

## Chapter One. General introduction and thesis outline



## Introduction

The coolibah (*Eucalyptus coolabah* subsp. *coolabah* Blakely & Jacobs) floodplain woodlands of Australia are iconic, endangered and almost unstudied. Dense regeneration of coolibah trees occurred in the Darling Riverine Plains bioregion (ERIN 2005), which includes the floodplains of inland northern New South Wales (NSW), following floods in the mid 1970s (Maher 1995; Freudenberger 1998). These stands are still dense (~3000 stems ha<sup>-1</sup>) even though they are now over 40 years old, and it has been suggested that the trees are not self-thinning in a timely manner and may require mechanical or chemical thinning to increase groundstorey vegetation cover (Maher 1995; Freudenberger 1998). Landholders have expressed concern about the negative effect of these stands on pasture production and biodiversity since it appears that the dense coolibah trees have excluded almost all groundstorey vegetation (Freudenberger 1998). Yet coolibah woodlands in the Darling Riverine Plains bioregion (ERIN 2005) have been so heavily cleared and modified since European occupation that they have been listed as an endangered ecological community federally – as part of ‘Coolibah – Black Box Woodland of the Darling Riverine Plains and Brigalow Belt South bioregions’ (EPBC Act 1999) and in NSW as ‘Coolibah – Black Box Woodland of the northern riverine plains in the Darling Riverine Plains and Brigalow Belt South bioregions’ (NSW Scientific Committee 2004; 2009). The aim of my thesis is to explore these contrasting issues – that of woody plant encroachment and woodland decline – by investigating the structure of remnant coolibah woodlands and stands of dense regeneration, the population dynamics of coolibah, and the effects of dense coolibah regeneration on groundstorey plant communities. Most of the remainder of this chapter consists of a literature review of relevant topics, viz. woody plant encroachment, the ecology of savannas, Australian woodlands, and coolibah woodlands specifically. In doing so, I explore global issues such as tree–grass coexistence in savannas, rangeland management and biodiversity conservation in agricultural landscapes. The chapter concludes with a section setting out the aims of the research and the aims of each of the remaining five chapters in the thesis.

## Woody plant encroachment

Woody plant encroachment is an increase in the abundance or extent of woody plants in previously open ecosystems. This phenomenon has occurred globally in grasslands, savannas and open woodlands in recent decades (e.g. Brown and Carter 1998; Knapp and Soule 1998; Archer *et al.* 2000; Van Auken 2000; Bowman *et al.* 2001; Lett and Knapp 2005; Graz 2008; Lunt *et al.* 2010). Ecosystems that are most commonly affected by encroachment include savannas and rangelands in North and South America, Africa and Australia (Burrell 1981; Archer *et al.* 2000; Van Auken 2000; Roques *et al.* 2001; Lunt *et al.* 2010). The consequences of woody encroachment include changes to nutrient cycling, soil chemistry, plant species composition and richness, herbaceous productivity, and carbon storage (Archer *et al.* 2000; Costello *et al.* 2000; Hibbard *et al.* 2001; Norris *et al.* 2001; Jackson *et al.* 2002; Lett and Knapp 2003; Butler *et al.* 2006; Hughes *et al.* 2006; Zarovali *et al.* 2007; Price and Morgan 2008; Van Els *et al.* 2010; Eldridge *et al.* 2011). However, these effects are not universal. A review by Eldridge *et al.* (2011) concluded there were few consistent effects of encroachment and that woody plants can have positive, neutral or negative effects on ecosystem attributes. The consequences of encroachment tend to be specific to the type of woody plant and the properties of the encroached ecosystem (Eldridge *et al.* 2011).

One of the few consistent effects of woody plant encroachment is a decrease in herbaceous biomass or productivity (Eldridge *et al.* 2011). Increased woody plant abundance and decreased grass or forb production substantially reduces the profitability of grazing enterprises. Hence, there is increasing pressure on government regulators to allow selective clearance of native species that are thought to be encroaching even though native vegetation clearance is illegal in many developed nations (Briggs *et al.* 2005). Alternative viewpoints have been expressed regarding the value of woody plant encroachment. Eldridge *et al.* (2011) and Maestre *et al.* (2003; 2009a) have highlighted possible benefits of increased woody plant abundance, especially in previously degraded systems. Maestre *et al.* (2009a) found increased plant species richness, fungal biomass, soil fertility and N mineralisation rates following encroachment in degraded Mediterranean grasslands. Other authors (Fensham and Fairfax 2005; Fensham *et al.* 2005; Wiegand *et al.* 2005;

Wiegand *et al.* 2006; Fensham and Fairfax 2007; Fensham 2008; Fensham *et al.* 2009) have questioned the directionality of vegetation change, suggesting that over broad spatial and temporal scales, mortality of woody plants during sub-optimal conditions balances out increases in abundance under favourable conditions.

The mechanisms responsible for increased woody plant abundance are understood to varying degrees in different systems, but there is no single explanation for all cases. Changes to disturbance regimes, above-average rainfall, changes to soil moisture availability, and increases in atmospheric carbon (CO<sub>2</sub>) concentration or some combination of these factors favour woody plant expansion in most systems (Bennett 1994; Archer *et al.* 1995; Knapp and Soule 1998; Van Auken 2000; Bowman *et al.* 2001; Roques *et al.* 2001; Heisler *et al.* 2003; Briggs *et al.* 2005; Kraaij and Ward 2006; Morgan *et al.* 2007a; Graz 2008).

Above-average rainfall and fine-scale changes in soil moisture availability may favour woody plant germination and establishment. Indeed, recruitment events are often associated with high rainfall years (Archer *et al.* 1988; Schlesinger *et al.* 1990; Archer *et al.* 1995; Roques *et al.* 2001; Fensham *et al.* 2005). Increased grazing pressure has also been implicated as a mechanism because grazing can reduce fuel loads, altering fire frequency and intensity, and this may favour the establishment of fire-sensitive woody species (Van Auken 2000; Roques *et al.* 2001; Briggs *et al.* 2005). Grazing also reduces herbaceous vegetation cover, which may reduce competition and suppression of woody plants by grasses and lead to an increase in woody plant abundance (Van Auken 2000). Humans can directly change fire regimes and this affects proportions of fire-sensitive and fire-tolerant species (Higgins *et al.* 2000; Roques *et al.* 2001; Bond *et al.* 2003; Heisler *et al.* 2003; Bond *et al.* 2005; Kraaij and Ward 2006; Bond 2008; Nano and Clarke 2010). It is thought that anthropogenic changes in savanna or rangeland management underlie most instances of encroachment, though the evidence is equivocal and a better understanding of the dynamics and processes underlying savanna stability is required.

## The ecology of savannas

Savannas consist of a continuous ground layer of herbaceous vegetation (forbs and grass, hereafter ‘grass’), and a discontinuous cover of woody plants (shrubs or trees, hereafter ‘trees’) (Scholes and Archer 1997). Savannas cover about a fifth of the global land surface and occur on most continents (Asia, Africa, America and Australia) and across a range of climates and soil types (Sankaran *et al.* 2004; Moustakas *et al.* 2010).

Both the grass and tree components have important functions in the savanna biome. Grasses provide food for herbivores, habitat for ground dwelling animals, and carry fire in more productive savannas. Scattered and clumped trees provide habitat for birds, mammals, reptiles and invertebrates, and plants. Trees also provide coarse litter and debris which can result in the ‘fertile island’ effect whereby the area surrounding an isolated tree is more fertile than treeless areas elsewhere in the landscape (Belsky *et al.* 1989; Belsky *et al.* 1993). Thus, changes in the dominance of the grass or tree component can have a variety of consequences for the composition, structure and function of savannas.

The tendency for savannas to occur in climatic regions that could support a much higher biomass of woody plants has led to a number of hypotheses about what limits trees in these systems (Bond 2008). Top-down (e.g. fire and grazing) and bottom-up (e.g. soil and climate) explanations alone are often insufficient and there are complex interactions among the many factors that constrain woody plant recruitment, growth and reproduction in savannas (Bond 2008; Midgley *et al.* 2010). Modelling climatic variables against tree abundance rarely predicts the actual distribution of savannas (Jeltsch *et al.* 1996; Bond *et al.* 2005; Midgley *et al.* 2010; Lehmann *et al.* 2011).

So, what factors limit tree abundance in savannas? Walter’s (1971) rooting niche separation theory, also known as the ‘two layer hypothesis’, proposes that trees are able to capture moisture in deeper layers whereas grasses can more efficiently obtain resources from shallow soil layers, thereby limiting available resources for woody plants and limiting their abundance. Some studies have reported an increase in woody plant abundance with increased grazing pressure (van Vegten 1983; Skarpe 1990), whereas others have found no effect of grass abundance on woody plant

establishment (Brown and Archer 1999). Given that the two layer hypothesis does not apply to all savanna systems, new theories have been developed, which may be broadly referred to as ‘demographic bottleneck’ approaches to understanding savanna dynamics.

Demographic bottleneck theories propose that savannas do not become dominated by trees due to factors that limit tree recruitment (Sankaran *et al.* 2004). Two broad processes responsible for limiting tree recruitment have been proposed: disturbance and environmental variability (Bond 2008). Disturbances – for example fire – tend to destroy plants or plant tissue, thereby directly altering vegetation structure. Environmental variability – rainfall or temperature extremes – tends to limit recruitment opportunities and can also kill plants. In general, disturbances that kill trees before they are established are important in mesic environments (Bond *et al.* 2005; Sankaran *et al.* 2005) where rainfall is high and does not limit tree recruitment. These savannas tend to be described as ‘disequilibrium’ systems, which if left undisturbed should transition toward a closed forest ecosystem (Jeltsch *et al.* 2000; Sankaran *et al.* 2004). Alternatively, ‘non-equilibrium’ systems are governed by the variability in environmental conditions, which favours grass or tree dominance at different spatial and temporal scales and prevents either life-form from becoming dominant across the landscape (Wiegand *et al.* 2005; Wiegand *et al.* 2006). This situation is most common in arid environments where inter-annual rainfall variability is high and droughts are common. These demographic bottleneck models are increasingly being studied and tested (Sankaran *et al.* 2004; Wiegand *et al.* 2006; Moustakas *et al.* 2010).

### **Australian woodland and savanna dynamics**

Woodlands and savannas dominated by eucalypts (*Angophora*, *Corymbia* and *Eucalyptus*) are extensive in Australia, covering 30% of the continent (Fig. 1; Benson 1991; Yates and Hobbs 1997a; Johnson 2003). Since European occupation and subsequent development of agriculture, especially in the wheat–sheep belt, eucalypt woodlands have been substantially modified with those occurring in the most productive lowlands now only remaining as small degraded fragments (Fig. 2; Benson 1991; Yates and Hobbs 1997a; Cox *et al.* 2001).

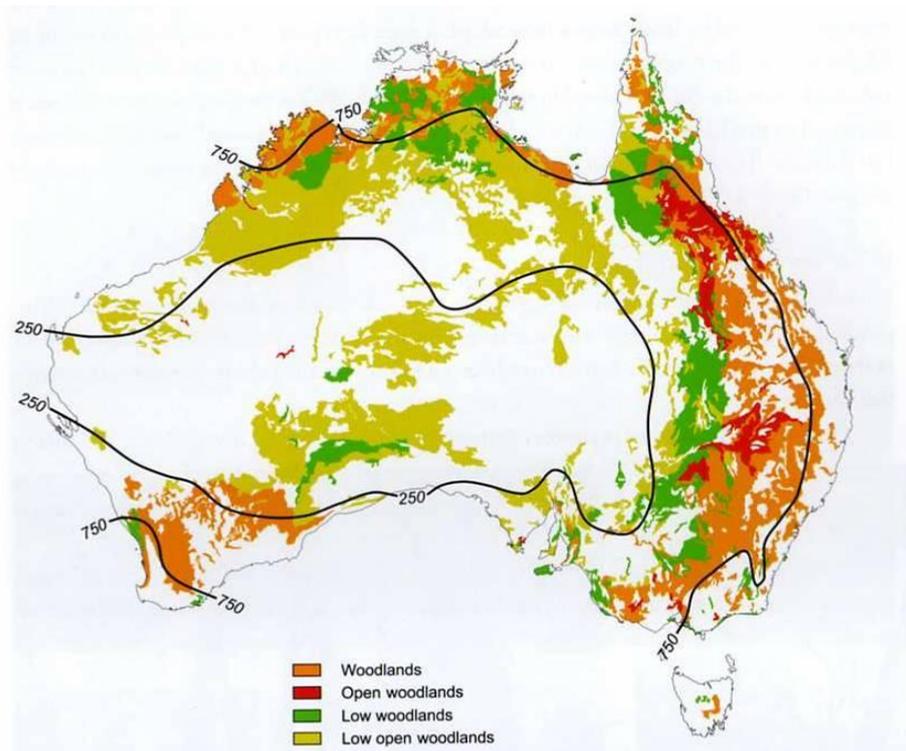


Figure 1. The distribution of broad woodland types in Australia with 250 mm and 750 mm isohyets. Source: (Johnson 2003).

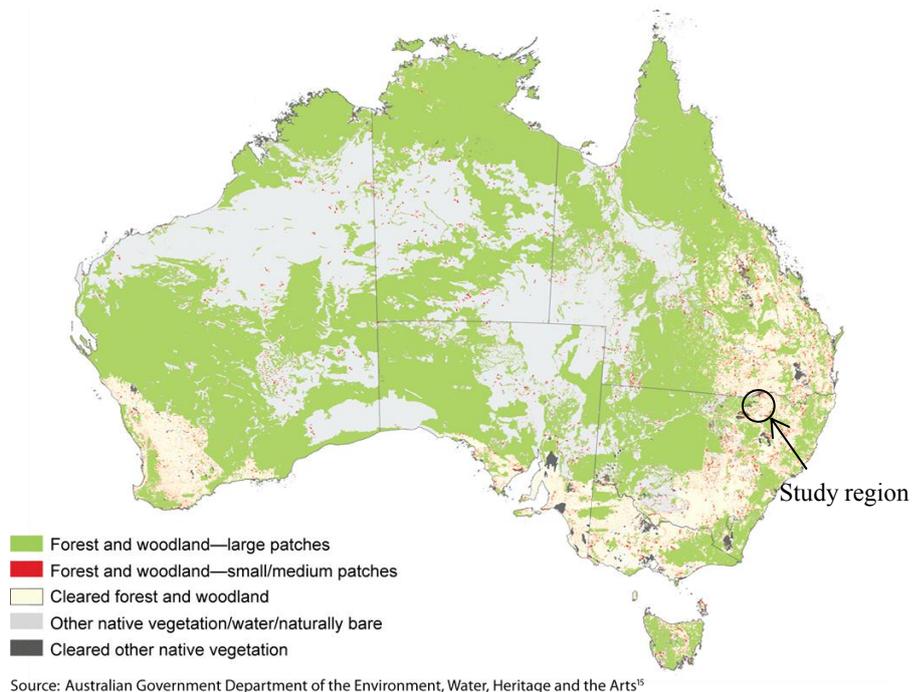


Figure 2. Land clearance map showing areas of cleared forest and woodland. The wheat-sheep belt through eastern and south-western Australia has been most heavily cleared and clearing continues, albeit at a reduced rate since the introduction of more stringent laws. My study region in eastern Australia is circled in black. Source: Australian Government Department of the Environment, Water, Heritage and the Arts (2011).

The historical tree density in Australia's woodlands and savannas is the source of ongoing debate among ecologists and land managers in Australia. In particular, the importance of fire in structuring pre-European vegetation is controversial (Benson and Redpath 1997; Bowman 2001; Griffiths 2002; Jurskis 2002; Fensham 2008; Jurskis 2009). In coastal areas of southern Australia, empirical studies have demonstrated a directional increase in shrub abundance due to changes in disturbance regimes (Burrell 1981; Gleadow and Ashton 1981; Bennett 1994; Lunt 1998; Costello *et al.* 2000; Gent and Morgan 2007; Lunt *et al.* 2010). In eastern and northern Australia, dense woodland regeneration tends to occur in times of above-average rainfall, but this process is thought to be balanced over time by widespread tree mortality in times of low rainfall (Fensham and Holman 1999; Sharp and Bowman 2004; Fensham *et al.* 2009). Areas of dense scrub are mentioned in early explorers records from eastern Australia prior to European occupation, indicating that changed management is not a prerequisite for dense woody cover (Fensham 2008).

Woody plant increases have also been reported in the rangelands of western NSW (Noble 1997). In these regions, changes in disturbance regimes (grazing and fire) are implicated (Noble 1997), but widespread clearing is likely to have preceded shrub encroachment (Harrington *et al.* 1979; Benson 1999; but see Ross *et al.* 2012). In Australia's semi-arid rangelands, concerns about woody encroachment are centred on the negative effects of woody plants on pasture production and profitability of grazing enterprises (Harrington and Johns 1990; Harris *et al.* 2003). In these regions, the processes driving woody encroachment, the natural dynamics of the vegetation and the effect of encroachment on biodiversity are poorly understood and require further investigation.

Understanding the conditions required for woodland tree recruitment may provide insight into the mechanisms responsible for changes in woody plant abundance in Australia. The biology of some eucalypts is well understood, especially those that are economically important (forestry) species, which generally occur in higher rainfall zones of Australia (Florence 1996). Eucalypts occurring in woodlands and open woodlands in lower rainfall zones are less well understood. However, the need to restore heavily cleared landscapes and ensure replacement of remnant woodlands has led to some advancement in this area (Yates and Hobbs 1997a; Vesk and Mac Nally 2006). For most

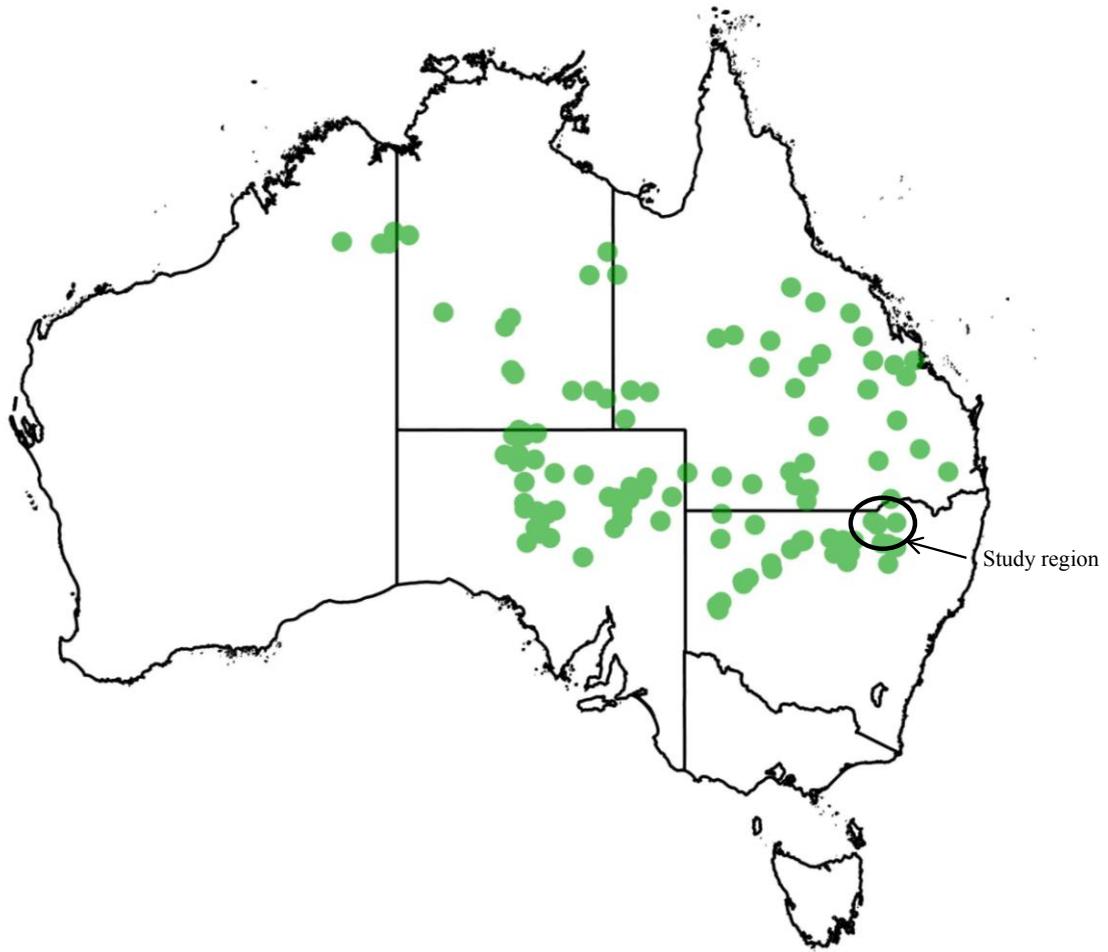
eucalypt species, seed supply and favourable seedbed conditions are required for successful germination and resources such as light and soil moisture determine seedling success (Facelli and Ladd 1996; Florence 1996; Yates *et al.* 1996; Clarke and Davison 2001). Eucalypt recruitment in temperate woodlands and cleared agricultural land is thought to be limited by seed dispersal, competition from introduced species, overgrazing and changes to fire regimes (Semple and Koen 2003; Vesk and Dorrough 2006; Standish *et al.* 2007). Recruitment in semi-arid woodlands tends to be driven by rare events such as fire and floods as well as periods of above-average rainfall (Wellington and Noble 1985a; 1985b; Yates *et al.* 1996; Yates *et al.* 2000). Therefore, changes in land management, such as the addition of fertilisers that favour exotic species, the introduction of livestock and continued grazing pressure, changes to fire and flooding regimes and clearing and fragmentation of woodlands may contribute to changes in tree abundance in Australia – either by increasing or decreasing opportunities for tree recruitment.

Changes in woody plant abundance in Australia – through clearing or woody encroachment – are likely to affect ecosystem structure, function and composition. Plant composition beneath woody plant canopies can be quite distinct from the composition of inter-canopy areas (Scanlan and Burrows 1990; Vetaas 1992; Belsky *et al.* 1993; Gibbs *et al.* 1999; Prober *et al.* 2002), thus changes in woody plant abundance may alter understorey composition. Shrubs that form a dense thicket can significantly reduce light availability such that just a few species can persist in the understorey (Costello *et al.* 2000; Price and Morgan 2008). Alternatively, shading may provide benefits in arid environments, such as reduced evapotranspiration, which might have facilitative effects on some species (Maestre *et al.* 2003). Indeed, the net effects of woody plant cover on herbaceous plants is likely to depend on climate and edaphic factors (Belsky *et al.* 1993; Scholes and Archer 1997). Trees have been associated with elevated soil fertility relative to treeless areas, most likely due to litter accumulation beneath canopies (Belsky *et al.* 1989; Vetaas 1992; Jackson and Ash 2001; Ludwig *et al.* 2004). Increased eucalypt cover will most likely have different effects on ecosystem properties compared to other woody species. Possibly the most important aspect of eucalypt woodland trees is their continuous litter deposition, which can alter soil chemistry and

microbial communities and also physically impede seed germination (Facelli and Pickett 1991; Prober *et al.* 2002). Eucalypts have been shown to reduce herbaceous productivity but can increase nutrient value of herbaceous vegetation (Harrington and Johns 1990; Scanlan and Burrows 1990; Jackson and Ash 1998). Eucalypt trees also increase microsite heterogeneity and reduce competitive exclusion from dominant herbaceous species, resulting in increased groundstorey species richness (Price and Morgan 2010). Thus, changes in woody plant abundance can have varying effects on ecosystem properties.

### **Coolibah woodlands**

Coolibah woodlands occur throughout seasonally inundated alluvial plains of northern New South Wales, southern Queensland and southern Northern Territory (Fig. 3). They occur as woodlands or open woodlands and have a predominantly grassy understorey with chenopods becoming more abundant with increasing aridity (Fig. 4a). Due to their occurrence on fertile floodplains, most coolibah woodlands have been cleared for food and fibre production in NSW and are an endangered ecological community listed under the Threatened Species Conservation Act 1995 (NSW Scientific Committee 2004; 2009) as the ‘Coolibah – Black Box Woodland of the northern riverine plains in the Darling Riverine Plains and Brigalow Belt South bioregions’. Coolibah woodland is also listed as endangered under federal legislation (Environmental Protection and Biodiversity Conservation Act 1999) as the ‘Coolibah – Black Box Woodland of the Darling Riverine Plains and the Brigalow Belt South bioregions’. Clearing, weed invasion and livestock grazing continue to threaten this community (Benson 1999; Keith *et al.* 2009).



**Figure 3. Distribution of *Eucalyptus coolabah* subsp. *coolabah* in Australia. Source: Australia's Virtual Herbarium (2012).**

Little is known of the biology or population dynamics of coolibah though the species is likely to have similarities with other floodplain eucalypts such as *E. camaldulensis* and *E. largiflorens* (Dexter 1968; Bren 1992). The few studies of coolibah and closely related floodplain coolibah species – *E. coolabah* subsp. *arida* and *E. victrix* – suggest that recruitment is dense, episodic and rare in space and time (Roberts 1993; Sharp and Whittaker 2003; Fox *et al.* 2004). Fox *et al.* (2004) found that the seedlings of *E. victrix* (a floodplain eucalypt from the Pilbara, Western Australia) rarely survive to become saplings even if germination is widespread, but they could not predict the conditions required for successful recruitment of this species. It is widely accepted that coolibah germinates following floods (Roberts 1993; Pettit 2000; Roberts and Marston 2000), but recruitment events are much less common than flooding so it is likely that other factors determine

recruitment establishment. Optimal germination of coolibah seed occurs at 30–35°C (Doran and Boland 1984), which suggests that floods in warmer months are more likely to stimulate recruitment. Based on studies of many other *Eucalyptus* species it is unlikely that coolibah forms a persistent soil seed bank and is likely to store seed in the canopy (Boland *et al.* 1980; Doran and Boland 1984). There are few phenological studies of coolibah but they are thought to flower between December and February and set seed from January to March (Boland *et al.* 1980). The importance of environmental cues for seed rain is not known.

Coolibah regenerated densely following floods in the mid 1970s and patches of dense coolibah woodland occur throughout the Darling Riverine Plains of NSW (Fig. 4b; Maher 1995; Freudenberger 1998). Dense regeneration of coolibah in the mid 1970s was also reported on the Victoria River floodplains in the Northern Territory where overgrazing was proposed as the reason for the high density of trees (Sharp and Whittaker 2003). The effect of these dense stands on the biomass and cover of groundstorey vegetation has raised concerns about the effect of dense regeneration on plant diversity and ecosystem function (Maher 1995; Freudenberger 1998; Sharp and Whittaker 2003). However, there are no studies assessing the effects of dense regeneration on groundstorey vegetation composition or richness. Dense regeneration occurs on productive grazing land and is said to reduce the amount of feed available for stock, which reduces the profitability and value of the land (Maher 1995). The perception that dense regeneration is a degrading process – as most studies of woody plant encroachment suggest – which is a threat to biodiversity has led to the listing of coolibah as an invasive native species under the NSW Government’s Native Vegetation Regulation 2005 (Environmental Outcomes Assessment Methodology, DECCW 2011). As such, stands of coolibah which are deemed to be ‘acting invasively’ may be cleared with the only requirement being that all trees with stems over 20 cm diameter and 20 additional stems per hectare be retained in any configuration (i.e. if a 100-ha area is cleared, 2000 stems must be retained in a patch and need not be distributed throughout the 100-ha). We know very little about the population biology of coolibah, the effects of dense regeneration on associated plant communities, where dense regeneration occurs and what conditions are necessary for coolibah

recruitment. Management decisions, such as tree clearing or thinning, should be based on a sound understanding of these aspects of dense regeneration.



**Figure 4. (a) Remnant coolibah woodlands and (b) dense coolibah regeneration on the northern riverine plains of New South Wales.**

## **Thesis outline**

This thesis investigates aspects of the community and population dynamics of coolibah woodlands in the semi-arid floodplains of the Darling Riverine Plains bioregion of New South Wales. I examine patterns of groundstorey community composition, biomass and soil properties in relation to coolibah stand structure as well as the processes governing the coexistence of the woody and herbaceous components of floodplain savannas. In particular, I aim to determine whether or not dense coolibah regeneration is associated with a reduction in plant biodiversity and changes in community composition relative to alternative woodland and derived grassland states. I also investigate landscape scale woodland dynamics and the stability of tree–grass coexistence by measuring differences in stand structure between dense regeneration and remnant woodlands and by experimentally examining the recruitment requirements of coolibah and the ability of grasses to limit recruitment. Together, these studies aim to assess the role of dense regeneration for biodiversity conservation and woodland persistence in this cleared and modified landscape. The following provides a brief outline of the thesis structure, which includes four chapters describing the results of field surveys and experiments and a final synthesis chapter that summarises the findings of the thesis.

In chapter 2, I compare areas of dense coolibah regeneration with adjacent open vegetation in order to determine if there are consistent differences between the two vegetation states in terms of soil properties and groundstorey vegetation richness and composition. The aim of this chapter was to determine if areas of dense regeneration were less species rich than surrounding vegetation. This chapter has been published in the *Australian Journal of Botany*.

Chapter 3 investigates differences in plant community composition in different vegetation states: remnant woodlands, derived grasslands and dense regeneration. This chapter provides insight into the relationship, or lack thereof, between tree density and herbaceous community dynamics and considers the importance of environmental and management variables for groundstorey plant community composition. This chapter has been published in *The Rangeland Journal*.

Chapter 4 focuses on the population dynamics of coolibah woodlands. In particular, I investigate the potential stability of the floodplain savanna system and the importance of dense regeneration for the persistence of coolibah woodlands in the landscape.

In chapter 5, the ability of coolibah seedlings to establish among native perennial grasses was investigated experimentally. The study involved three experiments where grass density was manipulated to investigate competition and facilitation between grasses and coolibah seedlings in various seasonal conditions. The aim of this chapter was to identify factors (abiotic and biotic) that may limit tree establishment in grasslands.

The findings of the previous four data chapters are summarised in chapter 6, and I discuss their implications for woody plant encroachment and savanna management. I present a state and transition model to describe common vegetation states in the study region and transitions between these states based on the findings from my thesis. Finally, I make management recommendations and suggest future research directions.

**Chapter Two. Densely regenerating coolibah (*Eucalyptus coolabah*) woodlands are more species-rich than surrounding derived grasslands in floodplains of eastern Australia**



**STATEMENT OF AUTHORS' CONTRIBUTION**

We, the PhD candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated in the *Statement of Originality*.

	<b>Author's Name (please print clearly)</b>	<b>% of contribution</b>
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Tables and figures	23 – 29
Text	16 – 33

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**Chapter Three. Dense regeneration of coolibah: degraded novel state or passive restoration of an endangered woodland community?**



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Tables and figures	41, 43, 45, 47 –49, 51
Text	36 –55

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**Chapter Four. Eucalypt floodplain woodlands have structural characteristics of a patch-dynamic system**



Source: Google Earth 2012

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Tables and figures	64, 68 – 72
Text	58 – 77

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**Chapter Five. Tree establishment in floodplain savannas: seasonal changes in plant–plant interactions**



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Tables and figures	93-95, 97-102
Text	80 – 108

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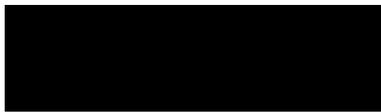
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## Chapter six. Conclusions and synthesis



**Introduction**

This thesis explores the population and community dynamics of coolibah woodlands in semi-arid floodplains of eastern Australia. In the first part of the thesis I compared soil and groundstorey species composition and richness among vegetation states to determine what effects dense regeneration has on plant biodiversity and soil function and to investigate the potential trajectory of dense regeneration towards the remnant woodland state. In the second part of the thesis I investigated landscape scale woodland dynamics and the stability of tree–grass coexistence by measuring differences in stand structure between dense regeneration and remnant woodlands and by measuring the recruitment requirements of coolibah and the ability of grasses to limit recruitment.

In Australia, there is a lack of empirical data about the structural and community dynamics of eucalypt woodlands in general and coolibah woodlands in particular (Yates and Hobbs 1997a; Freudenberger 1998; Fox *et al.* 2004; Dorrough and Moxham 2005; George *et al.* 2005; Clarke *et al.* 2010; Colloff and Baldwin 2010). Coolibah woodlands are protected under state and federal law, yet dense regeneration of coolibah is listed as an ‘invasive native species’ and can be legally cleared under certain conditions. The listing of coolibah as invasive native scrub was based the assumption that dense regeneration of coolibah reduces groundstorey plant diversity and on the perception that dense regeneration poses a threat to the endangered coolibah woodland community (NSW DNR 2006). These assumptions are largely based on studies of woody plant encroachment in other systems. There have been no attempts to test these assumptions in coolibah woodlands or to understand the processes governing woody plant abundance in these systems. This thesis aimed to fill these knowledge gaps to inform management and policy decisions pertaining to coolibah woodlands and potentially other floodplain woodlands dominated by eucalypt species with similar recruitment patterns (such as *E. camaldulensis* and *E. largiflorens*) throughout the Murray–Darling Basin.

In this chapter, I discuss the key findings of my thesis in the context of ecological theory. I then integrate these findings into a state and transition framework describing key characteristics of

vegetation states in the study region along with potential processes leading to transitions between states. Finally, I discuss the management and policy implications of my study and suggest future research questions and tests of the hypotheses proposed in the thesis.

### **Key findings**

In chapters 2 and 3, I investigated the effects of dense regeneration of coolibah on groundstorey plant community richness, composition, groundstorey biomass and soil properties in relation to alternative vegetation states. A review by Eldridge *et al.* (2011) demonstrated that increased woody plant abundance does not always result in loss of biodiversity or ecosystem function and these two chapters were aimed at measuring potential impacts of dense regeneration as well as investigating the relative contributions of different vegetation states to biodiversity conservation and restoration in the study region.

These two chapters described some key aspects of plant community dynamics in the study system. My findings indicated that dense regeneration is not associated with a loss of plant biodiversity, and that dense regeneration is compositionally and functionally similar to remnant woodlands and could be important for biodiversity conservation and landscape restoration in the study region. I found that:

1. Dense regeneration patches contain more groundstorey plant species (per 400 m<sup>2</sup>) than adjacent open areas (chapter 2);
2. Groundstorey plant communities are not strongly linked to overstorey tree density and most species are common in open grasslands and wooded states irrespective of tree density (chapter 3);
3. Dense regeneration contains a few woodland associated species that are not common in open vegetation (chapter 3), and
4. Soil C:N is similar in dense regeneration and remnant woodlands and higher than in grasslands, indicating that some aspects of nutrient cycling processes in the wooded states are functionally similar compared with open grasslands where litter accumulation is low and decomposition occurs rapidly (chapter 3).

In chapter 4, I investigated the population biology of coolibah trees by comparing tree size frequency distributions and tree spacing in dense regeneration and remnant woodlands. I described the patterns observed in the current structure of remnant woodlands and dense regeneration patches and inferred potential processes responsible for these patterns. I hypothesised that dense patches of coolibah may replace remnant stands, consistent with the patch-dynamics model, that is thought to explain woody plant dynamics in the Kalahari desert (Wiegand *et al.* 2006).

Four lines of evidence in chapter 4 suggest that dense regeneration could occur as part of a patch-dynamic system:

1. Remnant woodlands tend to be dominated by just one or two size-classes of trees indicating that they may be the result of episodic regeneration in the past;
2. Remnant woodlands do not contain trees in smaller size-classes indicating that they are an aging population with few or no young trees to replace them in the future;
3. When the mean biomass of all stands of trees, remnant woodlands and dense regeneration, were plotted against tree density, the slope of the relationship was close to  $-1.5$  indicating that self-thinning of even-aged stands may have led to the current structure of both remnants and dense stands, and
4. Tree size was positively correlated with distance between trees. Hence, the spacing of trees within stands may be due to competitive interactions and self-thinning.

This was the evidence presented in chapter 4, but there may be alternative explanations for each. For example, the lack of recruitment in remnant woodlands does not mean that there will be no recruitment in the future. These woodlands may not require frequent recruitment to ensure their persistence in the landscape. The same pattern may also be explained by grazing by livestock, which has been shown to prevent eucalypt recruitment in other woodlands, or perhaps by a lack of fire, which might stimulate recruitment (Dorrough and Moxham 2005; Vesk and Dorrough 2006). However, dense regeneration of coolibah occurred on both set-stocked and intermittently grazed land (chapter 3) and fire did not precede the 1970s recruitment event, which suggests that these are not factors limiting recruitment. Dense regeneration did occur where large tree density was low, so

I hypothesise that recruitment does not occur within woodlands due to competition from mature trees or microsite requirements. These hypotheses require further testing.

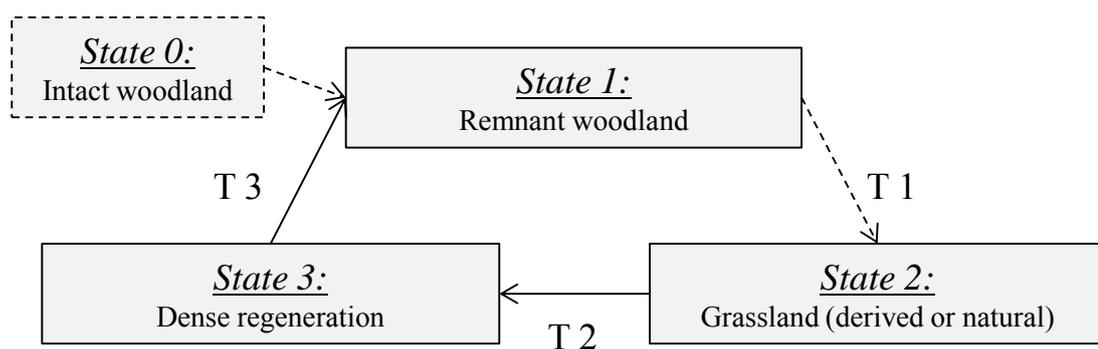
Despite the inferential nature of this study, the evidence, when considered together, provides some support for the hypothesis that coolibah woodlands are a patch-dynamic system in which dense regeneration occurs as patches in the landscape, eventually replacing aging remnant woodland stands. Therefore, clearing patches of dense regeneration, effectively the only regeneration in the landscape, may jeopardise the persistence of coolibah in this floodplain environment.

Chapter 5 described a series of experiments testing the effects of grass competition and season on coolibah recruitment success. This study was developed to investigate some of the climatic and competitive factors that might limit coolibah establishment in grasslands and to investigate changes in plant–plant interactions along a temporal stress gradient. In some savanna and semi-arid woodlands grasses are thought to limit woody plant establishment by outcompeting tree seedlings and this has been cited as a possible mechanism for tree–grass coexistence in savannas (van Vegten 1983; Scholes and Archer 1997; Van Auken 2000; Briggs *et al.* 2005).

Contrary to these studies, I found that hot and dry conditions following germination were more limiting to seedling survival and growth than grass competition. In cooler months, when seedling survival was not completely prevented by abiotic stress, grasses tended to facilitate seedling survival by ameliorating abiotic stressors and protecting seedlings from herbivory. These results indicate that coolibah establishment in grassy, open areas of the landscape is reliant on favourable climatic conditions as well as facilitation from grasses, and not release from herbaceous competition. Grass competition with woody seedlings and increased grazing pressure that reduces grass biomass is often cited as a potential explanation for woody encroachment in savannas (van Vegten 1983; Bennett 1994; Van Auken 2000; Briggs *et al.* 2005). I found that facilitation from grass may be vital for tree seedling establishment in this semi-arid floodplain system. Competition may still be important for regulating tree seedling recruitment in more mesic environments.

### A state and transition model for coolibah floodplain savannas

State and transition models were designed as an alternative to Clementsian and other specific succession models as a framework for describing the dynamic nature of rangeland vegetation, particularly systems characterised by multiple stable states (Westoby *et al.* 1989; Bestelmeyer *et al.* 2003; Stringham *et al.* 2003). They have become a popular tool among land managers and government agencies because they specify the conditions necessary for a shift from one vegetation state to an alternative state, which means that management opportunities and hazards can be identified. There are many different approaches to state and transition modelling (e.g. Westoby *et al.* 1989; Yates and Hobbs 1997b; Beisner *et al.* 2003; Bestelmeyer *et al.* 2003; Briske *et al.* 2005; Bashari *et al.* 2009). Here, I simply use the framework to organise my findings in a logical manner. I am not suggesting that any of the states below are stable (i.e. they are not sustained by feedbacks and need not cross a threshold in order to transition between states) and a continuum of intermediate states may exist between the three mentioned below. In floodplains in the study region dominated or formerly dominated by coolibah woodlands, the three states, along with the transitions between them, are of primary concern because they are the most common in the landscape, are distinct from one another structurally, and transitions between the states are abrupt and irreversible (without significant intervention) at management time scales.



**Figure 34. A state and transition (T) model of coolibah woodland dynamics in the northern riverine plains of New South Wales. States and transitions are expanded in the text.**

*Description of states:**State 0: Intact woodland*

This state does not exist anymore, within the study area, but I have included it because it is important to note that significant alterations have occurred to the whole of the landscape and what is left is a series of altered vegetation states. There is no way to know what the structure or composition of coolibah woodlands might have been prior to widespread ringbarking, clearing and sheep and cattle grazing. It has been suggested that there might have been a higher abundance of palatable chenopods, which have been replaced by grasses and unpalatable chenopods due to overgrazing of NSW floodplains (Moore 1953; Benson 1991).

*State 1: Remnant woodland*

Structure: Woodlands dominated by mature coolibah trees (DBH  $\geq$  20 cm). Tree density is generally around 20 trees ha<sup>-1</sup> to a maximum of 45 trees ha<sup>-1</sup>, but most stands have been ringbarked to some extent in the past. There are very few, if any, trees below 20 cm DBH indicating that recruitment in woodlands is rare (chapter 4).

Composition: Groundstorey vegetation is dominated by grasses, forbs and low shrubs. The dominant grasses are *Paspalidium jubiflorum*, *Sporobolus mitchellii* and *Enteropogon acicularis*. The dominant forbs are *Einadia nutans* subsp. *nutans* and *Sida trichopoda* (chapter 3).

Status: Remnant coolibah woodlands are rare in the landscape as most have been thinned or cleared. Most woodlands are grazed by livestock either continuously or intermittently. Due to ongoing threats to the groundstorey (grazing) and overstorey (clearing), coolibah woodlands are listed as an endangered ecological community both in NSW and federally (NSW Scientific Committee 2004;2009; EPBC Act 1999).

*State 2. Grassland (derived or natural)*

Structure: Grasslands dominated by native perennial C<sub>4</sub> grasses with scattered large coolibah trees (0 – 5 ha<sup>-1</sup>). Standing biomass of herbaceous vegetation can be high (>400 g m<sup>-2</sup>), when rainfall is high and grazing intensity is low (as in the grasslands used in the competition experiment in chapter 5). During droughts, biomass can be low, especially when grazing pressure is high (as in some of the degraded grasslands sampled in chapter 3).

Composition: Depending on grazing regime and rainfall, these grasslands are usually dominated by grasses such as *Panicum* spp., *Enteropogon acicularis*, *Astrebla* spp., *Eriochloa pseudoacrotricha*, along with forbs such as *Oxalis perenans* and *Solanum esuriale* (chapter 3). Grasslands can become dominated by *Sclerolaena muricata* if overgrazed or cultivated (Orr 1975).

Status: Native grasslands, especially those dominated by *Astrebla* spp., are relatively uncommon due to their conversion to cropping land and as such these grasslands are a listed endangered ecological community (EPBC Act 1999). Other, more common grasslands in the region are dominated by *Panicum* spp. and *Enteropogon* spp. and may be derived from the woodland state through tree removal (chapters 3 and 4).

*State 3: Dense regeneration*

Structure: Dense regeneration patches consist of woodlands dominated by small coolibah trees (<20 cm DBH). The density of trees may depend on the age of the stand, but most stands in the northern riverine plains of NSW regenerated following 1970s flooding (Freudenberger 1998) and contain between 1000 and 4000 trees ha<sup>-1</sup> (chapters 3 and 4). Groundstorey vegetation is sparse, generally lower than 20% cover, but litter cover is high, usually more than 50% (chapters 2 and 3).

Composition: Dense regeneration patches contain groundstorey vegetation the composition of which is similar to remnant woodlands, but this may depend on grazing intensity and rainfall. *Paspalidium jubiflorum* is the most common groundstorey species along with other native grasses and forbs which make up the bulk of species richness. Species richness is variable and depends on

the scale of sampling and rainfall: in chapter 2 we recorded between 20 and 30 groundstorey species per 400 m<sup>2</sup> whereas in chapter 3 we found around ten species per 16 m<sup>2</sup> and around 20 species per site (when all quadrats were pooled). Field sampling for chapter 2 followed above-average rainfall whereas field sampling for chapter 3 followed a low rainfall spring/summer.

Status: Dense regeneration of coolibah can be cleared under certain circumstances in NSW (DECCW 2011). Areas of coolibah regeneration are not common or widespread throughout the Darling Riverine Plains region (from my extensive observations) and will become rarer if clearing of dense regeneration is permitted.

*Description of transitions:*

*Transition 1 (Woodland → Grassland)*

This transition involves the death of trees either gradually (through self-thinning; chapter 4) but most likely episodically (due to drought or mechanical clearing; Fensham and Fairfax 2007; Keith *et al.* 2009). Episodic tree death due to drought is thought to be common among semi-arid eucalypts and has been reported in similar systems in Qld (Fensham and Fairfax 2007; Fensham *et al.* 2009). This may have resulted in open grassy patches throughout the landscape. The most common cause of tree death in recent years is clearing to increase pasture production or for cropping, so the area of remnant woodlands in the study region has decreased markedly (Keith *et al.* 2009).

*Transition 2 (Grassland → Dense regeneration)*

This transition requires the germination and establishment of coolibah trees at high density in areas of low tree abundance (grassland; chapter 4). Several conditions must be met for this to happen and this is potentially why dense regeneration is not widespread in the landscape (personal observation) and has only occurred a few times in the past century (Maher 1995; Roberts and Marston 2000). The following is a list of conditions required for successful establishment of coolibah trees:

1. A flood or local inundation (Freudenberger 1998);

2. Viable seed which is most likely stored in the canopy and is not long-lived once shed from fruit (Doran and Boland 1984);
3. Soil surface temperatures around 35°C for optimal germination (Doran and Boland 1984);
4. Mild temperatures in the months following germination (<30°C; chapter 5);
5. Regular rainfall in the first few months following germination (however, saturated soil following flood recession may be adequate; chapter 5);
6. Protection from direct sunlight and amelioration of temperature extremes, either from grasses or some other source of shade (chapter 5), and
7. Protection from herbivory, for example, grasses shielding seedlings from herbivores (chapter 5).

*Transition 3 (Dense regeneration → Woodland)*

I propose that the transition from dense regeneration to more open woodland dominated by larger trees is possible through self-thinning. Thinning occurs due to competition between neighbouring trees which leads to the death of competitively inferior trees. I cannot be sure that self-thinning of dense regeneration leads to a state that is similar to the remnant woodland structure, but there is some evidence that the structure of remnant woodlands today is the result of episodic recruitment and subsequent self-thinning in the past (chapter 4). This suggests that dense regeneration patches could become much less dense, given adequate time to self-thin. Therefore, all that may be required for this transition to occur is time, but drought might speed up the process.

**Management implications**

My findings should initiate a reassessment of the current selective clearing laws in NSW since I have found no evidence that dense regeneration of coolibah has negative effects on biodiversity other than a reduction in groundstorey biomass and the same could be true of other species on the invasive native species list. Indeed, dense regeneration patches are not compositionally different to surrounding vegetation and can be more species-rich than adjacent open areas. Further, evidence presented in this thesis suggests that dense episodic regeneration could be an important part of

landscape-scale woodland dynamics and may replace and resemble remnant woodlands in the future. Dense regeneration is rare in space and time and is valuable habitat for native flora and fauna in a heavily cleared landscape. In conclusion, I recommend that dense regeneration should be completely protected from clearing and delisted as an invasive native species to ensure the persistence of coolibah woodlands in the Darling Riverine Plains of NSW.

### **Future research questions**

This thesis is one of the first attempts to understand the dynamics of coolibah woodlands so there are still many questions that need to be answered. My state and transition model can be used as a hypothesis-generating framework. For example, experimental testing of the patch-dynamics model is needed. The patch-dynamics model predicts that recruitment will not occur within woodland patches due to inhibition from mature trees and as such patchy dense recruitment in open areas is required for woodland persistence in the landscape. This could be tested by transplanting seedlings at different distances from mature trees and following their success over a number of years. Alternatively, eucalypt litter could be a physical barrier preventing seed germination (Facelli and Ladd 1996) and this could be tested in controlled glasshouse germination experiments. Landscape-scale assessment of woodland distribution, as well as determination of the spatial arrangement of trees in the landscape (clumped, random or regular) could help to further understand the dynamics of coolibah woodlands. The effects of fire and flooding on woodland dynamics should also be considered since it is probable that both have been substantially altered since European occupation.

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## Appendices

### Appendix 1. Two-way ANOVA results for soil attributes in dense regeneration and grassland plots at three sites.

Significant results are bold ( $P < 0.05$ ). MS = Mean Squares.

Factor	Source	df	MS	F	P
Total C	Vegetation state	1	0.21	7.4	<b>0.009</b>
	Site	2	0.09	3.4	<b>0.043</b>
	Site × Vegetation state	2	0.14	4.9	<b>0.012</b>
	Error	42	0.03		
Total N	Vegetation state	1	0	0.2	0.616
	Site	2	0.01	8.9	<b>0.001</b>
	Site × Vegetation state	2	0.01	6.9	<b>0.002</b>
	Error	42	0.001		
C:N ratio	Vegetation state	1	51.33	31.9	<b>&lt;0.001</b>
	Site	2	17.31	10.8	<b>&lt;0.001</b>
	Site × Vegetation state	2	0.26	0.2	0.853
	Error	42	1.61		
pH	Vegetation state	1	0.01	5.6	<b>0.022</b>
	Site	2	0.01	6.4	<b>0.004</b>
	Site × Vegetation state	2	0.01	2.9	0.063
	Error	42	0.002		
ECEC	Vegetation state	1	64.91	2.2	0.147
	Site	2	65.67	2.2	0.122
	Site × Vegetation state	2	195.38	6.6	<b>0.003</b>
	Error	42	29.67		
Ca (cmol kg <sup>-2</sup> )	Vegetation state	1	32.38	6.0	0.13
	Site	2	81.63	2.4	<b>0.005</b>
	Site × Vegetation state	2	81.96	6.0	<b>0.005</b>
	Error	42	13.58		
Mg (cmol kg <sup>-2</sup> )	Vegetation state	1	13.1	3.9	0.055
	Site	2	70.18	20.8	<b>&lt;0.001</b>
	Site × Vegetation state	2	20.54	6.1	<b>0.005</b>
	Error	42	3.37		
K (cmol kg <sup>-2</sup> )	Vegetation state	1	0.27	2.4	0.126
	Site	2	0.01	0.1	0.903
	Site × Vegetation state	2	0.18	1.6	0.204
	Error	42	0.11		
Na (cmol kg <sup>-2</sup> )	Vegetation state	1	0.55	22.3	<b>&lt;0.001</b>
	Site	2	0.3	12.1	<b>&lt;0.001</b>
	Site × Vegetation state	2	0.07	3.0	0.059
	Error	42	0.02		
Al (cmol kg <sup>-2</sup> )	Vegetation state	1	0.00	0.4	0.519
	Site	2	0.00	2.9	0.068
	Site × Vegetation state	2	0.00	1.5	0.244
	Error	42	0.00		
Ca:Mg	Vegetation state	1	0.05	0.8	0.379
	Site	2	6.51	95.9	<b>&lt;0.001</b>
	Site × Vegetation state	2	0.01	0.2	0.798
	Error	42	0.07		

**Appendix 2. Two way ANOVA results for vegetation attributes of dense regeneration and grassland plots at three sites.**

Significant results are bold ( $P < 0.05$ ). MS = Mean Squares.

<b>Factor</b>	<b>Source</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>P</b>
Species richness	Vegetation state	1	294.7	20.5	<b>&lt;0.001</b>
	Site	2	271.5	18.9	<b>&lt;0.001</b>
	Site × Vegetation state	2	13.6	0.9	0.395
	Error	42	14.4		
Species diversity	Vegetation state	1	14.5	94.6	<b>&lt;0.001</b>
	Site	2	6.3	41.1	<b>&lt;0.001</b>
	Site × Vegetation state	2	1.9	12.4	<b>&lt;0.001</b>
	Error	42	0.1		
Standing biomass	Vegetation state	1	12.3	63.7	<b>&lt;0.001</b>
	Site	2	0.2	1.4	0.256
	Site × Vegetation state	2	0.7	3.5	<b>0.038</b>
	Error	42	0.2		
Groundstory vegetation cover	Vegetation state	1	8.2	131.8	<b>&lt;0.001</b>
	Site	2	0.3	4.6	<b>0.002</b>
	Site × Vegetation state	2	0.1	1.5	0.241
	Error	42	0.1		
Bare ground	Vegetation state	1	125.1	0.8	0.377
	Site	2	4241.6	26.8	<b>&lt;0.001</b>
	Site × Vegetation state	2	586.1	3.7	<b>0.017</b>
	Error	42	158.0		
Litter	Vegetation state	1	1.3	15.4	<b>&lt;0.001</b>
	Site	2	16.5	197.9	<b>&lt;0.001</b>
	Site × Vegetation state	2	1.7	21.0	<b>&lt;0.001</b>
	Error	42	0.1		
Forb cover	Vegetation state	1	0.3	7.8	<b>0.008</b>
	Site	2	0.6	15.2	<b>&lt;0.001</b>
	Site × Vegetation state	2	0.5	14.9	<b>&lt;0.001</b>
	Error	42	0.1		
Graminoid cover	Vegetation state	1	1.3	58.7	<b>&lt;0.001</b>
	Site	2	1.0	46.8	<b>&lt;0.001</b>
	Site × Vegetation state	2	1.0	46.1	<b>&lt;0.001</b>
	Error	42	0.1		
Low shrub cover	Vegetation state	1	0.9	47.9	<b>&lt;0.001</b>
	Site	2	1.1	54.3	<b>&lt;0.001</b>
	Site × Vegetation state	2	0.6	27.1	<b>&lt;0.001</b>
	Error	42	0.1		
<i>S. muricata</i> cover	Vegetation state	1	0.4	19.2	<b>&lt;0.001</b>
	Site	2	0.6	27.0	<b>&lt;0.001</b>
	Site × Vegetation state	2	0.2	8.1	<b>0.001</b>
	Error	42	0.1		

### Appendix 3. Nested ANOVA table for soil variables.

Significant results are bold ( $P < 0.05$ ). MS = Mean Squares

Factor	Source	df	MS	F	P
Total C	Vegetation state	3	1.8	1.1	0.380
	Site (Vegetation state)	15	1.6	25.4	<b>&lt;0.001</b>
	Error	76	0.1		
Total N	Vegetation state	3	0.1	0.4	0.738
	Site (Vegetation state)	15	0.3	31.8	<b>&lt;0.001</b>
	Error	76	0.1		
C:N ratio	Vegetation state	3	51.8	34.8	<b>&lt;0.001</b>
	Site (Vegetation state)	15	1.5	1.8	<b>0.043</b>
	Error	76	0.8		
pH	Vegetation state	3	1.5	1.7	0.213
	Site (Vegetation state)	15	0.9	19.3	<b>&lt;0.001</b>
	Error	76	0.1		
ECEC	Vegetation state	3	390.1	3.1	0.063
	Site (Vegetation state)	15	129.7	5.2	<b>&lt;0.001</b>
	Error	76	25.1		
Ca (cmol kg <sup>-2</sup> )	Vegetation state	3	129.8	1.8	0.181
	Site (Vegetation state)	15	70.2	6.4	<b>&lt;0.001</b>
	Error	76	10.9		
Mg (cmol kg <sup>-2</sup> )	Vegetation state	3	65.5	3.7	<b>0.034</b>
	Site (Vegetation state)	15	17.4	6.7	<b>&lt;0.001</b>
	Error	76	2.6		
K (cmol kg <sup>-2</sup> )	Vegetation state	3	0.5	1.2	0.351
	Site (Vegetation state)	15	0.5	8.3	<b>&lt;0.001</b>
	Error	76	0.1		
Na (cmol kg <sup>-2</sup> )	Vegetation state	3	0.4	1.3	0.298
	Site (Vegetation state)	15	0.3	7.5	<b>&lt;0.001</b>
	Error	76	0.1		
Al (cmol kg <sup>-2</sup> )	Vegetation state	3	0.002	8.7	<b>0.001</b>
	Site (Vegetation state)	15	0.001	2.5	<b>0.004</b>
	Error	76	0.001		
Ca:Mg	Vegetation state	3	0.4	0.5	<b>0.709</b>
	Site (Vegetation state)	15	0.9	38.6	<b>&lt;0.001</b>
	Error	76	0.1		

### Appendix 4. Nested ANOVA table for floristic variables

Significant results are bold ( $P < 0.05$ ). MS = Mean Squares

Factor	Source	df	MS	F	P
Groundstorey biomass (g m <sup>-2</sup> )	Vegetation state	3	16.3	18.2	<b>&lt;0.001</b>
	Site (Vegetation state)	15	0.9	6.4	<b>&lt;0.001</b>
	Error	76	0.1		
Groundstorey vegetation cover	Vegetation state	3	6883	5.1	<b>0.012</b>
	Site (Vegetation state)	15	1336	21.8	<b>&lt;0.001</b>
	Error	76	61.4		
Species richness	Vegetation state	3	149.3	1.1	0.387
	Site (Vegetation state)	15	138.2	23.6	<b>&lt;0.001</b>
	Error	76	5.9		

**Appendix 5. Two-way ANOVA results for light and root competition effects on seedling growth.**

Significant results are bold ( $P < 0.05$ ). MS = Mean Squares.

<b>Factor</b>	<b>Source</b>	<b>df</b>	<b>MS</b>	<b>F</b>	<b>P</b>
First 3 months	Light	1	349.2	1.55	0.215
	Root competition	1	110.2	0.49	0.485
	Light × Root competition	1	349.7	1.55	0.215
	Error	110	224.9		
Species richness	Light	1	45.5	0.01	0.931
	Root competition	1	41004.7	6.78	<b>0.014</b>
	Light × Root competition	1	3571.4	0.59	0.448
	Error	110	6051.4		