying capacity (Campbell 1998).

The nutrient content and palatability of foliage declines as plants age. Hence, livestock preferentially select young plants and green leaves (Crawley 1983; Prache *et al.* 1998). Livestock may also avoid eating dominant grasses if these species are largely composed of old, dead leaves. This can lead to the development of grazing mosaics as livestock avoid areas dominated by coarse unpalatable species and selectively graze other areas (Arnold and Dudzinski 1978; McIvor *et al.* 2005).

Both of the processes described above restrict the ability of livestock to increase small-scale plant diversity within areas dominated by coarse, unpalatable species. Traditionally, many graziers burnt natural areas to promote palatable 'green pick' for livestock (e.g. Banks 1989). However, from a conservation perspective, if the only reason for using livestock is to increase

plant diversity by reducing dominant species, then burning alone would achieve this aim, without subsequent livestock grazing. Burning followed by grazing is likely to have different ecological impacts than grazing or burning alone (Collins 1987; Collins *et al.* 1998; Archibald *et al.* 2005).

The decision tree (Fig. 2) includes an option which asks whether dominant species are palatable and available to livestock. This option is relevant only at productive sites which are capable of supporting dense stands of dominant species. At productive sites, livestock grazing may promote small-scale plant diversity if the dominant species are palatable and available to stock.

Species-specific factors influencing plant recruitment

Grazing affects plant diversity and composition (and, over the long-term, vegetation structure) by influencing patterns of plant establishment, growth and mortality. The above models of grazing-induced increases in plant diversity assume that the creation of canopy gaps or bare ground will actually promote seed germination and seedling establishment. This assumption is valid for many species in Australia and elsewhere, especially for herbaceous species (Gilfedder and Kirkpatrick 1994; Morgan 1998b, 1998c; Clarke et al. 2000).

However, gap creation is less likely to promote establishment of species that have evolved germination cues tied to other disturbances regimes such as burning. Unfortunately, most global grazing-diversity models (e.g. Milchunas et al. 1988; Milchunas and Lauenroth 1993; Olff and Ritchie 1998) give scant attention to the implications of evolutionary exposure, and consequent species adaptations, to other disturbance regimes such as fire. Many species in Australia and other Mediterranean regions (e.g. South Africa) have evolved mechanisms to promote seedling establishment after fires, including serotiny and a variety of seed-dormancy mechanisms (Gill 1981; Lamont et al. 1991; Bond and van Wilgen 1996; Bell 1999; Tieu et al. 2001). These adaptations are especially prevalent in sclerophyllous ecosystems such as heathlands and heathy forests. Grazing is unlikely to promote establishment of these species as the ecological changes invoked by grazing (canopy removal and soil disturbances) are relatively ineffective at stimulating seed germination (e.g. Clarke 2002). Thus, grazing is most likely to promote small-scale plant diversity in ecosystems (such as grasslands) where few species have germination requirements for fire, flooding or other specific disturbances.

Species-specific factors influencing plant recruitment are recognised at three places within the decision tree in relation to (1) plant establishment cues, (2) potential positive responses by native species to soil disturbances and (3) the presence of regionally significant species or attributes. Establishment cues receive a prominent position in the decision tree to highlight that livestock grazing is unlikely to promote plant diversity in ecosystems in which many species have specific requirements for other establishment cues (e.g. flooding or burning). By contrast, potential requirements of native species for grazing-induced soil disturbances need only to be explicitly acknowledged in the decision hierarchy at unproductive sites at which grazing has little potential to play other positive roles. The presence of regionally significant species or attributes is included in

the decision tree as a precautionary warning. The presence of regionally significant species in grazed areas does not imply that grazing is promoting these taxa or attributes (it may be hastening their decline; e.g. Dorrough and Ash 2004). However, significant taxa may be promoted by grazing (e.g. *Leucochrysum albicans*: Gilfedder and Kirkpatrick 1994) and managers should be alert to the possibility that the removal of grazing stock could adversely affect these significant attributes.

Controlling exotic species

Most pastoral grazing studies consider native and exotic species to be of equal value, provided that plants are palatable and nutritious to livestock. By contrast, conservation managers aim to promote the diversity of native species and to minimise the cover or abundance of exotic species. The factors that promote establishment of exotic species are, to a large extent, siteand species-specific. However, in general, native and exotic species are likely to be promoted by any processes that enhance the availability of resources (Davis et al. 2000). Invasion of Australian ecosystems by exotic species is often favoured by high resource levels, including elevated water and nutrient levels (Chalmers et al. 2005; Leishman and Thomson 2005; Lenz and Facelli 2005). Under high resource levels, many common exotic grasses and forbs grow faster and larger than native species that evolved in low-nutrient soils (Begg 1963; Allcock 2002; Groves et al. 2003; Lenz and Facelli 2005; Prober et al. 2005). Consequently, Huston's suggestion that disturbance impacts will vary between productive and unproductive environments may also apply in a general fashion to exotic species in grazed areas (Huston 2004), and grazing exclusion may lead to different outcomes for exotic species in unproductive and productive environments (Lunt et al. 2007), as described in Table 1. Thus, grazing exclusion is most likely to promote dominance by exotic species in degraded ecosystems on well watered, fertile soils (e.g. degraded riparian areas). Strategic grazing or other disturbances may help control vigorous exotic species in these conditions.

Exotic species are accommodated in two places in the decision tree (Fig. 2), namely, 'invasion risk from adjacent areas' and 'degradation and increaser species'. The attribute 'invasion risk from adjacent areas' highlights that managers need to consider not only the area being grazed (and from which grazing

stock may be excluded) but also adjacent areas. Livestock often promote dispersal of weed seeds (Brown and Archer 1988; Radford *et al.* 2001). However, they can also reduce the potential for grazing-sensitive invading species to invade from adjacent areas (Tiver *et al.* 2001).

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In the decision tree (Fig. 2), the factor 'degradation and increaser species' accommodates the degree of site degradation and the origin of potential increaser species. At intact sites, where many native 'increaser' species are present, grazing has the potential to boost diversity. By contrast, at highly degraded sites, this may not occur if most responsive species are exotic.

Spatial-scale and landscape context

The effects of grazing on plant diversity may vary across spatial scales for at least the following three reasons: (1) grazing patterns vary spatially, and not all areas are grazed in the same way; (2) small-scale impacts may cumulatively affect larger-scale landscape processes, such as water and nutrient flows; and (3) impacts observed at one spatial scale are not necessarily transferable across other spatial scales. These processes are described below.

First, grazing animals choose where to graze as well as what to graze (Arnold and Dudzinski 1978; van Rees and Hutson 1983; Prache et al. 1998). Hence, grazing patterns vary spatially and consequent impacts on vegetation vary spatially. For example, areas close to water points are typically heavily grazed and areas distant from water less intensively grazed (Andrew 1988; James et al. 1999). However, many methods for increasing the efficiency of commercial grazing enterprises aim to reduce the variability in grazing patterns across the landscape by, for example, reducing paddock sizes and installing more watering points, thereby potentially homogenising vegetation patterns. Second, alterations to large-scale ecosystem processes, especially water and nutrient flows, can affect vegetation patterns in unpredictable ways across large scales, as described earlier. Third, grazing impacts vary according to the scale of observation. At any one place, grazing is likely to reduce the abundance of some plant species ('decreaser species') while promoting others ('increaser species'). Small-scale plant diversity will be boosted if the number of increasers exceeds the number of decreaser species. However, at landscape scales, plant diversity will be maximised if increaser and decreaser

Table 1. Potential responses in vegetation structure following grazing exclusion in contrasting situations of site degradation and productivity (after Lunt et al. 2007)

Site	Productivity	
degradation	Low	High
Low	Native dominance	Native dominance
	 Small increase in biomass 	 Large increase in biomass
	 Small change in exotic biomass 	 Potential increases in large exotic species
	• Possible minor increase in small-scale richness of low biomass species	 Decline in small-scale plant richness, especially in low-biomass species
High	Native: exotic co-dominance	Exotic dominance
	 Small increase in biomass 	 Large increase in biomass
	 Possible minor increase in small-scale richness of low-biomass species 	Decline in small-scale plant richness, especially in low-biomass species
	 Limited increase in native richness owing to propagule constraints 	 Negligible increase in native diversity owing to competition and propagule constraints

species are both abundant. If livestock grazing causes 'decreaser' species to decline everywhere, then overall landscape diversity must decline, even if small-scale diversity increases. Thus, Landsberg *et al.* (2002, p. 427) found that grazing increased plant species richness at small scales but reduced richness at landscape scales 'by removing the most grazing-sensitive species from the regional species pool'. Similar results have been found elsewhere (Chaneton and Facelli 1991). At a national level, Moore suggested that livestock grazing acted to reduce landscape diversity by homogenising natural ecosystems by promoting a small suite of grazing-tolerant species (mostly exotics) across a wide variety of naturally variable ecosystems (Moore 1962; Moore and Biddiscombe 1964).

Fortunately, the homogenising potential of widespread grazing (or any widespread disturbance regime) may be moderated to some extent by natural environmental heterogeneity. Like all disturbances, grazing commonly has different effects in different localities (McIntyre and Martin 2001; Vesk and Westoby 2001; Landsberg *et al.* 2003) and species that decline in some areas may be promoted in others (Vesk and Westoby 2001; Landsberg *et al.* 2002). Consequently, in some cases, small-scale impacts may not be apparent when larger regions are studied (e.g. Stohlgren *et al.* 1999). Like most geographical phenomena, outcomes are likely to become more variable as spatial scale increases (Vesk and Westoby 2001).

From a conservation perspective, in ecosystems where grazing has some potential to promote conservation goals, landscape species diversity is likely to be promoted by maximising the diversity of disturbance regimes implemented (including grazing). In landscapes dominated by grazing, removal of livestock from some areas may boost landscape species diversity, regardless of impacts within the ungrazed areas. Within grazed areas, patch diversity is likely to be boosted by promoting spatially variable grazing patterns (Leonard and Kirkpatrick 2004). This approach assumes that grazing-tolerant species are well catered for elsewhere in the landscape, and that the management objective within conservation areas is to cater for grazing-intolerant species. The approach also assumes that grazing promotes some native 'increaser' species. In some landscapes, grazing promotes few native increaser species, e.g. semi-arid shrublands and woodlands (Landsberg et al. 2003) and temperate white box woodlands (Prober and Thiele 1995; Dorrough et al. 2007). In the decision tree (Fig. 2), spatial-scale issues are largely confined to the 'landscape context' option which asks whether grazing is a rare or widespread activity in the region, since information is rarely available on many other complex issues associated with spatial scales (as described above).

Synthesis through the decision support tool

The above review highlights that livestock grazing can have positive or negative impacts on plant diversity and composition, depending on a range of factors which vary within and among ecological communities (Milchunas *et al.* 1988; Olff and Ritchie 1998; Huston 2004). Like any disturbance regime (e.g. fire), livestock grazing cannot be deemed to be intrinsically 'good' or 'bad' for biodiversity conservation in Australia (as elsewhere). Instead, potential outcomes are context-specific. Understanding

this context will provide conservation managers with a means of making decisions that are pertinent to their local situation rather than seeking generic policy approaches to encompass all management directions.

The decision tree (Fig. 2) integrates the reviewed processes into a simple framework to guide decisions relating to livestock grazing in conservation reserves. For each set of circumstances, the potential impact of livestock grazing on conservation values is evaluated as being either positive, negative or uncertain. Although the decision tree suggests that only one potential outcome is obtained under each set of circumstances (e.g. a negative outcome), conflicts may exist between different values in some circumstances. For example, grazing may assist rare fauna but deplete rare plants, or have negative impacts at landscape scales but enhance plant diversity at small scales (Outcome J in Fig. 2). These complexities exist for all types of ecosystem management, not just livestock grazing. Resolution of these complexities is beyond the simple tool proposed here.

The decision tool highlights the fact that livestock grazing is likely to be detrimental to biodiversity conservation in many ecological contexts, e.g. in relatively intact, uninvaded ecosystems on unproductive soils (Fig. 2). The most common circumstance in which it may be a useful management tool for conservation purposes is where it controls the biomass of existing potentially dominant, grazing-sensitive, palatable plants (native or exotic) on productive soils (Outcome D in Fig. 2). Less commonly, grazing may theoretically also be useful where it (1) prevents encroachment or invasion by undesirable, grazingsensitive, potential dominants (Outcome A), (2) provides disturbance niches required by particular rare or significant species (e.g. Gilfedder and Kirkpatrick 1994) (Outcome D and F) or (3) where it contributes to the diversity of species and vegetation structures across landscape scales, especially when grazing occupies a relatively small part of the landscape (Outcome H). These examples are restricted to plants. Livestock grazing may also help to maintain a suitable habitat structure for significant fauna species in some places (e.g. plains wanderers; Baker-Gabb 1993, 1998). In all cases, however, managers may choose to use other disturbance regimes to achieve their objectives such as burning. However, in many cases, there is no a priori reason why fire will necessarily be more effective (or more efficient) than grazing, especially in degraded or invaded areas.

In addition to the scenarios provided, livestock grazing may also be a useful tool to help restore degraded ecosystems, in combination with other management interventions (e.g. Prober and Thiele 2005). However, these options are likely to require the use of specific grazing strategies which require considerable research and development. Specific grazing strategies (i.e. tactical or strategic grazing) are likely to give better outcomes than continuous set-stocking wherever grazing has potential to give positive ecological outcomes (Kemp *et al.* 1996; Lodge *et al.* 1998; Friend and Kemp 2000).

Conclusions

Historically, livestock grazing has caused enormous damage to many Australian ecosystems, and current grazing regimes continue to damage many areas. However, in some cases, Livestock grazing in Australia Australia Australia Australia

livestock grazing can provide a practical management tool to help achieve conservation objectives, as in other continents of the world (Bakker 1989; Perevolotsky and Seligman 1998; Rook *et al.* 2004). Positive outcomes from livestock grazing are not confined to situations involving compromises between production and conservation goals, but may also occur in areas devoted solely to conservation purposes. However, livestock grazing is expected to give positive conservation outcomes in a relatively small range of ecological circumstances.

Hopefully, the decision tree presented here will provide a useful framework to allow ecologists and managers to predict, interpret and compare the impacts of livestock grazing on natural ecosystems. This framework should not be used to advocate the wholesale removal or retention of livestock grazing from any particular site or ecosystem. Instead, it provides a coarse-level filter to inform management decisions and to allow the findings from individual studies to be placed in a broader ecological context. As always, ecological research and adaptive management trials should be used to gather high-quality evidence to support large-scale land management decisions (Parma and NCEAS Working Group on Population Management 1998).

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