Valentine, Leonie (2006) ***The impacts of human-mediated disturbances on birds and reptiles in tropical savannas.*** **PhD Thesis, James Cook University.**

The impacts of human-mediated disturbances on birds and reptiles in tropical savannas.

PhD thesis submitted by
Leonie Ellen Valentine
B.Sc., Dip. Res. Met. James Cook University
December 2006

For the degree of Doctor of Philosophy
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A land ethic… reflects the existence of an ecological conscience, and this in turn reflects a conviction of individual responsibility for the health of the land. Health is the capacity of the land for self-renewal. Conservation is our effort to understand and preserve this capacity.

Aldo Leopold

Top – Rufous Whistler (*Pachycephala rufiventris*), management burning along roadsides, rubber vine (*Cryptostegia grandiflora*) flower bud, *Carlia pectoralis* (male)

Bottom – Grazed tropical savanna, Dreghorn Property, Einasleigh Uplands.

Photo credit: Leonie Valentine.

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Abstract

Disturbances influence the structure of many ecosystems, determining environmental and biological heterogeneity. Human-mediated disturbances, including introduced plant species and fire, have the ability to alter ecosystem-level processes and properties, modify habitat structure and, as a consequence, influence faunal assemblages. This thesis examines the impacts of introduced plant species and fire management practices on vertebrate assemblages in grazed tropical savannas in northern Queensland.

Invasive introduced plant species pose a major threat to native environments. Rubber vine (*Cryptostegia grandiflora*) is an environmental weed that invades native riparian habitats in northern Australia. Small ground-dwelling lizards may be negatively affected as rubber vine replaces and fragments native habitat. Field observations of reptiles in habitat invaded by rubber vine recorded only a single lizard in rubber vine vegetation, compared to 131 lizards in nearby native vegetation. As rubber vine vegetation contains features that superficially resemble native habitat, such as leaf litter, the avoidance of rubber vine suggests that rubber vine has underlying characteristics that create a suboptimal environmental for lizards.

Two species of native skinks (*Carlia munda* and *C. pectoralis*) and the invasive plant rubber vine were used as a model system to determine possible underlying mechanisms driving avoidance of non-native plants by fauna. In semi-natural enclosures, lizards discriminated between leaf litter types: 85% of *C. pectoralis* and 80% of *C. munda* chose native leaf litter over rubber vine, indicating a clear preference for native habitat. In comparison to native habitat, rubber vine provided a suboptimal environment for litter-dwelling lizards with lower ambient temperatures, reduced availability of prey and a reduction in camouflage from predators (dissimilar leaf and lizard shapes). Thus, three possible mechanisms were identified by which an introduced plant species can alter the availability of resources in an environment, making it less attractive to native fauna. As rubber vine is a Weed of National Significance, management of this species is a priority.

Fire plays a pivotal role in structuring ecosystems and often occurs as a human-mediated disturbance for land management purposes, including management of introduced plants. Rubber vine is susceptible to fire, and burning for weed control may be implemented in riparian zones of tropical savannas where rubber vine is prevalent. Although tropical savannas are considered fire-adapted ecosystems, riparian vegetation and associated fauna may be less resilient to the effects of fire. Variations in fire regimes alter the environment in different ways, and the type of fire may govern the response of faunal assemblages. Using replicated experimental fire treatments, imposed on two habitats (riparian and adjacent woodland), I examined the responses of reptiles and birds in the short- and longer-term to a range of fire management practices used to control rubber vine.

An important component of fire regime is the season of burn. In tropical savannas, most fire management occurs during the dry season; however, wet season burning is often used for pastoral management and may be useful for controlling introduced plant species. Initially, only one species of reptile responded strongly to burning, with few differences detected between burning seasons. Abundances of the skink *C. munda* were higher in burnt sites and may reflect temporary changes in food availability, or a reduction in rubber vine. However, the overall structure of the reptile community was driven by habitat type (riparian versus woodland) rather than burning, suggesting most reptiles were responding to broader environmental factors. Within three years of burning, reptiles were least abundant in dry season burnt sites, a result mostly driven by the abundance of the small terrestrial gecko, *Heteronotia binoei*, which was commonly observed in unburnt and wet season burnt sites. In addition, litter-associated species, including the skink *C. pectoralis*, were rarely observed in burnt habitat and fewer species were detected in the wet season burnt sites.

Both season of burn and time since fire also significantly influenced bird assemblage responses. Within 12 months of fire, burning tended to benefit several bird species and feeding groups, with higher overall abundances of birds observed in the sites, although species that favoured dense vegetation (e.g. red-backed fairy-wren, *Malurus melanocephalus*) were rarely observed in burnt habitat. Responses of feeding groups, including insectivores, nectarivores and carnivores, suggest that burning may have temporarily increased food resources. In the short-term, assemblage of birds tended to

reflect whether or not a site was burnt, rather than burning season. However, four years following burning, dry season burnt sites were composed of a different bird assemblage than unburnt and wet season burnt sites. In addition, dry season burnt treatments were characterised by lower bird abundances, especially nectarivore and granivore feeding groups and the insectivorous white-throated honeyeater (*Melithreptus albogularis*). As dry season burning removed more vegetation than wet season burning, birds may be responding to a reduction in habitat complexity, and subsequent changes in food resources.

The frequency with which a habitat is burnt is another critical component of fire regime, and may ultimately determine faunal assemblage responses. Using a fully replicated Before-After-Control-Impact (BACI) design I examined the impacts of repeated burning on bird assemblages. In contrast to unburnt or singularly burnt sites, the repeated burning significantly reduced bird abundance and species richness. Repeat burning also altered the feeding group structure of sites. In particular, frugivorous and insectivorous birds were adversely affected by the second fire. Vegetation complexity was lower in both burning treatments, but the repeatedly burnt sites contained less native fruiting shrubs, especially currant bush (*Carissa ovata*), which was an important food and shelter source for several species. Repeatedly burning an area in a short time frame may reduce key resources, other than vegetation complexity, such as food availability or foraging opportunities.

The use of fire is considered necessary for the maintenance of tropical savannas. However, high impact individual fires may detrimentally affect habitat structure and faunal assemblages at a local scale. In particular, my results suggest that overall bird and reptile assemblages are strongly influenced by management burning, including variations in burning season and fire frequency. In an attempt to overcome potential negative impacts of burning, ecologists have suggested implementing mosaic burning, where a variety of burning regimes are employed. Although mosaic burning theoretically provides a diversity of habitat types that consequently maintain high faunal diversity, my results suggest that some measures of diversity (e.g. species evenness) may be compromised by mosaic burning.

In summary, this study provides evidence that introduced invasive plants and management burning play a key role in shaping landscapes and associated faunal communities. Fauna respond to disturbance-induced changes in microhabitat and vegetation structure, food availability or foraging opportunities, and habitat requirements (e.g. temperature). The role of multiple human-mediated disturbances in influencing faunal responses in my study is of particular importance. My research was conducted in landscapes already disturbed by grazing and invasive species, and the responses of fauna may be caused by cumulative impacts. In areas where multiple disturbances already influence landscapes, the resilience of faunal assemblages to fire management practices may be lower than previously predicted.

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Bottom – Grazed tropical savanna, Dreghorn Property, Einasleigh Uplands.

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reflect whether or not a site was burnt, rather than burning season. However, four years following burning, dry season burnt sites were composed of a different bird assemblage than unburnt and wet season burnt sites. In addition, dry season burnt treatments were characterised by lower bird abundances, especially nectarivore and granivore feeding groups and the insectivorous white-throated honeyeater (*Melithreptus albogularis*). As dry season burning removed more vegetation than wet season burning, birds may be responding to a reduction in habitat complexity, and subsequent changes in food resources.

The frequency with which a habitat is burnt is another critical component of fire regime, and may ultimately determine faunal assemblage responses. Using a fully replicated Before-After-Control-Impact (BACI) design I examined the impacts of repeated burning on bird assemblages. In contrast to unburnt or singularly burnt sites, the repeated burning significantly reduced bird abundance and species richness. Repeat burning also altered the feeding group structure of sites. In particular, frugivorous and insectivorous birds were adversely affected by the second fire. Vegetation complexity was lower in both burning treatments, but the repeatedly burnt sites contained less native fruiting shrubs, especially currant bush (*Carissa ovata*), which was an important food and shelter source for several species. Repeatedly burning an area in a short time frame may reduce key resources, other than vegetation complexity, such as food availability or foraging opportunities.

The use of fire is considered necessary for the maintenance of tropical savannas. However, high impact individual fires may detrimentally affect habitat structure and faunal assemblages at a local scale. In particular, my results suggest that overall bird and reptile assemblages are strongly influenced by management burning, including variations in burning season and fire frequency. In an attempt to overcome potential negative impacts of burning, ecologists have suggested implementing mosaic burning, where a variety of burning regimes are employed. Although mosaic burning theoretically provides a diversity of habitat types that consequently maintain high faunal diversity, my results suggest that some measures of diversity (e.g. species evenness) may be compromised by mosaic burning.

In summary, this study provides evidence that introduced invasive plants and management burning play a key role in shaping landscapes and associated faunal communities. Fauna respond to disturbance-induced changes in microhabitat and vegetation structure, food availability or foraging opportunities, and habitat requirements (e.g. temperature). The role of multiple human-mediated disturbances in influencing faunal responses in my study is of particular importance. My research was conducted in landscapes already disturbed by grazing and invasive species, and the responses of fauna may be caused by cumulative impacts. In areas where multiple disturbances already influence landscapes, the resilience of faunal assemblages to fire management practices may be lower than previously predicted.

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CHAPTER 1. GENERAL INTRODUCTION

Understanding the role of disturbances in shaping ecosystem function and patterns of biodiversity is a fundamental aspect of ecology (Connell & Slatyer 1977; Connell 1978; Sousa 1984; Pickett & White 1985). Environmental disturbances are broadly defined as 'any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, or the physical environment' (Pickett & White 1985, page 7). Disturbances are crucial determinants of environmental and biological heterogeneity, vary greatly across different spatial and temporal scales (Sousa 1984), and can be perceived as either natural or human-mediated events. The occurrence of natural disturbances (e.g. cyclones, floods) and subsequent habitat modification promotes change in environments, altering species composition. The classic example where disturbance plays a pivotal role in structuring communities are rocky inter-tidal shores. Here, space is often a limiting factor, and sessile organisms are reliant on disturbances to create room for colonisation by offspring (Sousa 1985). However, when humans modify natural disturbance regimes, ecosystem processes and biodiversity may be subsequently altered in undesirable ways (Chapin *et al.* 2000).

Disturbances in natural communities – the impacts of human activities

Humans are major contributors to environmental change and substantially modify ecosystems and alter natural disturbance patterns (Vitousek *et al.* 1997; Chapin *et al.* 2000; Sala *et al.* 2000). Broad-scale human-mediated disturbances are usually conducted to further financial goals and increase economic growth, but the consequences of our actions on ecosystem processes and biodiversity may be catastrophic (Chapin *et al.* 2000; Sala *et al.* 2000; Williams *et al.* 2003c). Humans modify environments in a number of ways, including habitat clearing and fragmentation, urbanisation, grazing and agriculture, the introduction of alien species, the use of fire, and anthropogenically induced climate change. Research is urgently required to examine how human-mediated disturbances alter environments so that land managers can reduce negative effects and establish appropriate management priorities. With a multitude of disturbances occurring throughout the world, identifying and quantifying community responses is challenging and will often require complex and expensive experimental designs. Natural ecosystems are simultaneously threatened by a variety of anthropogenic disturbances and understanding the influence of concurrent disturbances is therefore particularly important for appropriate management objectives. My study focuses on the impacts of two human-mediated disturbances, specifically fire management and introduced plant species.

Fire occurs as a natural disturbance via lightning in many ecosystems (Bond & Van Wilgen 1996), and plays a key role in modifying landscapes and promoting ecosystem changes. Fire-induced ecosystem changes subsequently influence environmental and biological heterogeneity, vegetation floristics and faunal assemblages (Whelan 1995; Bond & Van Wilgen 1996; Angelstam 1998; Brawn *et al.* 2001). Humans have long altered natural fire regimes by employing fire as a land management tool to modify environments (Kauffman *et al.* 1993; Russell-Smith *et al.* 2003b). Where natural disturbance regimes have been interrupted, prescribed burning may be useful for restoring conservation values in some ecosystems (Askins 1993; Angelstam 1998; Davis *et al.* 2000). For instance, fire is the principal management tool for restoring oak savannas in mid-western North America (Peterson & Reich 2001), and provides important habitat for declining bird species (Davis *et al.* 2000; Brawn 2006). However, inappropriate human-mediated fire regimes may have undesirable consequences for native biodiversity (Barlow & Peres 2004).

Invasive species of alien plants are another disturbance that severely threaten native communities and modify ecosystem process and functions (Vitousek *et al.* 1997; Gordon 1998; Hulme 2006). The introduction of non-native plants is usually deliberately facilitated by humans, and although most introduced plant species do not deleteriously impact ecosystems, a small proportion become invasive (Hulme 2006). Invasive species alter natural dynamics by changing nutrient levels, hydrological cycles and fire regimes (Vitousek & Walker 1989; D'Antonio & Vitousek 1992; Le Maitre *et al.* 1996; Brooks *et al.* 2004; Yurkonis *et al.* 2005). For example, the non-native nitrogen-fixing tree *Myrica faya,* has invaded volcanic sites in Hawaii and increased soil nitrogen levels, which has subsequently altered community composition of plant and soil organisms (Vitousek & Walker 1989). Native wildlife community structure and composition is also affected by invasive plant species (Griffin *et al.* 1989; Wilson & Belcher 1989; Herrera & Dudley 2003; Yurkonis & Meiners 2004), however few studies have examined the ecological responses of vertebrates to invasive plants (Blossey 1999; Levine *et al.* 2003).

Human-mediated disturbances in Australian tropical savannas

Tropical savannas are landscapes of scattered trees and grass, characterised by a distinct wet-dry season and cover nearly one-third of the world's land surface. Tropical savannas are predominantly found in Australia, Africa and South America. Although rainfall amounts vary in space and time, most rainfall predictably occurs during the summer months (Taylor & Tulloch 1985), and is subsequently followed by an extended dry season. This distinct wet-dry seasonality is conducive to grassy fuel production that promotes fires, and thus low-moderate intensity fires are frequent events (Russell-Smith *et al.* 2003b; Govender *et al.* 2006). Tropical savannas are areas with high biodiversity values, but are currently facing increasing pressure from a variety of human-mediated disturbances. Furthermore, the ecological integrity of tropical savannas is threatened by intensification of grazing practices, introduction of plant species and inappropriate fire regimes (Hudak 1999; Woinarski & Ash 2002; Smart *et al.* 2005; Whitehead *et al.* 2005).

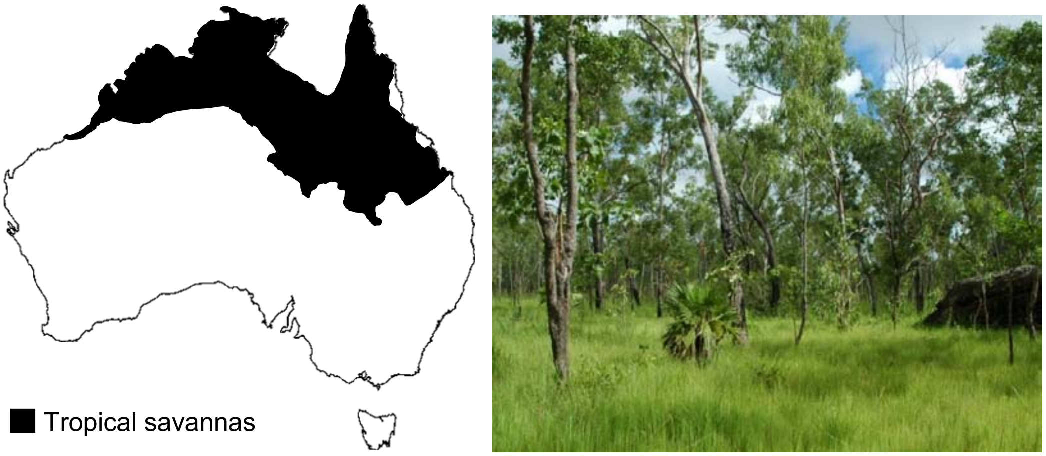

Figure 1. Distribution of tropical savannas in Australia and a photo of typical savanna habitat in Kakadu National Park, Northern Territory. Photo credit: Leonie Valentine.

In Australia, nearly one-quarter of the mainland surface (~ 2,000,000 km^2) comprises tropical savannas (Figure 1; Mott *et al.* 1985), most of which are sparsely populated with little broad-scale clearing (Williams *et al.* 2003b). Australian tropical savannas are primarily managed for pastoral production, although in northern Western Australia and the Northern Territory, large areas have also been established as aboriginal and conservation reserves (Russell-Smith *et al.* 2003b). Grazing in Australian tropical savannas consists mostly of low-intensity operations on large properties, except in some parts of Queensland where properties are smaller and grazing is more intensive (Russell-Smith *et al.* 2003b). Although the direct impacts of grazing on native biodiversity are many (see: Fensham *et al.* 1999; Fairfax & Fensham 2000; Ludwig *et al.* 2000; Woinarski & Ash 2002; Kutt & Woinarski 2006), pastoralism has also heralded other changes that subsequently affect native biodiversity, including the introduction of plant species (Lonsdale 1994; Martin *et al.* 2006), such as para grass (*Urochloa mutica*; Humphries *et al.* 1991), and altered fire regimes (Braithwaite & Estbergs 1985; Dyer *et al.* 2001). As the majority of tropical savannas are managed as grazing landscapes, understanding the synergistic impacts of additional human-mediated disturbances in these environments is pivotal.

History of fire in Australian tropical savannas

Fire is a key component influencing the Australian environment, and Australian tropical savannas have a history of fire association, both natural and human-mediated. Prior to human arrival, fire was a natural disturbance primarily initiated by lightning strikes (Kershaw *et al.* 2002), probably during the late dry and early wet season when lightning storms are frequent. From the late Cainozoic, increasing aridity and climatically variable conditions were, presumably, associated with an increase in fire activity (Kershaw *et al.* 2002). Where bioclimatic conditions favoured the common occurrence of lightning (e.g. tropical savannas), fire may have exerted evolutionary pressure on ecosystems (Goldhammer 1993). For example, Australian flora show a range of adaptations, including insulating bark, lignotubers and vegetative regrowth, that increase survival after fire events (Gill 1981; Kemp 1981; Whelan 1995).

The arrival of humans in Australia, some 45,000 years ago (O'Connell & Allen 2004), heralded a change in disturbance patterns, although the extent of impact of aboriginal-mediated disturbances, including the use of fire, on Australian landscapes remains a contentious issue (Singh *et al.* 1981; Flannery 1994; Bowman 1998; Kershaw *et al.* 2002; Johnson 2006). However, there is no question that human-mediated fire has been an important disturbance influencing Australian landscapes for the last 5,000 years

(Russell-Smith *et al.* 1997a; Bowman 1998; Johnson 2006). Fire was, and still is in parts of northern Australia, employed as a land management tool by aborigines for a variety of purposes, including the skilful modification of food resources (Jones 1969, 1980; Haynes 1985; Russell-Smith *et al.* 1997a). Aboriginal burning practices often have a distinct seasonal component, with low-intensity fires most frequent during the early dry season, tapering off during the late dry but increasing again in the early wet season (Jones 1980; Haynes 1985; Russell-Smith *et al.* 1997a). The protection of certain habitats was also an essential part of aboriginal fire management (Haynes 1985; Bowman 1998). Burning in this fashion, with fires occurring in different seasons and at varying frequencies presumably created a mosaic of habitat with variable-aged post-fire vegetation (Jones 1980; Haynes 1985).

European colonisation of Australia throughout the 19th century substantially modified traditional burning practices across much of the continent. During this time, European settlers viewed fire as a hazard and burning was suppressed, leading to the build up of high fuel levels that eventually resulted in devastating wild fires (Gill 1981). Subsequently, fire management practices were adopted to reduce the threat of high intensity wild fires. In northern Australia, changing fire regimes were also associated with the introduction of pastoralism in the late 19th century (Henderson & Chase 1985). The subsequent displacement of aborigines altered fire regimes as pastoralists began using frequent, extensive, late dry season fires to facilitate land clearing, improve access to habitat for mustering, and increase ‘green-pick’ for cattle (Tothill 1971; Braithwaite & Estbergs 1985; Russell-Smith *et al.* 1997b; Crowley & Garnett 2000; Dyer *et al.* 2001).

Today, the dominant land use in Australia’s tropical savannas is pastoralism, although substantial parts are also managed as Aboriginal reserves and conservation areas (Russell-Smith *et al.* 2003b). Land managers frequently and extensively exploit fire as a management tool (Russell-Smith *et al.* 2003b) for a variety of purposes, including human safety (Dyer *et al.* 2001), pastoral management (Tothill 1971; Ludwig 1990; Winter 1990; Crowley & Garnett 2000; Myers *et al.* 2004; Lankester 2005), traditional aboriginal purposes (Haynes 1985; Russell-Smith *et al.* 1997a; Yibarbuk *et al.* 2001), weed control (Stanton 1995; Grice 1997; Bebawi & Campbell 2002), and conservation management (Russell-Smith & Bowman 1992; Andersen *et al.* 2005; Price *et al.* 2005).

However, there are often distinct differences in the way fire is employed to meet these management objectives (see Yibarbuk *et al.* 2001; Russell-Smith *et al.* 2003b; Williams *et al.* 2003b; Vigilante *et al.* 2004; Whitehead *et al.* 2005).

Fire influences the environment by modifying the habitat matrix, with vegetation structure and floristic composition responding variably to differences in fire regimes, including changes in intensity, frequency and burning season (Christensen 1993; Glitzenstein *et al.* 1995; Whelan 1995; Russell-Smith *et al.* 1998; Williams *et al.* 1999; Williams *et al.* 2003a; Williams *et al.* 2005; Govender *et al.* 2006). Despite the relative resilience of tropical savanna landscapes to fire regimes (Andersen *et al.* 2005), inappropriate fire regimes have been linked to the decline of several taxa of plants (Russell-Smith & Bowman 1992; Russell-Smith *et al.* 1998), mammals (Woinarski *et al.* 2001; Pardon *et al.* 2003; Andersen *et al.* 2005), and birds (Franklin 1999; Franklin *et al.* 2005). Hence, variations in the way fire is used as a land management tool is likely to influence the responses of wildlife in the post-fire environment, and understanding the consequences of human-mediated burning practices is important to balance conservation and management objectives and outcomes.

Introduced plants in Australian tropical savannas

Invasions of native ecosystems by introduced plant species is a serious environmental issue in Australia. Most alien plant species have been introduced intentionally for agricultural, pastoral or ornamental purposes (Humphries *et al.* 1991; Lonsdale 1994; Martin *et al.* 2006). Approximately 2,700 alien plant species are now naturalised in Australia (Groves *et al.* 2003). Although only a small number become invasive, the proportion of invasive species differs between land-use types, with up to 26% of non-native plant species considered a threat in Australian rangelands (Martin *et al.* 2006). Invasive species in tropical savannas create substantial economic costs, particularly for the pastoral industry, and compromise native biodiversity (Humphries *et al.* 1991; Adair & Groves 1998; Grice 2006). However, relatively few studies have quantified the impacts of invasive plant species, especially with regard to the effects on native fauna (for review see Humphries *et al.* 1991; Adair & Groves 1998; Grice 2004, 2006).

Invasive plant species in tropical savannas have been associated with reduced native floristic diversity (Adair & Groves 1998; Fairfax & Fensham 2000; Fernandes &

Botelho 2003) and vegetation structure (Tomley 1998; Grice 2004) as well as altered light levels (Braithwaite *et al.* 1989) and changes to fire regimes (Rossiter *et al.* 2003). By altering plant diversity and habitat structure, the introduction of invasive plants will likely have flow-on effects for faunal communities. For example, in the Northern Territory, lower abundances of reptiles and birds were observed in areas dominated by the introduced shrub prickly mimosa (*Mimosa pigra*; Braithwaite *et al.* 1989) and in wetlands, fewer birds were associated with the exotic weed Para grass (*Urochola mutica*), originally introduced to increase pasture production (Ferdinands *et al.* 2005). Further studies quantifying the impacts of introduced plant species, and the mechanisms driving responses, are necessary to appreciate the changes that may occur in native environments following plant introduction (Levine *et al.* 2003).

Rubber vine – an invasive weed in Australia

Rubber vine, *Cryptostegia grandiflora* (Roxb.) Brown (Asclepiadaceae), is a globally distributed, invasive species. Originally endemic to Madagascar, rubber vine was introduced throughout the world in the late 1800s and early 1900s as an ornamental shrub, or a potential source of rubber (Tomley 1998). Rubber vine principally occupies tropical regions, but also extends into equatorial and sub-tropical climatic zones and is now distributed in a number of biogeographical regions; including northern, central and southern America, south-east Asia, Australia and some Pacific islands (McFadyen & Harvey 1990; Kriticos *et al.* 2003). Rubber vine is categorised as one of Australia's 20 Weeds of National Significance (Commonwealth of Australia 1999). In particular, rubber vine is a serious environmental weed in Queensland where it currently affects over 30,000 km^2 (McFadyen & Harvey 1990). With the potential to spread throughout most of northern Australia (Kriticos *et al.* 2003), rubber vine is capable of irreversible damage to the structure and function of native ecosystems (Humphries *et al.* 1991; Tomley 1995). Described as a woody liane, rubber vine grows as a free-standing shrub and also climbs over native plants, eventually smothering them (Humphries *et al.* 1991; Tomley 1998). Major infestations of rubber vine typically occur along watercourses and riparian zones, and then extend into nearby eucalypt woodland (McFadyen & Harvey 1990; Humphries *et al.* 1991; Tomley 1998). Surprisingly, no studies have quantified the impacts of rubber vine on native fauna (Grice 2004, 2006), although there is anecdotal evidence that rubber vine may disadvantage some riparian associated species, including white-browed robins (*Poecilodryas superciliosa*) and squirrel gliders (*Petaurus norfolcensis*) (see Humphries *et al.* 1991; Tomley 1998).

Techniques for managing rubber vine include chemical and mechanical methods, bio-control and fire, however, the success of these methods varies. Mechanical and chemical treatment can be effective at removing small or isolated patches of rubber vine (McFadyen & Harvey 1990; Tomley 1998) but given the weed's extensive distribution, such treatments are unsuitable for broad-scale use. Instead, two non-native bio-control agents have been trialled in Australia; *i*) the Madagascan rubber vine moth (*Euclasta whalleyi*), the larvae of which feed on rubber vine leaves (McFadyen & Harvey 1990; Mo *et al.* 2000); and *ii*) a fungal rust, *Maravalia crptostegiae* that may be effective at defoliating plants and reducing seedling emergence (Radford 2003; Tomley & Evans 2004). Fire is by far the most economical tool for controlling rubber vine infestations (Tomley 1995), and effectively reduces rubber vine survival, density and vegetative growth (Grice 1997; Bebawi & Campbell 2000, 2002). However, techniques to control introduced plant species, sometimes have undesirable consequences for native fauna (Zavaleta *et al.* 2001; Bower *et al.* 2006). Management burning to control rubber vine may adversely affect native wildlife, particularly in riparian zones that are already sensitive to inappropriate fire regimes (Andersen *et al.* 2005). Understanding the impacts of management burning on native fauna is necessary for appropriate land management decisions, and may entail a trade-off between potential deleterious effects of rubber vine and the techniques used to control it.

This project examines two main disturbances in tropical savannas: *i*) the impact of invasive plant species, specifically rubber vine, on native fauna; and *ii*), the impacts of different fire regimes, used to control rubber vine, on native fauna in tropical savannas. This study is the first to quantify the impacts of rubber vine on fauna. More importantly, I identify mechanisms driving weed avoidance of native fauna and significantly contribute towards understanding the consequences of invasive alien plants in native habitats. My fire research provides a number of benefits to ecologists and land managers alike. Firstly, most studies on the impacts of fire on fauna in Australian tropical savannas have occurred in the Northern Territory (Woinarski 1990; Trainor & Woinarski 1994; Woinarski *et al.* 1999), and few studies have examined the responses of vertebrates to fire regimes in northern Queensland (Woinarski & Ash 2002; Kutt &

Woinarski 2006) where native species composition and land use practices differ. Secondly, studies examining the impacts of weed control techniques are sparse (Zavaleta *et al.* 2001), and understanding the consequences of weed removal is important for appropriate management decisions (Zavaleta *et al.* 2001; Bower *et al.* 2006).

This study focuses on the effects of rubber vine and fire management on reptiles and birds. Reptiles and birds are strongly influenced by habitat structure (MacArthur 1964; Pianka 1989) and are, thus, likely to respond to weed- or fire-induced changes in native habitat. Furthermore, most reptiles have relatively small home ranges and are often used as surrogate measures of faunal diversity in response to disturbances (e.g. grazing: Smith *et al.* (1996), Fleischner (1994); mining: Taylor and Fox (2001); introduced plant species: Griffin *et al*. (1989), Braithwaite et al. (1989); and fire: Cunningham et al. (2002), Letnic *et al*. (2004), Trainor and Woinarski (1994)). In contrast, most bird species have large home ranges and surveys at the population level are more challenging, however, the abundance of birds in an area is indicative of habitat use. Thus, birds are also often used to measure responses to disturbance (Woinarski 1990; Jansen & Robertson 2001; Bryce *et al.* 2002; Vickery *et al.* 2005). In addition, birds encompass a range of feeding groups and examining the responses of guilds to disturbance is a useful technique for evaluating changes in bird communities that may indicate concomitant changes in resource availability (Knopf *et al.* 1988; Barlow & Peres 2004). Further, in Australian tropical savannas, inappropriate fire regimes have been linked to the decline of granivorous birds (Franklin 1999; Franklin *et al.* 2005).

Thesis Organisation

To examine the impacts of human-mediated disturbances on native fauna in tropical savannas I addressed two specific issues:

- The use of rubber vine habitat by lizards, and differences in key traits between native and rubber vine habitat that may drive lizard responses.
- The impacts of fire regimes, including variations in burning season and repeated burns, on reptile and bird assemblages in tropical savannas.

This thesis is structured as a series of stand-alone, but conceptually interconnected, publications and is organised as follows: **Chapter 2** documents observations of rubber vine habitat use by lizards in riparian zones where rubber vine is a component of the vegetation. In **Chapter 3**, I experimentally examined the habitat choice of two species of lizards, *Carlia munda* and *C. pectoralis*, using semi-natural enclosures with rubber vine and native leaf litter. Differences between native and rubber vine habitat in the field, including temperature ranges, prey availability and leaf litter structure, were compared to identify mechanisms driving lizard habitat choice. The remaining thesis chapters examine the impacts of fire regimes on native fauna, using field experiment sites initially established by Commonwealth Science Industry and Research Organisation (CSIRO – Sustainable Ecosystems). In **Chapter 4**, the responses of reptiles to differences in the burning season (wet season versus dry season) are experimentally examined in the short-term (within 12 months of burning) and medium-term (within 3 years of burning). **Chapter 5** examines the responses of bird communities, including differences in feeding groups, to differences in burning season in the short- and longer-term (within 4 years of burning). In **Chapter 6**, I use a Before-After-Control-Impact (BACI) design to experimentally examine the impact of a repeat burn on bird feeding group assemblages. Finally, in **Chapter 7**, I discuss the implications of my findings, present preliminary information on the use of mosaic burning to maintain biodiversity, and discuss directions for future research.

CHAPTER 2. HABITAT AVOIDANCE OF AN INTRODUCED WEED BY NATIVE LIZARDS

Publication: **Valentine, L.E.** (2006) Habitat avoidance of an introduced weed by native lizards. *Austral Ecology*, **31**, 732-735.

Introduction

Invasion by alien plant species poses a major threat to natural ecosystems worldwide (Vitousek *et al.* 1997), and is of particular concern in Australia, with nearly 2000 naturalised, non-native species (Humphries *et al.* 1991; Adair & Groves 1998). Environmental weeds, defined as introduced species that are deleterious to native communities (Humphries *et al.* 1991), have serious ecological consequences for the ecosystems they invade, including changes in species richness, abundance or ecosystem function (Vitousek *et al.* 1997; Grice 2004). Despite the damaging effects weeds can have on ecosystems, there is little information on the responses of native vertebrates, including reptiles, to the environmental changes brought about by large-scale weed invasions (Adair & Groves 1998; Grice 2004). Although lizard species richness may decrease in areas with a high proportion of exotic plant species (Jellinek *et al.* 2004), only a few studies have examined the responses of Australian reptiles to introduced plants. Invasion of native habitats by weeds have been correlated with reductions in species richness (Griffin *et al.* 1989) and abundance (Braithwaite *et al.* 1989), suggesting that reptiles may be particularly sensitive to the consequent alteration of habitat caused by some weed species.

One of Australia's most serious environmental weeds is rubber vine (*Cryptostegia grandiflora*), which is listed as a weed of national significance (Commonwealth of Australia 1999). Rubber vine was originally introduced from Madagascar in the 1870's and is now widespread throughout central and northern Queensland (Figure 1; Humphries *et al.* 1991; Tomley 1998). Rubber vine threatens several plant communities, but favours riparian habitats (Humphries *et al.* 1991), where it grows as a free-standing shrub or a towering vine, smothering native vegetation (Tomley 1998). Although rubber vine has been implicated in threatening native biodiversity (Humphries *et al.* 1991), there have been no studies examining the impact of rubber vine on fauna. Lizards, particularly small ground-dwelling skinks, may be affected by rubber vine due to the replacement and fragmentation of native habitat. This study aims to compare the use of rubber vine and native vegetation by lizards along watercourses within tropical savannas in northern Australia.

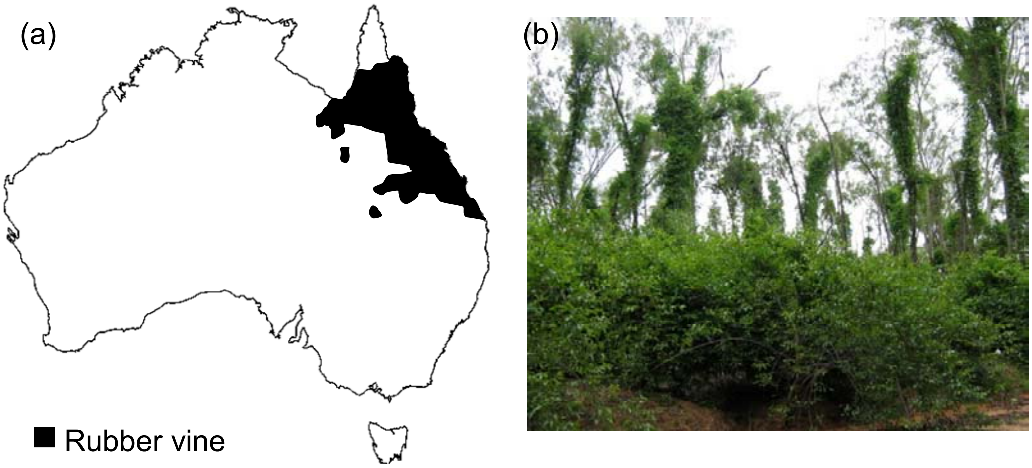

Figure 1. (a) Distribution of rubber vine (*Cryptostegia grandiflora*) in Australia (based on Tomley (1995) and Humphries *et al.* (1991)); and b) severe rubber vine infestation along a creek line showing shrubs and towers smothering native plants. Photo credit: Leonie Valentine.

Methods

The study was conducted in the Einasleigh Uplands bioregion, 110km south of Townsville, Queensland, Australia. All sites were located within grazed, tropical, open eucalypt woodland, along three seasonally dry watercourses: Bend Creek (20°16’07”S, 146°37’48”E), One Mile Creek (20°14’10”S, 146°40’35”E) and Cornishman Creek (20°12’18”S, 146°27’15”E), all tributaries of the Burdekin River. These sites were part of experimental plots used in a broader project that examined the responses of fauna to fire management strategies (Chapters 4, 5 and 6). At each site I surveyed two distinct vegetation types: riparian vegetation (within 50 m of the creek line) and the adjacent open woodland savanna. Rubber vine occurred in low to moderate infestations at each site, with much higher densities of plants in the riparian habitat than woodland habitat. In the riparian habitat, rubber vine occurred as a free-standing shrub (up to two metres high) in thickets interspersed amongst native habitat. In some areas, rubber vine also covered native trees, creating towering structures. In the woodland, rubber vine was more patchily distributed, occurring as small, isolated shrubs. In both habitats, rubber vine infestations were characterized by piles of shed leaves on the ground, superficially similar to native vegetation leaf litter piles found at the base of eucalypts.

Between mid-February and late-March 2003, 36 x ½ hr reptile surveys (6 surveys in each of the two habitats at each of the three creeks), were conducted between 0830 hrs and 1130 hrs. Surveys covered an area of approximately 1 ha and were conducted parallel to each water course, separated from other surveys by at least 50 m. During each survey, I actively searched the area by digging through leaf litter, turning logs and bark, peeling bark and visually examining tree trunks, shrubs and rubber vine. I did not preferentially search either rubber vine or native vegetation, but instead I haphazardly surveyed each vegetation type as it was encountered. Lizards were identified to species level according to Cogger (1996) and their abundance was recorded. As each lizard was encountered, the dominant habitat where they were first observed, rubber vine or non-rubber vine, was recorded. Henceforth, non-rubber vine vegetation will be referred to as native vegetation as the majority of the non-rubber vine plants observed were native species. Observations were also made of broad microhabitat types where lizards were first sighted, using the categories: leaf litter, bark, logs, open ground, shrubs or trees. The proportion of vegetation that was comprised of rubber vine was estimated to the nearest 10% within two 200 m^2 quadrats within each survey site (12 quadrats within each of riparian and woodland habitat at each of the three creeks). Assuming the expected occurrence of lizards in rubber vine versus native vegetation corresponded to the proportion of vegetation in each category, I compared lizard use of native and rubber vine vegetation in each habitat using a chi-squared goodness of fit test, with the expected values based on the proportion of rubber vine versus native vegetation.

Results

In total, 132 lizards from 17 species were observed during the surveys. The majority of lizard species were terrestrial, with only a few species observed arboreally. There was very little difference in overall reptile abundances or species richness between woodland and riparian habitat (Table 1). Only one lizard was observed in habitat dominated by rubber vine during the surveys (Table 1). A female *Carlia munda* (a small terrestrial skink) was observed at the base of a small rubber vine shrub, surrounded by rubber vine leaf litter in the woodland habitat. No reptiles were observed on rubber vine vegetation in the riparian habitat. Vegetation surveys showed that rubber vine comprised 43% (+/-5% SE) vegetation within riparian habitats, and only 5% (+/-3% SE) in woodland habitats. Since the occurrence of rubber vine in woodland habitat was approximately 5%, no useful statistical comparison could be made of the habitat use of reptiles in woodland habitats and these data were excluded from analyses. In riparian habitats, lizards occurred significantly less than expected in rubber vine vegetation ($\chi^2_{df=1} = 27.76$, $P < 0.001$; expected 70% native, 30% rubber vine, based on conservative estimates of rubber vine occurrence). However, a number of skinks (approximately five *C. munda*) were observed using native habitat that had a small proportion of rubber vine leaf litter mixed with native leaf litter.

Table 1. Abundance and species richness of lizards in riparian and woodland habitat.

	Riparian		Woodland	
	Native	Rubber vine	Native	Rubber vine
Total abundance	70	0	61	1
Total number of species	11	0	12	1

Most lizards were observed in leaf litter, under bark or on trees (Figure 2). However, the microhabitats used by lizards varied slightly between habitat types. Lizards in riparian environments were most often observed in leaf litter while lizards in woodland environments were commonly observed under bark (Figure 2). The majority of lizard captures (76%) were from 3 species, including two skinks (*Carlia munda* and *Cryptoblepharus virgatus*) and one gecko (*Heteronotia binoei*). *H. binoei* is a small terrestrial gecko that commonly occurs throughout Australia (Cogger 1996) and was nearly always observed under bark or logs. *C. munda* is a locally abundant, small, ground-dwelling skink that favours leaf litter (Cogger 1996), and was often observed in native leaf litter or within 2-3 metres of leaf litter piles. The other commonly encountered skink, *C. virgatus,* is a small arboreal skink that was always observed on tree trunks or branches.

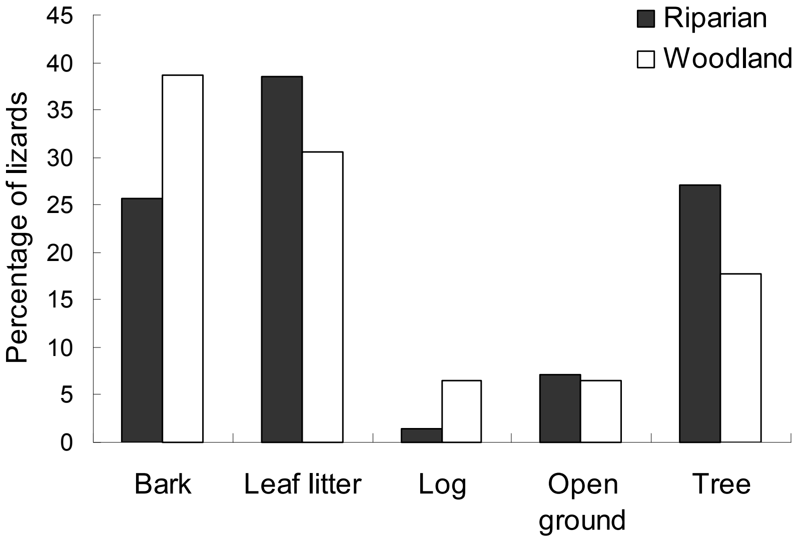

Figure 2. Microhabitat use by lizards in riparian and woodland habitats.

Discussion

Although the rubber vine habitat, particularly the leaf litter component, superficially resembles suitable habitat for lizards, only a single individual lizard was observed in the rubber vine vegetation. As rubber vine and associated leaf litter was prevalent in the riparian sites, and the majority of lizards observed were using leaf litter habitat, my observations suggest that lizards are avoiding rubber vine. Presumably, if rubber vine was suitable habitat for lizards, leaf-litter specialists, such as *Carlia munda* (Cogger 1996), would be observed utilising the readily available habitat. Instead, the apparent avoidance of rubber vine habitat by lizards suggests that rubber vine may contain underlying characteristics that are unfavourable for lizards. The responses of fauna to changes caused by introduced plant species are suspected to occur through changes in habitat structure and trophic interactions (Sakai *et al.* 2001). Differences in habitat structure between rubber vine and native vegetation may include the physical size of plants, growth form, characteristics of leaf litter and chemical attributes such as the latex content of rubber vine (Tomley 1998). These differences may alter the thermal environments available to lizards, the susceptibility of lizards to predation, and the habitat preference and subsequent availability of prey items.

As introduced species can alter characteristics of the invaded environment, they are often associated with changes in the native community structure and composition (Grice

2004). Other introduced species that have been found to create sub-optimal habitat for reptiles in Australia include the introduced tamarind (*Tamarisk aphylla*) and mimosa bush (*Mimosa pigra*). Reptiles were found to occur at lower abundances in areas dominated by mimosa (Braithwaite *et al.* 1989) and lower reptile species richness was observed in tamarind dominated areas compared to non-invaded areas (Griffin *et al.* 1989), with differences in species richness and abundance attributed to changes in habitat structure. Although my study did not specifically compare reptile abundance or species richness between rubber vine invaded and non-invaded areas, the avoidance of rubber vine by lizards observed in this study suggests that rubber vine also has the potential to reduce lizard species richness and abundance.

Since rubber vine is prolific throughout central and northern Queensland water courses (Tomley 1998) and has the potential to invade northern Australia (Kriticos *et al.* 2003), the consequences for reptile fauna in invaded habitat may be severe. The linear nature of riparian habitats may increase the negative consequences of these invasions, as obligate riparian species may be unwilling to move through an area dominated by rubber vine. This has the potential to lead to fragmentation of riparian reptile populations if areas of native vegetation are isolated by rubber vine infestations. Further studies are required to quantify the impact of introduced weeds, particularly rubber vine, on lizard fauna, and to elucidate the underlying mechanisms driving faunal responses to environmental weeds.

CHAPTER 3: MECHANISMS DRIVING WEED AVOIDANCE IN LIZARDS

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Introduction

Introduced plants, particularly invasive species, can have severe negative effects on environments and economies throughout the world (Sakai *et al.* 2001), and are a significant contributor to anthropogenically mediated, global environmental change (Daehler & Gordon 1997; Vitousek *et al.* 1997). Invading alien plant species threaten communities by changing ecosystem-level processes and properties (Gordon 1998), including nutrient cycles (Vitousek & Walker 1989; Witkowski 1991; Evans *et al.* 2001), hydrological cycles (Le Maitre *et al.* 1996; Blossey 1999), light levels (Standish *et al.* 2001), habitat structure (Ogle *et al.* 2000; Grice 2004) and fire regimes (D'Antonio & Vitousek 1992; Rossiter *et al.* 2003; Brooks *et al.* 2004). Invasive plants are also associated with changes in wildlife community structure and composition, including reduced native plant species richness (Groves & Willis 1999; Higgins *et al.* 1999) and colonization rates (Yurkonis *et al.* 2005), reduced vertebrate and invertebrate species richness or abundance (Friend 1982; Braithwaite *et al.* 1989; Griffin *et al.* 1989; Herrera & Dudley 2003; Ferdinands *et al.* 2005) and changes in plant and animal assemblage structure (Wilson & Belcher 1989). The loss of biodiversity caused by invasive alien plants may have cascading trophic effects (Sakai *et al.* 2001) that alter fundamental ecosystem processes (Knops *et al.* 1999; Hulme 2006). Occasionally, alien plant species benefit specific wildlife (Braithwaite & Lonsdale 1987; Safford & Jones 1998) and even increase faunal diversity (Marshall *et al.* 2003). However, the impacts of alien plants, particularly invasive species, are typically negative (see Hulme 2006).

The majority of research examining wildlife responses to alien plant species has focused on responses of the native floristic community. Few studies have examined the ecological responses of vertebrates to alien plant species, or the underlying mechanisms driving wildlife responses (Adair & Groves 1998; Blossey 1999; Levine *et al.* 2003;

Grice 2004). Understanding the mechanisms driving faunal responses to disturbances, including invasive alien plant species, is important for predicting how organisms will respond to increasingly modified habitats. The responses of fauna to invasive alien plant species are thought to occur as a consequence of habitat alteration and changes in trophic interactions (Sakai *et al.* 2001). For example, a change in habitat structure may lead to altered levels of predation compared to native habitat (Schmidt & Whelan 1999). Hence, differences among key traits of native and alien plant species are likely to alter the behaviour and survival of fauna in the habitats where alien plants occur (Levine *et al.* 2003), but this assumption remains untested.

Rubber vine (*Cryptostegia grandiflora*) is a widespread, globally distributed, invasive species. It is a free-standing woody liane with the ability to climb and smother trees. Endemic to Madagascar, rubber vine was introduced to several countries as an ornamental shrub or as a source of potential rubber in the late 1800s and early 1900s (Tomley 1998). In Australia, rubber vine invades several plant communities throughout Queensland, including eucalypt woodlands and vine thickets, but favours riparian habitats (Humphries *et al.* 1991; Tomley 1998). Due to the severe negative effects on the agricultural, economic and biodiversity values of invaded habitat (McFadyen & Harvey 1990; Humphries *et al.* 1991; Tomley 1998), and the potential to invade most of northern Australia (Kriticos *et al.* 2003) rubber vine is listed as a weed of national significance (Commonwealth of Australia 1999).

Reptiles are strongly dependent on habitat structure for their survival (Pianka 1989) and are therefore excellent model organisms with which to examine faunal responses to disturbances, such as invasions of alien plant species. Field observations of reptiles in habitat invaded by rubber vine recorded only a single lizard in rubber vine vegetation, compared to 131 lizards in nearby native vegetation (Chapter 2 / Valentine 2006). Further, several studies have recorded negative correlations between the presence of other alien plants and reptile species richness or abundance (Braithwaite *et al.* 1989; Griffin *et al.* 1989; Smith *et al.* 1996; Jellinek *et al.* 2004), suggesting that reptiles may be sensitive to changes in the environment caused by alien plant species.

If reptiles discriminate between alien and native vegetation, this process could influence habitat choice and provide a mechanism by which alien plant species affect local abundance and distribution patterns of reptiles. To examine the influence of alien plants on reptiles, I observed whether litter-dwelling lizards discriminated between litter from native vegetation and the introduced plant rubber vine in semi-natural enclosures. In addition, I compared habitat attributes, including temperature, prey (arthropod) availability and the physical structure of litter, between rubber vine and native habitat patches, in an environment invaded by rubber vine, to determine the possible underlying mechanisms driving habitat choice.

Methods

Behavioural experiments: leaf litter choice

The two species of lizards examined in this project, *Carlia pectoralis* and *Carlia munda*, are small (snout to vent: 44 - 52 mm), terrestrial, diurnal skinks that are locally common in the litter of open eucalypt forests of northern Queensland, Australia (Figure 1; Wilson & Swan 2003). I examined skinks occurring along seasonally dry creeks dominated by *Melaleuca fluviatilis, M. leucadendra*, *M. bracteates*, *Casuarina cunninghamiana*, and *Corymbia tessellaris*, where rubber vine was a component of the vegetation. In this environment, rubber vine occurred as a small shrub, with some towering structures that climbed trees.

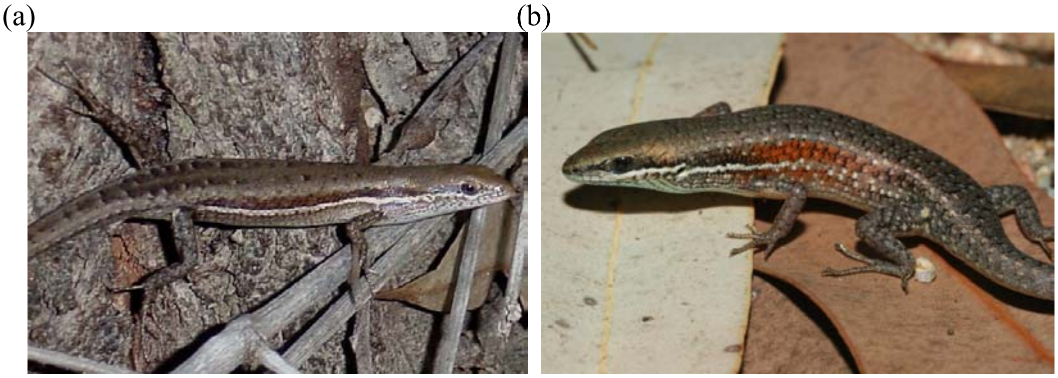

Figure 1. The two species of lizards examined in project; a) *Carlia pectoralis* (female) and b) *Carlia munda* (male). Photo credit: Leonie Valentine.

A sample of 20 adult *C. pectoralis* were captured by hand between 11 – 20 April 2005, from Campus Creek, James Cook University (19°19’33”S, 146°45’41”E), and Bohle Creek, Joleka homestead (19°22’31”S, 146°42’22”E) in Townsville, Queensland.

Twenty adult *C. munda* were also captured by hand between 25 – 29 April 2005 from Bend Creek (20°16’06”S, 146°37’52”E) and Camp Creek (20°16’35”S, 146°41’55”E) at Dreghorn station, 110 km south of Townsville. Both sexes were used in the experiments. Following capture, lizards were transferred to individual plastic cages (33 L x 22 W x 13 H cm) and provided with water, food (crickets, *Acheta domestica*), a thermal gradient and a neutral substrate (commercial potting soil) to avoid influencing habitat preference experiments, e.g. by causing chemosensory habituation to either native or rubber vine leaf litter. Behavioural experiments were conducted between 14 April and 12 May 2005 outdoors at James Cook University. Experiments were conducted in 1000 L oval, plastic enclosures (200 L x 50 H x 100 W cm). A mosaic of sun and shade was provided by commercially available “shade cloth” blocking 80% of incident solar radiation and attached to a plastic frame positioned at a 45° angle from the rim of each enclosure, allowing some direct sunlight to enter the enclosures, but always providing large patches of shade. Such a mosaic is typical of habitats used by these lizards (personal observations). The base of each enclosure was covered with washer river sand. Rubber vine and native eucalypt leaf litter (depth 4 cm) was provided at opposite ends of each enclosure, with allocation of leaf litter type randomly determined. The two leaf litter types were divided by a gap of bare sand, 35 cm wide, and water was provided at both ends of each enclosure.

All leaf litter used in the experiment had been stored in clear plastic bags in the sun for two days, killing most invertebrates. In addition, any visible prey items were removed from enclosures prior to use. Thus, prey availability during the experiments was assumed to be equally limited. To determine available temperatures within enclosures, data loggers (Thermochron iButtons™), programmed to record temperature every 15 min, were placed in the centre of each type of leaf litter in each enclosure during the *C. munda* experiments. Temperatures recorded on a typical sunny day showed that a similar thermal regime was available in both the rubber vine and native leaf litter sections of the enclosures. Temperature over a 24 hr period ranged from 18.8 °C (± 0.7 °C, 95%CI) to 32.2 °C (± 2.1 °C), with an average of 23.8 °C (± 0.4 °C) in the native leaf litter section and from 18.9 °C (± 0.8 °C) to 34.2 °C (± 4.0 °C), with an average of 24.1 °C (± 0.5 °C) in the rubber vine leaf litter section. This indicates that both ends of the enclosures experienced similar temperatures during the experiment.

After the enclosures were established, a single, randomly chosen lizard was released in the centre of the sand gap between the two leaf litter types in each enclosure, and initial choice of habitat was recorded. Lizards were left undisturbed for two days to become accustomed to the new environment. Previous behaviour experiments conducted in these enclosures indicated that exploratory and escape behaviour of lizards had decreased to a low level, and lizard behaviour was typical of field behaviour within 48 hrs of release (Langkilde *et al.* 2004). Habitat choice was quantified by quietly approaching each enclosure between 09.00 and 10.00 hrs and recording which habitat contained the lizard. A wooden barrier was placed across the sand gap separating the two habitat types, prohibiting the movement of lizards once observations began. If a lizard was detected immediately, its location (i.e. type of leaf litter) was recorded. If not, active searching was conducted until the lizard was located. Chi-squared goodness of fit tests, using Yate's correction, were used to determine habitat choice for each species.

Temperature in the field

Temperature is an important variable influencing habitat selection of lizards (Heatwole & Taylor 1987) and may vary between habitat types in the field. Seven piles of leaf litter dominated by rubber vine, and seven piles of native eucalypt leaf litter were selected along Camp Creek. Sites were chosen where leaf litter was deep (6 – 10 cm) and each site was separated by at least 50 m. I measured temperature at each pile by placing temperature data loggers (Thermochron iButtons™) at the top (1 – 2 cm below surface) and the bottom of each pile (6 – 10 cm below surface). Temperatures were recorded every 15 min for 2 sunny days from midnight, and an average temperature was calculated over a 24 hr period for each pile, allowing me to compare temperature at two depths between native and rubber vine leaf litter.

Prey availability in the field

Lizards from the genus *Carlia* are predators of small arthropods (Wilson & Swan 2003) and habitat choice of lizards may be influenced by potential prey availability. I compared arthropod abundance, taxon richness and assemblage composition between native and rubber vine habitat. Arthropods were collected on 7 August 2003 from six patches of native habitat and six patches of rubber vine habitat along Camp Creek, northern Queensland. Arthropods were collected from each site using equal-sized leaf litter samples (21 W x 30 L cm bags), and time-constrained (5 min) beating techniques of small shrubs (either native or rubber vine, depending on habitat type). Arthropods collected using beating techniques were captured on a 1 x 1 m calico fabric tray and transferred to alcohol. Leaf litter samples were placed into Berlese funnels for 6 days, until the litter was completely dry and searches of the remaining litter did not reveal any insects. Insects escaping the funnels were preserved in alcohol. Arthropods were later sorted and identified to order using the taxonomy of Harvey & Yen (1989). I combined arthropods captured at each patch using different techniques to examine average arthropod abundance and taxon richness between rubber vine and native habitat patches using t-tests (SPSS, version 12) on the log-transformed data. Arthropod assemblages (rare taxa removed) were compared between habitat patches using Principal Component Analysis (PCA; SPSS, version 12) using the covariance matrix, on the log (x + 1) transformed arthropod order abundance.

Characteristics of leaf litter piles in the field

I compared characteristics of leaf litter occurring in the field by measuring leaf litter structure and leaf shape between rubber vine and native leaf litter piles (sites described above). Leaf litter pile structure was examined by comparing the proportion of fine, coarse and very coarse particulate matter between rubber vine and native leaf litter piles. At each site, a 19 cm diameter core sample of leaf litter and debris was removed. All leaves and fine particulate matter were sieved through a series of 10, 5 and 1 mm sieves. For each size category, the total mass of material was weighed to the nearest gram using a 100 g Pesola™ spring balance. Average proportion of each size category in native and rubber vine leaf litter was compared using a MANOVA (SPSS, version 12), following arc-sine transformation of the proportional data (Quinn & Keough 2002). The average size of leaves (i.e. length and width) for each pile was also compared between native and rubber vine habitat. Eight randomly selected leaves were measured to the nearest millimetre at each pile using a transparent plastic ruler. Leaf length was measured from the base of the stem to the tip of the leaf, and leaf width was measured at three equidistant locations from 1 cm from the tip to 1 cm from the base to produce an average width per leaf. Average leaf length and width of leaves were compared between native and rubber vine leaf litter piles using a MANOVA on the log-transformed data.

To examine similarities in lizard and leaf shape, I compared the lengths of the two species of lizards to native and rubber vine leaf lengths. The total lengths of 20 *C. munda* and 20 *C. pectoralis* were measured from snout to tail tip, to the nearest millimetre, with a transparent plastic ruler. Leaf length measurements were obtained by compiling the data described above and randomly selecting 20 leaves from each litter type. An ANOVA on the log-transformed data compared mean lengths among lizard species and leaf litter types. I did not compare lizard widths to leaf widths as lizards from the genus *Carlia* are slender and both the species observed in this study were obviously much thinner than either rubber vine or native leaves (average lizard width approximately 5 mm).

Results

Behavioural experiment: leaf litter choice

During active searching for lizards in the field, I occasionally observed lizards in leaf litter piles that contained both native and rubber vine leaf litter, but lizards were never observed within leaf litter piles that were dominated by rubber vine. I captured 10 male and 10 female *C. pectoralis*, and 7 female and 13 male *C. munda*. Once animals were released into enclosures, the choice of leaf litter immediately sought was recorded. Both species of lizards dispersed evenly between the native and rubber vine leaf litter (*C. pectoralis*: $\chi^2_{df=1} = 0.05$, $P > 0.05$; *C. munda*: $\chi^2_{df=1} = 0.05$, $P > 0.05$). After two days in the semi-natural enclosures, significantly more individuals of both lizard species were observed in native leaf litter compared to rubber vine leaf litter (*C. pectoralis*: $\chi^2_{df=1} = 8.45$, $P < 0.01$; *C. munda*: $\chi^2_{df=1} = 6.05$, $P < 0.05$; Figure 2), clearly indicating a habitat preference by both lizard species for native leaf litter.

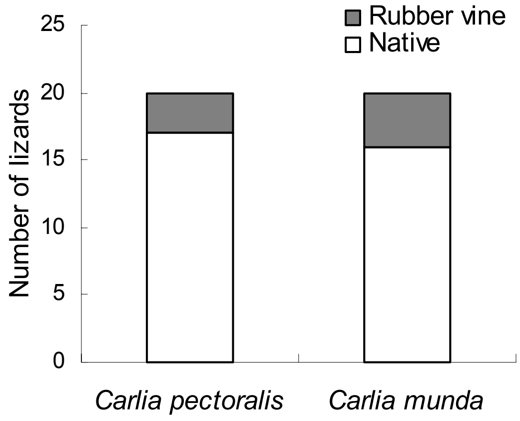

Figure 2. Number of C. pectoralis and C. munda observed in either rubber vine or native leaf litter after two days in semi-natural outdoor enclosures. 85% of *C. pectoralis* and 80% of *C. munda* were observed in native leaf litter compared to rubber vine leaf litter.

Temperature in the field

Temperature was recorded at two depths (top: 1 – 2 cm deep; below 6 – 10 cm deep) within leaf litter in the field to obtain average daily temperature ranges in rubber vine and native leaf litter (Figure 3). Temperatures at the bottom of leaf litter piles were similar. However, temperatures at the top of leaf litter piles differed considerably, with native leaf litter experiencing higher temperatures than rubber vine leaf litter for the majority of daylight hours (Figure 3). During peak periods of lizard activity, (7 - 11 am, Langkilde *et al.* 2003) native leaf litter was within the preferred body temperature range for the genus *Carlia*, typically between 28 – 32 °C (Wilhoft 1961; Singh *et al.* 2002b, L. Schwarzkopf unpublished data; Figure 3). In contrast, available temperature at the top of rubber vine leaf litter was similar to temperature at the bottom of both kinds of leaf litter for most of the day.

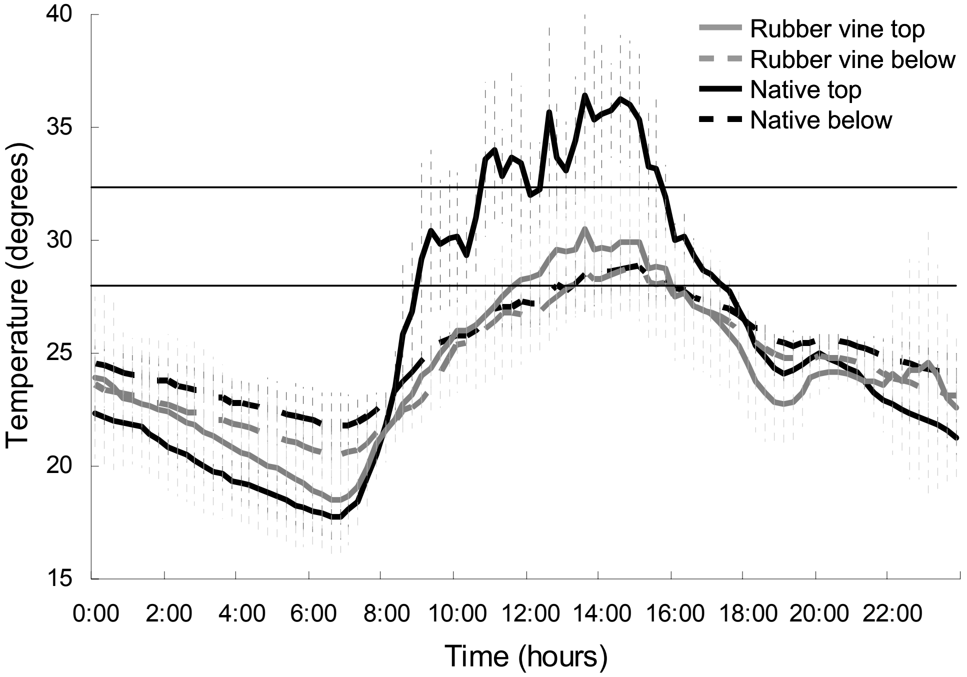

Figure 3. Average temperature throughout the day (± 95%CI, n = 7) at different depths in naturally occurring native vegetation and rubber vine leaf litter in the field. Line type represents depth of data logger in leaf litter piles (top 1 – 2 cm, below 6 – 10 cm deep). Horizontal lines through graph indicate the preferred body temperature ranges for *Carlia*, typically between 28 – 32 °C (Wilhoft 1961; Singh *et al.* 2002b, L. Schwarzkopf unpublished data).

Prey availability in the field

A total of 17 arthropod orders (Chelicerata: 3 orders; Uniramia: 14 orders) were identified from beating and leaf litter samples. Although there was a trend for lower abundances of arthropods in rubber vine habitat, there was no significant difference in abundance between habitat types (log abundance t-test, assuming equal variances: $t_{10} = 1.785$, $P > 0.05$; Figure 4a). However, lower arthropod taxon richness was observed in rubber vine habitat compared to native habitat (log order richness t-test, assuming unequal variances: $t_{6.44} = 2.430$, $P < 0.05$; Figure 4b). A PCA on arthropod composition of 12 orders of arthropods (observed in three or more sites) also revealed differences between rubber vine and native habitat (Figure 5), with significant separation of sites based on habitat type along the first principal component (PC1 site scores t-test, assuming equal variances: $t_{10} = 4.108$, $P = 0.002$). Native habitat was associated with higher number of bugs (Hemiptera), mites (Acarina) and spiders (Aranea), while rubber vine habitat was associated with larvae of butterflies or moths (Lepidoptera; Figure 5).

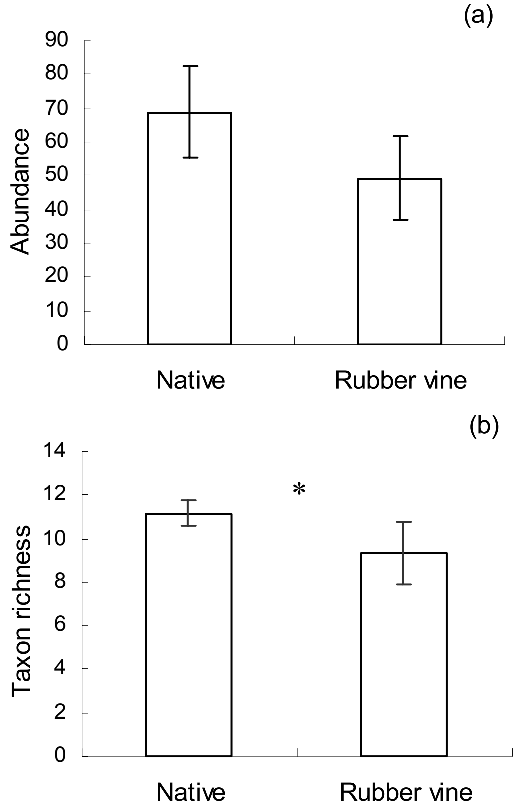

Figure 4. Average arthropod abundance (a), and arthropod taxon richness (b) in native plant and rubber vine habitat (± 95%CI). Asterisk (*) indicates significant difference between means based on t-tests.

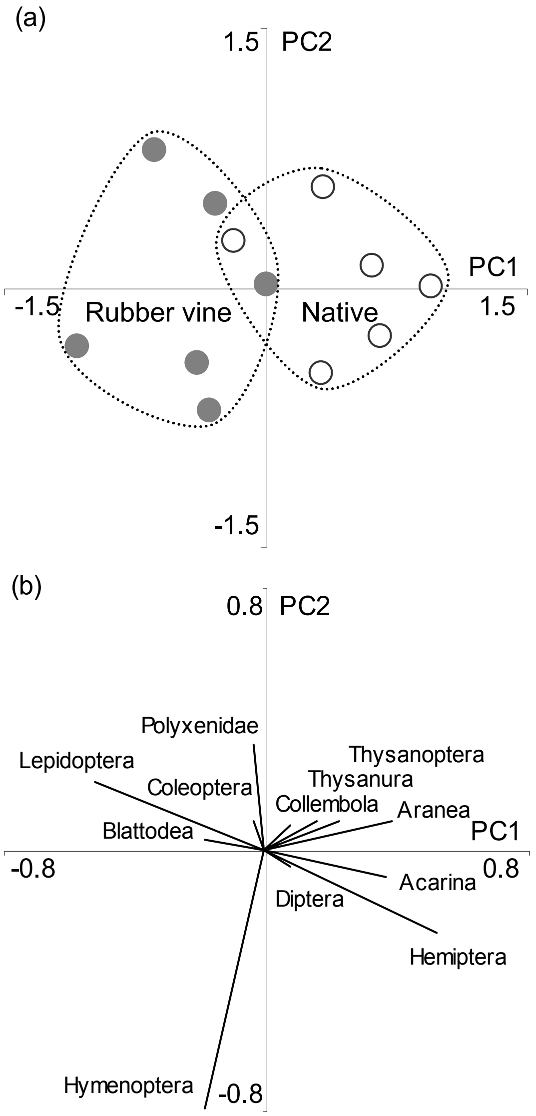

Figure 5. a) Principal Component Analysis based on the log (x + 1) covariance matrix of arthropod order abundance observed in native and rubber vine habitat. PC1 explains 34% variance, PC2 explains 21% variance. Filled symbols indicate rubber vine habitat, clear symbols indicate native habitat. Dotted lines represent significant grouping of sites based on habitat type. b) Taxon eigenvectors.

Characteristics of leaf litter piles in the field

The proportion of fine, coarse and very coarse organic matter (such as leaves, leaf debris and plant litter) was used to describe structural composition of the two types of leaf litter. Both native and rubber vine leaf litter piles were similar in overall organic matter composition and contained similar proportions of leaf litter within each sieve size category (MANOVA Wilks' Lambda: $F_{3,10} = 0.776$, $P > 0.05$). However, rubber vine leaf litter had shorter and thicker leaves compared to native leaf litter (Rubber vine leaves: mean length = 64.0 ± 3.9 mm, mean width = 30.1 ± 2.4 mm, 95%CI; Native leaves: mean length = 100.5 ± 10.1 mm, mean width = 20.8 ± 4.0 mm, 95%CI; MANOVA Wilks' Lambda: $F_{3,10} = 18.720$, $P < 0.001$; log leaf length ANOVA: $F_{1,12} = 53.367$, $P < 0.001$; log leaf width ANOVA: $F_{1,12} = 15.181$, $P = 0.002$).

In addition, rubber vine leaves were significantly shorter than *C. munda, C. pectoralis* and native leaves (Log length ANOVA: $F_{3,76} = 21.151$, $P < 0.001$; Tukey's HSD: $P < 0.01$; $P < 0.001$; $P < 0.001$, respectively; Figure 6). Interestingly, native leaves were not different in length from either lizard species, even though *C. pectoralis* was longer than *C. munda* (Tukey's HSD: $P < 0.01$). In summary, rubber vine leaves were markedly shorter than either species of lizard, with rubber vine on average 20 mm shorter than *C. munda* and 50 mm shorter than *C. pectoralis* (Figure 6).

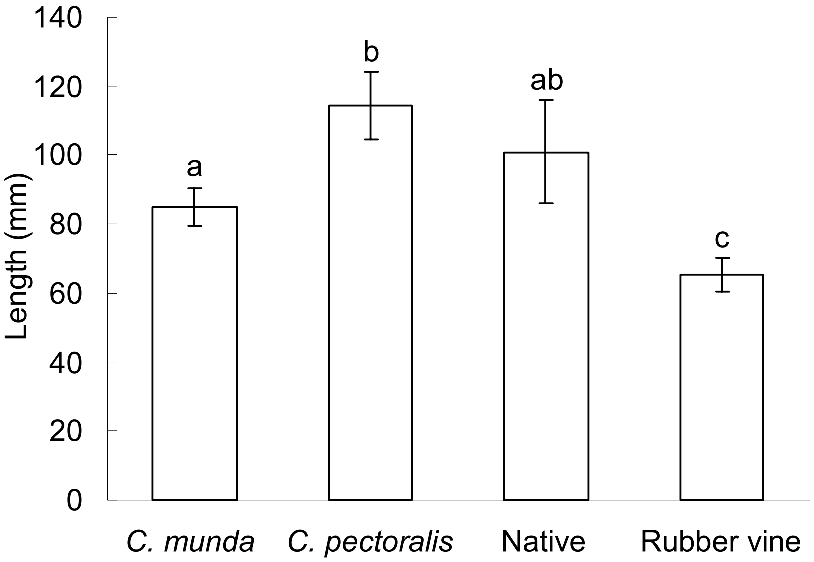

Figure 6. Average length of *Carlia munda*, *C. pectoralis*, native leaves and rubber vine leaves (± 95%CI). Letters indicate significant differences between means based on Tukey's HSD post-hoc tests.

Discussion

Behavioural experiments – leaf litter choice

Both *C. pectoralis* and *C. munda* discriminated between litter from native and rubber vine vegetation with a clear preference for native leaf litter. This confirms field observations showing that lizards, including both species of skinks examined here, were avoiding rubber vine vegetation (Valentine 2006). Low use of alien plant habitat has been observed previously in reptiles in *Mimosa pigra* and *Tamarix aphylla* dominated areas (Braithwaite *et al.* 1989; Griffin *et al.* 1989), where the alien plant species altered the vegetation structure or floristics in a manner presumed unfavourable to reptiles. Both of these studies compared reptile (and other vertebrate) abundances and species richness between native vegetation and habitat dominated by an alien plant species. My study focused on specific aspects affecting species' habitat selection in a semi-natural environment, and identified potential mechanisms driving lizard choice where introduced rubber vine is a component of the vegetation.

Temperature in the field

I measured aspects of native vegetation and introduced rubber vine habitat that may contribute to the discrimination made by lizards between these two habitats. Temperature differed markedly between native plant and rubber vine leaf litter. The biological and ecological functions of reptiles are dependent upon body temperature and thermal preferences may influence habitat selection of reptiles (Heatwole & Taylor 1987), including *Carlia* (Singh *et al.* 2002b). During peak periods of lizard activity, native leaf litter was within the preferred body temperature range of *Carlia* for longer, and throughout the day maintained higher temperatures than rubber vine leaf litter. As body temperature of small lizards is largely dependent upon habitat temperatures (Heatwole & Taylor 1987), native leaf litter may provide a more thermally suitable environment for the two *Carlia* species. Additionally, the lower temperatures observed within rubber vine leaf litter may preclude its use by other reptiles. Differences in temperature between litter types were probably related to the surrounding vegetation structure. Rubber vine has a smothering, weeping growth form that, although allowing dappled light to penetrate, produces larger shade patches than native under storey vegetation in the same community. The growth form of an introduced plant may amplify the impacts of changes in habitat structure, particularly when an introduced plant displays a growth form not normally encountered in the native environment (Grice 2004), as is the case with rubber vine in Australian tropical savannas.

Prey availability in the field

Small lizards are predators on a wide variety of arthropods (Wilson & Swan 2003) and the stomach contents of three species of *Carlia* indicated that the main prey items were spiders, grasshoppers, bugs and the larvae of beetles, butterflies and flies (James 1983). The higher taxon richness of native habitat, including greater numbers of spiders and bugs, may provide more foraging opportunities for lizards. In contrast, only the larvae of butterflies or moths were strongly associated with rubber vine habitat and these arthropods may be unpalatable to lizards. Rubber vine contains a latex (Tomley 1998), and lepidopteran larvae that feed on plants with toxic substances often sequester the compounds, rendering them unpalatable to predators (Nishida 2002). The lepidopterans observed in rubber vine habitat were most likely either larvae of the Madagascan rubber vine moth *Euclasta whalleyi*, introduced as a biological control for rubber vine (Mo *et al.* 2000), or larvae of the native common crow *Euploea core corinna*, a species that regularly uses rubber vine as a host plant (Scheermeyer 1985). Hence, rubber vine habitat, with lower taxon richness, fewer preferred prey items and potentially unpalatable caterpillars, may provide inferior food resources for lizards. The presence of a chemical compound, such as latex, in decaying leaf litter may also influence skink habitat choice.

Characteristics of leaf litter piles in the field

Although differences in the thermal range and food availability of native and rubber vine leaf litter were observed in the field, lizards selected native leaf litter over rubber vine leaf litter even in experiments when temperature ranges were similar and food was limited. Avoidance of rubber vine leaf litter under these conditions, suggests that either lizards have had previous experience of the negative properties of rubber vine leaf litter prior to capture, and have learned to avoid it, or that there are factors other than temperature and food that influenced their habitat choice in the enclosures. One factor that may contribute to the habitat selection of lizards is the appearance or structural properties of the environment (Losos 1990; Irschick & Losos 1999). I found no differences in the organic particulate composition of leaf litter types, but I did observe differences in the shape of leaves, particularly when compared to lizards. Differences in the appearance of leaves may influence habitat discrimination between native and rubber vine vegetation, as both colour and shape of background objects are important aspects of background matching for camouflage (Endler 1978, 1984; Merilaita & Lind 2005). Native leaf litter was composed of longer and thinner leaves, more similar to *Carlia* body shape, than rubber vine leaves. As rubber vine leaves are shorter than both species of lizards they may be visually more obvious on such litter, which may increase their susceptibility to detection by predators. In contrast, native leaf litter may provide more desirable habitat with the longer leaves perhaps concealing the lizards. In addition, although I did not do detailed colour analyses, the colour of native leaf litter appeared more similar to *Carlia* dorsal coloration to human eyes (both the lizards and the leaves appear light brown) than did the rubber vine leaf litter (which appears yellowish brown). Although I did not quantify the observation, it was much harder for me to see *Carlia* on native leaf litter than on rubber vine leaf litter, and this may be true for visual predators with similar visual abilities. Given this, the selection of native leaf litter may reflect background habitat matching by these cryptic skinks.

Ecological Significance and Management Implications

Our study provides conclusive evidence that two species of small litter dwelling skinks discriminate between leaf litter from native and rubber vine vegetation. This discrimination probably influences habitat choice in the field and provides a mechanism by which lizards may be affected by the introduced plant. Differences in native and rubber vine leaf litter piles observed in the field identified three possible underlying mechanisms influencing habitat choice of lizards. Firstly, the top of native leaf litter piles experienced warmer temperatures, in the preferred temperature range of *Carlia,* during peak lizard activity. Secondly, native habitat contained higher arthropod taxon richness, and more preferred prey items than rubber vine habitat. Thirdly, native leaves were similar to *Carlia* body size and shape, while rubber vine leaves were shorter than both species of lizards. Overall, rubber vine provides suboptimal habitat in comparison to native habitat, by having lower temperature ranges, supporting less favourable prey items and offering reduced opportunities for camouflage (dissimilar leaf size to lizard). Future directions for research may involve isolating the relative importance of each possible mechanism and any interactions. Whilst ambitious, a fully factorial experiment may be useful in elucidating these relationships. In addition, the presence of latex in rubber vine vegetation, and any role it might play in lizard habitat selection, also requires further investigation.

Rubber vine is a globally widespread invasive species and is one of Australia's most serious environmental weeds, with the ability to invade, dominate and degrade susceptible plant communities throughout northern Australia (Humphries *et al.* 1991; Adair & Groves 1998). Based on my results, I suggest that where rubber vine has invaded native communities, litter dwelling skinks are disadvantaged by the fragmentation and replacement of native habitat with a suboptimal environment. The absence of ground-dwelling lizards within rubber vine leaf litter is also likely to have flow-on effects to higher-order predators, including larger reptiles and birds. Given this, rubber vine represents a substantial threat to biodiversity, particularly to the fauna that utilize the riparian waterways where rubber vine is prolific.

Techniques for managing rubber vine include chemical and mechanical methods, biocontrol and fire, although the success of these methods varies. Mechanical and chemical treatments can be effective at removing small or isolated patches of rubber vine (McFadyen & Harvey 1990; Tomley 1998) but given the weed's extensive distribution such treatments are unsuitable for broadscale use. Instead, two biocontrol agents have been introduced in Australia, the leaf-feeding moth *E. whalleyi* (McFadyen & Harvey 1990; Mo *et al.* 2000) and a fungal rust *Maravalia crptostegiae* that may be effective at defoliating plants and reducing seedling emergence (Radford 2003; Tomley & Evans 2004). Fire is by far the most economical management tool and is often used for controlling other invasive alien plant species (Emery & Gross 2005). Fire effectively reduces rubber vine survival, density and vegetative growth (Grice 1997; Bebawi & Campbell 2000, 2002), but management burning may also adversely affect native wildlife, particularly in riparian zones. Further research is required to evaluate the effects of fire management on native fauna. Despite potential negative consequences of weed management practices, control of rubber vine is essential to address the deleterious environmental impacts of this invasive weed. As for all invasive alien species, a model for integrated weed management should incorporate a variety of management strategies (Hulme 2006), such as that recommended for the invasive shrub *Mimosa pigra* (Buckley *et al.* 2004).

Introduced invasive plant species are a cause of global environmental change (Vitousek *et al.* 1997) and can alter habitat structure, species composition, ecosystem pathways and ecological interactions in native communities (Gordon 1998; Blossey 1999; Sakai *et al.* 2001; Grice 2004). Such changes in habitat structure can have cascading consequences by altering the resources available to organisms in the modified environment. When this happens, the habitat created by the introduced species may not meet the requirements of native fauna, disadvantaging certain species. Knowledge of the mechanisms underlying differential uses of native and introduced plant habitat is crucial for understanding how introduced plants alter the environment and will enable managers to better predict faunal responses to disturbances from introduced species.

CHAPTER 4: WEED MANAGEMENT BURNING ALTERS REPTILE ASSEMBLAGES IN TROPICAL SAVANNAS

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Introduction

Disturbances, like fire, are crucial determinants of environmental and biological heterogeneity (Sousa 1984). However, when humans mediate disturbances, ecosystem dynamics of communities may be inappropriately modified, resulting in changes to biological diversity that may be undesirable (Chapin *et al.* 2000). Fire is a naturally occurring disturbance that is regularly imposed as a human-mediated land management tool (e.g. control of weeds: Briese (1996), Grice (1997), Emery and Gross (2005)). Since fire influences the structure of many ecosystems (Whelan 1995; Bond & Van Wilgen 1996), the widespread use of fire as a management tool will have important ramifications for biodiversity, and understanding the consequences of human-mediated fire is critical.

Reptiles, because they are strongly affected by habitat structure (Pianka 1989) and have relatively small home ranges, are often used as indicators to examine the impacts of disturbances, including fire (Trainor & Woinarski 1994; Cunningham *et al.* 2002; Letnic *et al.* 2004), on biodiversity. The use of burrows for shelter, preference of many species for open habitat and other adaptations to arid conditions (Bradshaw 1986) suggests that reptiles are fairly resilient to the short-term impacts of fire (Friend 1993; Nicholson *et al.* 2006). Further, in fire-prone environments, direct mortality of reptiles from fire is often minor (Christensen *et al.* 1981; Mushinsky 1985; Braithwaite 1987), although this varies with fire intensity. Instead, studies from a number of fire-prone environments (e.g. arid regions: Masters (1996), Letnic *et al.* (2004), Fyfe (1980); chaparral and forests: Greenberg *et al.* (1994), Taylor and Fox (2001); and tropical savannas Braithwaite (1987), Trainor and Woinarski (1994), Griffiths and Christian (1996), Faria *et al.* (2004)) indicate that reptiles respond to changes in the post-fire environment, with abundances of species presumably responding to changes in shelter, food and thermal resources caused by burning.

The longer-term responses of reptiles to fire have been well documented in spinifex dominated environments of Australia (Fyfe 1980; Pianka 1989; Masters 1996; Letnic *et al.* 2004). In these habitats, there is strong evidence that reptiles show a clear post-fire succession with species abundances and assemblages changing predictably with time since fire. In tropical savannas, however, a clear post-fire faunal succession with time since fire has not been observed, presumably because the high fire frequency of tropical savannas compared to temperate and arid regions (Lacey *et al.* 1982) may prohibit a clear successional response (Braithwaite 1987). Instead, changes in reptile assemblages may be related to the type of fire an area receives (Woinarski *et al.* 1999). Differences in fire intensity, frequency and season of burn variably alter habitat structure and composition (Glitzenstein *et al.* 1995; Whelan 1995; Russell-Smith *et al.* 1998; Williams *et al.* 2003a) and reptiles in tropical savannas may respond to these differences in fire regimes (Braithwaite 1987; Trainor & Woinarski 1994). Hence, how fire is used as a land management tool in tropical savannas may influence the responses of reptiles.

Fire and Australian tropical savannas

Tropical savannas are extensive, fire-prone environments, and stretch across the northern part of Australia, covering approximately 25% of the continent (Mott *et al.* 1985). The region has low population density and is primarily used for low-intensity cattle grazing, with large areas also set aside as Aboriginal lands and conservation reserves (Stocker & Mott 1981; Williams *et al.* 2003b). Fire is already frequently used as a contemporary land management tool (Russell-Smith *et al.* 2003b) and the characteristic seasonality of tropical savannas, with a distinct wet season followed by an extended dry season, ensures that fire is a frequent occurrence (Russell-Smith *et al.* 1997b). Burning season influences fire intensity and is an important aspect of fire regimes in tropical savannas. Grass biomass and leaf litter accumulated in the wet season cure in the high temperatures and low humidity of the ensuing dry season (Gill *et al.* 1996). As the dry season progresses, fire intensity typically increases and the most extreme fire weather occurs in the late dry season when fuel moisture content is low (Gill *et al.* 1996; Williams *et al.* 1999). Following the first rains at the start of the wet season, fires are less severe and generally more patchy (Braithwaite & Estbergs 1985;

Lonsdale & Braithwaite 1991). In tropical savannas, fire is already frequently used as a contemporary land management tool (Dyer *et al.* 2001; Russell-Smith *et al.* 2003b) and often involves the use of early-mid dry and wet season burning (Crowley & Garnett 2000; Williams *et al.* 2003b). Understanding the effects of burning season on reptile assemblages is critical. Season of burn is also likely to influence the responses of reptiles as it may interact with a species' highly seasonal activity and breeding patterns (Friend 1993).

An important element of tropical savannas is the extensive riverine systems and associated riparian zones interspersed throughout. Riparian environments are one of the most diverse and complex habitats (Naiman *et al.* 1993), often characterized by a distinct fauna (Woinarski *et al.* 2000). Although Australian tropical savannas, and associated riparian zones, are relatively intact, they are disturbed by inappropriate fire regimes (Andersen *et al.* 2005; Whitehead *et al.* 2005). The use of fire in riparian zones has been discouraged in some south-western United States ecosystems where invasive plant species have altered fire regimes (Bock & Block 2005; Keeley 2006). However, in Australia, fire may be an important management tool for controlling the spread and extent of invasive plant species, including the globally distributed woody weed, rubber vine (*Cryptostegia grandiflora*).

Rubber vine, a weed of national significance in Australia (Commonwealth of Australia 1999), was introduced from Madagascar in the late 1800's and damages the agricultural, economic and biodiversity values of northern Australia (Tomley 1998; Chapter 2 / Valentine 2006), particularly in riparian zones where rubber vine is prolific (Tomley 1998). Further, at a small-scale, reptiles tend to avoid rubber vine as it creates a suboptimal environment (Chapter 3 / Valentine *et al.* in press). As fire can significantly reduce rubber vine survival, density and vegetative growth, and may inhibit seed germination (Grice 1997; Bebawi & Campbell 2002), the use of fire in riparian zones may increase. The removal of weeds is often a priority, and few studies have examined the impacts of weed removal techniques on biodiversity and assemblage composition (Zavaleta *et al.* 2001). However, preliminary work suggests that broad-scale weed removal techniques, like burning, may alter faunal composition (Zavaleta *et al.* 2001; Bower *et al.* 2006). Understanding the consequences of management burning, including weed control, is crucial for informed land management decisions. I examined the short- and medium-term responses of reptile assemblages to weed management burning during different seasons in riparian zones of tropical savannas.

Methods

Study Site & Experimental Design

This study was conducted in the Einasleigh Uplands bioregion (Sattler & Williams 1999), 110 km south of Townsville in north-eastern Queensland, Australia (Figure 1). All sites were located in grazed, open, eucalypt woodland, along three seasonally dry watercourses: Bend Creek (20°16'07"S, 146°37'48"E), One Mile Creek (20°14’10”S, 146°40'35"E) and Cornishman Creek (20°12'18"S, 146°27'15"E), all sub-catchments of the Burdekin River. The study was carried out in three stratified, replicate, experimental blocks, each of which encompassed approximately three km of watercourse. The experimental design was initially established by the Commonwealth Science and Industry Research Organisation – Sustainable Ecosystems (CSIRO-SE) and Tropical Savannas Cooperative Research Centre (TS-CRC) in 1999 for investigating the effectiveness of fire regimes to control rubber vine. Prior to the experiment, sites were unburnt for at least 10 years (K. Smith personal communications). Although there is no detailed record of previous fire regimes for the area, sites were probably burnt every 5 – 20 years (K. Smith personal communications).

Experimental plots were established along each creek and included both riparian and adjacent non-riparian open woodland habitat. Riparian vegetation consisted of fringing woodland dominated by *Melaleuca fluviatilis, M. leucodendra, M. bracteata, Casuarina cunninghamiana* and *Corymbia tessellaris*. Adjacent non-riparian habitat, henceforth referred to as woodland, was dominated by *Eucalyptus crebra, E. brownii* and *Corymbia erythrophloia* with a predominantly grassy understorey of *Bothriochloa pertusa* and *Heteropogon contortus*. Rubber vine occurred in low to moderate infestations in both habitats, but was more prolific in the riparian habitat. Each plot was approximately 20 ha (10 ha either side of the watercourse) and plots were separated from each other by double fire breaks, spaced at least 50 m apart. At each creek, the same experimental treatments were randomly imposed and included: *i*) an unburnt control plot; *ii*) a dry season burnt plot, fire imposed August 2000; and *iii*) a wet season burnt plot, fire imposed December 1999 (Figure 1). Henceforth, time since fire will describe the time interval elapsed since the wet season fire. Two additional experimental treatments were imposed at each creek, but these were part of a larger study and were not included in analysis in the present study. In this study, site refers to either the riparian or woodland habitat of each fire treatment.

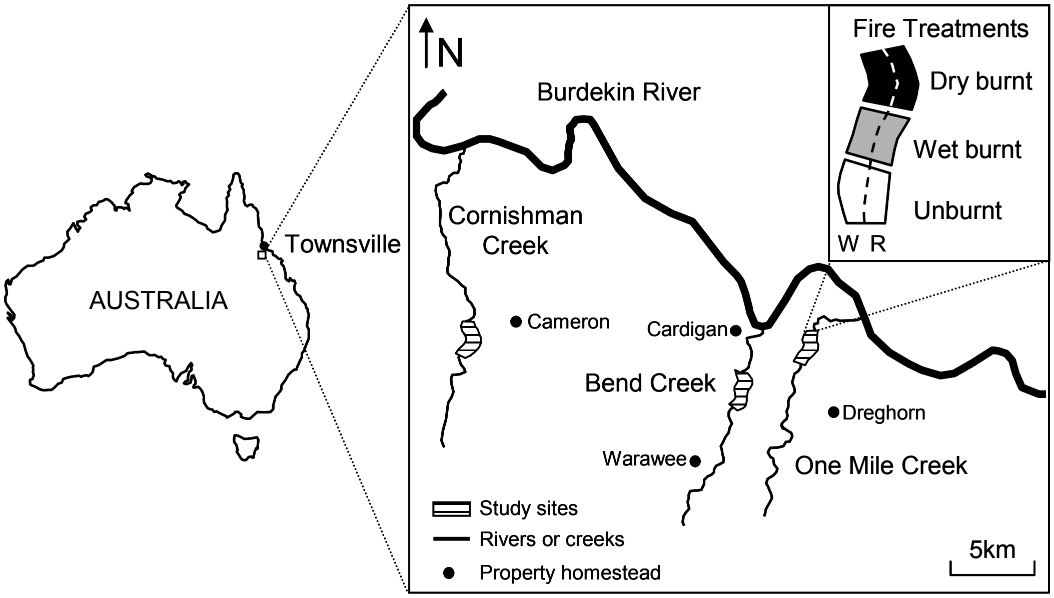

Figure 1. Map of study region. First inset shows location of study sites along tributaries of the Burdekin River, north-eastern Queensland. Second inset shows fire treatment plots and habitat (dashed line indicates separation of habitats; R = riparian, W = adjacent woodland) along One Mile Creek.

Sampling strategy

Data were collected during the tropical wet season, following the first rains of the season, between January and March 2001 & 2003. Sampling occurred over two years to examine the short term (12 months post-fire) and medium term (3 years post-fire) responses of reptile assemblages to burning. Sampling reptile fauna in tropical savannas during the wet season is ideal as reptile activity is at a peak, and coincides with the breeding season of several lizard species. Plots were surveyed randomly in each creek. Lizard assemblages were surveyed using a combination of active searching and pit-fall trapping techniques. At each site two 30-min time-constrained active searches (four surveys in each treatment at each watercourse) were conducted between 0830 hrs and 1130 hrs. Surveys were conducted parallel to each water course, separated from other surveys by at least 50 m, and covered an area of approximately 1 ha. During each survey the area was actively searched by digging through leaf litter, turning logs, peeling bark and visually examining vegetation. Reptiles were identified to species level according to Cogger (2000) and where possible, sex was determined. Two pit-fall trap arrays were established at each site (four arrays in each treatment at each watercourse). Each array consisted of two 20 L buckets connected by ten meters of shade cloth, erected 40 cm high. The buckets, with 2 mm holes drilled in the bottom for drainage, were dug flush with the ground 1.5 m from either end of the shade cloth. A moistened sponge and leaf litter were placed at the bottom of each bucket to provide shade and reduce the risk of desiccation. Traps were open for six days at each site and checked thoroughly daily. Captured reptiles were identified to species, sexed and measured, for individual identification purposes, and released near the pit-fall traps. Total reptile species and abundances observed using pit-fall trapping and active searching were pooled for each site, with recaptures excluded, to provide an estimate of reptile species richness and abundance per site. Data on vegetation structure were collected using four large quadrats (20 m x 10 m) that were established in each site. The number of trees and shrubs were counted and the proportion of rubber vine in the understorey (< 3 m high) was estimated to the nearest 10% in each quadrat. Microhabitat composition was described by recording the percentage cover of leaf litter, grass, branches (including logs), bare ground and vegetation cover (forbs and other plant material) using five 0.25 m^2 quadrats in each larger vegetation quadrat (20 small microhabitat quadrats per site).

Analysis

Species number and reptile abundance

Data were analysed within each sample year to examine the short- and medium-term responses of reptile assemblages to seasonal burning. A three-factor ANOVA (SPSS, version 12) was used to examine differences in mean reptile abundance and species number among fire treatments (unburnt, wet season burnt, dry season burnt) and between habitats (riparian and woodland), using creek as a blocking factor. As the likelihood of detecting animals using survey techniques may have varied between treatments, trends in the abundances of reptiles observed only using pit-fall trapping were also examined. The abundance of dominant species (≥ 5% of observed individuals) was also compared among factors using ANOVA models (described above). As the experiment only had modest replication, Bonferroni correction (Rice 1984) to sequential species ANOVAs was not applied.

Reptile assemblage

Community composition, defined as the observed abundance of each species per site, was recorded between treatments and habitats using perMANOVA (Anderson 2001). PerMANOVA is a distance-based nonparametric multivariate analysis of variance that provides a pseudo-F statistic, and an associated *P*-value derived from permutation tests (Anderson 2001). A two-way factorial perMANOVA, using Sorensen distance measure, was used to examine community composition between treatment and habitat in the statistical package PC-ORD (McCune & Mefford 1999). PerMANOVA was initially conducted on untransformed and log (x + 1) species abundance data. However, as reptiles assemblages were dominated by one or two species, I transformed data using relativisation by species maximum to decrease the influence of numerically dominant species. Post-hoc pair-wise comparisons were used to examine differences in reptile assemblages between fire treatments. Rare species (species that were observed in less than three sites) were not included in the analysis. Non-metric multidimensional scaling (NMDS; Kruskal 1964) was used to graphically depict the site assemblage relationships of the transformed similarity matrix using Sorensen distance measure and the ‘slow and thorough’ autopilot option of NMDS in PC-ORD (McCune & Mefford 1999). Dimensionality was determined using scree plots and Monte Carlo tests.

Vegetation composition, correlations and data transformations

The average number of trees, shrubs and proportion of rubber vine per quadrat in each site was compared using ANOVA models (described above). Microhabitat variables were also examined using ANOVA. Microhabitat and vegetation variables were correlated, using Pearson’s correlation coefficient (SPSS, version 12), with species number, reptile abundance, and the abundance of species that responded significantly to fire treatment or habitat. Microhabitat and rubber vine percentage data were adjusted by arcsine transformation of the square-root proportional data (Zar 1999). Count data (species number, reptile and individual species abundance, and vegetation variables) were examined for normality and heteroscedasticity using box plots, Q-Q plots and residual plots. Abundances of trees and shrubs were square-root transformed, and the abundance of individual species were log (x + 1) transformed to meet assumptions of

ANOVA and Pearson's correlations. To aid interpretation, graphs depict the untransformed data.

Results

Short-term Responses (12 months post-fire)

Reptile species number and abundance

During the first year of surveys, 485 reptiles from 22 species of lizards (four geckos, 15 skinks, two dragons and one goanna) and four species of snakes (one colubrid, two elapids and one blind snake) were observed during active searching and pit-fall trapping. Of these, eight species were only observed once. Only 14 skinks were recaptured, all within the same sites, indicating that only a small proportion of the reptile population was sampled. There was no difference in species number among fire treatments, however more species were observed in the woodland habitat (species number: riparian mean = 6.2 ± 1.4, woodland mean = 8.1 ± 1.5, 95%CI) and there were differences in the number of species observed between creeks (Table 1). Although abundances of reptiles were similar among factors, a significant interaction between fire treatment and habitat was detected (Table 1), indicating higher abundances of reptiles in the woodland habitat of dry season burnt sites (Figure 2a). This pattern was also observed when examining pit-fall trapping data without the active search data, suggesting the result was not entirely due to differences in detectability of reptiles among sites when searching actively.

Despite observing several species, the abundance of each survey was numerically dominated by only a couple of lizard species. By far the most abundant species (35% of all observations) was *Carlia munda*, a small, terrestrial skink. Abundances of *C. munda* were significantly higher in the dry season burnt and wet season burnt sites compared to the unburnt (Table 1, Figure 2b), and this pattern was also observed when examining only the pit-fall trapping data. Several juvenile *C. munda* (30 individuals) were observed during surveys, but the abundance of juveniles did not vary among fire treatments (ANOVA: $F_{2,10} = 1.814$, $P > 0.05$). Instead, the high abundance of *C. munda* in burnt sites was driven by differences in adult abundances among fire treatments (ANOVA: $F_{2,10} = 6.722$, $P < 0.05$). The abundance of other lizards, including the skinks *Carlia pectoralis, Cryptoblepharus virgatus*, *Menetia timlowi* and the gecko

Heteronotia binoei, did not significantly among fire treatments (Table 1). However, *Carlia pectoralis* were more abundant in riparian habitat while *H. bineoi* were more abundant in the woodland habitat (Table 1). The remainder of species comprised < 5% of the total observed individuals and were not examined using ANOVA.

Table 1. ANOVA F-values for species number, reptile abundance and the log (x + 1) transformed abundance of select species within 12 months post-fire. The proportion that each species contributed to total reptile abundance is given as a percent in parentheses. Significant values are in bold (* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$). Letters beside significant values indicate results from post-hoc Tukey HSD tests (unburnt = U, wet burnt = W, dry burnt = D) or identify the habitat with higher abundances (riparian = R, adjacent woodland = W).

	Treatment $_{df = 2,10}$	Habitat $_{df = 1,10}$	Trt*Hab $_{df = 2,10}$	Creek $_{df = 2,10}$
Species number	1.477	**10.947** W**	0.720	7.273*
Reptile abundance	1.353	1.458	**4.631***	3.522
Scincidae				
Carlia munda (35%)	**5.887* D&W > U**	0.125	2.126	0.336
Carlia pectoralis (8%)	0.059	**7.335* R**	0.142	**7.145***
Cryptoblepharus virgatus (15%)	2.078	3.461	0.382	0.307
Menetia timlowi (10%)	1.547	0.460	1.162	**8.012****
Gekkonidae				
Heteronotia binoei (11%)	2.028	**28.988*** W**	1.269	1.257

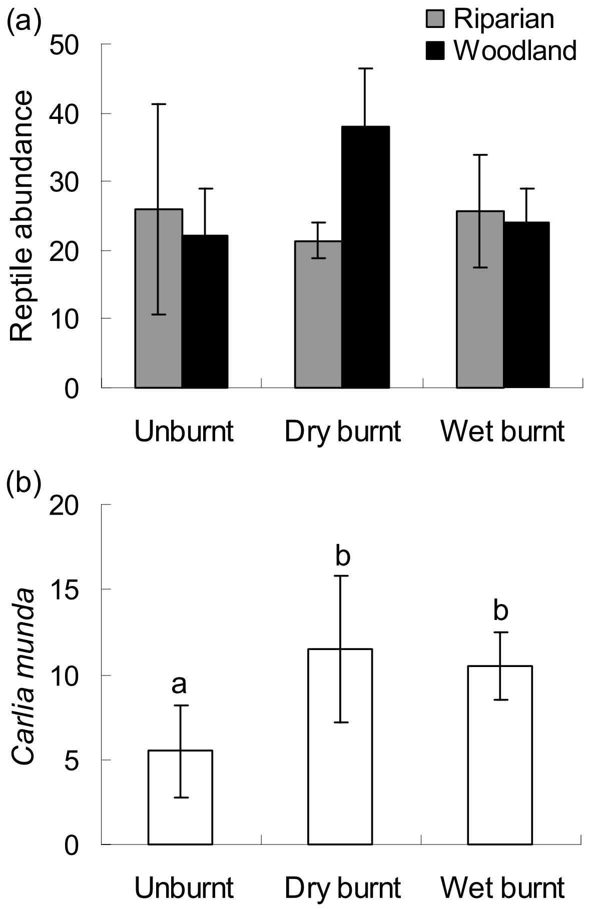

Figure 2. Mean abundance (± 95%CI) of a) reptiles in each habitat type, and b) untransformed mean abundance of *Carlia munda* among fire treatments 12 months post-fire. Note that reptile abundance was higher in the woodland habitat of the dry season burnt sites. Letters above error bars indicate significant differences between means in the abundance of *Carlia munda* (Tukey HSD, $\alpha \leq 0.05$).

Reptile assemblage

Twelve lizard species were observed in 3 or more sites and included in community analyses. PerMANOVA on data relativised by species maximum detected significant differences in community structure between habitats (perMANOVA: $F_{2,12} = 2.758$, $P = 0.008$) but not fire treatments (perMANOVA: $F_{2,12} = 0.867$, $P > 0.05$). Similar results were also observed on the untransformed and log (x + 1) transformed data. Using NMDS, I found a stable 2-dimensional solution (stress = 0.19) representing 69% variance (Figure 3). Woodland and riparian sites mostly separated along Axis 1. Most species were associated with woodland habitat, although *Carlia pectoralis* and *Cryptoblepharus virgatus* were associated with riparian habitat (Figure 3).

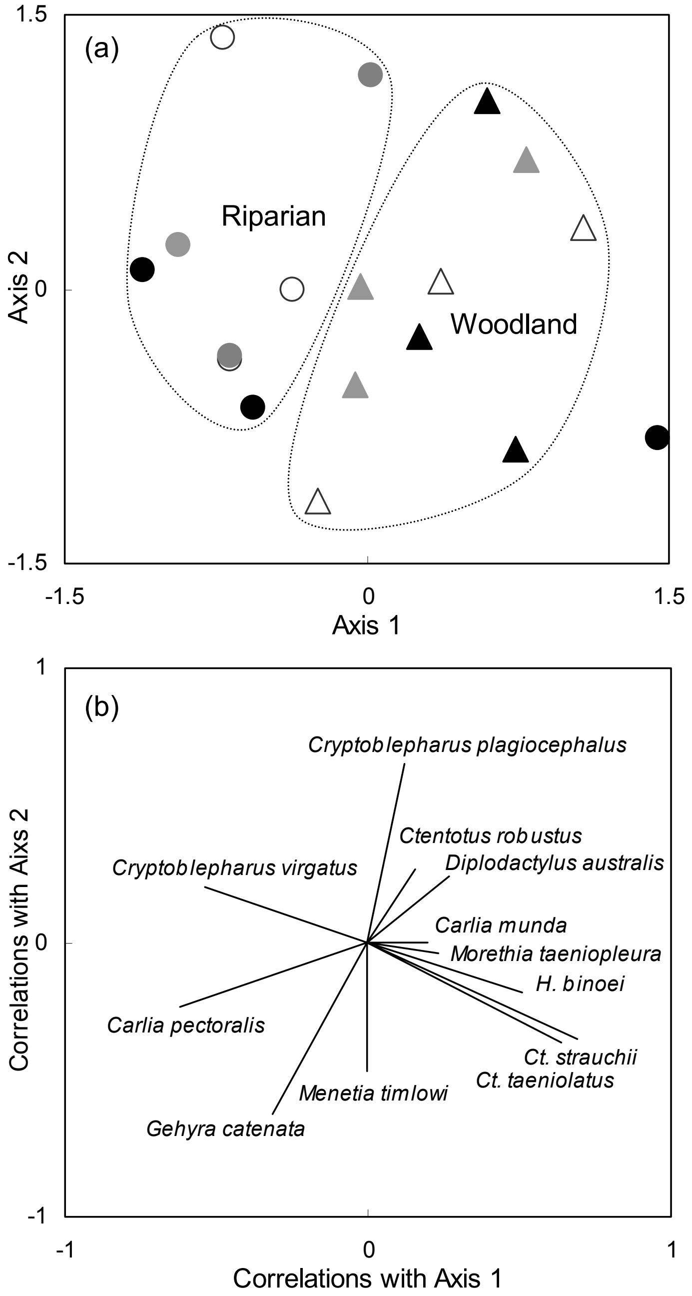

Figure 3. (a) Two dimensional NMDS ordination (stress = 0.19) on the assemblage of reptiles (n = 12, relativised by species maximum) at sites within 12 months of burning. Axis 1 represents 37% variance and axis 2 represents 32%. Colour represents fire treatment (clear = unburnt; grey = wet season burnt; black = dry season burnt) and symbols represent habitat type (circles = riparian; triangles = woodland). Dotted lines indicate groups of habitat. (b) Correlations of species ($r^2 > 0.2$) with NMDS ordination.

Vegetation composition

Microhabitat and vegetation structure varied between fire treatments and habitats (Table 2). There was a tendency for there to be less microhabitat and vegetation structure in the dry season burnt sites than the unburnt sites, with wet season burnt sites showing intermediate levels of these variables. Dry season burnt sites had significantly lower amounts of grass and shrubs, but higher amounts of bare ground than unburnt sites (Table 2). Wet season burnt sites also had lower numbers of shrubs than unburnt. There was a trend for lower amounts of rubber vine in the burnt sites, but the proportion of rubber vine did not significantly vary among fire treatments. Although the intensity of rubber vine infestations was visibly reduced in the burnt habitat, the recorded measure of rubber vine relates to understorey shrubs only and, therefore, did not reflect the reduction in rubber vine infestations or towers in the burnt sites (Radford, unpublished data). Substantial differences in microhabitat and vegetation structure were also detected between habitat types, with riparian sites containing higher amounts of leaf litter, branches, vegetation cover, shrubs and rubber vine but lower amounts of bare ground (Table 2).

Table 2. ANOVA F-values for microhabitat and vegetation variables per quadrat within 12 months of burning. No significant interaction terms were detected. Significant values are highlighted in bold (* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$) and values approaching significance are identified (^ $0.06 > P \geq 0.05$). Untransformed means (± 95%CI) for fire treatments and habitat are shown. Letters next to fire treatment means indicate results from post hoc Tukey HSD tests ($\alpha < 0.5$).

	F-values $_{\text{Error df = 10}}$			Treatment means			Habitat means	
	Treatment df = 2	Habitat df =1	Creek df = 2	Unburnt	Dry burn	Wet burn	Riparian	Woodland
Microhabitat Variables (%)								
Leaf litter	1.156	**34.623*** **	**5.297***	20.2 ± 3.3	20.6 ± 8.7	24.0 ± 7.3	28.9 ± 6.5	14.3 ± 5.2
Grass	**10.021** **	2.808	1.809	57.9 ± 8.2^{a}	29.1 ± 11.6^{b}	44.3 ± 9.6^{ab}	39.3 ± 9.1	48.3 ± 5.7
Branch	0.093	**7.088***	1.198	3.6 ± 0.5	4.1 ± 1.0	4.2 ± 2.4	5.1 ± 2.0	2.8 ± 0.7
Ground	**23.409*** **	**11.768** **	1.932	8.5 ± 3.6^{a}	38.9 ± 9.7^{b}	18.1 ± 9.6^{a}	15.6 ± 4.3	28.1 ± 9.5
Veg cover	0.652	4.680^	0.794	9.5 ± 3.5	6.0 ± 2.2	7.5 ± 5.8	9.8 ± 2.6	5.5 ± 2.8
Vegetation Variables (count data & %)								
Trees	0.301	**5.945***	1.031	4.4 ± 1.3	5.0 ± 1.7	4.5 ± 0.5	5.5 ± 0.7	3.8 ± 0.7
Shrubs	**7.903** **	**7.093***	0.474	1.8 ± 0.4^{a}	0.5 ± 0.4^{b}	$0.8 \pm 0.6^{b\wedge}$	1.3 ± 0.1	0.7 ± 0.3
RV	1.604	**33.853*** **	0.135	37.9 ± 16.1	21.7 ± 10.7	26.2 ± 13.7	49.4 ± 14.1	7.8 ± 6.1

Correlations of vegetation and reptile assemblage

The number of species per site was negatively correlated with logs possibly reflecting lower species richness in riparian habitat and the association of riparian habitat with logs (Table 3). Total reptile abundance was not correlated with any of the measured vegetation variables. However, the abundance of *Carlia munda* was negatively associated with shrub abundance and grass cover, but positively associated with bare ground (Table 3; Figure 4), reflecting the higher abundances of this species in burnt habitat. Similarly, the abundances of *Carlia pectoralis* were positively associated with leaf litter and abundances of *Heteronotia binoei* were negatively correlated with vegetation cover and branches, reflecting these species habitat preferences (Table 3).

Table 3. Pearson's correlations (r) of species number, reptile abundance and the log (x + 1) abundance of species that responded significantly to fire treatment or habitat with microhabitat and vegetation structure. Significant values are highlighted in bold (* $P < 0.5$, ** $P < 0.01$) and values approaching significance are identified (^ $0.06 > P \geq 0.05$).

	Microhabitat (%)					Vegetation		
	Leaf litter	Grass	Branch	Ground	Veg cover	Trees	Shrubs	RV
Species number	-0.365	0.132	**-0.582***	0.205	-0.385	-0.326	-0.244	-0.426
Reptile abundance	0.043	-0.350	-0.301	0.425	-0.296	-0.187	-0.428	-0.259
Carlia munda	0.291	**-0.590***	0.087	**0.522***	-0.244	0.069	**-0.520***	-0.133
Carlia pectoralis	**0.540***	-0.352	0.112	0.008	0.025	0.451^	0.185	0.413
Heteronotia binoei	-0.426	0.283	**-0.520***	0.199	**-0.471***	**-0.480***	-0.345	**-0.614****

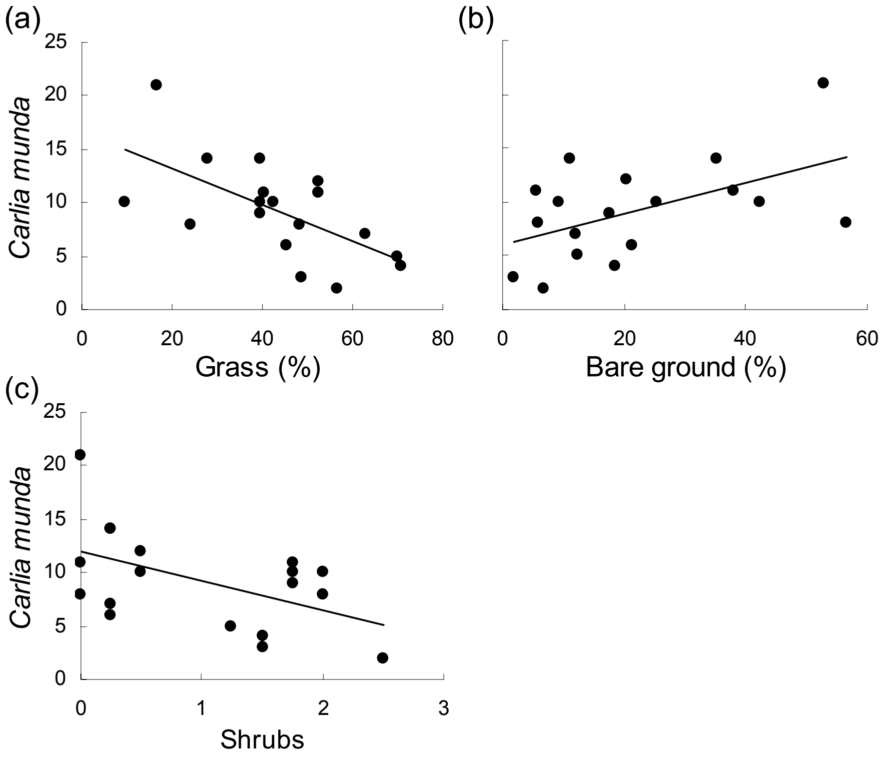

Figure 4. Significant associations between the abundance of *Carlia munda* and microhabitat and vegetation structure within 12 months of burning. Linear trend lines are fitted on the data for each graph.

Medium-term responses (3 years post-fire)

Reptile species number and abundance

The final year of surveys detected far fewer reptiles, with only 203 individuals from 18 species of lizards (three geckos, 1 legless lizards, 12 skinks, one dragon and one goanna) and two species snakes (one elapid and one blind snake) observed during active searching and pit-fall trapping. Of these, six species were observed only once and three skinks were recaptured. A significant difference in species number and reptile abundance was detected among fire treatments but not habitat (Table 4). Wet season burnt sites had significantly lower species number than unburnt sites and reptile abundance was lower in the dry season burnt sites compared to the unburnt (Figure 5a-b). The small, terrestrial gecko *Heteronotia binoei* was the most abundant lizard but was rarely observed in the dry season burnt sites (Table 4, Figure 5c). Although abundances of *Carlia pectoralis* were generally low, this small terrestrial skink was only observed once in the burnt sites and was most often observed in unburnt riparian habitat (Table 4). The abundances of three other skinks, *Carlia munda*, *Cryptoblepharus virgatus* and *Ctenotus robustus* did not vary among factors (Table 4).

Table 4. ANOVA F-values for species number, reptile abundance and the log (x + 1) transformed abundance of selected species three years after burning. The proportion that each species contributed to total reptile abundance is given as a percent in parentheses. Significant values are highlighted in bold (* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$) and values approaching significance are identified (^ $0.06 > P \geq 0.05$). Letters beside significant values indicate results from post-hoc Tukey HSD tests (unburnt = U, wet burnt = W, dry burnt = D) or identify the habitat with higher abundances (riparian = R, adjacent woodland = W).

	Treatment $_{df = 2,10}$	Habitat $_{df = 1,10}$	Trt*Hab $_{df = 2,10}$	Creek $_{df = 2,10}$
Species number	**6.695* U > W**	0.763	2.288	3.136
Reptile abundance	**8.766** U > D**	0.075	1.363	0.467
Scincidae				
Carlia munda (24%)	1.929	4.606^	1.423	3.095
Carlia pectoralis (5%)	**9.773** U > W&D**	**7.533* R**	3.413	1.088
Cryptoblepharus virgatus (11%)	0.684	0.536	0.034	0.251
Ctenotus robustus (6%)	0.505	0.116	0.809	0.158
Gekkonidae				
Heteronotia binoei (36%)	**13.328** U&W > D**	2.719	1.211	0.160

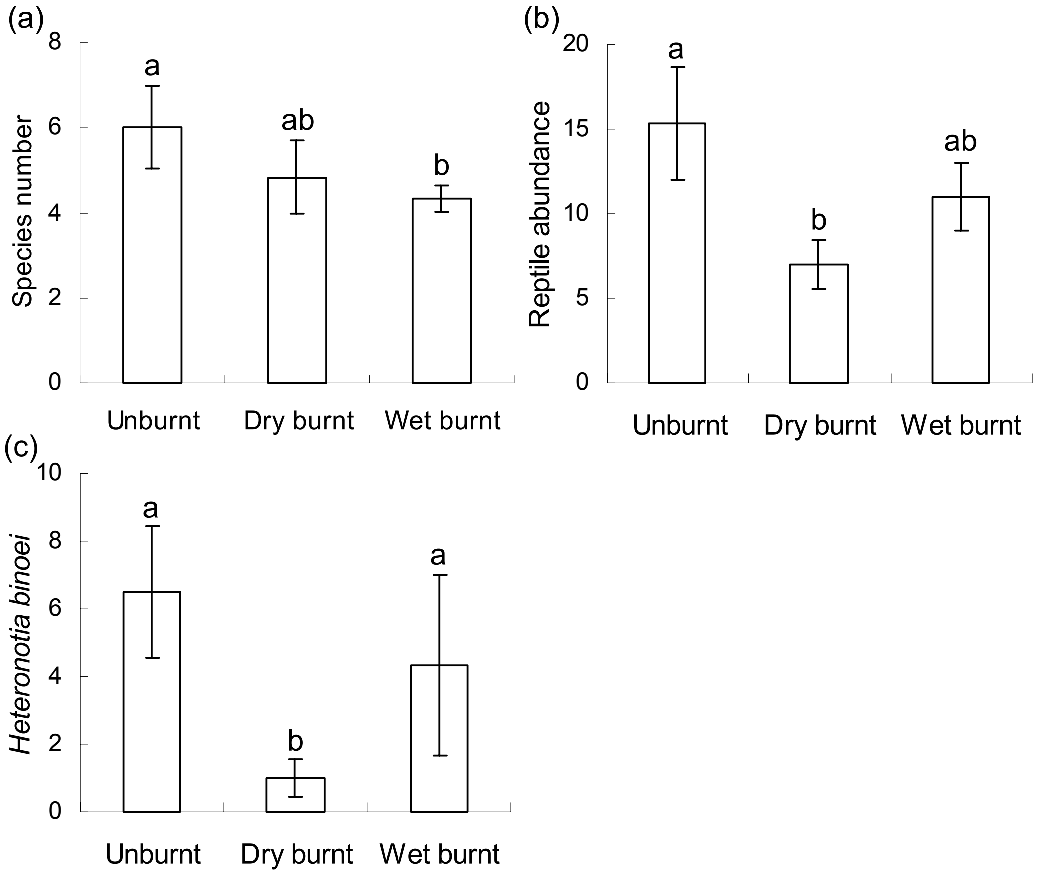

Figure 5. Mean a) species number (± 95%CI), b) reptile abundance (± 95%CI) and c) untransformed mean abundance of *Heteronotia binoei* (± 95%CI) between fire treatments three years after burning. Letters above error bars indicate significant differences between means (Tukey HSD, $P \leq 0.05$).

Reptile assemblage

Ten reptile species were observed in 3 or more sites and included in community analyses. Initial perMANOVA on untransformed or log (x + 1) transformed species abundances detected differences in community structure among fire treatments (perMANOVA: $F_{2,12} = 2.386$, $P = 0.01$), with pair-wise comparisons showing differences in unburnt sites compared to dry season burnt ($t = 1.53$, $P = 0.04$) and wet season burnt sites ($t = 1.77$, $P = 0.008$). However, these differences were driven by the most abundant species, *Heteronotia binoei*. After relativisation by species maximum to reduce the influence of the most abundant species, perMANOVA detected significant differences in community structure among fire treatments (perMANOVA: $F_{2,12} = 2.160$, $P = 0.025$), but only between unburnt and wet season burnt sites ($t = 1.77$, $P = 0.008$).

Using NMDS, I found a stable 2-dimensional solution (stress = 0.18) representing 67% of the variance (Figure 6). Fire treatments separated along Axis 1. In particular, the unburnt sites grouped away from the wet season burnt sites, with the dry season burnt sites scattered throughout. Most species were associated with unburnt sites, and only the ground-dwelling skink *Ctenotus robustus* was associated with wet season burnt sites (Figure 6). This pattern tends to reflect the differences in species number observed in fire treatments.

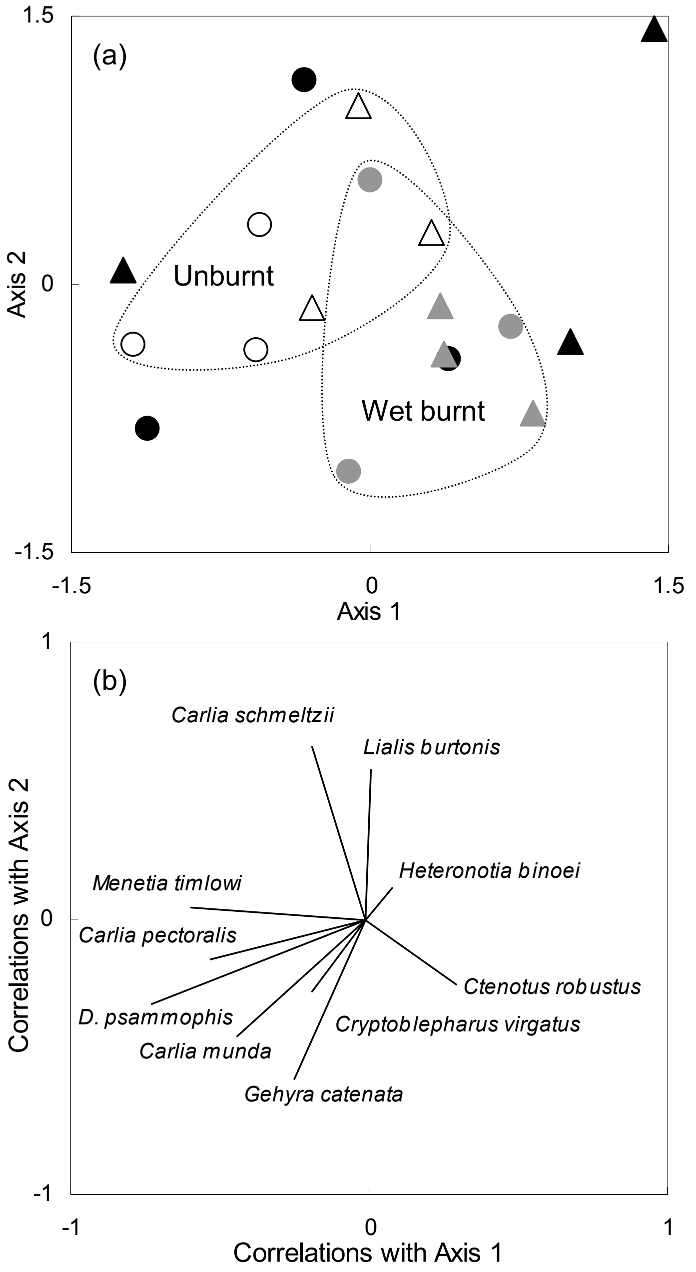

Figure 6. (a) Two dimensional NMDS ordination (stress = 0.18) on the assemblage of reptiles (n = 10, relativised by species maximum) at sites within three years of burning. Axis 1 represents 43% variance and axis 2 represents 25%. Colour represents fire treatment (clear = unburnt; grey = wet season burnt; black = dry season burnt) and symbols represent habitat type (circles = riparian; triangles = woodland). Dotted lines indicate groups of fire treatments. (b) Correlations of species ($r^2 > 0.2$) with NMDS ordination (*D. psammophis* = *Demansia psammophis*).

Vegetation Composition

Microhabitat and vegetation structure varied among fire treatments and between habitats (Table 5), with a tendency for more complexity in the unburnt and riparian habitat. Dry season burnt sites had significantly lower amounts of grass than unburnt and wet season burnt sites (Table 5). In addition, dry season burnt sites had fewer shrubs and rubber vine but more bare ground than unburnt sites. Differences in microhabitat and vegetation structure were also detected between habitats, with higher amounts of leaf litter, branches, trees and rubber vine, but lower amounts of bare ground in riparian habitats (Table 5).

Table 5. ANOVA F-values for microhabitat and vegetation variables per quadrat within three years of burning. No significant interaction terms were detected. Significant values are highlighted in bold (* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$). Untransformed means (± 95%CI) for fire treatments and habitat are shown. Letters next to fire treatment means indicate results from post hoc Tukey HSD tests ($\alpha < 0.5$).

	F-values $_{\text{Error df = 10}}$			Treatment means			Habitat means	
	Treatment df = 2	Habitat df =1	Creek df = 2	Unburnt	Dry burn	Wet burn	Riparian	Woodland
Microhabitat Variables (%)								
Leaf litter	0.531	**18.288****	4.159	26.1 ± 6.1	23.5 ± 4.6	26.5 ± 5.9	31.1 ± 6.1	19.7 ± 8.7
Grass	**6.172***	3.657	0.866	31.2 ± 6.3^{a}	18.8 ± 5.3^{b}	30.8 ± 2.3^{a}	23.6 ± 3.9	30.4 ± 7.2
Branch	0.373	**15.093****	1.634	4.5 ± 0.9	5.5 ± 1.7	4.7 ± 2.2	6.6 ± 2.5	3.2 ± 0.5
Ground	**7.358***	**6.437***	**4.461***	21.9 ± 4.4^{a}	36.7 ± 8.3^{b}	22.0 ± 8.9^{a}	22.2 ± 4.3	31.5 ± 10.1
Veg cover	1.035	3.577	**27.044*****	15.5 ± 5.8	13.6 ± 11.2	14.5 ± 9.2	16.2 ± 8.4	13.0 ± 8.9
Vegetation Variables (count & %)								
Trees	2.010	**6.562***	1.024	5.6 ± 0.7	5.5 ± 1.5	4.0 ± 2.1	6.0 ± 0.9	4.0 ± 0.7
Shrubs	**4.460***	0.318	0.699	2.0 ± 1.2^{a}	0.5 ± 0.4^{b}	1.1 ± 0.5^{ab}	1.1 ± 0.3	1.3 ± 0.8
RV	**4.092***	**43.005*****	0.551	35.8 ± 18.8^{a}	14.2 ± 6.5^{b}	23.8 ± 7.1^{ab}	43.6 ± 10.9	5.6 ± 5.0

Correlations of vegetation and reptile assemblage

The number of species was not correlated with any of the vegetation variables (Table 6). However, total reptile abundance was positively associated with the amount of grass and shrubs, but negatively associated with bare ground (Table 6; Figure 7). Only two species responded significantly to fire treatment and were correlated with habitat variables (Table 6). The small, terrestrial gecko *Heteronotia binoei* was strongly associated with the amount of grass, reflecting the preference of *H. binoei* for unburnt sites (Figure 7). The other lizard that responded to fire treatment, *Carlia pectoralis*, was positively associated with the amount of leaf litter and rubber vine (Table 6). Although *C. pectoralis* tend to avoid rubber vine on a small scale (Chapters 2 and 3), the skinks occurred more frequently in unburnt or riparian habitat where rubber vine was prevalent.

Table 6. Pearson's correlations (*r*) between species number, reptile abundance, and the log (x + 1) abundance of species that responded significantly to fire treatment or habitat, with microhabitat and vegetation structure. Significant values are highlighted in bold (* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$) and values approaching significance are identified (^ $0.06 > P \geq 0.05$).

	Microhabitat (%)					Vegetation		
	Leaf litter	Grass	Branch	Ground	Veg cover	Tree	Shrub	RV
Abundance	-0.052	**0.596****	-0.022	**-0.494***	0.210	0.118	**0.600****	0.350
Species richness	0.043	0.061	0.212	-0.142	-0.063	0.360	0.220	0.154
Heteronotia binoei	-0.133	**0.740*****	-0.205	-0.343	-0.018	0.071	0.453^	0.155
Carlia pectoralis	**0.477***	-0.249	0.233	-0.359	0.374	0.379	0.008	**0.638****

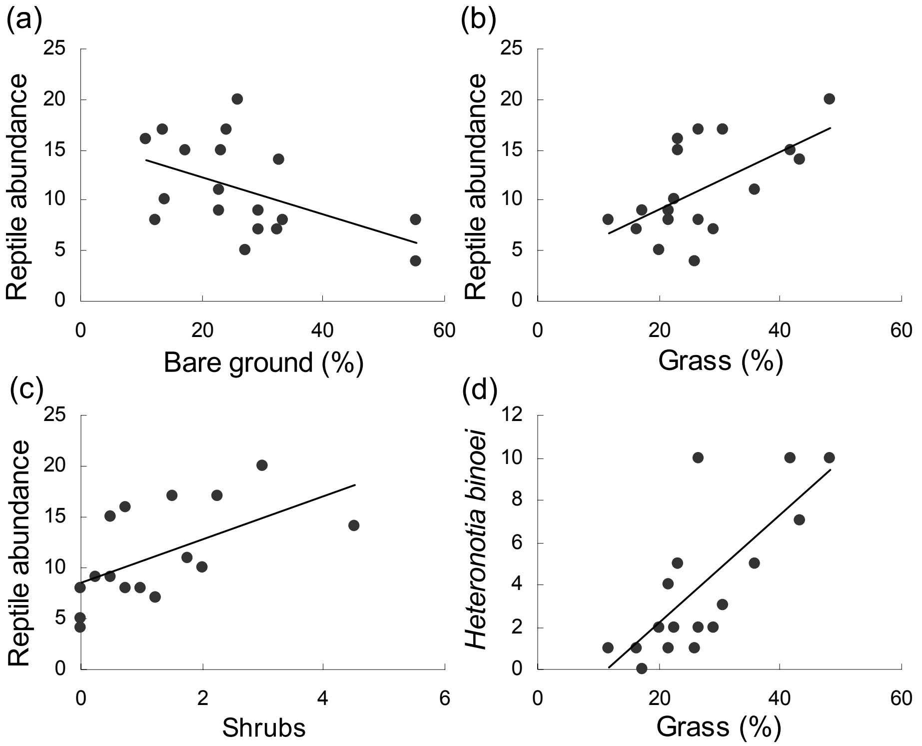

Figure 7. Significant associations between total reptile and *Heteronotia binoei* abundance per site and the amount of microhabitat and vegetation structure within 3 years of burning. Linear trend lines are fitted on the data for each graph.

Discussion

Short-term responses

Although higher overall abundances of reptiles were observed in the woodland habitat of dry season burnt sites, only one species, *Carlia munda*, responded significantly to fire treatment, with higher abundances in burnt sites. Other reptile responses were mostly influenced by habitat type. With reduced vegetation complexity (fewer shrubs and more bare ground) in burnt sites, lizards may have been easier to detect in burnt sites. However, abundance counts from pit-fall trapping data showed similar patterns to the combined survey and trapping data, suggesting that differences in active searching detection may not be the only cause for high abundances in burnt sites. Other studies have also recorded similar increases in the abundance of reptiles shortly following burning (Hannah & Smith 1995; Cunningham *et al.* 2002; Moseley *et al.* 2003) and these responses are often linked to changes in thermoregulatory, shelter and foraging resources available in the post-fire environment (Mushinsky 1992; Friend 1993; Masters 1996; Singh *et al.* 2002a; Moseley *et al.* 2003). Some species may prefer the early post-fire habitat (Cunningham *et al.* 2002) and are often observed in higher abundances compared to unburnt habitat, particularly species with preferences for open ground, such as the north American six-lined racerunner *Cnemidophorus sexlineatus* (Mushinsky 1985) or the Australian two-lined dragon *Diporiphora bilineata* (Braithwaite 1987; Trainor & Woinarski 1994). In contrast, species that are associated with habitat cover, such as the Australian skink *Carlia vivax*, may be disadvantaged by a change in vegetation complexity in the early post-fire environment (Singh *et al.* 2002a).

Despite being a leaf-litter specialist (Wilson & Swan 2003), the skink *Carlia munda* was positively associated with bare-ground, a characteristic of burnt habitat. This observation contrasts with Trainor and Woinarski (1994), where *C. munda* was negatively associated with bare-ground and was more frequently observed in unburnt or low-intensity burnt habitat. The intensity of fire used in my study was mostly low-moderate and may not have detrimentally effected *C. munda* abundances in the short-term. Alternatively, *C. munda* may be responding to other changes in resources, including food availability. Low intensity burning may provide enhanced foraging opportunities for a range of vertebrate taxa, including birds (Braithwaite & Estbergs

1987), mammals (Vernes & Haydon 2001) and reptiles (Griffiths & Christian 1996). Lizards tend to be generalist arthropod consumers (Cogger 2000), but stomach contents of skinks from the genus *Carlia* indicate that preferred prey items include spiders, bugs, grasshoppers and beetle larvae (James 1983). In tropical savannas, the abundance of spiders, bugs and beetles may increase following burning (Nicholson *et al.* 2006) and *C. munda* may benefit from a temporary increase in food availability. The use of recently burnt habitat for foraging has also been observed in two Australian dragons, *Chlamydosaurus kingii* (Griffiths & Christian 1996) and *Gemmatophora gilberti* (Woinarski *et al.* 1999). However, both dragons have comparatively large home ranges (c.f. *Carlia munda*) and sought shelter in nearby unburnt habitat.

The higher abundances of *C. munda* observed in the burnt sites may also be related to a reduction in the amount of rubber vine leaf litter caused by burning. Field observations and behavioural experiments indicate that *C. munda* prefers native litter to rubber vine litter (Chapter 2 / Valentine 2006; Chapter 3 / Valentine *et al.* in press). Although my measure of rubber vine (percent cover in the understorey) was not sensitive enough to detect significant differences, due to burning treatments the density of rubber vine infestation (height and thickness of towers) was visibly reduced in the burnt sites.

In the short-term, the assemblage structure of lizards was mostly influenced by habitat type, not fire treatment, with more species associated with the woodland habitat, including the small gecko *Heteronotia binoei*, and two arid-adapted *Ctenotus* species. In contrast, the leaf-litter specialist, C*arlia pectoralis*, and arboreal skink *Cryptoblephaurus virgatus* were associated with riparian habitat. Similarly, Trainor and Woinarksi (1994) observed that reptile assemblages were strongly structured by habitat variables, particularly a moisture gradient, even though individual species abundance varied among fire treatments. In tropical savannas, there are a large number of factors that influence faunal assemblages, and detecting changes in reptiles assemblages due to fire may be difficult (Woinarski *et al.* 2004). Instead lizards may be responding to broader environmental factors, rather than the effect of fire (Trainor & Woinarski 1994), at least in the short-term.

Medium-term responses

Very different responses to fire were observed three years following burning, with overall reptile abundance lower in the dry season burnt sites and fewer species observed in the wet season burnt sites. Differences in abundance were mostly driven by the small terrestrial gecko *Heteronotia binoei* and the small terrestrial skink *Carlia pectoralis*. Higher abundances and species richness in habitat unburnt for long periods has been observed in spinifex-dominated environments (Masters 1996) where burnt sites tend to comprise a subset of the species present in unburnt sites (Pianka 1989). In contrast, results from mallee woodland and sand-pine scrub habitats, suggest that overall reptile abundance and species richness remain steady following burning, but the species composition changes (Caughley 1985; Greenberg *et al.* 1994).

As reptile species tend to occupy sites with suitable thermal, shelter and food resources (Friend 1993; Masters 1996; Letnic *et al.* 2004), burning may have removed components of the habitat that are desirable to some reptiles. Within a few years of burning, the abundance of insects may decline (Force 1981), and although arthropod assemblages in tropical savannas are fairly resilient to fire (Andersen & Muller 2000; Parr *et al.* 2004), the initial increase in prey availability may be a short-lived event. Subsequently, when there is no immediate benefit in the form of increased prey availability, reptiles may respond to changes in vegetation structure caused by burning. Abundance of reptiles was correlated with several vegetation variables, with higher abundances observed in sites with greater vegetation complexity, typically unburnt sites. Vegetation structure is often correlated with reptile abundance (Schlesinger *et al.* 1997), and species that rely on vegetation cover for shelter, for example *H. binoei* and *C. pectoralis*, will be disadvantaged in the dry season burnt sites. Low abundances of *H. binoei* have previously been observed within 12 months following fire (Trainor & Woinarski 1994) and *H. binoei* may be disadvantaged by high intensity or late dry season fires (Braithwaite 1987). The fire-induced change of vegetation in the dry season burnt sites, including fewer shrub and grass cover, suggests that the availability of shelter sites was low, changing predation susceptibility or appropriate thermal resources.

Long-term changes in reptile assemblage composition in arid regions (Fyfe 1980; Pianka 1989; Masters 1996; Letnic *et al.* 2004), forests (Caughley 1985; Taylor & Fox

2001) and sand-pine scrub (Greenberg *et al.* 1994) suggest that reptile assemblages change with time since fire as different species dominate when appropriate habitat presides. The high fire frequency of tropical savannas may prevent clear succession and the type of fire may be more important in determining reptile assemblages (Braithwaite 1987), although tropical savanna reptile assemblages may be fairly resilient to the effects of fire (Trainor & Woinarski 1994; Andersen *et al.* 2005). In my study, different responses of reptiles were observed between unburnt and burnt sites, but few significant differences occurred between sites burnt in different seasons. Burnt sites were not characterised by different species to the unburnt, rather, certain species, including the legless lizard *Lialis burtonis*, the skinks *C. pectoralis* and *Menetia timlowi*, and the elapid *Demansia psammophis*, were absent in wet season burnt sites, and rarely observed in dry season burnt sites. Further, no species dominated the burnt sites, and only the open-foraging skink *Ctenotus robustus*, was associated with wet season burnt sites. This suggests that serial species replacement following burning, or selection of habitat based on burning season, is not occurring for the majority of species. Rather, burning modified resources and a few species were disadvantaged. Tropical savannas in northern Queensland are landscapes with multiple human-mediated disturbances, including cattle grazing and introduced plant species, and impacts of cumulative disturbances need to be considered. Previous studies have observed deleterious responses of reptiles to both grazing (Woinarski & Ash 2002; Kutt & Woinarski 2006) and weeds (Braithwaite *et al.* 1989; Chapter 2 / Valentine 2006; Chapter 3 / Valentine *et al.* in press). In areas where disturbances already influence reptile responses, the threshold of resilience to additional disturbances (e.g. burning) may be lower, or species may already be precluded from the environment.

Conservation and management implications

This study observed that the post-fire environment may initially provide some benefits to reptiles, particularly ground-foraging skinks, possibly due to a temporary increase in food availability. However, once the immediate benefit was gone (i.e., three years post-fire), reptiles responded to fire, with fewer species observed in wet season burnt sites and lower abundances in the dry season burnt sites. Reduced cover and vegetation structure in burnt sites, particularly dry season burnt sites, may alter shelter requirements, food resources and predation risk (Masters 1996; Letnic *et al.* 2004) making the habitat less desirable for certain species. Further, the cumulative impacts of disturbances from cattle-grazing and introduced plant species in the same habitats may reduce the resilience of reptiles to burning.

Introduced plant species threaten ecosystems throughout the world, however, the process of weed removal can also unintentionally effect biodiversity (Zavaleta *et al.* 2001), and burning for weed control may adversely affect some native species (Bower *et al.* 2006; this study). Burning along creek lines visibly reduced rubber vine density. As rubber vine habitat is not generally used by lizards (Chapter 2 / Valentine 2006), the subsequent changes in reptile assemblages are unlikely to be caused by removal of rubber vine, Instead, differences in reptile assemblages relate to burning, suggesting that control of rubber vine using fire may adversely effect reptiles. However, rubber vine is a serious environmental weed that deleteriously affects native biodiversity values and its control is of paramount importance (Tomley 1998; Commonwealth of Australia 1999). Fire is the most effective removal technique currently available (Grice 1997; Tomley 1998). Given that fire is already frequently used by humans (Crowley & Garnett 2000; Russell-Smith *et al.* 2003b), burning to control rubber vine will be incorporated in land management strategies. When controlling rubber vine with fire, land managers will need to maintain a clear perspective on management objectives, while considering the consequences of burning for native fauna. Burning riparian zones, particularly in areas with additional disturbances, will affect some native species and if possible, management should retain unburnt refuges.

CHAPTER 5: BURNING SEASON INFLUENCES THE RESPONSE OF BIRD ASSEMBLAGES TO FIRE IN TROPICAL SAVANNAS

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Introduction

Fire often occurs as a human-mediated disturbance and is frequently used as a land management tool. Disturbances, like fire, influence the structure of many ecosystems (see Whelan 1995; Bond & Van Wilgen 1996) by playing a pivotal role in determining environmental and biological heterogeneity (Brawn *et al.* 2001). Variations in the temporal and spatial aspects of disturbances alter the environment in dissimilar ways (Sousa 1984), and thus, may consequentially influence fauna that are susceptible to changes in the environment, including birds. Bird assemblages are strongly influenced by habitat structure (MacArthur & MacArthur 1961) and variations in the type of fire an area receives may govern the response of bird assemblages in the post-fire habitat (Smucker *et al.* 2005). Hence, the widespread use of fire as a land management tool will have important ramifications for conservation of biodiversity.

Previous studies in a variety of habitats have observed a great variety of bird assemblage responses to fire (e.g., grasslands: Pons *et al.* (2003); tropical savannas: Woinarksi (1990), Woinarski *et al.* (1999), Mills (2004); oak savannas and forests: Artman *et al.* (2001), Brawn (2006); conifer and pine forests: Hutto (1995), Saab (2005); and rainforests: Barlow *et al.* (2002; 2006)). The responses of birds to fire are often related to changes in vegetation structure and the availability of resources in the post-fire environment (Woinarski & Recher 1997; Davis *et al.* 2000; Brawn *et al.* 2001). Because the post-fire environment is influenced by fire regime, (Whelan 1995), the responses of birds may also be dependent on fire regime (Woinarski & Recher 1997; Smucker *et al.* 2005). Given that humans alter fire regimes by using fire as a land management tool, understanding how birds respond to fire regimes, including variations in intensity, frequency and season of burn, is crucial for conservation purposes.

Season of burn: Fire in Australian savannas as a model system

Fire influences the structure of many biomes, and is a key component in the maintenance of grassland and savanna ecosystems (Gillon 1983), including Australian tropical savannas. Prior to human arrival in Australia, some 50,000 years ago (Roberts *et al.* 1990), fire occurred via lightning strikes in the late dry or early wet season (Kemp 1981). However, the majority of fires have since been lit by humans for traditional or contemporary land management purposes (Russell-Smith *et al.* 1997a; Russell-Smith *et al.* 2003b). The distinct wet and dry seasons of tropical savannas ensure that fires are frequent events (Russell-Smith *et al.* 1997b) and season of burn is an important component of fire regime. Fire potential increases as the dry season progresses, and the habitat is extremely fire prone late in the dry season, when fuel moisture contents is low (Gill *et al.* 1996). In contrast, fires are less likely in the early dry and wet seasons, and fires at these times are usually of lower intensity and more patchy (Braithwaite & Estbergs 1985; Lonsdale & Braithwaite 1991).

Birds display a variety of responses to fire regimes in tropical savannas (Woinarski 1990; Woinarski *et al.* 1999; Mills 2004); although late dry season fires tend to detrimentally affect more bird species than early dry season fires. Additionally, inappropriate fire regimes have been linked to the decline of granivorous birds (Franklin 1999; Franklin *et al.* 2005). As land managers increasingly use early-mid dry and wet season fires to reduce the potential of destructive late dry season fires (Crowley & Garnett 2000; Williams *et al.* 2003b), understanding how season of burn influences bird assemblages is critical.

In Australia, fire may be an important management tool for controlling the spread and extent of invasive plant species, including the globally distributed wood weed, rubber vine (*Cryptostegia grandiflora* R. Br.). Endemic to Madagascar, rubber vine damages the agricultural, economic and biodiversity values of northern Australia (Tomley 1998; Chapter 2 / Valentine 2006; Chapter 3 / Valentine *et al.* in press). Fire can significantly reduce rubber vine survival, density, and vegetative growth, and may inhibit seed germination (Grice 1997; Bebawi & Campbell 2002). As rubber vine grows most prolifically in riparian zones (Tomley 1998), the use of fire in these environments may increase. Riparian environments are an important element of tropical savannas, often characterized by a distinct bird fauna (Woinarski *et al.* 2000), and may be inappropriately disturbed by management burning (Andersen *et al.* 2005). I experimentally examined the short and longer term changes of bird assemblages, in riparian and non-riparian habitat, in response to wet and dry season burning for weed control in tropical savannas in north-eastern Australia.

Methods

Study Site & Experimental Design

The study took place in the Einasleigh Uplands bioregion (Sattler & Williams 1999), 110km south of Townsville in north-eastern Queensland, Australia. All sites were located in open eucalypt woodland, along three seasonally dry watercourses: Bend Creek (20°16’07”S, 146°37’48”E), One Mile Creek (20°14’10”S, 146°40’35”E) and Cornishman Creek (20°12’18”S, 146°27’15”E), all sub-catchments of the Burdekin River on lease-hold grazing properties. The study was carried out using experimental fire treatments previously described in Chapter 4. To reiterate, experimental plots were established along each creek and included both riparian and adjacent non-riparian open woodland habitat. Each plot was approximately 20 ha, separated from other plots by double fire breaks. Along each creek the following fire treatments were randomly imposed: *i*) an unburnt control plot; *ii*) a dry season burnt plot, fire imposed August 2000; and *iii*) a wet season burnt plot, fire imposed December 1999 (see Figure 1 for photos of treatments). Henceforth, time since fire will describe the time interval elapsed since the wet season fire.

Sampling Strategy

Data were collected during the wet season, following the first rains of the season, between January and March 2001 & 2004. Plots were surveyed randomly in each creek. Bird assemblages were surveyed using thirty-minute timed surveys along 250 m line transects running through the middle of each site (habitat/treatment replicate). Although visibility of birds was consistently high over all sites, as the denser habitats were still open, I constrained width of transects to 50 m either side of observer to minimize differences in detection probability among sites. Surveys were conducted within the first three hours after sunrise and recorded the species and abundance of all birds either observed or heard within the limits of each transect. Birds observed flying more than 10 m above the canopy were not included in analyses. Surveys were conducted twice along each transect within ten days, but were not undertaken on days with poor weather (e.g. rain or high wind). Abundance of birds observed during the two surveys of each transect were averaged, while the numbers of species observed were summed to estimate species number for each site based on two surveys. As sites were unlikely to encompass the home range of all species, I used observed species number and species abundance as estimates for habitat use of fire treatments by birds. Data on broad vegetation variables were collected using four large quadrats (20 m x 10 m) that were established in each site. In each quadrat, the number of trees and shrubs were recorded. The proportion of rubber vine in the understorey was estimated to the nearest 10% in each quadrat. Data were averaged among the four quadrats to provide an estimate of average vegetation structure within each site.

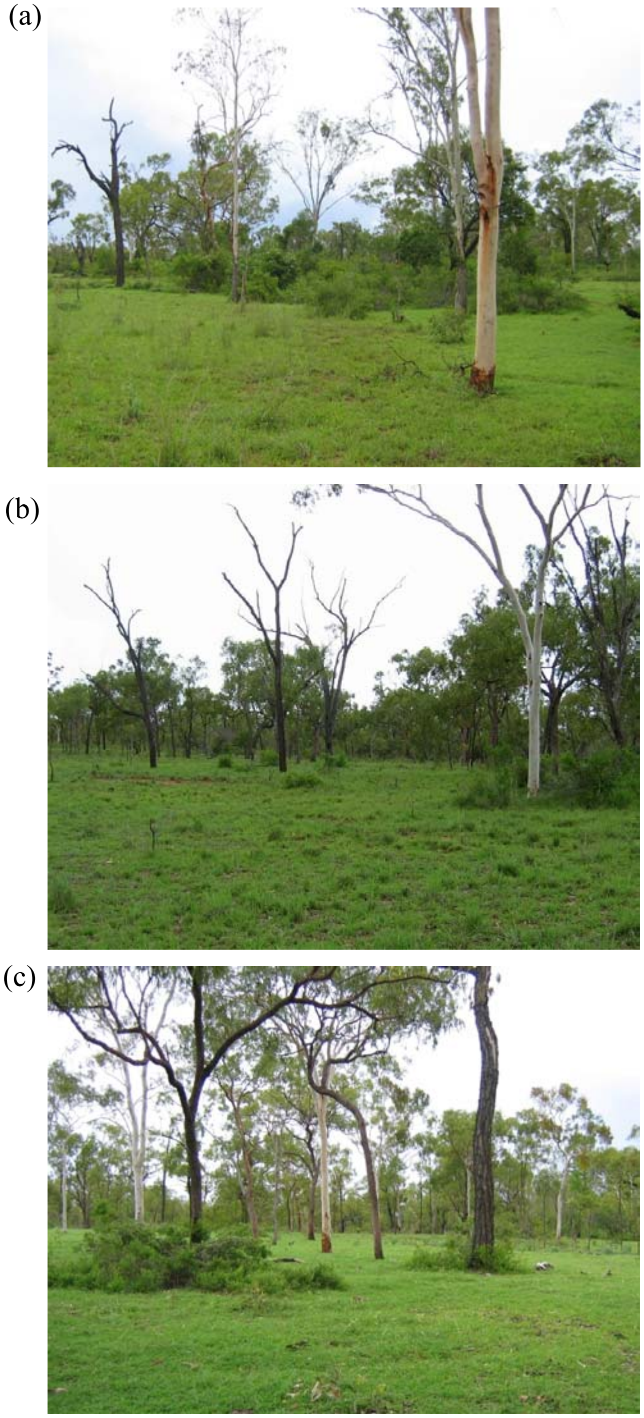

Figure 1. Photos of fire treatments four years following burning in the woodland habitat of Bend Creek; a) unburnt, b) dry season burnt, and c) wet season burnt. Photo credit: Leonie Valentine.

Analysis

Data were analysed within each sample year to examine the short-term and longer-term responses of bird assemblages. The experiment was in the form of a randomized block design with treatment and habitat as main effects terms and creek as a blocking factor. A three-factor ANOVA (SPSS, version 12) was used to examine differences in mean bird abundance and species number among fire treatments (unburnt, wet season burnt, dry season burnt) and habitats (riparian and woodland), using creek as a blocking factor (i.e. same model used in Chapter 4). The responses of selected individual species (species observed in 3 or more sites, with a total abundance ≥ 5) were also examined within each year survey.

Examining the responses of guilds to disturbance is a useful technique of evaluating changes in bird communities that may be indicative of changes in resources. Bird species were assigned to one of five feeding groups (carnivore, granivore, frugivore, insectivore and nectarivore) based on their dominant source of food, using dietary information from the literature (Marchant & Higgins 1990a, b, 1993; Higgins & Davies 1996; Higgins 1999; Higgins *et al.* 2001; Higgins & Peter 2002; Catterall & Woinarski 2003; Higgins *et al.* 2005). I used a MANOVA (SPSS, version 12) to compare the assemblage of feeding groups between sites.

Community composition, defined as the average abundance of each species per site, was compared among treatments and between habitats using perMANOVA (Anderson 2001). I used a Sorensen distance measure on the untransformed data in the statistical package PC-ORD (McCune & Mefford 1999). Similar results were observed with square-root transformed or log (x + 1) data. Post-hoc pair-wise comparisons were used to examine differences in bird assemblages between fire treatments. Rare species (species that were observed in less than three sites) were not included in the analysis. Non-metric multidimensional scaling (NMDS; Kruskal 1964) was used to graphically depict the site assemblage relationships. The same similarity matrix used for perMANOVA was ordinated using NMDS with a Sorensen distance measure in PC-ORD (McCune & Mefford 1999). Where 3-dimension ordinations were deemed more appropriate (determined using scree plots and Monte Carlo tests), I have displayed the two axes that represent the highest proportion of variance explained in the ordination.

Vegetation structure was examined by comparing the average number of trees, shrubs and the proportion of rubber vine per quadrat in each site using a MANOVA (SPSS, version 12). Species number, bird abundance, the abundance of feeding groups and individual species that responded to fire treatment were correlated using Pearson's correlation coefficient. Rubber vine percentage data were adjusted by arcsine transformation of the square-root proportional data (Zar 1999). Count data (species number, birds, feeding group and vegetation abundances) were examined for normality and heteroscedasticity using box plots, Q-Q plots and residual plots. Multivariate linearity was examined using scatter plots of variables used in MANOVA analysis. Abundances of feeding groups, trees and the 2001 shrub abundances were square-root transformed, and the abundance of individual species were log (x + 1) transformed to meet assumptions of ANOVA and correlations. To aid interpretation, graphs depict the untransformed data.

Results

Short-term responses: 12 months since fire

A total of 50 bird species were recorded during surveys in 2001. Although differences in species richness were found among creeks (ANOVA: $F_{2,10} = 8.505$, $P = 0.007$), no significant differences were observed among treatments or between habitat types. Average bird abundance was significantly higher in the dry and wet season burnt sites compared to unburnt (ANOVA: $F_{2,10} = 11.316$, $P = 0.003$; Figure 2a). Slight differences in bird abundances were also observed among creeks (ANOVA: $F_{2,10} = 4.145$, $P = 0.049$).

Of 26 species with sufficient data for analysis, I detected a significant response to fire treatment for seven species, with several species observed in higher abundance in the burnt sites, particularly the dry season burnt sites. Striated pardalotes (*Pardalous striatus*) and yellow-throated miners (*Manorina flavigula*) had higher abundances in the dry season burnt compared to unburnt sites, and pale-headed rosellas (*Platycercus adscitus*) were more abundant in the dry season burnt compared to unburnt and wet season burnt sites (Table 1). Significant interactions among fire treatments and habitats were detected for two species, pied butcherbirds (*Cracticus nigrogularis*) were more abundant in the woodland habitat of burnt sites while little friarbirds (*Philemon* *citreogularis*) was more abundant in dry season burnt sites and the riparian habitat of the wet season burnt sites (Table 1). Two species, red-backed fairy-wren (*Malurus melanocephalus*) and cicadabird (*Coracina tenuirostirs*), were less abundant following burning (Table 1). The red-backed fairy-wren was mostly observed in low shrubs and was never recorded in the dry season burnt sites. Australian magpies (*Gymnorhina tibicen*), yellow-throated miners (*Manorina flavigula*) and weebills (*Smicrornis brevirostris*) were more abundant in the woodland habitat, and only grey butcherbirds (*Cracticus torquatus*) were detected in higher abundance in the riparian habitat (Table 1).

Table 1. ANOVA F-values for the log (x + 1) transformed abundance of select species showing the short-term and longer-term responses to fire treatment. Significant values (and corresponding species) are in bold (* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$), values approaching significance are identified (^ $0.06 > P \geq 0.05$). Letters beside significant values indicate results from post-hoc Tukey HSD tests (unburnt = U, wet burnt = W, dry burnt = D) or which habitat had higher abundances (riparian = Ri, adjacent woodland = W). No significant interaction terms were observed in the longer-term responses. F-values for the blocking factor creek are not shown.

	Short-term Responses			Longer-term Responses	
	Treatment $_{df = 2,10}$	Habitat $_{df = 1,10}$	T*H $_{df = 2,10}$	Treatment $_{df = 2,10}$	Habitat $_{df = 1,10}$
Carnivores					
Torresian crow	0.633	0.656	0.175	-	-
Pied butcherbird	**6.083* U < W, D**	**44.224*** W**	**4.272***	0.841	1.910
Grey butcherbird	1.026	**29.335*** Ri**	1.573	2.416	**6.726* Ri**
Laughing kookaburra	3.329	0.099	1.624	-	-
Forest kingfisher	-	-	-	2.485	0.792
Frugivores					
Bowerbird	-	-	-	1.080	0.937
Mistletoebird	-	-	-	1.513	0.095
Granivores					
Red-wing parrot	1.052	0.049	0.383	2.372	1.915
Crested pigeon	0.826	2.012	1.511	-	-
Pale-headed rosella	**11.232** U, W < D**	0.610	2.067	2.188	0.748
Insectivores					
Black-faced cuckoo-shrike	2.154	0.950	3.004	2.253	**8.500* Ri**
Cicadabird	**21.825*** U > W, D**	3.403	1.123	**3.567^ U < D**	2.683
Dollarbird	1.726	2.839	0.032	1.935	**8.800* Ri**
White-throated gerygone	1.583	0.286	0.657	-	-
Magpie-lark	0.563	0.632	1.081	1.661	**8.382* Ri**
Australian magpie	0.752	**24.198** W**	0.146	0.008	1.424
Red-backed fairy-wren	**12.507** U > W, D**	0.734	1.963	0.236	**10.746** W**
Yellow-throated miner	**4.125* U < D**	**9.874* W**	0.263	-	-
White-throated honeyeater	2.983	2.996	2.223	**17.622** U, W > D**	3.940
Olive-backed oriole	0.266	1.483	0.266	1.256	0.895
Rufous whistler	1.795	0.311	0.461	-	-
Striated pardalote	**6.897* U < D**	1.597	0.766	0.009	**7.446* W**
Weebill	2.439	**16.047** W**	0.147	**5.901* U < W**	**17.396** W**
Apostlebird	1.596	0.866	0.056	-	-

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Table1. continued…

	Short-term Responses			Longer-term Responses	
	Treatment $_{df = 2,10}$	Habitat $_{df = 1,10}$	T*H $_{df = 2,10}$	Treatment $_{df = 2,10}$	Habitat $_{df = 1,10}$
Nectarivores					
Blue-faced honeyeater	1.931	0.924	0.529	1.057	**5.970* Ri**
Yellow honeyeater	2.622	3.150	0.236	0.673	**5.507 Ri**
Little friarbird	**11.071** U, W < D**	0.705	**4.933***	**6.820* U, W > D**	1.335
Noisy friarbird	0.879	0.271	0.072	-	-
Rainbow lorikeet	2.520	1.027	0.606	**4.559* W > D**	1.014

A MANOVA on the square-root transformed feeding group abundances detected a significant difference in feeding group assemblage among treatments (MANOVA Wilks' Lambda: $F_{10,12} = 3.410$, $P = 0.024$) and habitats (MANOVA Wilks' Lambda: $F_{5,6} = 4.757$, $P = 0.042$). Insectivore abundance was higher in the dry season burnt sites compared to the unburnt (ANOVA: $F_{2,10} = 5.486$, $P = 0.025$; Figure 2b), and in the woodland habitat (ANOVA: $F_{1,10} = 8.156$, $P = 0.017$). Similarly, nectarivore abundance was higher in the dry burnt sites compared to the unburnt (ANOVA: $F_{2,10} = 6.118$, $P = 0.018$; Figure 2c), and varied among creeks (ANOVA: $F_{2,10} = 12.300$, $P = 0.002$). The abundance of carnviores was significantly higher in the wet season burnt sites compared to the unburnt (ANOVA: $F_{2,10} = 4.288$, $P = 0.045$; Figure 1d). Granivore and frugivore abundance did not vary among factors, although there was a trend for higher granivore abundance in the dry season burnt sites.

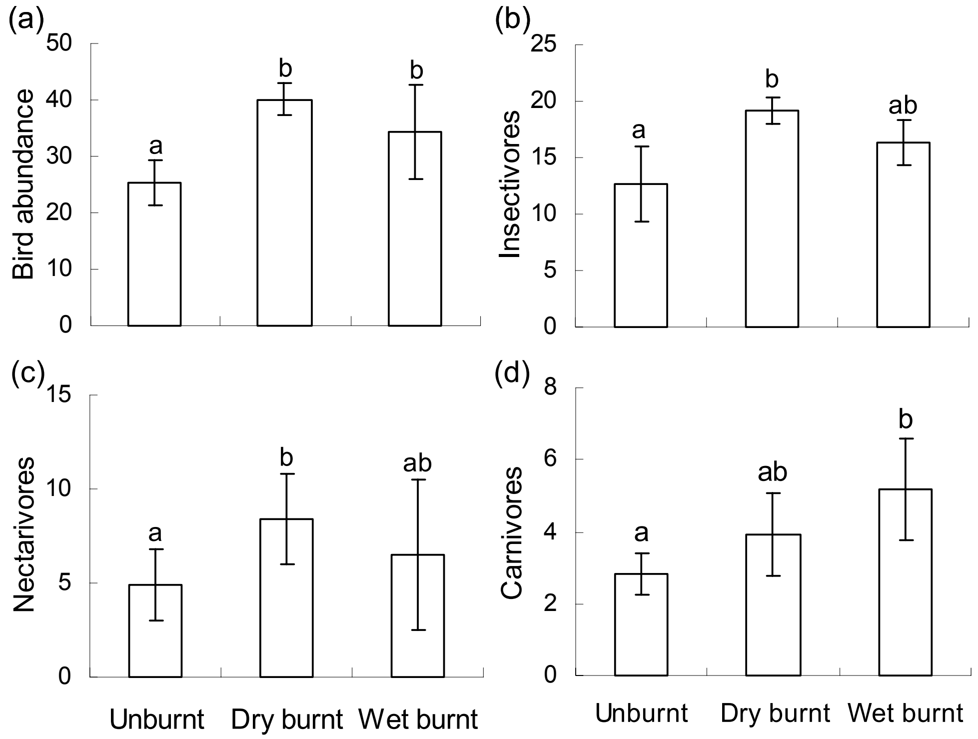

Figure 2. Significant differences in mean (± 95%CI) abundance of (a) birds, (b) insectivores, (c) nectarivores, and (d) carnivores in fire treatments within 12 months of burning. Letters above error bars indicate significant differences of means between fire treatments (Tukey HSD, $\alpha < 0.05$).

Of the 50 bird species recorded during surveys, 37 were observed in three or more sites and were included in community analyses. PerMANOVA detected differences in community structure among fire treatments (perMANOVA: $F_{2,12} = 1.795$, $P = 0.025$) and habitats (perMANOVA: $F_{1,12} = 2.702$, $P = 0.005$). Pair-wise comparisons showed that the unburnt sites differed to the dry season burnt sites ($t = 1.66$, $P = 0.002$), but were not significantly different to wet season burnt sites ($t = 1.30$, $P = 0.100$). NMDS ordination found a stable 3-dimension solution representing 84% of the community variation, with the first two axes representing 59% of variation (Figure 3). Fire treatments were separated along axis 1 with burnt sites clustering away from the loose grouping of unburnt sites (Figure 3). In particular, the burnt woodland sites formed a relatively tight cluster, furthest from the unburnt sites, indicating a high degree of similarity in community composition in burnt woodland sites. Most bird species were associated with burnt sites, but yellow honeyeaters (*Lichenostomus flavus*), red-backed fairy-wrens (*Malurus melanocephalus*), cicadabirds (*Coracina tenuirostris*) and grey butcherbirds (*Cracticus torquatus*) were associated with unburnt sites (Figure 3b).

Vegetation structure was significantly different among treatments (MANOVA Wilks' Lambda: $F_{6,16} = 2.772$, $P = 0.048$) and habitat (MANOVA Wilks' Lambda: $F_{3,8} = 9.751$, $P = 0.005$). The abundance of shrubs was lower in the dry season burnt sites compared to the unburnt (Table 2), and there was a strong trend for fewer shrubs in the wet season burnt sites. Shrub abundance was higher in the woodland habitat compared to the riparian habitat as were the number of trees (Table 2). The proportion of rubber vine was lower in the woodland sites, and there was a trend for less rubber vine in the burnt treatments (Table 2). The intensity of rubber vine infestations was visibly reduced in the burnt habitat. However, the measure of rubber vine recorded in my study refers to understorey shrubs only and, therefore, did not reflect the reduction in rubber vine infestations or towers in burnt sites (Radford, unpublished data).

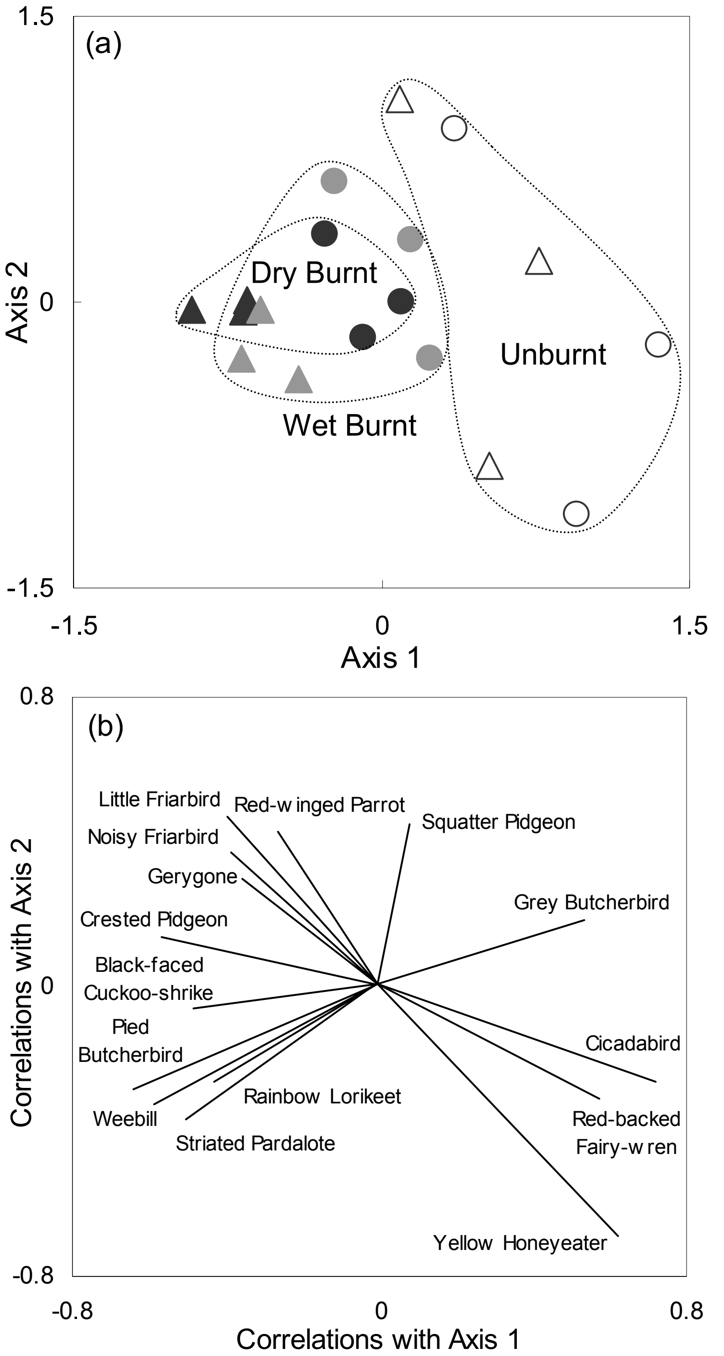

Figure 3. (a) NMDS ordination (Sorensen distance measure) on the assemblage of birds (n = 37) at sites within 12 months of burning. Ordination is in three dimensions (stress = 0.11), with axis 1 and 2 plotted ($r^2 = 0.316$ and 0.273 respectively). Colour represents fire treatment (clear = unburnt; grey = wet season burnt; black = dry season burnt) and symbols represent habitat type (circles = riparian; triangles = woodland). Dotted lines indicate groups of fire treatments, with burnt sites grouping away from unburnt. (b) Correlations of species ($r^2 > 0.2$) with NMDS ordination.

Table 2. ANOVA F-values for the number of trees and shrubs per quadrat and the proportion of rubber vine in the understorey within 12 months of burning. No significant interaction terms were detected. Significant values are highlighted in bold (* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$). Untransformed means (± 95%CI) for fire treatments and habitat are shown. Letters next to fire treatment means indicate results from post hoc Tukey HSD tests ($\alpha < 0.5$).

	F-values $_{\text{Error df = 10}}$			Treatment means			Habitat means	
Vegetation	Treatment $_{\text{df = 2}}$	Habitat $_{\text{df =1}}$	Creek $_{\text{df = 2}}$	Unburnt	Dry burn	Wet burn	Riparian	Woodland
Trees	0.301	**5.945***	1.031	4.4 ± 1.3	5.0 ± 1.7	4.5 ± 0.5	5.5 ± 0.7	3.8 ± 0.7
Shrubs	**7.903****	**7.093***	0.474	1.8 ± 0.4^{a}	0.5 ± 0.4^{b}	0.8 ± 0.6^{ab}	1.3 ± 0.1	0.7 ± 0.3
Rubber vine	1.604	**33.853*****	0.135	37.9 ± 16.1	21.7 ± 10.7	26.2 ± 13.7	49.4 ± 14.1	7.8 ± 6.1

In the short-term, shrub abundance was negatively correlated with overall bird and insectivore abundance, and a number of individual species that responded to fire treatment (Table 3). The abundances of striated pardalotes (*Pardalotus striatus*) and pied butcherbirds (*Cracticus nigrogularis*) were negatively correlated with shrub abundance (Table 3). In contrast, other species were positively correlated with shrub abundance, including cicadabirds (*Coracina tenuirostris*) and red-backed fairy-wrens (*Malurus melanocephalus*). Rubber vine was negatively correlated with pied butcherbirds (*Cracticus nigrogularis*), yellow-throated miners (*Manorina flavigula*) and overall insectivore abundance, (Table 3). However, the abundance of cicadabirds (*Coracina tenuirostris*) was positively associated with rubber vine. The bird responses to rubber vine tend to reflect differences in bird abundances between riparian and woodland habitat.

Table 3. Pearson's correlations (r) among bird abundance, species number, evenness, abundance of feeding groups and species that responded significantly to fire treatment, with the number of trees, shrubs and proportion of rubber vine per quadrat. Information is provided for 12 months and 4 years after burning.

	Short-term			Longer-term		
	Trees	Shrubs	Rubber vine	Trees	Shrubs	Rubber vine
Abundance	-0.094	**-0.652****	-0.361	-0.172	0.195	**0.584***
Species number	-0.072	-0.283	-0.210	0.107	0.259	**0.698****
Evenness	0.207	0.032	-0.029	0.278	0.192	0.243
Carnivores	0.247	-0.354	-0.239	0.157	**0.689****	0.399
Pied butcherbird	-0.296	**-0.615****	**-0.724****	-	-	-
Frugivores	-0.317	-0.190	-0.290	0.398	0.178	0.221
Granivores	0.046	-0.268	-0.183	-0.181	0.250	0.453^
Pale-headed rosella	0.198	-0.277	-0.109	-	-	-
Insectivores	-0.279	**-0.650****	**-0.505***	**-0.496***	-0.196	0.165
Cicadabird	-0.089	**0.505***	**0.526***	0.260	-0.452^	0.114
Red-backed fairy-wren	-0.378	**0.506***	0.091	-	-	-
Yellow-throated miner	-0.072	-0.429^	**-0.767*****	-	-	-
White-throated honeyeater	-	-	-	-0.050	0.108	0.287
Striated pardalote	-0.250	**-0.587***	-0.327	-	-	-
Weebill	-	-	-	-0.364	-0.292	**-0.602****
Nectarivores	0.158	-0.390	0.149	0.015	0.314	**0.609****
Little friarbird	0.238	-0.328	-0.041	-0.072	0.361	0.279

Longer-term responses: four years since fire

A total of 53 bird species were observed during surveys in the 2004 sampling period. The number of species observed in surveys did not differ among fire treatments, but was significantly higher in riparian habitat (ANOVA: $F_{1,10} = 13.028$, $P = 0.005$). Average bird abundance was significantly lower in the dry season burnt sites than unburnt, with a strong trend for higher abundances in the wet season burnt sites (ANOVA: $F_{2,10} = 4.826$, $P = 0.034$; Figure 4a). Bird abundance was also higher in the riparian habitat (ANOVA: $F_{2,10} = 6.426$, $P = 0.030$).

The abundance of 21 species were analysed to examine the specific species responses to fire treatment (Table 1). In contrast to the initial results, three of the five species that responded to fire treatment had lower abundances in dry season burnt treatments, including little friarbirds (*Philemon citreogularis*), rainbow lorikeets (*Trichoglossus haematodus*) and white-throated honeyeaters (*Melithreptus albogularis*). Weebills (*Smicrornis brevirostris*) were more abundant in wet season burnt sites, while cicadabirds (*Coracina tenuirostris*) were more abundant in dry season sites (Table 1). Pied butcherbirds (*Cracticus nigrogularis*), black-faced cuckoo-shrikes (*Coracina novaehollandiae*), dollarbirds (*Eurystomus orientalis*), magpie-larks (*Grallina cyanoleuca*), blue-faced honeyeaters (*Entomyzon cyanotis*) and yellow honeyeaters (*Lichenostomus flavus*) had higher abundance in the riparian habitat while striated pardalotes (*Pardalotus striatus*), weebills (*Smicrornis brevirostris*) and red-backed fairy-wrens (*Malurus melanocephalus*) were more abundant in woodland habitat.

A MANOVA on the square-root transformed feeding group abundances detected a significant difference in feeding group assemblage between treatments (MANOVA Wilks' Lambda: $F_{10,12} = 4.010$, $P = 0.013$) and habitats (MANOVA Wilks' Lambda: $F_{5,6} = 6.722$, $P = 0.019$). The abundance of nectarivores was significantly higher in the unburnt and wet season burnt sites (ANOVA: $F_{2,10} = 8.974$, $P = 0.006$; Figure 4b) and the riparian habitat (ANOVA: $F_{1,10} = 15.633$, $P = 0.003$). Granivorous bird abundance was also higher in the wet season burnt sites compared to the dry season burnt sites (ANOVA: $F_{2,10} = 4.566$, $P = 0.039$; Figure 4c). The abundance of carnivores, frugivores and insectivores did not vary among factors.

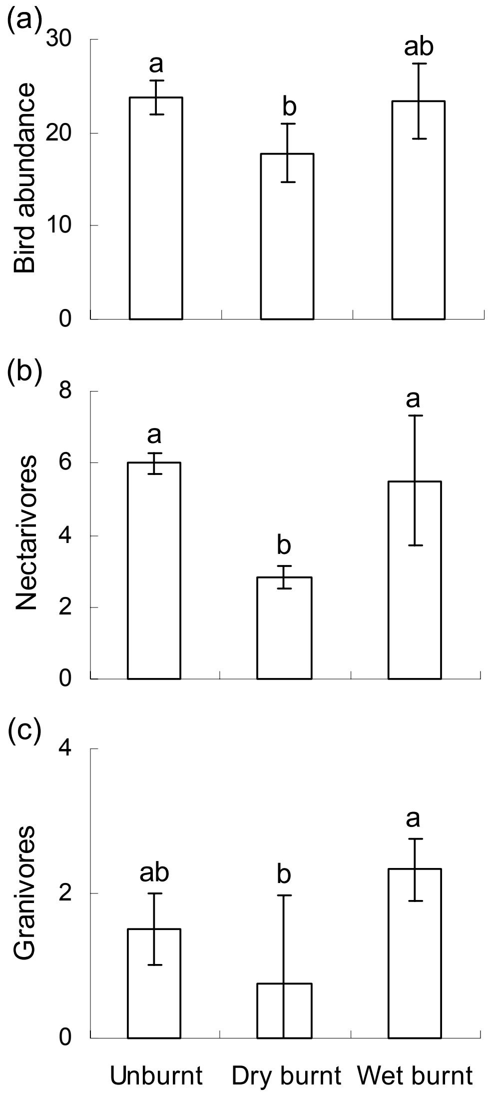

Figure 4. Significant differences in mean (± 95%CI) abundance of (a) birds, (b) nectarivores, and (c) granivores in fire treatments four years post burning. Letters above error bars indicate significant differences of means between fire treatments (Tukey HSD, $P < 0.05$).

Of the 53 bird species observed during surveys, 37 were record in more than two sites and were included in community analyses. PerMANOVA detected differences in community structure between fire treatments (perMANOVA: $F_{2,12} = 1.728$, $P = 0.022$) and habitat (perMANOVA: $F_{2,12} = 2.811$, $P = 0.002$). Pair-wise comparisons showed that the dry season burnt sites differed to the wet season burnt sites ($t = 1.57$, $P = 0.003$) and showed a trend for differences with the unburnt sites ($t = 1.26$, $P = 0.087$). NMDS ordination found a stable 3-dimensional solution representing 85% variance, with axes 1 and 2 representing 61% of the community variation (Figure 5). Woodland and riparian sites were mostly separated along Axis 1, and there was a clear separation of fire treatments along Axis 2 (Figure 5). Most species were associated with riparian habitat in unburnt or wet season burnt treatments (Figure 5b). In particular, white-throated honeyeaters (*Melithreptus albogularis*), little friarbirds (*Philemon citreogularis*), rainbow lorikeets (*Trichoglossus haematodus*), pale-headed rosellas (*Platycercus adscitus*) and weebills (*Smicrornis brevirostris*) were associated with wet season burnt and unburnt sites (Figure 5b). In contrast, only cicadabirds (*Coracina tenuirostris*) were associated with dry season burnt sites.

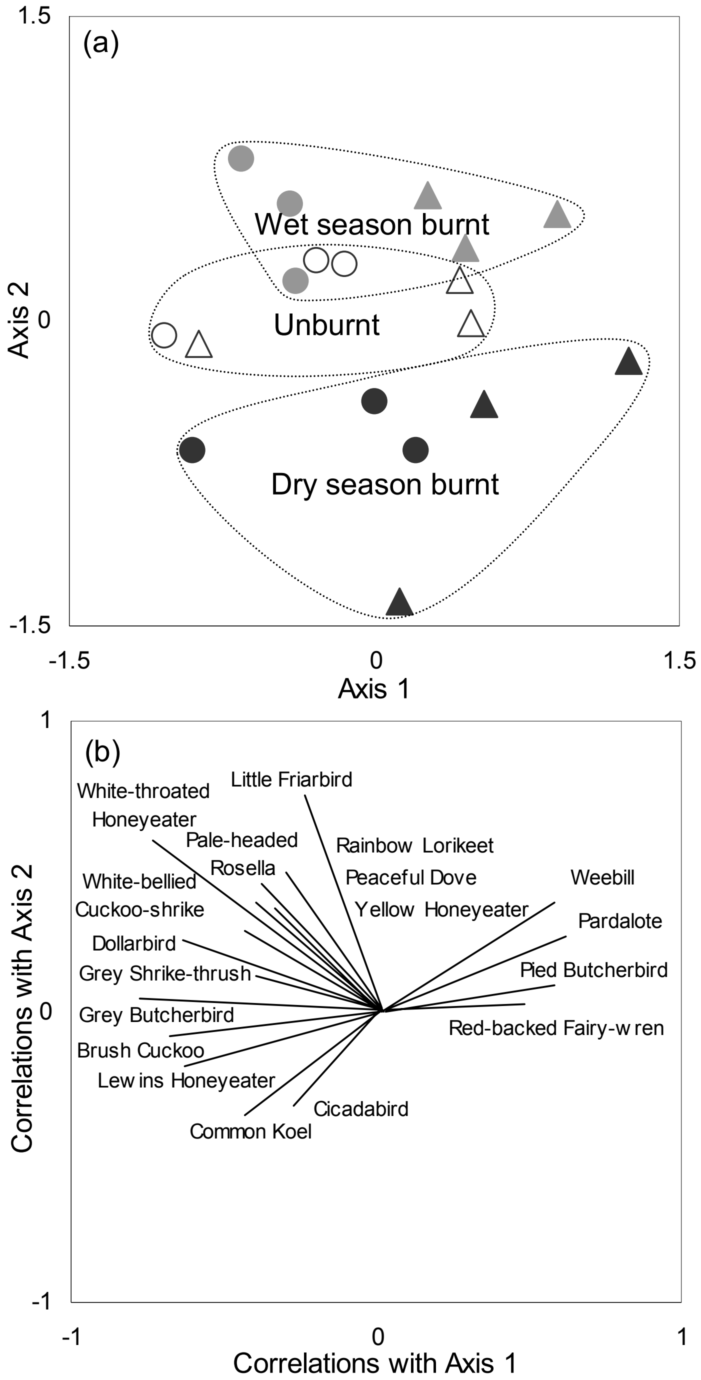

Figure 5. (a) NMDS ordination (Sorensen distance measure) on assemblage of birds (n = 37) at sites four years post burning. Ordination is in three dimensions (stress = 0.11), with axis 1 and 2 plotted ($r^2 = 0.295$ and 0.309 respectively). Colour represents fire treatment (clear = unburnt; grey = wet season burnt; black = dry season burnt) and symbols represent habitat type (circles = riparian; triangles = woodland). Dotted lines indicate grouping of fire treatments, with the dry season burnt sites separating from

unburnt and wet season burnt sites along Axis 2. Note that sites are also separated by habitat along Axis 1. (b) Correlations of species ($r^2 > 0.2$) with NMDS ordination.

Vegetation structure was significantly different among fire treatments (MANOVA Wilks' Lambda: $F_{6,16} = 7.290$, $P < 0.001$) and habitats (MANOVA Wilks' Lambda: $F_{3,8} = 27.343$, $P < 0.000$). The number of trees was higher in the riparian habitat and there were fewer shrubs in the dry season burnt sites compared to unburnt (Table 4). The proportion of rubber vine was higher in riparian habitat, but lower in burnt sites, although a significant difference was only detected between unburnt and dry season burnt sites (Table 4).

Table 4. ANOVA F-values for the number of trees and shrubs per quadrat and the proportion of rubber vine in the understorey within 4 years of burning. No significant interaction terms were detected. Significant values are highlighted in bold (* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$). Untransformed means (± 95%CI) for fire treatments and habitat are shown. Letters next to fire treatment means indicate results from post hoc Tukey HSD tests ($\alpha < 0.5$).

	F-values $_{\text{Error df = 10}}$			Treatment means			Habitat means	
Vegetation	Treatment df = 2	Habitat df =1	Creek df = 2	Unburnt	Dry burn	Wet burn	Riparian	Woodland
Trees	0.917	**6.598***	1.139	4.5 ± 0.5	5.4 ± 1.8	4.3 ± 1.5	5.5 ± 0.9	3.8 ± 1.0
Shrubs	**4.241***	1.954	1.636	3.0 ± 1.5^{a}	0.9 ± 0.5^{b}	1.4 ± 1.0^{ab}	1.3 ± 0.5	0.7 ± 0.6
Rubber vine	**4.226***	**43.918*****	0.430	35.4 ± 6.0^{a}	12.5 ± 10.0^{b}	25.0 ± 15.0^{ab}	49.4 ± 10.4	7.8 ± 7.0

Rubber vine was positively correlated with species number, bird and nectarivore abundance, but negatively correlated with the abundance of weebills (*Smicrornis brevirostris*), probably reflecting differences in habitat type. The abundance of shrubs and carnivores were positively correlated, while insectivore abundance was negatively correlated with trees.

Discussion

Short-term responses: 12 months since fire

In the short-term, I observed higher overall abundances of birds in both the wet and dry season burnt treatments. Differences in community structure and the abundance of feeding groups and particular species were also detected. Changes in bird abundance and community composition following a fire suggest that burning has altered the quantity or quality of habitat resources (Woinarski & Recher 1997; Smucker *et al.* 2005). High abundance of birds in recently burnt habitat is often observed in the first year post-fire (Woinarski 1990; Hutto 1995; Woinarski *et al.* 1999; Smucker *et al.* 2005), and may be related to an increase in food or greater accessibility to food resources (Woinarski & Recher 1997; Brawn *et al.* 2001). For example, a short-term increase in the abundance of some granivorous bird species has been attributed to the release of seeds following fire (Hutto 1995). In tropical savannas, the removal of dense understorey vegetation may expose seed resources, temporarily increasing granivore abundance (Woinarski 1990; Woinarski *et al.* 1999), and in my study may have promoted higher abundance of pale-headed rosellas (*Platycercus adscitus*). Similarly, carnivores, like pied butcherbirds (*Cracticus nigrogularis*) may be attracted to recently burnt habitat by greater accessibility to prey following the removal of understorey vegetation (Braithwaite & Estbergs 1987).

The higher abundances of insectivores and nectarivores in the dry season burnt treatments may reflect similar changes in resource availability. Although burning may reduce the amount of vegetation, remaining plants often exhibit traits that enhance survival in the post-fire environment, including flushes of new growth *via* epicormic shoots, vegetative regrowth and resprouting, and flowering events (Gill 1981; Whelan 1995). New foliage on remaining vegetation may attract arthropods (Force 1981; Recher *et al.* 1985; Swengel 2001), temporarily increasing food resources for some insectivorous birds (Hutto 1995; Barlow & Peres 2004). Although assemblages of arthropods in tropical savannas are perceived as resilient to the effects of fire (Parr *et al.* 2004; Andersen *et al.* 2005), short-term changes in arthropod abundance may be promoting higher abundance of the some species, including yellow-throated miners (*Manorina flavigula*) and striated pardalotes (*Pardalotus striatus*). Likewise, post-fire flowering events may attract nectar-feeding species (Recher *et al.* 1985), although a conspicuous flowering event was not observed during my study. As several non-obligatory nectarivores (e.g., little friarbird, *Philemon citreogularis*) include invertebrates as a component of their diet (Higgins *et al.* 2001), high abundance of nectarivores in dry season burnt treatments may be caused by a temporary shift in diet preferences, from nectar to invertebrates.

Bird assemblage showed that most species were associated with burnt sites, but some species, notably red-backed fairy-wrens (*Malurus melanocephalus*) and cicadabirds (*Coracina tenuirostris*) were adversely affected by burning. Birds with specialized habitat requirements, including prey and vegetation structure, may decline following burning if their preferred resource has been adversely affected by fire (Artman *et al.* 2001). The red-backed fairy-wren (*Malurus melanocephalus*) tends to avoid recently burnt habitat (Woinarski *et al.* 1999), presumably because the removal of understorey vegetation by fire disadvantages this shrub-foraging species.

Although bird abundance was higher in both burning treatments, differences in the abundance of feeding groups and certain species were most obvious between unburnt and dry season burnt sites. As pied butcherbirds (*Cracticus nigrogularis*) were the only species detected with significantly higher abundances in the wet season burnt sites, small changes in the abundance of other bird species presumably contributed to higher overall bird abundances. As dry season burning is typically more intense than wet season burning (Braithwaite & Estbergs 1985), a more prolific post-fire vegetative response, temporarily benefiting some species, may have occurred.

Long-term responses: four years since fire

Within four years of burning, distinct differences in the composition of birds and vegetation structure were apparent between fire regimes. Dry season burnt sites were characterized by lower overall abundance of birds, nectarivores, granivores, shrubs and rubber vine. Differences were mostly detected between dry season burnt and unburnt sites, although dry season burnt sites had fewer granivores and a different bird assemblage than wet season burnt sites. As responses of birds to burning reflect changes in the food or vegetation structure (Woinarski & Recher 1997; Smucker *et al.* 2005), burning during the dry season may have removed elements of the habitat that disadvantaged some species.

The initial flush of post-fire vegetative regrowth may be a short-term event (Gill 1981; Whelan 1995) and abundance of arthropods may decline a few years following burning (Force 1981), possibly to the detriment of insectivores, including white-throated honeyeaters (*Melithreptus albogularis*). The higher intensity of dry season fires may also cause high grass-seed mortality, reducing longer-term resources for granivores

(Woinarski 1990). Similarly, a reduction in the abundance of nectarivores may reflect changes in food availability as rainbow lorikeets (*Trichoglossus haematodus*) and little friarbirds (*Philemon citreogularis*) are suspected of tracking food resources in a landscape (Franklin & Noske 1999). As the abundance and accessibility of food resources declines, and birds that were initially attracted to the burnt areas disperse (Woinarski & Recher 1997), the changes in vegetation structure caused by burning may subsequently determine the suitability of the post-fire environment for birds.

Lower vegetation complexity was observed in the dry season burnt sites compared to unburnt, and the woodland habitat compared to riparian. Given that bird diversity is strongly influenced by habitat structure (MacArthur & MacArthur 1961) and often reflects the degree of habitat complexity in tropical savannas (Woinarski *et al.* 1988), the distinct bird assemblage and higher species number observed in the riparian habitat is unsurprising. Similarly, the low abundance of birds in the dry season burnt treatments probably reflects the lower vegetation complexity caused by a higher intensity burn. Changes in vegetation caused by burning are associated with differences in assemblages of birds (Davis *et al.* 2000; Barlow *et al.* 2006), presumably as species abundances increase or decrease according to their preferred habitat structure (Woinarski & Recher 1997). In my study, the long-term results of burning during the dry season created dissimilar assemblage of birds to wet season burnt sites and probably reflects differences in resources. In contrast, the wet season burnt sites did not significantly vary from unburnt sites in vegetation structure and maintained a similar bird assemblage.

Conservation and Management Implications

Our results confirm suggestions that the type of fire an area receives, and the time since fire, are important components influencing species responses (Woinarski 1990; Saab & Powell 2005; Smucker *et al.* 2005). In particular, my study shows that season of burn is a significant aspect of fire regime, and may have longer-term consequences on bird assemblages that differ from the short-term responses. As the intensity of fire in tropical savannas is always influenced by fuel moisture content, and hence season of burn, my results emphasize the importance of incorporating seasonality in fire management strategies.

The frequent occurrence of mid-late dry season fires, and the resulting simplification of vegetation structure, may lead to changes in the assemblage of birds. Indeed, an increased frequency of late dry season burning following the cessation of traditional Aboriginal burning practices (Braithwaite & Estbergs 1985; Russell-Smith *et al.* 1997b), may have already substantially altered bird assemblages across Australian tropical savannas. In my study, burning during the wet season least altered the riparian zone and adjacent woodland, and may offer a possible alternative to potentially destructive mid-late dry season burning. However, the effects of wet season burning on breeding birds are unknown, although it is likely that low-shrub nesting species will be disadvantaged. Dry season burning offered short-term benefits that may promote an increase in the abundance of some species. However, the broad scale use of dry season burning may disadvantage some granivorous and nectivorous species in the longer term. This is especially likely in Australian tropical savannas where high intensity fires, typically in the late dry season, are a possible factor contributing to the decline of granivorous species (Franklin 1999; Franklin *et al.* 2005).

Despite possible negative consequences for fauna, the contemporary use of prescribed burning for management purposes needs to continue. In particular, fire is an important weed management tool and burning may reduce rubber vine towers, infestations levels and understorey shrubs (Radford unpublished data, Grice 1997). Given that rubber vine is a problematic weed that deleteriously affects biodiversity (Tomley 1998; Chapter 2 / Valentine 2006; Chapter 3 / Valentine *et al.* in press), the use of fire to control rubber vine in riparian habitats may be justified, particularly if used in conjunction with other control methods. However, the long-term effect of burning riparian zones needs to be considered. As with other fire management practices, adopting a landscape scale approach, incorporating a variety of burning techniques and unburnt refugia, may maintain overall biodiversity (Hutto 1995; Woinarski *et al.* 1999). Considering that fire is an integral component of tropical savannas and exerts a strong influence on bird assemblages, I recommend small scale burns and the retention of unburnt habitat to reduce homogenisation of vegetation structure and bird assemblages.

CHAPTER 6. RESPONSES OF BIRDS TO REPEAT FIRES IN TROPICAL SAVANNAS

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Introduction

Fire is a widespread and significant agent of disturbance that influences the structure of many habitats. Today, the occurrence of fire is determined mainly by human land-use practices, with land managers using fire for pastoral management (Tothill 1971; Taylor 2003; Myers *et al.* 2004), hazard reduction burning (Cheney 1996; Fernandes & Botelho 2003), weed control (Briese 1996; Grice 1997) and conservation management of ecosystems (Abrams 1992; Angelstam 1998). Additional human-mediated disturbances, like introduced plant species (Rossiter *et al.* 2003; Brooks *et al.* 2004) and grazing (Lacey et al. 1982), can also alter natural fire regimes. Human-mediated use of fire has important ramifications for the environment, and fire frequency is emerging as a key land management issue (Williams *et al.* 2003b).

Fire frequency is a powerful driver of community composition for plants and animals (Brawn *et al.* 2001; Peterson & Reich 2001; Williams *et al.* 2003b; Andersen *et al.* 2005). Repeatedly burning an area predictably changes the habitat structure, leading to simplification of the vegetation complexity (Christensen *et al.* 1981; Bowman *et al.* 1988), particularly in the lower strata. Such changes have implications for faunal composition and fire frequency has been identified as a major factor influencing bird assemblages (Woinarski & Recher 1997; Woinarski *et al.* 1999; Engstrom *et al.* 2005). In grasslands or pine and oak savannas, where fire frequency has been reduced, and bird species have declined, frequent fires may be beneficial by increasing the abundance of bird species associated with disturbed environments (Askins 1993; Davis *et al.* 2000; Pons *et al.* 2003; Engstrom *et al.* 2005; Brawn 2006). In contrast, frequent fires have been linked to the decline of some bird species in Amazonian tropical forests (Barlow & Peres 2004) and Australian open forests (Woinarski & Recher 1997).

Australian tropical savannas are often considered resilient to the effects of fire (Andersen *et al.* 2005) with most habitat types receiving fire at least once every five years (Lacey *et al.* 1982) and large areas are burnt annually (Russell-Smith *et al.* 1997b). However, certain elements of tropical savannas, such as riparian habitat or monsoon forests, may be adversely affected by high fire frequencies (Russell-Smith & Bowman 1992; Andersen *et al.* 2005), and there is evidence that inappropriate fire regimes are linked to the decline of several bird and mammal species (Franklin 1999; Pardon *et al.* 2003; Franklin *et al.* 2005). Further, the cumulative effects of repeatedly burning an already-disturbed habitat may be significant. Although Australian tropical savannas are relatively intact, with little broadscale clearing, they are subject to inappropriate disturbances from cattle grazing, invasive species and fire regimes (Whitehead *et al.* 2005), and there is growing concern that human-mediated fire frequency in tropical savannas is too high.

The invasive weed rubber vine (*Cryptostegia grandiflora*) is currently spreading through Australia’s northern savannas, especially in riparian habitats. Fire can reduce rubber vine survival, and fire may be a useful tool to control rubber vine infestations (Grice 1997; Bebawi & Campbell 2000, 2002). Work already presented in this thesis showed that differences in burning season altered bird assemblages, with wet season burnt sites showing greater similarity to unburnt areas than dry season burnt sites (Chapter 5). Burning during the wet season is already used by land managers in tropical savannas (Crowley & Garnett 2000) and may be implemented as a potential weed management tool. However, repeatedly burning an area may be required to control woody weeds (Vitelli & Pitt 2006), including rubber vine, and understanding the impacts of repeated fires is critical for land managers.

Ideally, to understand the impact of a repeat burn, a before-after/control-impact (BACI; Stewart-Oaten *et al.* 1986) design should be used. As manipulative fire experiments are understandably complicated and expensive ventures, few studies allow this approach (but see Smucker *et al.* 2005), and most fire experiments compare elements of biodiversity between areas burnt with different fire frequencies (Woinarski 1990; Woinarski *et al.* 1999; Andersen *et al.* 2005). Here, I examine the impact of repeated fires by comparing bird assemblages between experimentally replicated fire treatments using an extended BACI approach.

Methods

Study Site and Experimental Design

The study took place in the Einasleigh Uplands bioregion (Sattler & Williams 1999), 110 km south of Townsville in north-eastern Queensland, Australia. All sites were located in open eucalypt woodland, along three seasonally dry watercourses: Bend Creek (20°16’07”S, 146°37’48”E), One Mile Creek (20°14’10”S, 146°40’35”E) and Cornishman Creek (20°12’18”S, 146°27’15”E), all sub-catchments of the Burdekin River on lease-hold grazing properties (Figure 1). The study was carried out in three stratified, replicate, experimental blocks, each of which encompassed approximately three km of watercourse. As described in Chapter 4, experimental plots were established along each creek that included both riparian and adjacent non-riparian open woodland habitat (see Chapter 4 for habitat description). At each creek, the following experimental treatments were randomly imposed: *i*) an unburnt control plot; *ii*) a singularly burnt plot, fire imposed December 1999, and *iii*) a repeatedly burnt plot, initial fire imposed December 1999 and second fire imposed December 2001 (Figure 1).

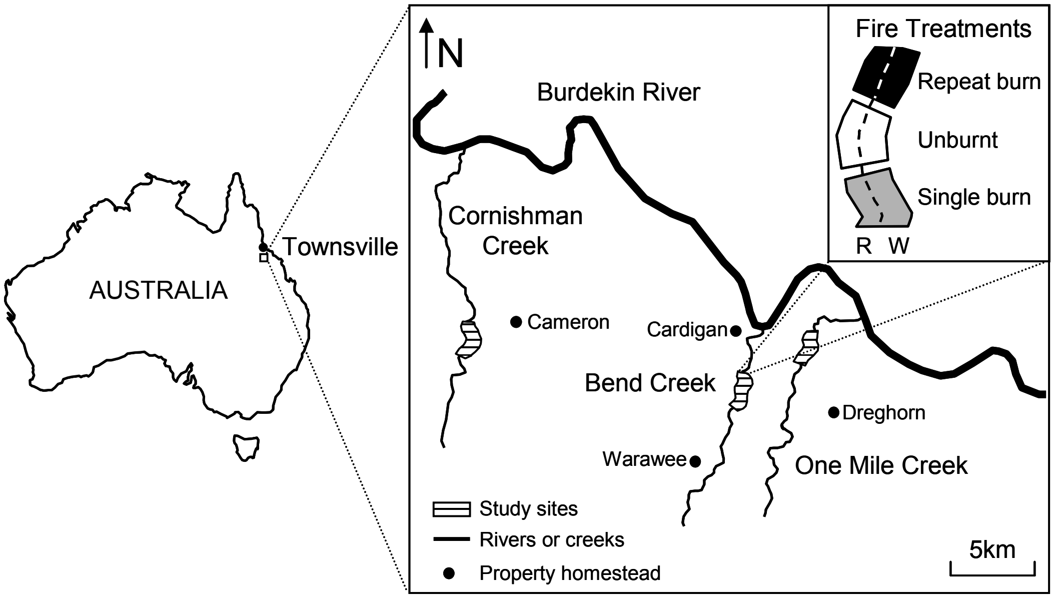

Figure 1. Map of study region in northern Australia. First inset shows location of study sites along tributaries of the Burdekin River, north-eastern Queensland. Second inset shows fire treatment plots and habitat (dashed line indicates separation of habitats; R = riparian, W = adjacent woodland).

Sampling Strategy

Faunal sampling began in 2001, one year after CSIRO had imposed the initial fires. Data were collected during the wet season, following the first rains of the season, between January and March 2001, 2003 & 2004. Sampling at these times allowed data collection one year prior to the second burn, one year after the second burn and two years after the second burn. Plots were surveyed randomly in each creek. Bird assemblages were surveyed using thirty-minute timed surveys along 250 m line transects running through the middle of each site (habitat/treatment replicate). Although visibility of birds was consistently high over all sites due to the generally open vegetation structure, I constrained the width of transects to 50 m either side of the observer to minimize differences in detection probability among sites. Surveys were conducted within the first three hours after sunrise and recorded the species and abundance of all birds either observed or heard, within the limits of each transect. Birds observed flying more than 10 m above the canopy were not included in analyses. Surveys were conducted twice along each transect within ten days, but were not undertaken on days with poor weather (e.g., rain or high wind). Abundance of birds observed during the two surveys of each transect were averaged, while the number of species observed were summed to estimate total species richness for each site. Data on vegetation variables were collected using four large quadrats (20 m x 10 m) that were established in each site. In each quadrat, the number of trees and shrubs were recorded. The proportion of rubber vine in the understorey was estimated to the nearest 10% in each quadrat. In the last two years of surveys, several plants were observed fruiting, particularly the commonly occurring native shrub currant bush (*Carissa ovata*). To examine the potential change in food resources, I estimated the area (m^2) of currant bush within each quadrat in the last two years of surveys. Data were averaged among the four quadrats to provide an estimate of average vegetation structure within each site.

Analysis

Species richness and bird abundance

The experiment was in the form of a randomized block design and when combined with the sampling protocol provided the opportunity to use a Before-After-Control-Impact (BACI; Stewart-Oaten *et al.* 1986) approach to examine the impact of the second fire on mean bird abundance and species number. The BACI ANOVAs (SPSS, version 12) included time (before 2nd fire, 1 year after 2nd fire and 2 years after 2nd fire), treatment (unburnt, single burn and repeat burn) and habitat (riparian and woodland) as main effects terms, and creek as a blocking factor. Interaction terms between time*treatment and time*treatment*habitat were also included to examine the impact of the second burn. If a significant interaction was detected, indicating a significant impact of the second burn, post-hoc ANOVAs were used to further explore sources of variation among factors within each year of survey. Post-hoc ANOVAs used treatment and habitat as main effects terms (including an interaction term) and creek as a blocking factor. The response of 24 commonly occurring species (observed in at least 20 of the possible 54 time*treatment*habitat sites) was also examined within each year of survey using ANOVAs.

Feeding group assemblage

Bird species were assigned to one of five feeding groups (carnivore, granivore, frugivore, insectivore and nectarivore) based on their dominant source of food, using dietary information from the literature (Marchant & Higgins 1990a, b, 1993; Higgins & Davies 1996; Higgins 1999; Higgins *et al.* 2001; Higgins & Peter 2002; Catterall & Woinarski 2003; Higgins *et al.* 2005). Feeding group assemblage was examined by comparing the average number of carnivores, granivores, frugivores, insectivores and nectarivores at each site using a MANOVA (SPSS, version 12) with the BACI design (described above). A Canonical Discriminant Analysis (CDA) was used to interpret significant interaction terms and to examine the influence of time and fire treatments on feeding group assemblage.

Vegetation structure and correlations

Vegetation structure was examined by comparing the average number of trees, shrubs and the proportion of rubber vine per quadrat in each site using a MANOVA (SPSS, version 12), with the BACI design (described above). The area of currant bush was compared each year surveyed using ANOVAs. Species number, bird abundance and feeding group abundance and the abundance of species that responded significantly to the second fire were correlated with vegetation variables within each year of survey using Pearson's correlation coefficients.

Data transformations

Rubber vine percentage data were adjusted by arcsine square-root transformation (Zar 1999). Species richness, abundance counts (birds, feeding groups, trees and shrubs) and amount of currant bush were examined for normality and heteroscedasticity using box plots, Q-Q plots and residual plots. Multivariate linearity was determined by examination of scatterplots of variables used in MANOVA. Species richness and abundance of birds, trees and shrubs and the amount of currant bush were square-root transformed and individual species abundances and feeding group abundances were $\log_{10}(x + 1)$ transformed to meet assumptions of ANOVA and Pearson's correlation. To aid interpretation, graphs depict the untransformed data.

Results

Species richness and bird abundance

Species richness

A total of 67 bird species were identified during the three years of surveys. An additional three species were observed once during surveys but not positively identified. The unknown species were included in abundance and species richness analyses but were excluded from feeding group analyses. BACI analysis on the square-root transformed species number revealed significant differences among creeks (ANOVA: $F_{2,34} = 14.090$, $P < 0.001$) and a significant interaction between time and fire treatment (ANOVA: $F_{4,34} = 2.903$, $P = 0.036$; Figure 2), where the number of species was lower in repeatedly burnt sites following the second fire. Prior to the second fire, post-hoc ANOVAs revealed similar number of species in all fire treatments (Figure 2), although species number differed among creeks (ANOVA: $F_{2,10} = 7.722$, $P = 0.009$). One year after the second fire species number in the repeatedly burnt sites was significantly lower than in unburnt and singularly burnt sites (ANOVA: $F_{2,10} = 10.941$, $P = 0.003$; Figure 2) and varied among creeks (ANOVA: $F_{2,10} = 4.539$, $P = 0.040$). Two years following the second fire species number was still significantly lower in repeatedly burnt sites compared to unburnt and singularly burnt sites (ANOVA: $F_{2,10} = 9.539$, $P = 0.005$; Figure 2). A number of species, including great bowerbird (*Chlamydera nuchalis*), red-backed fairy-wren (*Malurus melanocephalus*), yellow honeyeater (*Lichenostomus flavus*), Lewin's honeyeater (*Meliphaga lewinii*), noisy friarbird (*Philemon corniculatus*) and rainbow lorikeet (*Trichoglossus haematodus*), were observed in the unburnt and singularly burnt sites, but were absent from the repeatedly burnt sites at least one of the years following the second fire. During the final year of survey, species number was also lower in the woodland habitat compared to the riparian habitat

(ANOVA: $F_{1,10} = 9.408$, $P = 0.012$). This finding probably contributed to a significant interaction between time, fire and habitat in the original BACI analysis (ANOVA: $F_{8,34} = 2.610$, $P = 0.024$) as the trends in species number over time and fire were similar in both habitat types.

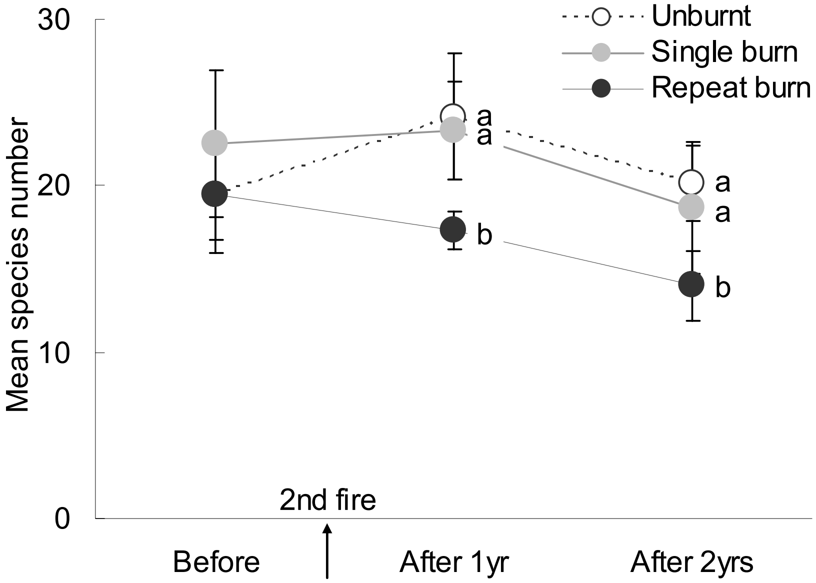

Figure 2. Mean species number (± 95%CI) observed in fire treatments over time. Lines follow fire treatments through time. Letters indicate differences between fire treatments within each year of survey based on post-hoc Tukey HSD tests ($\alpha < 0.05$). Note that the unburnt treatment in the 'Before' time period is obscured by the repeat burn treatment.

Bird abundance

BACI analysis on the square-root transformed bird abundance detected a significant interaction between time and fire treatment (ANOVA: $F_{4,34} = 7.310$, $P < 0.001$; Figure 3), where the abundance of birds decreased following the second fire. Post-hoc ANOVAs, conducted within each year of survey, initially showed higher abundances of birds in the burnt sites compared to the unburnt sites (ANOVA: $F_{2,10} = 6.224$, $P = 0.018$; Figure 3). However, one year following the second fire, abundances of birds in the repeatedly burnt sites were lower than the unburnt (ANOVA: $F_{2,10} = 5.463$, $P = 0.025$; Figure 3) and by two years following the second fire abundances were lower than both unburnt and singularly burnt sites (ANOVA: $F_{2,10} = 8.422$, $P = 0.007$; Figure 3). In the final year of survey, abundances of birds were also lower in the woodland habitat (ANOVA: $F_{1,10} = 13.988$, $P = 0.004$).

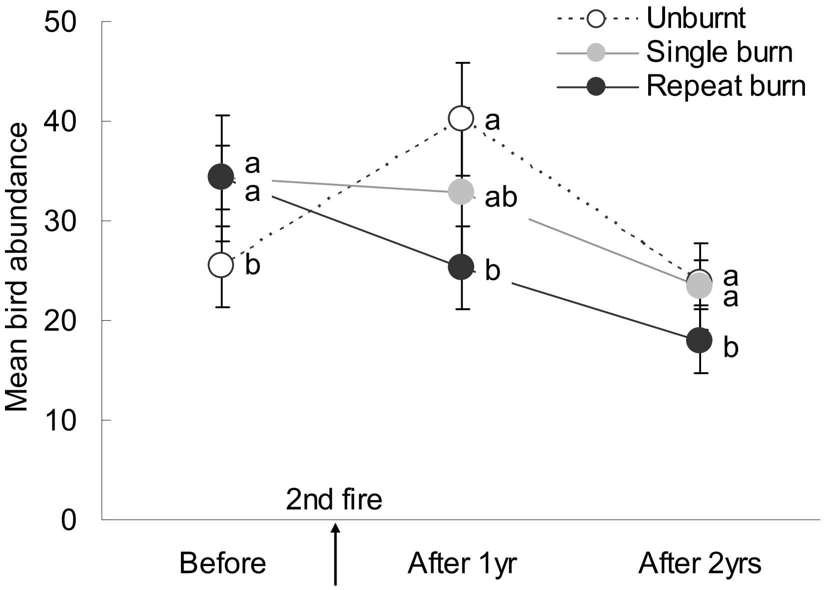

Figure 3. Mean bird abundance (± 95%CI) per survey in fire treatments over time. Lines follow fire treatments through time. Letters indicate differences between fire treatments within each year of survey based on post-hoc Tukey HSD tests ($\alpha < 0.05$). Note that the single burn treatment in the 'Before' time period is obscured by the repeat burn treatment.

Individual Species Responses

A number of species showed differences in abundances among fire treatments and between habitats (Table 1). Before the second fire, striated pardalotes (*Pardalotus striatus*) were more abundant in burnt sites, pied butcherbirds (*Cracticus nigrogularis*) and black-faced cuckoo-shrikes (*Coracina novaehollandiae*) were more abundant in the woodland habitat of burnt sites. In contrast, the red-backed fairy-wren (*Malurus melanocephalus*) showed a strong trend for lower abundances in the burnt sites. In the two years following the second fire, a few species, including the frugivore mistletoebird (*Dicaeum hirundinaceum*), the granivore red-winged parrot (*Aprosmictus erythropterus*), the insectivore white-throated honeyeater (*Melithreptus albogularis*), and the nectarivores noisy friarbird (*Philemon corniculatus*) and rainbow lorikeet (*Trichoglussus haematodus*) decreased in abundance in the repeatedly burnt sites compared to either the singularly burnt sites, unburnt sites, or both (Table 1). In addition, great bowerbirds (*Chlamydera nuchalis*) were less abundant in repeatedly burnt sites and the woodland habitat of singularly burnt sites. A number of species were absent from repeatedly burnt sites following the second fire, including red-backed fairy-wrens (*Malurus melanocephalus*), yellow honeyeaters (*Lichenostomus flavus*) and Lewin's honeyeaters (*Meliphaga lewinii*), although significant differences in abundance among fire treatments were not detected. Birds associated with riparian habitat at some point in time included grey butcherbirds (*Cracticus torquatus*), white-throated honeyeaters (*Melithrepus albogularis*), dollarbirds (*Eurystomus orientalis*), peaceful doves (*Geopelia striata*) and magpie-larks (*Grallina cyanoleuca*). Birds associated with woodland habitat at some point in time include pied butcherbirds (*Cracticus nigrogularis*), weebills (*Smicrornis brevirostris*), Australian magpies (*Gymnorhina tibicen*), yellow-throated miners (*Manorina flavigula*) and red-backed fairy-wrens (*Malurus melanocephalus*; Table 1). In addition, the abundances of white-throated honeyeaters (*Melithreptus albogularis*), striated pardalotes (*Pardalotus striatus*), mistletoebirds (*Dicaeum hirundinaceum*), black-faced cuckoo-shrikes (*Coracina novaehollandiae*), olive-backed orioles (*Oriolus sagittatus*) and weebills (*Smicrornis brevirostris*) varied among creeks at some point during surveys.

Table 1. ANOVA F-values for select species within each year of survey. Significant values are in bold (* P< 0.5, ** $P < 0.01$, *** $P < 0.001$) and values approaching significance are identified (^ $0.06 > P \geq 0.05$). Letters beside significant values indicate results from post-hoc Tukey HSD tests (treatment: S = singularly burnt, R = repeatedly burnt, U = unburnt) or which habitat had highest abundances (habitat: W = woodland, Ri = riparian). Species with a significant response to the 2nd fire are highlighted in bold. F-values for the blocking factor Creek are not shown.

	Before 2nd fire			After 1 year			After 2 years		
Species	Treatment $_{df = 2,10}$	Habitat $_{df = 1,10}$	T*H $_{df = 2,10}$	Treatment $_{df = 2,10}$	Habitat $_{df = 1,10}$	T*H $_{df = 2,10}$	Treatment $_{df = 2,10}$	Habitat $_{df = 1,10}$	T*H $_{df = 2,10}$
Carnivores									
Pied butcherbird	**11.976**** S & R >U	**124.116***** W	**11.976****	0.567	**16.520**** W	0.619	1.004	4.463	0.480
Grey butcherbird	0.454	**33.843***** Ri	2.885	0.560	**23.946**** Ri	0.547	3.979^ R > S	**9.541*** Ri	0.645
Frugivores									
Great bowerbird	0.493	0.281	0.493	**8.557**** U & S > R	0.332	**11.013****	1.570	0.240	1.186
Mistletoebird	0.683	0.155	1.739	**5.396*** U > R	0.014	1.316	**6.094*** U > R	0.001	0.685
Granivores									
Red-winged parrot	0.679	0.642	1.348	**6.879*** S > R	3.713	2.657	3.983^ U > R	0.068	1.718
Peaceful dove	2.156	0.111	1.089	0.080	0.003	0.581	0.455	**7.723*** Ri	3.182
Pale-headed rosella	0.825	0.770	0.377	0.861	0.061	0.145	1.068	1.047	0.944
Insectivores									
Black-faced cuckoo-shrike	**4.750*** R > U	0.101	**4.273***	1.087	2.886	0.148	0.388	4.665^ Ri	2.997
Dollarbird	1.980	3.337	0.064	1.667	**20.000**** Ri	1.667	0.454	**16.848**** Ri	2.627
White-throated gerygone	1.517	0.496	0.585	0.637	0.004	0.657	Only one individual observed – no tests performed		
Magpie-lark	0.285	2.185	0.352	0.368	0.044	0.105	0.791	**6.060*** Ri	0.484
Australian magpie	0.118	**8.857*** W	0.048	0.132	0.304	0.804	0.354	1.687	0.306
Red-backed fairy-wren	3.888^ U > S & R	1.927	1.173	2.318	**5.163*** W	2.079	0.424	**7.809*** W	0.424
Yellow-throated miner	1.728	**5.293*** W	0.092	2.270	3.845	2.270	1.221	0.010	0.561
White-throated honeyeater	0.152	**5.636*** Ri	2.843	**4.786*** U > R	0.283	1.707	**27.022***** S & U > R	2.157	0.749
Olive-backed oriole	0.333	1.748	0.199	1.731	1.199	0.127	1.315	0.322	0.902
Striated pardalote	**4.402*** S & R > U	1.115	0.673	0.172	0.080	0.189	1.251	2.256	1.587
Weebill	0.898	**5.560*** W	0.428	0.121	**9.574*** W	0.092	3.162	**6.134*** W	0.278
Apostlebird	2.431	0.170	1.366	2.895	0.258	0.841	2.576	4.896^ Ri	1.025

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Table 1. continued.

	Before 2nd fire			After 1 year			After 2 years		
Species	Treatment $_{\mathrm{df = 2,10}}$	Habitat $_{\mathrm{df = 1,10}}$	T*H $_{\mathrm{df = 2,10}}$	Treatment $_{\mathrm{df = 2,10}}$	Habitat $_{\mathrm{df = 1,10}}$	T*H $_{\mathrm{df = 2,10}}$	Treatment $_{\mathrm{df = 2,10}}$	Habitat $_{\mathrm{df = 1,10}}$	T*H $_{\mathrm{df = 2,10}}$
Nectarivores									
Blue-faced honeyeater	1.404	0.047	0.145	0.104	0.569	3.221	0.758	3.737	0.351
Yellow honeyeater	2.054	3.552	0.450	2.284	1.247	0.538	3.328	3.280	1.590
Little friarbird	2.506	0.424	3.994^	0.037	0.110	1.432	0.454	2.286	0.122
Noisy friarbird	2.422	0.286	0.074	**7.329*** S & U > R	1.538	0.582	0.776	0.551	0.053
Rainbow lorikeet	0.536	1.938	2.794	2.021	0.008	0.365	**4.559*** S > R	1.014	0.506

Feeding group assemblage

A MANOVA on the five log(x + 1) abundance of feeding group variables using the BACI design detected a significant interaction between time and fire treatment (MANOVA Wilks' Lambda: $F_{20,100.5} = 1.857$, $P = 0.024$) and a significant difference in abundance was also detected among creeks (MANOVA Wilks' Lambda: $F_{10,60} = 13.674$, $P < 0.001$) and habitats (MANOVA Wilks' Lambda: $F_{5,30} = 2.568$, $P = 0.048$). A Canonical Discriminant Analysis (CDA) was used to examine the influence of the time*treatment interaction on feeding group assemblage (Figure 4). Time separated along the first discriminant axis while fire treatments separated along the second (Figure 4). Before the second fire, burnt sites grouped together and were influenced by granivores and carnivores (Figure 4b and 4e). However, following the second fire, unburnt sites grouped away from the repeatedly burnt sites and appeared to be influenced by frugivores, insectivores and nectarivores, while singularly burnt sites were scattered throughout (Figure 4a and 4e). The pattern of separation between unburnt and repeatedly burnt sites continued two years following the second fire and was mostly influenced by frugivores, with singularly burnt sites clustering between the two fire treatments (Figure 4c).

The log(x + 1) abundance of each feeding group was further examined individually using the BACI analysis. A significant interaction between time and treatment was detected for the abundance of frugivores (ANOVA: $F_{4,34} = 3.299$, $P = 0.022$; Figure 5a). The abundance of frugivores was low in all sites during the first year of survey. However, following the second fire, frugivores were least abundant in repeatedly burnt sites (Figure 5a). The abundance of frugivores also varied among creeks (ANOVA: $F_{2,34} = 3.546$, $P = 0.040$). A significant interaction between time and treatment was also detected for insectivores (ANOVA: $F_{4,34} = 3.608$, $P = 0.015$), where 12 months following the second burn, the repeatedly burnt sites contained lower abundances of insectivores than the unburnt (Figure 5b). Similarly, a significant interaction between time and treatment was detected for nectarivores (ANOVA: $F_{4,34} = 3.010$, $P = 0.031$; Figure 5c) and showed comparable patterns to the abundance of insectivores. Nectarivore abundance was also highest in the riparian habitat (ANOVA: $F_{1,34} = 11.173$, $P = 0.002$) and varied among creeks (ANOVA: $F_{2,34} = 4.967$, $P = 0.013$). BACI analysis did not detect a significant interaction term for either granivores or carnivores

(Figures 5d and 5e). Granivore abundance showed a marked decline over time (ANOVA: $F_{2,34} = 18.218$, $P < 0.001$) and was particularly low in the final year of surveys (Figure 5d). The abundance of carnivores similarly varied over time (ANOVA: $F_{2,34} = 11.175$, $P < 0.001$) but was greatest in the first year of surveys (Figure 5e). There was also some variation in the abundance of carnivores among creeks (ANOVA: $F_{2,34} = 3.378$, $P = 0.046$).

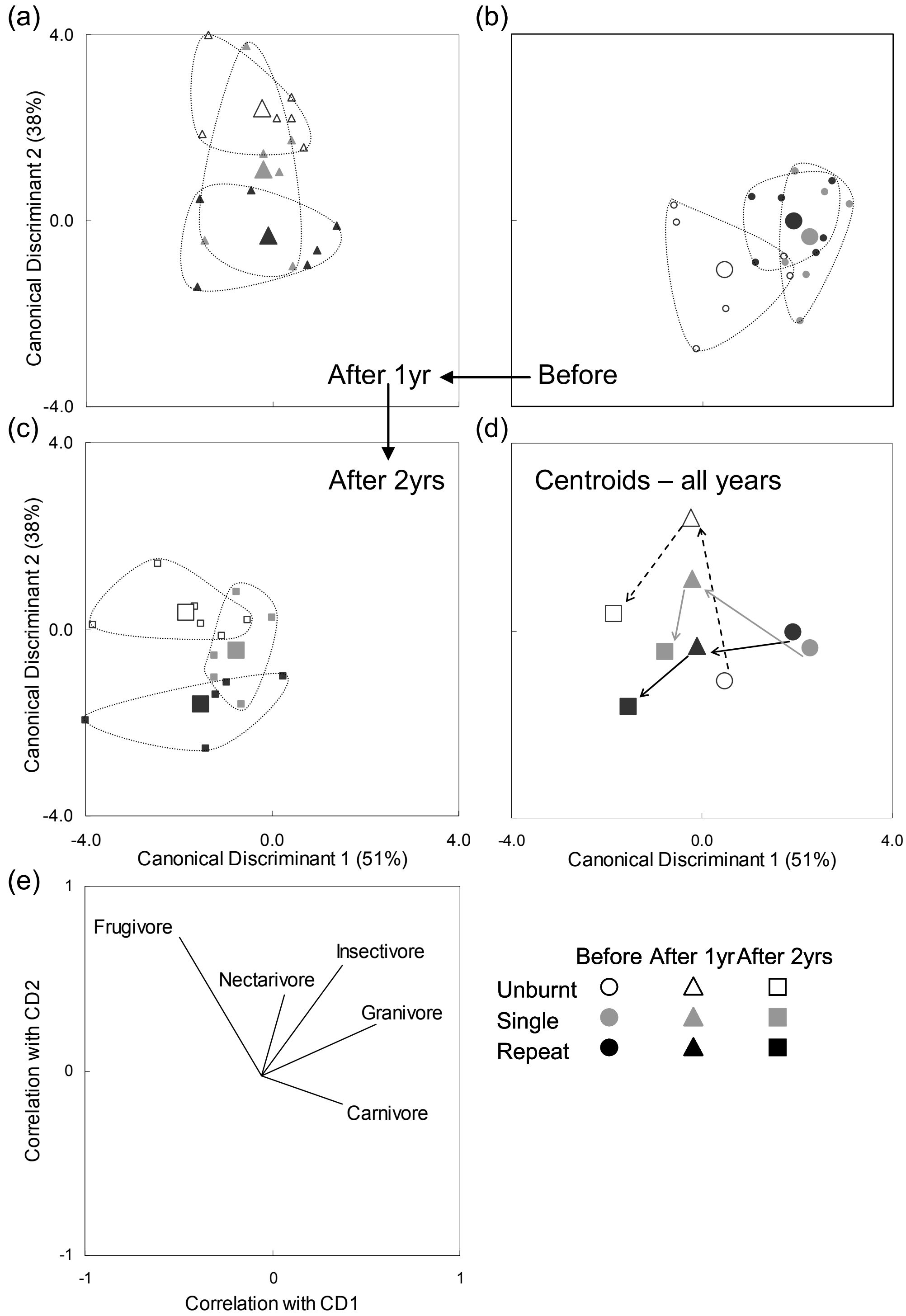

Figure 4. Canonical Discriminant Analysis of feeding group in fire treatments over time. a-c) The position of each site and centroids of fire treatments displayed in each year to ease interpretability. Dashed lines define the range of sites within each fire treatment*year combination. d) Centroids for each group. Arrows show change in centroid over time. e) The correlation between feeding groups and the canonical value.

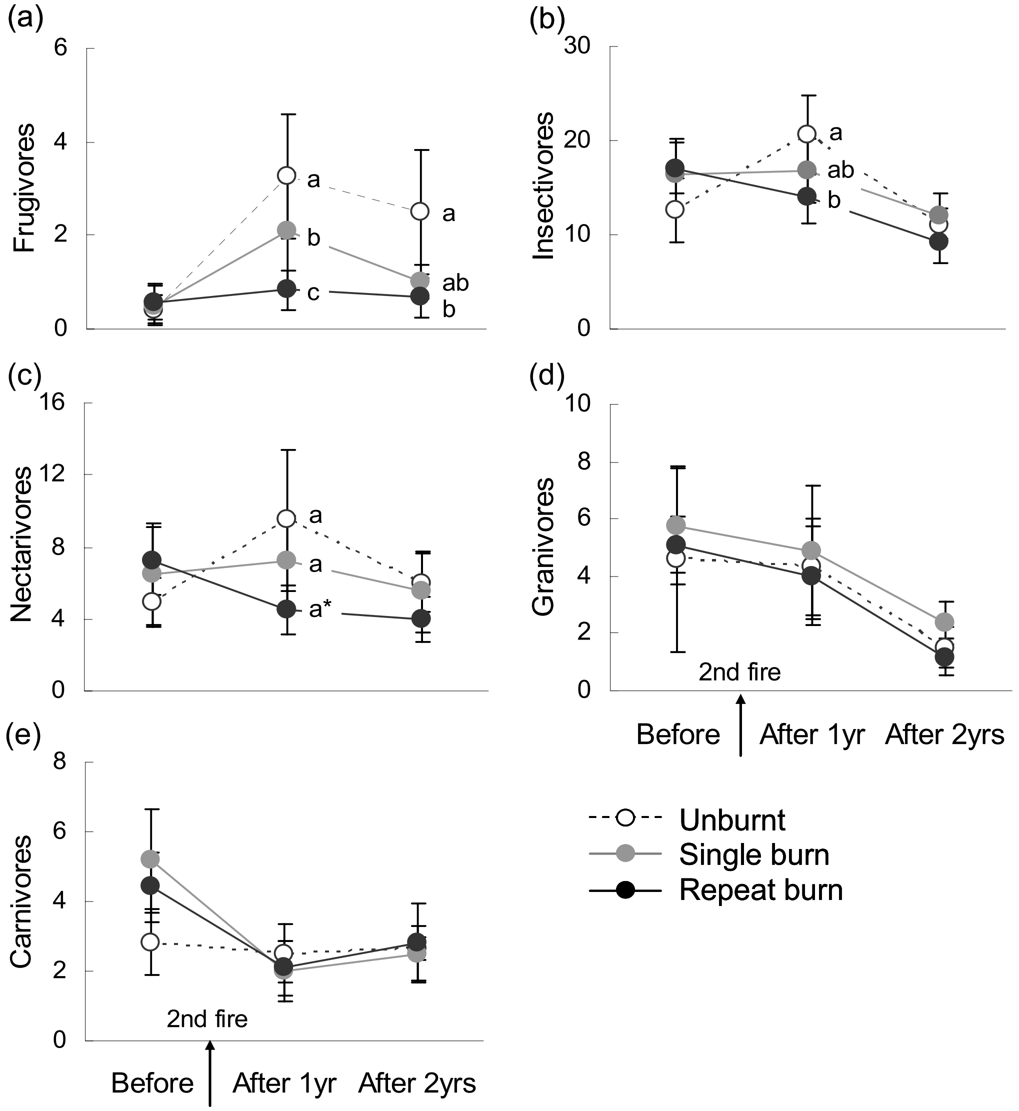

Figure 5. Untransformed mean feeding group abundance (± 95%CI) of a) frugivores, b) insectivores, c) nectarivores, d) granviores and e) carnivores per survey in fire treatments over time. Lines follow fire treatments through time. Letters within graph indicate significant differences between fire treatments within each year of survey based on post-hoc Tukey HSD tests ($\alpha < 0.05$) and the asterisk (*) indicates that the fire treatment was approaching significance ($0.06 < P \geq 0.05$).

Vegetation structure and correlations

A MANOVA on the three vegetation variables (square-root tree abundance, square-root shrub abundance and arcsine percentage of rubber vine) using the BACI design detected significant differences between habitats (MANOVA Wilks' Lambda: $F_{3,32} = 51.589$, $P <$

0.001), and among treatments (MANOVA Wilks' Lambda: $F_{6,64} = 4.499$, $P < 0.001$) and creeks (MANOVA Wilks' Lambda: $F_{6,64} = 2.756$, $P = 0.019$), but no significant interaction between time and treatment. The abundance of trees was higher in the riparian habitat and varied among creeks (Table 2). Shrub abundance was lower in the burnt sites compared to the unburnt sites and also varied among creeks (Table 2). The proportion of rubber vine was lower in the woodland habitat and in the burnt sites (Table 2).

Table 2. BACI ANOVA F-values for the number of trees and shrubs per quadrat and the proportion of rubber vine in the understorey. No significant interaction terms were detected. Significant values are highlighted in bold (* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$). Untransformed means (± 95%CI) for fire treatments and habitat are shown. Letters next to fire treatment means indicate results from post hoc Tukey HSD tests ($\alpha < 0.5$).

	F-values $_{\text{Error df} = 34}$				Treatment means			Habitat means	
Vegetation	Time $_{\text{df} = 2}$	Treatment $_{\text{df} = 2}$	Habitat $_{\text{df} = 1}$	Creek $_{\text{df} = 2}$	Unburnt	Single	Repeat	Riparian	Woodland
Trees / quadrat	0.437	2.292	**6.577***	**3.848***	4.8 ± 0.8^a	4.3 ± 0.6^a	3.9 ± 0.7^a	4.8 ± 0.5	3.8 ± 0.5
Shrubs / quadrat	0.188	**6.839****	3.164	**5.501****	2.3 ± 0.6^a	1.1 ± 0.5^b	1.3 ± 0.5^b	1.7 ± 0.5	1.4 ± 0.5
Rubber vine %	0.751	**7.101****	**146.944*****	0.588	36.4 ± 5.5^a	25.0 ± 6.3^b	20.4 ± 5.0^b	48.6± 6.2	5.9 ± 3.5

During the first year of surveys few plants were observed fruiting. However, in the remaining two sample years, surveys coincided with fruiting plants. One of the most prevalent fruiting plants was the low native shrub currant bush (*Carissa ovata*). One year following the repeat burn, the amount of currant bush (*Carissa ovata*) was lower in the repeatedly burnt sites compared to the unburnt (ANOVA: $F_{2,10} = 7.472$, $P = 0.010$; mean square-root m^2 per quadrat ± 95%CI: Unburnt = 2.5 ± 1.0, Single = 1.4 ± 1.3, Repeat = 0.5 ± 0.5) and varied among creeks (ANOVA: $F_{2,10} = 9.596$, $P = 0.005$). Similarly, the amount of currant bush was lower in the repeatedly burnt sites two years following the second fire (ANOVA: $F_{2,10} = 5.720$, $P = 0.022$; mean square-root m^2 per quadrat ± 95%CI: Unburnt = 2.9 ± 1.3, Single = 1.1 ± 1.0, Repeat = 0.7 ± 0.5).

Bird and vegetation correlations

Prior to the second fire the abundance of both frugivores and insectivores were negatively correlated with the number of trees and the proportion of rubber vine in the understorey (Table 3), indicating that frugivores and insectivores were associated with woodland habitat, and insectivores may also have preferred burnt sites. However, following the second fire, the abundance of birds, frugivores and nectarivores, as well as species number were positively associated with trees, rubber vine or current bush (Table 3), indicating that several birds were associated with unburnt or riparian habitat. In particular, a strong relationship was observed between the abundance of frugivores and the amount of currant bush (Figure 6). Several great bowerbirds (*Chlamydera nuchalis*) were incidentally observed feeding on the berries of currant bush, and great bowerbirds and mistletoebirds (*Dicaeum hirundinaceum*) showed strong associations with the amount of currant bush (Table 3). The abundance of nectarivores, including noisy friarbirds (*Philemon corniculatus*), was also strongly associated with the amount of currant bush.

Table 3. Pearson correlations (*r*) of average square-root bird abundance, square-root species number, abundance of log (x + 1) feeding groups and abundance of log (x + 1) species that responded significantly to the second fire with the square-root number of trees, shrubs, asine proportion of rubber vine and square-root area of current bush per quadrat. Significant values are highlighted in bold (* $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$).

	Before			After 1 year				After 2 years			
	Tree	Shrub	Rubber	Tree	Shrub	Rubber	Current	Tree	Shrub	Rubber	Current
Abundance	-0.202	-0.402	-0.418	**0.576***	0.441	**0.507***	**0.623****	0.022	0.189	**0.645****	0.364
Species number	-0.280	-0.380	-0.320	0.374	0.126	0.433	0.184	0.115	0.188	**0.650****	0.417
Carnivores	0.040	-0.466^	-0.350	0.215	0.366	0.170	0.224	-0.328	0.182	0.231	-0.112
Frugivores	**-0.587***	0.351	-0.381	**0.529***	0.285	0.367	**0.763*****	0.242	0.083	0.361	**0.728****
Great Bowerbird	0.105	-0.335	0.037	0.406	**0.483***	0.343	**0.537***	0.012	-0.170	0.153	**0.504***
Mistletoebird	-0.382	0.080	-0.050	0.466^	0.156	0279	**0.754*****	0.365	0.064	0.279	**0.748*****
Granivores	0.110	0.015	-0.211	0.200	0.040	0.301	0.110	0.244	0.290	0.388	0.183
Red-winged Parrot	0.031	-0.123	-0.077	0.255	0.020	0.340	0.144	-0.159	0.386	0.151	-0.213
Insectivores	-0.279	-0.329	**-0.494***	0.394	0.401	0.241	0.365	-0.052	0.152	0.387	0.079
White-throated HE	-0.078	-0.266	0.209	0.154	0.068	0.267	0.248	0.105	0.133	0.315	0.406
Nectarivores	0.041	-0.122	0.242	**0.562***	0.407	**0.540***	**0.600****	-0.002	0.062	**0.492***	0.241
Noisy Friarbird	0.443^	0.001	-0.148	0.280	0.105	0.022	**0.571***	-0.056	-0.040	-0.104	0.087
Rainbow Lorikeet	-0.168	-0.118	0.124	0.468^	0.038	0.366	0.346	-0.046	-0.255	0.298	-0.032

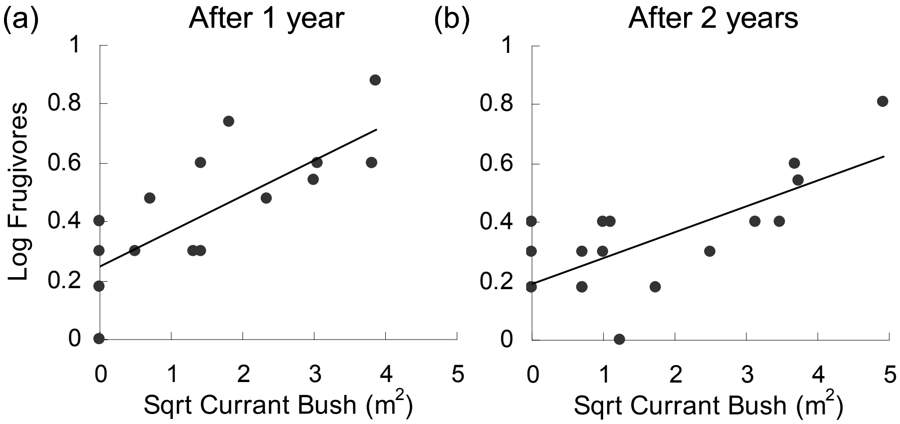

Figure 6. Associations of frugivore abundance and the amount of currant bush following the second fire.

Discussion

The impact of a repeat fire

Clearly, repeated fires have very different effects from single fires, and these effects change with time post-fire. Before the second fire, when both burning treatments were 12 months post-fire, burnt sites contained higher overall abundance of birds. The phenomenon of increased bird abundance or species richness in recently burnt sites has been observed in a variety of studies (Braithwaite & Estbergs 1987; Woinarski 1990; Hutto 1995), and is assumed to occur because of a temporary change in resource availability that benefits some species (Woinarski & Recher 1997; Brawn *et al.* 2001; Saab & Powell 2005). For instance, a post-fire flush of new vegetation may attract invertebrates to recently burnt sites (Force 1981; Swengel 2001), facilitating a temporary glut of food resources for insectivorous birds (Christensen *et al.* 1981; Hutto 1995; Barlow & Peres 2004; Chapter 5 / Valentine *et al.* accepted). In contrast, following the second fire there was a marked reduction in species richness, overall bird abundance, the abundance of some feeding groups and particular species. This suggests that burning a second time within two years of the first fire did not offer any immediate benefit, but instead altered the habitat in a manner unfavourable to birds. As the response of birds to disturbances are often associated with changes in the availability of resources and vegetation structure (Woinarski & Recher 1997; Davis *et al.* 2000; Brawn *et al.* 2001; Kutt & Woinarski 2006), it is likely that the second fire detrimentally modified the quantity or quality of resources important for some species. Dissimilarity in bird assemblages between comparatively high frequency burning and low frequency burning has been previously observed in oak savannas (Davis et al. 2000) and Brazilian forests (Barlow & Peres 2004; Barlow *et al.* 2006) where differences were attributed to changes in vegetation structure and resource availability. Similarly, previous studies in tropical savannas have identified fire frequency as an important component influencing bird feeding groups (Woinarski 1990; Woinarski *et al.* 1999), although there were few consistent differences among study results due to fire regime, rather, birds seem to respond to time since fire (Woinarski et al. 1999) or whether or not a site was burnt (Woinarski 1990).

Changes in food availability – the response of feeding groups

Feeding group assemblages varied among year of survey and fire treatments. In particular, the assemblages of feeding groups were strongly separated by year of survey, and probably reflect differences in environmental characteristics (e.g. mean annual rainfall). Year-to-year variability in bird assemblages is fairly common in tropical savannas (Woinarski & Tidemann 1991) and is best explained by changes in resource availability that relate to the extremes of within-year seasonality (Woinarski & Tidemann 1991), or differences in the wet season characteristics among years (Taylor & Tulloch 1985). However, within each year of survey, fire treatments showed distinct feeding group assemblages. Although burnt sites initially grouped together, in the two years following the second fire, feeding group assemblages of repeatedly burnt sites diverged increasingly from unburnt and singularly burnt sites.

Frugivore abundance was initially low in all fire treatments when few plants were observed fruiting. However, in later years, fruiting shrubs coincided with bird surveys and the abundance of frugivores, including mistletoebrids (*Dicaeum hirundinaceum*) and great bowerbirds (*Chlamydera nuchalis*), were lowest in the repeatedly burnt sites. Frequent fires can reduce the abundance and composition of understorey shrubs (Fox & Fox 1986) and burning may also reduce the number of fruiting species (Sanaiotti & Magnusson 1995) or the amount of fruit production (Setterfield 1997) in the post-fire environment. Berries of the native shrub currant bush (*Carissa ovata*) provide a food resource for frugivores like great bowerbirds (*Chlamydera nuchalis*), and may also provide foraging opportunities or shelter for other species. As the amount of currant bush was reduced in repeatedly burnt sites, frugivores may have been affected by the loss of food resources, while other species, including red-backed fairy-wrens (*Malurus melanocephalus*) were affected by reduced shelter or foraging opportunities.

Following the second fire, the overall abundance of insectivores was also lower in repeatedly burnt sites. This pattern was probably driven by lower abundances of white-throated honeyeaters (*Melithreptus albogularis*) in repeatedly burnt sites. Frequent low intensity fires can reduce invertebrate abundance, taxon richness and alter composition in subtropical *Eucalypt* forests (York 1999, 2000). Although, tropical savanna arthropod communities tend to show resilence to fire (Parr *et al.* 2004; Andersen *et al.* 2005), burning does disadvantage certain arthropods and alter the overall composition of arthropod communities (Andersen & Muller 2000; Parr *et al.* 2004), potentially to the disadvantage of some insectivorous species. Further, the change in invertebrate communities caused by repeated burning may be exaggerated in environments where arthropod communities are affected by additional disturbances, such as introduced species (Chapter 3 / Valentine *et al.* in press) and grazing (Abensperg-Traun *et al.* 1996). A reduction in preferred arthropod abundance may also influence the response of some nectarivores that include arthropods in their diet, including noisy friarbirds (*Philemon corniculatus*) (Higgins *et al.* 2001).

Changes in habitat structure

Burnt sites had a lower vegetation complexity than unburnt, characterised by fewer shrubs and less rubber vine. Although I did not detect a significant time*treatment interaction the recorded vegetation variables, frequent fires in tropical savannas may reduce seedling establishment in shrub and tree species (Andersen *et al.* 2005) and reduce plant species richness (Fensham 1990), particularly of obligate seeding species (Russell-Smith *et al.* 1998). Further, frequent fires in tropical savannas typically lead to a reduction in vegetation complexity (Christensen *et al.* 1981; Bowman *et al.* 1988). Lower vegetation complexity in repeatedly burnt sites may disadvantage bird species by removing important nesting or foraging habitat (Artman *et al.* 2001). In addition, the repeatedly burnt sites in my study did contain lower amounts of currant bush than the unburnt sites. Given that currant bush creates a dense shrubby understorey, the removal of this plant may reduce available shelter and foraging opportunities for birds.

Conservation and Management Implications

Given that rubber vine is a weed of national significance in Australia (Commonwealth of Australia 1999), controlling the spread and extent of rubber vine is of vital importance. Rubber vine degrades the biodiversity values of native habitat (Tomley 1998) and may preclude some species (Chapter 2 / Valentine 2006; Chapter 3 / Valentine *et al.* in press). Further, the pastoral industry incurs a substantial economic cost from the reduced production capability caused by rubber vine (Tomley 1998), and there is strong incentive to remove rubber vine. Fire is by far the most economical and effective tool for reducing rubber vine infestations (Grice 1997; Tomley 1998). In my study, burning reduced the amount of rubber vine, and elements of rubber vine vegetation (e.g. rubber vine towers) were visibly reduced in the repeatedly burnt sites. However, when implemented in riparian habitat that is already disturbed by grazing and introduced plants, there may be undesirable consequences of burning for rubber vine control on the faunal elements of the environment. A management approach that incorporates a variety of techniques, possibly burning to reduce the intensity of infections, followed by mechanical or chemical control, may represent a compromise between weed removal and retention of native fauna.

In this study, I showed that burning riparian habitat within two years of a fire reduces species richness and the abundance of some bird species. Frequent burning in tropical savannas can simplify habitat structure, especially in the riparian zones, and in my study, reduced the area of a plant that provides important foraging and shelter resources for birds. In areas where there is a range of disturbance impacts, including grazing and introduced plant species, frequent fires may further compound habitat simplification. The current burning paradigm is fairly variable throughout tropical savannas, but there is a tendency for human-mediated fire to occur in the mid-dry and wet seasons to reduce the likelihood of destructive, late dry season fire (Crowley & Garnett 2000; Russell-Smith *et al.* 2003b). When implementing fires, I recommend that land managers exercise caution in respect to the frequency with which they burn. Specifically, repeatedly burning within two years of a fire will have negative affects on bird diversity. Most importantly, further work is necessary to determine appropriate fire-free intervals that meet both land management and conservation objectives.

CHAPTER 7. GENERAL DISCUSSION

Natural ecosystems are subjected to human-mediated disturbances that substantially modify ecosystem processes and patterns (Vitousek *et al.* 1997; Chapin *et al.* 2000; Sala *et al.* 2000). Variations in the scale and extent of disturbances alter the environment in dissimilar ways and subsequently play a pivotal role in determining biodiversity (Sousa 1984). Thus, understanding the influences of human-mediated disturbances is important for setting appropriate management and conservation priorities. My study examined the small-scale habitat use of an invasive alien plant species, rubber vine (*Cryptostegia grandiflora*), by native lizards. I identified differences in key traits between rubber vine and native habitat that may provide potential mechanisms driving lizard habitat choice. I also examined the impact of burning in different seasons, as a management tool to control rubber vine, on native reptiles and birds. Finally, I investigated the impacts of a repeat management burn on birds in riparian habitat in grazed tropical savannas of northern Australia.

Impacts of introduced plants on reptiles

Invasive alien plant species are a major threat to native ecosystems throughout the world (Vitousek *et al.* 1997). My study is one of the first to document possible mechanisms driving avoidance of an introduced plant. Specifically, lizards were able to discriminate between native and rubber vine habitat in the field and in semi-natural enclosures, and displayed a distinct preference for native leaf litter (Chapters 2 and 3). The ability to discriminate between introduced and native vegetation provides a mechanism by which lizards may be affected by alien plant species and I identified three characteristics of rubber vine that may drive lizard habitat choice (Chapter 3). Firstly, rubber vine leaf litter piles provided a limited range of available temperatures (c.f. native habitat) and were generally cooler than either native leaf litter or the preferred temperature range of *Carlia*. Secondly, rubber vine habitat had fewer preferred prey items of *Carlia* and, instead, contained potentially unpalatable arthropods. Thirdly, the shape and colour of rubber vine leaf litter differed to lizards (and native leaf litter), offering reduced opportunities for camouflage from visual predators. Differences in these key attributes suggest that rubber vine may be unfavourable habitat for several reptiles and where rubber vine is the dominant habitat (rather than a component of the vegetation) the effects on native fauna are likely to be amplified. Given that rubber vine has the potential to spread throughout northern Australia (Kriticos *et al.* 2003), management of this invasive plant is a top priority. Understanding the impacts of rubber vine management strategies, including the use of fire, is important for appropriate management decisions.

Impacts of fire management strategies

Burning season influences faunal composition

The responses of fauna to fire management practices may be influenced by variations in fire regimes (Woinarski 1990; Saab & Powell 2005; Smucker *et al.* 2005). My results support this notion by experimentally demonstrating that burning season is indeed a significant aspect of fire regime that differentially affects birds and reptiles. Faunal responses to different burning strategies were complex depending on taxa, fire regime and time since fire. However, some common patterns were identified.

Fire-induced changes in habitats potentially alter the availability of resources including food, shelter and risk of predation (Masters 1996; Woinarski & Recher 1997; Brawn *et al.* 2001; Letnic *et al.* 2004). The short-term impact of burning in my study may have altered habitat resources in a manner favourable to some species. Regardless of burning season, single low-intensity fires initially tended to benefit several species, and resulted in an increase of overall bird abundance and the abundance of a common skink, *Carlia munda*. Many species that responded positively to fire (e.g. the skink *C. munda*, and members of the insectivorous bird feeding group) preyed on arthropods. Burning is likely to have increased the availability of some arthropods by encouraging new plant growth that subsequently attracts insects (Force 1981; Swengel 2001). The abundance of arthropods may peak in the first 12 months post-fire (Force 1981; Swengel 2001), and some taxa, including spiders, crickets, beetles and bugs may increase following fire in tropical savannas (Andersen & Muller 2000; Nicholson *et al.* 2006). Thus, the short-term increase in the abundance of some species may have been caused by a concomitant change in food resources. However, species that commonly occur in dense vegetation, such as the red-backed fairy-wren, *Malurus melanocephalus*, were notably absent from burnt sites (Chapter 5).

Both birds and reptiles are strongly influenced by habitat complexity (MacArthur & MacArthur 1961; Pianka 1989) and the fire-induced changes in vegetation cover probably reduced the longer-term availability of potential shelter sites or foraging opportunities. In stark contrast to the short-term responses, substantial differences were detected for both birds and reptiles in the longer-term, with distinct differences in the response of birds to burning season. In particular, dry season burning substantially reduced the overall abundances of reptiles and birds (Chapters 4 and 5), and created a dissimilar assemblage of birds to the wet season burnt sites (Chapter 5). Burning during the dry season is typically more intense than burning during the wet season (Braithwaite & Estbergs 1985), and may have removed elements of the habitat that ultimately disadvantaged certain species, including nectarivorous and granivorous birds. As some bird species (e.g. little friarbird, *Philemon citreogularis*) track resources throughout the landscape (Franklin & Noske 1999), low abundances of birds in the dry season burnt sites may reflect longer-term reductions in food resources, potentially caused by the higher-intensity burn (Chapter 5). Furthermore, dry season burnt sites were typically characterised by lower vegetation complexity (Chapters 4 and 5), and species that relied on vegetation cover for shelter (e.g. the gecko *Heteronotia bineoi*) were disadvantaged in the dry season burnt sites.

In contrast to studies in other habitats (Masters 1996; Taylor & Fox 2001; Letnic *et al.* 2004), a serial replacement of reptile species following burning was not evident (Chapter 4). In addition, unlike previous work in tropical savannas, reptiles did not appear resilient to the effects of fire (Trainor & Woinarski 1994; Andersen *et al.* 2005), and few species selected habitat based on burning season (c.f. Braithwaite 1987). Instead, certain litter-associated reptiles (e.g. the skink *Carlia pectoralis*) were absent from wet season burnt sites and rarely observed in dry season burnt sites (Chapter 4). Burning *per se* tended to modify resources that disadvantaged litter-associated species, although dry season burning substantially reduced reptile abundances. The lack of open-foraging species (e.g. the arid-adapted skink *Ctenotus* spp. and dragon *Diporiphora* spp.) in burnt sites is perplexing, particularly because such species were recorded in the local region, albeit in fairly low numbers. One possible explanation is that prior disturbances in the region, including grazing, drought and invasive plants, have already lowered the resilience of reptiles to additional disturbances. Thus, in areas with multiple disturbances, reptiles may be more susceptible to burning.

Repeated fires reduce bird species richness

Frequent burning predictably changes habitat structure and ultimately leads to simplification of vegetation complexity (Fox & Fox 1986; Bowman *et al.* 1988; Fensham 1990; Russell-Smith *et al.* 2003a) that has subsequent implications for fauna. In my study, repeatedly burning riparian zones within two years had a profound effect on bird assemblages (Chapter 6). Following the second fire, there was a marked reduction in bird species richness, overall bird abundance and the abundance of some feeding groups, including frugivores and insectivores. Unlike the first fire, burning a second time within two years did not offer any immediate benefit to birds *via* increased food resources (Chapter 5). Instead, the habitat was modified in a manner unfavourable to birds, and it is likely that the availability of food and shelter resources were altered in a negative way for several species (Woinarski & Recher 1997; Brawn *et al.* 2001). The reduction of a commonly occurring native shrub, currant bush (*Carissa ovata*), was strongly related to low numbers of frugivores in repeatedly burnt sites (Chapter 6). Currant bush berries provided a food source for frugivores, including the great bowerbird (*Chlamydera nuchalis*) and the low-shrubby habitat probably offered foraging opportunities and shelter for several other species (e.g. red-backed fairy-wren, *Malurus melanocephalus*). In addition, although the feeding group assemblage of burnt sites initially grouped together, following the second burn, feeding group assemblages increasingly diverged from both unburnt and singularly burnt sites. This suggests that to maintain bird assemblages similar to that of unburnt or single-burnt sites, fire-free intervals should be longer than two years.

The results of my study provide a number of important conclusions regarding fire management of riparian zones in grazed tropical savannas of northern Queensland. Firstly, patterns in faunal responses were generally consistent across habitat types, suggesting that burning influenced the riparian and adjacent woodland habitat in a similar fashion (Chapters 4, 5 and 6). Secondly, single low-moderate intensity burning may benefit some bird and reptile species in the short-term (Chapters 4 and 5), probably via increased food resources. Thirdly, if burning has a greater impact on the environment (e.g. moderate intensity dry season burning or applied frequently) bird assemblages may differ from unburnt areas and singularly low-intensity burnt areas; and several species are disadvantaged by the longer-term fire-induced changes in resources (Chapters 4, 5 and 6). Finally, I did not observe a serial replacement of species in the higher impact burnt sites, rather species were simply not associated with sites under a higher level of disturbance. My results suggest that overall bird and reptile assemblages are strongly influenced by management burning, and may not be as resilient to the impacts of fire management as previously expected (Andersen *et al.* 2005). In order to meet conservation and land management objectives, caution is therefore required when developing fire management regimes.

Fire management practices: is mosaic burning the answer?

Fire is an essential land management tool and is frequently employed by humans to modify environments (Russell-Smith *et al.* 2003b), particularly in the fire-prone tropical savannas. As some fires, particularly higher impact burns, may adversely affect components of biodiversity at a local scale (e.g. Chapters 4, 5 and 6), managers are presented with a conservation dilemma between burning for pastoral, weed or safety purposes, and meeting conservation objectives. Previous research has shown a variety of faunal responses to burning regimes, indicating that a single fire regime will not suit all species (Woinarski 1990; Trainor & Woinarski 1994; Woinarski *et al.* 1999; Letnic *et al.* 2004). Instead, ecologists have suggested that incorporating a variety of burning techniques to generate a heterogenous environment may maintain overall biodiversity at a landscape scale, while meeting conservation objectives (Russell-Smith *et al.* 1997b; Parr & Brockett 1999; Woinarski *et al.* 1999; Brockett *et al.* 2001). Theoretically, mosaic burning incorporates a variety of small-scale management burns that include both low and higher impact fires that are variable in time and space (Parr & Andersen 2006). Thus at a region scale, mosaic burning theoretically provides a diversity of habitats that will presumably support a high diversity of fauna.

The theory of mosaic burning has been supported by a variety of work that suggests many species require heterogenous environments with variable post-fire habitats (Griffiths & Christian 1996; Masters 1996; Woinarski *et al.* 1999; Letnic 2003; Pardon *et al.* 2003). In addition, burning in a variable fashion in Australia's tropical savannas may simulate traditional aboriginal fire management practices which are presumed to have created a fine-grained mosaic of habitats that enhanced biodiversity (Haynes 1985; Yibarbuk *et al.* 2001; Whitehead *et al.* 2005). As contemporary fire practices have largely erased previous fire-induced habitat mosaics (Russell-Smith *et al.* 1997b), and are associated with the decline of some species (Russell-Smith & Bowman 1992;

Franklin 1999; Woinarski *et al.* 2001), recreating variably burnt habitat is viewed as a positive step towards conservation of tropical savannas. However, adopting mosaic burning as a management policy has provided some practical challenges (see Parr & Andersen 2006), and although the concept of mosaic burning intuitively makes sense, there is little supporting empirical evidence (Parr & Andersen 2006).

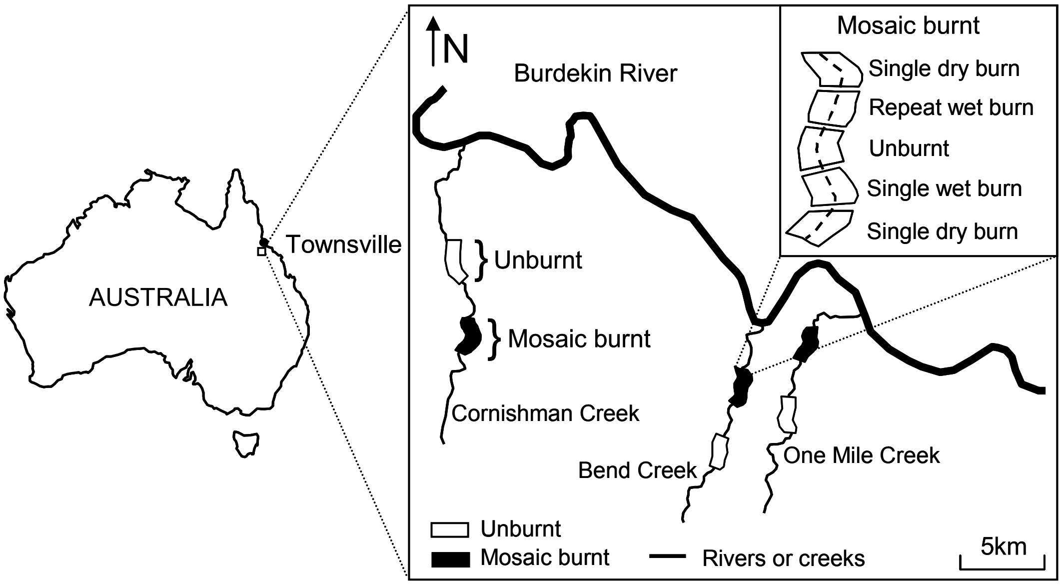

Figure 1. Map of study region. First inset shows location of study sites along tributaries of the Burdekin River, north-eastern Queensland. Mosaic burnt sites were established by CSIRO-SE. Similar sized unburnt sites are located upstream or downstream of mosaic burnt sites. Second inset shows fire treatment plots and habitat (dashed line indicates separation of habitats) along Bend Creek.

While investigating the impacts of different fire regimes on birds (Chapters 5 and 6), I had the opportunity to experimentally examine the concept of mosaic burning. As the preliminary results have important ramifications for my study (Chapters 4, 5 and 6), I present some initial findings here. At a broad scale, the experimentally burnt sites used in my study (Chapters 4, 5 and 6) are representative of a mosaic burnt area (Figure 1). My work has shown that the different fire regimes imposed alter bird assemblages at a local-scale (Chapters 5 and 6), but it is important to examine if bird assemblages vary at a broader level. I compared bird assemblages within three designated areas of mosaically burnt habitat (~ 3 km of creekline) to three similar sized areas with a fairly uniform fire history (unburnt) either upstream or downstream of the mosaically burnt sites (Figure 1). Five bird surveys were conducted in the woodland and riparian habitat within each site.

A three-factor ANOVA (SPSS, version 12) was used to examine differences in diversity (measured as species richness and evenness (E)) between fire treatments (mosaic burnt and unburnt) and habitats (riparian and woodland), using creek as a blocking factor; and non-metric multidimensional scaling (NMDS; Kruskal 1964) was used to examine assemblage composition. Species number was similar between mosaic burnt and unburnt sites (ANOVA: $F_{1,6} = 0.449$, $P > 0.05$; Figure 2a), but slightly higher in riparian habitats (ANOVA: $F_{1,6} = 7.922$, $P < 0.031$). Surprisingly, in contrast to theoretical predictions, evenness (E) was lower in the mosaic burnt sites compared to the unburnt sites (ANOVA: $F_{1,6} = 11.779$, $P = 0.014$; Figure 2b). In addition, although there were distinct differences between habitat types, the assemblage structure of mosaic burnt sites was more similar than that of unburnt (Figure 3). These results highlight two important issues, *i*) that mosaic burning may actually reduce a measures of diversity (evenness); and *ii*) that mosaic burning may homogenise bird assemblages.

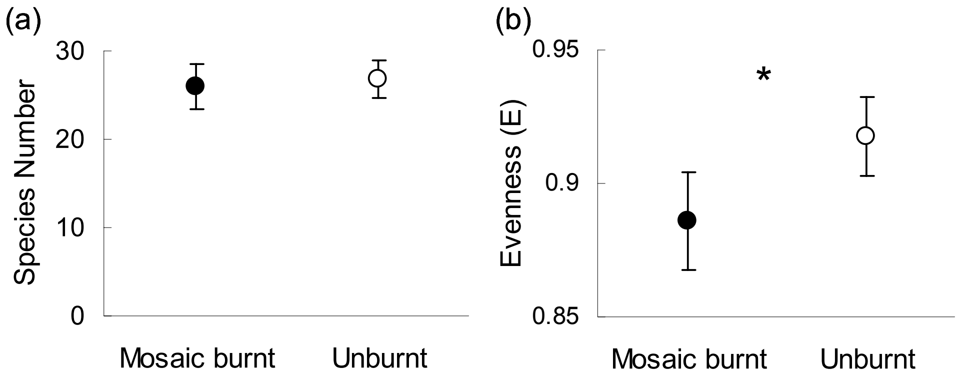

Figure 2. Mean (± 95% CI) a) species number of birds, and b) evenness measure between mosaic burnt and unburnt sites. Asterisk (*) indicates significant difference ($P < 0.05$).

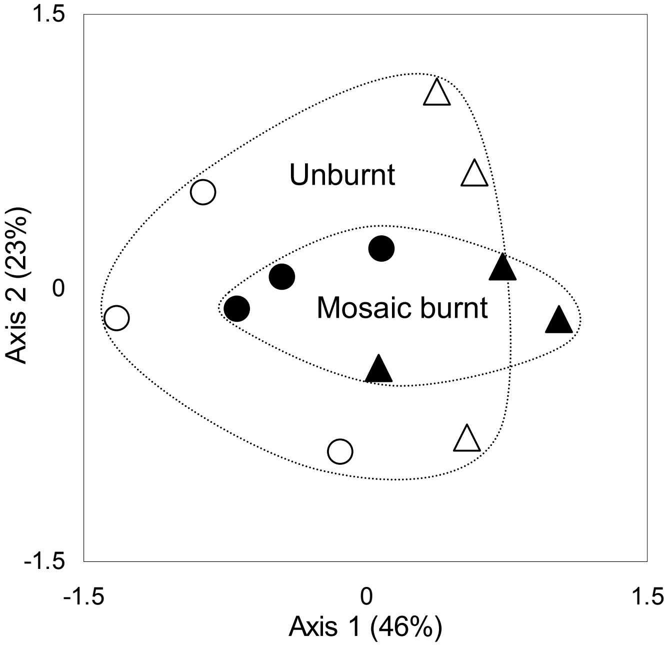

Figure 3. NMDS ordination (Sorensen distance measure) on the assemblage of birds (n = 47) at sites burnt in a variable-mosaic fashion (black) and unburnt (clear). Ordination is in three dimensions (stress = 0.07), with axis 1 and 2 plotted. Separation of sites is between riparian (circles) and woodland (triangle) habitat, however mosaic burnt sites tend to cluster together.

Theoretically, burning in a variable fashion will increase habitat heterogeneity and subsequently faunal diversity (but see Parr and Andersen 2006). However, my preliminary observations suggest that variable burning may actually homogenise assemblage structure and lower bird diversity. Not only do these preliminary findings suggest that our understanding of mosaic burning is still fairly limited, but they show that even at a broader scale, fire management strategies in riparian zones of grazed tropical savannas can alter faunal assemblages in unexpected, and perhaps undesirable ways. One distinct difference between my research and that of other studies in Australian tropical savannas (see Woinarski 1990; Trainor & Woinarski 1994; Andersen *et al.* 2005), is the extent of already-existing human-mediated disturbances. As my study occurred in landscapes already disturbed by grazing and introduced plants, the faunal responses to fire (Chapters 4, 5, 6 and 7) may be caused by cumulative disturbance impacts. Northern Queensland has a long history of human-mediated disturbances from cattle grazing and invasive plants, and these types of disturbances may independently affect birds and reptiles in tropical savannas (Braithwaite *et al.* 1989; Woinarski & Ash 2002; Kutt & Woinarski 2006; Chapters 2 and 3). Although cattle grazing occurs throughout tropical savannas, properties in northern Queensland are typically smaller with more intensive pastoral production (Russell-Smith *et al.* 2003b) and its likely that the cumulative impacts of multiple disturbances may be driving some of the longer-term faunal responses to fire (Chapters 4, 5, 6 and 7). In areas where disturbances already influence faunal assemblages, the threshold of resilience to additional disturbances may be lower, causing in a decrease in diversity when a variety of burning practices are employed.

Conservation and management implications

Introduced invasive plant species cause substantial global environment change (Vitousek *et al.* 1997), and can alter habitat resources to the detriment of native fauna (Braithwaite *et al.* 1989; Wilson & Belcher 1989; Bower *et al.* 2006; Chapters 2 and 3). Control of invasive plant species is an obvious management priority (Grice 2006; Hulme 2006; Martin & van Klinken 2006), however the process of weed removal can also unintentionally affect biodiversity (Zavaleta *et al.* 2001; Bower *et al.* 2006). To investigate this management dilemma, my study examined the impacts of rubber vine, on native fauna, and the impacts of fire management practices that may be useful for rubber vine control on native fauna. With the potential to spread throughout most of northern Australia (Kriticos *et al.* 2003), rubber vine is capable of irreversible damage to the structure and function of native ecosystems (Humphries *et al.* 1991; Tomley 1995). Rubber vine is a pervasive threat to the biodiversity values of riparian zones (Humphries *et al.* 1991; Tomley 1995; Chapters 2 and 3) and management of rubber vine is imperative. As for all invasive plants, an integrated weed management strategy should incorporate a variety of control measures (Hulme 2006). However, fire is by far the most useful, broad-scale method of controlling rubber vine (Grice 1997; Tomley 1998). Given that fire is already frequently used for land management purposes (Russell-Smith *et al.* 2003b), it is likely that rubber vine control will incorporate the use of fire in riparian areas. As my research has also shown that weed management burning may adversely affect some elements of native biodiversity (Chapters 4, 5 and 6), land managers are presented with an interesting conservation conundrum, and there is likely to be a trade-off between effective rubber vine management and conservation of native fauna. When using fire for rubber vine control, managers will need to maintain a clear perspective on management objectives, while considering the longer-term consequences of burning riparian zones.

Fire is an important influence on the environment (Whelan 1995) and this study confirms that variations in fire regimes influence wildlife responses (Woinarski 1990; Saab & Powell 2005; Smucker *et al.* 2005). Understanding the consequences of human-mediated fire is important for appropriate land management practices. Although most species in tropical savannas have evolved with fire and successfully persisted under indigenous fire regimes for at least 5 000 years (Johnson 2006), fauna are now confronted by multiple disturbances, often occurring simultaneously. The consequences of burning may be amplified by additional disturbance factors, including grazing and introduced plants. In particular, my study showed that, in grazed landscapes, the type of fire an area receives has important consequences for fauna, with both burning season and repeated burning significantly influencing faunal assemblages.

Given the variable faunal responses to fire regimes, it is not possible to set all-encompassing fire management guidelines. Instead, managers need to consider the desired objective when developing burning strategies. In particular, when burning landscapes already modified by human-mediated disturbances, management should include the retention of well-chosen minimally disturbed areas as potential refuges. From a wildlife conservation perspective, bird and reptile communities would probably benefit, in terms of maintaining high diversity at a local scale, from a reduction in the frequency of fires in grazed landscapes. In riparian and surrounding woodland areas, burning within 2-3 years of a fire will, at a minium, temporarily reduce bird diversity. Although both burning seasons negatively impacted some species, restricting burning to a single season will probably compound impacts, and varying the burning season in space and time is likely to alleviate some of these problems.

During my PhD research, I encountered numerous pastoralists with a very strong land ethic. The feeling I received from these graziers is a desire to implement pastoral management practices that also achieve conservation objectives. It is unfortunate that there are no clear wildlife-friendly fire management guidelines for grazing landscapes. In particular, pastoralists had two key fire-management questions: *i*) how often can I burn, and *ii*) how big an area should remain unburnt? If tropical ecologists can answer these two questions, there is hope for the integrity of grazed tropical savannas.

Future directions

A novel component of my research examined the impact of a weed on fauna, and identified some of the underlying mechanisms driving faunal responses to invasive plant species (Chapters 2 and 3). Further work is necessary to compare the relative importance of mechanisms driving weed habitat avoidance, and to determine if different invasive plants similarly affect faunal groups. With specific regard to rubber vine, further work is necessary to advance our understanding of the impacts of rubber vine on biodiversity, particularly on different taxonomic groups. Although I did not quantify my observations, commonly occurring bird species were often recorded using habitat (e.g. perching, alighting etc) where rubber vine was a component of the vegetation structure. However, in the mid-upper vegetation layers, where most birds were observed, rubber vine infestation was low to moderate and rubber vine occurred intermingled with native vegetation, adding to the structural complexity. Where rubber vine occurs at higher infestation levels, it is unlikely that the habitat requirements for birds (and other taxa) will be met. Quantifying faunal assemblages in areas with a gradation in levels of rubber vine infestation may enhance our understanding of the types of fauna resilient to rubber vine and identify those most at risk. As rubber vine is an insidious invasive plant, developing a comprehensive management strategy is a top priority for managers. My study also illustrates the potential negative consequences of weed management using fire (Chapters 4, 5 and 6). Understanding the consequences of weed removal is essential for appropriate management techniques and has mostly, at this stage, been over-looked.

Although our understanding of fire ecology is still inadequate, there has been a strong tradition of research on the impacts fire in a variety of environments throughout the world (e.g. Woinarski & Recher 1997; Brawn *et al.* 2001; Swengel 2001; Parr *et al.* 2004; Andersen *et al.* 2005; Barlow *et al.* 2006). Further, in fire-prone tropical savannas a number of manipulative experimental projects (including my study) have examined the impacts of burning on fauna and flora (for review see: Parr & Chown 2003; Williams *et al.* 2003b), however the majority of this research has been phenomological. To further fire ecology, it will be necessary to adopt a mechanistic approach. Several studies have identified possible causes for faunal responses to fire, namely, changes in vegetation structure or food resources (Woinarski & Recher 1997; Davis *et al.* 2000; Brawn *et al.* 2001; Chapters 4, 5 and 6) and the role these factors play in determining responses needs to be clarified. A recurring theme throughout my study was a link between faunal responses and the role of modified food resources (Chapters 4, 5 and 6). A logical next step would be to quantify how food resources change with different types of management burning. Such work could incorporate faunal behavioural observations and experimental manipulation of food resources in conjunction with fire experiments.

Considering the increasing use of management burning for conservation, understanding the influence of mosaic burning strategies on biodiversity and the practicality of its application is also important (Parr & Andersen 2006). Specifically, further research is necessary to empirically test the 'pyrodiversity begets biodiversity' paradigm (Martin & Sapsis 1992; Parr & Andersen 2006), both on and off conservation reserves. As the majority of tropical savannas are principally managed for purposes other than conservation, the cumulative impact of human-mediated disturbances needs to be examined, necessitating a multidisciplinary approach. The role of additional disturbances in shaping biodiversity is particularly important in light of human-mediated global climate change. Given that climate change predictions for tropical savannas include extended dry seasons, more intensive fires and the spread of invasive species (D'Antonio & Vitousek 1992; Goldhammer & Price 1998; Gritti *et al.* 2006), knowledge of the synergistic effects of multiple disturbances will enable better predictions of possible environmental consequences. Understanding the intricate ecology of tropical savannas, and how humans can fit into the system, is a key challenge facing scientists and conservation researchers.

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APPENDICES

Appendix 1. Reptile species list

Table 1. Reptile species captured during pit-fall trapping and active searching of fire treatments in 2001 and 2003.

Species	Common Name	2001	2003
Gekkonidae (geckos)			
Diplodactylus steindachneri	Box-pattern gecko	X	-
Diplodactylus williamsi	Spiny-tailed gecko	X	-
Gehyra catenata	Gecko	X	X
Heteronotia binoei	Bynoe's gecko	X	X
Nephrurus asper	Knob-tailed gecko	-	X
Pygopodidae (legless lizards)			
Lialis burtonis	Burton's snake-lizard	-	X
Scincidae (skinks)			
Carlia munda	Rainbow skink 1	X	X
Carlia pectoralis	Rainbow skink 2	X	X
Carlia schmeltzi	Robust rainbow skink	X	X
Cryptoblepharus plagiocephalus	Fence skink 1	X	X
Cryptoblepharus virgatus	Fence skink 2	X	X
Ctenotus robustus	Striped skink 1	X	X
Ctenotus strauchii	Striped skink 2	X	X
Ctenotus taeniolatus	Copper-tailed skink	X	X
Egernia striolata	Tree skink	-	X
Lerista orientalis	Lerista	X	X
Menetia greyii	Common dwarf skink	X	-
Menetia timlowi	Dwarf litter skink	X	X
Morethia taeniopleura	Fire-tailed skink	X	X
Notoscincus ornatus	Notoscincus	X	-
Proablepharus tenuis	Proablepharus	X	-
Species A	Unknown	X	-
Agamidae (dragons)			
Diporiphora australis	Eastern two-lined dragon	X	X
Pogona barbatus	Bearded dragon	X	-
Varanidae (goannas)			
Varanus storri	Storr's monitor	X	X

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Table 1. continued…

Species	Common Name	2001	2003
Typhlopidae (blind snakes)			
Ramphophtytops proximus	Blind nnake	X	X
Colubridae (rear-fanged/tree/water snakes)			
Tropidonophis mairii	Keelback snake	X	-
Elapidae (front-fanged snakes)			
Demansia psammophis	Yellow-faced whip snake	X	X
Furina diadema	Red-naped snake	X	-
	Total species number	26	20

Appendix 2. Bird species list

Table 1. List of bird species, sorted by feeding group, observed during surveys for Chapters 4, 5 and 6.

Species	Common Name	Chapter 4	Chapter 5	Chapter 6
Carnivore				
Aviceda subcristata	Pacific baza	X	X	X
Corvus orru	Torresian crow	X	X	X
Cracticus nigrogularis	Pied butcherbird	X	X	X
Cracticus torquatus	Grey butcherbird	X	X	X
Dacelo leachii	Blue-winged kookaburra	X	X	X
Dacelo novaeguineae	Laughing kookaburra	X	X	X
Falco berigora	Brown falcon	X	X	X
Falco peregrinus	Peregrine falcon	-	X	-
Milvus sphenurus	Whistling kite	-	X	-
Ninox novaeseelandidae	Southern boobook	-	-	X
Todiramphus macleayii	Forest kingfisher	X	X	X
Todiramphus sanctus	Sacred kingfisher	-	X	X
Frugivore				
Chlamydera nuchalis	Great bowerbird	X	X	X
Dicaeum hirundinaceum	Mistletoebird	X	X	X
Dromaius novaehollandiae	Emu	X	-	-
Eudnamys scolopacea	Koel	X	X	X
Grantiella picta	Painted honeyeater	X	-	-
Scythrops novaehollandidae	Channel-billed cuckoo	X	X	X
Specotheres viridis	Figbird	X	-	X
Granivore				
Aprosmictus erythropterus	Red-winged parrot	X	X	X
Cacatua galerita	Sulphur-crested cockatoo	X	X	X
Cacatua roseicapilla	Galah	-	X	X
Geopelia humeralis	Bar-shouldered dove	-	X	X
Geopelia striata	Peaceful dove	X	X	X
Geophaps scripta	Squatter pigeon	X	X	X
Ocyphaps lophotes	Crested pigeon	X	X	X
Phaps chalcoptera	Common bronzewing	X	X	X
Platycercus adscitus	Pale-headed rosella	X	X	X
Taeniopygia bichenovii	Double-barred finch	X	X	X
Insectivore				
Alectura lathami	Australian brush-turkey	X	X	-
Artamus cinereus	Black-faced woodswallow	X	X	-
Centropus phasianinus	Pheasant coucal	X	X	X
Chrysococcyx basalis	Horsfield's bronze-cuckoo	-	X	-
Collurincincla harmonica	Grey shrike-thrush	X	X	X
Coracina maxima	Ground cuckoo-shrike	-	X	-
Coracina novaehollandiae	Black-faced cuckoo-shrike	X	X	X
Coracina papuensis	White-bellied cuckoo-shrike	X	X	X
Coracina tenuirostris	Cicadabird	X	X	X

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Table 1. continued…

Species	Common Name	Chapter 4	Chapter 5	Chapter 6
Insectivores cont…				
Corcorax melanorhamphos	White-winged chough	X	X	-
Cuculus variolosus	Brush cuckoo	X	X	X
Daphoenositta chrysoptera	Varied sitella	X	X	X
Dicrurus bracteatus	Spangled drongo	X	X	-
Eurystomus orientalis	Dollarbird	X	X	X
Gerygone olivacea	White-throated gerygone	X	X	X
Grallina cyanoleuca	Magpie-lark	X	X	X
Gymnorhina tibicen	Australian magpie	X	X	X
Lalage sueurii	White-winged triller	-	X	X
Lichenostomus plumulus	Grey-fronted honeyeater	-	X	-
Lichenostomus virescens	Singing honeyeater	X	X	X
Malurus melanocephalus	Red-backed fairy-wren	X	X	X
Manorina flavigula	Yellow-throated miner	X	X	X
Melithreptus albogularis	White-throated honeyeater	X	X	X
Merops ornatus	Rainbow bee-eater	X	X	X
Myiagra rubecula	Leaden flycatcher	X	X	X
Oriolus sagittatus	Olive-backed oriole	X	X	X
Pachycephala rufiventris	Rufous whistler	X	X	X
Pardalotus striatus	Striated pardalote	X	X	X
Podargus papuensis	Papuan frogmouth	X	-	X
Podargus strigoides	Tawny frogmouth	-	X	-
Pomatostomus temporalis	Grey-crowned babbler	-	X	X
Rhipidura fuliginosa	Grey fantail	X	X	-
Rhipidura leucophrys	Willie wagtail	X	X	X
Smicrornis brevirostris	Weebill	X	X	X
Struthidea cinerea	Apostlebird	X	X	X
Vanellus miles	Masked lapwing	-	-	X
Nectarivore				
Entomyzon cyanotis	Blue-faced honeyeater	X	X	X
Lichenostomus flavus	Yellow honeyeater	X	X	X
Lichmera indistincta	Brown honeyeater	-	X	-
Meliphaga lewinii	Lewin's honeyeater	X	X	X
Philemon citreogularis	Little friarbird	X	X	X
Philemon corniculatus	Noisy friarbird	X	X	X
Trichoglossus haematodus	Rainbow lorikeet	X	X	X
	Total Species Number	58	66	58