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Using strategically applied grazing to manage invasive alien plants in novel grasslands

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Abstract

Introduction: Novel ecosystems that contain new combinations of invasive alien plants (IAPs) present a challenge for managers. Yet, control strategies that focus on the removal of the invasive species and/or restoring historical disturbance regimes often do not provide the best outcome for long-term control of IAPs and the promotion of more desirable plant species.

Methods: This study seeks to identify the primary drivers of grassland invasion to then inform management practices toward the restoration of native ecosystems. By revisiting both published and unpublished data from experiments and case studies within mainly an Australian context for native grassland management, we show how alternative states models can help to design control strategies to manage undesirable IAPs by manipulating grazing pressure.

Results: Ungulate grazing is generally considered antithetical to invasive species management because in many countries where livestock production is a relatively new disturbance to grasslands (such as in Australia and New Zealand as well as Canada and the USA), selective grazing pressure may have facilitated opportunities for IAPs to establish. We find that grazing stock can be used to manipulate species composition in favour of the desirable components in pastures, but whether grazing is rested or strategically applied depends on the management goal, sizes of populations of the IAP and more desirable species, and climatic and edaphic conditions.

Conclusions: Based on our findings, we integrated these relationships to develop a testable framework for managing IAPs with strategic grazing that considers both the current state of the plant community and the desired future state—i.e. the application of the principles behind reclamation, rehabilitation, restoration or all three—over time.

Review

Introduction

Research into invasive alien plants (IAPs) has largely been focused on understanding *why* and *how* some plant species can colonise, persist, expand their ranges, and sometimes even dominate plant communities over relatively short evolutionary timeframes—this, often under the guise of informing and improving the design of control strategies (Sax and Brown 2000; Levine et al. 2003; MacDougall and Turkington 2005; Vila et al. 2011). Yet, the most common control strategies remain centred on removing IAPs with various rudimentary physical, chemical or biological measures, such as bulldozers, herbicides and insects. In some control programs, particularly within an Australian context for land management, strategies are put into place to return historical disturbance regimes, e.g. by excluding grazing and/or prescribing seasonal burning. Despite these efforts, many control programs continue to prove ineffectual, resulting in the re-establishment of the same IAP or others (Gardener et al. 2010), a phenomenon referred to as *filling a 'weed-shaped' hole* (Firn et al. 2008). That being said, common control strategies—e.g. where the IAP is killed or removed and the historical/bioregional disturbance regime applied—are largely based on traditional models of succession. These models suggest that plant assemblages are dynamic but still progress towards a final state (or climax community) along a continuum that is regulated by internal forces (i.e. changes resulting from interactions among organisms and the physical

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environment) as well as climatic conditions. Disturbance and/or intra- and inter-specific competition can shift vegetation community composition forward or backward along a continuum (Clements 1916). This notion of a continuum of states suggests that alterations to a plant community are reversible, yet we now know that this is not always the case (cf. Perring et al. 2013). In addition, weed control has commonly been approached from principles of population ecology, being focused on the behaviour and requirements of single species, as opposed to the holistic behaviour of vegetation communities undertaking active recruitment following control measures—the so-called and aforementioned *weed-shaped hole* (Booth et al. 2003).

The problem with these approaches is that the original community is usually not restored once the causal disturbance has been reduced or mitigated; instead, what mostly results is a new assemblage of plant species, not predicted along the historical continuum (cf. Suding et al. 2004). Novel ecosystems and the underlying theory (representing a central theme for this special issue) have recently (and contentiously) arisen in the field of restoration ecology to address the unique management issues that are presented by these altered systems (Hobbs et al. 2006, 2009). As discussed further below, this is particularly relevant to IAP-dominated ecosystems in which many new assemblages are achieved by human-mediated dispersal (Richardson and Gaertner 2013).

Novel ecosystems and alternative states models

Recent novel ecosystem theory proposes that threshold models such as alternative states models are effective restoration tools for managing systems altered by direct and indirect human-induced disturbances (Hobbs and Suding 2009), particularly since not all novel ecosystems are necessarily desirable (Richardson and Gaertner 2013). In this case, the goal may be, e.g., to alter the conditions of the novel ecosystem to a more desirable state. Alternative states models suggest that historical disturbance regimes will not work where the functioning of the ecosystem has changed (i.e. nutrient cycling, hydrology and energy flows; Zavaleta et al. 2001; Suding et al. 2004; Hobbs et al. 2006). These models have evolved within the context of rangeland ecology (Westoby et al. 1989; Cingolani et al. 2005), restoration ecology (Suding et al. 2004) and ecological resilience theory (Gunderson 2000) but have only recently been applied within invasion ecology (Cox and Allen 2008; Firn et al. 2010; Gaertner et al. 2012). In contrast to traditional models of succession, alternative states models explain how different communities can exist at the same site depending on conditions. Transitions between states are regulated by both internal forces (that are also included in succession models) as well as external ones. External forces are defined as newly imposed or alterations to existing disturbance(s) and climatic conditions. For instance, if a community has transitioned to a new state and the feedback relationships have shifted permanently from negative to positive within this state, restoring it back to the previous state may no longer be possible simply by reducing or mitigating the causative disturbance (Richardson and Gaertner 2013). Instead, alternative management actions may be required to initiate a transition, and the disturbance applied to initiate a transition may have little to do with the historical disturbance regime (Suding et al. 2004). Understanding the historical context of *why* and *how* IAPs dominate is important for the design of preventative measures, but this is only one piece of the puzzle. To use alternative states models as the underlying framework for invasive species management bringing together fields of restoration and invasion ecology (Hobbs and Richardson 2011), we then need:

1. An understanding of how the new IAP-dominated ecosystem functions (Hobbs et al. 2006; Richardson and Gaertner 2013), and
2. A clear, realistic and flexible set of restoration goals aimed at gradually shifting the community towards a more desirable state over the short and long term (Hobbs 2007; Hobbs and Suding 2009).

This is particularly important when IAPs are considered transformers (or drivers of ecological change) because they may alter both subtle and obvious components of ecosystem functions and services, e.g. by being excessive users of nutrients, donors of limiting nutrients, fire promoters/suppressors or salt accumulators/redistributors (Richardson et al. 2000; Richardson and Gaertner 2013). Otherwise investing time, effort and money into the application of common control strategies may lead to even further degradation (Zavaleta et al. 2001).

Methods

Objectives, hypotheses and investigative approach

Human activities such as recently introduced ungulate grazing imposed at high rates and/or intensities in either productive or unproductive regions (or, likewise, regions prone to drought—as in many parts of Australia) may lead to the dominance of undesirable plant species (Cingolani et al. 2005). These species, which are typically difficult to control over expansive landscapes (e.g. *Nitraria billardieri* in semi-arid NSW; Noble and Whalley 1978), are generally either unpalatable or respond quickly to disturbance through vegetative growth and/or germination. Even though many restoration efforts stipulate biodiversity conservation as a main objective, a solution to this management dilemma is not necessarily to remove grazing entirely (as in traditional models of succession); instead, some evidence suggests that modifying grazing pressure either (a) directly through the manipulation of the timing, frequency and intensity of grazing or (b) indirectly through the manipulation of resource availability to increase the palatability of the dominant IAP are more effective solutions (or alternative states) at least in the short term (Davies et al. 2009; Firn et al. 2010). We know from extensive research that, on the one hand, grazing can reduce species richness and abundance where herbivores are exotic or newly introduced to an area (particularly in regions that are low in nutrients and rainfall) and where grazing pressure is high in both intensity and frequency (Milchunas et al. 1988; Cingolani et al. 2005). On the other hand, grazing can increase species diversity where herbivores are native to an area (particularly in regions that have moderate to high nutrients and rainfall) and where grazing pressure is low in both intensity and frequency (Milchunas et al. 1988; Olff and Ritchie 1998; Cingolani et al. 2005; Parker et al. 2006; Hillebrand et al. 2007). Grazing can also produce genetic changes within native grass species, for instance, where there are marked spatial differences in grazing pressure or in the distribution of introduced perennial pasture grasses within a paddock (Scott and Whalley 1984; Magcale-Macandog and Whalley 2000, 2007). This is particularly true of Australian native grasses because of the breeding systems that many of them have evolved over geological time (Whalley et al. 2011) Based on this evidence, it is suggested that grazing, if used strategically, could then facilitate increased native diversity (Lunt et al. 2007).

In this study, we synthesize evidence that strategically applied grazing can be used successfully for the control of invasive plants and the return of more desirable species, in particular natives. By revisiting both published and unpublished data from studies of invasive species within an Australian context for grassland management, we describe two management options: (1) directly manipulating grazing pressure and (2) indirectly manipulating grazing pressure. We then make recommendations on scenarios where direct and indirect manipulation of grazing pressure can be applied. Finally, we suggest a set of generic management goals depending on the current and future desirable state of the grassland or pasture, in accordance with the principles of adaptive management. Studies included in our retrospective analysis were selected if they included a treatment where grazing was manipulated to control an IAP. This provided a suitable investigative context to ultimately present our testable conceptual depiction of alternative states models work as a theoretical underpinning for IAP control using grazing management. Detailed methodology explaining data collection and analyses for all of the presented data (particularly Figures S1 and S3) is presented in Additional file 1.

Results and discussion

Control strategies

Directly manipulating grazing pressure To reduce IAP dominance with strategic grazing, management needs to alter those variables that enable species persistence under grazing, i.e. selectivity and palatability. There are several ways in which selectivity and/or palatability can be altered by directly modifying grazing pressure. Grazing intensity can be increased to reduce selectivity and increase the uniformity of grazing among the desirable and undesirable species. The resulting community composition will depend on the ability of the species to recover from grazing in the rest period following defoliation (Gardener et al. 2005). High intensity rotational grazing has been used successfully for the control of several invasive species (e.g. *Cirsium arvense*; De Bruijn and Bork 2006) and *Chrysanthemum leucanthemum* (Olson et al. 1997)). Pywell et al. (2010) found the most effective control strategy for *Cirsium arvense* was low intensity grazing because it maintained a competitive cover of other plant species. Many unpalatable species have life-history stages that are palatable and sensitive to grazing, and the timing of grazing (and the intensity) can be altered to periods when the invasive species is most susceptible (Hartley et al. 1984; Thomsen et al. 1993; Rinella and Hileman 2009). The duration of grazing is also important as many invasive species require repeated defoliations to have an effect (e.g. leafy spurge; Kirby et al. 1997). Grazing has been used strategically for invasive species control in two ways: (1) biocontrol, where grazing animals are used to reduce the growth, survival or reproduction of invasive plants (Popay and Field 1996), and (2) competition, by increasing the cover of resident species to suppress invasive species.

An example of when grazing management can aid in invasive species management is with thistle. Thistle species are generally unpalatable and as such tend to increase in grazed systems. However, strategic grazing can reduce thistle densities by targeting the life-history stage when the shoots are palatable (newly emerging) and beyond the rosette stage (available to stock) (Grace et al. 2002; Holst et al. 2004; De Bruijn and Bork 2006; Wallace et al. 2008). The timing of grazing that provides the best control will depend on the species as well as environmental variables. Grazing intensity and duration are important; low intensity continuous grazing increased Canadian thistle populations by favouring selective grazing, whereas high intensity rotational grazing reduced populations (De Bruijn and Bork 2006). High intensity rotational grazing also minimised the impact on resident species, which increased competition. Rest from grazing in autumn to increase competition altered the morphology of *Carduus* spp. causing plants to become more upright and accessible to stock, and grazing at this stage provided control (Bendall 1973). Control methods that indirectly alter grazing pressure have also provided thistle control, e.g. applying herbicides can alter physiology, vigour and palatability (Holst et al. 2004; Shea et al. 2006). Thistles are a well studied example of an invasive species which increases under grazing but can be controlled with modifications to the grazing regime.

Resting from grazing can also be beneficial for the development of competitive species that may be more palatable than the target weed (Lodge and Whalley 1985. A number of studies have found rest from grazing can reduce the abundance of undesirable species and increase the abundance of desirable species by matching rest periods with species phenologies (e.g. Ash et al. 2011; Kemp et al. 1996). This strategy will depend, however, on whether desirable species remain in the community, their phenology (Kemp et al. 1996; Fischer et al. 2009) and whether the dominance of the IAP has been reduced prior to resting (Lunt et al. 2007). Rest from grazing in novel ecosystems also may not work because remaining original species may have experienced genetic changes that allow them to survive and persist with grazing pressure (Scott and Whalley 1984; Magcale-Macandog and Whalley 2000, 2007; Waters et al. 2010, 2011), but they may then lack the genetic variability to persist without grazing. Original species that are lost or have become rare and endangered within the ecosystem may have had inflexible breeding systems that meant they were incapable of responding to grazing pressure (Yu et al. 2000, 2003). Several studies have found that excluding grazing from sites where populations of an unpalatable plant species are high indeed favour the further expansion of the IAP (Firn et al. 2010; Hayes and Holl 2011; Isbell and Wilsey 2011; Price et al. 2011b). In these cases, it may be that the undesirable species itself should be removed using herbicides, the palatability of the species be modified by using fertilisers or some other form of disturbance occur to initially perturb the population and open opportunities for other species.

Indirectly manipulating grazing pressure Selectivity and palatability can also be altered by indirectly modifying grazing pressure. Prescribed burning within IAP-dominated ecosystems will break down mature tissue and litter, which in turn will increase light and nutrient availability and stimulate germination from the seed bank and vegetative growth. Because of this flush of resources, plant species that colonise after fire will be more palatable and nutrient rich, and these patches will then attract grazing stock and reduce selective pressure (Cummings et al. 2007). In some cases, prescribed burning may reduce dominant IAPs and promote other desirable species without livestock grazing being necessary, although evidence has shown that prescribed burning is more effective when incorporated into an integrated vegetation management program (DiTomaso et al. 2006).

Lespedeza cuneata is a perennial legume that was introduced into the USA as a forage species specifically because the species has persistence mechanisms that maintain its dominance under grazing. Patch burning was found to reduce invasion in tallgrass prairies by maintaining the invasive species in a young and palatable stage of growth (Cummings et al. 2007). The size of the patch that is burnt matters, however, with small burnt patches more likely than large ones to result in increased grazing pressure on all species present not just the most palatable. Applying herbicides or fertilisers can also alter the palatability of IAPs. Fertilisers have been used to increase the palatability of *Eragrostis curvula*, and in combination with grazing management provided good control (Firn et al. 2010). A treatment combination of herbicides and grazing has been effective for the control of *Echium plantaginuem* (Huwer et al. 2005) and *Carduus nutans* (Shea et al. 2006). Herbicides alter the morphology of *E. plantaginuem* making the rosettes more erect and available to grazing stock (Piggin 1979).

Alternative states models work as a theoretical underpinning for IAP control using grazing management

Most of the literature on grazing management and invasive species control has been conducted in rangelands or pastures where conservation of biodiversity or native dominance is secondary to production and where the major land use is grazing. Because of this, in many cases grazing exclusion has not been experimentally tested as a management option, rather just the grazing regime has been modified. This means that models that incorporate restoring historical conditions are largely untested in the bulk of the agricultural literature. What is evident, however, from this literature is that sometimes a modification of the current grazing regime may be what is needed to provide control of invasive species. In addition to this, some recent studies have found that restoring historical conditions has not provided the best control options, supporting the notion that novel ecosystems may need novel management options (Seastedt et al. 2008).

Restoration of historical disturbance regimes (ungrazed and burnt) facilitated the invasion of the annual grass species *Bromus tectorum* and other exotic forbs into sagebrush communities (Davies et al. 2009). In comparison, treatments that combined historical and non-historical disturbances (grazed and burnt) did not facilitate an invasion and resulted in greater cover of perennial vegetation. Livestock grazing is a causal factor in *B. tectorum* invasion but can also, depending on the grazing regime, provide resilience to invasion. The mechanism cited here is increased litter accumulation in the ungrazed condition resulting in greater post-fire mortality of native species providing space and resources for invasion. The intensity of grazing determines the outcome because heavy grazing facilitates invasion by decreasing the cover of native plant species. The authors highlight that best management practices are counterintuitive to the assumption that restoring historical disturbances will provide best management of ecosystems.

The best control strategy for the invasive perennial grass *Eragrostis curvula* was the maintenance of grazing (non-historical disturbance) and the use of fertilisers (non-historical conditions) to increase the palatability of the IAP (Firn et al. 2010). Invasion of *E. curvula* is facilitated by selective grazing because of its low palatability in unproductive environments, but the same disturbance, when used strategically, can reduce the population of IAPs. This treatment combination also gave the best results for restoring native dominance. Interestingly, the control strategy of removing the causal disturbance and applying herbicide reduced IAP abundance but led to an increase in abundance of another invasive species, a perennial forb, *Verbena tenuisecta*. In this case, the best approach for the restoration of a novel ecosystem dominated by an invasive species was a combination of non-historical management techniques.

Testable framework for strategically using grazing to reduce IAPs in novel pastures The underlying ecological theory behind common control strategies for IAPs is based on traditional successional theory, which, after decades of research, is known to explain the dynamics of few natural systems. Recent studies that explicitly examine the efficacy of control strategies based on traditional models of succession have found that the resultant plant community either remained dominated by the same or another invasive species. Evidence suggests instead that new theoretical models are needed to underpin invasive species control in undesirable novel ecosystems—alternative states models (Wiess 1999; Cox and Allen 2008; Davies et al. 2009; Firn et al. 2010). When these theories are applied to invasion scenarios where ungulate grazing is a relatively recently applied disturbance, and the ecosystem is degraded, manipulating grazing pressure towards the IAP may be a more effective control measure than grazing exclusion (Figure 1) because a threshold to recovery has been crossed (Westoby et al. 1989; Gaertner et al. 2012; Richardson and Gaertner 2013). This can be accomplished either directly by changing the timing, frequency and intensity of grazing animals or indirectly by increasing resource availability if the dominant IAP is a plastic species capable of increasing in palatability (Firn et al. 2012).

We know from general ecological theory on the effects of grazing and from invasive species literature that certain preconditions should be met for strategically applied grazing to be a benefit for management (Wiess 1999; Lunt et al. 2007; Cox and Allen 2008; Davies et al. 2009; Firn et al. 2010). Native diversity or other more desirable species should be present at the site or in the surrounds as a source of new recruits, and soil moisture and nutrient levels should be adequate for recruiting species to germinate and survive. The decision to use direct or indirect manipulation of grazing will depend on the palatability of the IAP and the economic and technical feasibility of each strategy. Direct manipulation requires decreasing, increasing or maintaining herd numbers, and in some cases intensively guiding their movements. Indirect manipulation will require fertiliser addition, irrigation or prescribed burning. Whether or not these actions are feasible at a site will depend on the characteristics and pressures that are specific to an individual site, landscape and region.

An example of the complexities of using grazing to manipulate an IAP is the establishment of the perennial forb lippia [*Phyla canescens* (Kunth) Greene, native to South America], in the wetlands of Eastern Australia. The relative abundance of this species is affected by grazing as well as by the frequency, season and depth of flooding (Price et al. 2010, 2011a). Further complications are that flooding affects the distribution of grazing animals and therefore their direct and indirect impact on the competing native vegetation of the area (Price et al. 2011b; Whalley et al. 2011). However, there are some indications that high intensity rotational grazing can reduce the abundance of this IAP (Southwell and Reid 2012). Evidence has shown that continuous grazing at dry sites increases bare ground and subsequently increases lippia spread, whereas high intensity rotational grazing at dry and wet sites maintains higher levels of groundcover in general and lower lippia abundance (Figure 2, reproduced with permission from Southwell and Reid 2012). Research by Price et al. (2011a), however, found rest from grazing at different times of the year was not an effective control strategy, probably because stocking intensity was low and did not reduce selectivity, and native species also did not respond to calendar-determined rest periods. Hence, a grazing strategy which reduces selective grazing (high intensity) and its duration, allowing native species a chance at recovery, provided best control of lippia.

Direct manipulation of grazing will be most effective where the IAP is palatable at certain times of the year, the IAP is not toxic or poisonous to stock, and the IAP demonstrates a different phenology to more desirable species, native or exotic. Other important considerations are whether infrastructure is available for managing

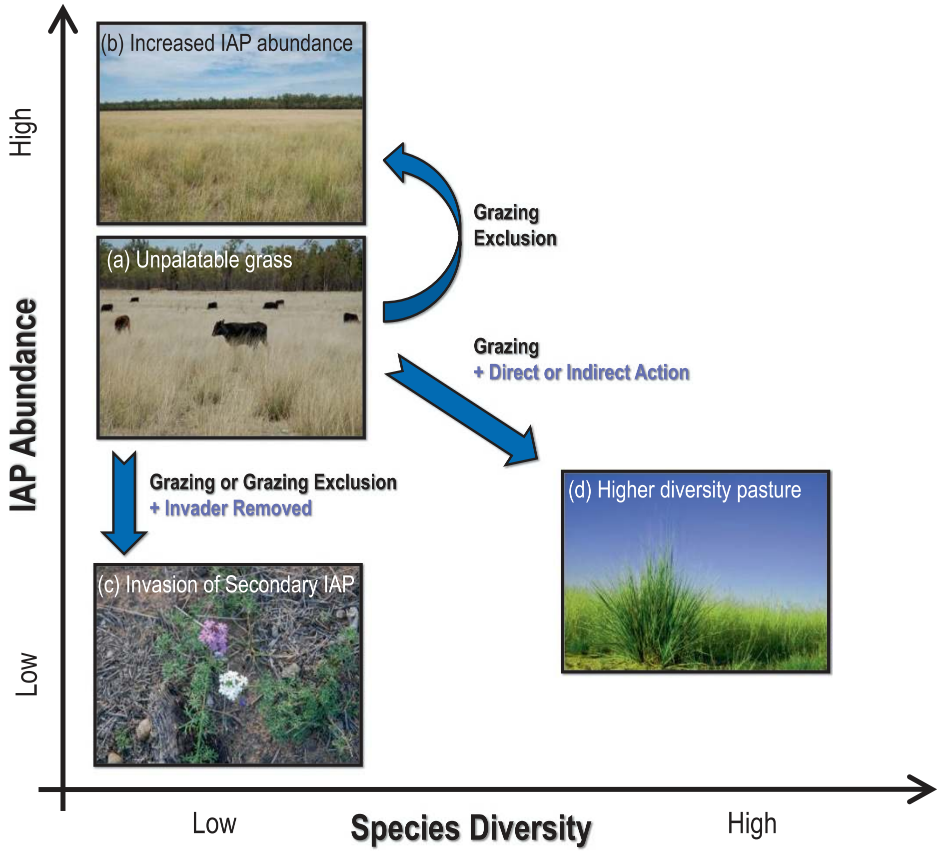

Figure 1 Summary of the results from Firn et al. (2010) on how grazing exclusion and grazing manipulation can alter the abundance of a dominant invasive plant species and small-scale richness of the subsequent plant community. a) Dominant invasive alien plant (IAP) has low palatability and a high growth rate, and the plant community shows low species diversity. **b)** If grazing is excluded from the site (and not replaced by another disturbance regime), the abundance of the IAP will increase in the short to mid-term and species diversity remains low. **c)** If grazing is excluded or grazing continued and the dominant invasive plant species killed and/or removed, there is a high probability that a secondary IAP will become dominant. If successful the abundance of the IAP may be low, but species diversity also remains low. **d)** If grazing is continued but a change is made to the grazing regime, either through direct manipulation of the intensity, frequency and timing of grazing or through indirect manipulation where additional strategies are used to manipulate the palatability of the dominant IAP such as nutrient addition or prescribed burns, then the plant community can be gradually shifted towards a more diverse native species composition.

targeting grazing such as moveable fencing that will allow for ‘cell grazing’ or for small paddocks to be created to concentrate stock at the desired locations. In this strategy, grazing herds are forced to remain in certain locations for a given period of time ensuring that IAP abundance is reduced. Although identifying the most appropriate grazing regime is not as simple as targeting the growth and survival of undesirable species, the grazing regime must also reduce negative impacts on the more desirable species. Even if detailed information on phenology is known, finding the best grazing regime is challenging. For example, leafy spurge (*Euphorbia esula*) is an invasive forb that is generally avoided by cattle but eaten by sheep (Rinella and Hileman 2009). Some direct manipulation of grazing pressure has been successful in reducing the density of leafy spurge in rangelands in the USA (Lym et al. 1997) but not in others (Olson and Wallander 1998; Seefeldt et al. 2007). Rinella and Hileman (2009) clarified some of the inconsistencies in leafy spurge research by simulating grazing at different intensities, timing and frequencies. They found that treatments targeting early vegetative stages reduced the IAP and increased resident species, whereas defoliating more intensively at later growth stages often had the opposite effect. These results clearly show that finding the proper timing of grazing is crucial to the success of control efforts.

Indirect manipulation of grazing will be most effective when the palatability of the IAP is highly dependent on resource availability. For example, a highly plastic species, such as *Eragrostis curvula* (Firn et al. 2012), can increase in palatability when a small quantity of fertiliser is applied in a good rainfall year. The key to successfully applying indirect measures for manipulating grazing

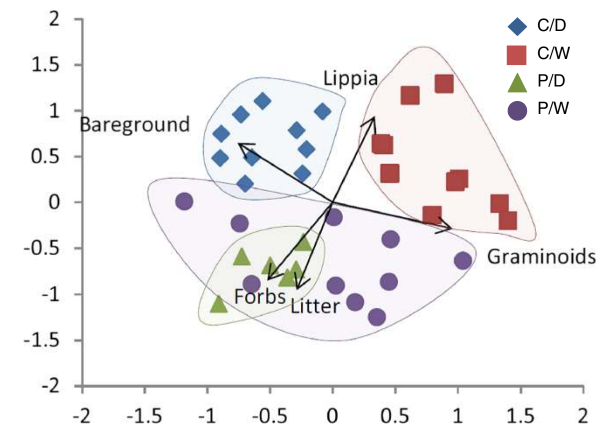

Figure 2 Non-metric dimensional scaling plot for May 2008 sampling period showing changes in invasive alien plant (IAP) abundance for *Phyla canescens* (lippia) under treatments of continuous grazing in dry areas (C/D), continuous grazing in wet areas (C/W), periodic grazing in dry areas (P/D) and periodic grazing in wet areas (P/W). Arrows represent principal component correlation factors > 0.5. Reproduced with permission from Southwell and Reid (2012).

pressure is that the conditions that make the dominant IAP palatable must also be the same conditions that are most conducive for the recruitment of more desirable species (Firn et al. 2010).

Framework for managing IAPs with direct or indirect grazing management In order to consider the unknowns associated with site-specific variables, we suggest three possible restoration goals to maximise short- and long-term benefits (see Figure 3 for a flowchart summary), and these goals will change considerably based on whether the main land use is farming or conservation. For farming, desired species may include other alien plants that are palatable as the main ecosystem service may be forage value, while for conservation native plants are most likely more desirable. A fundamental issue when using grazing for invasive species management when the goal is conservation and/or to maintain native diversity is when to stop grazing and allow natural recovery to take place. Continuing grazing, whether with a direct or indirect strategy, can result in a community of plant species that are fast-growing and tends to favour the establishment of annuals over perennials, short over tall, unpalatable over palatable, and stoloniferous and rosette over tussock architecture (Diaz et al. 2007). Depending on the disturbance regime of the original community and micro-evolutionary changes that may have occurred in important components, this may not represent the key traits of the previous plant community and may not lead to the control of the IAP. Restoration is a goal-oriented science. For this reason, there must be a set of clearly defined goals for the short and long term. The length of time that a site should be managed under each restoration goal (and the starting point) will depend on the extent to which biotic and abiotic factors of the ecosystem are degraded (e.g. nutrient cycling, hydrology, energy flows, and native species richness). For these reasons, restoration goals should also be flexible so that changes can be made to management strategies when systems do not react according to predictions.

When the original species composition is unknown then a potentially useful indicator to assess the 'functional quality' of plant species assembling in response to management in novel ecosystems may be 'soft traits' (defined as easily measured) such as leaf dry matter content (LDMC, mg/g), growth form (e.g. short basal, long basal, semi-basal tussock, erect leafy) and dispersal mode (e.g. anemochory, ballistichory, hydrochory) (Diaz et al. 2004; Garnier et al. 2004; Wright et al. 2004; Westoby and Wright 2006). As previously discussed, Firn et al. (2010) found fertiliser increased the palatability of an IAP grass, *Eragrostis curvula*, and a treatment of continuous grazing saw a reduction in its abundance and an increase in more desirable native plant species. This result did not, however, provide any indication as to how the new assemblages of species function and whether they are functioning any differently to the IAP dominated system. Figure 4 shows trait diversity (i.e. LDMC, growth form and dispersal modes) versus species diversity (both calculated with Shannon's diversity index) in each of the grazing and fertiliser treatments (unpublished data from the Firn et al. 2010 study). Here, species diversity increased under grazing treatments because the IAP was reduced in abundance. While LDMC decreased, both growth form and dispersal mode diversity increased with the grazing treatments. A decrease in functional diversity of LDMC with grazing suggests plant species are increasing in similarity with increased prevalence of fast-growing resource acquisition specialists, but this treatment opens up opportunities for a more diverse group of species in terms of growth form and dispersal mode to colonise.

Excluding grazing and killing or removing the invasive plant species may be a viable control option at sites where the original functioning of an ecosystem is intact. However, if an ecosystem is found in a new and undesirable state from its historical state, we recommend that the management goal be reclamation. Reclamation is defined as returning some function to a degraded ecosystem generally to ensure continued production (Lamb and Gilmour 2003). At this stage, the prime objective is not likely the return of species diversity, as the system is degraded to such a stage where simply removing the IAP could lead to its re-establishment or the recruitment of another invasive species. Although research has

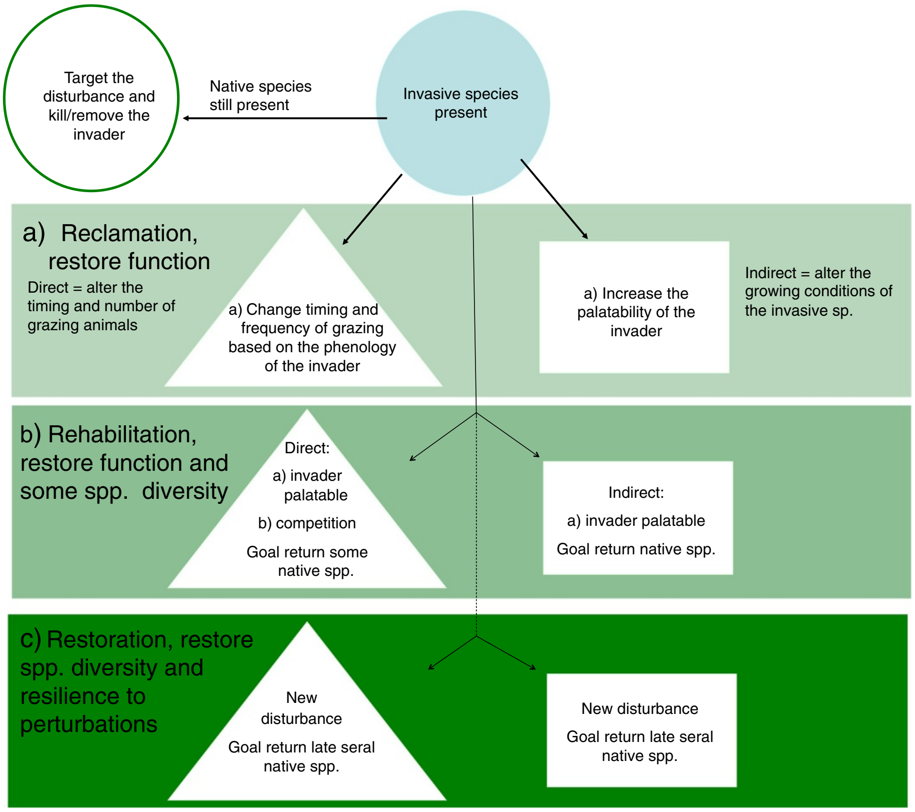

Figure 3 Alternative or a continuum of restoration goals that may help to gradually shift a degraded site, dominated by an invasive plant species, towards a more desirable state with increased species diversity and improved ecosystem functioning. If a grazed pasture has not lost its original ecosystem functioning, then excluding grazing and removing/killing the IAP may be the best option. If, however, the system has changed to a novel state then direct or indirect manipulation of grazing pressure is a better option. If a grassland community is highly degraded, the main goal may be reclamation. **a)** At the reclamation stage, the main aim will be to return some form of functioning back to the degraded site. This may be accomplished using either direct or indirect strategies depending on the plasticity of the IAP, economic and social constraints and the phenology of the IAP in comparison to the natives. Evidence that this early stage is working is the return or increase in the abundance of some early seral native species to the site. **b)** Rehabilitation is where management strategies should aim to maintain key ecosystem functions, while also focusing on encouraging the return of more native diversity to the site. When using direct manipulation of grazing, if the IAP has a different phenology than some of the native species present, then grazing can be applied at a time when the IAP is most susceptible, thereby manipulating competition among species within the community. **c)** Restoration goals are the hardest to achieve from a management perspective because restoration involves shifting the species diversity from a set of early colonising native species to a system characterised by late seral species. This may not be possible with continued grazing at the site. Instead, what might be needed is a new grazing regime of lower intensity or the application of an alternative disturbance regime, possibly one that resembles more the historical disturbance regime.

shown that increasing plant species diversity may increase ecosystem services such as productivity, nutrient cycling and resilience to perturbations (Isbell et al. 2011; MacDougall et al. 2013), this is not a realistic goal in the short term. With some invasive species, more intensive management that ensures the continued production of young tissue may be the best option. Evidence that some original functioning has returned could be the recruitment of more desirable species.

Another goal may be rehabilitation, which involves maintaining key ecological functions and encouraging the return of some more desirable species (Figure 1) (Lamb et al. 2005). With this goal, grazing may still be used as a control strategy by focusing management actions on maintaining the grazing pressure on the IAP or by resting grazing at an appropriate time (in terms of phenology) to enable other species to outcompete the IAP (Kemp et al. 1996; Fischer et al. 2009). At this stage of the restoration process, the original levels of species diversity will not be returned, but gradually more species may establish. Again these will most likely be early colonists or species that are favoured by disturbance, and the invasive species will likely remain present within the community. For example, Californian serpentine grasslands are renowned for high levels of endemic species that are adapted to low N soils. Nitrogen deposition from cars has provided opportunities for Mediterranean grasses to establish in these grasslands, but cattle grazing

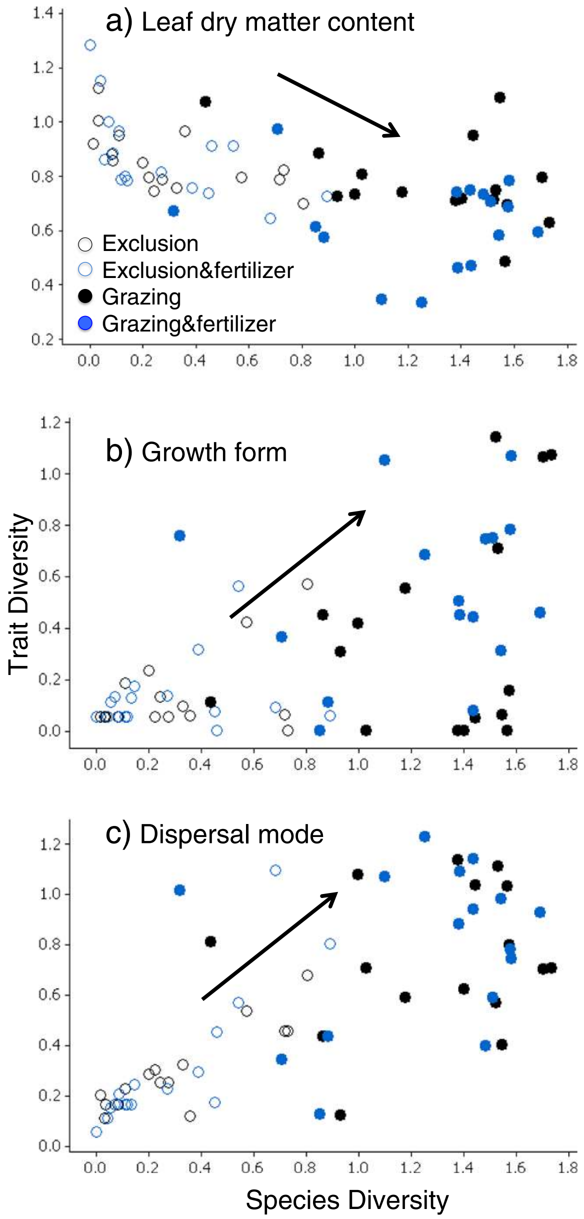

Figure 4 Trait diversity (i.e. leaf dry matter content, growth form and dispersal mode) versus species diversity (both calculated with Shannon's diversity index) across three years of grazing exclusion and fertiliser treatments established to reduce the abundance of an IAP, *Eragrostis curvula* (unpublished data from Firn et al. 2010). Panel **a)** shows Leaf dry matter content, **b)** growth form and **c)** dispersal mode. For detailed data collection methods and for species diversity and leaf dry matter content, please see Additional file 1.

can be beneficial by reducing the biomass levels of the IAPs, and trampling reduces thatch that suppresses native species (Wiess 1999). In some cases, where the seed sources of more desirable species have been depleted from the site and surrounding area, enrichment planting or direct seeding may be necessary to encourage species diversity.

The longest-term goal is restoration—re-establishing the species diversity, productivity and structure of the original ecosystem. There is considerable argument as to whether complete historical restoration is an achievable goal (Lamb and Gilmour 2003; Suding et al. 2004; Hobbs et al. 2006) because the original suite of species may not be known or present in the seed bank. Because information on the precise dynamics that governed the original ecosystem is likely also not known, setting targets and milestones for assessing progress is challenging (Lamb and Gilmour 2003; Suding et al. 2004). For these reasons, the goal of restoration may need to be altered from the re-establishment of the original suite of species, function and structure to the establishment of late seral species that are favoured by a different disturbance regime other than ungulate grazing. In this case, it may be desirable to exclude ungulate grazing to ensure the colonisation of secondary species not favoured by grazing. Once a diverse set of more desirable species has returned to a site, although overall composition may still include a small population of the IAP, attempting to return the original disturbance regime and excluding grazing may then be the best option for encouraging late seral species.

Conclusions

There is now strong empirical evidence that the explicit implementation of an alternative states approach for invasive species management can be more effective than control strategies based on traditional models of succession, particularly where grazing is a key mechanism facilitating IAP dominance. Where grasslands are degraded by grazing pressure, the best control strategy is not necessarily to exclude grazing, as is the tendency when biodiversity values are the chief concern. Instead the optimal strategy may be to manipulate the timing, intensity and spatial distribution of grazing to gradually transition the state of the grassland towards a more diverse plant community. It is likely that applying an alternative states approach would be beneficial to other invasion scenarios, but the evidence is not yet available. More research is needed that compares the efficacy of returning historical disturbance regimes and the application of novel disturbances for invasive species control where grazing is not the disturbance, e.g. changes to water flow rates to intermittent wetlands.

Based on current evidence, to explicitly apply this framework, it is essential that the dynamics of the new ecosystem be understood. In a situation where a site is not found in a novel state then excluding grazing could be a viable option. Managing a novel ecosystem to a more desirable state will require a more complex set of management strategies than the generic implementation of common control strategies. To add to this complexity, this approach will also require active monitoring so that the management strategies can be changed over time in response to changes within the ecosystem—adaptive management (McCarthy and Possingham 2007). Based on these requirements, an alternative states approach is more difficult to implement than current generic approaches to IAP management, e.g. herbicides, and may require more effort, money and resources in the short term. In the long term, however, an alternative states approach has the potential to lead to more effective management strategies, even if the historical conditions cannot be recreated, and in this way may prove more cost-effective.

Additional file

Additional file 1: Figure S1 and S3. Data collection and sampling design.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

JF, JNP and RDW collaboratively researched and wrote the review paper. JF collected data shown in Figure 4. All authors read and approved the final manuscript.

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References

Ash AJ, Corfield JP, McIvor JG, Ksiksi TS (2011) Grazing management in tropical savannas: utilization and rest strategies to manipulate rangeland condition. Rangeland Ecol Manage 64:223–239

Bendall GM (1973) The control of slender thistle, Carduus pycnocephalus L. and C. tenuiflorus Curt. (Compositae), in pasture by grazing management. Aust J Agric Res 24:831–837

Booth BD, Murphy SD, Swanton CJ (2003) Ecology of weeds. In: Booth BD, Murphy SD, Swanton CJ (eds) Weed ecology in natural and agricultural systems. CABI, Oxford, UK

Cingolani AM, Noy-Meir I, Diaz S (2005) Grazing effects on rangeland diversity: a synthesis of contemporary models. Ecol Appl 15:757–773

Clements FE (1916) Plant succession. Carnegie Institute, Washington DC

Cox RD, Allen EB (2008) Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. J App Ecol 45:495–504

Cummings DC, Fuhlendorf SD, Engle DM (2007) Is altering grazing selectivity of invasive forage species with patch burning more effective than herbicide treatments? Rangeland Ecol Manage 60:253–260

Davies KW, Svejcar TJ, Bates JD (2009) Interaction of historical and nonhistorical disturbances maintains native plant communities. Ecol Appl 19:1536–1545

De Bruijn SL, Bork EW (2006) Biological control of Canada thistle in temperate pastures using high density rotational cattle grazing. Biol Control 36:305–315

Diaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Marti G, Grime JP, Zarrinkamar F, Asri Y, Band SR, Basconcelo S, Castro-Diez P, Funes G, Hamzehee B, Khoshnevi M, Perez-Harguindeguy N, Perez-Rontome MC, Shirvany FA, Vendramini F, Yazdani S, Abbas-Azimi R, Bogaard A, Boustani S, Charles M, Dehghan M, de Torres-Espuny L, Falczuk V, Guerrero-Campo J, Hynd A et al (2004) The plant traits that drive ecosystems: evidence from three continents. J Veg Sci 15:295–304

Diaz S, Lavorel S, McIntyre S, Falczuk V, Casanoves F, Milchunas DG, Skarpe C, Rusch G, Sternberg M, Noy-Meir I, Landsberg J, Zhang W, Clark H, Campbell BD (2007) Plant trait responses to grazing—a global synthesis. Glob Change Biol 13:313–341

DiTomaso JM, Brooks ML, Allen EB, Minnich R, Rice PM, Kyser GB (2006) Control of invasive weeds with prescribed burning. Weed Technol 20:535–548

Firn J, Rout T, Possingham HP, Buckley YM (2008) Managing beyond the invader: manipulating disturbance of natives simplifies control efforts. J App Ecol 45:1143–1151

Firn J, House APN, Buckley YM (2010) Alternative states models provide an effective framework for invasive species control and restoration of native communities. J App Ecol 47:96–105

Firn J, Prober SM, Buckley YM (2012) Plastic traits of an exotic grass contribute to its abundance but are not always favourable. PLoS One 7:e35870

Fischer J, Stott J, Zerger A, Warren G, Sherren K, Forrester RI (2009) Reversing a tree regeneration crisis in an endangered ecoregion. PNAS 106:10386–10391

Gaertner M, Holmes PM, Richardson DM (2012) Biological invasions, resilience and restoration. In: van Andel J, Aronson J (eds) Restoration Ecology - The New Frontier. Wiley-Blackwell, Oxford, pp 265–280

Gardener MR, Sindel BM, Whalley RDB, Earl JM (2005) Can *Nassella neesiana*, Chilean needle grass, be incorporated into a grazing management system in Australia? Plant Protect Q 20:36–40

Gardener MR, Atkinson R, Renteria JL (2010) Eradications and people: lessons from the plant eradication program in Galapagos. Rest Ecol 18:20–29

Garnier E, Cortez J, Billes G, Navas ML, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C, Toussaint JP (2004) Plant functional markers capture ecosystem properties during secondary succession. Ecology 85:2630–2637

Grace BS, Whalley RDB, Sheppard AW, Sindel BM (2002) Managing saffron thistle in pastures with strategic grazing. Rangeland J 24:313–325

Gunderson LH (2000) Ecological resilienc— in theory and application. Annu Rev Ecol Syst 4:1–23

Hartley MJ, Lyttle LA, Popay I (1984) Control of Californian thistle by grazing management. In: Proceedings of the 37th New Zealand Weed and Pest Control Conference. New Zealand Weed and Pest Control Society, Hastings, New Zealand, pp 24–27

Hayes GF, Holl KD (2011) Manipulating disturbance regimes and seeding to restore mesic Mediterranean grasslands. App Veg Sci 14:304–315

Hillebrand H, Gruner DS, Borer ET, Bracken MES, Cleland EE, Elser JJ, Harpole WS, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. Proc Natl Acad Sci USA 104:10904–10909

Hobbs RJ (2007) Setting effective and realistic restoration goals: key directions for future research. Rest Ecol 15:354–357

Hobbs RJ, Richardson DM (2011) Invasion ecology and restoration ecology: parallel evolution in two fields of endeavour. In: Richardson DM (ed) Fifty years of invasion ecology: the legacy of Charles Elton. Wiley-Blackwell, Malden, pp 61–69

Hobbs RJ, Suding KN (2009) Synthesis: are new models for ecosystem dynamics scientifically robust and helpful in guiding restoration projects? In: Hobbs RJ, Suding KN (eds) New models for ecosystem dynamics and restoration. Island Press, Washington DC

Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, Norton D, Ojima D, Richardson DM, Sanderson EW, Valladares F, Vila M, Zamora R, Zobel M (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. Glob Ecol Biogeograp 15:1–7

Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. Trends Ecol Evol 24:599–605

Holst PJ, Allan CJ, Campbell MH, Gilmour AR (2004) Grazing of pasture weeds by goats and sheep. 1. Nodding thistle (Carduus nutans). Aust J Exp Agric 44:547–551

Huwer RK, Briese DT, Dowling PM, Kemp DR, Lonsdale WM, Milchalk DL, Neave MJ, Sheppard AW, Woodburns TL (2005) Can an integrated management approach provide a basis for long-term prevention of weed dominance in Australian pasture systems? Weed Res 45:175–192

Isbell FI, Wilsey BJ (2011) Rapid biodiversity declines in both ungrazed and intensely grazed exotic grasslands. Plant Ecol 212:1663–1674

Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES, Loreau M (2011) High plant diversity is needed to maintain ecosystem services. Nature 477:199–202

Kemp DR, Dowling PM, Michalk DL (1996) Managing the composition of native and naturalised pastures with grazing. N Zealand J Agri Res 39:569–578

Kirby DR, Hanson TP, Krabbenhoft KD, Kirby MM (1997) Effects of simulated defoliation on leafy spruge (*Euphorbia esula*)-infested rangeland. Weed Technol 11:586–590

Lamb D, Gilmour D (2003) Rehabilitation and restoration of degraded forests. IUCN and WWF, Gland Switzerland and Cambridge, UK

Lamb D, Erskine P, Parotta J (2005) Restoration of degraded tropical forest landscapes. Science 310:1628–1632

Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proc R Soc B Biol Sci 270:775–781

Lodge GM, Whalley RDB (1985) The manipulation of species composition of natural pastures by grazing management on the Northern Slopes of N.S.W. Aust Rangel J 7:6–16

Lunt ID, Eldridge DJ, Morgan JW, Witt GB (2007) A framework to predict the effects of livestock grazing and grazing exclusion on conservation values in natural ecosystems in Australia. Aust J Bot 55:401–415

Lym RG, Sedivec KK, Kirby DR (1997) Leafy spurge control with angora goats and herbicides. J Range Manage 50:123–128

MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42–55

MacDougall AS, McCann KS, Gellner G, Turkington R (2013) Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. Nature 494:86–89

Magcale-Macandog DB, Whalley RDB (2000) Genotypic differentiation in *Microlaena stipoides* populations: morphological and ecological patterns. Phil Agri Sci 83:159–172

Magcale-Macandog DB, Whalley RDB (2007) Competitive abilities and divergence of *Microlaena stipoides* populations with associated perennial grass species in New South Wales, Australia. Asia Life Sci 16:35–52

McCarthy MA, Possingham HP (2007) Active adaptive management for conservation. Conserv Biol 21:956–963

Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized-model of the effects of grazing by large herbivores on grassland community structure. Am Nat 132:87–106

Noble JC, Whalley RDB (1978) The biology and autoecology of *Nitraria* L. in Australia I. Dist Morphol Potent Utilisation Aust Ecol 3:141–163

Olff H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. Trends Ecol Evol 13:261–265

Olson BE, Wallander RT (1998) Effect of sheep grazing on a leafy spurge-infested Idaho fescue community. J Range Manage 51:247–252

Olson BE, Wallander RT, Fay PK (1997) Intensive cattle grazing of oxeye daisy (*Chrysanthemum leucanthemum*). Weed Technol 11:176–181

Parker JD, Burkepile D, Hay ME (2006) Opposing effects of native and exotic herbivores on plant invasions. Science 311:1459–1461

Perring MP, Standish RL, Hobbs RJ (2013) Incorporating novelty and novel ecosystems into restoration planning and practice in the 21st century. Ecol Proc 2013:2–18

Piggin CM (1979) Control of *Echium plantagineum* L. with 2,4-D and grazing management. Weed Res 19:17–23

Popay I, Field R (1996) Grazing animals as weed control agents. Weed Technol 10:217–231

Price JN, Gross CL, Whalley RDB (2010) Prolonged summer flooding switched dominance from the invasive weed lippia (*Phyla canescens*) to native species in one small, ephemeral wetland. Ecol Manag Restor 11:61–63

Price JN, Berney PJ, Ryder D, Whalley RDB, Gross CL (2011a) Disturbance governs dominance of an invasive forb in a temporary wetland. Oecologia 167:759–769

Price JN, Whalley RDB, vanKlinken RD, Duggin JA, Gross CL (2011b) Periodic rest from grazing provided no control of an invasive perennial forb. Rangeland J 33:287–298

Pywell RF, Hayes MJ, Tallowin JB, Walker KJ, Meek WR, Carvell C, Warman LA, Bullock JM (2010) Minimizing environmental impacts of grassland weed management: can *Cirsium arvense* be controlled without herbicides? Grass Forage Sci 65:159–174

Richardson DM, Gaertner M (2013) Plant invasions as builders and shapers of novel ecosystems. In: Hobbs RJ, Higgs EC, Hall CM (eds) Novel ecosystems: intervening in the new ecological world worder. Wiley-Blackwell, Oxford, pp 102–114

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Diver Distrib 6:93–107

Rinella MJ, Hileman BJ (2009) Efficacy of prescribed grazing depends on timing intensity and frequency. J App Ecol 46:796–803

Sax DF, Brown JH (2000) The paradox of invasion. Glob Ecol Biogeograph 9:363–371

Scott AW, Whalley RDB (1984) The influence of intensive sheep grazing on genotypic differentiation in *Danthonia linkii*, *D. richardsonii* and *D. racemosa* on the New England Tablelands. Austral Ecol 9:412–429

Seastedt TR, Hobbs RJ, Suding KN (2008) Management of novel ecosystems: are novel approaches required? Front Ecol Environ 6:547–553

Seefeldt SS, Taylor JB, Van Vleet S (2007) Reducing *Euphorbia esula* with a combination of sheep grazing and imazapic. J Arid Environ 69:432–440

Shea K, Sheppard A, Woodburn T (2006) Seasonal life-history models for the integrated management of the invasive weed nodding thistle *Carduus nutans* in Australia. J App Ecol 43:517–526

Southwell M, Reid M (2012) Lippia fact sheet. Central West Catchment Management Authority. Wellington, NSW

Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. Trends Ecol Evol 19:46–53

Thomsen CD, Williams WA, Vayssieres MP, Bell FL, George MR (1993) Controlled grazing on annual grassland decreases yellow starthistle. California Agri 47:36–40

Vila M, Espinar JL, Hejda M, Hulme PE, Jarosik V, Maron JL, Pergl J, Schaffner U, Sun Y, Pysek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species communities and ecosystems. Ecol Lett 14:702–708

Wallace JM, Wilson LM, Launchbaugh KL (2008) The effect of targeted grazing and biological control on Yellow Starthistle (Centaurea solstitialis) in canyon grasslands of Idaho. Rangeland Ecol Manage 61:314–320

Waters CM, Murray BR, Melville GJ, Coates DJ, Young A, Virgona J (2010) Polyploidy and possible implications for the evolutionary history of some Australian Danthonieae. Aust J Bot 58:23–34

Waters CM, Melville GJ, Coates DJ, Virgona J, Young A, Hacker RB (2011) Variation in morphological traits among and within populations of *Austrodanthonia caespitosa* (Gaudich.) H.P.Linder and four related species. Aust J Bot 59:324–335

Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. Trends Ecol Evol 21:261–268

Westoby M, Walker B, Noy-Meir I (1989) Opportunistic management for rangelands not at equilibrium. J Range Manage 42:266–274

Whalley RDB, Price JN, Macdonald MJ, Berney PJ (2011) Drivers of change in the social-ecological systems of the Gwydir wetlands and Macquarie marshes in northern New South Wales, Australia. Rangeland J 33:109–119

Wiess SB (1999) Cars, cows, checkerspot butterflies: nitrogen deposition and management of nutrient poor grasslands for a threatened species. Conserv Biol 13:1476–1486

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC et al (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Yu P, Prakash N, Whalley RDB (2000) Comparative reproductive biology of the vulnerable and common grasses in Bothriochloa and Dichanthium. In: Jacobs SWL, Everett J (eds) Grasses: systematics and evolution. CSIRO, Melbourne

Yu P, Prakash N, Whalley RDB (2003) Sexual and apomictic seed development in the vulnerable grass *Bothriochloa biloba* S.T.Blake. Australian. Aust J Bot 51:75–84

Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. Trends Ecol Evol 16:454–459

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