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The fire ecology of *Callitris intratropica*:  
Tracing the legacy of Aboriginal fire  
management to inform contemporary  
responses to a conservation crisis on the  
Arnhem Plateau, northern Australia

by  
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Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy  
University of Tasmania <Month, year of submission>

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## DISSERTATION ABSTRACT

The decline of Northern Cypress Pine (*Callitris intratropica*) throughout the tropical savannas of northern Australia has become an iconic example of the ecosystem-wide effects of destructive fire regimes. The persistence of *C. intratropica*, a conspicuous, long-lived, obligate-seeding conifer with limited fire-tolerance, in one of the world's most fire-prone ecosystems is ecologically puzzling. An appealing hypothesis is that habitat mosaics created by Aboriginal burning maintained enough long unburnt patches throughout the landscape for fire-sensitive plant species like *C. intratropica* to successfully recruit. However, widespread depopulation of Aboriginal lands within the past century across much of northern Australia has resulted in the shift from small-scale patch burning to landscape-scale wildfires. On the Arnhem Plateau, this change in fire pattern is widely blamed for current declines in *C. intratropica* as well as other species, notably native mammals and granivorous birds, which were able to persist for more than 50,000 years of continuous Aboriginal occupation. Within the last several years, in an attempt to simulate Aboriginal fire regimes, contemporary managers across much of the Arnhem Plateau have implemented programs consisting of frequent burning, largely from helicopters, in the early dry season when higher fuel moisture and cooler temperatures result in smaller, patchier fires. However, continued and dramatic species declines, especially in the World Heritage listed Kakadu National Park, urgently signals the need for some means by which to better direct and monitor current strategies. If, as the above hypothesis implies, the presence of *C. intratropica* in Australian savannas is a relict of past fire regimes, then maintaining the species in the landscape may provide a powerful benchmark for evaluating contemporary management and conservation efforts. Therefore, this research examines the utility of *C. intratropica* as a proactive indicator

both of ecologically beneficial fire regimes and critical habitat for other fire-sensitive species by addressing four key components:

- 1) Exploring the role of human management in driving habitat heterogeneity in flammable ecosystems worldwide using fire simulations and the spatial scale of *C. intratropica* grove occurrence as a case study
- 2) Patch-level assessment of the interaction between *C. intratropica* groves and savanna fires and its implication for vegetation heterogeneity and diversity
- 3) Population modelling of *C. intratropica* to understand the role of patch dynamics in driving population stability under prevailing and hypothetical fire regimes
- 4) Landscape-scale survey of *C. intratropica* grove condition to examine patterns of habitat heterogeneity and plant diversity across differing management regimes in Kakadu National Park (KNP) and central Arnhem Land (CAL)

The results demonstrated that under low-intensity fire regimes, fire exclusion by *C. intratropica* groves effectively creates small-scale fire refugia, which have implications for both the persistence of *C. intratropica* populations as well as increasing the heterogeneity, diversity, and structural complexity of savanna vegetation. Disturbance and population models further implicated human intervention – specifically via the reduction of high intensity fires – in maintaining conditions that favour the establishment and persistence of *C. intratropica*, despite high fire frequencies in this savanna. Better overall *C. intratropica* grove condition in CAL provided evidence that continued Aboriginal fire management – and possibly the presence of feral water buffalo – supports greater savanna heterogeneity and diversity than in neighboring KNP.

## INTRODUCTION: Shifting perspectives on *Callitris intratropica*

Can an indicator of northern Australia's ecological history provide a look forwards?



Low intensity surface fire set by Joshua and Rahab Roston, Traditional Owners at Dukladjarranj, an Aboriginal estate in central Arnhem Land

### Background

Fire is an integral component of savanna ecology; however, changing patterns of fire activity in tropical savannas worldwide have serious implications for carbon emissions, local livelihoods, species diversity and overall ecological integrity (Rackham 2008, Butz 2009, Romme et al. 2009, Russell-Smith et al. 2009). The crucial question for management and conservation is how to maintain fire regimes that sustain biological diversity. In northern Australia, there is good evidence that around 50,000 years of Aboriginal fire management has created an utterly unique biological heritage. This is well illustrated by the long record of Aboriginal occupation on the Arnhem Plateau

(Roberts et al. 1994), a regional centre of vertebrate and plant endemism. Sadly, declines in flora and fauna have recently signalled the need for proactive management on the Plateau. These declines are widely interpreted as a direct result of the abandonment of ancestral Aboriginal lands over the past century as family groups have relocated to permanent settlements along the fringes of the region (Bowman et al. 2001, Russell-Smith et al. 2003). The consequence of this depopulation has been a shift in fire regimes from intentional, small-scale patch burning towards landscape-scale wildfires. While the causal relationships are not fully understood, homogenization of habitat patches due to large and intense burns may be a key driver of changes in species composition. Therefore understanding whether and how Aboriginal patterns of burning contributed to habitat heterogeneity provides a critical baseline for land managers attempting to reconfigure current fire regimes on the vast and largely uninhabited Arnhem Plateau. Unfortunately, destructive fires still prevail (Edwards and Russell-Smith 2009) and researchers have yet to determine reliable indicators of management success.



The 'Escarpment' - the western edge of the Arnhem Plateau in Kakadu National Park.





Rangers set a prescribed fire at the start of the early dry season in the lowlands of Kakadu National Park, Australia

In response to the ecological and cultural degradation wrought by uncontrolled wildfires on the Arnhem Plateau, the Western Arnhem Land Fire Abatement Project (WALFA) and Kakadu National Park's (KNP) Stone Country burning program have recently been established in collaboration with Aboriginal landowners (Petty et al. 2007, Russell-Smith et al. 2009). The approach of both programs is to set fires on the ground and from helicopters early in the dry season when higher moisture and favourable winds result in smaller, patchy burns (Price et al. 2003). The objective of these burns is to break up available fuel loads and minimize the extent of destructive, late dry season wildfires. On a landscape scale, managers use burns to link topographic features such as rivers and gorges in a network of firebreaks so that late season fires can at least be contained (Price et al. 2007, Pickworth 2008). Yet with current management on the plateau

ranging widely from small-scale “country cleaning” on Aboriginal outstations (Yibarbuk et al. 2001) to systematic aerial burns across the landscape, the variability of ecological outcomes among different strategies is, arguably, poorly understood. Moreover, given the sheer size of the Arnhem Plateau and the relative scarcity of management resources, there is an urgent need to identify ecological features that can aid in prioritizing management efforts and provide some measure of success (Edwards and Russell-Smith 2009).

### **Callitris intratropica and fire**

*Callitris* is a genus of 15-19 species of tree and shrubs, depending on the treatment, in the Cypress family (Cupressaceae) found only in Australia and New Caledonia (Pye et al. 2003; Farjon 2005). The genus has been interpreted as Gondwanan in origin (Crisp et al. 2004) and possibly originating from an ancestral rainforest species (Farjon 2005), however, the ancestral habitat is disputed (Paull and Hill 2010). Indeed *Callitris* is currently found across a wide range of habitats in Australia, from arid zones to the monsoon tropics. The closest relatives of the genus are *Actinostrobus* (3 species), endemic to southwestern Australia, and *Neocallitropsis*, a single-species genus restricted to serpentine soils on New Caledonia. The Gondwanan and potential rainforest origins suggest that *Callitris* and related genera evolved under conditions of low fire occurrence. However, *Actinostrobus* and several species of *Callitris* have evolved fire-mediated serotinous cones. Still, contemporary ecological comparisons to the dominant eucalypt species in Australia clearly demonstrate a limited tolerance to fire among *Callitris* species in terms of survival and, especially, the highly limited ability of *Callitris* to resprout after burning and dependence on reproduction by seed (Bradstock and Cohn 2002; Bowman and Panton 2003; Prior et al. 2011).



Aboriginal landowners have long known the Northern Cypress Pine, *Callitris intratropica*, to be an indicator of fire regime change on the Arnhem Plateau (Haynes 1985). *C. intratropica* is widespread across the monsoon tropics of northern Australia. Bowman and Panton (1993) outline the characteristics of the species that essentially provide a window into the ecological history of Australia's tropical savannas. In brief, *C. intratropica* is a widely distributed, fire-sensitive conifer with a life history (c. 250 yrs) long enough to span the shift from Aboriginal occupation and management of the Arnhem Plateau (and elsewhere) to contemporary patterns of unmanaged wildfires. Whereas the common occurrence of *C. intratropica* among rainforest patches and rocky outcrops illustrates its limited tolerance of fire, the species' presence in open, highly fire-prone savanna vegetation remains a puzzle. Although repeated low-intensity burns do not harm adult trees (Russell-Smith 2006; Lawes et al. 2011), hot fires may result in severe canopy damage and eventual mortality (Figure 1). The advantage of *C. intratropica*'s biology is that dead snags remain in the landscape due to its termite-resistant wood and their overabundance stands as evidence of high-intensity fires. Unlike the eucalypts that dominate Australia's tropical savannas, *C. intratropica* is unable to resprout in response to fire and is wholly dependent on regeneration from seed (i.e., an obligate-seeder). Demographic studies estimate that fire-free periods of 8-10 years are necessary for *C. intratropica* seedlings to reach a size at which they can withstand even low-intensity burns (Bowman et al. 2001, Russell-Smith 2006). Thus, the occurrence of *C. intratropica* in open, fire-prone eucalypt savannas suggests that long-unburnt habitat patches are (or were) a relatively common component of the landscape (Bowman and Panton 1993, Russell-Smith et al. 1998, Bowman et al. 2001, Russell-Smith et al. 2003).



*Callitris intratropica* adult tree at Dukladjarranj, central Arnhem Land

The long fire-free period required for *C. intratropica* recruitment has been used as an argument for the “skilful manipulation of fire” by Aboriginal managers and the maintenance of unburnt habitat patches (Price and Bowman 1994). Moreover, counts of dead *C. intratropica* stems across the Arnhem Plateau indicate a decline in the species that generally coincides with the abandonment of the region by Aboriginal family groups (Bowman and Panton 1993). If contemporary unmanaged wildfires are resulting in a decline in *C. intratropica*, the logical inference, notwithstanding climate change, is that 50,000 years of fire management by Aborigines allowed for its persistence. While the degree to which Aboriginal land managers anticipated the long-term ecological consequences of fire remains a contentious issue (Russell-Smith et al. 1997, Whitehead et al. 2003), the current declines in *C. intratropica* provides some of the strongest evidence of an ecosystem-scale response to shifting fire regimes. There are clear examples of the application of traditional patch burning in mesic Australian savannas for

a variety of purposes such as manipulating food resources for game species, protecting valuable food plants, 'cleaning' vegetation to improve access, and controlling pest species (Jones 1969, Lewis 1982, Russell-Smith et al. 1997, Yibarbuk et al. 2001, Vigilante and Bowman 2004, Murphy and Bowman 2007). *Callitris intratropica* is valued for its wood and providing habitat for feral water buffalo (J. Rostron, pers. Comm.), however, the manipulation of habitat by Aborigines for the direct benefit of *C. intratropica* has not been reported. Thus its persistence in the landscape has been interpreted as an ecological relict of traditional burning regimes (Bowman and Panton 1993, Bowman et al. 2001).



Thus far, the application of *C. intratropica* as an indicator of changes to fire regimes has essentially been to look “backwards” into ecological history (Bowman 2000). The deeper question of whether *C. intratropica* may be representative of broader aspects of ecosystem composition and integrity remains unanswered. The breakdown of Aboriginal patch burning is generally presumed by ecologists to be influencing the decline of multiple taxa in

Australian savannas, including granivorous birds, obligate-seeding shrubs, and, notably, small mammals (Braithwaite 1995, Russell-Smith et al. 1998, Franklin 1999, Woinarski et al. 2001, Yibarbuk et al. 2001, Woinarski and Ash 2002, Fraser et al. 2003). Two key factors implicate fire in these changes: (i) the dependency of some species on long-unburnt habitat patches (Russell-Smith et al. 1998, Bowman et al. 2001, Andersen et al. 2005) and (ii) the declining availability of long-unburnt patches under contemporary fire

regimes (Russell-Smith et al. 2003, Yates and Russell-Smith 2003, Edwards and Russell-Smith 2009). Yet given the difficulties in tracking the cumulative effects of repeated fires, causal evidence of species' responses to different fire regimes is arguably weak (Bradstock et al. 2005). The ecology and longevity of *C. intratropica*, however, may provide a metric by which patch burning and the distributions of other plant and animal species can be related. By using healthy and fire-damaged *C. intratropica* populations to differentiate the legacies of burning among landscape patches, the effects of fire history on species composition can be further clarified. For example, on the Arnhem Plateau, traditionally managed Aboriginal estates support high overall species diversity despite declines elsewhere (Yibarbuk et al. 2001), indicating the benefits of patchy fires. However, no research has examined the possible associations between *C. intratropica* and other taxa. From a management perspective, the use of *C. intratropica* as a surrogate for species diversity may greatly aid in prioritizing conservation efforts in a landscape as large, complex and remote as the Arnhem Plateau.



The “Stone Country” of the Arnhem Plateau. Deeply dissected canyons provide refugia from fire for fire-sensitive vegetation such as rain forest, heaths, and *Callitris intratropica*.

### **Study Site**

The Arnhem Plateau is an ancient sandstone tableland rising 300-400 m above the tropical lowland savannas of northern Australia (Figure 2). Also known locally as the “Stone Country”, the plateau is vast, rugged and remote, covering over 30,000 km<sup>2</sup> from the eastern portion of Kakadu National Park eastwards into central Arnhem Land. The plateau’s geological stability and extremely dissected topography has resulted in the highest rates of endemism for both plants and vertebrates in the Northern Territory (Freeland et al. 1988, Woinarski et al. 2006). The region is dominated by mesic savanna with annual rainfall (c. 1500 mm) driven by the Asian monsoon, with 90% of precipitation.

Although fire is a pervasive ecological disturbance in all savannas, the greater primary

productivity of mesic supports more frequent and intense fires and more continuous fuel beds may decrease the spatial heterogeneity of fire events relative to more arid savannas (Bond and Keeley 2005). Fire – and fire management – therefore plays a stronger role in shaping the ecology of mesic savannas, whereas rainfall may be more critical in arid savannas. With annual, abundant, and highly seasonal monsoon rainfall across northern Australia, the dominant eucalypt-grassland savannas of the Arnhem Plateau experience frequent and widespread seasonal bushfires, often with very short fire return times of 1–3 years (Gill et al. 2000, Russell-Smith et al. 2003). The Plateau's rugged landscape, however, provides natural fire breaks which have allowed pockets of fire-sensitive, endemic sandstone heath and rainforest communities to persist (Bowman 1991, Russell-Smith et al. 1993, Russell-Smith et al. 1998). Thus, in addition to climate, the influence of fire on the vegetation of the Arnhem Plateau must be considered within the context of the heterogeneity wrought by factors such as topography and hydrology (Skarpe 1992).

Evidence suggests humans colonized the region over 50,000 years ago (Roberts et al. 1994) and the abundance of Aboriginal rock art across the plateau provides one of the longest continuous cultural records on the planet (Chaloupka 1993). Apart from a small number of Aboriginal families still managing ancestral lands on the north-eastern edge of the Plateau in Central Arnhem Land, most of the “Stone Country” has been depopulated over the past century as a result of disease, displacement, the inaccessibility of the terrain, and changing economies (Yibarbuk et al. 2001, Whitehead et al. 2003).

Consequently, fire regimes changed from patchy, low intensity burns by Aborigines manipulating resources throughout the dry season to ecologically destructive, high intensity, landscape-scale wildfires ignited mostly by lightning in the late dry season



(Bowman et al. 2001, Yibarbuk et al. 2001, Russell-Smith et al. 2003, Whitehead et al. 2003).



Burning a fire break in the early dry season using aerial incendiaries from a helicopter on the Arnhem Plateau. In remote regions of the Stone Country, rangers burn along topographic features such as ridges and rivers in an effort to contain higher intensity, late dry season fires should they ignite.

### **Project Aim**

The objective of this study is to evaluate the potential of *Callitris intratropica* as an indicator species for ecologically beneficial fire regimes on the Arnhem Plateau in northern Australia. Researchers and managers are still piecing together the ecological consequences of the shift in fire regimes from small-scale patch burning to landscape-scale wildfires after the depopulation of Aboriginal lands across the Top End.

Meanwhile, the emergent paradigm driving contemporary management on the Arnhem Plateau is “burn-early, burn-often” in an attempt to re-create Aboriginal patterns of burning and reduce the incidence and extent of hot, late dry season wildfires. Under this strategy frequent burns are set, largely from helicopters, in the early dry season (June-July) when higher fuel moisture and cooler temperatures result in smaller, patchier fires. The degree to which a burn-early, burn-often strategy actually simulates Aboriginal burning is highly debatable. However, continued and dramatic species declines, especially among small mammals in Kakadu National Park, urgently signals the need for some measure of effectiveness for a relatively novel management strategy being implemented at regional scales across the Arnhem Plateau.



Joshua, Leanna, and Rebekkia Rostron in the Stone Country at Dukladjarranj estate, central Arnhem Land



The decline of *Callitris intratropica* throughout the tropical savannas of northern Australia has become an iconic example of the ecosystem-wide effects of destructive fire regimes. If, as the hypothesis above implies, the presence of *C. intratropica* in Australian savannas is a relict of past Aboriginal fire regimes, then understanding how the species persists in the landscape may provide a powerful benchmark for evaluating contemporary management and conservation efforts. Therefore, this research examines the utility of *Callitris intratropica* as a proactive indicator both of ecologically beneficial fire regimes and critical habitat for other fire-sensitive species by addressing four key components:

- 1) Exploring the role of human management in altering habitat heterogeneity in flammable ecosystems worldwide using fire simulations and the spatial scale of *C. intratropica* grove occurrence as a case study
- 2) Patch-level assessment of the interaction between *C. intratropica* groves and savanna fires and its implication for vegetation heterogeneity and diversity
- 3) Population modelling of *C. intratropica* to understand the role of patch dynamics in driving population stability under prevailing and hypothetical fire regimes
- 4) Landscape-scale survey of *C. intratropica* grove condition to examine patterns of habitat heterogeneity and plant diversity across differing management regimes in Kakadu National Park and central Arnhem Land



Dukladjarranj base camp

### **Project Significance**

Once considered a bastion for native Australian fauna, the current and, as yet unexplained, declines in mammals and other species on the Arnhem Land Plateau urgently require further study. A variety of management approaches are currently employed on the Arnhem Land Plateau and clarifying patterns of fire heterogeneity and their relationship to the ecology of *Callitris intratropica* has immediate applications for assessing the effectiveness of these programs. Relating *C. intratropica* stand structure to the diversity and abundance of other species may shed light onto interpretations of species' responses to variation in fire heterogeneity. Moreover, although managers are already concerned with the conservation of *C. intratropica* as a landscape component on the Arnhem Plateau, this research will determine whether other species may also benefit from the protection of *C. intratropica*. Given the sheer size of the Arnhem Land Plateau and the limited resources available to manage it, there is a desperate need to identify landscape elements by which conservation and management efforts can be prioritized.



Jim Jim Falls in the wet season careens over the western edge of the Arnhem Plateau in Kakadu National Park





Joshua Rostron, Traditional Owner at Dukladjarrandj, central Arnhem Land burning country.

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Figure 1. *Callitris intratropica* commonly occurs in distinct groves within an open savanna matrix dominated here by *Eucalyptus miniata* and *E. tetradonta*. The panels to the left (a & c) show *C. intratropica* groves with intact, healthy canopies, whereas those on the right (b & d) illustrate groves with significant canopy scorching from high intensity fires.

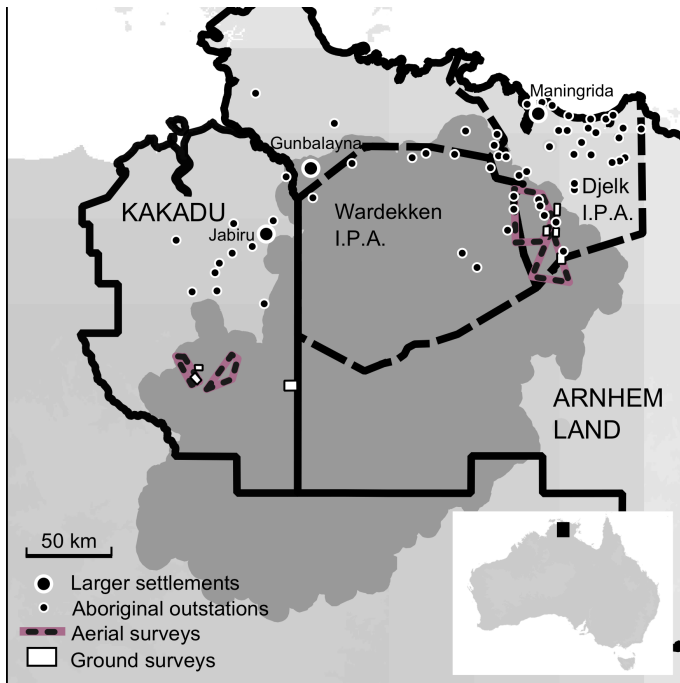


Figure 2. Research sites on the Arnhem Plateau Stone Country (shaded dark grey). Solid borders indicate Kakadu National Park and Arnhem Land and dashed borders indicate the Wardekkeren and Djelk Indigenous Protected Areas (IPAs).

## CHAPTER 2: Indigenous landscape burning creates habitat diversity

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Joshua Rostron walking with fire-stick, Dukladjarranj, central Arnhem Land

## **Abstract**

There is tension among historians and ecologists in how to interpret the impact of anthropogenic fire on the past and present composition of flammable landscapes. Some argue humans have manufactured habitat diversity, whereas others remain skeptical of the influence of anthropogenic burning. Here we examine patterns of convergence among traditional fire management systems to interpret their potential effects on pyrodiversity – landscape heterogeneity wrought by fire – in a more generalized ecological framework. We first review the objectives and global extent of indigenous and rural landscape burning, and then consider an example where the persistence of fire-sensitive vegetation in Australian savannas provides a signal of the ‘patch mosaics’ created by Aboriginal burning. Using a simple stochastic landscape simulation, we explore how anthropogenic burning can increase both spatial and temporal aspects of habitat diversity. We suggest major, shared objectives of habitat manipulation and resource protection among indigenous and contemporary fire managers provide opportunities for cultural dialogue and management innovation.

## **Introduction**

The antiquity and legacy of human influence are increasingly apparent among ‘natural’ systems worldwide (Liu et al. 2007). One of the most contentious, yet potentially significant, social-ecological interactions affecting ecosystem composition is anthropogenic fire (Pyne 1997, Bowman et al. 2011). Major ecological shifts – for instance shrub encroachment in African rangelands (Angassa and Oba 2008), forest degradation in South America (Bilbao et al. 2010), continental-scale vegetation shifts in North America and Australia (Nowacki and Abrams 2008, Gammage 2011), and the decline of multiple plant and animal taxa in Australia (Bowman and Panton 1993,

Woinarski et al. 2010) – are variously attributed to changing patterns of landscape burning associated with social-ecological change. Although the biophysical drivers of fire are well studied, improving our capacity to manage and coexist with fire requires equal consideration of how human activities have been, and remain, integrated with fire disturbance.

The difficulty in quantifying human interactions with fire is partly due to the complex relationship between fire disturbance and the composition of flammable ecosystems. Fire regimes – defined by their characteristics of intensity, frequency, extent, and spatial patterns of burning across landscapes – are driven by multiple ecological and climatic interactions (Archibald et al. 2009). The resultant spatial and temporal heterogeneity of successional habitat stages maintained by prevailing fire regimes has been coined 'pyrodiversity' (Martin and Sapsis 1992). Research on both modern (e.g. prescribed) and traditional anthropogenic burning demonstrates that human intervention can increase pyrodiversity by altering the frequency and seasonality of ignitions beyond the range of natural sources (Laris 2002, Bowman et al. 2004, Knapp and Keeley 2006, Bird et al. 2008). These activities effectively jumpstart the fire season before fuels are completely cured, thereby reducing the size and intensity of individual fire events and creating a more heterogeneous landscape of habitat 'patch mosaics'. Most attempts at quantifying the effects of anthropogenic burning examine these visible patterns in vegetation. However, the invisibility of historical patterns of fire and its legacy effects on vegetation make pyrodiversity inherently difficult to study (Bradstock et al. 2005) and, thus, the influence of humans difficult to assess.

Adding to this are the historical, economic and cultural contexts that affect the human use of landscape fire. The extraordinary diversity of cultural knowledge and

management practices defy deterministic interpretation and are difficult to incorporate into ecological theory (Balée 1998). However, the challenges and available strategies to coexist with fire may be more universal than site specific. For instance, contemporary managers of flammable ecosystems worldwide share fundamental priorities, namely the protection of natural and economic resources and the maintenance of desired ecological communities (Driscoll et al. 2010). Among rural and indigenous people, ethnographic comparisons suggest that intentional burning meets common aims of increasing landscape productivity and access to resources (Lewis and Ferguson 1988). Yet contemporary managers and conservationists often discount both the legacy of indigenous burning and the current relevance of traditional knowledge.

History suggests that the practice of landscape burning was once widespread among pre-industrial societies (Pyne 1997). Tension arises among historians and ecologists, however, in how to interpret the impact of these practices on the past and present composition of flammable landscapes. Whereas some argue that humans have manufactured landscape diversity with fire (Lewis and Ferguson 1988, Pyne 1997, Gammage 2011), others remain skeptical of the influence of anthropogenic burning and the links between pyrodiversity and species composition (Parr and Andersen 2006).

Understanding the relationship between humans and pyrodiversity requires integrating multiple perspectives – culture, biology, and landscape. Our objective in this paper is therefore to explore patterns of convergence among systems of traditional fire management in order to interpret their potential effects on pyrodiversity in a more generalized ecological framework. We first survey the literature to provide a global perspective on the objectives and extent of indigenous and rural landscape burning. We then provide a biological example from Australia to illustrate how the heterogeneity of

vegetation provides a signal of the ‘patch mosaic’ created by Aboriginal landscape burning. Finally we present a simple spatial disturbance model to explore how patch burning alters fundamental aspects of pyrodiversity across a landscape. Ultimately, we hypothesize that the needs and available strategies among indigenous and contemporary approaches to fire management share more in common than is generally acknowledged.

### **Cultural parallels among flammable landscapes**

We surveyed 79 research papers (including 48 ethnographic accounts) on intentional landscape burning among rural and indigenous communities (see Supplementary Material). Mapping the research presents a widespread geography of landscape burning – or at least where it has been studied (Figure 2). Ethnographic accounts also point to regions where the practice may still persist. Despite the wide cultural and ecological diversity captured in our survey, the most frequently encountered purpose of burning was ‘cleaning’ landscapes, attributing practicality – access to resources – as well as positive aesthetic value to landscapes altered by fire (Table 1). This suggests a perception of fire, consistent across five continents, that is quite different from negative views of fire encountered in industrialized societies (Pyne 1997). Sixty-five per cent of ethnographic studies also found the prevention of destructive (e.g., destructive, hot) fires as an explicit objective of landscape burning (Table 1). Thus the practice is widely recognized as a risk-reduction strategy. This parallels the view of contemporary fire management in which destructive wildfires, unlike most natural disasters, can be proactively mitigated. A second important implication – that anthropogenic patch mosaics may be common among flammable social-ecological systems – is discussed below.

By limiting the occurrence of large, intense fires, preventative burning effectively increases the heterogeneity of fire disturbance and thus the patchiness of available successional habitat (Laris 2002, Knapp and Keeley 2006, Trauernicht et al. 2012). Thus the widespread practice of preventative burning among cultures worldwide suggests the link between anthropogenic fire and pyrodiversity is a global phenomenon. Demonstrating the ecological footprint of humans in flammable systems, however, is problematic. Modern studies of indigenous burning – relegated to strongholds of indigenous culture where practices are often threatened by various socio-political factors (e.g. Yibarbuk et al. 2001, Bird et al. 2008, Bilbao et al. 2010) – are difficult to replicate and often disregarded as exceptional rather than typical. Also, given the challenges assessing pyrodiversity discussed above, few studies track the ecological outcomes of cultural practices. Remote sensing provides insight into the effects of anthropogenic burning on ignition seasonality and increased habitat heterogeneity (Laris 2002, Bowman et al. 2004, Bird et al. 2008). But the spatial resolution of satellite imagery (generally >30 m) may miss ecologically significant patterns (e.g. Price et al. 2003) and datasets only cover decadal timespans. Alternatively, deep longitudinal paleoecological research appears equivocal about human effects. Whereas some studies identify changes to burning patterns coeval with pre-industrial human activity (e.g. Pinter et al. 2011), others point to climate as the primary driver (Marlon et al. 2008). Critical to this discrepancy is the ecological evidence that human intervention (i.e. fire management) can significantly alter fire intensity and heterogeneity with little effect on the total extent of landscape burnt, which appears to be climate-driven (Gill et al. 2000, Archibald et al. 2009). Therefore, many paleoecological studies using proxies of biomass burning, such as charcoal sediments, are likely dominated by climate-driven signals of landscape burning and possibly miss the effects of human activities.



## Case Study – Pyrodiversity and the northern cypress pine

The northern cypress pine (*Callitris intratropica*) provides an iconic example of the relationship between cultural degradation and landscape change in the tropical savannas of northern Australia (Bowman and Panton 1993, Trauernicht et al. 2013). Extant adult trees of this remnant, Gondwanan conifer recruited in a landscape extensively managed via anthropogenic burning (Yibarbuk et al. 2001). Yet relative to the ecologically dominant eucalypts, cypress pine individuals are particularly vulnerable to fire, especially in juvenile stages (Russell-Smith 2006). Hence contemporary, widespread mortality in the species has been attributed to the shift in recent decades from Aboriginal patch burning to unmanaged, large-scale wildfires (Bowman and Panton 1993). A prevailing hypothesis is that Aboriginal burning allowed cypress pine to 'invade' open savanna vegetation from extant forest patches and topographically fire-protected sites. Cypress pine tends to occur in small (<0.5 ha), compositionally distinct 'bush islands' within the surrounding savanna matrix. Thus, the distribution of remnant cypress pine groves essentially provides a window into fine-scale patterns of pyrodiversity maintained under Aboriginal management.

We surveyed cypress pine groves in open savanna vegetation across three regions of Kakadu National Park and three Aboriginal estates in central Arnhem Land (see Trauernicht et al. 2013 for site descriptions). The density of groves across the landscape was determined by counting all groves (N=182) within 50 m of 12 transects ranging in length from 1.5 to 5 km. We estimated a mean density of  $1.1 \text{ groves ha}^{-1} \pm 0.1$  (S.E.). A median grove size of 0.025 ha (ranging from 0.005-0.34 ha) was calculated from the dimensions of 134 groves. Although these groves can actually suppress the

spread of low-intensity fires (Trauernicht et al. 2012), juvenile trees require upwards of 10 years before they can survive even mild fires (Russell-Smith 2006). Given average fire return times of 1-3 years in these savannas under the current management regime, the establishment of new groves – occasionally observed in the field – remains a puzzle. The capacity for indigenous burning to increase the spatial heterogeneity of vegetation has been demonstrated in Arnhem Land and elsewhere (Laris 2002, Bowman et al. 2004, Bird et al. 2008). By starting fires earlier in the dry season before fuels have completely cured, anthropogenic burning can effectively decrease the intensity and size of disturbance events. Indeed, the density and size of cypress pine groves in the landscape lends support to the spatial outcomes of the ‘patch mosaic’ model. However, the mechanism by which patch burning could affect temporal aspects of pyrodiversity – in this instance creating the long-unburnt habitat required for Cypress pine establishment – remains unexplored.

### **Modeling the patch mosaic**

Traditional ecological knowledge of fire management – such as burning under cooler temperatures, favorable winds, and before fuels completely cure – has enabled people worldwide to mitigate destructive wildfires (see previous section). The outcomes of these practices are decreased fire intensity, which reduces damage to vegetation, and smaller fire size, which alters the spatial configuration of habitat patches. We explored the potential consequences of altering fire size using a simple, spatially explicit stochastic disturbance model. We constructed two-dimensional cellular automata (lattice model) to simulate fire regimes that contrast in fire size but burn the same mean proportion of the landscape. For each time step, the model randomly placed a given number of square ‘fire footprints’ of a specified size range across a 150×150 pixel

landscape. The fire history of a given pixel had no effect on subsequent time steps, allowing for annual fire return times (more typical of frequently burnt biomes such as mesic savannas). We varied fire size and number to 'burn' the same proportion of the landscape at each time-step (approximately 40%, adjusting for fire overlap) and ran 100 replications of each parameterization for 150 time steps. At the end of each model run, we sampled the total count of fires at each pixel and the time since the last fire at each pixel (TSF) from a 50x50 pixel 'plot' at the landscape center (to compensate for unwanted boundary effects). These data provided a measure of fire frequency and habitat composition, respectively, where TSF values represented habitat age classes with contiguous pixels of the same value interpreted as discrete habitat patches.

The simplicity of our disturbance model provides an explicit perspective on a fundamental question of anthropogenic burning; namely, how does reducing disturbance size alter emergent patterns of pyrodiversity? Intuitively, smaller fire sizes increased spatial heterogeneity (measured as adjacency – the degree of similarity between each pixel and its adjacent pixels averaged across the entire 'landscape') and decreased mean habitat patch size (Figs 3 a,b). Less intuitive were the effects of disturbance size on the temporal aspects of pyrodiversity. Although median values for fire return time and patch age were consistent across all fire size 'treatments', smaller fires generated larger maximum values for these metrics (Figure 3c). This suggests that those disturbance regimes characterized by many small fires increase the occurrence of habitat patches that are older and burned less frequently, when compared to fewer, larger fires burning the same proportion of the landscape. This pattern is also evident in higher Shannon index of patch age diversity (Figure 3d) and greater counts of older available patches as fire size decreases (Figure 4).

Considering the cypress pine case study above, the disturbance model suggests a mechanism by which anthropogenic patch burning drives the creation of 'islands' of unburnt vegetation in which fire-sensitive species could successfully recruit, as a simple 'emergent' property of fire size. If we assume our simulation represents a 3×3 km landscape, the count of habitat patches >5 and >10 years old (Fig. 4) under the smallest fire size regime (1 ha fires) are still far fewer than the actual densities of cypress pine groves encountered in the field ( $1.1 \text{ groves ha}^{-1} \pm 0.1$ ). Median patch sizes in the simulations were also larger than typical cypress pine grove areas (Figure 3a), although evidence of degradation suggests groves may be contracting under current fire regimes (C. Trauernicht, pers. obs). In addition, extant groves are unlikely to have established contemporaneously. Therefore the availability of long-unburnt habitat patches need not be exactly concordant with current grove densities. Yet these results (e.g. Fig 4) strongly suggest that the likelihood of long-unburnt habitat patches occurring in landscapes dominated by large fires is extremely low.

The model results appear to be a simple scale effect – if we sampled a large enough landscape, we may encounter the same diversity of patch ages under any of the simulated fire regimes. However, ecosystems and the organisms within them are bounded in space. Thus, our model suggests disturbance size, when measured relative to habitat patch size, may be a critical driver of ecologically relevant patterns of pyrodiversity – both in terms of resource patchiness and the available range of successional habitat stages. Of course the processes driving fire regimes and habitat configurations are far more complex than our simulation. However, by shedding light on the creation and maintenance of long-unburnt habitat patches, our results address a phenomenon that perplexes managers and ecologists alike. They also suggest how fire

size may be used to maintain landscape configurations required by constituent species (Bradstock et al. 2005, Driscoll et al. 2010).

### **Tending the land with fire**

Pioneering researchers of indigenous burning – Carl Sauer, Omer Stuart, Rhys Jones, Henry Lewis, Sylvia Hallam, Stephen Pyne, and others – have long made the case that flammable landscapes are ultimately cultural landscapes. Here, we present the case study of cypress pine in Australia and used stochastic simulation to explore how anthropogenic burning can alter the disturbance regimes that shape vegetation in fire-prone ecosystems. Obviously, the fixed fire size and lack of ‘memory’ in our simulation result in an oversimplified model of real-world disturbance dynamics. For instance, large fires will likely occur under any management regime and may create habitat heterogeneity in some systems (Knapp and Keeley 2006). Thus, questions remain regarding the degree to which anthropogenic fires actually reduce the occurrence of large fires and how quickly patch mosaics re-establish after large disturbances. However, the link between disturbance size and the age distribution of habitat patches has significant implications for understanding the ecology of flammable systems and guiding their feasible maintenance. The existence of long-unburnt patches of vegetation appears to be critical for many species, yet creating these poses a difficult management challenge in highly flammable landscapes (e.g. Woinarski et al. 2010). Still, despite the common presumption that ‘pyrodiversity begets biodiversity’, the extent to which patch mosaics increase species diversity is debated (Parr and Andersen 2006). The successional mosaic hypothesis lends theoretical support to the positive relationship between spatial heterogeneity and species coexistence (Chesson and Huntly 1997). In the field, the persistence of floristically distinct cypress pine groves increases the

diversity of vegetation in Australian savannas (Trauernicht et al. 2013), however, other taxa suggest pyrodiversity may be less important (Davies et al. 2012).

Although the links between pyrodiversity and biodiversity are yet to be fully resolved, social-ecological interactions have been part of the baseline processes shaping the composition of most fire-prone ecosystems for millennia (Bowman et al. 2011). The influence of anthropogenic burning varies with ecosystem flammability and the density of natural ignitions. However, our ecological understanding of these systems, today and historically, is arguably incomplete without considering the effects of human-mediated disturbance. The outcomes of indigenous landscape burning – reductions in fire intensity and fire size and consequent increases in pyrodiversity – have been demonstrated outright among several ecosystems (Laris 2002, Bowman et al. 2004, Bird et al. 2008, Bilbao et al. 2010). Furthermore, the widespread ethnographic parallels in fire use, knowledge and intent – preventing destructive fires, “cleaning” landscapes, manipulating resources – suggest the link between humans and pyrodiversity is a global phenomenon.

Unfortunately, the vast majority of traditional land management systems described in the literature have disappeared or deteriorated due to dispossession, increasing sedentariness, economic development, and fire suppression. It is not coincidental that these systems align with the needs of contemporary land managers, especially mitigating ecologically and economically destructive fires and maintaining historical habitat configurations. However, it is probably unfeasible and unrealistic to replicate exact patterns of indigenous burning in most cases. Yet managers can certainly draw on the rich body of traditional ecological knowledge where it remains and reassess current approaches and cultural misconceptions. Our findings suggest not only that



pyrodiversity has important ecological implications but that it can be effectively manipulated by land managers via fire size. Landscape burning is a cultural process – whether conducted by hunter-gatherers, pastoralists, or park rangers. Identifying the common needs of fire management across seemingly disparate cultures provides a unique opportunity to reciprocate knowledge and develop innovative approaches.

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Table 1. The frequency of mention of uses and objectives of intentional landscape burning in the ethnographic literature (N=48) and all surveyed literature (N=78) – including ethnographic, historical (N=20) and descriptive accounts (i.e. without specific reference to sources; N=11) – on indigenous and rural burning.

Purpose for Burning	Ethnographic studies		All studies (+ historical, descriptive)	
	Count	Proportion	Count	Proportion
"Cleaning"/clearing land	36	0.75	54	0.68
Protection of resources/property	31	0.65	39	0.49
Attracting game	28	0.58	45	0.57
Nontimber forest product harvest	27	0.56	46	0.58
Driving game	26	0.54	33	0.42
Manipulation of wild plant traits	26	0.54	41	0.52
Forest management†	26	0.54	42	0.53
Pest management	25	0.52	35	0.44
Cultivation	25	0.52	42	0.53
Animal safety‡	24	0.50	27	0.34
Pasture management	23	0.48	35	0.44
Animal gathering	13	0.27	16	0.20
Communication	11	0.23	13	0.16
Ownership/responsibility	9	0.19	10	0.13
Drying/curing firewood	9	0.19	10	0.13
Medicinal/ceremonial	9	0.19	9	0.11
Warfare/conflict	7	0.15	12	0.15
Fishing	3	0.06	3	0.04

†Refers explicitly to burning within forests, for example to open the understory or promote recruitment.

‡Refers to reducing risk to lives and livelihoods, such as predators and venomous snakes.



Figure 1. Nineteenth century paintings depicting landscape burning in a) Australia by Joseph Lycett in *Drawings of the Natives and Scenery of Van Diemens Land*, London 1830, PIC R5689, National Library of Australia and b) North America by Alfred Sully entitled *Prairie Fire*, no date, oil on academy board, Great Plains Art Museum, Lincoln, NE.

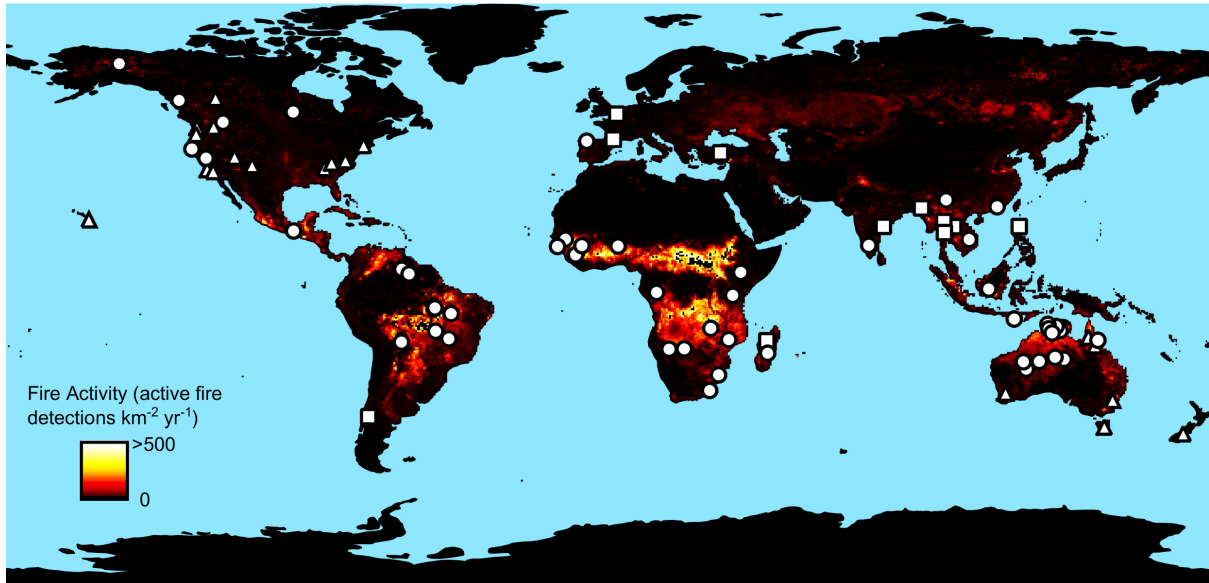


Figure 2. The global distribution of indigenous and rural landscape burning covered in the literature. Circles indicate ethnographic studies (N=48), triangles research using historical accounts (N=19), and squares studies that provide descriptive accounts (N=11) without reference to specific sources or data. Color coding illustrates ecosystem flammability using the mean annual density of active fire detections from MODIS satellite data between 2001-2006 (Giglio et al. 2006).



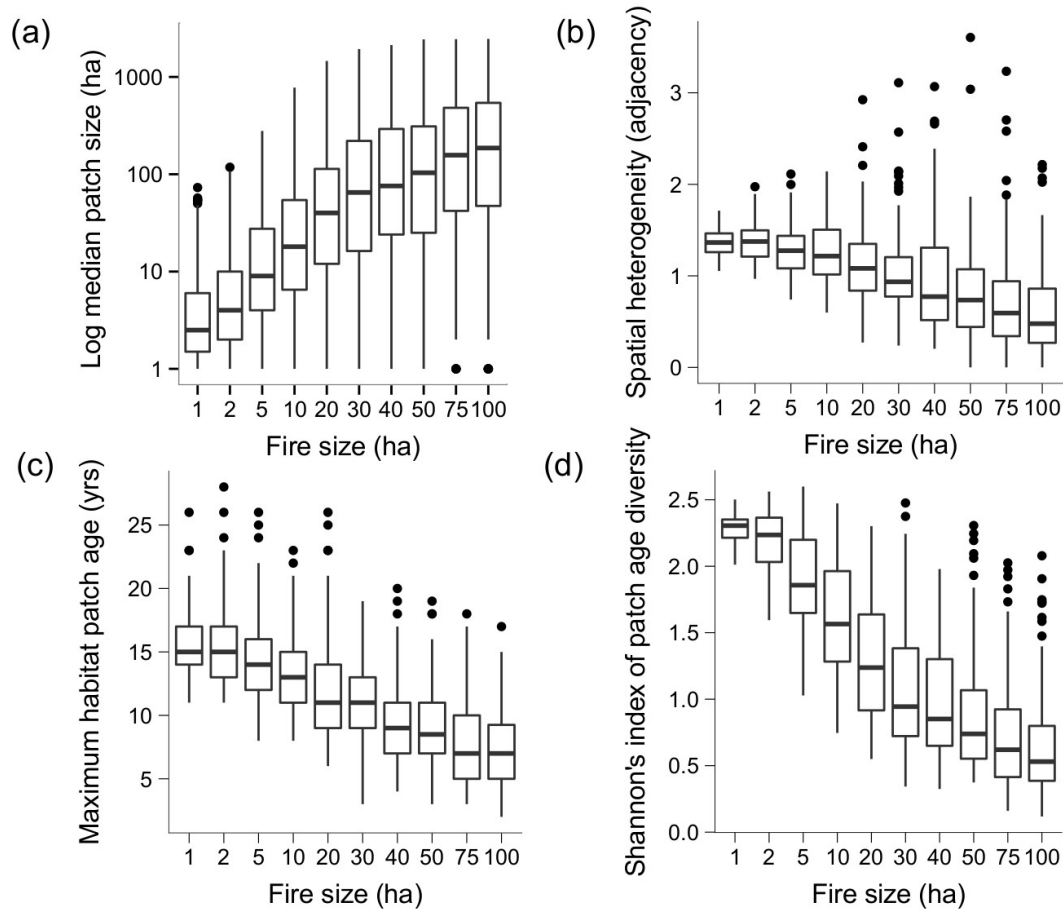


Figure 3. The results of the fire disturbance simulation, illustrating the effect of fire size on emergent habitat configurations sampled from a 100 ha plot at the center of a 900 ha landscape: (a) Median habitat patch size; (b) Spatial heterogeneity measured as adjacency (the degree of similarity between each pixel and its adjacent pixels averaged across the entire 'landscape'); (c) Maximum habitat patch age; and (d) Shannon's index of patch age diversity. Horizontal bars represent median values, boxes indicate the first and third quartiles, whiskers show the highest and lowest values within 1.5\*IQR (the interquartile range), and points represent data lying outside this range.

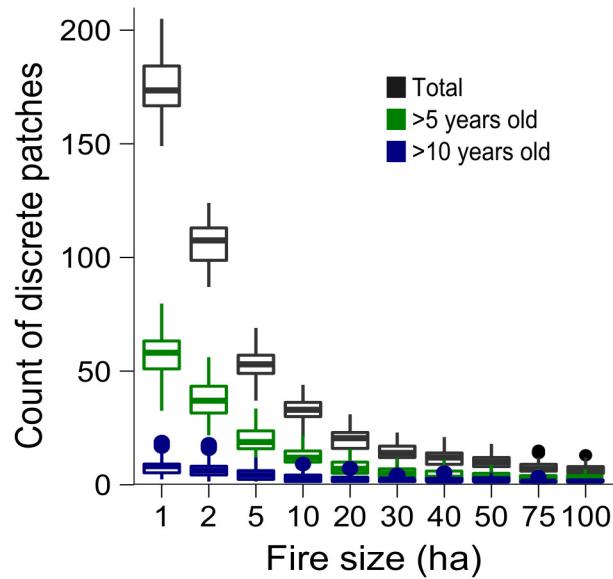


Figure 4. Results of fire simulations under different prevailing fire sizes for the total count of (i) discrete habitat patches (grey), (ii) the count of habitat patches >5 years old (green), and (iii) the count of habitat patches >10 years old (blue), as sampled from a 100 ha plot at the center of a 900 ha landscape. Horizontal bars represent median values, boxes indicate the first and third quartiles, whiskers show the highest and lowest values within 1.5\*IQR (the interquartile range), and points represent data lying outside this range.

**Chapter 2 - Supplementary Material.** Research papers addressing the objectives of rural and indigenous landscape burning organized by data source (direct ethnography, historical accounts, and descriptive accounts without reference to sources) and biome ('mixed' refers to multiple habitat types such as forest-savanna mosaics).

Data	Biome	References
Ethnographic	Arid savanna	Gould 1971, Kimber 1983, Bird et al. 2005, Vaarzon-Morel and Gabrys 2009
	Boreal forest	Gottesfeld 1994, Natcher et al. 2007, Miller 2010
	Subtropical forest	Coggins 2002
	Subtropical mixed	Johansson et al. 2012
	Subtropical savanna	Warren et al. 2001, Cassidy 2003, Kepe 2005, Sheuyange et al. 2005, Eriksen 2007, Angassa and Oba 2008, Butz 2009, Shaffer 2010
	Temperate forest	Barrett and Arno 1982, Anderson 2005
	Temperate mixed	Lewis 1989, Seijo 2005
	Tropical forest	Hill and Baird 2003, Maxwell 2004
	Tropical mixed	Fairhead and Leach 1996, Mistry 1998, Kull 2002, Dampha et al. 2003, Lichang et al. 2003, Dennis et al. 2005, McDaniel et al. 2005, Russell-Smith et al. 2007, Roveta 2008, Huffman 2011, Rodriguez et al. 2011
	Tropical savanna	Thomson 1949, Lewis 1973, Jones 1980, O'Connell et al. 1983, Haynes 1985, Hough 1993, Russell-Smith et al. 1997, Mbow et al. 2000, Laris 2002, Mistry et al. 2005, Rodriguez 2007, Hecht 2009, Walters 2010, Melo and Saito 2011
Historical	Temperate forest	DeVivo 1991, Brose et al. 2001, Gammage 2008
	Temperate mixed	Stewart 1951, Day 1953, Hallam 1975, Norton 1979, Timbrook et al. 1982, Lewis and Ferguson 1988, Patterson III and Sassaman 1988, Brown 2000, Williams 2000, Condie and Raish 2002, Keeley 2002, Gott 2005, Storm and Shebitz 2006, Williams 2009
	Tropical mixed	McEldowney 1979, Fensham 1997
	Tropical savanna	Preece In Press
Descriptive	Temperate forest	Kurtulmuslu and Yazici 2003, Aagesen 2004
	Temperate mixed	Webb 1998, Métaillé and Agnoletti 2006
	Tropical forest	Masipiqueña et al. 2000, Darlong 2002, Makarabhirom et al. 2002, London 2003
	Tropical mixed	Stott 1986, Bloesch 1999, Nanda and Sutar 2003

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### **CHAPTER 3: Tree cover–fire interactions promote the persistence of a fire-sensitive conifer in a highly flammable savanna\***

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The boundary between a *Callitris intratropica* grove (to the left) and open eucalypt savanna (to the right), during a 2010 wet season survey in Kakadu National Park. Note the difference in grass cover.

## Abstract

1. *Callitris intratropica* is a long-lived, obligate-seeding, fire-sensitive overstorey conifer that typically occurs in small groves (<0.1 ha) of much higher tree densities than the surrounding, eucalypt-dominated tropical savanna in northern Australia. We used *C. intratropica* groves of varying canopy cover to examine the role of feedbacks between fire and tree cover in the persistence of a fire-sensitive tree species and the maintenance of habitat heterogeneity in a highly flammable savanna.

2. We examined the population structure and floristic composition of *C. intratropica* groves and conducted controlled burns with Aboriginal landowners to test the prediction that groves of *C. intratropica* with closed canopies inhibit savanna fires by physically altering the fuel arrays below trees. We measured pre- and post-burn fuel availability, the probability of burning, and fire intensity along transects (55–75 m) spanning entire *C. intratropica* groves and extending into the surrounding savanna matrix.

3. We found that closed-canopy groves of *C. intratropica* had higher densities of seedlings and saplings than open-canopy groves and supported a distinct plant community. Closed-canopy groves also had a lower probability of burning and less severe fires due to a lower availability of fine fuels than the surrounding savanna.

4. *Synthesis.* Our results suggest that the observed regeneration within closed-canopy *C. intratropica* groves within frequently burnt savanna reflects a vegetation–fire feedback. A significant, negative relationship between canopy cover and the probability of burning provides strong evidence that closed-canopy *C. intratropica* groves are capable of excluding low-intensity savanna fires, thereby enabling the persistence of patches of fire-

sensitive forest or woodland amid open, highly flammable savanna vegetation. We present our findings as evidence that alternative stable state dynamics may play a role in determining savanna diversity and structure.

Keywords: Aboriginal landscape burning, alternative stable states, determinants of plant community diversity and structure, fire ecology, habitat complexity, patch dynamics, pyrodiversity, tropical savanna, vegetation boundaries, fire-sensitive species

## **Introduction**

In addition to topography, hydrology and soils, the diversity in size and age of habitat patches within an ecosystem is closely linked to the heterogeneity of disturbance across the landscape (Denslow 1995; Hobbs 1996; Turner 2005; Collins & Smith 2006; Peterson & Reich 2008). Thus, in flammable ecosystems, the ecological interactions that influence burning heterogeneity have important implications for understanding broader patterns of biological diversity and composition. While climate-driven factors such as short-term fire weather, rainfall seasonality and fuel productivity shape the general conditions under which fire occurs in ecosystems, positive and negative feedbacks among plants, animals and their environment further modulate patterns of burning. For instance, high herbivore densities can reduce fuel loads while high graminoid productivity increases fuel availability, consequently affecting ecosystem flammability at different temporal and spatial scales (de Knegt *et al.* 2008; Fuhlendorf *et al.* 2009; Setterfield *et al.* 2010; Mayer & Khalyani 2011). Contrasting fire regimes observed across habitat boundaries also suggest that overstorey woody plant composition and abundance play an important role in altering a system's propensity to burn (Peterson & Reich 2008; Hoffmann *et al.* 2009; Warman & Moles 2009; Staver,



Archibald & Levin 2011). Trees and shrubs display a wide range of adaptations that have the potential to facilitate or inhibit fire at the individual level (Bond & Midgley 1995; Schilck 2003; Kane, Varner & Hiers 2008). How woody plant–fire interactions scale up to affect flammability and burning heterogeneity at the patch, community, or ecosystem scale is therefore an important aspect of savanna and forest ecology (Mourik *et al.* 2007; Nowacki & Abrams 2008; Beckage, Platt & Gross 2009; Engber *et al.* 2011; Mandle *et al.* 2011; Kitzberger *et al.* *In press*).

In this paper we examine the potential of a fire-sensitive savanna tree species to exclude fires and thereby contribute to habitat heterogeneity and the persistence of other fire-sensitive species in an Australian tropical savanna. *Callitris intratropica* R.T. Baker & H.G. Smith (syn. *Callitris collumellaris* var. *intratropica* Silba) is a long-lived (>200 y), obligate-seeding conifer of Gondwanan origin that is widespread throughout northern Australia. The persistence of *C. intratropica* in one of the most fire-prone ecosystems on earth (Russell-Smith *et al.* 2007) is a key question concerning the composition of these savannas. Region-wide declines in the species' abundance had been noted by biologists as early as the 1920s and continue into the present across much of northern Australia (Easton 1922; Bowman & Panton 1993). These, as well as recent and dramatic declines in other species assemblages, notably small mammals and granivorous birds, have been attributed to the shift in fire regimes from Aboriginal patch burning to unmanaged, higher intensity wildfires within the past century (Franklin 1999; Bowman *et al.* 2001; Woinarski *et al.* 2010). Aboriginal landowners have long recognized high *C. intratropica* mortality as a sign of poor fire management (Haynes 1985). Thus, adapting this traditional knowledge and using *C. intratropica* as an indicator of ecologically beneficial fire regimes is of great interest to contemporary

management and conservation programs in Aboriginally-owned Arnhem Land and World Heritage Kakadu National Park.

In northern Australian savannas, *C. intratropica* can occur as isolated, mature trees but commonly forms small (typically <0.1 ha), discrete groves with higher tree densities than the scattered eucalypts which otherwise dominate the savanna overstorey. *C.*

*intratropica* groves vary in canopy cover and can be broadly delineated into two types – open- and closed-canopy groves (Fig. 1). Aside from differences in canopy cover, open-canopy groves appear to differ from closed-canopy groves in their lack of seedling and sapling regeneration and the continuity of the grass understorey. Despite these distinct spatial patterns in *C. intratropica* distribution, the mechanisms and temporal dynamics that maintain these groves remain unclear. It is well-established that frequent savanna fires limit the establishment and recruitment of woody plants (Mourik *et al.* 2007; Hoffmann *et al.* 2009) – especially if they are obligate-seeding species (i.e. incapable of resprouting after fire) like *C. intratropica* (Cohn *et al.* 2011; Prior *et al.* 2011).

Conversely, high rates of *C. intratropica* recruitment have been observed in savannas where fire has been excluded (Bowman, Wilson & Davis 1988). *C. intratropica* is a long-lived species and larger trees appear capable of surviving decades of high-frequency surface fires typical of Australian savannas (Prior, Bowman & Brook 2007). We therefore suspect that these open-canopy groves represent a state in which the grove structure has been degraded by one or several severe fires, however, demonstrating a longitudinal degradation from closed- to open-canopy groves to individuals is beyond the temporal scope of the present study. Rather, we suggest that groves with varying canopy cover (open vs. closed) provide important clues to the mechanisms behind both the persistence of *C. intratropica* and broader patterns of heterogeneity and diversity in

these savannas. Our objective is therefore to provide a clear ecological description of these two grove types and examine the fine-scale interaction between *C. intratropica* and savanna fires.

The spatial clumping of *C. intratropica* parallels patterns in other fire-prone systems, including congeners elsewhere in Australia (Cohn *et al.* 2011; Prior *et al.* 2011), *Pinus* and *Quercus* species dynamics in North American grasslands (Guerin 1993; Platt 1999; Nowacki & Abrams 2008), shola forests of India (Mohandass & Davidar 2009) and tree groves or bush islands in African and South American savannas (Couteron & Kokou 1997; Furley 2007). It has been argued that the persistence of vegetation boundaries under identical climatic and edaphic conditions is due to alternative stable state dynamics. Alternative stable state theory essentially attributes vegetation with the potential to alter abiotic conditions, thereby deterministically maintaining distinct ecological "regimes" (Scheffer *et al.* 2001; Folke *et al.* 2004). In the context of fire, for example, the theory has been proposed to explain abrupt ecosystem boundaries between savanna and rain forest (Hoffmann *et al.* 2009; Warman & Moles 2009; Staver, Archibald & Levin 2011) and sclerophyllous shrubland and forest (Perry & Enright 2002; Odion, Moritz & DellaSala 2010). But alternative stable state theory also has conceptual implications for habitat composition at smaller spatial scales, whereby feedbacks between vegetation and disturbance by fire may shape patch-level heterogeneity (Laycock 1991). The classic example of a positive feedback is the grass-fire cycle (D'Antonio, Hughes & Vitousek 2001). Yet fire-impeding species (e.g. Kane, Varner & Hiers 2008) as invaders in flammable systems may alter the probability of disturbance at the patch level, thereby creating a self promoting negative feedback (Buckley, Bolker & Rees 2007; Stevens & Beckage 2009). Therefore examining the patterns of burning

across the boundary between open- and closed-canopy vegetation within savannas may help elucidate whether and how fire feedbacks affect the persistence of fire-sensitive vegetation at the local scale and habitat heterogeneity at the landscape scale.

Here, we first describe the floristic composition and community and population structure of open- and closed-canopy groves of *C. intratropica* in relation to the surrounding matrix of eucalypt savanna. Using controlled burns conducted with Aboriginal landowners, we then empirically test the prediction that closed-canopy groves of *C. intratropica* inhibit savanna burning by physically altering the habitat below trees. We specifically address the following hypotheses:

- 1) The composition and structure of woody understorey vegetation in closed-canopy groves of *C. intratropica* differs from that of open-canopy *C. intratropica* groves and savanna;
- 2) *C. intratropica* regeneration is greater in closed- than in open-canopy groves;
- 3) Fine fuel cover and biomass is lower within closed-canopy groves of *C. intratropica* than in the surrounding savanna;
- 4) The probability of burning and fire intensity are lower within closed-canopy groves of *C. intratropica*.

## Methods

### Study site

Surveys of *C. intratropica* groves and experimental savanna fires were conducted at Dukladjarranj along the Cadell River on the northern rim of the Arnhem Plateau, within the Djelk Indigenous Protected Area of north-central Arnhem Land, Northern Territory (Fig. 1d). The Arnhem Plateau is a low massif (<400 m) of deeply dissected Middle

Proterozoic quartzose sandstone and is a regional centre of species endemism (Woinarski et al. 2006). The region is characterized by very short fire return times (1–3 years) and 40–60% of the landscape may burn annually (Gill *et al.* 2000; Edwards & Russell-Smith 2009). A general trend within the past century towards unmanaged, higher intensity wildfires occurring in the late dry season is widely attributed to the decline of Aboriginal patch burning across most of the region (Bowman *et al.* 2001; Yibarbuk *et al.* 2001; Russell-Smith *et al.* 2007). Our study site Dukladjarranj is a Gunei language group Aboriginal clan estate comprising an area of c. 90 km<sup>2</sup> and has been under nearly continuous management since before European colonisation. Detailed descriptions of the study area are provided by Yibarbuk *et al.* (2001) and Murphy and Bowman (2007).

#### Survey of *Callitris* groves

In the mid-dry season (July-August) 2010, a total of 21 discrete *C. intratropica* groves were randomly selected at Dukladjarranj ranging in size from 100–650 m<sup>2</sup>. Ten closed-canopy (> 50% canopy cover) and five open-canopy groves were situated east of the Cadell River in an area of open savanna which had last burned in 2008. In addition, three groves of each type were located to the west of the Cadell River among more rocky country which had experienced a late dry season, intense burn in October 2009. LANDSAT-derived fire history for the study site is currently available only as far back as 2006. Vegetation surrounding groves in both areas consisted of open savanna-woodland dominated by *Eucalyptus tetradonta* and *E. miniata* (mean basal area=7.5 m<sup>2</sup> ha<sup>-1</sup> ± 0.7 [SE]; mean density=168 stems ha<sup>-1</sup> ± 18 [SE]).

Sampling at *C. intratropica* groves consisted of between two and five adjacent 5 m-wide

transects, depending on the size of the grove. Transects ran from 25 m outside the grove, completely through the grove, and extended 25 m beyond the far side of the grove into the eucalypt savanna matrix. Hence, transect length varied from 55–75 meters and all transects ran parallel to the prevailing south-easterly trade winds which spread dry season fires. In each transect we recorded the diameter at breast height (DBH) and x,y coordinates of all trees  $\geq 130$  cm tall.

A line was marked down the centre of each transect at 5 m intervals beginning at 2.5 m, effectively defining a plot centre for adjacent  $5 \times 5$  m plots along the length of each transect. In alternating  $5 \times 5$  m plots, we recorded the species and counted all shrubs and small trees ( $< 5$  cm DBH) in each of two size classes (50–200 cm and  $\geq 200$  cm). Vouchers were collected and identified at the Northern Territory Herbarium in Darwin. At each  $5 \times 5$  m plot centre, hemispherical canopy photographs were taken 1 m above ground level using a fish-eye lens (Pentax DA 10–17 mm) mounted on a tripod. For sites consisting of only two parallel transects, photos were taken every 5 m along the centre line joining the two transects due to the time constraints of taking canopy photographs at dawn and dusk to prevent sun flares. Canopy cover was measured from each photograph as the percentage of closed-canopy pixels using the Gap Light Analyzer software (Frazer, Canham & Lertzman 1999). Tree coordinates were plotted in a GIS database in order to derive tree counts for each  $5 \times 5$  m plot and the distance of the *C. intratropica* individual nearest to each plot centre.

#### Burning heterogeneity and experimental fires

The heterogeneity of habitat burning was measured at all 21 *C. intratropica* groves by recording the centre of each  $5 \times 5$  m plot as burnt or unburnt after fires had passed

around and/or through the grove. We also recorded scorch heights (maximum height of damaged, browned foliage) on 12 trees in the savanna matrix around each *C.*

*intratropica* grove, a metric that has been shown to be correlated with fire intensity in this region (Williams, Gill & Moore 1998; Setterfield *et al.* 2010). However, it is important to note that scorch height may better reflect the effect of fire on vegetation (i.e. fire damage) than the actual behaviour of the fire (Hood 2010). Burn measurements at the 15 groves east of the Cadell River were recorded within several days of fires which occurred during the course of the study whereas measurements at the six groves west of the river were recorded approximately 8 months after a late fire in the previous dry season.

Variation in fuels and fire behaviour across the boundary between savanna and closed-canopy *C. intratropica* groves was examined in greater detail by intentionally setting fires under the supervision of Aboriginal landowners at seven of the 21 *C. intratropica* groves. One additional grove was accidentally burned from helicopter by local rangers in our absence and we were therefore able to record fuel data but not aspects of fire behaviour and fire intensity (see below). The area of savanna surrounding all eight of these groves last burned in 2008.

At each of the eight groves, percent cover was estimated and mean height measured for available fuels within 1 × 1 m quadrats at each 5 × 5 m plot centre before burning and immediately after fires had passed the transects. Fuel categories included tree litter (the leaf litter layer above humus and soil horizons), live graminoids, dead graminoids, shrubs <50 cm tall, and coarse fuels (woody debris >0.64 cm diameter). Three 10 g samples of litter and grass fuels were also collected and sealed in plastic bags inside and outside each *C. intratropica* grove. Samples were weighed before and after oven-



drying to determine fuel moisture. In addition, before burning at each grove, the standing biomass of litter, dead graminoids and live graminoids was cut and weighed from three, randomly placed 1 × 1 m quadrats inside the *C. intratropica* grove and three quadrats outside the grove.

These fires enabled us to measure fire behaviour and fuels before, during and after burning. Fires were lit as an arc of patch fires c. 50 m upwind from each *C. intratropica* grove, so that the fires connected into a single front moving parallel with the transects. As fires approached *C. intratropica* groves, rate of spread was measured at three locations and height of the flame front was measured at five locations. Wind speed was measured with a hand-held anemometer while temperature and humidity were derived from observations at Jabiru and Maningrida airports, the nearest meteorological stations located c. 150 km and 65 km from the field site, respectively. During the burns, we used the amount of water vaporised from open calorimeters to measure the energy released by the fire as a proxy for fire intensity (Perez & Moreno 1998). Aluminium cans were filled with 50 g of water, weighed to the nearest 0.01 g, and placed at ground level at each 5 × 5 m plot centre before burning. Five control cans were placed outside the burn area to account for ambient evaporation. Cans were collected and reweighed immediately after the fire passed and water loss due to vaporisation was determined by subtracting the mean water loss in the control cans from the water loss of the burnt cans.

## Analyses

All data modelling employed linear and generalised linear models with model selection based on Akaike's Information Criterion (AIC<sub>c</sub>) as outlined in the Information-Theoretic framework (Anderson & Burnham 2002). We used mixed models wherever possible,

incorporating site (i.e. each *C. intratropica* grove) as a random effect in order to account for the slight random variation in both environmental conditions and fire events among groves (Bolker *et al.* 2009). For all response variables that produced normal errors, we employed spatially explicit linear mixed models (LMM) which incorporated the x,y coordinates of all sample points to account for spatial autocorrelation (Crawley 2007) using the 'lme' function in the 'nlme' package in R (Pinheiro *et al.* 2010). For analyses of data with binomial and Poisson distributed errors, we used generalized linear models (GLM) or generalised linear mixed models (GLMM; 'lmer' package in R) which do not allow for spatial structure to be incorporated into the analyses. For clarification, all model types, data transformations, and global parameterizations are listed for each response variable in the Chapter 2 Supplementary Material.

The hypothesis that woody plant composition differs among open- and closed-canopy *C. intratropica* groves and the eucalypt savanna matrix was explored using non-metric multi-dimensional scaling (NMDS) as part of the 'vegan' package in R (Oksanen *et al.* 2011). The ordination used 3-dimensions (based on scree plots of NMDS stress values) and Bray-Curtis dissimilarities to model the differences among all 5 × 5 m plots based on the composition and abundance of 59 plant species (excluding *C. intratropica*). We also tested the strength of this separation as a function of plot location (eucalypt savanna vs. open-canopy vs. closed-canopy *C. intratropica* groves) with a permutational multivariate analysis of variance (PERMANOVA) also based on Bray-Curtis dissimilarities using the 'vegan' package in R.

We tested for structural differences in the woody plant community among closed-canopy groves, open-canopy groves and savanna by modelling the total count of shrubs and small trees in each plot as a function of grove type (open- vs. closed-canopy) and plot

location using a GLMM with log-normal Poisson errors for overdispersed data (Elston et al. 2001). Plot location was based on the distance of each plot centre to the nearest *C. intratropica* individual to group plots into three categories: (i) Inside grove (<5 m); (ii) Grove edge (5–10m); and (iii) Outside grove (>10m). We selected a categorical over a continuous distance variable in this and subsequent analyses because we expected our dependent variables to display a threshold rather than a continuous response across the habitat boundary.

We tested the hypothesis that open- and closed-canopy *C. intratropica* groves differ in regeneration patterns by examining population structures based on tree size classes. We calculated the mean and standard error of stem density among *C. intratropica* groves of each type (open- vs. closed-canopy groves) for 5 cm DBH classes, beginning with 0–4.9 cm.

To test the hypothesis that closed-canopy groves of *C. intratropica* have lower fine fuel availability, we employed LMMs to examine the importance of plot location to the following fuel measurements: (i) Index of grass fuel abundance: total grass cover × height; (ii) Litter cover; (iii) Cover of shrubs <50 cm tall; and (iv) Index of coarse fuel abundance: coarse fuel cover × height. We used a least-squares linear model ('lm' function in R) of fuel moisture as a function of fuel type, site, and sample location (inside vs. outside grove) in order to determine fuel moisture content for estimates of fuel biomass. Biomass of live graminoids, dead graminoids and litter were modelled as a function of sample location (inside vs. outside grove) using non-spatial LMMs with site as a random factor.

In order to test the hypothesis that closed-canopy groves of *C. intratropica* are capable

of reducing the spread of savanna fires, we used a binomial GLMM to examine the importance of canopy cover to the proportion of plot centres burnt, a binary response variable. Using canopy cover as a single, continuous explanatory variable in this analysis captured the key ecological feature distinguishing closed-canopy groves of *C. intratropica* from both open-canopy groves and eucalypt savanna (Fig. 1c).

The hypothesis that closed-canopy groves of *C. intratropica* reduce the intensity of fires was tested by modelling the amount of water vaporised from calorimeters as a function of plot location using LMMs. In order to see which of the fuel measurements were important to fire intensity, we also used LMMs to model water loss as a function of net change in fuel cover (i.e. fuel consumed) for the fuel variables described above.

## Results

### Compositional differences among *C. intratropica* groves

Plotting the first two dimensions of the NMDS ordination illustrated a clear distinction between plots in closed-canopy groves and plots within the eucalypt savanna matrix, with those in open-canopy groves intermediate (Fig. 2a). The NMDS reached a stress level of 0.20, which suggested a  $\leq 1\%$  chance of the ordination having a random structure (Sturrock & Rocha 2000). The PERMANOVA also supported this pattern, with plot location supported as a significant factor explaining the separation of points ( $F=18.6$ ,  $P<0.01$ ). *C. intratropica* groves and eucalypt savanna also differed structurally in their associated woody plant community, with higher stem counts of shrubs and small trees inside closed-canopy groves than inside open-canopy groves or outside groves ( $w_i>0.99$ ; Fig. 2b). In terms of regeneration patterns, closed- and open-canopy groves of *C. intratropica* showed clear differences with notably lower densities of *C. intratropica*

individuals among smaller size classes in open-canopy groves (Fig. 3). Despite this difference, the mean total basal area of *C. intratropica* was similar between the two grove types (closed groves:  $19.4 \pm 2.9$  [SE]; open groves:  $23.3 \pm 3.8$  [SE]).

#### Negative feedback between *C. intratropica* cover and fire

Fire weather and fuel conditions during our experimental burns resulted in low-intensity surface fires. Mean wind speed during the fires was moderate, ranging from 15–20 km hr<sup>-1</sup> from the east-northeast, mean relative humidity was 38% and temperature was 31°C. ANOVAs of fuel moisture predicted differences among fuel types with no differences among sites (live graminoids:  $57\% \pm 2$  [SE]; dead graminoids:  $27\% \pm 2$  [SE]; litter:  $15\% \pm 2$  [SE]). ANOVAs of rate of spread (mean =  $1.4 \text{ ms}^{-1} \pm 0.1$  [SE]) and flame height (mean =  $0.81 \text{ m} \pm 0.15$  [SE]) indicated no significant differences among the seven fires intentionally lit at *C. intratropica* groves. The mean intensity along fire fronts outside *C. intratropica* stands was  $640 \text{ kW m}^{-1}$  (Byram 1959) based on rate of spread data, estimates of graminoid fuel consumption (mean =  $261 \text{ kg ha}^{-1} \pm 74$  [SE]) from cover and biomass measurements along transects, and mean heat of combustion for grass fuels ( $17,781 \text{ kJ/kg}$ ; Trollope 1984). This estimate falls within the range of low intensity savanna fires that are typical of the mid-dry season for the region (Russell-Smith & Edwards 2006).

The fuels data supported the hypothesis that closed-canopy groves of *C. intratropica* reduce the availability of fine fuels. LMMs predicted lower graminoid fuel abundance (% cover  $\times$  height) and lower graminoid biomass inside closed-canopy groves (Figs 4a, 4d, 4e; Abundance:  $w_i = 0.98$ ; Dead biomass:  $w_i > 0.99$ , Live biomass:  $w_i > 0.99$ ). Our analyses indicated an increase in the abundance of coarse fuels (% cover  $\times$  height; Fig. 4c;

$w_i > 0.99$ ) and a decrease in low shrub cover inside closed-canopy groves (Fig. 4b;  $w_i > 0.99$ ). Although no relationship was found between litter cover and the presence of a *C. intratropica* canopy, our analyses demonstrated higher litter biomass within closed-canopy *C. intratropica* groves (Fig. 4f;  $w_i > 0.99$ ). Analyses of calorimeter water loss as a function of fuel consumed found the change in cover of low shrubs and litter were both important to fire intensity measurements ( $w_i = 0.99$ ,  $R^2 = 0.29$ ).

Our analyses showed that the probability of habitat burning decreases with increasing canopy cover based on the GLMM (Fig. 5a;  $w_i > 0.99$ ;  $R^2 = 0.32$ ), thus supporting our hypothesis that closed-canopy *C. intratropica* groves are able to limit the spread of fire. We present  $R^2$  values calculated from model deviances based on log-likelihood (Nagelkerke 1991), however, it is important to note that deriving  $R^2$  for models with random effects is problematic (e.g. Xu 2003). The analyses of the calorimeter data also supported the hypothesis that fire intensity is lower inside closed-canopy *C. intratropica* groves relative to open savanna (Fig. 5b;  $w_i = 0.97$ ).

## Discussion

Fire is considered a principal driver of habitat heterogeneity in savannas (e.g. Scholes & Archer 1997; Sankaran *et al.* 2005), yet the ways in which feedbacks between fire and woody vegetation affect the spatial patterns of disturbance within plant communities and ecosystems remain unclear. Here we focused on the occurrence of open- and closed-canopy groves of *C. intratropica* (Fig. 1), a fire-sensitive savanna conifer, in a highly fire-prone ecosystem to better understand the mechanisms which shape and maintain savanna heterogeneity. Our results showed marked differences in the floristics and community and population structures between closed-canopy groves and both open-canopy groves and the surrounding savanna matrix. For example, the NMDS ordination

(Fig. 2a) illustrates a clear pattern of separation among plots into closed-canopy *C. intratropica* groves and eucalypt savanna, indicating that the boundary between closed-canopy groves and savanna (Fig. 1a) is also characterized by differences in the woody plant community. These compositional patterns are mirrored by differences in the stem counts of woody plants over 50 cm tall (Fig. 2b) which was highest in closed-canopy groves and, importantly, very similar for open-canopy groves and eucalypt savanna.

Fire is the primary disturbance limiting woody plant establishment in Australian savannas and therefore the lack of juveniles and saplings (<15 cm DBH) in open-canopy groves may be an indication that these groves are more likely to burn than groves with closed canopies (Fig. 3). Of course fire can affect tree establishment in other ways, for example, by altering fecundity (Quintana-Ascencio & Menges 2000; Caddy & Gross 2006). However, high counts of *C. intratropica* seedlings have been observed to establish between fire events in both grove types (C. Trauernicht, unpublished data), indicating adult trees in open-canopy groves maintain their reproductive capacity. *C. intratropica* seedlings take many years to reach maturity and are much more vulnerable to fire than adult trees (C. Trauernicht, unpublished data; Russell-Smith 2006).

Therefore, we argue that the population structure of open groves is ultimately shaped by higher rates of seedling and sapling mortality due to fire. Although an admittedly static representation of demography, the lower densities in smaller size classes for both open- and closed-canopy groves suggest that, at the patch-scale, these populations may be declining (Rubin, Manion & Faber-Langendoen 2006). Gaps in size class structures may also reflect the fact that *C. intratropica* is a mast seeder and relies on episodic recruitment (e.g., Stocker 1966; Drewa *et al.* 2008; Prior *et al.* 2010). However, the temporal variability among the processes limiting seedling recruitment can make

population structures difficult to interpret and a forthcoming paper will examine *C. intratropica* demography in greater detail. Modelling long-term population stability at the patch-scale will be critical in determining whether *C. intratropica* groves are expanding and/or whether the species relies on the initiation of new patches in a meta-population context. Given the longevity of *C. intratropica* adults (> 200 y), population dynamics may also provide a strong indication of the degree to which current fire regimes have changed since extant groves established. Yet the key aspect of the data we present here is that the higher density of seedlings and saplings in closed-canopy groves (Fig. 3) strongly implies that some kind of feedback mechanism is reducing the likelihood of disturbance within these groves (e.g. Stevens & Beckage 2009), thereby allowing smaller trees to escape mortality.

Previous anecdotal descriptions have linked fire exclusion by *C. intratropica* to the litter layer forming within groves (Stocker & Mott 1981; Bowman & Wilson 1988). Our results support this assertion with closed-canopy groves having greater litter biomass than the surrounding savanna (Fig. 4f). However, it is more likely the reduction in fine fuel cover and biomass – specifically graminoids and low shrubs (Figs 4a,4b,4d,4f) – within groves that ultimately reduces the probability of habitat burning. Grasses are the primary fuel source for fires in these savannas (e.g. Setterfield *et al.* 2010) and our analyses found low shrubs to be an important factor driving observed fire intensities. Increased litter cover has been shown to negatively affect grass establishment (Schramm & Ehrenfeld 2010; Scott *et al.* 2010; Viard-Cretat *et al.* 2010). Alternatively, multiple studies have found shading to be a limiting factor to the growth and survival of C<sub>4</sub> grasses which are dominant fuels in temperate and tropical savannas (Veenendaal, Shushu & Scurlock 1993; Lett & Knapp 2003; Scott *et al.* 2010). Light limitation is an obvious physical effect



of closed-canopy *C. intratropica* groves on the local environment (Fig. 1c). However, it is difficult to disentangle the effects of shading and litter on fuels with our data and both processes may be important. Regardless of the mechanism, the reduction in grass biomass within *C. intratropica* groves has direct consequences for limiting both fire intensity, critical for adult survival and stand persistence, and fire occurrence, critical for juvenile recruitment (e.g. Thaxton & Platt 2006; Engber *et al.* 2011).

We examined the potential for a feedback between fire and *C. intratropica* more explicitly by measuring the extent of habitat burnt along transects extending across the boundary of eucalypt savanna and closed- and open-canopy groves after fires had passed through our field sites. Our data provide compelling evidence that closed-canopy groves of *C. intratropica* have a lower probability of being burnt (Fig. 5a). In addition, calorimeter measurements suggest that those areas that do burn within closed-canopy *C. intratropica* groves experience fires of lower intensity than outside or along the edges of groves (Fig. 5b). These results have important implications for understanding how *C. intratropica* persists in such a flammable ecosystem. The apparent feedback between closed-canopy *C. intratropica* groves and fire has the potential to maintain long fire-free intervals within groves even under frequent, low intensity, ambient fire conditions. From a demographic perspective, the ability of these groves to exclude fires would be critical to maintaining recruitment among smaller, highly fire-sensitive size classes (Russell-Smith 2006). This not only provides an explanation of observed differences in population structure among grove types (Fig. 3), but also suggests the mechanism by which the species self-organizes into groves. The persistence of *C. intratropica* in the landscape requires further examination to determine the ultimate fate of damaged groves, as well as the degree to which the species depends on the tree cover–fire feedback we describe

versus the initiation of new groves. Nonetheless, our results suggest the decline and degradation of *C. intratropica* groves are due to increases in fire intensity rather than in fire frequency (Russell-Smith *et al.* 2010), although establishing specific thresholds for fire impacts on canopy cover and tree survival would require observations of fires at varying intensities (e.g. Cohn *et al.* 2011).

A growing body of literature has explored the potential of woody plants to both facilitate and impede fire in flammable ecosystems (Bond & Midgley 1995; Schwilk 2003; Kane, Varner & Hiers 2008). On broader scales, alternative stable state theory has been invoked to explain how vegetation–fire feedbacks maintain contrasting disturbance regimes across ecosystem boundaries (Hoffmann *et al.* 2009; Odion, Moritz & DellaSala 2010; Staver, Archibald & Levin 2011). We argue that the potential for a feedback between fire and closed-canopy groves of *C. intratropica* suggests a similar mechanism may be operating at the patch- and community-level in savannas. A canopy cover–fire feedback has obvious and direct implications for the demography and persistence of *C. intratropica*. However, the community composition data (Figs 2a, 2b) also suggests that fire exclusion by *C. intratropica* has implications for broader patterns of vegetation structural complexity and diversity. At larger spatial scales, the persistence of closed-canopy *C. intratropica* groves essentially maintains a mosaic of small-scale forest or woodland patches within the wider eucalypt savanna matrix. Unfortunately, establishing a longitudinal decline due to fire damage from closed-canopy to open-canopy groves and eventually to isolated, individual trees is beyond the temporal scope of the present study. However, we hypothesize that open-canopy groves provide evidence of a state change, in terms of both canopy cover (Fig. 1c) and habitat flammability (Fig. 5a), from *C. intratropica* woodland to eucalypt savanna conditions, despite the survival of *C.*

*intratropica* adults.

While the fire feedback we describe is critical to the persistence of *C. intratropica* and potentially other fire-sensitive species, continued regional declines in *C. intratropica* abundance suggest that this mechanism cannot withstand the high intensity fires typical of current fire regimes (Bowman & Panton 1993; Edwards & Russell-Smith 2009; Cohn *et al.* 2011). There is a strong case that the prevailing pattern of landscape-scale habitat degradation in northern Australia (Russell-Smith *et al.* 1998; Bowman *et al.* 2001; Franklin *et al.* 2005; Woinarski *et al.* 2010) is related to the breakdown of Aboriginal fire management. The life histories of extant *C. intratropica* groves in this region span the transition across much of the region from >50,000 years of Aboriginal management to what can be aptly described as modern wilderness (Bowman *et al.* 2001). Thus, the spatial patterns of *C. intratropica* groves and their potential to tolerate frequent, low-intensity burning likely hold further clues to disentangling the complex relationships between people and savanna landscapes (e.g. Price & Bowman 1994). We hope that by establishing the mechanism by which *C. intratropica* can exclude fire, we can better understand the species' potential as an indicator of fine-grain landscape heterogeneity, the availability of long-unburnt habitat, and the system's response to changing fire regimes. Although still a contentious issue, the maintenance of habitat heterogeneity by fire is currently thought to be crucial for the integrity of communities across multiple guilds of species (Schwilk, Keeley & Bond 1997; Bradstock *et al.* 2005; Van Dyke *et al.* 2007; Yarnell *et al.* 2007; Clarke 2008; Fuhlendorf *et al.* 2009). Our research on vegetation–fire feedbacks at the patch scale provides further insight into the processes driving habitat complexity in Australian savannas and raises the question of how alternative stable state dynamics may shape patterns of savanna structure and burning

worldwide.

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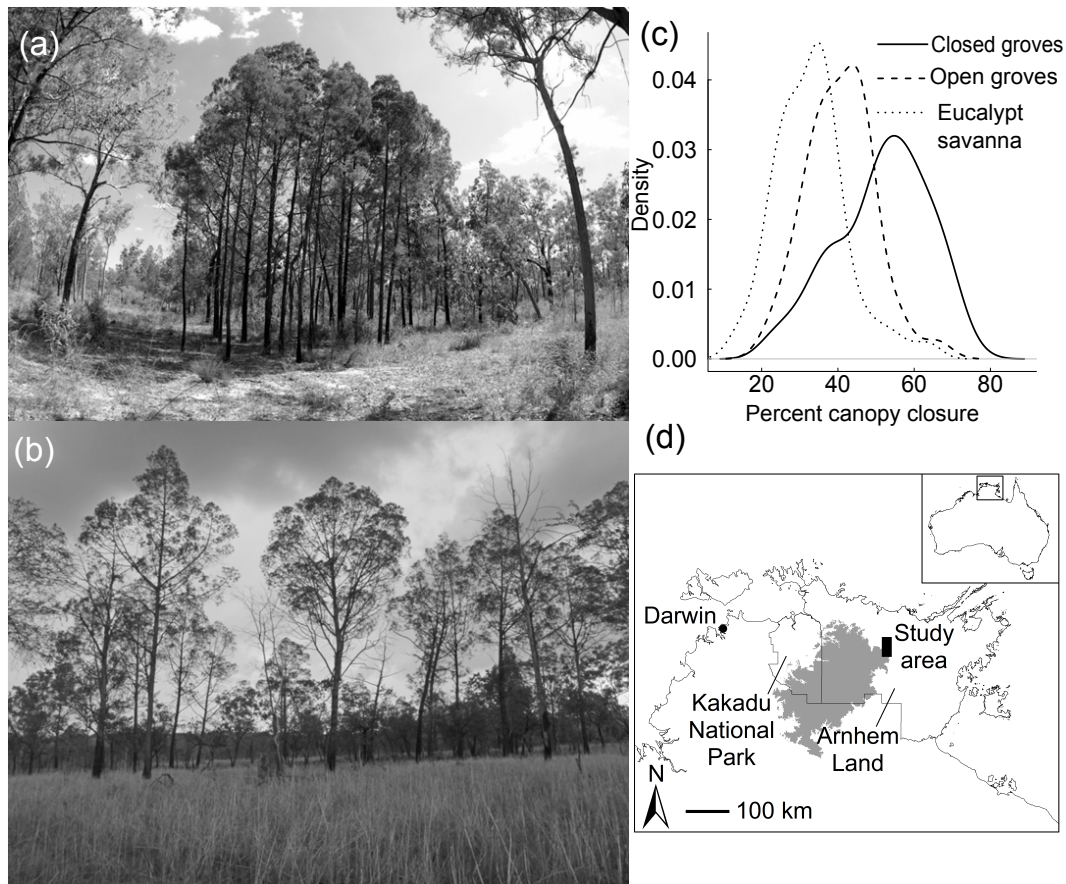
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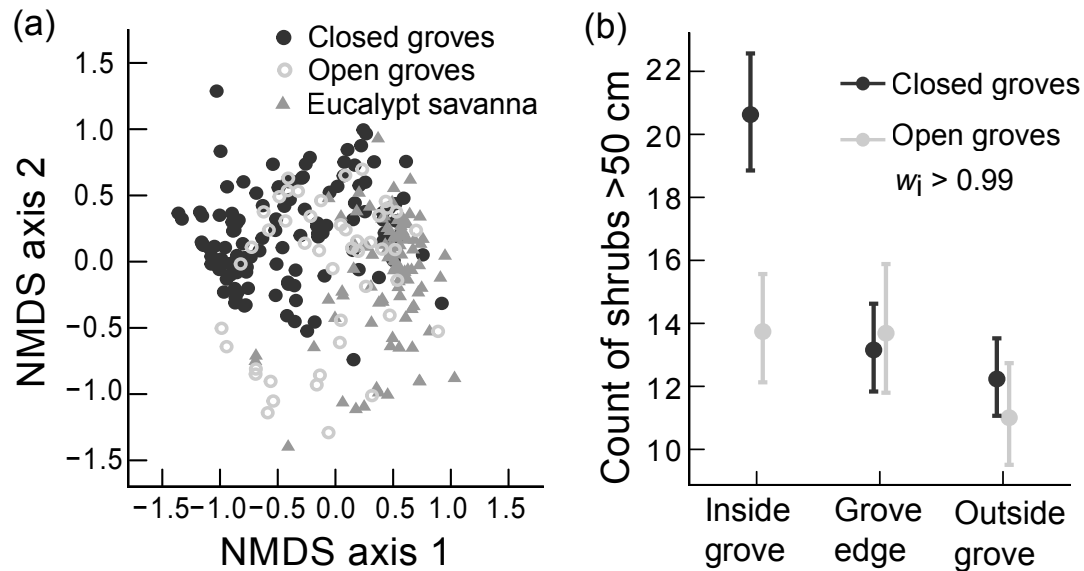


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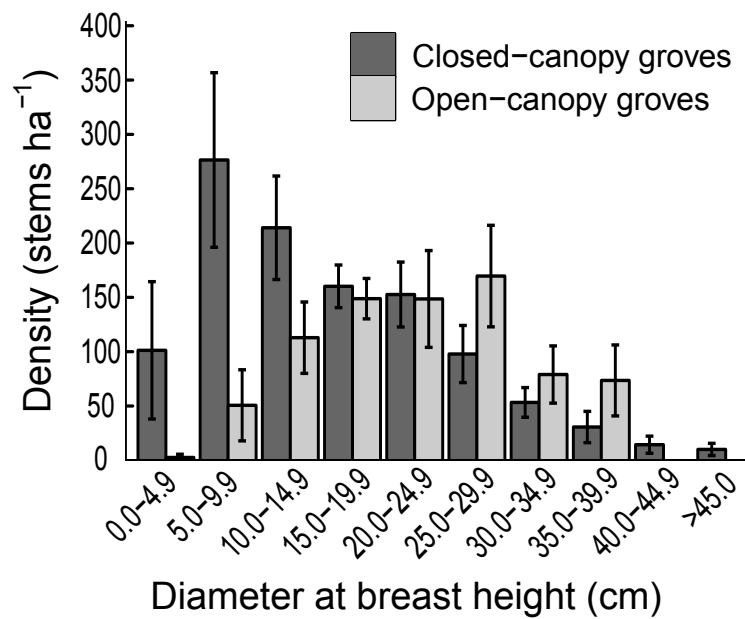
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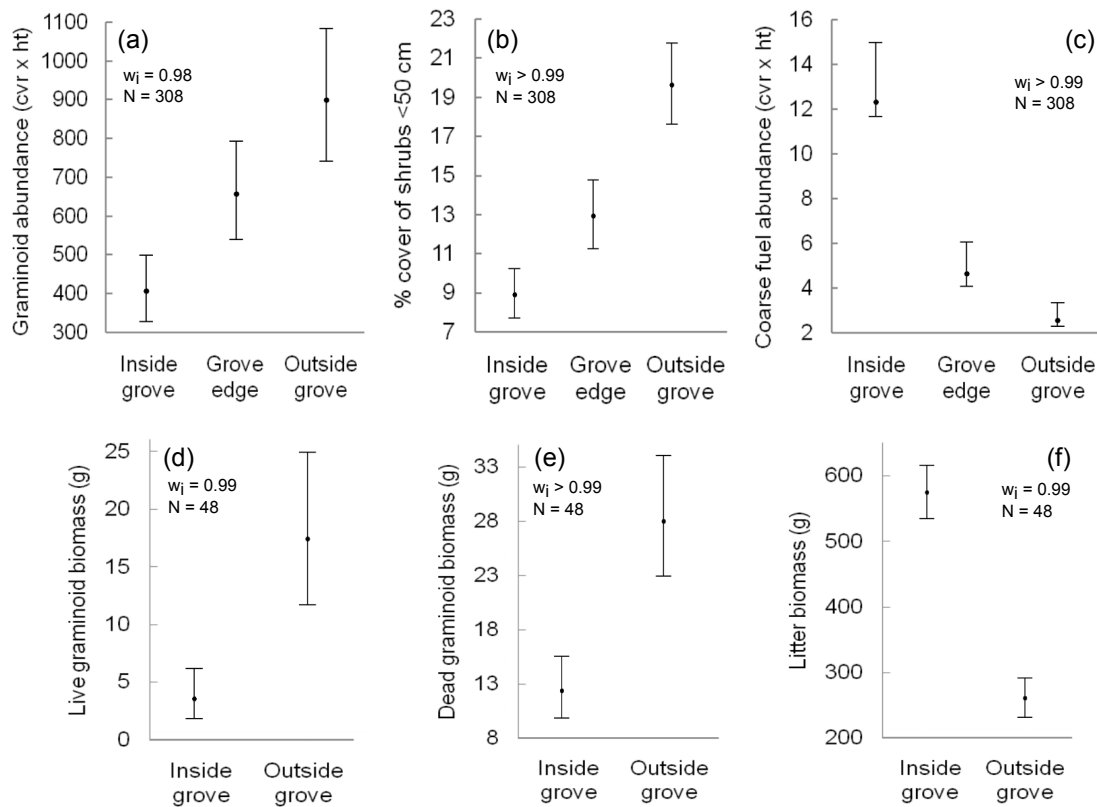
**Fig. 1.** The context of the study system. (a) Closed-canopy groves of *C. intratropica* form clearly defined habitat boundaries with the matrix of open savanna dominated by *Eucalyptus tetradonta* and *E. miniata*, and are clearly distinguishable from (b) open-canopy *C. intratropica* groves. (c) Canopy cover distributions (derived from hemispherical photographs) illustrate differences among plots in closed-canopy groves, open-canopy groves, and open eucalypt savanna. (d) A map of Arnhem Land shows the study site in relation to Kakadu National Park and the Arnhem Plateau (shaded gray; from Yibarbuk et al. 2001).



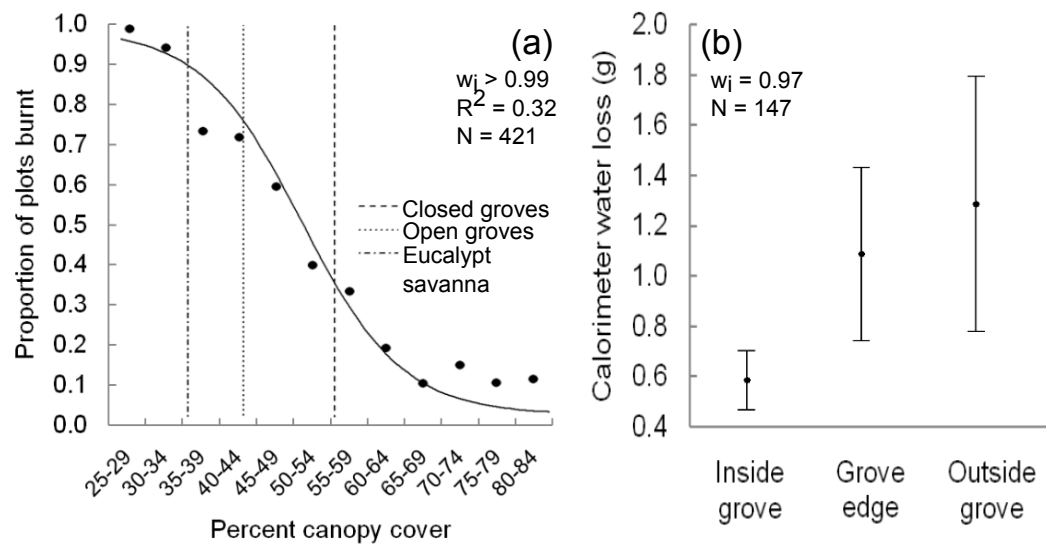
**Fig. 2.** The structural and compositional aspects of the woody plant community among closed-canopy and open-canopy *C. intratropica* groves and the surrounding eucalypt savanna matrix. (a) A scatterplot of the first two axes of an ordination using nonmetric multidimensional scaling (stress = 0.20) is based on woody plant species composition (excluding *C. intratropica*) from 25 m<sup>2</sup> plots sampled among closed-canopy groves, open-canopy groves and eucalypt savanna. (b) GLMM predictions of counts of shrubs > 50 cm tall are presented as a function of plot location relative to *C. intratropica* and *C. intratropica* grove type. Error bars represent standard errors and the Akaike weight ( $w_i$ ) relative to the null model is presented.



**Fig. 3.** Mean *C. intratropica* stem densities per DBH size class are shown for closed- and open-canopy groves. Error bars represent standard errors.



**Fig. 4.** Relationships between available fuels (i.e. before burning) and plot locations relative to *C. intratropica* groves. The upper panels present spatially-explicit LMM predictions for fuel cover measurements taken along transects for (a) graminoid abundance, (b) low shrub cover, and (c) coarse fuel abundance. The lower panels present LMM predictions based on biomass collected from 1 × 1 m plots inside and outside closed-canopy groves for (d) live graminoids, (e) dead graminoids and (f) litter. Error bars represent the standard error of model predictions and Akaike weights ( $w_i$ ) relative to the null model are presented.



**Fig. 5.** Relationships between *C. intratropica* groves and savanna fires. Panel (a) presents the relationship between the proportion of plots burnt (binned in 5% cover increments) and canopy cover, which is a key factor distinguishing closed-canopy *C. intratropica* groves from open-canopy groves and the eucalypt savanna matrix. Dashed vertical lines show median canopy cover values for closed-canopy groves, open-canopy groves, and eucalypt savanna. Panel (b) presents LMM predictions of fire intensity, measured by water loss from open calorimeters, as a function of plot location relative to closed-canopy *C. intratropica* groves. Error bars represent standard errors and Akaike weights ( $w_i$ ) are presented relative to the null model.

### Chapter 3 Supplementary Material. Summary of statistical models and data

transformations employed in the analyses. Model acronyms are as follows: GLM - general linearised model, GLMM - general linearised mixed model, LM - linear model, LMM - linear mixed model. Spatial LMMs incorporated the x,y coordinates of sample points to account for spatial autocorrelation. All mixed models incorporated site as a random effect. Plot location refers to the position of sampling points relative to *C. intratropica* groves either as 3-level categorical variable (†; Inside grove/Grove edge/Outside grove) from transect data or a 2-level variable (‡; Inside grove/Outside grove) from randomly placed sample points.

Response Variable	Fixed effects in global model	Transformation	Model
Shrub Count >50 cm high	Grove type*Plot location	None	GLMM (log-normal Poisson)
Survival (plantation)	Tree size*Mass of kerosene	None	GLM (binomial errors)
Graminoid abundance (cover x height)	Plot location†	response <sup>0.2</sup>	spatial LMM
Litter cover	Plot location†	response <sup>0.2</sup>	spatial LMM
Shrub ≤50 cm cover	Plot location†	response <sup>0.5</sup>	spatial LMM
Coarse fuel abundance (cover x height)	Plot location†	log(response)	spatial LMM
Fuel moisture (g)	Site+Fuel type+Plot location‡	None	ANOVA
Rate of spread (m s <sup>-1</sup> )	Site	response <sup>0.75</sup>	ANOVA
Flame height (m)	Site	response <sup>0.5</sup>	ANOVA
Live graminoid biomass (g)	Plot location‡	response <sup>0.25</sup>	LMM
Dead graminoid biomass (g)	Plot location‡	response <sup>0.2</sup>	LMM
Litter biomass (g)	Plot location‡	response <sup>0.75</sup>	LMM
Proportion of plots burnt	Canopy cover	None	GLMM (binomial errors)
Calorimeter water loss (g)	Plot location†	response <sup>0.35</sup>	spatial LMM
Calorimeter water loss (g)	Δ Grass cover+Δ low shrub cover+Δ litter cover+ Δwoody cover	response <sup>0.35</sup>	spatial LMM



#### **CHAPTER 4: Aboriginal fire management, patch mosaics, and the population stability of a fire-sensitive conifer in northern Australia**



Aerial photo of an intact, closed canopy *Callitris intratropica* grove amid open savanna vegetation in Kakadu National Park

## Abstract

Differences among woody plant species in their adaptive responses to fire provide important insight into shifts in ecosystem composition due to changing fire regimes. In Australian tropical savannas, the switch from patchy landscape burning by Aborigines to unmanaged wildfires across much of the region within the past century has been implicated in the widespread declines of the fire-sensitive conifer, *Callitris intratropica*. The species occurs as singleton trees but also commonly forms small, closed-canopy groves that are capable of excluding fire and thereby contributing both to conspecific recruitment and the persistence of a distinct community of fire-sensitive woody plants. Despite *C. intratropica*'s contribution to savanna heterogeneity, the mechanisms underlying its persistence and decline at the population level remain poorly understood. In this paper, we examined the hypothesis that the presence of *C. intratropica* in highly flammable, open savanna is dependent upon a regime of low-intensity fires maintained by Aboriginal management. We combined integral projection models of *C. intratropica* population behavior with an environmental state change matrix to examine how the contributions of demography, grove dynamics, and the frequency of high and low intensity fires contribute to the species' long term population stability. We found that closed canopy *C. intratropica* groves make a disproportionately large contribution to population stability by promoting seedling/sapling recruitment. Conversely, singleton trees account for a larger proportion of adult mortality. Our results suggested that *C. intratropica* decline is a successional process likely requiring multiple, high intensity fire events and that the recruitment of new groves plays a critical role in the species' persistence. As expected, our patch-based population model projected negative population growth rates under current fire probabilities. However, manipulating fire

disturbance probabilities also suggested that reductions in fire intensity – a primary outcome of Aboriginal burning – lead to positive *C. intratropica* population growth. These findings provide critical insight into the role of human management as a driver of the vegetation mosaics encountered in flammable ecosystems.

## Introduction

The accumulation of woody biomass provides a key signal of the role of fire in driving the composition of savannas (Bond and Keeley 2005, Murphy and Bowman 2012). Fire can affect the growth, survival, and fecundity of woody species which, in turn, shape ecosystem biomass and structural complexity (Quintana-Ascencio and Morales-Hernández 1997, Murphy et al. 2010). Importantly, differences among plant species in their adaptive response to fire have provided insight into compositional shifts related to changes in fire disturbance regimes. For instance, fire suppression has been implicated in the encroachment of fire-sensitive shrubs into African and North American grasslands (Roques 2001, Heisler et al. 2004) as well as continental-scale increases in the abundance of fire-sensitive trees in North America (Nowacki and Abrams 2008), while increases in fire intensity have been linked to the degradation of forest patches in South American and Australian savannas (Bilbao et al. 2010, Russell-Smith et al. 2012). Modeling the effects of fire on woody plants at the population level can therefore provide critical insight into how fire disturbance affects and interacts with the spatial heterogeneity of vegetation (Hoffmann 1999, Caswell and Kaye 2001, Keeley et al. 2006, Hoffmann et al. 2009b).

*Callitris intratropica* is a long-lived, fire-sensitive conifer that has persisted in Australian tropical savannas, which are among the most fire-prone environments on Earth. *Callitris*

*intratropica* is one of the few non-eucalypt overstory trees in these savannas and it provides a model system with which to understand the effects of fire disturbance on ecosystem composition. Widespread declines in *C. intratropica* have coincided with declines in other species assemblages, notably small mammals (Woinarski et al. 2010), and provide some of the best, direct evidence of landscape scale ecological degradation wrought by changing fire regimes in recent decades (Bowman and Panton 1993, Edwards and Russell-Smith 2009). Research on the interactions between fire and *C. intratropica* regeneration, mortality, and patch dynamics has led to the hypothesis that the species' establishment and persistence in open savanna vegetation is largely dependent upon a regime of low-intensity, patchy fires maintained by Aboriginal burning (Price and Bowman 1994, Russell-Smith 2006, Trauernicht et al. 2012). The species occurs as singleton trees but is also commonly found in small (0.01-0.3 ha) and abundant groves (c. 1 grove ha<sup>-1</sup>), within the savanna matrix (Trauernicht et al. submitted). Structurally intact *C. intratropica* groves alter fuel availability and are capable of excluding low-intensity savanna fires (Figure 1a). This feedback allows for conspecific recruitment (Figure 1c) as well as the establishment of a distinct woody plant community with a greater abundance of other fire-sensitive species than are present in the savanna matrix (Trauernicht et al. 2012). Canopy damage from high intensity fires disrupts this feedback, however, causing a state change among degraded groves in which the abundance of grass fuel, probability of fire, and plant community composition are equivalent to open savanna, even though adult *C. intratropica* individuals persist (Figure 1b). Thus the proportions of intact and degraded *C. intratropica* groves across the landscape provide insight into changes in the structural complexity and diversity of savanna plant communities. For example, a greater prevalence of intact *C. intratropica* groves in central Arnhem Land – one of the few regions of Australian savanna still under

direct Aboriginal management – than in neighboring Kakadu National Park (KNP) indicates greater structural complexity and plant species diversity in Arnhem Land savannas (Trauernicht et al. 2013). Yet, importantly, the presence of degraded groves in KNP indicates that the ecological integrity of the savannas in KNP has degraded over time. Examining the potential of humans to influence *C. intratropica* establishment and persistence ultimately requires an understanding of the relationship between the patch dynamics of *C. intratropica* groves and the species' population behavior.

The cessation of Aboriginal burning regimes across much of northern Australia following widespread depopulation within the last century has been a major driver of fire regime change (Bowman and Panton 1993, Russell-Smith et al. 1997, Whitehead et al. 2003, Trauernicht et al. 2013). Proactive landscape burning to manipulate resources, 'clean' country and mitigate destructive fires is prevalent among indigenous management systems worldwide, often providing templates for contemporary land management (Trauernicht et al. submitted). In regions with pronounced rainfall seasonality, indigenous and contemporary managers effectively 'jumpstart' the process of landscape burning in the early dry season (EDS) before fuels have completely cured, thereby disrupting fuel continuity and reducing the occurrence and extent of higher intensity, larger fires in the late dry season (LDS; Gill et al. 2000, Mbow et al. 2000, Laris 2002, Bowman et al. 2004, Bird et al. 2008, van Wilgen et al. 2008, Price et al. 2012). For example, the relatively recent adoption of strict EDS-only burning in Kakadu, conducted largely from helicopters, is explicitly an attempt to 're-impose' Aboriginal burning practices and mitigate the 'wilderness effect' of decades of unmanaged, large scale and high intensity LDS wildfires (Kakadu National Park Board of Management 2007). More even temporal distributions of fire ignitions throughout the dry season on lands under the

tenure of indigenous people in both Africa and Australia suggest that the implementation of EDS fires allows for the continuation of controlled burning into the LDS (Laris 2002, Petty and Bowman 2007, Franklin et al. 2008). Thus, the extent to which modern, 'remedial' EDS burning and 'traditional' Aboriginal fire management overlap remains debated (Lewis 1989).

The EDS/LDS dichotomy provides a useful proxy for relative fire intensity, which can be combined with frequency to refine our characterization of fire regimes (Knapp and Keeley 2005, Govender 2006, Russell-Smith and Edwards 2006). Fire frequency alone remains, by far, the more common metric. For example, tropical savannas worldwide are generally characterized by their short (1-3 years) fire return times (Coutinho and Goldammer 1990, Gill et al. 2000, Trollope 2008) and changes in fire frequencies are used to frame anthropogenic effects on landscape burning such as fire suppression or increased frequency of ignitions (Guyette et al. 2002, Hoffmann and Solbrig 2003). Fire frequency also lends itself well to modeling disturbance effects on plant demography by sequencing population vital rates recorded before and after fire events (Menges and Kimmich 1996, Hoffmann 1999, Caswell and Kaye 2001, Caswell 2006). Frequency alone, however, may be inadequate to assess both the effects of fire on vegetation and how human management has altered fire regimes. Fire intensity has variable and critical effects on woody plant survival, growth, and reproduction (Knapp and Keeley 2006, Hoffmann et al. 2009b) and is positively correlated with the spatial extent of fire, affecting heterogeneity and diversity of savanna vegetation at broader spatial scales (Bessie and Johnson 1995, Yates and Russell-Smith 2003). In addition, research in savannas suggests that the annual extent of landscape burnt (the equivalent of fire frequency) is largely unaffected by human management (Gill et al. 2000, Van Wilgen et al. 2004,

Archibald et al. 2009).

Given the difficulties apparent in altering fire frequency via management intervention, we instead consider how Aboriginal burning may have affected the establishment and persistence of *C. intratropica* by altering the intensity of fires in open savanna vegetation. We hypothesize that on a landscape scale, intact groves make a disproportionately large contribution to population stability, and that the decline of *C. intratropica* is a successional process from intact to degraded groves, then to singleton trees and eventually to local extirpation. In this paper, we combine integral projection models of *C. intratropica* population behavior with an environmental state change matrix to examine how the contributions of demography, the grove dynamics described above, and the frequency of high and low intensity fires contribute to the species' long term stability in savanna vegetation. By manipulating patterns of fire disturbance in this patch-based population model, we intend to shed light on how the cessation of Aboriginal burning may be implicated in *C. intratropica* declines, as well as the general, contemporary trend of homogenization of savanna vegetation in northern Australia (Russell-Smith et al. 2010a, 2012).

## **Methods**

### **Study Species and Location**

*Callitris intratropica* (Cupressaceae) is the only conifer species in tropical savannas, occurring as singleton trees and in small, scattered groves often in fire-protected rocky areas and rainforest patches. However, the species is also common in open, fire-prone savanna where it co-occurs as an overstory tree with the dominant eucalypts (*Eucalyptus miniata* and *E. tetrodonta*). Relative to the eucalypts, however, *C.*

*intratropica* is much more vulnerable to fire damage, with low-growing crowns and a poor ability to resprout new shoots after burning (Prior et al. 2007, Lawes et al. 2011).

Whereas *C. intratropica* adults can survive lower intensity surface fires, any burning may result in high mortality among seedlings and saplings (Russell-Smith 2006, Lawes et al. 2011). *C. intratropica* is monecious and although cone and seed production may vary considerably year to year (Hawkins 1966), the species does not form persistent seed banks either in the soil or in cones retained in the canopy. Thus, recruitment in a given year depends on cone production and short-distance (i.e. <25 m) dispersal of seeds by wind during the wet season (Russell-Smith 2006).

Censuses of *C. intratropica* growth and survival were conducted at Dukladjarranj, an Aboriginal 'estate' on the Cadell River on the northeastern edge of the Arnhem Plateau and owned and managed by a Gunei-speaking clan within the Djelk Indigenous Protected Area of Arnhem Land, Northern Territory, Australia (Figure 2a). The Arnhem Plateau is a low massif (<400 m elevation) of deeply dissected Middle Proterozoic quartzose sandstone and is a regional centre of species endemism (Freeland et al. 1988, Woinarski et al. 2006). The region is dominated by mesic savanna with annual rainfall (c. 1500 mm) driven by the Asian monsoon, with 90% of precipitation occurring from November to May. The region is characterized by very short fire return times of 1–3 years (Gill et al. 2000, Russell-Smith et al. 2003). Detailed descriptions of the study area are provided elsewhere (Yibarbuk et al. 2001, Murphy and Bowman 2007).

Observations of cone and seed production used to estimate fecundity were made in a climatically and compositionally similar savanna in Litchfield National Park, about 200 km west of Dukladjarranj (Lawes et al. 2013).

#### Demographic Surveys



We recorded the growth and survival of 722 *C. intratropica* individuals ranging from 1 to 650 mm in stem diameter (measured at 1 m from the ground) and 563 *C. intratropica* seedlings ranging from 35 to 1300 mm in height over three growing seasons between 2006-2009. The former, hereafter referred to as 'adults', were scattered across a 2.5 km stretch of open savanna dominated by *Eucalyptus tetradonta* and *E. miniata* with a grass understory (Figure 2b). Seedlings were tagged and monitored in thirteen 30 m<sup>2</sup> circular plots in the same area. Sampling encompassed a range of grove condition and fire disturbances. Adult trees were identified as occurring within an intact, closed-canopy grove (N=215 among 12 groves), within a degraded, open-canopy grove (N=208 among 24 groves), or as lone, singleton trees (>5 m from any other adult conspecific; N=299) following Trauernicht et al. (2012). LANDSAT satellite-derived fire scar maps (~30 m resolution; Edwards and Russell-Smith 2009) were used to establish whether adult trees and seedling plots were exposed to low intensity EDS fires (May-July), high intensity LDS fires (August-October), or no fire in the year prior to measurements. These data were corroborated on the ground by recording fire damage for each individual.

Fecundity was determined by measuring cone and seed production and seed germination rates from 31 trees sampled from closed-canopy ('dense') groves, open-canopy ('open') groves, and singleton trees (Lawes et al. 2013).

### Analyses of Vital Rates

We modeled *C. intratropica* adult survival and growth increment and seedling survival and size at time  $t+1$  as continuous functions of tree diameter or seedling height at time  $t$  using linear and generalized linear models, including random effects where possible. We included (i) fire disturbance (unburnt, low intensity burn, high intensity burn) and (ii) grove state (intact grove, degraded grove, singleton tree) as categorical covariates in our

global models wherever appropriate (Table S1). Adult growth and survival models included both fire disturbance and grove state as covariates. Seedling growth included fire disturbance and stand density (basal area of adult *C. intratropica* per seedling plot), whereas seedling survival included only fire disturbance as a covariate (Table S1). Wherever possible, we included individual and year as random effects to account for pseudo-replication in re-censusing individuals and annual climatic variation, respectively. Global models of adult growth and survival included two-way interactions between fire disturbance and grove state and size at time  $t$  and grove state. Linear mixed models of adult and seedling growth included exponential variance structures to account for heterogeneous variance in the relationship between size at  $t$  and diameter increment and size at  $t+1$ , respectively (Zuur et al. 2009).

Fecundity models were constructed using the count of cones produced as a function of adult tree diameter and grove state, including an interaction term. These models were combined with mean counts of seeds per cone and percentage of seed germination for each grove type (Lawes et al. 2013) to construct a size-based predictive model of viable seed production for adult *C. intratropica* trees. We also incorporated the effects of fire on fecundity in the IPMs described below using the findings of Hawkins (1966), in which severe fires were found to reduce seed production of *C. columellaris* – considered synonymous with *C. intratropica* by some authorities (Farjon 2005) – by 98.4%. We determined the probability of seedling establishment as the proportion of newly established seedlings in our Arnhem Land seedling plots to the total *potential* seed production of the *C. intratropica* adults in each plot based on this predictive model. The best-supported models of growth, survival, and cone production were determined via multi-model inference based on the Akaike Information Criterion (AICc) according to the

Information-Theoretic approach (Anderson and Burnham 2002). All analyses were completed in R using the lme4 (Bates et al. 2011) and nlme packages (Pinheiro et al. 2010).

### Modeling Population behavior

We used an integral projection model (IPM) that combined the continuous, size-based functions of *C. intratropica* growth, survival, and fecundity described above into a single function - the kernel – to project population behavior (see Supplementary Methods; Easterling et al. 2000, Ellner and Rees 2006). IPMs provide the same projections as traditional matrix models, such as long-term population stability, or lambda ( $\lambda$ ), long-term population structure, or stable stage distribution (SSD), in addition to sensitivity and elasticity analyses, but are considered more accurate for slow-growing plant species (Zuidema et al. 2010). The use of fire disturbance and grove state (see above) as categorical covariates in our IPM kernel function effectively resulted in nine separate IPMs, corresponding to each of the possible combinations of the three levels in the covariates. We calculated the projected, long-term population growth rate ( $\lambda$ ) for each IPM with the popbio package in R (Stubben and Milligan 2007). Values of  $\lambda > 1$  indicate a growing population whereas  $\lambda < 1$  indicates a population expected to decline, although lambda may best be interpreted as a measure of relative growth rate among populations, rather than a prediction of actual future population growth (Menges 2000).

### Environmental State Change Transition Matrix

To model *C. intratropica* patch dynamics relative to fire disturbance, we constructed matrix  $F$ , a  $9 \times 9$  discrete state Markov chain of transition probabilities from time  $t$  to time  $t+1$  for all grove state categories across all fire disturbance categories (see

Supplementary Methods; Horvitz and Schemske 1986, Valverde and Silvertown 1997, Pascarella and Horvitz 1998). Grove state transitions were derived from the responses of intact groves, degraded groves and singleton *C. intratropica* trees to low and high intensity fires observed from surveys and experimental burns (Figure 3; Prior et al. 2011, Trauernicht et al. 2012, 2013). We calculated the probability of fire disturbance from LANDSAT satellite imagery (~30 m resolution) of early and late dry season fire scars for each annual time-step between 1990 and 2011 across the entire 28,000 km<sup>2</sup> region encompassing our field site and comprising the Western Arnhem Land Fire Abatement project (Edwards and Russell-Smith 2009). We used matrix  $F$  to project stable stage distributions (SSDs) of each of the nine possible 'fire-states', from which we derived the predicted proportions of grove states across the landscape under known or hypothetical fire disturbance probabilities. We also used grove state SSDs to examine the sensitivity of these outputs to changes in the grove state transition parameters (see Supplementary Methods).

### The Megamatrix

Finally, we combined our environmental state change matrix,  $F$ , with the IPMs derived for each of the nine combinations of fire disturbance and grove state using a 'megamatrix' to project population demography across different environmental patches (Figure 4 & Supplementary Methods; Valverde and Silvertown 1997, Pascarella and Horvitz 1998). This approach produced the probabilities of a plant of a given size within a given environmental state transitioning to another combination of size and state. Thus this model describes individuals moving from patch to patch as opposed to patches 'carrying' populations through successional states (Caswell 2006). In other words, the megamatrix models population behaviour using the transition probabilities of individual

trees remaining in or changing both size class and environmental state (defined by grove state and fire disturbance), rather than tracking the fate of patches – and the trees within them – across the landscape. The megamatrix enabled us to project long-term stability ( $\lambda$ ) for the entire population across all environmental states, thereby incorporating demography, patch dynamics and fire disturbance into a single model. We also tested the sensitivity of  $\lambda$  to changes in the fire-dependent grove state transition probabilities (see Supplementary Materials). This allowed us to assess the robustness of the final  $\lambda$  outputs as well as the influence of the patch dynamics described by the environmental state change matrix relative to the IPM outputs derived from population census data and the effects of fire described below. To our knowledge, this is the first application of this approach to patch-based environmental state changes using IPMs in place of traditional population matrix models.

#### Fire regime scenarios

In order to examine the effects of changing fire frequencies on our model projections, we maintained the probabilities of no fire occurring at time  $t+1$  (established from the LANDSAT data in matrix  $D$  above), while altering the probabilities of fire occurring as a low intensity or high intensity burn at time  $t+1$ . Thus, we varied the transition probabilities in our fire disturbance matrix  $D$  such that the total proportion of the landscape burnt annually remained unchanged (c. 40%), enabling us to test just the effects of changing the proportion of fires occurring as low or high intensity fires.

Maintaining the overall frequency of fire occurrence better reflects the effects of actual savanna fire management which alters fire seasonality and thus intensity (Gill et al. 2000, Van Wilgen et al. 2004). However, we also created hypothetical fire regime scenarios in which we compare the effects of varying both overall fire frequency (the

probability of fire occurring) as well as the probability of fire occurring as a low vs. high intensity burn.

## Results

### Vital Rates

Our analyses confirmed tree diameter, fire disturbance and grove state as important predictors of both growth increment and survival of *C. intratropica* adults (Growth increment: Akaike weight ( $W_i$ ) = 0.95,  $R^2$  = 0.45,  $N$  = 2112, Table 1, Figure 5; Survival:  $W_i$  = 0.65,  $R^2$  = 0.11,  $N$  = 2342, Figure 6). The slight but significant effect of tree diameter on growth increment differed among grove types, with a positive relationship in intact groves, a small negative relationship among singleton trees, and with almost no size effect among degraded groves. Low intensity fires actually increased growth increment among trees in intact groves but had very little effect on singletons and trees in degraded groves. High intensity fires decreased growth increment across all grove types, however, they had the greatest deleterious effect on intact groves (Figure 5c). For survival, fire disturbance increased *C. intratropica* mortality across all grove types, with high intensity fires having the strongest effect on tree mortality (Figure 6). Degraded groves experienced slightly higher mortality than intact groves, whereas singleton trees experienced much higher rates of mortality across all disturbance types, with the difference being most pronounced for high intensity fires (Figure 6c). Although we did not explicitly include density effects in adult vital rate functions, *C. intratropica* basal area correlated with grove state (e.g., mean of 12.65 m<sup>2</sup>/ha for intact groves, 12.18 m<sup>2</sup>/ha for degraded groves, and 4.99 m<sup>2</sup>/ha for singletons; Figure 1d) and therefore adult density effects were implicitly modeled by including the grove state covariate.

Our seedling plots experienced only low intensity fires over the census period, thus we included two levels of fire disturbance (unburnt vs. low intensity burn) in our global models of seedling growth and survival. Our analysis of *C. intratropica* seedling growth only supported height at time  $t$  and ‘adult competition’ (i.e., basal area of adult *C. intratropica* trees within seedling plots) as important factors affecting seedling size at time  $t+1$ , but we found no effect of fire on growth ( $W_i=0.82$ ,  $R^2=0.91$ ,  $N=367$ ). The effect of adult density on seedling growth was incorporated into the IPM using the mean adult density values for each grove type. Analyses of seedling survival identified both height at time  $t$  and fire disturbance as important predictors ( $W_i=0.70$ ,  $R^2=0.08$ ,  $N=972$ , Figure 7a), with early dry season fires negatively affecting survival. We assumed no seedling survival under late dry season fires in the parameterization of our IPMs (Russell-Smith 2006). In our models of fecundity, only adult tree size was supported as an important predictor the count of cones produced with no effect of grove state ( $W_i=0.55$ ,  $R^2=0.024$ ,  $N=31$ , Figure 7b).

#### Population dynamics

The individual IPMs enabled us to examine population behavior for each grove state under each fire disturbance. On their own, these models assumed a continuous state of fire disturbance and are therefore unsuitable for projecting the overall population stability of *C. intratropica*, which would experience variable probabilities of disturbance among patches across the landscape. The lambda values from these individual IPMs (Figure 8a), however, are useful for understanding how the different grove states contribute to overall population stability as well as susceptibility of each grove state to different conditions of burning. Our models indicated population growth ( $\lambda>1$ ) among all grove states under conditions of no fire and for intact groves under low intensity burns. IPMs

projected negative population growth ( $\lambda < 1$ ) for all other combinations of grove state and fire disturbance, with high intensity fires having a strongly negative effect on the stability of degraded groves and singleton trees.

#### Patch dynamics and the megamatrix

The grove state SSDs projected from the environmental state change matrix,  $F$ , were robust to changes in the transition probabilities of intact groves under low intensity burns, and for both intact and degraded groves under high intensity burns (Supplementary Methods; Figure S1). Grove state SSDs were sensitive to changes in the recruitment of intact groves (i.e., increasing contributions to intact groves from degraded groves and singleton trees; Figure S1d). However the probabilities used in matrix  $F$ , based on actual observed frequencies of occurrence of newly recruiting *C. intratropica* groves (i.e., patches of seedling/sapling cohorts), provided very conservative estimates for this value. Overall population stability values projected by the megamatrix also suggested our patch-based population model was very robust to changes in the grove state transition probabilities (Supplementary Methods; Figure S2). Negligible shifts in overall lambda ( $< 1$  under all parameterizations) suggested that overall population stability is principally governed by the population-level patterns in growth, survival and recruitment (via the IPM) and the probabilities of burning (via the environmental state change matrix)

Altering the probability of fire occurring as a low intensity fire had effects on both the projected proportion of grove states and the overall population stability projected by the megamatrix (Figures 8b, 9). Thus, although the total projected proportion of the landscape burnt (total fire frequency) remained unchanged, Figure 6b illustrates how, as the proportion of fire occurring as low intensity burns increases, so does the projected



proportion of intact *C. intratropica* groves. The SSD of grove states under the current fire probabilities projected higher proportions of singleton trees and lower proportions of intact and degraded groves (Intact: 5%, Degraded: 11%, Singletons: 84%) than the actual proportions of the population among grove states observed in the field (Intact: 30%, Degraded: 29%, Singletons: 41%). It must be noted, however, that the environmental state change matrix alone does not include singleton mortality – this is accounted for in the megamatrix by including singleton tree mortality from the IPM. Therefore, some of the singleton grove state proportion in the SSD actually represent patches that are unoccupied by *C. intratropica*. The megamatrix projected negative population growth ( $\lambda=0.97$ ) for the overall *C. intratropica* population across all grove types under observed probabilities of fire disturbance. The values of projected overall *C. intratropica* population stability,  $\lambda$ , increased as the prevalence of low intensity increased relative to high intensity fires (Figure 9a). Altering both the probability of fire occurrence and low vs. high intensity burns, indicated that decreasing total fire frequency in the model also increased *C. intratropica* population stability. However, these results also suggested that increasing the prevalence of low intensity fires may increase *C. intratropica* population growth even under very high total fire frequencies (Figure 9b).

## Discussion

The recruitment bottleneck imposed by fire is a major determinant of the demography of woody plants and, therefore, the composition and structural complexity of savannas and other grassland mosaic systems worldwide (Bond 2008, Hoffmann et al. 2009a, Wood et al. 2011, Murphy and Bowman 2012, Ellair and Platt 2013). Our analyses of population behavior using grove state and fire disturbance as categorical variables simplify complex ecological processes into a heuristic model (Figure 3). Yet given the high fire

frequencies in some Australian savannas (eg. 1-3 years between fires) and the high sensitivity of *C. intratropica* seedlings and saplings to burning, the negative fire feedback/alternative state imposed by intact groves is obviously a major factor in shaping the species' demography (Trauernicht et al. 2012). Importantly, our findings suggest that this feedback, when coupled with a predominance of low intensity fires, has the potential to allow *C. intratropica* expansion in one of the world's most flammable ecosystems. Evidence that human intervention largely influences the seasonality, intensity and spatial extent of fire, as opposed to fire frequency (Gill et al. 2000, Van Wilgen et al. 2004, Archibald et al. 2009), suggests that the use of fire intensity and *C. intratropica* spatial configuration as covariates in our demographic analyses targets the parameters that are most critical to elucidating the relationship between Aboriginal patch burning and *C. intratropica* persistence (Price and Bowman 1994, Trauernicht et al. 2012).

The decline of *C. intratropica* has provided a strong signal of change in both the fire regime and in the structural complexity and plant diversity of Australian savannas over the course of radical changes in the social-ecological relationships shaping this ecosystem (Bowman and Panton 1993, Edwards and Russell-Smith 2009, Russell-Smith et al. 2012, Trauernicht et al. 2013). Importantly, the life history of extant *C. intratropica* groves across the region span the shift from widespread Aboriginal landscape burning to what has become, largely, a 'modern wilderness' within the past century (Bowman et al. 2001). Widespread contemporary declines in *C. intratropica* pose an evocative hypothesis that prescribed burning by humans enabled this relatively fire-sensitive conifer to 'invade' and persist in highly fire-prone vegetation. The negative feedback between *C. intratropica* adult canopy cover and savanna fires illustrates how, under low

to moderate intensity fires, intact groves contribute to fine-scale ecological heterogeneity across the landscape, promoting both conspecific recruitment as well as the maintenance of fire-sensitive plant communities (Trauernicht et al. 2012, 2013). By including the difference in this feedback – effectively an ecological state change – among intact and degraded groves, our patch-based modeling approach provides critical insight into whether and how the establishment and persistence of intact groves contributes to the long-term persistence of the *C. intratropica* population as a whole. Equally compelling, the integration of the frequency of low and high intensity burns allow us to explore how, by altering the occurrence of high intensity burns, patchy landscape burning by Aboriginal managers may have contributed to the current distribution of *C. intratropica* in these savannas. Thus, *C. intratropica* provides a window into a management legacy that extends back over 40 millennia and, arguably, must underlie any attempt to understand the current and grave declines in biodiversity across the region.

It is clear from previous research that the strongest impact of fire on *C. intratropica* demography is via seedling and sapling mortality (Bowman and Panton 1993, Price and Bowman 1994, Russell-Smith 2006, Prior et al. 2007, 2011). *C. intratropica* populations are not limited by reproductive capacity, as illustrated by fecundity measurements (Figure 7b) and reports of abundant recruitment when protected from fire (Bowman et al. 1988, Lawes et al. 2013). Yet even low intensity fires can have major effects on seedling survival (Figure 7a; Russell-Smith 2006), reinforcing the importance to *C. intratropica* demography of the negative fire feedback among intact groves. Although the effects of this recruitment bottleneck due to fire on *C. intratropica* population dynamics have been demonstrated and discussed elsewhere (Price and Bowman 1994,

Prior et al. 2007), the critical role of the species' patch dynamics has been missing from previous models. Similarly, our approach of constructing separate IPMs for each combination of fire disturbance and grove state provides an incomplete picture of *C. intratropica* demography. Yet the IPMs do illustrate how under conditions of no fire, all grove types are capable of maintaining similar positive population growth rates (Figure 8a). The IPMs also reveal that despite little change in growth rates among degraded groves and singletons exposed to low intensity fires (Figure 5b), the reduction in seedling survival (Figure 7a) is sufficient to project negative population growth ( $\lambda < 1$ ; Figure 8a). Assumptions of complete seedling mortality under high intensity (LDS) fires drove IPM projections well below levels of stable population behavior across all grove states.

Although we expected greater survival among trees in intact than in degraded groves (Trauernicht et al. 2012), our survival models clearly support the importance of grove formation to *C. intratropica* persistence, even under high intensity fires (Figure 6). Just as intact groves contribute disproportionately to seedling and sapling recruitment (Figure 1c), singleton trees conversely account for a larger proportion of the mortality events among adult trees (Figure 6c). These findings support our hypothesis that degraded groves and singleton trees represent successional stages in the process of *C. intratropica* decline. In the absence of the negative fire feedback found in intact groves, degraded groves and singleton trees do little to promote seedling/sapling survival and therefore do not represent intermediate stages of grove formation. Moreover, the dependence of seedling/sapling recruitment on this fire feedback suggests that most extant *C. intratropica* adults in open savanna vegetation – whether currently part of a grove or a singleton tree – originated through this process of grove formation.

The establishment of new groves is occasionally observed in the field as patches of seedling/sapling cohorts (C. Trauernicht, pers. obs.). Any extant adult tree may therefore contribute to the process of grove formation as a seed source – indeed, our patch dynamic model allows for this via the contribution to intact groves from degraded groves and singleton trees (Figure 3). However, we hypothesize that the ultimate driver of grove formation is the availability of habitat patches remaining unburnt long enough for seedling cohorts to establish, suppress fuels, and thereby alter the local disturbance regime. Although the availability of long-unburnt habitat in highly fire-prone savannas seems an unlikely phenomenon, the presence of new *C. intratropica* groves demonstrates that it does occur. Even if low-intensity burns predominate, the inevitable occurrence of intense fires means that *C. intratropica* groves will not persist indefinitely and, thus, the rate of grove establishment is a likely a critical driver of grove dynamics (Figure S1d; see below) and long-term population stability. Yet, whereas low fire intensity fire is critical to the persistence of established *C. intratropica* groves, the creation and maintenance of long-unburnt patches – and thus the formation of new groves – is more difficult to explain. Habitat modeling, however, suggests increasing the spatial heterogeneity of fire disturbance – which is also correlated with lower intensity fire regimes – may increase the age diversity of available habitat patches (Trauernicht et al., submitted).

The differences in growth rates of adult trees among grove states and fire disturbance types were also significant, albeit small (Figure 5). There are likely several processes shaping these growth relationships. For example, the inverse effects of diameter on growth among singletons versus trees in intact groves are possibly due to differences in intraspecific competition. Higher *C. intratropica* density in fire-protected areas can

reportedly arrest growth, especially among smaller individuals (Bowman et al. 1988, Lawes et al. 2013). Thus the smaller singleton trees may be experiencing faster growth rates due to reduced competition. Although we did not explicitly model density-dependent growth, *C. intratropica* basal area was clearly greater among degraded and intact groves (Figure 1d). In addition, reduced growth rates for larger singleton trees than for trees in intact groves may be due to canopy damage from greater exposure to repeated fires. Degraded groves may simply be experiencing the worst of both worlds, with competition and canopy damage reducing growth for trees across all size classes. The negligible impacts of high intensity fires on degraded groves and singleton trees, relative to the effect on intact groves, also suggests that tree growth may be permanently impaired from accumulated canopy damage from previous fires.

The environmental state Markov chain (matrix  $F$ ) provided a broader context from which to interpret the individual IPM results discussed above. The SSDs, or projected proportions, of grove states derived from matrix  $F$  under observed LANDSAT fire frequencies were fairly robust to changes in the transition probabilities among *C. intratropica* grove states (Figure S1). For example, plotting the projected grove state SSDs against changing probabilities of intact and degraded groves remaining in their respective states under high fire intensities (Figure S1b,c) suggested our parameterizations of grove state transitions were conservative with respect to the process of transitioning to singleton trees. Increasing 'recruitment' rates of intact groves (modeled as the transitions to intact groves from degraded groves and singleton trees) dramatically altered projections of grove state proportions (Figure S1d). The grove recruitment rates used in our parameterization of matrix  $F$  (Figure 3) were based on field observations of the frequency of seedling/sapling cohorts establishing new groves

relative to counts of mature degraded and intact groves sampled across a landscape of variable fire conditions (Trauernicht et al. submitted). Thus our model parameterizations for recruitment were similarly conservative because they likely underestimate the potential for grove establishment under conditions of no fire. The sensitivity of grove state SSDs to grove recruitment also indicates the potential of *C. intratropica* to expand under conditions that favor seedling/sapling survival and thus the establishment of new groves. The effects of altering the probability of fire occurring as a low intensity vs. high intensity burn on grove states SSDs in the environmental state change matrix  $F$  revealed two important patterns. First, the difference between projected and observed proportions of grove states under observed fire probabilities suggests that grove state proportions are ‘drifting’ towards lower proportions of intact and degraded groves and higher proportions of singleton trees (Figure 8b). Although this patch dynamic model alone does not account for ‘mortality’ among singleton patches (see Methods), the dominance of this grove state corroborates field observations of *C. intratropica* declines and, more generally, the homogenization of Australian savannas under contemporary fire regimes (Russell-Smith et al. 2010b, 2012, Trauernicht et al. 2013). However, the patch dynamic model also suggests that increasing the prevalence of low intensity burns may increase the abundance of intact *C. intratropica* groves (Figure 8b), which has been linked to greater structural heterogeneity and diversity of savanna vegetation (Trauernicht et al. 2013).

The megamatrix approach allowed us to effectively ‘insert’ the demographic models of *C. intratropica* (the IPMs) into the environmental state change matrix  $F$  (Horvitz and Schemske 1986, Valverde and Silvertown 1997, Pascarella and Horvitz 1998). We do not presume to model the reality of complex savanna dynamics. However, the

megamatrix,  $M$ , provides a synthetic model of patch-based population behavior, which incorporates the negative fire feedback in intact groves, and is ultimately driven by the probabilities of low and high intensity fire occurrence. Furthermore, the lack of sensitivity of the megamatrix to changes in grove state transition probabilities (Figure S2) suggests our model provides a robust test of *C. intratropica*'s response to fire at the population level. Specifically, the megamatrix has important implications for distinguishing the ecological effects of *how* a landscape burns from simply *how much* of it burns. In other words, evidence suggests management has little influence on the proportion of landscape burnt annually – directly analogous to overall fire frequency – but has major effects on fire seasonality and thus, the intensity and heterogeneity of fire events (Gill et al. 2000, Knapp and Keeley 2006, Russell-Smith and Edwards 2006, Archibald et al. 2009). Thus, understanding the influence of Aboriginal burning on Australian savannas requires exploring metrics of fire regimes other than overall frequency. Given the well documented declines in *C. intratropica* across northern Australia (Bowman and Panton 1993, Bowman et al. 2001, Edwards and Russell-Smith 2009, Trauernicht et al. 2013), the negative population growth ( $\lambda = 0.97$ ) projected by the megamatrix under current frequencies of low and high intensity fires is no surprise. However, the critical finding here is that increasing the frequency of low intensity burns relative to high intensity burns, without altering total fire frequency, increases the overall stability of *C. intratropica* populations (Figure 9a). Further, this relationship appears to hold even under conditions of very high total fire frequencies (Figure 9b). Thus, our results not only suggest that managing fire intensity can contribute to *C. intratropica* persistence, but that this practice may also mitigate shifts in overall fire frequency which may be climate driven (i.e., Bliege Bird et al. 2012).



The relationship between fire intensity and *C. intratropica* persistence evident in our patch-based population model has implications beyond understanding the potential of Aboriginal burning to influence the distribution of a single, fire-sensitive tree species. It also suggests a potential mechanism by which fire feedbacks may drive mosaics of fire-sensitive and fire-tolerant vegetation in other systems. In Australian savannas, there is a clear relationship between the abundance of intact *C. intratropica* groves and the heterogeneity of fire disturbance, availability of refugia for other fire-sensitive species, and overall structural complexity and plant diversity (Trauernicht et al. 2012, 2013). Thus, in addition to linking biodiversity to pyrodiversity (ie, landscape heterogeneity wrought by fire), our findings also suggest that human management has the potential to engineer fundamental aspects of ecosystem composition. The use of proactive landscape burning to mitigate destructive fires is widespread among indigenous land management systems in flammable ecosystems worldwide (Trauernicht, submitted). Therefore, understanding the relationship between disturbance and species composition/conservation may require reshaping our perspective of what constitutes the ecological baseline in these systems. For instance, it may be coincidental that the current species declines among birds, mammals, and fire-sensitive plants in northern Australia have occurred within decades of the abandonment of Aboriginal lands (Franklin 1999, Edwards and Russell-Smith 2009, Woinarski et al. 2010). However, the persistence of these species through more than 40,000 years of Aboriginal management strongly implicates the ‘wilderness effect’ as a contributing factor to these declines. Our findings therefore provide critical insight into a millennial-scale relationship between human–fire interactions and ecosystem composition. Although we maintain that this interaction is critical to rehabilitating Australian savannas as social-ecological systems, the role of humans in ‘natural systems’ will, doubtless, continue to raise contentious

debate.

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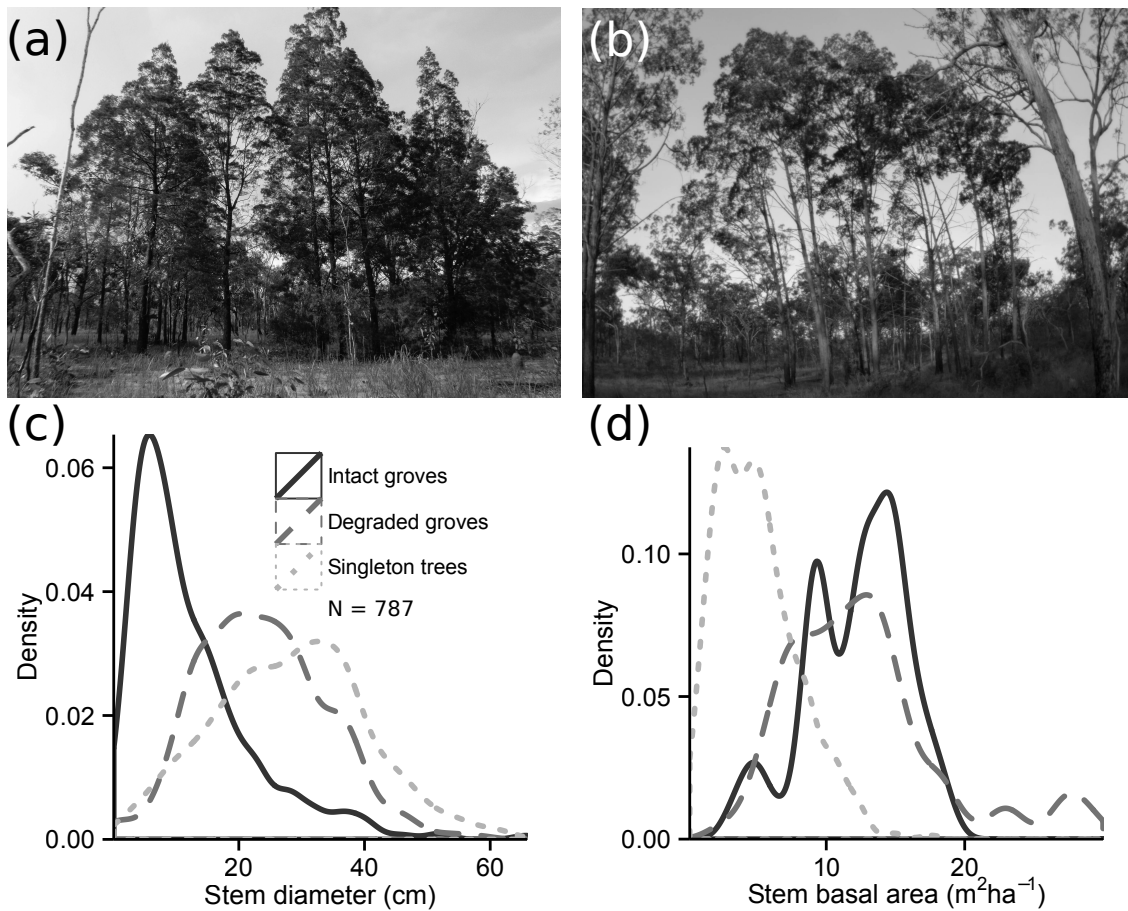


Figure 1. Characteristics of *C. intratropica* groves sampled in open eucalypt savanna vegetation. (a) A typical intact grove with closed canopy and woody understory development. (b) Example of a degraded grove with damaged canopy and open, grassy understory. The bottom panels are kernel density plots showing the distributions of *C. intratropica* (c) stem diameter and (d) basal area (sampled within a 10 m radius of each individual) for each of the *C. intratropica* grove states: (i) intact groves, (ii) degraded groves, and (iii) singleton trees.

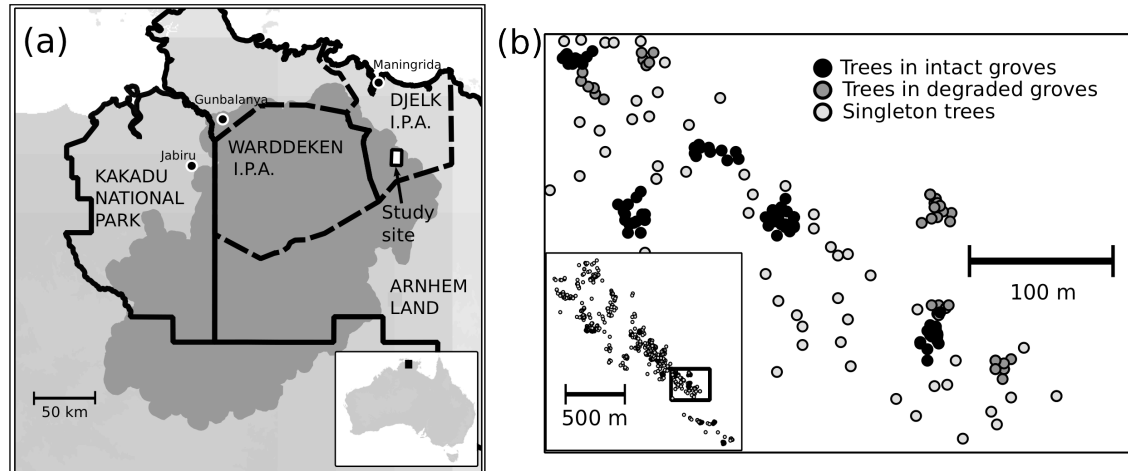


Figure 2. Maps of (a) the study site in Arnhem Land (the shading indicates the extent of the Arnhem Plateau ‘Stone Country’) and (b) the trees surveyed the *Callitris intratropica* census. Black circles show the location of trees classified as intact groves, white circles are trees classified as degraded groves, and grey circles are singleton trees.

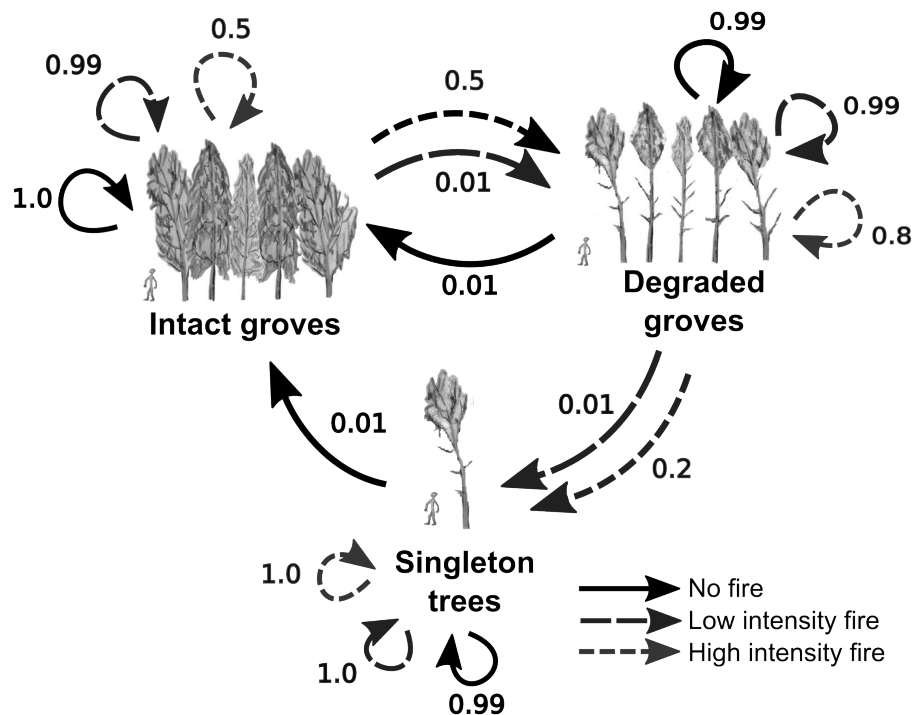


Figure 3. A model of *Callitris intratropica* 'grove state' transitions under conditions of no fire, low intensity fire and high intensity fire. Values adjacent to arrows indicate the fire-dependent probabilities used in the construction of Markov chain probability matrices of patch dynamics. These probabilities were based on field observations of the response of groves to fire events in Kakadu National Park and central Arnhem Land. Low frequencies of grove 'recruitment' is allowed via 'transitions' to intact groves from degraded groves and singleton trees. There is no grove 'extinction' category because we are not modeling the entire landscape – only patches occupied by *C. intratropica*. However, grove 'extinction' was included in our final patch-based model by integrating the population vital rates of *C. intratropica*. Thus, survival models of singleton trees under each fire disturbance type ultimately defined the proportion of singleton 'patches' remaining after high and low intensity fires.

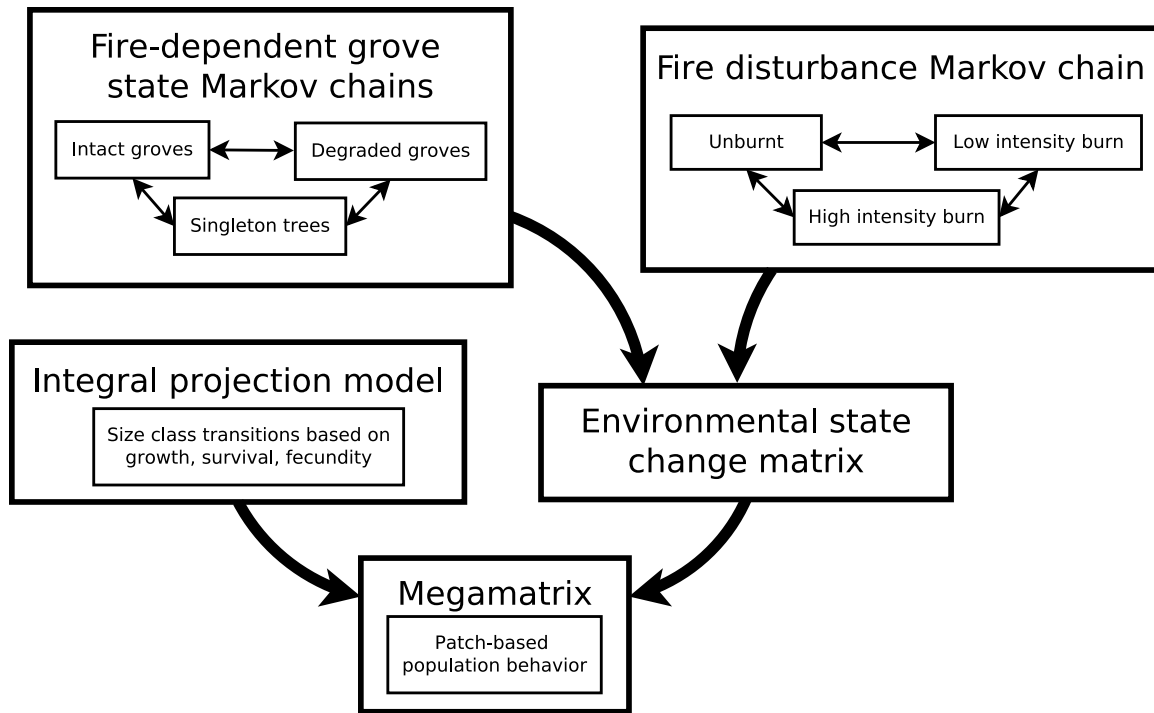


Figure 4. Flow chart of analyses employed to develop a patch-based model of *Callitris intratropica* population behavior. Markov chains of *C. intratropica* grove state transition probabilities were developed for each type of fire disturbance and then combined with a Markov chain of actual fire disturbance probabilities (derived from LANDSAT satellite imagery) to construct the environmental state change matrix. This matrix was then combined with matrices of size-based transition probabilities derived from integral projection models of *C. intratropica* population behavior to construct an integrated 'megamatrix' accounting for the transition of individual trees among size classes and environmental states. The megamatrix was used to project overall population stability (Lambda) across grove states and disturbance types. Probabilities in the fire disturbance Markov chain were manipulated to examine the response of population stability to hypothetical changes in fire disturbance.

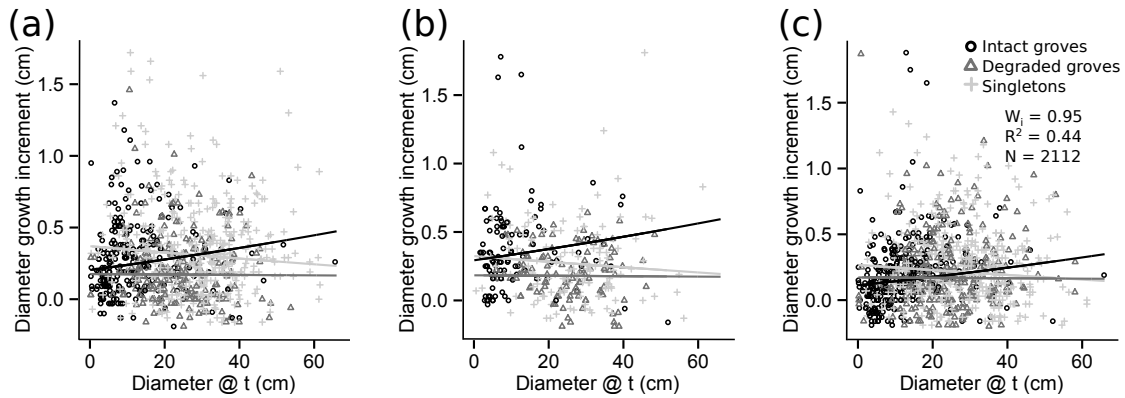


Figure 5. *Callitris intratropica* diameter growth increment as a function of diameter at time  $t$  for (a) unburnt conditions, (b) low intensity burns, and (c) high intensity burns.

Akaike weight ( $W_i$ ) are presented relative to the null model.

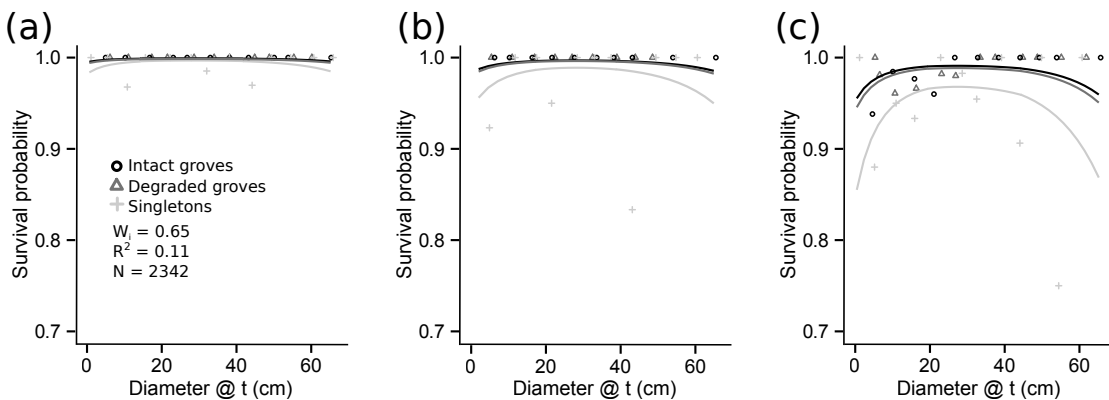


Figure 6. Probability of *C. intratropica* survival under (a) unburnt conditions, (b) low intensity burns, and (c) high intensity burns. Akaike weights ( $W_i$ ) are presented relative to the null model.

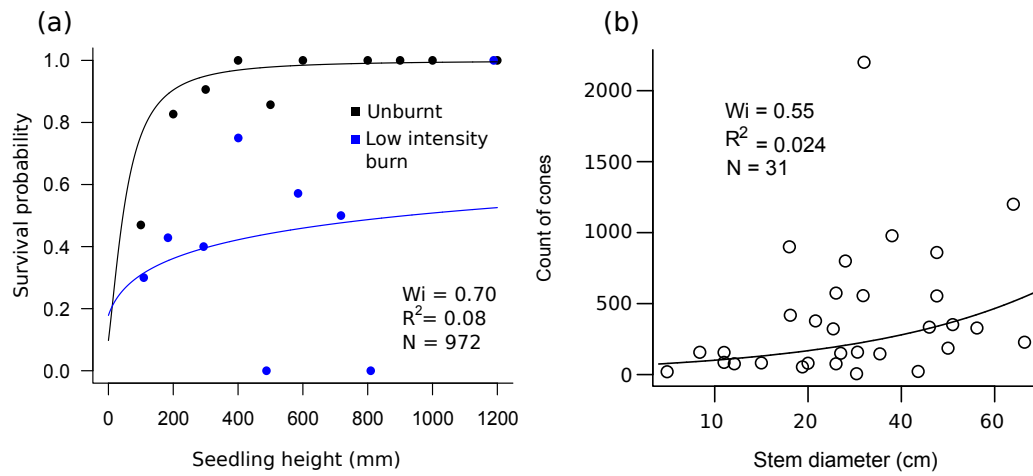


Figure 7. *Callitris intratropica* (a) seedling survival under no fire and low intensity burns and (b) adult cone production as a function of stem diameter. Akaike weights ( $W_i$ ) are presented relative to the null model.



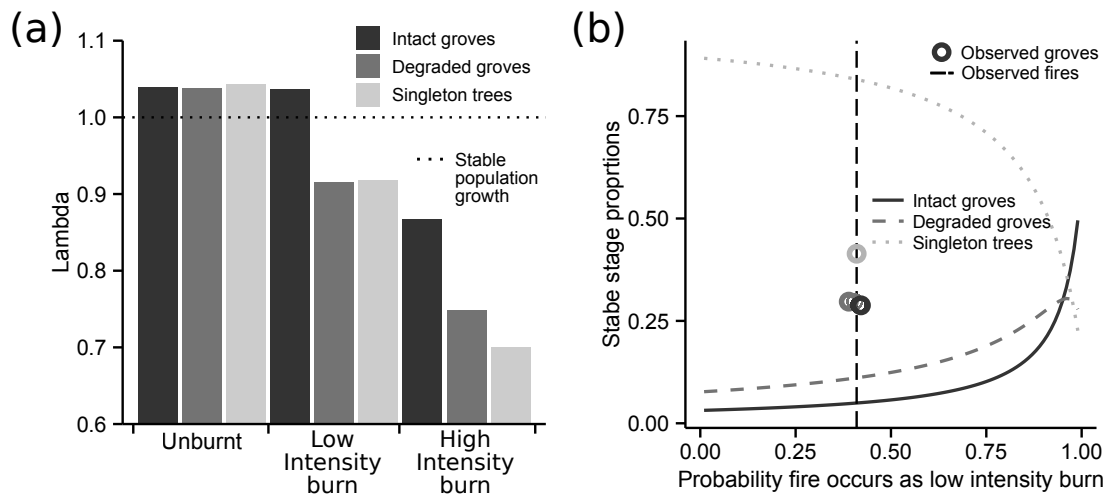


Figure 8. *Callitris intratropica* (a) population stability ( $\lambda$ ) derived from integral projection models for each combination of fire disturbance type (unburnt, low intensity, and high intensity burns) grove state (intact groves, degraded groves, and singleton trees) and (b) stable stage proportions of grove states derived from the environmental state change matrix.  $\lambda > 1$  indicates positive population growth and  $\lambda < 1$  indicates populations are declining. The vertical dashed lines indicate the actual observed probability of fire occurring as a low intensity burn, derived from LANDSAT data for western Arnhem Land. 'Observed groves' are the actual proportions of the surveyed *C. intratropica* population occurring among the three grove states. The environmental state change matrix is a Markov chain transition matrix integrating the probabilities of each fire disturbance type above with the fire-dependent transition probabilities among *C. intratropica* groves states.

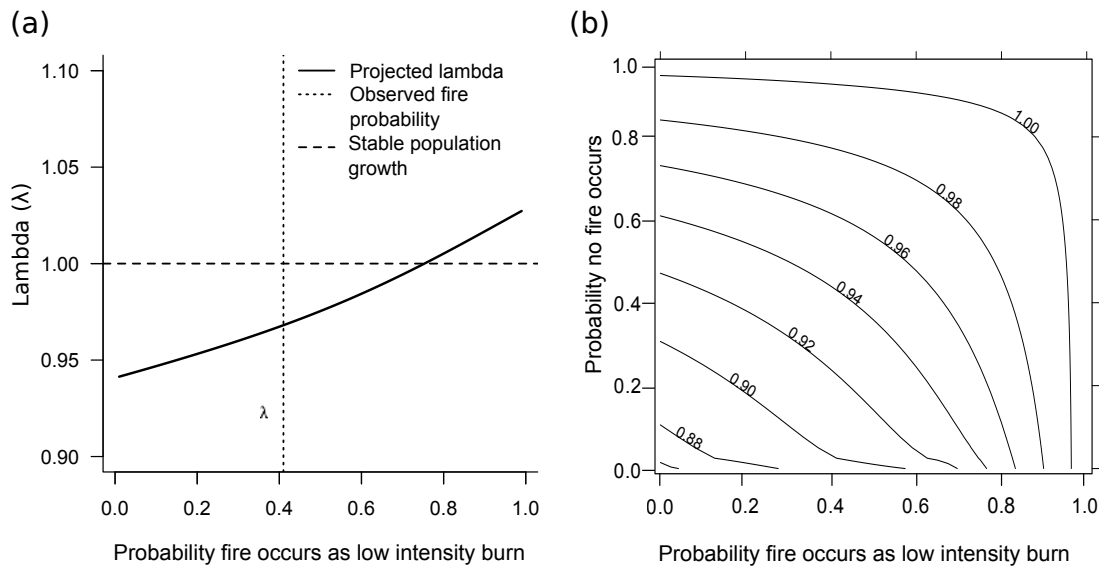


Figure 9. Overall *C. intratropica* population stability ( $\lambda$ ) projections from the megamatrix integrating patch-level (i.e., grove) dynamics and population behavior from integral projection models. Panel (a) illustrates the response of  $\lambda$  to changing the probability that fire occurs as a low intensity burn, keeping total fire frequency constant (c. 40%; observed from LANDSAT data for western Arnhem Land). The dashed vertical line indicates that under actual observed probabilities of low intensity burns,  $\lambda$  is 0.97. Panel (b) is a surface plot of the response of  $\lambda$  to hypothetical changes in both total fire frequency (y-axis) and the probability that fire occurs as a low-intensity burn (x-axis). In both panels,  $\lambda < 1$  indicates declining populations and  $\lambda > 1$  indicates population growth.

## CHAPTER 4: Supplementary Material – Population modeling methods

### Patch-based integral projection models

Our analysis of *Callitris intratropica* demography incorporated two covariates – (i) fire disturbance (no fire vs. low intensity fire vs. high intensity fire) and (ii) grove state (intact groves vs. degraded groves vs. singleton trees) – into size-dependent linear and generalized linear models of *C. intratropica* survival, growth and fecundity (see Methods). We used these vital rate functions to construct integral projection models (IPMs) of population dynamics (Easterling et al. 2000, Ellner and Rees 2006) and assess the population stability of each grove state under each fire disturbance type. We also constructed an environmental state transition matrix (Horvitz and Schemske 1986) using a Markov chain of grove state transition probabilities per fire disturbance type. This enabled us to examine how the frequency of low-intensity and high intensity fires affects the long-term projected proportions of intact grove, degraded groves and singleton trees. We then integrated the IPM and environmental state transition matrix into a ‘megamatrix’ that modeled the patch- and size-based population dynamics of *C. intratropica* (Valverde and Silvertown 1997, Pascarella and Horvitz 1998) and thereby allowed us to examine how changes in the frequency of low and high intensity fires affects overall population stability of *C. intratropica* across all grove states.

The IPM combines continuous vital rate functions (see Methods) into a single function – the kernel - to derive probabilities of individuals among size stages remaining in that stage, transitioning to another stage, and/or producing new individuals the next year. Thus, they are effectively operationalized as very large population matrix models from which one can derive long-term population stability,  $\lambda$  as the dominant

eigenvalue of the resultant matrix. Values of  $\lambda > 1$  indicate a growing population whereas  $\lambda < 1$  indicates a population expected to decline, although  $\lambda$  may best be interpreted as a measure of relative growth rate among populations, rather than a prediction of actual future population growth (Menges 2000). The advantages of IPMs over matrix models are twofold. First, whereas matrix models have limited capacity to handle environmental covariates, the use of linear and generalized linear models of vital rate functions in IPMs allows the inclusion of covariates derived from data collected within a single population. Second, continuous vital rate functions enable IPMs to effectively estimate transition probabilities across many more size class divisions (i.e., 100s) than traditional matrix models (typically  $< 10$ ). These probabilities are therefore based on size transitions observable in the field and provide more accurate predictions of population behavior, especially for slow-growing, long-lived plants (Zuidema et al. 2010).

We constructed the IPM kernel using four sections of transition probabilities, derived from *C. intratropica* vital rates, according to Zuidema et al (2010). These sections included (i) seedlings remaining seedlings ( $k_{SS}$ ), (ii) seedlings transitioning to adults ( $k_{AS}$ ), (iii) adults remaining to adults ( $k_{AA}$ ), and (iv) adults contributing to seedlings ( $k_{SA}$ ). Each of these sections was then combined to create the complete kernel:

$$\begin{bmatrix} k_{SS} & k_{SA} \\ k_{AS} & k_{AA} \end{bmatrix}$$

Thus, the left hand side of the kernel is determined by the product of seedling growth and survival, with  $k_{AS}$  representing the growth of seedlings beyond  $> 1300$  mm in height (ie into the 'adult' size range). The lower right hand quadrant,  $k_{AA}$ , represents adult growth and survival. The production of new seedlings by adults,  $k_{SA}$ , was determined using a fertility function based on the product of (i) adult survival, (ii) the size-based

probability of cone production, (iii) the number of seeds germinated per cone, and (iv) the probability of seedling establishment.

We used the midpoint rule according to Zuidema et al. (2010) to numerically integrate the demographic kernel and produce transition probabilities across *C. intratropica* size classes. Each statistical model was a function of adult or seedling size and incorporated fire disturbance and grove state as categorical covariates where possible and appropriate (see Table S1). The use of these covariates effectively resulted in nine separate IPMs, each accounting for a different combination of fire disturbance and grove state categories: (i) unburnt, intact groves, (ii) unburnt, degraded groves, (iii) unburnt singletons, (iv) low intensity burn, intact groves, (v) low intensity burn, degraded groves, (vi) low intensity burn, singletons, (vii) high intensity burn, intact groves, (viii) high intensity burn, degraded groves, and (ix) high intensity burn, singletons. We calculated the projected population growth rate ( $\lambda$ ) for each IPM with the popbio package in R (Stubben and Milligan 2007).

### **Environmental State Change Transition Matrix**

We used the differential responses to low and high intensity fires among intact groves, degraded groves and singleton *C. intratropica* trees derived from field observations and experimental burns (Prior et al. 2011, Trauernicht et al. 2012, 2013) to develop fire-dependent transition probabilities among *C. intratropica* grove states (Fig 2). We used these probabilities to constructed three  $3 \times 3$  Markov chain matrices for grove state transition probabilities from time  $t$  to time  $t+1$  under each fire disturbance type: (1)  $G_U$  for unburnt groves, (ii)  $G_E$  for early burnt groves, and  $G_L$  for late burnt groves. Thus, for example, grove states remain mostly stable under no fires in  $G_U$ , whereas proportions of

intact and degraded groves switch to the degraded and singleton states, respectively, under late dry season (high intensity) burns in  $G_L$ .

These grove state transitions do not include ‘empty patches’ (ie, dead groves/eucalypt savanna) because we are not modeling the abundance/proportion of *C. intratropica* patches relative to all patches in the landscape. Rather, we are only interested in linking fire disturbance to the proportion of the *C. intratropica* population occurring among these three grove states to understand how differences in population behavior among grove states contributes to overall population stability. ‘Grove mortality’ under high intensity fires, although not explicitly accounted for in the grove state transitions, is modeled using population-level mortality integrated via the megamatrix model that combines patch and population dynamics (see below). Singleton trees are a category both in the patch-dynamic model as well as the population dynamic model (the IPM). In the megamatrix, when an individual transitions into the singleton environmental state, that tree’s mortality (and thus the mortality of the ‘grove state’) is determined by the vital rate models for singleton trees under the given fire disturbance. In addition, although the formation of new groves via the recruitment of *C. intratropica* seedling/sapling cohorts occurs in the field, we do not include ‘new groves’ as a category. Instead, we model grove ‘recruitment’ by allowing for small contributions to intact groves from degraded groves and singleton trees under conditions of no fire (See Figure 2). In the field, seed production from adult trees in any grove state may result in abundant seedling establishment and therefore contribute to the formation of new groves. However, this process is ultimately dependent on seedling survival and thus the maintenance of unburnt habitat – a rare phenomenon in these savannas. Yet to account for the low frequencies at which grove establishment has been observed in the field, we allowed for

very small rates of grove recruitment in our patch dynamic model.

We then derived the probability of fire disturbance from LANDSAT imagery of early and late dry season fire scars for each annual time-step between 1990 and 2011 across the entire 28,000 km<sup>2</sup> region encompassing our field site and comprising the Western Arnhem Land Fire Abatement project (Edwards and Russell-Smith 2009). We used these data to derive a fire disturbance matrix,  $D$ : a  $3 \times 3$  Markov chain consisting of the probability of a given patch of landscape experiencing one of three disturbance states (unburnt, early burnt, or late burnt) at time  $t+1$  based on its disturbance state at time  $t$ :

		Time $t$		
		Unburnt	Early burnt	Late burnt
Time $t+1$	Unburnt	0.586	0.605	0.709
	Early burnt	0.173	0.201	0.093
	Late burnt	0.241	0.194	0.198

The stable stage distributions (SSD) of fire disturbance types based on matrix  $D$  (Unburnt: 62%; Early burnt: 16%; Late burnt: 22%) were similar to the actual mean proportions of the landscape under each disturbance type derived from the LANDSAT data (Unburnt: 64%; Early burnt: 12%; Late Burnt: 24%).

We combined the Markov chains for fire disturbance and grove state transitions to construct an environmental state change matrix,  $F$  (Horvitz and Schemske 1986, Valverde and Silvertown 1997, Pascarella and Horvitz 1998), by multiplying the elements of matrix  $D$  by the individual grove state matrices  $G_U$ ,  $G_E$ , and  $G_L$  as follows:

$$F = \begin{bmatrix} D_{1,1} \times G_U & D_{1,2} \times G_U & D_{1,3} \times G_U \\ D_{2,1} \times G_E & D_{2,2} \times G_E & D_{2,3} \times G_E \\ D_{3,1} \times G_L & D_{3,2} \times G_L & D_{3,3} \times G_L \end{bmatrix}$$

This yielded a  $9 \times 9$  discrete state Markov chain of transition probabilities for all grove states across all fire disturbance states from time  $t$  to time  $t+1$  (Table S2). We used matrix  $F$  to project stable stage distributions (SSDs) of each of the nine possible 'fire-states', from which we derived the predicted proportions of grove states across the landscape under known or hypothetical fire disturbance probabilities. We also used these SSDs to examine the sensitivity of the patch dynamic model to changes in the grove state transition parameters (Figure S1).

### **The Megamatrix**

Finally, we combined our environmental state change matrix,  $F$ , with the IPMs derived for each of the nine fire-states using a 'megamatrix' to project population demography across different environmental patches (Valverde and Silvertown 1997, Pascarella and Horvitz 1998). By classifying individuals both by size stage and patch type, this approach produces probabilities of a plant of a given size within a given environmental state transitioning to another combination of size and state. Thus this model describes individuals moving from patch to patch as opposed to patches 'carrying' populations through successional states (Caswell 2006). Our censuses occurred in June and July, after *C. intratropica* trees grow and recruit during the wet season (December-May) and before the occurrence of the environmental state transitions that are driven by fire disturbance later in the dry season (June–October). Therefore, as with Pascarella and Horvitz (1998), our megamatrix first modeled the size stage transitions (using IPMs) followed by the environmental state transitions (matrix  $F$ ).

IPMs were operationalized as  $265 \times 265$  matrices of transition probabilities among *C. intratropica* size stages and integrated with the  $9 \times 9$  environmental state change matrix



$F$  to construct megamatrix  $M$ , following Pascarella and Horvitz (1998), as follows:

$$M = (F \otimes I) \times A_{1,9}$$

Where  $F \otimes I$  is the Kronecker product of  $F$ , the environmental state change matrix described above, and  $I$ , an identity matrix of the same dimensions as each IPM output. In the equation above,  $A_{1,9}$  is a sparse matrix constructed of each of the nine IPMs ( $A_1, A_2, \dots, A_9$ ; corresponding to each combination of fire disturbance type and grove state) arranged diagonally as submatrices among equally sized submatrices ( $Z$ ) composed of all zeros:

$$\begin{bmatrix} A_1 & Z & \dots & Z \\ Z & A_2 & \dots & Z \\ \vdots & \vdots & \ddots & \vdots \\ Z & Z & Z & A_9 \end{bmatrix}$$

This produced a final,  $2385 \times 2385$  matrix, megamatrix  $M$ , from which it was possible to project long-term stability ( $\lambda$ ) for the entire population across all environmental states. To our knowledge, this is the first application of this approach to patch-based environmental state changes using IPMs in place of traditional population matrix models.

In order to examine the reliability of the overall population stability projected from the megamatrix, we also tested the sensitivity of the megamatrix to changes in the grove state parameters. We altered the fire-dependent grove state transition probabilities used in the environmental state change matrix described above and incorporated them into megamatrices using the population transition probabilities derived from our field measurements. We then calculated  $\lambda$ , the overall population stability, for each incremental change in a) the probability that intact groves remain intact under low intensity fires, b) the probability that intact groves remain intact under high intensity fires,

c) the probability that degraded groves remain degraded groves under high intensity fires, d) the probability of intact grove recruitment under no fire (Figure S2).

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Table S1. Summary of statistical analyses used to model *Callitris intratropica* vital rates in the integral projection model. Fixed effects included In tree/seedling size in addition to two categorical explanatory variables: Fire (no fire, early dry season fire, late dry season fire) and Grove state (intact grove, degraded grove, singleton tree). The seedling growth model also included the density of adult trees within plots (basal area per ha) as a fixed effect. Model acronyms are as follows: GLM - general linearized model, GLMM - general linearized mixed model, LMM - linear mixed model.

Model	Form (R Package)	Response Variable	Fixed Effect in Global Model	Random effect	Interactions	Transformation
Adult Growth	LMM (nlme)	Adult size@ $t+1$	Size@ $t$ , Fire, Grove state	Individual	Size:Grove state & Grove state:Fire	response <sup>0.7</sup>
Adult Survival	Binomial GLM*	Adult survival from time $t$ to time $t+1$ †	Size, Fire, Grove state	None	Size:Grove state & Grove state:Fire	None
Seedling Growth	LMM (nlme)	Seedling size@ $t+1$	Size@ $t$ , Fire, Density	Individual	None	$\log(\text{response})$
Seedling Survival	Binomial GLMM (lme4)	Seedling survival from time $t$ to time $t+1$	Size, Fire	Time step	None	None
Cone Production	Log-normal Poisson GLMM (lme4)‡	Count of cones produced	Size, Grove state	Individual	None	None
Cone Probability	Binomial GLM	Probability of cones produced	Size, Grove state	Individual	None	None

\*Model convergence issues prevented the use of a mixed-effects model

†Response variable was modeled as a quadratic term

‡Log-normal Poisson GLM used for overdispersed data (Elston et al. 2001)

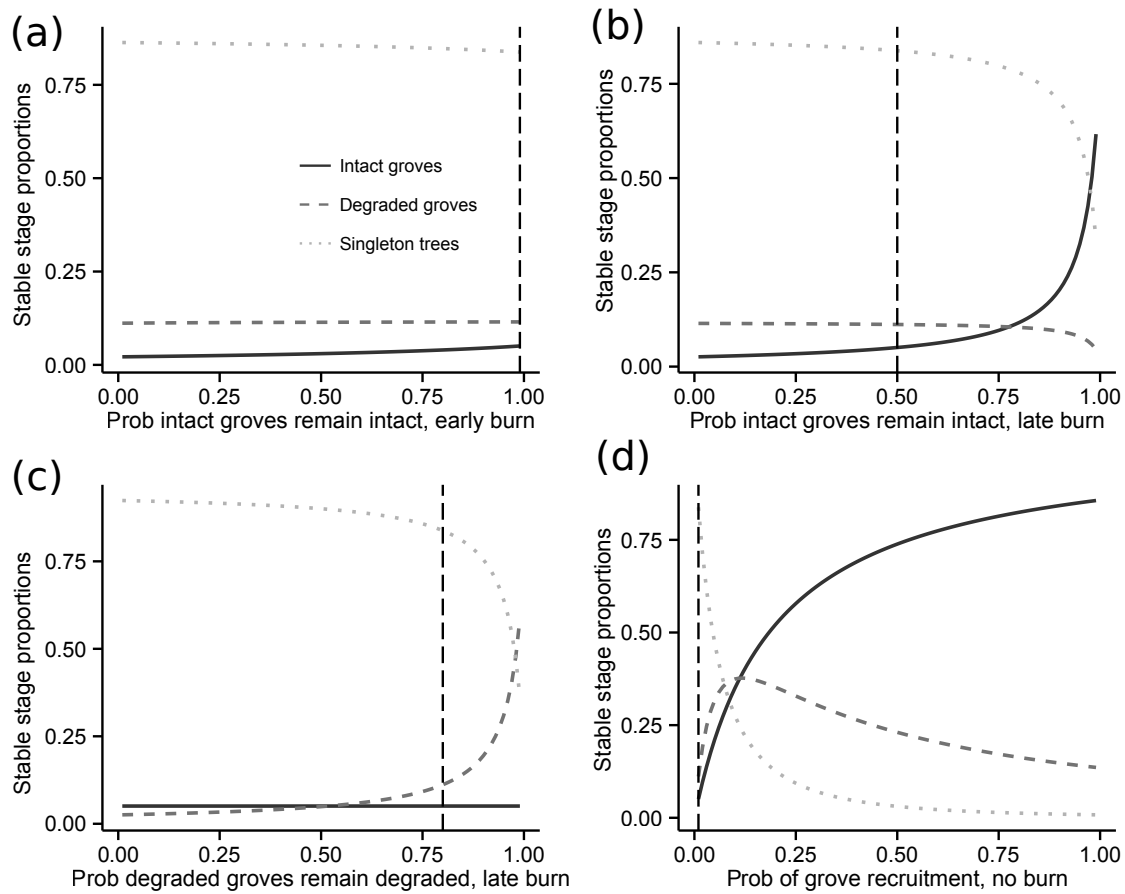


Figure S1. The sensitivities of the environmental state change Markov chain (matrix  $F$  described in the Methods) to changes in fire-dependent grove state transition probabilities, illustrated via stable stage projections of the proportions of *Callitris intratropica* grove states (right eigenvectors summed across fire disturbance types; solid lines) under the actual probabilities of regional fire occurrence in Arnhem Land. Panels illustrate sensitivities to changes in (a) the probability that intact groves remain intact under low intensity fires, (b) the probability that intact groves remain intact under high intensity fires, (c) the probability that degraded groves remain degraded under high intensity fires, and (d) the probability of grove recruitment under no fire. Dashed lines indicate the grove transition probabilities used in the final model parameterizations, estimated from field observations.

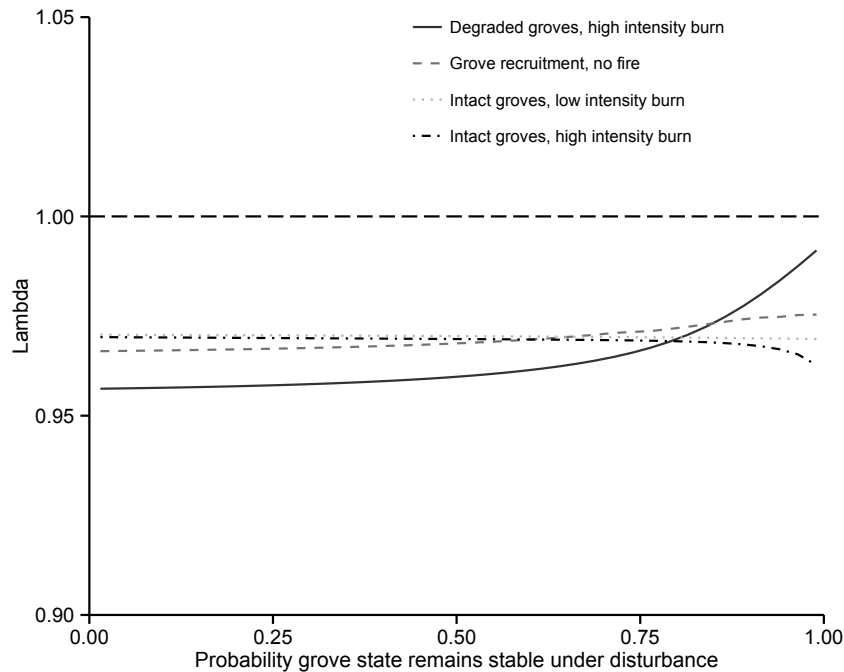


Figure S2. The sensitivity of lambda, the overall population stability projected from the patch-based population model of *Callitris intratropica* demography, to changes in environmental state change parameters. The patch-based population model is a megamatrix combining size class transitions (from integral projection models) and an environmental state change Markov chain. The environmental state change matrix integrates fire-dependent transitions among *C. intratropica* grove states (intact groves, degraded groves vs. singleton trees) and the probability of fire occurrence (as no fire, low intensity burn vs. high intensity burn). We altered the probability that grove states remain stable vs. degrade to the next successional state (i.e., intact groves → degraded groves, degraded groves → singleton trees) for individual grove state categories under the given fire disturbance type and projected lambda for each incremental change in these transition probabilities. Grove recruitment refers to the probability that degraded groves and singleton trees ‘transition’ to intact groves under no fire. Grove state transition probabilities used in the actual model parameterization (based on field observations) projected a lambda of 0.97. Lambda values  $\geq 1.0$  (the dashed horizontal line) indicates stable or increasing population growth.

## **CHAPTER 5 - Cultural legacies, fire ecology and environmental change in the Stone Country of Arnhem Land and Kakadu National Park, Australia\***

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Feral water buffalo tracks block the spread of a low-intensity surface fire at Dukladjarranj, central Arnhem Land. The species has become integrated into Aboriginal cosmology and is a valued food resource in Arnhem Land. In Kakadu National Park feral buffalo have been the targets of eradication campaigns.

## Abstract

**Aim:** We describe the contrasting landscape histories of Kakadu National Park (KNP) and adjacent central Arnhem Land (CAL) in terms of Aboriginal occupation and management institutionalization. We use the fire ecology and biogeographical patterns of *Callitris intratropica*, a fire-sensitive conifer, and the Asian water buffalo (*Bubalus bubalis*), an introduced mega-herbivore to examine the hypothesis that the continuation of Aboriginal burning and cultural integration of buffalo have contributed to greater landscape heterogeneity and plant diversity in CAL.

**Location:** The 'Stone Country' of the Arnhem Plateau, extending from KNP to CAL, is a globally renowned social-ecological system, managed for millennia by Bininj-Kunwok Aboriginal clans. Regional species declines have been attributed to the cessation of patchy burning by Aborigines across much of the landscape. Whereas the KNP Stone Country is a modern wilderness, managed through prescribed burning and buffalo eradication, CAL remains a stronghold for Aboriginal management where buffalo have been culturally integrated.

**Methods:** We surveyed the woody plant community and presence of buffalo tracks among intact and fire-damaged *C. intratropica* groves and the savanna matrix at 102 sites across KNP and CAL. Aerial surveys of *C. intratropica* grove condition were then used to compare landscape-scale patterns of savanna vegetation across the KNP and CAL Stone Country.

**Results:** The plant community in intact *C. intratropica* groves differed compositionally and structurally from degraded groves and the savanna matrix, with higher stem counts of shrubs and small trees and higher proportions of fire-sensitive, obligate-seeding plant species. A higher proportion of intact *C. intratropica* groves in CAL therefore indicated greater gamma diversity and habitat heterogeneity than the KNP Stone Country. Interactions among buffalo, fire and *C. intratropica* suggested buffalo also contributed to these patterns.

**Main Conclusions:** Our results provide evidence for the linkages between ecological and cultural integrity at broad spatial scales across a complex landscape. Buffalo may provide a tool for mitigating destructive fire regimes, however, their role in this system requires further study. Sustainability in the Stone Country depends upon adaptive management programs that maintain and rehabilitate the coupling of indigenous culture, disturbance regimes, and natural resources.

**Keywords:** Aboriginal landscape burning, Coupled human natural systems, fire ecology, landscape history, fire management, plant community diversity, habitat heterogeneity, tropical savanna

## **Introduction**

Fire is an ancient and pervasive disturbance among terrestrial ecosystems yet poses formidable challenges for conservation and socio-economic development (Bowman et al. 2009). Although climate undoubtedly affects fire regime dynamics (Marlon et al. 2008, Mooney et al. 2011), the relative influence of human management versus biophysical constraints on fire activity is still debated. Fire has been a fundamental aspect of human culture throughout our history (Pyne 1997, Bowman et al. 2011), and there is growing evidence that anthropogenic burning, even among pre-industrial societies, has had ecosystem-scale effects worldwide (Nowacki and Abrams 2008, Fletcher and Thomas 2010, Archibald et al. 2012). Indeed, the current challenges facing many flammable landscapes (e.g. increases in fire intensity and extent, diversity declines) are associated with the breakdown, via colonization and dispossession, of culturally integrated, indigenous approaches to fire management (Russell-Smith et al. 1997, Laris 2002, Rodriguez 2007). Coupled social-ecological systems can provide critical insight into how the changing human dimension of fire affects the sustainability of flammable ecosystems and demonstrate the need to integrate historical and cultural legacies with ecological research (Foster et al. 2003).

The Arnhem Plateau in northern Australia provides a compelling case study of the collision and integration of European and Aboriginal fire management (Fig. 1a). Colloquially referred to as the 'Stone Country', the 23,000 km<sup>2</sup> sandstone massif is located in one of the world's most flammable landscapes (e.g. 1-3 year fire return intervals; Russell-Smith et al. 2003, Yates et al. 2008), straddling the border of World Heritage Kakadu National Park (KNP) and Arnhem Land. A millennial-scale history of fire management by Bininj-Kunwok Aboriginal clans was only recently disrupted by European expansion into the region at the turn of the 20<sup>th</sup> Century. The Stone Country is a conservation priority with high levels of species endemism and vast tracts of unmodified tropical savanna (Woinarski et al. 2006). However, the increasing prevalence of high intensity wildfires, associated with the cessation of patchy landscape burning by Aborigines, has been linked to recent declines of fire-sensitive plant communities, mammals, and granivorous birds across the region (Bowman and Panton 1993, Franklin et al. 2005, Edwards and Russell-Smith 2009, Woinarski et al. 2010, Russell-Smith et al. 2012). Yet despite attempts to 'reimpose' traditional burning by contemporary, institutionalized programs, as exemplified in KNP (Kakadu National Park Board of Management 2007), continued species declines contrast with high ecological integrity among areas still under Aboriginal management (Yibarbuk et al. 2001, Whitehead et al. 2003, Franklin et al. 2008), particularly in central Arnhem Land (CAL). We suggest critical differences between KNP and CAL provide a unique natural experimental setting in which to understand complex social-ecological interactions involving fire, human history, megafauna and cultural perceptions that would be impossible to manipulate, especially at large spatial scales (Diamond 1986). Our objective is therefore to provide a landscape-scale contrast between KNP and CAL in order to understand how history and culture have shaped current management regimes and, consequently, savanna heterogeneity and diversity in a region globally renowned for its biology and culture, yet faced with daunting challenges in sustaining these values.



## Fire, megafauna and humans on the Stone Country

The Arnhem Plateau is over a billion years old, yet fire probably became prevalent in the region with the strengthening of the Asian Monsoon c. 20 Ma (Bowman et al. 2010).

Evolutionary fire regimes likely consisted of less frequent, more intense fires than at present with higher forest cover (Kershaw et al. 2002). Climatic shifts throughout the Quaternary altered vegetation and fire, yet arguably the greatest ecological disruption in Australia occurred 40-60 ka with the largely coeval arrival of humans, extinction of megafauna, and an hypothesized increase in landscape burning (Jones 1969, Flannery 1990, Head 1996, Johnson 2009, Rule et al. 2012). The palaeoecological evidence for changes in fire regime around this time remains equivocal (Kershaw et al. 2002, Mooney et al. 2011). However, the potential impacts of these changes on ecosystem composition is supported by contemporary research on the coupled effects of fire and megafaunal grazing (Knapp et al. 1999, Archibald et al. 2005, Waldram et al. 2008, Fuhlendorf et al. 2009) and the deliberate use of fire by indigenous people worldwide (Laris 2002, Bowman et al. 2011, Archibald et al. 2012).

The Bininj-Kunwok clans of the Stone Country maintain one of the world's oldest continuous cultures and few debate that Aboriginal burning is adaptive and ancient (Russell-Smith et al. 1997, Yibarbuk et al. 2001, Murphy and Bowman 2007). Sadly, the degradation of this tradition defines the region's next major ecological shift. European expansion into northern Australia in the late 19<sup>th</sup> Century devastated Aboriginal culture through disease and dispossession, leading to widespread abandonment of the Stone Country by the 1940s and 1950s (Cooke 2009). Consequently, fire regimes shifted from fine-scale burning by a widely dispersed population to high intensity wildfires ignited largely in the late dry season by lightning (Ritchie 2009). Yet the abandonment of the Stone Country was not ubiquitous.

The plateau's eastern flank in CAL has remained under nearly continuous Aboriginal management (Yibarbuk et al. 2001). Scattered among more than a dozen outstations (small, family-based settlements) on ancestral lands, the Aboriginal population of the CAL Stone

Country is smaller, more sedentary and dependent on imported goods than before European contact. However, the continuation of land management traditions is clear, with evidence of healthier lifestyles tied to subsistence resource extraction among outstation residents (Johnston et al. 2007, Garnett et al. 2009) and high ecological integrity of savannas on Aboriginal lands (Yibarbuk et al. 2001, Whitehead et al. 2003, Franklin et al. 2008).

The colonial introduction of a novel mega-herbivore, the Asian water buffalo (*Bubalus bubalis* L.), has further crystallized contrasts both in cultural perspectives and ecological conditions in KNP and CAL. Expanding from a few individuals in the mid-1800s to widespread populations within decades, buffalo became an icon of the Australian frontier, providing a common enterprise for white settlers and Aborigines via a hide industry that thrived until the 1950s (Bradshaw et al. 2007, Petty et al. 2007). As the industry declined, buffalo populations irrupted from 1960-80, leading to severe impacts in wetlands and rainforests due to trampling and grazing (Werner et al. 2006, Petty et al. 2007). Yet as their range expanded, Aboriginal Traditional Owners (TOs) integrated buffalo into their cosmology and subsistence resource base (Bowman and Robinson 2002, Robinson and Whitehead 2003). An eradication campaign targeting KNP, but not Arnhem Land, was eventually initiated, largely to protect the regional cattle industry from disease. Although buffalo impacts were of concern to both European and Aboriginal land managers (Petty et al. 2007, Ens et al. 2010), the new perspective of buffalo as an environmental menace polarized many. Significantly, many TOs still viewed buffalo as a cultural component of the landscape and strongly disagreed with full-scale eradication (Haynes 2009). Buffalo densities in KNP were eventually driven to  $<0.01 \text{ km}^{-2}$ , however, populations in Arnhem Land were not targeted and continue to immigrate into the park (Robinson and Whitehead 2003, Petty et al. 2007).

Divergent Stone Country management paradigms

The Stone Country's ecological history shows clear divergences in patterns of human occupancy and the institutionalization of land management (Fig. 1b). Established under a mandate of joint management in 1979, KNP's regulation of landscape burning and the highly contentious buffalo eradication program have led to conflict between TOs and park officials (Lewis 1989, Bradshaw et al. 2007, Trigger 2008, Haynes 2009). The current strategy for fire management in KNP's Stone Country (as well as western Arnhem Land) is, explicitly, an interpretation of Aboriginal burning imposed on a wilderness area (Kakadu National Park Board of Management 2007). Frequent fires are ignited in the early dry season, largely from helicopter, to disrupt fuel continuity, maintain habitat mosaics, and limit the extent of high-intensity fires in the late dry season. In practice, and largely out of necessity given limited resources and the landscape's size (e.g. one ranger, one helicopter for >5,000 km<sup>2</sup> in KNP), the program focuses on creating fire breaks along topographic features such as rivers and ridgelines, as opposed to patch mosaic burning *per se*. Park policy also imposes strict seasonal burning cut-offs to minimize the risk of late season fires.

In contrast in Arnhem Land, the "outstation movement" of the 1970s established small Aboriginal settlements, facilitating the management of ancestral lands by TOs. Although centralized Aboriginal Ranger groups have recently implemented aerial burning in CAL, the communities on the Stone Country's eastern flank remain a stronghold for Aboriginal culture (Yibarbuk et al. 2001). Thus, to the west is a highly institutionalized park system managing a wilderness area both for tourism and species conservation through regulated fire management and systematic buffalo eradication, while to the east is one of the most culturally intact social-ecological systems left in Australia, in which landscape burning and buffalo remain closely integrated with Aboriginal livelihoods. Aboriginal lands in CAL have been found to have high ecological integrity at the local scale (Yibarbuk et al. 2001, Whitehead et al. 2003) and, at the regional scale, more evenly distributed fire ignitions throughout the dry season compared to the early season burning models under European

tenure (Petty and Bowman 2007, Franklin et al. 2008). Thus, if the contrasting management paradigms in the KNP and CAL Stone Country affect the ecology of the region differently, then it should be possible to identify an ecological signal, despite the ‘noise’ associated with biophysical variation across the landscape. Here we consider the biogeographical patterns of *Callitris intratropica* R.T. Baker & H.G. Smith and feral buffalo in order to examine ecological variation across the Stone Country and discuss the region’s ecological and management trajectories.

## Methods

### *Callitris intratropica* as a Witness Tree

*Callitris intratropica*, one of the savanna’s few non-eucalypt overstorey trees, is a fire-sensitive, Gondwanan cypress, which has provided insight into ecological change at regional and continental scales (Bowman and Panton 1993, Prior et al. 2011). Importantly, the life histories of extant *C. intratropica* individuals (>200 years) in northern Australia span the decline in Aboriginal burning and the introduction of buffalo. TOs have long recognized declines in *C. intratropica* as a signal of destructive fire regimes due to the species’ vulnerability to intense fires, inability to resprout after burning and longevity of dead stems (Haynes 1985). Widespread mortality in *C. intratropica* across northern Australia provides clear evidence of fire regime change (Bowman and Panton 1993, Edwards and Russell-Smith 2009, Russell-Smith et al. 2012). Closed-canopied groves of *C. intratropica* can also exclude low-intensity savanna fires via fuel suppression and maintain small (e.g. 0.02-0.5 ha), compositionally distinct forest patches within the savanna matrix (Trauernicht et al. 2012). Yet among open-canopied, degraded groves, flammability and plant community structure are identical to open savanna conditions, despite the persistence of *C. intratropica* adults. The clear distinction between intact and degraded groves allows for rapid evaluation of the likelihood of groves to exclude fires. Thus, the condition of *C. intratropica* groves

across the landscape can indicate both the prevalence of high intensity fires as well as habitat heterogeneity not apparent from assessments of *C. intratropica* mortality alone.

### Plant Community Surveys

We surveyed the woody plant community associated with *C. intratropica* groves at 102 sites across the KNP and CAL Stone Country, restricting sampling to open, *Eucalyptus tetrodonta*/*E. miniata* savanna. Further logistic constraints included site access via seasonally flooded 4x4 tracks, multi-day walks and permission from Aboriginal landowners. Survey sites consisted of discrete groves of *C. intratropica*, ranging in size from 100 to 3000 m<sup>2</sup>, located >500 m from one another. At each site, we randomly selected a reproductive *C. intratropica* adult within 5 m of the grove centre and a reproductive *Eucalyptus miniata* or *E. tetrodonta* individual 30–100 m from the grove edge. Each tree marked the centre of a 25 m<sup>2</sup> circular plot in which we recorded canopy cover at the plot centre using a spherical densiometer, the count and species of all woody plants >50 cm tall and the count of all *C. intratropica* seedlings <50 cm tall. At each plot, percent cover and mean height of graminoid fuels was measured in a randomly placed, 1×1 m<sup>2</sup> quadrat. In addition, we scored the presence–absence of buffalo tracks as well as bowers of the great bowerbird (*Chlamydera nuchalis*) within or adjacent to each 25 m<sup>2</sup> circular plot.

### Aerial Surveys

Surveys of *C. intratropica* grove condition were conducted by helicopter across the KNP and CAL Stone Country (Fig 1a). As with ground surveys, we stratified sampling to open sandsheet savanna dominated by *E. tetrodonta* and *E. miniata*, avoiding rocky outcrops that afforded protection from fires. Each of the 33 groves in KNP and 54 in CAL were circled by the pilot while observers recorded (i) population structure by estimating the proportion of trees in each of 3 height classes relative to the established adult canopy (c. 15m): saplings (1–3m tall), juveniles (3–6m tall), adults (>6m tall), as well as dead adult trees; (ii) shrub

understory as absent, partial or continuous; (iii) lowest mean height of *C. intratropica* foliage (indicating prior canopy scorching); (iv) buffalo track density as absent, few, or many; and (v) *Sorghum brachypodium* (a native species currently driving ecologically destructive grass-fire cycles in KNP) cover as low, moderate or high.

## Analyses

In order to assess each *C. intratropica* grove sampled in the aerial surveys, the relevant attributes described above were weighted as 0, 0.5, or 1, with a higher weight indicating better ecological condition (Table 1). Attribute weights were added to derive a condition score for each grove, ranging from 0 (highly degraded) to 5 (highly intact). We examined the distributions of grove scores in KNP and CAL to compare the condition of *C. intratropica* between these management areas and statistically examined effect of management on grove score using a simple least-squares linear model ('lm' function in R software; R Core Team) with a log-transformed response variable. We also separately modelled the effect of management area on aerial assessments of buffalo track density (absent/moderate/high) using ordinal logistic regression and *S. brachypodium* cover (low/moderate/high) using a Chi-square test.

For the ground survey data, we used the same criteria above to classify groves as either intact (grove score 3-5) or degraded (grove score 0-2). Thus our primary explanatory variable, 'plot type', categorized plots as within intact *C. intratropica* groves, degraded *C. intratropica* groves, or *E. tetradonta/miniata* savanna. Wherever possible, analyses employed multi-model inference using the Akaike Information Criterion based on the Information-Theoretic approach (Anderson and Burnham 2002). Unless stated otherwise, we used linear mixed models (LMM; 'lme' in R; Pinheiro et al. 2010) for variables with normally-distributed errors and generalized linear mixed models (GLMM; 'glmer' in R; Bates et al. 2011) for variables with binomial- or Poisson-distributed errors, with site as a random

factor.

To examine the woody plant community associated with *C. intratropica* groves, we calculated the frequency of occurrence for the top 25 most frequent species among intact groves, degraded groves, and eucalypt savanna. We also examined the importance of *C. intratropica* groves to savanna gamma diversity by compiling species accumulation curves using random sampling from three different pools of plot types: (i) eucalypt plots only, (ii) eucalypt and degraded *C. intratropica* plots only, and (iii) eucalypt and intact *C. intratropica* plots only. To examine structural differences in the woody plant community, we modelled the count of all non-*C. intratropica* woody plant species as a function of plot type and the presence–absence of buffalo tracks using a log-normal Poisson GLMM for overdispersed data. *C. intratropica* seedling counts were modelled similarly. In order to examine the association of other fire-sensitive species with *C. intratropica* stands, we determined the proportion of obligate-seeder species and stems per plot (i.e. plants that do not resprout after burning and decline under high fire frequencies; Northern Territory Ecological Response Database, J. Russell-Smith et al., unpubl. data). We then modelled each of these proportions as a function of plot type using binomial GLMMs. In order to corroborate buffalo observations between the aerial and ground surveys, we modelled the presence–absence of buffalo tracks in plots as a function of management area and plot type using a binomial GLM. The effects of plot type on percent graminoid cover and graminoid height were modelled using a binomial GLMM for proportional data and LMM, respectively. Finally, in order to further explore the effects of buffalo in this system, we revisited an analysis on the probability of savanna burning as a function of canopy cover – driven by *C. intratropica* – conducted in CAL (Trauernicht et al. 2012) and included the presence–absence of buffalo tracks in the global model.

## Results

The frequency of occurrence of plant species illustrated a distinct community association with intact *C. intratropica* groves (Fig. 2a). Plotting species accumulation curves using plots in eucalypt savanna and intact *C. intratropica* groves increased woody plant richness beyond that sampled in eucalypt plots alone, while including degraded stands had a much smaller effect on richness (Fig. 2b). The plant community within intact *C. intratropica* groves also had significantly higher proportions of species and stems of obligate-seeding plants than the eucalypt savanna (Fig. 2c). Interestingly, 30% of the intact *C. intratropica* groves surveyed in KNP contained greater bower bird (*Chlamydera nuchalis*) bowers, while none were encountered in other plot types. Bowers were not encountered among *C. intratropica* groves in CAL. In terms of plant community structure, our statistical models suggested that *C. intratropica* patch dynamics (Trauernicht et al. 2012) extend across the landscape, with lower graminoid (i.e. grassy fuel) cover and height (Fig. 3a) and higher woody plant density among intact groves, but that buffalo reduced woody stem counts (Fig. 3b). Our results also demonstrated a clear association between buffalo and intact *C. intratropica* groves (Fig. 3c) and the presence of buffalo tracks was associated both with higher counts of *C. intratropica* seedlings and a lower probability fire occurrence (Figs 3d, 4).

Scaling patch-level (i.e. individual grove) dynamics to the landscape scale (i.e. multi-kilometer transects; Fig. 1a) via aerial surveys, the distribution of grove condition scores clearly showed a higher proportion of intact *C. intratropica* groves in CAL (Fig. 5). Aerial surveys also confirmed higher buffalo densities in Arnhem Land noted in other studies (Koenig et al. 2003, Franklin et al. 2008) with 26% of sites in CAL containing moderate to high buffalo track density vs. <1% in KNP ( $\chi^2=6.09$ , d.f.=1,  $P=0.014$ ;). Aerial surveys indicated low *S. brachypodum* cover at all our CAL sites vs. 22% and 53% of sites in KNP with partial and high cover, respectively ( $\chi^2=56.2$ , d.f.=2,  $P<0.0001$ ).



## Discussion

The distinct plant community associated with intact *C. intratropica* groves provides evidence that the presence of this grove type within open eucalypt savanna increases plant gamma diversity and structural complexity across the landscape. Reaching densities of more than one per hectare (C. Trauernicht, unpubl. data), *C. intratropica* groves clearly provide refugia for fire-sensitive, obligate-seeding plants and at least one bird species within the matrix of more open, fire-adapted vegetation. Thus, the higher proportion of intact *C. intratropica* groves in the CAL Stone Country recorded from aerial surveys (Fig. 2) not only suggests a lower prevalence of high intensity fires, but also that the savanna in CAL is more structurally and biologically diverse than KNP. Given the differences in ecological history between these regions (Fig. 1b), our results implicate the role of Aboriginal management in shaping patterns of vegetation, and suggest there is a relationship between cultural and ecological integrity in these savannas. Previous research has demonstrated the ecological benefits of Aboriginal management at local scales (Yibarbuk et al. 2001, Whitehead et al. 2003, McGregor et al. 2010). Our findings suggest these ecological benefits may extend to the landscape-scale given the spatial extent of our surveys across a large area of CAL Stone Country accessed and utilised regularly by TOs via multiple outstations (Fig. 1a). Furthermore, it is important to note that the presence of degraded *C. intratropica* groves in KNP implies that conditions there were once very similar to CAL. Evidence suggests the process of grove degradation and, more generally, the homogenization of savanna vegetation are unidirectional processes (Russell-Smith et al. 2012, Trauernicht et al. 2012). Thus, based on intact KNP grove composition, we can infer that degraded groves in KNP once also contributed to the heterogeneity and diversity of savanna vegetation. The patch dynamics of *C. intratropica* therefore provide a powerful tool for understanding the patterns and processes of landscape change in the Stone Country.

People and buffalo as ecosystem engineers?

We suggest that in addition to differences in Aboriginal occupation, the control of feral buffalo has had major effects on patterns of landscape burning across the Stone Country.

Megafaunal grazers have been described as ecosystem engineers based on their strong effects on herbaceous vegetation and the coupling of these impacts with fire disturbance (Knapp et al. 1999, WalDRAM et al. 2008, Fuhlendorf et al. 2009). Our results for fire occurrence and *C. intratropica* recruitment (Figs 3d and 4) suggest buffalo are interacting similarly in the Stone Country. This indicates that the compartmentalization of buffalo and fire as separate phenomena by contemporary management programs may be misguided, certainly according to the cultural perspectives of TOs (Bowman and Robinson 2002, Robinson and Whitehead 2003, Trigger 2008), and also ecologically.

Although buffalo–fire interactions may benefit *C. intratropica*, the hypothesis that buffalo may be beneficial to the Stone Country savannas is likely to produce contentious debate.

Outside wetlands, however, little vegetation change was observed in the KNP Stone Country over the course of buffalo expansion and decline (Petty et al. 2007). Further landscape-scale assessments in KNP have found little to no effect of buffalo density on tree dynamics in upland savannas (Bowman et al. 2008, Lehmann et al. 2008), while at the site level, buffalo grazing has been shown to decrease fire damage and mortality among woody savanna species (Werner 2005, Werner et al. 2006). Thus, although critical wetland habitats certainly require protection (Petty et al. 2007, Ens et al. 2010), we are far from a complete understanding of buffalo interactions in the system. Ultimately, given the high costs and logistic difficulties of eradication, the Aboriginal view of buffalo as an active ecological component in the system likely provides a more realistic perspective for management.

Hybrid land management – the way forward?

Contemporary Stone Country burning programs were only established after extensive fires in 2004 and 2006 and the region presents myriad challenges. For instance, with one ranger

handling KNP's program, covering the entire landscape during the early dry season is difficult, even by helicopter, and limits the opportunities for TOs to burn on the ground (though several "footwalks" are organized each year; A. Pickworth, pers. comm.). KNP is simultaneously saddled with huge tourism responsibilities and managing both objectives stretches the limits of funding and human resources. East of KNP, the Western Arnhem Land Fire Abatement project (WALFA) provides yet another model of joint management for the Stone Country (Whitehead et al. 2009). WALFA is funded through carbon offsets for corporations, employing aerial and ground burns in the early dry season to reduce biomass consumed by late dry season fires (Russell-Smith et al. 2009). Among WALFA's major achievements has been the establishment of the Warddeken Ranger group, providing access and culturally appropriate employment to TOs in one of the most remote regions of the Stone Country. Similarly, the Djelk Ranger group has augmented Aboriginal participation in land management in CAL in addition to the activities of outstation residents. Though these programs stand at the forefront of progressive fire management, the reciprocity among differing objectives – carbon offsets, biodiversity conservation, cultural identity, etc. – is still unresolved and leaves potential both for collaboration and conflict (Andersen 1999, Yibarbuk et al. 2001, Russell-Smith et al. 2003).

Feral buffalo may present even greater controversy. Though we cannot extract the ways in which buffalo effects confound the influence of people on savanna integrity from our data, we argue that the interactions between buffalo and fire is an implicit component of contemporary Aboriginal land use, in which the species is valued and managed for hunting (Bowman and Robinson 2002). Given the fact that eradication is, in the end, financially unsustainable, it seems far more productive to examine the role of grazing as a management tool. In KNP, the grass–fire cycle involving the native annual *Sorghum brachypodum* provides a prime example where continuous, monotypic fuel beds of the species in many areas drive more intense, large-scale fires (Elliott et al. 2009). Though the same species is present in Arnhem

Land, aerial surveys indicated low *S. brachypodum* cover at all CAL sites versus high cover at over half the sites in KNP. High numbers of buffalo are clearly ecologically destructive (Petty et al. 2007, Ens et al. 2010) – even among *C. intratropica* groves (Fig. 4b) – however, targeted stocking rates may provide both a tool with which to combat current and impending grass–fire cycles as well as the opportunity to engage TOs.

A legacy of research in Australia has pioneered the ecological significance of humans in flammable systems (Jones 1969, Bowman and Panton 1993, Head 1996, Russell-Smith et al. 1997, Yibarbuk et al. 2001, Whitehead et al. 2003, Murphy and Bowman 2007, Bird et al. 2008, Fletcher and Thomas 2010), a dynamic that is increasingly apparent elsewhere (Laris 2002, Rodriguez 2007, Archibald et al. 2012). Although it is difficult to ascertain the degree of replicability or consistency in land use among outstations, the greater heterogeneity and diversity in the CAL Stone Country indicated by *C. intratropica* (Fig. 5) suggests an association between greater ecological integrity and a more holistic, culturally based approach to land management. Our findings also contribute to the current debate over the ecological benefits of landscape heterogeneity wrought by fire, or ‘pyrodiversity’ (Parr and Andersen 2006, Parr and Brockett 2008). The persistence of *C. intratropica* groves in these savannas is clearly tied to the maintenance of lower intensity, patchier fires (Bowman and Panton 1993, Edwards and Russell-Smith 2009, Russell-Smith et al. 2012, Trauernicht et al. 2012). Thus, given the occurrence of a distinct, fire-sensitive plant community in intact groves but *not* degraded groves (Fig. 2), our findings provide a clear link between pyrodiversity and biodiversity.

Equally compelling as the potential ecological benefits, TOs living “on country” enjoy greater mental and physical well-being than those in larger settlements, as unequivocally demonstrated by Aboriginal testimony and socio-medical research (Johnston et al. 2007, Garnett et al. 2009). The scenarios in CAL and WALFA suggest that increasing and/or reintegrating the direct involvement of TOs in land management is a tenable goal. Though

we and others contend that the contemporary institutions like KNP must prioritize the rehabilitation of Aboriginal lands as social-ecological systems (Altman and Whitehead 2003, Whitehead et al. 2003, Johnston et al. 2007), many barriers persist: sociopolitical opposition to outstations, loss of traditional knowledge, and limited access to ancestral lands are but a few. Buffalo will also remain a flashpoint for conservationists, yet similarly, burning restrictions and tourism may not align with the wishes of TOs. The story of people, fire, and buffalo on the Stone Country affirms the resilience and adaptability of a culture that has persisted for more than 50 millennia. Clearly, the sustainability of the Stone Country, as well as other Aboriginal lands, depends upon sustainable futures for indigenous people. This challenges all actors to confront conflicting needs and perspectives, yet also find common ground, in order to develop and improve management paradigms.

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Table 1. The aerial survey observations, scored for each *Callitris intratropica* grove. At each grove, we measured the percentage (relative to the total population) of (i) *C. intratropica* saplings (1-3 m), (ii) juveniles (3-6 m), and (iii) dead adult stems, as well as (iv) the mean lowest height of the canopy foliage (i.e. scorch damage) and (v) the cover of the understory shrub community. Scores were added to determine a total score for grove condition ranging from 0 (highly degraded) to 5 (highly intact).

<b>Score</b>	<b>% Saplings</b>	<b>% Juveniles</b>	<b>% Dead trees</b>	<b>Foliage Ht</b>	<b>Shrub Cover</b>
0	0	0	>20	>4 m	Absent
0.5	≤20	≤20	≤20	3-4 m	Partial
1	>20	>20	0	<3 m	Continuous

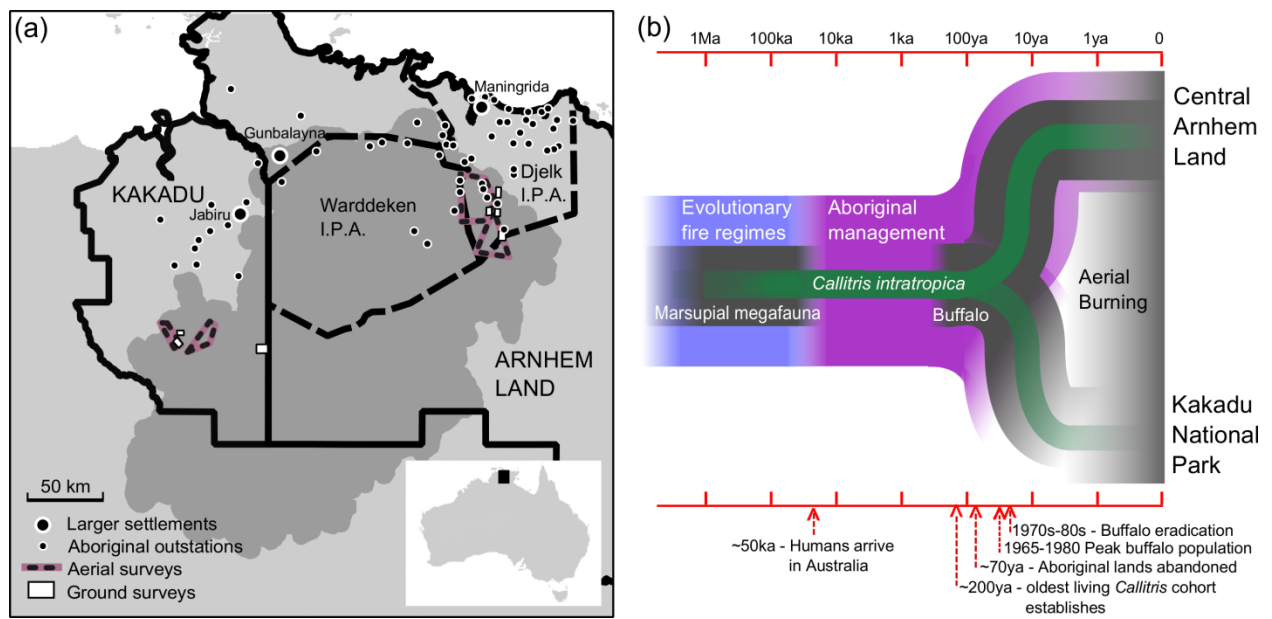


Figure 1. (a) Map of the Arnhem Plateau region illustrating the extent of sandstone outcrops comprising the Stone Country (shaded dark grey), settlements, and sampling areas. (b) Timeline showing the historical divergences in ecological conditions and management between Kakadu National Park and central Arnhem Land.

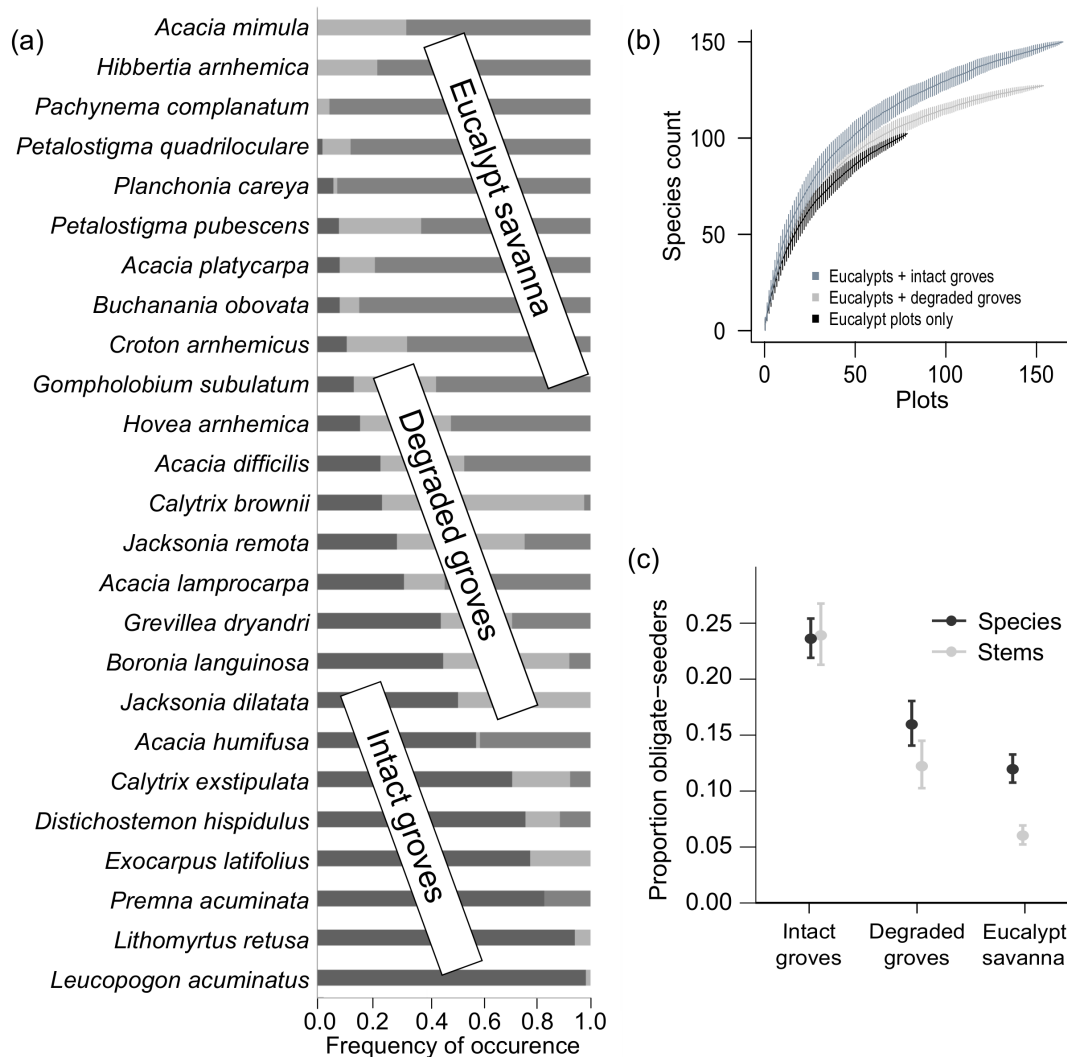


Figure 2. Woody plant species composition recorded in plots (N=197) among intact and degraded *Callitris intratropica* groves as well as adjacent eucalypt savanna. (a) Frequencies among plot types for the 25 most frequent species of shrubs and small trees. (b) Species accumulation curves by random sampling from plots in eucalypt savanna and intact *C. intratropica* groves, eucalypt savanna and degraded *C. intratropica* groves, and eucalypt savanna only. (c) Proportions of species and stems of fire-sensitive, obligate seeding plants (i.e. do not resprout after burning) sampled in each plot type (Akaike weight=0.99 relative to the null model for both analyses; error bars represent standard errors).

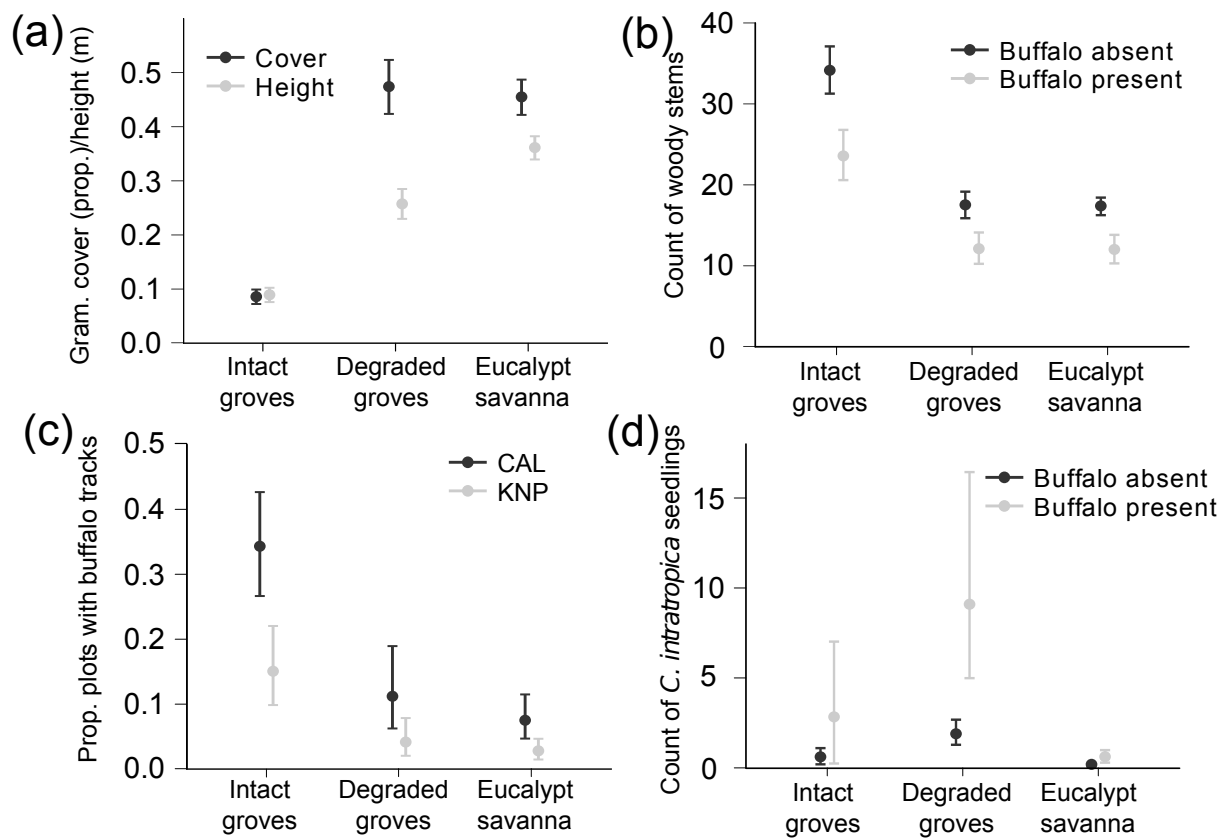


Figure 3. Comparisons among plots (N=197) in intact and degraded *Callitris intratropica* groves and the surrounding eucalypt savanna matrix for (a) graminoid fuels height and cover (Akaike weight ( $w_i$ )=0.99, both analyses), (b) the count of woody plants (excluding *C. intratropica*) including the effect of the Asian water buffalo ( $w_i$ =0.92) (c) the proportion of plots containing buffalo tracks in central Arnhem Land (CAL) and Kakadu National Park (KNP;  $w_i$ =0.79) and (d) the count of *C. intratropica* seedlings including the effect of buffalo ( $w_i$ =0.97). Akaike weights are presented relative to the null model and error bars represent standard errors.

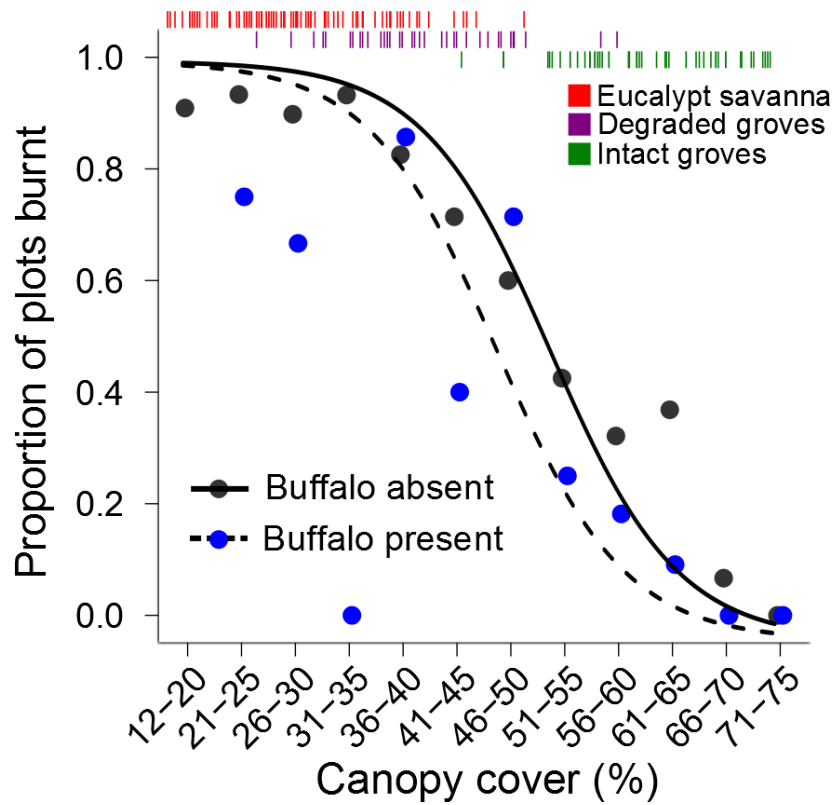


Figure 4. The probability of savanna burning as a function of canopy cover and the presence–absence of buffalo tracks (N=421, Akaike weight=0.76,  $R^2=0.30$ ). Rug plots at the top of the figure indicate canopy cover distributions among intact and degraded *Callitris intratropica* groves and the adjacent eucalypt savanna.

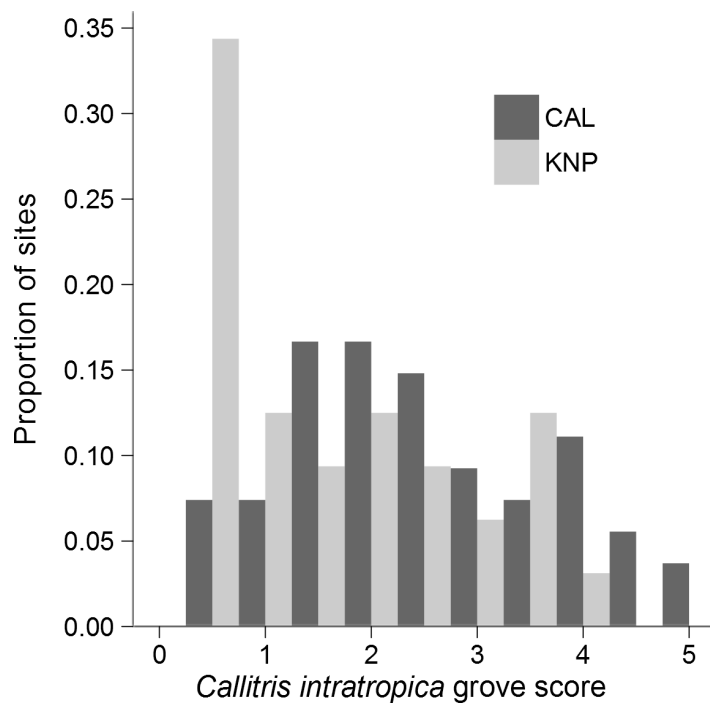


Figure 5. Distributions of *Callitris intratropica* grove condition scores in Kakadu National Park (KNP; N=33) and central Arnhem Land (CAL; N=54). Scores were derived from aerial surveys of population structure (including dead stems), the height of canopy scorching, and the cover of the understory shrub community. A least squares linear model of log-transformed scores supported the importance of region (KNP vs. CAL) in explaining this difference (Akaike weight=0.99 relative to null model).



## Chapter 6: CONCLUSION - Summary and management applications



Joshua, Leroy and Rahab Rostron along with the author and his wife, Talia at Dukladjarranj, central Arnhem Land

### Why Fire? Why *Callitris*?

That fire would become a major research theme in my doctoral dissertation was more serendipity than calculation. In pursuing my education and career, I have had the great fortune to work among rural and indigenous people in many different habitats throughout the world. It was entirely opportunistic that this path introduced me to forest–savanna mosaics – first in the hills of Southern India, later the Rupununi-Rio Branco savannas of interior Guyana and northern Brazil, and even the little known occurrence of this biome in Micronesia. Throughout these experiences, my focus remained on the management and socioeconomic

interdependencies between communities and local resources – nontimber forest management, enrichment planting, agroforestry, hunting, and even conservation intervention. Yet the saliency of the ecological influence of people was never clearer than through the use of fire in these mixed forest–savanna ecosystems. Thus, for me, fire has emerged not as simply the subject, but as the vehicle for understanding the historical and contemporary ecological role that people of have played in shaping ecosystem composition.

The emergence of *Callitris intrtropica* as a subject of study was also serendipitous. Australia was a logical place to work – the opportunity to ‘begin at the beginning’ in terms of building upon established research on ecological and cultural perspectives of fire management. The immediate impetus for my research program was the invitation by my supervisor, David Bowman, first to join his research group as a doctoral student and second to join him on a field trip to Arnhem Land at the start of the dry season in June of 2009. Within a few hours of our arrival, my wife and I were packed into a ‘troopie’ and after an 8 hour ride east out of Darwin, we arrived at Dukladjarranj, an ‘estate’ in central Arnhem Land which has been under nearly continuous Aboriginal management for millennia (Yibarbuk et al. 2001) and met Traditional Owners Wesley Campion and Tom Noydduna, and Anna, Joshua, and Rahab Rostron. In addition to our introduction to Aboriginal Australia, Dukladjarranj also introduced us to this conifer that David and his research team seemed rather obsessed with, *Callitris intrtropica*. Although I was convinced part of my research program would take place at Dukladjarranj, my own fate with *Callitris intrtropica* was not sealed until several weeks later. While my wife and I were establishing the basic necessities far away in the Tasmanian winter, David had plotted the next course in my dissertation. On the heels of the Arnhem Land trip, he’d had a conversation with the manager of Kakadu National Park, Sarah Kerin. She had just returned from a helicopter ride over the Arnhem Plateau ‘Stone Country’ and was appalled by the fire damage among the *Callitris intrtropica* trees up there. There was a small pot of money to start a student project and David reckoned he had the perfect

candidate. Within a couple weeks I was back in the Northern Territory, flying over the Arnhem Plateau with Anna Pickworth, Kakadu's fire ranger. Despite being completely overwhelmed by the sheer magnitude of the Stone Country and having no idea what I was going to do, my relationship with *Callitris* had begun.

### **Relevance of *Callitris***

I soon realized that *Callitris intratropica* provides a unique opportunity to apply the ecological knowledge of Australian Aborigines to understanding fundamental aspects of savanna disturbance ecology and human–fire relationships. Aboriginal Traditional Owners were the first to point out that damaged *Callitris* trees are an indication of destructive fires and, therefore, poor management of 'country' (Haynes 1985). In addition to the species' vulnerability to high intensity fires, terpenoids in its stem confer long-term termite resistance to *Callitris* – live or dead. The sensitivity of *Callitris* to increased fire intensity and the persistence of its dead stems has provided a signal with which to examine a fundamental question concerning these savannas: What are the ecological consequences of the cessation of Aboriginal fire management? Vast expanses of Australian tropical savannas became depopulated over the past century – particularly among the rugged 'Stone Country' of the Arnhem Plateau – due to disease, dispossession and radical shifts in material culture among the Aboriginal clans who had culturally adapted to this landscape over the past 40-60 millennia (Cooke 2009, Ritchie 2009). *Callitris* has arguably provided one of the first tests of whether Rhys Jones' 'fire-stick farming' hypothesis – the use of proactive landscape burning by Aborigines to deliberately shape the availability of resources – had implications for savanna composition at the ecosystem scale (Jones 1969). Thus, surveys of *Callitris* across much of the tropical savannas encompassing Australia's 'Top End' of the Northern Territory have indeed revealed that the species is declining across much of the landscape (Bowman and Panton 1993, Bowman et al. 2001, Edwards and Russell-Smith 2009). This

compositional shift remains some of the best evidence for landscape-scale, deleterious effects of the change from patchy burning by a widely dispersed Aboriginal population to unmanaged wildfires occurring in a 'modern wilderness'.

## **Research Accomplishments**

The window provided by *Callitris* declines into past fire regime change – and its implications for the ecological effects of Aboriginal management – marks the entry point of the research presented in this dissertation. Two fundamental questions about *Callitris* remained unanswered: (1) By what mechanisms does the species persist in such a flammable landscape? and (2) How can the species be used proactively to inform contemporary management? It is well known that frequent savanna fires limit the establishment and recruitment of woody plants (Mourik 2007, Hoffmann et al. 2009a) – especially if they are obligate-seeding species (i.e. incapable of resprouting after fire) like *Callitris* (Cohn and Lunt 2011, Prior et al. 2011). Still, fire-sensitive vegetation contributes to the complexity of habitat mosaics found in nearly all flammable ecosystems. Although this landscape heterogeneity wrought by fire – pyrodiversity – is a known property of fire-prone ecosystems, uncertainty and debate ensues regarding the mechanisms that create and maintain pyrodiversity (via management intervention or otherwise) as well as the dependencies of constituent species on patterns of pyrodiversity (Bradstock et al. 2005, Parr and Andersen 2006, Clarke 2008, Davies et al. 2012, Taylor et al. 2012).

As a complete body of work, this research suggests a dual, synergistic role of human management (via fire) and alternative stable state dynamics (via the negative fire feedback imposed by intact *Callitris* groves) as a mechanism that enables the persistence of fire-sensitive species in flammable systems. It also provides some of the best available evidence for the relationship between fire-generated habitat diversity and species diversity. The evidence presented in chapter two suggested that proactive landscape by both

indigenous and contemporary managers in flammable ecosystems worldwide decreases fire intensity and increases the spatial heterogeneity of burning. Through habitat modelling, it was revealed that even if these practices have little effect on total fire frequency (analogous to the annual extent of landscape burnt), reductions in the size of individual fire events can increase the availability of long-unburnt habitat (Chapter 2, Figure 4) – a critical requirement for the establishment of species such as *Callitris*. This strongly implicates the role of proactive landscape burning in creating conditions of habitat heterogeneity and low-intensity fires under which *Callitris* groves would have been capable of ‘invading’ highly fire-prone savanna vegetation. However, it is ultimately the negative fire feedback imposed by *Callitris* groves, demonstrated in Chapter 3, through which *Callitris* influences savanna composition. Alternative stable state theory has been generally invoked to explain the coarse boundaries between biomes, such as savanna and rain forest (Warman and Moles 2009, Staver et al. 2011, Murphy and Bowman 2012) as opposed to small-scale patterns of heterogeneity (but see Laycock, 1991). However, the results from our experimental burns illustrate how the lower probability of burning within intact *Callitris* groves contributes to the fine-grain habitat diversity of savannas (i.e., on the scale of tens to hundreds of m<sup>2</sup>; Chapter 3, Figure 5).

Under low-intensity fire regimes, *Callitris*’ patch dynamics effectively create small-scale fire refugia, which have implications for both *Callitris* populations as well as the heterogeneity, diversity, and structural complexity of savanna vegetation. The negative fire feedback allows for higher conspecific recruitment among intact groves, which, through population modelling in Chapter 4, was found to play a critical role in maintaining population stability among *Callitris* groves across the landscape. The patch-based population models also further implicated human intervention – specifically via the reduction in fire intensity – in maintaining conditions favouring the long-term persistence of *Callitris*, despite high overall fire frequencies (Chapter 4, Figure 7). The negative fire feedback also allows *Callitris* groves to provide habitat for a distinct plant community (and bowerbirds) – initially demonstrated by

the data in Chapter 3 (Figure 2) and definitively established via surveys at more than 100 sites across multiple regions on the Arnhem Plateau (Chapter 5, Figure 2). Thus, the ecological relationships we have explored in this research not only support the ‘pyrodiversity begets biodiversity’ hypothesis, but offers a mechanistic explanation of how anthropogenic burning and *Callitris* grove dynamics contribute to maintaining pyrodiversity.

From the perspective of Aboriginal traditional ecological knowledge, linking the persistence of *Callitris* to Aboriginal management practices is, of course, far from novel. The novelty of this research thus far lies instead in fine-tuning the characterization of the effects of human fire management beyond the limited metric of overall fire frequency (Chapter 2), the establishment of the negative fire feedback among closed canopy, intact *Callitris* groves (Chapter 3) and the application of these interactions into models of savanna heterogeneity and composition (Chapters 2 and 4). The *true* application of these findings, however, is presented in Chapter 5 in which we establish the use of *Callitris* as an indicator of savanna integrity by comparing contrasting management histories on the Arnhem Plateau ‘Stone Country’ in Kakadu National Park (KNP) and central Arnhem Land (CAL). Importantly, the distinct ‘state change’ between intact and degraded *Callitris* groves (Chapter 3) allows for a robust and rapid assessment of *Callitris* ‘grove condition’. Thus whereas intact groves create refugia for *Callitris* recruitment and other fire-sensitive species, degraded groves are equivalent to open savanna vegetation in terms of woody composition and fire disturbance, despite the persistence of adult *Callitris*. Thus, the abundance of intact groves and degraded groves can provide a relative measure of disturbance heterogeneity and the structural complexity and diversity of savanna vegetation. In addition, the relative abundance of degraded groves can suggest the degree to which savanna integrity has declined. Thus, the greater abundance of intact groves in CAL than KNP illustrates how the areas of savanna in CAL which remain under Aboriginal management, are more diverse and structurally complex. The contrast in management regimes incorporates differences in fire

management but also complex ecological interactions involving feral water buffalo. However, the comparison pits one of the most intact traditional management systems left in Australia against an unmanaged, modern wilderness area. This research therefore raises the issue of confounding interactions between an introduced mega-herbivore and patterns of burning (i.e., Archibald, Bond, Stock, & Fairbanks, 2005; Fuhlendorf, Engle, Kerby, & Hamilton, 2009) but ultimately supports indigenous people as key engineers of ecosystem composition in Australian savannas – and perhaps elsewhere (e.g., Anderson, 2005; Bilbao, Leal, & Mendez, 2010; Bird, Bird, Coddington, Parker, & Jones, 2008; Keeley, 2002; Laris, 2002; Mistry et al., 2005; Nowacki & Abrams, 2008).

### **A Tool for Management**

Finally, elucidating the mechanism by which *Callitris* interacts with fire provides a unique opportunity to develop monitoring protocols for managers of Australian savannas. The threshold between intact and degraded *Callitris* groves, and the ecological implications of this state change, translates into practical and easy-to-interpret monitoring methods. To that end, I have worked with the Djelk Aboriginal Ranger group of central Arnhem Land to develop a protocol for the rapid assessment of *Callitris* groves. The protocol will allow Aboriginal ranger groups and park rangers to implement surveys of *Callitris* grove condition using the Cybertracker program on handheld GPS units. These surveys will enable ranger groups to assess the overall integrity of savanna plant diversity and habitat heterogeneity where *Callitris* occurs. As data accumulates, it will also establish a landscape-scale baseline from which to monitor changes in *Callitris* condition – from the degradation of groves to the formation of new patches – and thereby assess the outcomes of fire management efforts. The surveys incorporate illustrations by Joshua Rostron, a Traditional Owner residing at Kolorbidahdah outstation in the Djelk IPA in order to provide clear and culturally appropriate data collection methods based on the results from this research.

The protocol is nearly identical to that applied during the aerial surveys in Chapter 5, in which specific traits were ranked and summed to determine scores for individual groves. Similarly, the Cybertracker program consists of a series of survey 'steps' (see Appendix). For each grove, the users are required mark the location, estimate the size, and then assess whether the grove is 'new', 'established', or 'dead'. For established groves, the user is led through a step-wise assessment the condition of a specified set of grove 'characters': (i) sapling abundance, (ii) dead tree abundance (iii) canopy health, (iv) shrub abundance, and (v) buffalo track abundance. Each character is described visually by one of three conditions. The conditions of each character (apart from buffalo abundance; see below) are attributed with a value of 0,1, or 2 according to how it relates to grove health based on the research findings. Summing the grove character values produces a 'grove score' for each surveyed grove, ranging from 0 (highly degraded) to 8 (highly intact). Put in the hands of rangers across Australia's Top End, these surveys will provide direct quantitative assessments of *Callitris* grove abundance and plant community structural complexity. It will also provide indirect but relative measurements of plant community diversity and prevailing fire heterogeneity and intensity. Assessments of buffalo tracks, although not incorporated into 'grove scores' will help to clarify the effects of this species on established grove condition and the recruitment of new groves.

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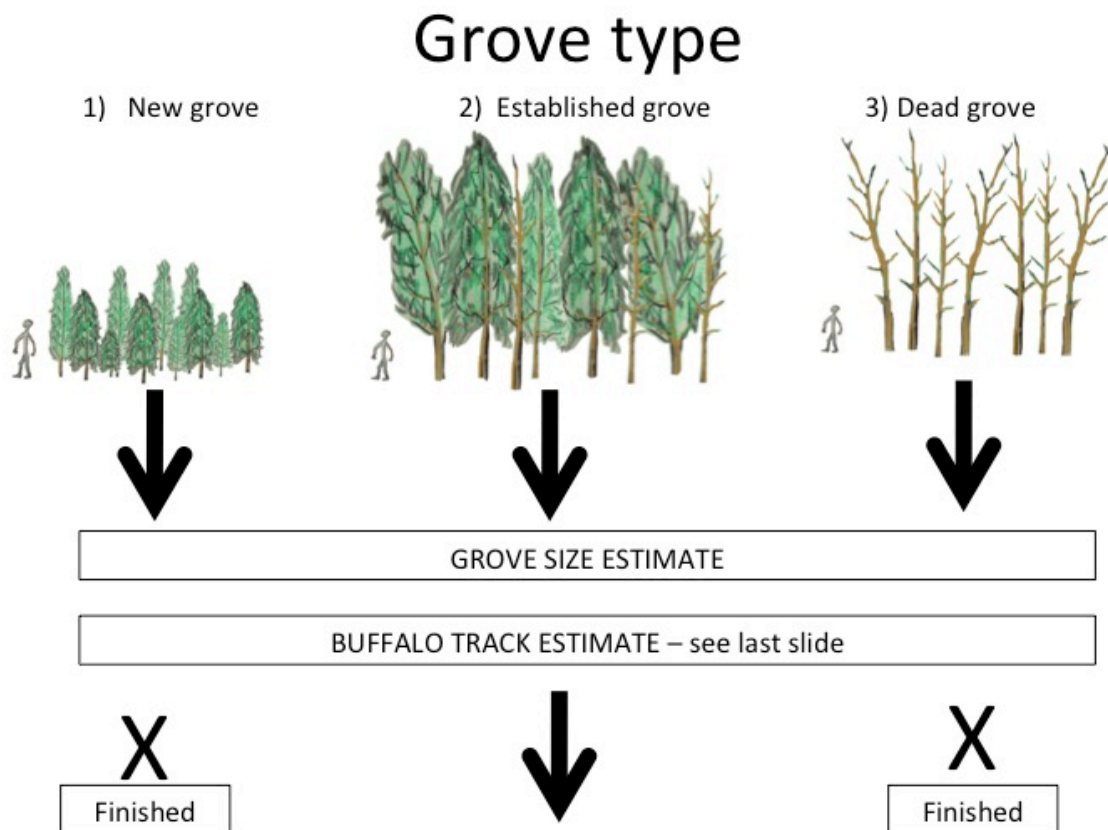
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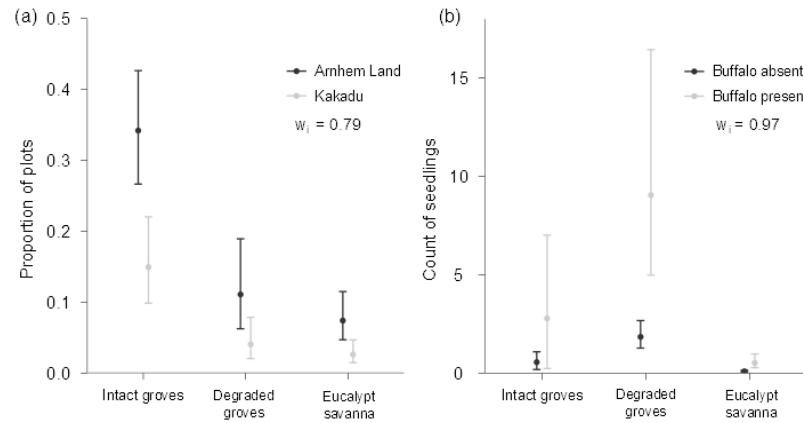
**Appendix.** *Callitris* Rapid Assessment. The panels below present the survey steps comprising the *Callitris* rapid assessment protocol. For each panel, data is presented in the upper right corner in order to illustrate the correspondence of each grove character to the research findings.



Steps 1-2. After taking a GPS point of *Callitris* grove location, the user selects whether the grove is new, established, or dead. For all groves, the user is also required to estimate grove area (by pacing the length and width) and assess the abundance of buffalo tracks (see last slide). For established groves, the survey continues.

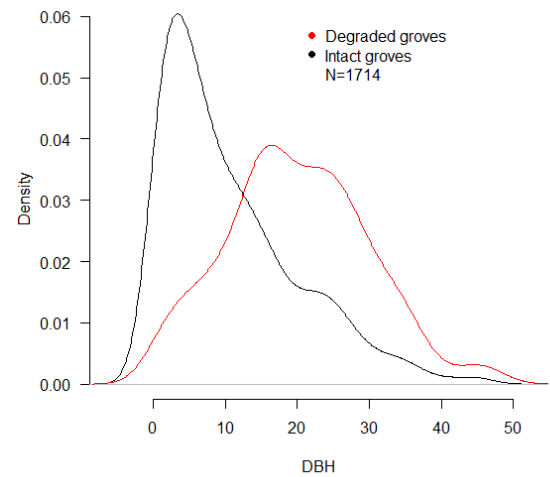


## Buffalo tracks



Step 3. For all grove types, the user assess the relative abundance of buffalo tracks. This does not contribute to the overall 'grove score' but will provide managers with an indirect measure of buffalo abundance with which it will be possible to assess their effects on *Callitris* condition and recruitment. The figures illustrate (a) the proportion of plots containing buffalo tracks in Arnhem Land and Kakadu National Park and (b) the correlation between buffalo presence/absence and the count of *Callitris* seedlings. Error bars illustrate standard errors.

## Saplings



SCORE: 2



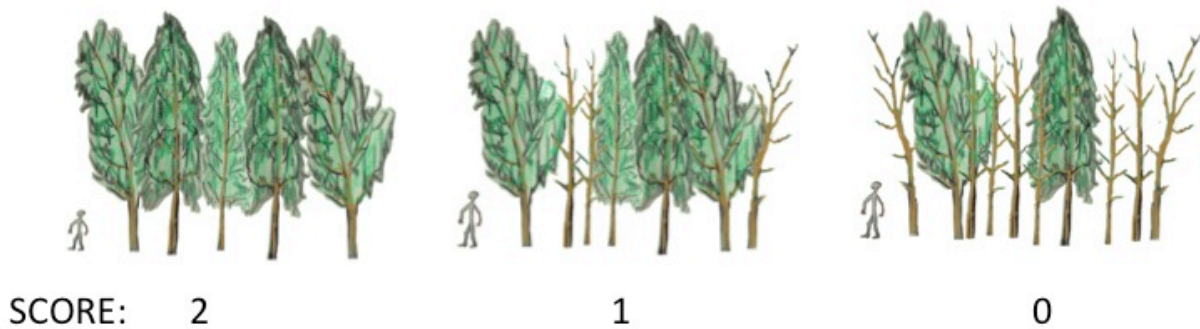
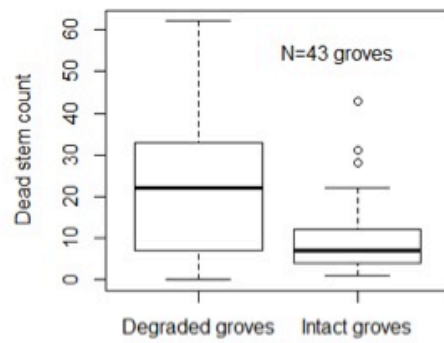
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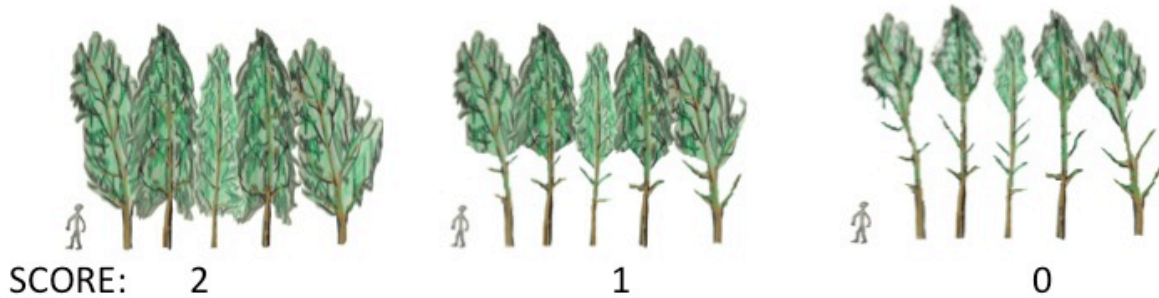
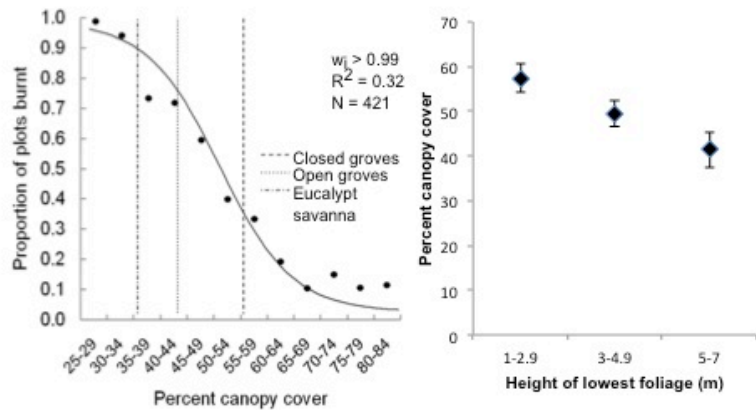
Step 4. The user assesses the relative abundance of *Callitris* saplings. Scores represent the 'weight' attributed to each condition, ranging from 0 (degraded condition) to 2 (intact condition). The figure in the upper right illustrates the kernel density of the diameter at breast height (DBH) distribution for *Callitris* individuals among intact and degraded groves.

# Dead trees



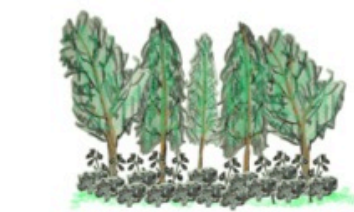
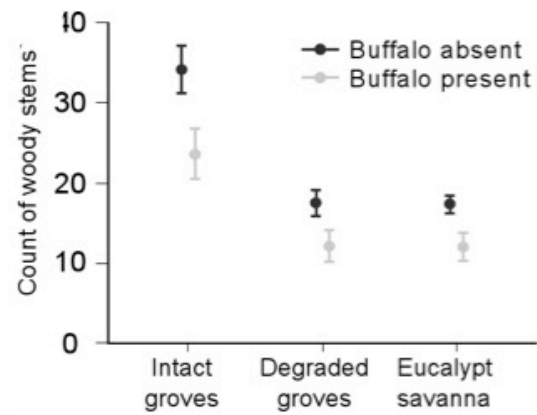
Step 5. The user assesses the relative abundance of dead adult *Callitris* stems. Scores represent the ‘weight’ attributed to each condition, ranging from 0 (degraded condition) to 2 (intact condition). The boxplot illustrates the difference in the count of dead stems between degraded and intact *Callitris* groves. Horizontal bars represent median values, boxes indicate the first and third quartiles, whiskers show the highest and lowest values within 1.5\*IQR (the interquartile range), and points represent data lying outside this range.

## Canopy health

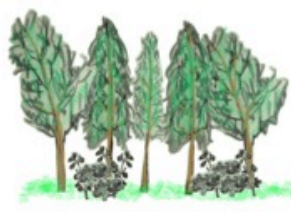


Step 6. The user assesses canopy condition of the *Callitris* grove. Scores represent the 'weight' attributed to each condition, ranging from 0 (degraded condition) to 2 (intact condition). The data plots illustrate the relationships between foliage height and canopy closure and canopy closure and the probability of burning (see Chapter 3, Figure 5), respectively. Error bars represent standard errors.

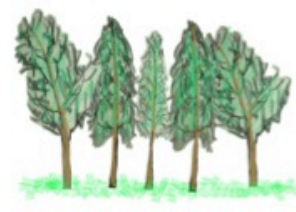
## Shrub layer



SCORE: 2



1



0

Step 7. The user assesses the relative abundance of woody shrubs in the understory of the *Callitris* grove. Scores represent the 'weight' attributed to each condition, ranging from 0 (degraded condition) to 2 (intact condition). The data figure illustrates the counts of woody stems among intact and degraded groves, as well as eucalypt savanna (see Chapter 5, Figure 3b). Error bars represent standard errors.