

Are shrubs really a sign of declining ecosystem function? Disentangling the myths and truths of woody encroachment in Australia

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Abstract. Since European settlement, there has been a dramatic increase in the density, cover and distribution of woody plants in former grassland and open woodland. There is a widespread belief that shrub encroachment is synonymous with declines in ecosystem functions, and often it is associated with landscape degradation or desertification. Indeed, this decline in ecosystem functioning is considered to be driven largely by the presence of the shrubs themselves. This prevailing paradigm has been the basis for an extensive program of shrub removal, based on the view that it is necessary to reinstate the original open woodland or grassland structure from which shrublands are thought to have been derived. We review existing scientific evidence, particularly focussed on eastern Australia, to question the notion that shrub encroachment leads to declines in ecosystem functions. We then summarise this scientific evidence into two conceptual models aimed at optimising landscape management to maximise the services provided by shrub-encroached areas. The first model seeks to reconcile the apparent conflicts between the patch- and landscape-level effects of shrubs. The second model identifies the ecosystem services derived from different stages of shrub encroachment. We also examined six ecosystem services provided by shrublands (biodiversity, soil C, hydrology, nutrient provision, grass growth and soil fertility) by using published and unpublished data. We demonstrated the following: (1) shrub effects on ecosystems are strongly scale-, species- and environment-dependent and, therefore, no standardised management should be applied to every case; (2) overgrazing dampens the generally positive effect of shrubs, leading to the misleading relationship between encroachment and degradation; (3) woody encroachment *per se* does not hinder any of the functions or services described above, rather it enhances many of them; (4) no single shrub-encroachment state (including grasslands without shrubs) will maximise all services; rather, the provision of ecosystem goods and services by shrublands requires a mixture of different states; and (5) there has been little rigorous assessment of the long-term effectiveness of removal and no evidence that this improves land condition in most cases. Our review provides the basis for an improved, scientifically based understanding and management of shrublands, so as to balance the competing goals of providing functional habitats, maintaining soil processes and sustaining pastoral livelihoods.

Additional keywords: shrublands, thickening, woodland.

Received 24 June 2014, accepted 21 November 2014, published online 19 February 2015

Introduction

Shrub encroachment, also known as woody encroachment or thickening, is a global phenomenon characterised by an increase in the density and cover of native shrubs, particularly in grasslands and open woodlands (Van Auken 2009). The causes of shrub encroachment are relatively well known and include historical overgrazing, reduced fire frequency, past clearing, increases in CO₂ and N deposition (e.g. Segoli *et al.* 2008; Archer 2009; Eldridge *et al.* 2011; Daryanto *et al.* 2013a, 2013b, 2013c). The effects of encroachment on ecosystem properties and processes are less clearly defined. It is generally believed that shrub encroachment has increased dramatically in

eastern Australia over the past century and certainly occurs currently over large areas in temperate, subhumid, semiarid and arid environments (Gardiner *et al.* 1998; Burrows *et al.* 2002; Fensham *et al.* 2005; Lunt *et al.* 2010). Although there is evidence that encroachment rates for species deemed as particularly ‘invasive’ may not have risen, at least substantially, over the past two decades, it is still unclear whether the rate of shrub encroachment in eastern Australia has stabilised since European settlement, or whether there is still potential for further encroachment (Witt *et al.* 2009; Witt 2013). Analysis of changes in shrub cover between 1990 and 1999 at the New South Wales (NSW) Rangeland Assessment

Program monitoring sites in semiarid NSW, Australia, indicates that canopy cover increased at 68% of sites and declined at only 15% (Russell Grant, unpubl. rept). However, recent research from south-western Queensland has shown that the rate of thickening in the mulga (*Acacia aneura*) woodlands has been ~3.6% over the past 50 years ($0.072\% \text{ year}^{-1}$; Witt *et al.* 2009), contrasting strongly with the generally held view among some landholders and agency staff (e.g. Burrows *et al.* 2002) that rates of ~1% per year are normal. Although *Acacia aneura* is a tree rather than a shrub, these reports have suggested that increases and decreases in woody cover vary widely across the semiarid woodlands. Overall, the sparse evidence available suggests that there is a tendency for a greater rate of encroachment on previously cleared or thinned land than on uncleared land (Beale 2004).

Irrespective of the real rates of encroachment or whether it is a natural or human-induced process, encroachment by both shrubs and trees is seen as a major issue by many land managers, who consider that it threatens the viability of their pastoral enterprises (Inter-Departmental Committee 1969). The majority of the criticism of encroachment derives from the pastoral community and relates to lost opportunities for grazing. It is, therefore, a contextual issue and is highly land-use dependent. Encroachment is also viewed by both the pastoral and scientific communities as being associated with declining ecosystem functioning, landscape degradation or desertification (Noble 1997; MEA 2005; Archer 2009). Active programs to encourage or support the removal of shrubs have resulted in the expenditure of tens of billions of dollars by governments worldwide (Teague *et al.* 1997), with the aim of restoring land condition (see, for example, the Restore New Mexico Program at http://www.blm.gov/nm/st/en/prog/restore_new_mexico.html, verified 18 December 2014). Legislation enacted in the NSW Parliament that aimed to bring about an end to broad-scale vegetation clearance allowed for the removal of shrubs that were deemed to be 'invasive,' so as to improve or maintain environmental outcomes (*Native Vegetation Act* 2003). In NSW, woody plant removal has recently been defined as a routine agricultural management activity (New South Wales Government 2013), allowing landholders to remove many species of shrubs and trees according to specific guidelines. However, despite the large investment in woody removal in Australia, there has been little rigorous assessment of its long-term effectiveness, and, to the best of our knowledge, few studies of the extent to which removal encourages natural regeneration of more favourable species, or indeed improves ecosystem structure and functions (Bollard *et al.* 2010).

The present paper aims to assemble current scientific evidence on the impacts of shrub encroachment in eastern Australia. Even though the emphasis is on shrubs (woody plants <3 m tall), it is also relevant to trees that recruit in dense patches, such as *Callitris glaucophylla* or various small *Eucalyptus* species that self-thin extremely slowly (e.g. Thompson and Eldridge 2005). However, our intention is not to restate the extensive body of literature on shrub encroachment currently in the public arena (see, for example, Noble 1997; Van Auken 2000; House *et al.* 2003; Archer 2009; Eldridge *et al.* 2011), nor the body of work on tree regrowth and clearing (e.g. Fensham 2008; Witt *et al.* 2009, 2011; Silcock *et al.* 2013; Witt 2013). Rather, we seek to address several

misconceptions in the literature that relate specifically to functional decline associated with the encroachment of shrubs into former grasslands or the infilling by shrubs of open areas in woodlands. We present a theoretical framework that seeks to reconcile the apparent conflicts between the oft-reported positive effects of individual shrubs (the patch-level effect) and the upscaled, generally negative effects assumed when shrubs occur in large aggregations (landscape-level effects). We document how two principal management practices, livestock grazing and shrub removal, alter ecosystem goods and services derived from shrublands, and highlight existing idiosyncrasies among different shrub species, questioning the 'one size fits all' approach to shrub management. Finally, we identify several knowledge gaps in our understanding of the impacts of shrublands on competing ecosystem goals. It is our hope that this review can provide the basis for an improved understanding and management of shrublands to balance the competing goals of providing functional habitats, maintaining essential soil processes and sustaining pastoral livelihoods.

Linking the effects of shrubs at patch and landscape scales

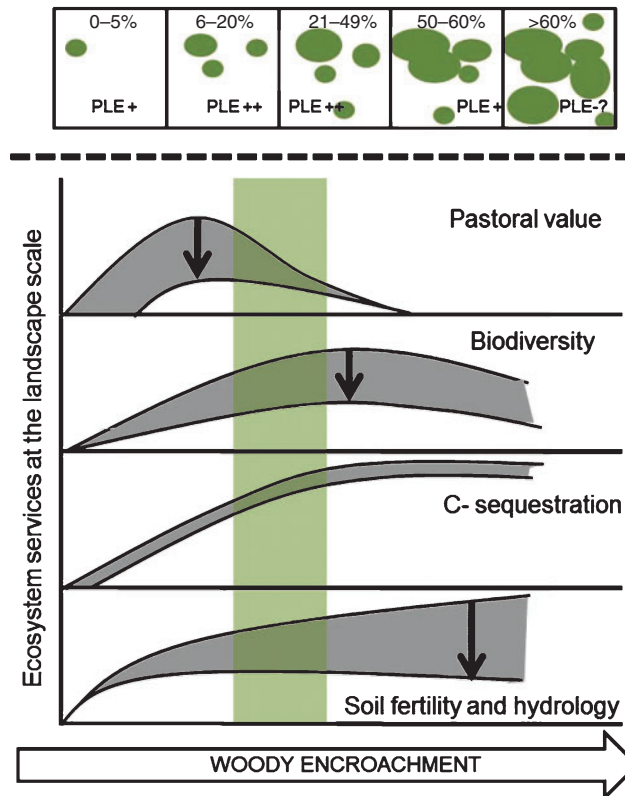
'There is no single natural scale at which ecological phenomena should be studied' (Simon Levin 1992).

Probably one of the most striking conundrums in the woody-encroachment literature is the issue of scale. This relates specifically to the contrast between the well known positive effects of individual shrubs or trees on their understorey soils and plants (the patch-level effect) and their putative roles as drivers of ecosystem degradation, desertification and dysfunction at landscape scales (landscape-level effects; MEA 2005; Daryanto *et al.* 2012). Here, we build on the linkages between the patch- and landscape-level effects of shrubs and discuss the factors that arise to explain this conundrum.

The first, and perhaps more intuitive, explanation for the contrasting patch- and landscape-level effects is density dependence of woody plants forming patches of varying sizes (Breshears 2006; Riginos *et al.* 2009; Soliveres and Eldridge 2014). Woody plants can have a very strong positive effect on their understorey community when they grow at low densities, because they often have more fertile soil conditions, and an improved microclimate, sheltering the understorey neighbours from drought stress or even grazing pressure (the 'fertile island' effect, Niering *et al.* 1963; Weltzin and Coughenour 1990; Warnock *et al.* 2007). However, this positive effect might become less positive or even negative at higher woody densities when viewed at the scale of entire landscapes or paddocks (Box 1). This is so because the ability of individual shrubs to capture runoff and therefore provide more fertile soil conditions may decline with the number of shrubs in the area (e.g. Breshears 2006). Woody canopies also provide habitat for shade-tolerant or drought-sensitive species (e.g. Prider and Facelli 2004; Liancourt *et al.* 2005; Warnock *et al.* 2007; Howard *et al.* 2012), resulting in greater species diversity at the level of entire landscapes (Tewksbury and Lloyd 2001; Soliveres *et al.* 2011). If shrubs or trees grow in denser stands, however, their canopies tend to close up, reducing the habitat for open-habitat

Box 1. Patch-level effects in relation to woody density

At the landscape level, the effects of individual woody plants (patch-level effect; PLE) change across the gradient in woody densities (uppermost panel). Here, the PLE of individual shrubs (the green ellipses) remains positive until woody cover reaches ~60%, which is close to the maximum cover found in eastern Australia (Soliveres and Eldridge 2014). In the lower panel, different ecosystem services that we have assessed (C sequestration, biodiversity conservation, hydrology, plant pastoral nutrients, pastoral production, soil fertility; see Box 4) are likely to respond differently to increasing woody densities (adapted from Blaum *et al.* 2007; Sirami *et al.* 2009; Eldridge *et al.* 2013). The grey-shaded envelope indicates the range of values that occur under varying levels of grazing, with downward arrows indicating increasing grazing pressure. The positive responses of plant biomass (the main component of the pastoral production score), plant richness (biodiversity), soil fertility and infiltration dampen under increasing grazing pressure (indicated by the downward arrows and the lower limits of the shaded envelopes; Eldridge *et al.* 2013). Grazing, however, has little effect on C sequestration, which stabilises at a maximum once woody cover reaches $\geq 30\%$ (Reich *et al.* 2001; Breshears 2006), at least in the short to medium term (see also Box 2). The lack of grazing effect on C sequestration occurs because soil C is relatively slow to respond to increased grazing, and plant biomass makes up only a small proportion of total C compared with soil and woody C (Daryanto *et al.* 2013a). The green stripe indicates the range in woody cover that maximises the level of all ecosystem services simultaneously.



specialists (Breshears 2006; Riginos *et al.* 2009). Studies in eastern Australia have indicated that these closed woody canopies are more likely to support vulnerable birds or 'declining woodland birds' (Smallbone *et al.* 2014), whereas grassland-dependent species will be adversely affected (e.g. Coffman *et al.* 2014). This change in the effect of individual shrub canopies (i.e. patch-effect) across a shrub density and/or cover gradient may generate hump-shaped relationships between diversity and the degree of woody encroachment at the landscape level (Box 1). Interestingly, these aforementioned studies accord with an optimum woody canopy cover of 30%, a level that corresponds to peaks in richness of a range of different taxa, including plants (Soliveres *et al.* 2014; but see Báez and Collins 2008), birds (Sirami *et al.* 2009) and mammals (Blaum *et al.* 2007). It should be noted, however, that in some Australian shrub species, the positive patch-level effect on plant richness and soil fertility holds for woody canopy cover levels of ~50% (Soliveres and Eldridge 2014), which is close to the maximum cover level observed for shrubs in eastern Australia (Daly and Hodgkinson 1996).

When ecosystem services or functions other than biodiversity conservation are considered, the situation becomes more complex. Ground-storey plant biomass, for example, has been shown to peak at levels of woody cover much lower than 30% in

some areas, or even decline in a linear fashion with increasing encroachment in others (Eldridge *et al.* 2013). If the aim of shrub management (e.g. removal for pastoralism) is to increase or maintain pastoral values, then cover of shrubs of ~15% might be more desirable. From a pastoral perspective, however, it could be argued that pasture quality (which includes biomass production, forage digestibility, and nutrient and fibre contents) is a better surrogate of pastoral value than productivity or biomass *per se*. We are unaware of any Australian studies that have linked shrub or tree cover or density relationships to plant nutrient analyses. In African savannas, however, grass N and P contents have been shown to vary with tree size and level of herbivory (Treydte *et al.* 2009), and N : P ratios have been shown to decline with increasing tree density (Riginos *et al.* 2009; Sitters *et al.* 2013), following the same trend as that in soil. Similarly, foliage concentrations of fibre and lignin have been shown to increase with increasing shrub cover, although with no clear responses for organic matter digestibility (Zarovali *et al.* 2007). More studies are needed, therefore, to examine the links between the degree of shrub encroachment and the nutrient value of plants at the landscape scale.

A different set of ecosystem services or functions are those related to C sequestration, soil fertility and hydrology (water capture, infiltration), which are important functions in drylands

globally (Reynolds and Acock 1997; Jackson *et al.* 2002; Maestre *et al.* 2009; Okin *et al.* 2009). Consistent with existing scientific evidence, these functions are predicted to increase linearly with woody encroachment, reaching a plateau at ~40% of woody cover (Wilcox *et al.* 2003b; Barger *et al.* 2011; Eldridge *et al.* 2013; Box 1; but see Jackson *et al.* 2002). Of particular importance is C sequestration, because this may provide opportunities to increase the economic value of many pastoral properties (e.g. C-farming initiative). Given the emerging interest in C farming, we see a strong need for further research on the relationship between shrub encroachment and C storage values. For example, it is assumed that C sequestration increases linearly with woody encroachment, at least until woody covers of ~30–40%, potentially stabilising at higher shrub covers (Box 1; e.g. Reich *et al.* 2001; Breshears 2006). However, this relationship depends on the level of aridity, with stronger (Jackson *et al.* 2002; Barger *et al.* 2011; de Graaff *et al.* 2014) or weaker (Knapp *et al.* 2008; Soliveres *et al.* 2014) effects of shrubs on C budgets towards drier environments. Contrasting results may depend on the particular functional traits of the encroaching shrubs under investigation (see below), or environmental factors other than aridity. Thus, more research is needed to better understand under which scenarios shrub-encroached landscapes are more effective C sinks and, therefore, where government-funded C programs should direct their investments.

A second potential mechanism to explain the conundrum between patch- and landscape-level effects is the influence of environmental factors. As with C sequestration, the relationship between shrubs and their understorey plant community is known to vary with changes in rainfall and evapotranspiration (modelled as aridity) and/or herbivory pressure. Moderate levels of grazing or aridity are likely to increase the positive effect of shrubs on ground-storey plant diversity and biomass production. This occurs because woody patches provide either protection from grazing or more benign environmental conditions, which allow their understorey neighbours to cope better with such low levels of grazing or aridity (reviewed in Vandenberghe *et al.* 2009; Soliveres *et al.* 2012). Under extremely high levels of grazing or aridity, however, these positive effects of shrubs will vanish, because the improved microclimatic conditions or safe sites are no longer effective under such harsh environments (Tielbörger and Kadmon 2000; Maestre and Cortina 2004; Smit *et al.* 2007). A recent synthesis of woody effects on soil C for North America showed that, compared with open areas, the relative value of woody canopies for sequestering C increased with increasing aridity (de Graaff *et al.* 2014), being consistent with other published data on woody plants (Jackson *et al.* 2002; Barger *et al.* 2011). This is because woody patches have almost constant values of soil C across a wide variety of environmental conditions, which maximises their difference, when compared with open areas whose soil C linearly declines with aridity (de Graaff *et al.* 2014 and references therein). These trends, however, are not always consistent among response variables, as demonstrated by reports of increases in the positive effect of shrub encroachment on plant biomass production towards wetter environments (Knapp *et al.* 2008).

Regulation of shrub effects, however, is not the only influence that environmental conditions have on the relationship between

patch- and landscape-level effects. Overgrazing leads to reductions in several ecosystem functions such as plant biomass, nutrient-cycling rates or C sequestration, and these reductions are likely to be greater under a more variable climate (e.g. Kéfi *et al.* 2007; Harris 2010; Maestre *et al.* 2012; Hilker *et al.* 2014). Soil erosion might well reduce soil fertility and its ability to capture and retain water, and overgrazing may also reduce the available number of plant species that are favoured by shrubs (see Howard *et al.* 2012). Existing data suggest that these negative effects of overgrazing might be more evident in open areas than under the shrubs. For example, soil erosion on grazing properties has been shown to reduce concentrations of soil C in the interspaces, but not under the shrubs or trees, resulting in lower estimated site-level infiltration rates and a higher contrast between open and shrub microsites (Eldridge *et al.* 2014; see also de Graaff *et al.* 2014). Thus, although the positive patch-level effect of shrubs might remain unchanged under different levels of grazing, the overall result at the landscape level is a decline in the ability to capture and retain water, and declines in plant richness, C sequestration and soil fertility (Schlesinger *et al.* 1990).

Does woody encroachment lead to declines in ecosystem function or are the effects attributed to shrub encroachment confounded by different levels of grazing?

‘Confounding means that differences due to experimental treatments, i.e. the contrast specified in your hypothesis, cannot be separated from other factors that might be causing the observed differences’ (Gerry P. Quinn and Michael J. Keough 2002).

The notion that shrub encroachment is a driver of declining ecosystem function comes largely from studies from the western United States where overgrazing of grasslands has led to changes in the spatial distribution of critical resources such as nutrients and water (Gutierrez and Hernandez 1996; Okin and Gillette 2001). Overgrazing also promotes invasion by shrubs, which further exacerbate the localisation of soil resources under their canopies via runoff capture and litter deposition. This positive feedback leads to the desertification of formerly productive grassland, and the mechanisms are described in the Schlesinger *et al.* (1990) desertification model. Despite the explicit recognition of long-term grazing as the trigger for changes in resource distribution, many authors have invoked the Schlesinger *et al.* (1990) model to support the notion that shrub encroachment equates with, or leads universally to, desertification, degradation or ecosystem dysfunction (e.g. Ludwig and Tongway 1995; Huenneke *et al.* 2002; Goslee *et al.* 2003; Peters *et al.* 2006; Blaum *et al.* 2007; Eldridge *et al.* 2009, to name a few).

A considerable and growing body of evidence indicates that encroachment does not lead to declines in ecosystem functioning (e.g. Maestre *et al.* 2009; Eldridge *et al.* 2011). Indeed, Maestre *et al.* (2009) demonstrated that increasing density of shrubs was associated with an improvement in a range of ecosystem functions across a large area of central–south-eastern Spain. More locally, Collard and Fisher (2010) identified the many biodiversity benefits of shrubs in environmental plantings. A regional study

across 35 sites in western NSW demonstrated no declines in plant, vertebrate and invertebrate richness with increasing shrub cover or density (Ayres *et al.* 2001). The latter study showed that the abundance of some pastorally important perennial grasses (*Panicum subxerophilum*, *Thyridolepis mitchelliana*) increased with increasing shrub cover (Ayres *et al.* 2001). Similarly, a NSW Government report to the Native Vegetation Advisory Council in 2003 endorsed by a panel of experts showed that there were no clear links between the risk of soil erosion and the presence of regrowth vegetation, which included dense patches of shrubs as well as trees (Eldridge *et al.* 2003). Overall, scientific evidence suggests that woody encroachment enhances important ecosystem services by maintaining healthy soils, mitigating dryland salinity, capturing water, removing atmospheric pollutants, sequestering CO₂ and providing habitat for other species (Scholte 1989; Fisher 2000; Burrows *et al.* 2002; Bhark and Small 2003; Wilcox *et al.* 2003a, 2003b; Maestre *et al.* 2009; Witt *et al.* 2011; Fensham *et al.* 2012; Howard *et al.* 2012; Eldridge *et al.* 2014).

How can we reconcile the science that reports the positive benefits of shrubs with the perception that they are associated with degraded or dysfunctional systems? A glance to any statistical book will draw the readers' attention to the issue of a *confounding factor*; a factor that can influence the course of a study if it is not properly accounted for. For example, there may be a strong statistical relationship between the application of sun cream and drownings, that is, the two are strongly correlated. It does not mean that using sun cream will cause drowning. The confounding variable (season, i.e. summer) influences both variables. We argue that overgrazing, which is both a well known driver of woody encroachment and a cause of land degradation (Schlesinger *et al.* 1990; Burrows *et al.* 2002; Noble *et al.* 2005; Lunt *et al.* 2007; Archer 2009; Okin *et al.* 2009; Harris 2010; Hilker *et al.* 2014) might well be one of the *confounding factors* behind the perceived relationship between woody encroachment and land degradation. Grazing by native and exotic herbivores has substantial biotic and abiotic effects on ecosystems, and is one of the main pressures on biodiversity in semiarid and arid systems (Milchunas *et al.* 1988; Lunt 2005; Lunt *et al.* 2007). Grazing is also the principal cause of grass decline in drylands, irrespective of the cover or density of shrubs (Dawson and Boyland 1974; Burrows *et al.* 2002). Despite the considerable allocation of resources to the control of shrubs over the past half century (e.g. Noble 1997), there have been few attempts to critically question the contention that the widely reported negative effects of shrub encroachment might be confounded by high levels of grazing. Indeed, that would not be the first case in which ecosystems are poorly managed because of confounding factors. Rodents, such as the native plateau zoker (*Myospalax baileyi*), are poisoned extensively across China and Tibet because they disturb large areas of soil and are thought to compete with cattle for pasture (see review in Harris 2010). However, scientific evidence shows that zoker activity leads to increased plant diversity and substantially reduces runoff and sedimentation in nearby rivers (Smith and Foggin 1999). Best available evidence suggests that it is overgrazing by cattle that is responsible for the loss of pastoral productivity attributed to the zoker (Zhang *et al.* 2003).

Anecdotal evidence from sites north of Cobar, NSW, that have adopted time-controlled grazing (Ashley McMurtrie, pers. comm.), and empirical data from sites where goats and rabbits have been controlled suggest that grazing has a larger effect on grass biomass than do shrub cover or density (Robson 1995; Daryanto and Eldridge 2010). At other sites south of Cobar, extensive overgrazing by sheep and goats has altered interspace infiltration (e.g. by reducing grass cover and compacting the soil surface), resulting in site-level reductions in infiltration regardless of the positive effect of shrubs on it (Eldridge *et al.* 2014). Recent studies from south-western NSW have also demonstrated that increasing shrub cover is associated with increases, or no change, in functional and structural measures indicative of healthy systems, and that any positive effects were dampened under increasing grazing pressures (Eldridge *et al.* 2013). We re-analysed data reported in Eldridge *et al.* (2012) by separating shrub effects into sites with low and high grazing based on an assessment by the authors of the original papers, or by using our own data from regional surveys or government monitoring programs (e.g. NSW Rangeland Assessment Program). Our re-analysis indicated that the generally positive effects of shrubs on important ecosystem features such as biodiversity or pastoral productivity are dampened by grazing (Box 2), although this depends on the ecosystem service considered.

Shrub effects are strongly trait-specific

'Biological specificity is the major problem about understanding life' (Linus Pauling 1995).

Different shrub species are often treated as one and the same. In reality, they are likely to have different effects on soils, associated fauna and understorey plant communities (Whitford 2002). Thus, although the same management strategies are often applied in encroached landscapes everywhere, it is likely that the effects of woody encroachment on ecosystem functioning will be highly dependent on which species are encroaching. Different species have different root systems, and this influences their capacity to access groundwater and to scavenge resources from the interspaces (Schlesinger *et al.* 1990). Canopy architectures and canopy density, which typically vary among a wide range of shrub and tree species, can affect the capacity of shrubs to capture and redirect rainfall (Whitford 2002) or alter the amount of radiation reaching the soil surface (Jankju 2013). Shrub species are also likely to vary in their effects on soil fertility and may even exhibit allelopathy. For example, N fixation of some woody species influences nutrient pools, decomposition rates and facilitation of ground-storey species (Rodríguez-Echeverría and Pérez-Fernández 2003; Throop and Archer 2007; Liao and Boutton 2008; Riginos *et al.* 2009; Sitters *et al.* 2013). Indeed, the increased soil fertility of N-fixing species such as *Senna* spp. may account for the initially relatively high levels of plant biomass after shrub removal (Hughes *et al.* 2006). Overall, it seems that mean plant height is among the strongest species-specific traits explaining differences in ecosystem function in encroached landscapes globally (Eldridge *et al.* 2011). A reassessment of data from 35 sites across a large area of eastern Australia (Ayres

et al. 2001) showed that ant community composition in shrub-encroached landscapes differed markedly with differences in shrub height (Gabriella Radnan, unpubl. data), perhaps because larger shrubs would be expected to support greater levels of biological activity, providing a greater number and diversity of niches and more resources for ants (e.g. seed, fruit, sap, flowers, aphids).

As explained in the preceding sections, it is crucial to consider density-dependence in relation to these idiosyncratic shrub effects. For example, shrub traits such as the ability to resprout or produce root suckers after disturbance may also affect rates of thickening (Maestre *et al.* 2009; Iannone *et al.* 2014). Similarly, tall shrubs or trees enhance understorey diversity and productivity when they grow at low densities or cover (e.g. <10%), but have a negative effect as their density increases (Riginos *et al.* 2009). N-fixing woody species enhance plant biomass and soil fertility until they reach densities sufficient to promote P limitation, which reduces forage quantity and quality (Riginos *et al.* 2009; Sitters *et al.*

2013). Surprisingly, only a handful of studies has addressed the relationship between woody traits and their density-dependent effects. The wide variety of Australian species and their diverse traits make this an important area of future research.

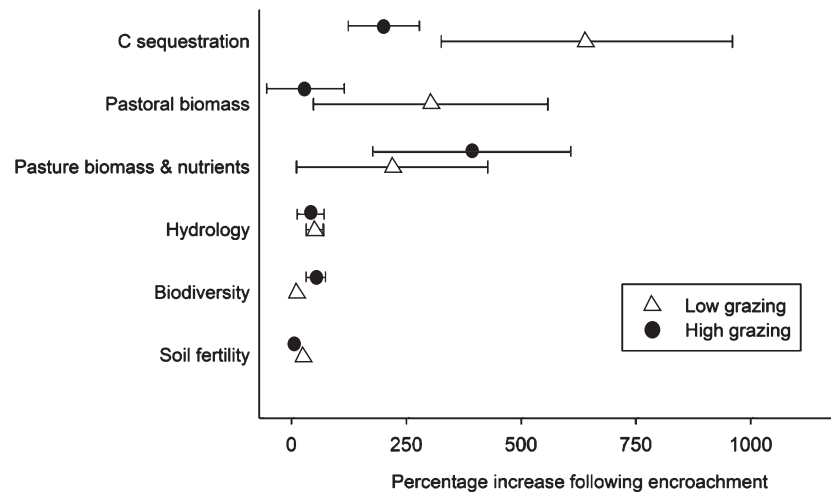
The provision of ecosystem services depends on the encroachment state

Our analyses of published and unpublished literature on shrub encroachment and ecosystem services indicated that shrub encroachment is associated with increases in six ecosystem services associated with ground-storey biomass production, forage quality, C sequestration, hydrological function, biodiversity and soil fertility (Box 2). However, different configurations of degree of encroachment, shrub cover, shrub traits, richness of ground-storey plants and soil condition will largely determine the extent of benefits likely to accrue from shrublands, and this is likely to be mediated by grazing intensity (Box 2). To quantify these services, therefore, we advance a state-and-transition model (Box 3) for shrublands in eastern

Box 2. Relationships between shrub encroachment and ecosystem services

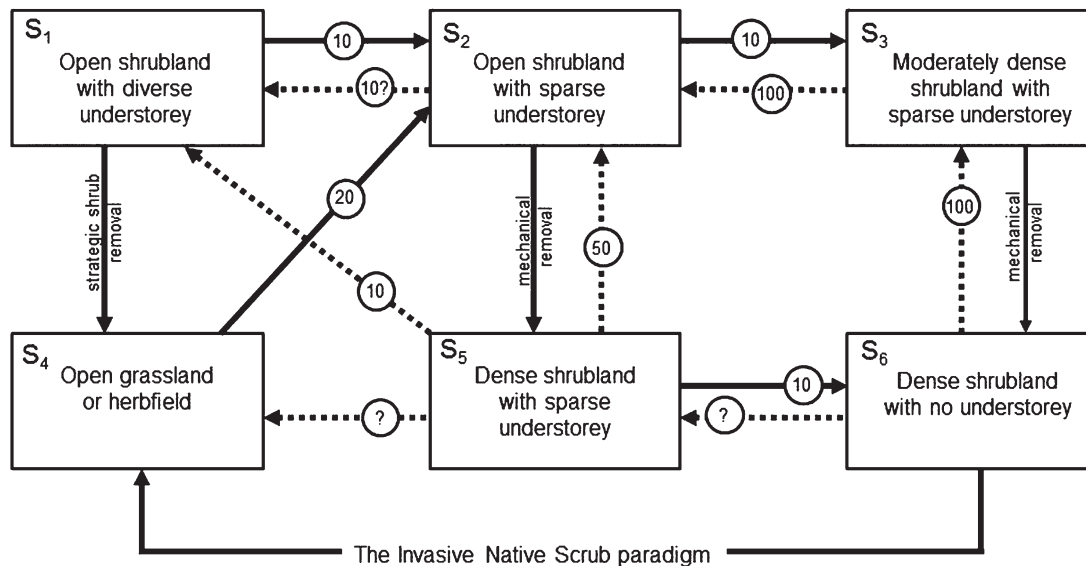
Mean percentage increase ($\pm 95\%$ CI) in six ecosystem services provided by shrublands under two levels of grazing by domestic livestock. Encroachment effects on ecosystem services were always positive, even under high levels of grazing. In order to critically examine the evidence for or against the notion of a positive effect of shrub encroachment, we re-analysed a database consisting of 528 pairs of data. The data were derived from 15 peer-reviewed publications across a range of environmental conditions in NSW and Queensland (Eldridge and Wang (unpublished data), Oliver (undated), Scanlan (1986), Baker *et al.* (1992), Ayres *et al.* (2001), Eldridge (2002), Thompson & Eldridge (2005), McHenry *et al.* (2006), Doerr *et al.* (2009), Tighe *et al.* (2009), Bollard *et al.* (2010), Good *et al.* (2011), Muñoz-Robles *et al.* (2011a, 2011b), Eldridge *et al.* (2013)). One piece of data of each pair reported an effect for open grasslands or woodlands (unencroached) and the other member an effect when that grassland or woodland was encroached by shrubs (encroached). Each of the 528 pairs of data reported a change in one of 36 compositional, structural or functional ecosystem response variables. Data on grazing intensity for each data pair, reported as either low or high, were also recorded. This grazing intensity was based on an assessment by the authors of each original paper, or on regional surveys or government monitoring programs (e.g. NSW Rangeland Assessment Program).

The 36 response variables were categorised into six ecosystem services comprising the following: i) the biomass of pasture (using data on above-ground plant biomass and grass cover), ii) biomass and nutrient content of pasture (using above-ground plant biomass, grass cover, and measures of soil N and P), iii) carbon sequestration (above-ground plant biomass, above-ground carbon, biocrust cover, grass, litter, forb, shrub and tree cover, soil labile, total and organic carbon, and soil aggregate stability), iv) hydrological function (various measures of steady-state infiltration and sorptivity, infiltration index and soil volumetric moisture content), v) biodiversity (ant, bird, grass, forb, shrub, tree and vertebrate richness), and vi) soil fertility (microbial biomass, soil available, extractable and total P, inorganic and total N, labile, organic and total carbon, soil respiration). For each of the six services we plotted the mean percentage change ($\pm 95\%$ CI) against the two levels of grazing.



Box 3. A State and Transition Model for shrublands

A state and transition model for shrublands, describing changes in shrub cover (or density) among six different shrubland states (S1–S6) in a semi-arid woodland. Broken arrows indicate removal of grazing (destocking), and numbers in circles, the years taken to transition between states. The transition from S4 to S6 underlies the assumption implicit in the invasive native scrub (INS) paradigm (see Hassall and Associates 2006), i.e. that removal of shrubs from densely encroached landscapes, often with little or no understorey, will lead to an open, productive and diverse grassland. Transition from S2 to S5 or S3 to S6 has been shown to result from one-off mechanical removal, generally blade ploughing, the method most commonly used in many areas to control shrubs (Robson 1995; Daryanto and Eldridge 2010; Daryanto *et al.* 2012). Other forms of mechanical removal such as roller-chopping, which disturb the surface soil (Adema *et al.* 2004), are likely to result in other transitions. Unless otherwise indicated, continuous arrows represent the effects of grazing.



Australia. This model has been developed using a combination of data from published and unpublished reports and field observations.

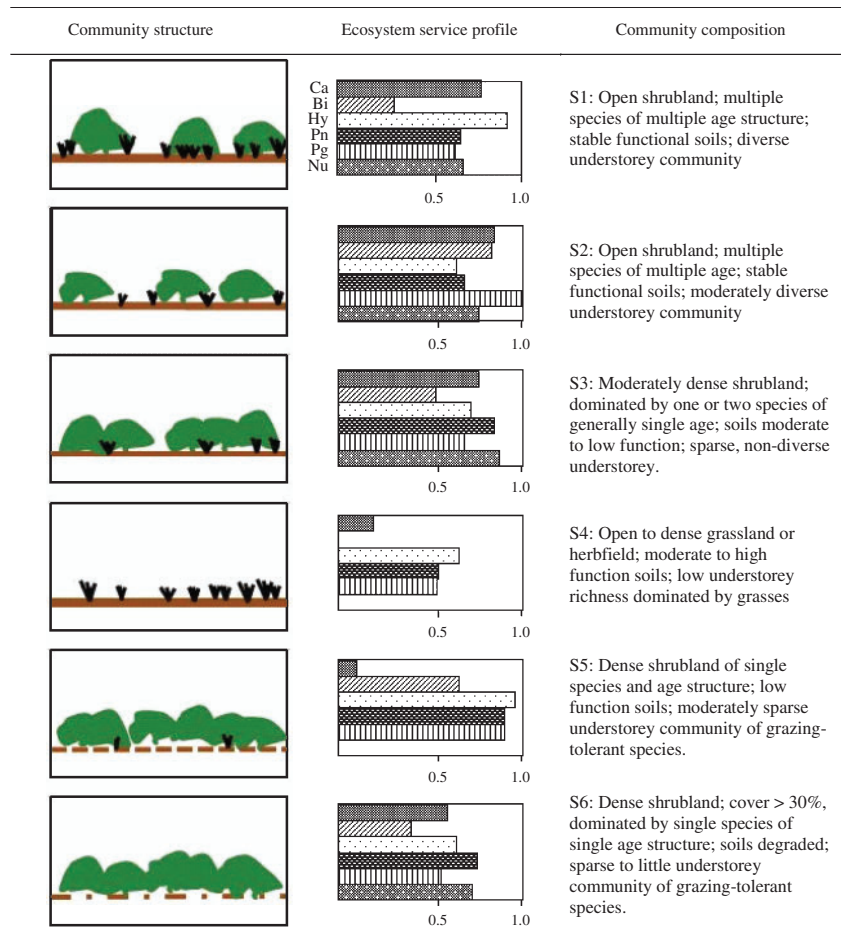
Our model shows that a change from open shrubland with diverse understorey (S1) to moderately dense shrubland with sparse understorey (S3) can occur rapidly, and this change has been observed to occur within a decade at sites monitored under the NSW Rangeland Assessment Program (Green *et al.* 2000; Eldridge and Koen 2003). A transition from dense shrubland with sparse understorey (S3) to that with no understorey (S6) can occur directly through mechanical shrub removal (e.g. by blade ploughing; Robson 1995; Daryanto and Eldridge 2010); however, the prognosis for its return to either dense shrubland with sparse (S3) or open shrubland with sparse (S2) or diverse (S1) understorey is highly unlikely in less than a century, even in the absence of grazing and under conditions of high rainfall (see Hodgkinson 1991). The transition from open shrubland with sparse understorey (S2) to the same shrubland with a diverse understorey (S1) has been demonstrated in some areas in western NSW, through the use of stock-proof (particularly goat-proof) fencing to manage total grazing pressure. This can be achievable within a decade, depending on the soil seed-bank and rainfall conditions, although this will likely depend on initial soil conditions. An unreported, but feasible, transition would be that between a diverse open shrubland (S1) and open

grassland (S4), which would involve strategic removal of individual shrubs without soil disturbance (e.g. through chemical removal of selected plants), although key 'habitat' shrubs would need to be retained to ensure the persistence of those ground-storey plants that require shrubs for critical habitat (i.e. Howard *et al.* 2012; Soliveres *et al.* 2012). Finally, it is unclear how long it would take for dense shrubland with little (S5) or no (S6) understorey to move back to an open grassland (S4), although we suspect it would be in the order of many tens of years or a century in the absence of physical intervention (Box 3).

We derived a relative value for each of six ecosystem services provided by different shrubland states identified in our state-and-transition model (see Box 4). These services (C sequestration, biodiversity conservation, hydrology, forage value for livestock production, biomass production and soil fertility) are the same as those described previously. The data used to value these services were obtained from published and unpublished studies. Several trends are apparent in our service scores. First, levels of C sequestration are very low in open to dense grassland (State 4) and dense shrubland with sparse understorey (State 5; Box 4). Second, although the pastoral value of grasslands would be expected to be greatest in State 4, owing to more grasses and forbs, it is actually greater in the presence of moderate shrubs (near maximum in open

Box 4. Ecosystem services derived from semi-arid shrublands

Schematic diagram showing the community structure of six contrasted states of shrub encroachment, a diagrammatic representation of the relative cover of woody and herbaceous plants, a description of the community composition, and relativised values for the six ecosystem services derived from each state. The six ecosystem services are C sequestration (Ca), biodiversity conservation (Bi), hydrology (e.g. infiltration of water; Hy), plant pastoral nutrition (provision of nutrients N and P that are critical for pasture grass growth and nutrition, Pn), pastoral grass production (plant biomass; Pg), and soil fertility (i.e. organic matter content, soil nutrients; Nu). To derive an overall value for each of the six services, we searched the literature for studies reporting empirical data on various attributes related to the six services. First, we collected any data that allowed us to derive a value for any of the six attributes from a range of publications (see below). Each value was relativised by dividing it by the largest number. This has the effect of rescaling values to a maximum of 1 and improves the comparison among variables with different units and ranges. For each of the six services for each state, the relativised values are then averaged. Some data were unavailable (fertility for States 4 and 5, biodiversity for State 4), so these values have been left blank. Sequestration of C relates to the potential of a given state to fix and store atmospheric C and was calculated using measures of plant, litter and biological soil crust cover, plant biomass, total and labile soil C, and total ecosystem (above- and below-ground) pools of C (e.g. Burrows *et al.* 2002; Daryanto and Eldridge 2010; Stefani Daryanto, unpubl. data). Biodiversity relates to the capacity of a given state to provide habitat for plants and animals. We could find very little information on fauna from the six encroachment phases (apart from limited information in Ayres *et al.* 2001; and Doerr *et al.* 2009), so we based our assessment only on plant richness (e.g. Daryanto and Eldridge 2010; Daryanto *et al.* 2012, and unpublished material). Hydrology was related to the capacity of each state to conduct water through the soil profile and was assessed using various indices and empirical measures of infiltration capacity such as infiltrability (e.g. Daryanto *et al.* 2013a), sorptivity and steady-state infiltration under ponding and tension from different shrub states in western New South Wales (NSW) (Bowker *et al.* 2013; Eldridge *et al.* 2014; D. J. Eldridge, unpubl. data from Cobar and Griffith, NSW) and assorted soil infiltration indices relating to landscape-function analysis (LFA; Eldridge *et al.* 2013). Pastoral nutrients relate to the service provided by soil in supplying P and N to plants. These elements are critical components of grass biomass and essential for livestock growth and production (Belsky 1994; Treydte *et al.* 2011). Information was obtained on various forms of N and P, including organic, inorganic and mineralisable N, total soil N, net N mineralisation potential; Tighe *et al.* 2009; Eldridge *et al.* 2013). Pastoral grass production is the service most closely aligned to pastoralism, and is related directly to biomass production, particularly grasses. Even though this is not strictly an ecosystem service, we calculated its value because it is the attribute that is most valued by pastoralists and often the only attribute considered to have real utility. Data were obtained from a range of published and unpublished sources (e.g. Tothill 1971; Robson 1995; Snowdon and Ryan 2005, Thompson and Eldridge 2005). Soil fertility was derived from soil N, P and C, and specific nutrient indices (e.g. LFA nutrient index) using data from Eldridge (2011), Daryanto and Eldridge (2012), Daryanto *et al.* (2012, 2013a) and unpublished reports.



shrubland with moderate understorey; State 2) because of the presence of plant-facilitatory mechanisms (Soliveres *et al.* 2011) and is also very high where shrubs are dense and understorey moderate (State 5). Third, biodiversity values are highest in open shrubland with diverse understorey (State 2), but unknown in the grassland state (State 4) because of lack of data. Fourth, hydrological services are maximised where shrublands support a diverse understorey (State 1) or where a single shrub species dominates and the understorey is moderately sparse (State 5), reinforcing the value of both diverse, multi-species shrubs (State 1) and perennial grasses (State 4) as conduits for water flow (e.g. Eldridge *et al.* 2014). Finally, soil-fertility data are lacking for two of the six states, although the little available evidence suggest that it peaks in landscapes with moderate shrub densities or cover (State 3).

Calculations of the ecosystem-service values across the six shrubland states indicate that there is no one state that maximises all services; rather, the provision of services by shrublands requires a mix of different states (i.e. a mosaic of structures). Our data suggest that shrublands that are open to moderately dense, supporting more than one shrub species and having relatively stable surface with a moderate cover of ground-storey plants (States 2 and 3), have the highest mean overall service values. However, shrublands dominated by single species and with moderately sparse understorey (State 6) or perennial grasslands (State 4) have the lowest score (although additional data on State 4 may well alter this). However, the question is not which state is better, but rather, what mix of services are required, and therefore, what loadings should be given to these services in any upscaling to the community level?

Managing shrublands: how sustainable is shrub removal?

'People love chopping wood. In this activity one immediately sees results' (Albert Einstein).

Despite the substantial investment by governments in shrub-removal programs, the long-term ecological and economic viability of shrub removal is surprisingly poorly understood. There is little scientific evidence to support the belief that shrub removal increases pastoral value. The best evidence lies in a comprehensive meta-analysis of published data on the effects of woody plant removal from North America (Archer *et al.* 2011). Their report showed that removal of woody shrubs (using physical or chemical methods) produced a range of responses in grass and forb diversity and ground-water recharge, from neutral to positive. Any effects of shrub removal were, however, relatively short-lived (<15 years; Archer *et al.* 2011).

In Australia, few economic analyses of shrub control have been made, and the results of such analyses are likely to depend on vegetation community and rainfall regime. One such study, based on a one-off control of *Callitris glaucophylla* regrowth from an area of relatively moderate rainfall (650 mm) in northern NSW, suggested that private costs borne by landholders would exceed the benefits that would accrue from increased livestock productivity, at least for 16 years following treatment. Although *Callitris* is a tree, it regenerates into dense

stands and individual plants remain relatively short (<3 m tall) and therefore shrub-like. Analyses also indicated that control of regrowth would result in a positive net social benefit through perceived reductions in erosion and improved native vegetation (Farquharson *et al.* 2010). These analyses make several assumptions for which data are currently unavailable. For example, they assume that (1) removing *Callitris* regeneration will reduce stream erosion, (2) any 'rejuvenated' native pasture will be 'close to a pre-European state', and (3) removing *Callitris* will revert the landscape to one resembling a pre-European state. Finally, no allowance was made for the potential biodiversity value of the existing vegetation before treatment nor the effect that current stocking rates had on reducing such biodiversity. We use this example not to criticise the modelling of Farquharson *et al.* (2010), which identifies most of these knowledge gaps, but simply to highlight the huge gaps in our knowledge of wooded communities and their values to the broader community. Government-sanctioned removal of woody vegetation, including shrubs and trees, may have social benefits such as improving the 'visual amenity' or leaving the property in a 'good state for [the] next generation' (Farquharson *et al.* 2010), but the net benefits in terms of the maintenance of ecosystem services through increased water and nutrient capture, reduced soil loss, C fixation or the maintenance of diversity are rarely considered. Economic analyses in the western United States indicated that any program of large-scale shrub removal will require a substantial investment by the state (Lee *et al.* 2001). Rigorous, science-based evidence is needed to determine objectively whether this removal is economically viable and whether woody removal actually results in enhanced ecosystem services and environmental benefits.

Shrub removal is likely to be less economically viable in areas of lower than in areas of higher rainfall because the economics of grazing are less certain in arid and semiarid areas than in more mesic environments. For example, results from one study near Bourke in western NSW (350-mm average annual rainfall) indicated that one-off shrub removal combined with continued grazing is likely to increase, rather than reduce, shrub density (Daryanto and Eldridge 2010). At this site, shrub removal failed to provide sustained increases in ground-storey plant richness or cover compared with a system that was ungrazed for the same time period (Robson 1995; Daryanto and Eldridge 2010). When grazing was removed following shrub removal, ground-storey plant cover was almost double that under a regime of continued grazing (Daryanto and Eldridge 2010). In these environments, landholders rarely destock after removing shrubs because they need to recoup the costs of treatment and the high opportunity cost (i.e. the foregone grazing value) of not grazing a large paddock that contains a relatively small area of treated shrubs. Evaluation of the economics of shrub control is limited, but control is likely to be viable, if only marginally, when wool or meat prices (and stocking rates) are high (Burgess 1988). The economics of ploughing for shrub removal will depend on many things such as the opportunity cost of not grazing and the cost of treatment (e.g. labour, machinery and fuel). These costs, however, may vary depending on soil texture, soil type, soil moisture, plough model, tractor type, and shrub size and density (Harland 1993). Furthermore, follow-up treatment is

likely to be needed, and this is likely to reduce the profitability of shrub control.

Reliance solely on a grazing-derived income and applying stocking rates close to the biological maximum (i.e. maximised profits per hectare instead of per animal) have been shown to be unsustainable in the long-term (e.g. Stafford Smith and Foran 1992; Solomon *et al.* 2007; but see Silcock and Fensham 2013). First, annual income will be highly dependent on annual rainfall, which is extremely variable in arid and semiarid environments (Whitford 2002). Second, overgrazing increases temporal unpredictability, and heavily grazed sites are less resilient than those that are moderately grazed (Stafford Smith and Foran 1992). Policies aimed at diversifying on-farm incomes should be promoted so as to increase the predictability and amount of annual income derived from pastoralism in a shrub-encroached ecosystem. For example, European agri-environment schemes pay farmers to manage their land for increasing environmental benefits (see review of the Lucid program in de Snoo *et al.* 2013). Funding directed to assisting pastoralists to adopt alternative strategies or supplementary enterprises has been suggested as a more efficient use of public money than spending it on shrub removal (Musters *et al.* 2001; de Snoo *et al.* 2013; and references therein), and will likely result in a reduced risk of land degradation (Dreber *et al.* 2014).

In the Australian case, money invested to promote shrub removal might be better invested in programs to maximise C sequestration (related to the reduction of greenhouse gases), enhancing biodiversity (related to conservation, e.g. New Mexico Comprehensive Wildlife Conservation Strategy Program on Piñon-Juniper Woodland/Shrubland), or measures to enhance soil fertility and conservation (related to pastoral production and the reduction in the frequency and size of dust storms; Williams and Young 1999). Projected profits derived from woody-focussed C farming may be comparable to those from pastoralism, as long as seasons are favourable and the C marked can be sustained (Daryanto *et al.* 2013a). There will likely also be co-benefits of thickening vegetation for flora and fauna (Dwyer *et al.* 2009). Other examples are programs aimed at rewarding pastoralists for sustaining minimum levels of ground cover (Hacker 2009), although these are relatively uncommon. Overall, therefore, there is little evidence that in Australia, government-funded programs to remove shrubs have provided real long-term economic or environmental benefits to landholders hoping to increase plant production. For those clearing for cropping, which is a more profitable enterprise, shrub removal may be more economical.

Implicit in current regulation in NSW is the premise that invasive native scrub is 'much more extensive and/or much denser than the previous natural condition of the vegetation' (Hassall & Associates 2006) and, therefore, its removal or reduction is warranted under the condition that it will 'improve or maintain' environmental outcomes, outlined in the 'Environmental Outcomes Assessment Methodology' of the Native Vegetation Regulations (2005). However, this underlying premise is still hotly debated (e.g. Noble 1997; Kerle 2009; Lunt *et al.* 2010; see Introduction above). Regardless of the exact nature of pre-European vegetation, existing data suggest that the opportunities for moving towards

an open woodland with very few shrubs, and maintaining this condition in the long-term, from a heavily grazed shrubland are highly unlikely (see Box 3).

Concluding remarks and future directions

Despite the well known positive effects of isolated shrub patches on their understorey communities, there is a long-established and widely held view that shrub encroachment is synonymous with the loss of ecosystem functioning at the landscape-level. We critically tested this paradigm and found three elements that contradict the prevailing view. First, there is little acknowledgement that the symptoms attributed to shrub encroachment, which in many areas are sparse cover and low diversity of vascular plants, and dysfunctional soils, could be due to anything other than the shrubs themselves. It is assumed, therefore, that reductions in ecosystem structure, function and composition under encroachment result directly from shrub-driven resource competition rather than being a response to changes in management actions such as prolonged grazing pressure. We have shown that grazing, rather than increases in shrub density *per se*, is the key driver of declines in function in shrublands. Second, shrubs are typically considered as a homogeneous collective, often in a pejorative sense (e.g. 'invasive' native scrub, woody 'weeds'), and are rarely considered as idiosyncratic species with a range of traits such as an ability to fix atmospheric N, access groundwater or provide specialised habitat for particular taxa. These species-specific attributes may well alter the effect of shrub encroachment on ecosystem services and should be considered when managing encroached landscapes. Third, much of the criticism of encroachment derives from a pastoral context. Encroachment is therefore a contextual issue, and is strongly dependent on the prevailing land use. Finally, current policy relating to the management of encroachment is not, in our opinion, based on best available science (Hassall & Associates 2006). There is clearly a role for further research to guide the management of encroachment at the ecosystem level. Greatly needed is a scientifically valid framework that considers encroached vegetation within a wider range of potential land uses, embracing the provision of ecosystem services such as habitat for biodiversity, C and water capture and ecotourism, as well as pastoralism.

It is clear from our paper that several key knowledge gaps constrain our ability to make decisions about the efficacy and economics of managing shrub-encroached landscapes, and these include the following:

- (1) We need to better understand which specific shrub traits have the greatest influence on the tendency of shrubs to encroach and how they influence ecosystem services derived from shrublands.
- (2) Separating the effects of encroachment from those of historic and contemporary grazing is required to clarify the encroachment–ecosystem dysfunction relationship commonly assumed.
- (3) There are very few scientifically rigorous studies where the effect of shrub removal has been rigorously tested. Thus, there is ample opportunity for studies focussed on how differing stages of shrub encroachment affect multiple

ecosystem functions and services, and how we could maximise them at the landscape scale (e.g. Archer *et al.* 2011). There is also a need to document response times for the return of understorey species from dense shrublands with no understorey (State 6) to the same shrubland with a sparse understorey (State 5; Box 3) and the eventual return to open grassland (State 4). Such studies will help promote cost- and ecologically effective techniques for managing regrowth vegetation.

- (4) Finally, there is a need for more economic studies of the benefits to be derived from clearing encroached communities compared with the returns from grazing and even alternative land uses such as recreational shooting or ecotourism. This evidence is needed to ensure that decisions made by pastoralists and governments are based on best available science.

Acknowledgements

We thank Ian Oliver and Chris Nadolny for comments on an earlier draft, and James Val, Niki Huang, Stefani Daryanto, Samantha Travers and Alan Kwok for assistance with various aspects of field work that has formed the basis for much of the material considered here. This work was funded by the Hermon Slade Foundation (RG133197). Finally, discussions with many colleagues, particularly Ian Lunt, over many years have helped us form our views about shrubs, shrublands and ecosystem processes. To all of these people, we are extremely grateful.

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