Dingo (*Canis dingo*) extirpation and associated trophic restructuring as a mechanism influencing shrub encroachment in arid Australia

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Statement of Authentication

The work presented in this thesis is, to the best of my knowledge and belief, original except as acknowledged in the text. I hereby declare that I have not submitted this material, either in full or in part, for a degree at this or any other institution.

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Preface

This thesis consists of five separate data chapters which are either in review, or intended for publication in peer-reviewed academic journals. Each chapter is formatted as a stand-alone manuscript with separate references and supplementary information. Because of this, there is some repetition in content among chapters.

The majority of the concepts and ideas tested in this thesis are my own, with guidance from my supervisors Mike Letnic and Ben Moore. I conceptualised the ideas and designed the experiments used in this thesis with help from Mike Lentic. I completed all the field work with help from Anna Feit and Jennifer Grüber, and conducted all the statistical analyses with help from Mike Letnic, Mathew Crowther, and Ben Moore. I wrote all the thesis chapters presented here. Editorial comments made by Mike Letnic and Ben Moore greatly benefited the writing of this thesis. At the beginning of each thesis chapter I have listed co-authors as they would be shown in a published article and have stated their involvement in compiling each manuscript.

My thesis research was conducted with approval from the Animal Care and Ethics committee, University of Western Sydney (project number: A8904) and the Wildlife Ethics Committee, South Australian Department of Environment and Natural Resources (project number: 26/2011). This research was funded by an Australian Postgraduate Award, a University of Western Sydney ‘top-up’ scholarship, and an Ecological Society of Australia student grant awarded to Christopher Gordon. This research was also funded by Australian Research Council grants (DP110103069 and FT110100057) and a Margret Middleton Fund grant awarded to Mike Letnic.

‘Trophic effects’ (species interactions mediated through predation or consumption) and the ‘trophic cascade’ (trophic effects that propagate between trophic levels within ecosystems) are reoccurring concepts throughout this thesis. In relation to trophic effects and trophic cascades, I frequently use the terminology, ‘positive and negative effects’, to describe interaction pathways between species. I note that this terminology refers to measured or predicted directional interactions occurring between species, and not value statements which cast judgment.

A section of Australia’s dingo-proof fence in the Strzelecki Desert is shown on the cover page of this thesis. Photo supplied by Ben Moore.

Acknowledgments

I acknowledge the patience, hard work, ideas, editing, and field-work skills of Mike Letnic. This thesis would not have happened without his help.

I acknowledge the hard work and critical editing of Ben Moore. A man who knows the value of a good pun. I thank him for stepping in halfway through my candidature and getting me to the finish line.

I acknowledge all the volunteers who helped me conduct my field work. I’m glad I could give you the opportunity to sleep in a swag, eat from a mulga wood fire, get dirty, dig holes, experience remote field work away from all the ‘mod-cons’, and more than anything else, have an adventure. We always had fun, often a little too much. Special thanks go to Meg Humphreys, Peri Bolton, Ben Twist, Ben Feit, Anna Feit, Rory Pie, Dodgy Roger Scott, Freya Gordon, Jennifer Grüber, Alison Naught, Josh Shorrock and Brenton von Takach Dukai.

I acknowledge the help that the wonderful staff at the Hawkesbury Institute for the Environment at the University of Western Sydney have given me throughout my candidature. Special note must go to Gillian Wilkins, Patricia Hellier and David Harland. I also thank the Hawkesbury Institute for the Environment for their financial support, especially in regards to the use of their four-wheel drive vehicle and their satellite phone.

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Finally, I thank my beautiful wife Freya for her patience, love and support throughout the course of this thesis. And I thank her for giving me my beautiful daughter Scout….. who loves cows.

Abstract

Large mammalian carnivores can initiate trophic cascades which influence the abundance of species occupying multiple trophic levels in ecosystems. Although these ‘top predators’ often play keystone roles within ecosystems, they have been extirpated from vast areas of the Earth due to conflict with pastoralists and habitat modification. The extirpation of top predators from areas where they were once common has often resulted in ecosystem restructuring and loss of biodiversity.

Shrub encroachment is a global phenomenon characterised by increases in the density of woody plants at the expense of grasses. Although top predator extirpation and shrub encroachment co-occur in many areas of the Earth, top predator extirpation has yet to be tested as a mechanism influencing shrub encroachment.

In this thesis I explore the hypothesis that the functional extinction of Australia’s largest terrestrial predator, the dingo (*Canis dingo*), has indirectly benefited the recruitment and ultimately the abundance of encroaching shrub species in areas of the Strzelecki Desert. Specifically, I test the hypothesis that dingoes (12 – 22 kg), by suppressing the abundance of red fox (*Vulpes vulpes*; 5 – 7 kg) and feral cat (*Felis catus*; 3-6 kg) mesopredators, facilitate an increase in the abundance and consumptive impact of browsing rabbits and granivorous rodents on shrub seedlings and seeds.

Much of my research uses Australia’s dingo-proof fence as a pre-established experimental treatment. The dingo-proof fence is over 5000 km long and was constructed in the early 1900s to exclude dingoes from sheep grazing areas of New South Wales, South Australia and Queensland. The dingo-proof fence provides an ideal setting to test hypotheses regarding

dingo effects in arid Australian ecosystems because dingoes have been and remain historically rare to the south and east of the fence (‘inside’ the dingo-proof fence), but have remained common in adjoining areas to the north and west of the fence (‘outside’ the dingo-proof fence).

I introduce this thesis by reviewing when and how keystone ‘top predators’ influence the structure of ecosystems, and whether dingoes might initiate trophic cascades in arid Australian ecosystems. I also discuss mechanisms which are classically thought to mediate shrub encroachment.

In my second chapter, I ask whether trophic cascades triggered by the extirpation of dingoes could be a driver of shrub encroachment in the Strzelecki Desert. Using aerial photographs spanning 51 years I show that suppression of dingoes co-occurred with increased shrub cover. I then quantify contemporary patterns of shrub cover, shrub seedling density and mammal abundance indices, describe recent fire history, and develope structural equation models which show that dingo removal has likely facilitated shrub encroachment by relaxing processes that function as recruitment bottlenecks for shrubs via two interaction pathways: 1) predators of shrub seedlings and seeds are suppressed by irrupting populations of mesopredators in the absence of dingoes and 2) fire-induced mortality of shrub seedlings is suppressed by higher levels of grazing in the absence of dingoes.

In chapter 3, I test the hypothesis that dingoes indirectly benefit the abundance of a small ground-nesting bird, *Turnix velox,* by suppressing the abundance and predatory impact of foxes and cats. I estimated the abundance of dingoes, foxes, cats and *T. velox*, quantify herbivore grazing pressure and ground cover (grasses and forbs), and assessed the occurrence of birds remains in predator scats on either side of the dingo-proof fence. My results suggest that the strong positive association which was observed between dingoes and *T. velox* can likely be explained by the suppression of foxes by dingoes, and not by the negative influence of livestock grazing pressure on *T. velox* abundance.

In my fourth chapter, I test the hypothesis that by suppressing the abundance and predatory impact of foxes and cats, dingoes create a safer foraging environment for a rodent, *Notomys fuscus*, which can then feed less apprehensively from food patches containing post-dispersal shrub seed. By conducting giving up density trials and indexing the activity and abundance of dingoes, foxes, cats and *N. fuscus*, I demonstrate that dingoes, by suppressing the activity of cats, indirectly benefited the foraging behaviour of *N. fuscus*. By conducting experiments which manipulated the 'risk' that *N. fuscus* experienced whilst foraging, I show that *N. fuscus* foraged less apprehensively from 'risky' exposed food patches where dingoes were common and cats were rare, but foraged more apprehensively from 'risky' exposed food patches where cats were common and dingoes were rare.

In chapter 5, I propose the hypothesis that the low levels of rodent granivory previously recorded in Australian deserts are an artefact of the historical decline of rodents. I hypothesise that where extant rodent communities occur, rodent granivory can negatively impact the fate of seed and vegetation dynamics more generally. I use artificially-provided foraging trays to compare rates of removal of *Dodonaea viscosa angustissima* (hopbush) shrub seed between areas where *N. fuscus* were rare and hopbush shrubs were common, and areas where *N. fuscus* were common and hopbush shrubs were rare and found that seed take was consistently higher where *N. fuscus* were common and hopbush were rare. By excluding ants and rodents from foraging trays I show that ants removed more seed than rodents where rodents were rare but rodents removed far more seeds than ants where rodents were common. By manipulating the access that rodents had to the soil seed bank I show that hopbush seed accumulated in greater numbers where rodents were excluded than where they were allowed to enter.

In chapter 6, I test the ‘mesopredator cascade’ hypothesis proposed in chapter 2; namely that the abundance and consumptive impact of rabbit browsers and rodent granivores on shrub seedlings and seeds is suppressed by irrupting populations of mesopredators in the absence of dingoes. By comparing mammal activity and abundance indices, shrub cover and shrub seed bank accumulation, and predator diets on either side of the dingo-proof fence over a 30-month period, I show that where dingo activity was high, fox activity, hopbush cover, and hopbush seed bank accumulation were consistently low, whereas rabbit and *N. fuscus* abundance were consistently high. I also followed the fate of hopbush seedlings and manipulate the local access of rodents to hopbush seed to show that 1) hopbush seedlings survived in greater numbers where rabbits and rodents were rare rather than common, and 2) hopbush seed accumulated in greater numbers where rodents were excluded than allowed entry.

Finally, I synthesise data collated from chapter 2 – 6 to propose a novel ‘top predator extirpation’ conceptual model to account for shrub encroachment not only in arid Australia, but also in other areas of the Earth where shrub encroachment has followed top predator extirpation.

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Chapter 1: General Introduction

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Photos showing shrub cover on sand dunes located ‘inside’ the dingo-proof fence in the Strzelecki Desert. The photo was taken from a sand dune which bisected the dingo-proof fence.

Chapter 1. General introduction

Keystone species have a disproportionately large influence on the structure of ecological communities relative to their abundance (Mills et al., 1993). Through biotic processes such as predation, competition or facilitation, or through the constructive or destructive interactions they have with their environment, these species instigate indirect effect pathways which influence the abundance of species at multiple trophic levels (Power et al., 1996; Jordán, 2009). Because of this, the extinction of keystone species can result in fundamental changes to how ecosystems are structured (Delibes-Mateos et al., 2011; Estes et al., 2011).

The Australian dingo (*Canis dingo*) is a keystone species which facilitates the abundance of rodents and small ground-dwelling marsupials by suppressing the abundance and impact of smaller predators (Johnson et al., 2007; Letnic et al., 2009a; Letnic et al., 2009b). In this thesis I aim to determine if dingoes initiate ‘ecosystem-wide’ trophic cascades in the Strzelecki Desert, which indirectly influence the abundance of plants. Specifically, I aim to understand if dingoes indirectly constrain the recruitment and ultimately the abundance of shrub species which have typically increased in abundance where dingoes are historically rare. In this general introduction I review when and how keystone ‘top predators’ and small and medium-sized mammals (< 5 kg) influence the structure and functioning of ecological communities, the extent to which dingoes initiate trophic cascades within arid Australian ecosystems, and the mechanisms which are classically thought to mediate shrub encroachment. I then outline my thesis objectives and give a brief synopsis of each data chapter.

1.1 Top predators as trophic regulators

Top or apex predators such as wolves (*Canis lupus*), sharks, sea otters (*Enhydra lutris*) and leopards (*Panthera pardus*) are carnivorous species which reside at the top of their respective food webs (Schmitz et al., 2000; Ripple et al., 2014). Mammalian top predators are typically large bodied species that have relatively high metabolic demands, occur at low population densities, occupy large home-ranges, and have few if any predators (Cardillo et al., 2005; Ripple et al., 2014). Because they can initiate trophic cascades which influence the abundance of many species occurring within ecosystems, top predators are often defined as keystone species (see 1.1.1 for further discussion).

Although top predators often play keystone roles within ecosystems, they have become functionally extinct from large areas of the globe largely due to persecution by humans and habitat destruction (Prugh et al., 2009; Ripple et al., 2014). For example, of the 31 largest extant mammalian carnivores (> 15 kg body mass), 61 % are listened as threatened by the International Union for the Conservation of Nature and 77 % are undergoing population declines (Ripple et al., 2014). A large number of these species have also experienced substantial range restrictions; 17 of the 31 species exhibited average historic range declines of 47 % (Ripple et al., 2014).

Because top predators interact strongly with other species within ecosystems, it is likely that their historic declines have dramatically altered the way ecosystems function. Further, given that top predators have been functionally absent from many ecosystems for decades (e.g. wolves have been functionally absent from much of North America for over 100 years; Ripple et al., 2013) their historical declines have often preceded understanding of the interactive roles they may have once have played within ecosystems (Jackson et al., 2001). This presents problems for the diagnosis of key threatening processes affecting ecosystems because a key driver of degradation - namely the absence of functionally active top predators - has been obscured by time.

1.1.1 Top predators and trophic cascades

A trophic interaction refers to the predatory or consumptive impact that one species has upon another. A trophic cascade occurs when the predatory or consumptive impact that one species has upon another indirectly influences the abundance of species occurring at sequentially lower trophic levels (Schmitz et al., 2000; Fig. 1.1). Thus, trophic cascades are controlled by ‘top-down’ forces. A wealth of literature has revealed that top predators initiate trophic cascades within ecosystems throughout the Earth (Schmitz et al., 2000; Ripple et al., 2014). For example, Coyotes (*Canis latrans*) indirectly benefit the abundance of song birds by suppressing the abundance and predatory impact of feral cat (*Felis catus*) mesopredators (Crooks and Soule, 1999).

In addition to top-down forces, ‘bottom-up’ forces can also influence the way species interact with one another within ecosystems (Elmhagen and Rushton, 2007; Elmhagen et al., 2010). Bottom-up forces are primarily dependant on productivity (e.g. rainfall, soil productivity) which increase or decrease food available to species occupying sequentially higher trophic levels (Hunter, 1992; Polis et al., 2000; Fig. 1.1). When productivity is extremely high, trophic interactions between species are often weak because food is not limited at any trophic level (Fig. 1.1). Conversely, when productivity is extremely low, trophic interactions between species are often strong because food is limited at every trophic level (Fig. 1.1). In environments which experience varied levels of ecosystem productivity (i.e. seasonal forests, deserts which experience variable rainfall) top-down and bottom-up forces often interact with one another to influence ecosystem structure (Hunter, 1992; Elmhagen and Rushton, 2007).

Trophic cascade theory predicts that the functional extinction of top predators will positively and negatively impact the abundance of organisms occurring at sequentially lower trophic levels (Hunter, 1992). The most obvious population-level effects of top predator extirpation are increases in the abundance and consumptive impacts of herbivores and smaller mesopredators owing to decreases in predation and competition (Beschta and Ripple, 2009; Letnic et al., 2012). Increases in the abundance of these species may then instigate trophic cascades which alter the abundance of species occurring at low trophic levels. For example, many studies have shown that plant biomass decreases in response to irrupting herbivore populations following localised top predator extinction (Polis et al., 2000; Ripple et al., 2013).

Although cascading effect pathways have been identified where consumptive effects are concerned, top predators may also initiate cascading effect pathways through non-consumptive effects (Ripple and Beschta, 2004). By forcing prey and mesopredators to respond to changing risks they encounter whilst foraging, top predators initiate behavioural changes in the way prey and mesopredators exploit habitat and food resources (Laundré et al., 2001). Similar to consumptive effect pathways, these behavioural changes may then indirectly influence the abundances or behaviour of organisms occurring at lower trophic levels, and in doing so influence ecosystem structure. For example, Pacific sleeper shark (*Somniosus pacificus)* declines are thought to allow harbor seal (*Phoca vitulina richardsi)* mesoconsumers to feed in areas where they were previously at high risk of predation and where prey are relatively seal naïve (Frid et al., 2008). Although non-consumptive effect pathways have great potential to propagate between trophic levels within ecosystems, few studies have experimentally shown this to occur (Laundré et al., 2001; Ripple and Beschta, 2004).

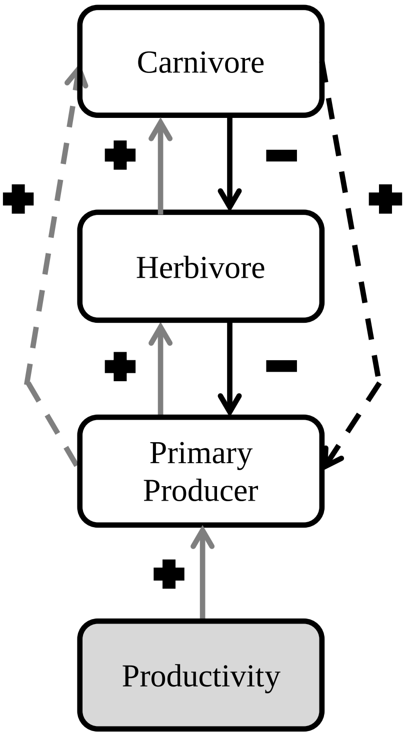

Figure 1.1. Conceptual diagram showing a simple three-level trophic cascade. Carnivores negatively impact herbivores through predation, herbivores negatively impact primary producers through herbivory, and carnivores indirectly benefit primary producers by reducing the impact of herbivores. Trophic cascades are often influenced by productivity and bottom-up forces. Increased productivity positively influences primary producers, herbivores and carnivores by increasing food availability. Black lines represent top-down forces and grey lines represent bottom-up forces. Solid lines represent direct effect pathways and dashed lines represent indirect effect pathways.

1.1.2 Mesopredator release hypothesis

The mesopredator release hypothesis predicts that reduced abundance of top predators releases smaller mesopredators from predation and competition constraints, and in doing so allows for population increases (Crooks and Soule, 1999; Prugh et al., 2009; Ritchie and Johnson, 2009). Abundant mesopredators may then negatively affect the abundance of species which fall below the weight range normally preyed on by top predators (Crooks and Soule, 1999; Johnson et al., 2007; Letnic et al., 2009b).

Trophic cascades initiated by top predator extirpation and mediated through mesopredator release pathways have resulted in losses of biodiversity and ecosystem restructure in many areas of the Earth (Ritchie and Johnson, 2009). For example, rodent species richness and diversity declines which co-occurred with increases in the density of one rodent species (*Dipodomys ordii*), have been attributed to increases in the abundance and impact of mesopredators such as badgers (*Taxidea taxus*), bobcats (*Felis rufus*), and gray foxes (*Urocyon cineroargenteus*) following coyotes (*Canis latrans*) removal in western Texas (Henke and Bryant, 1999). In islands in New Zealand, reduced breeding success of Cook's petrel (*Pterodroma cookii*) was attributed to increases in the abundance and impact of Pacific rat (*Rattus exulans*) mesopredators following feral cat (*Felis catus*) removal (Rayner et al., 2007). Reduced abundance of bay scallop (*Argopecten irradians*) was attributed to increases in the abundance and impact of cownose ray (*Rhinoptera bonasus*) mesopredators following the overfishing of large sharks along the east coast of North America (Myers et al., 2007; see Ritchie et al., 2009 for many more examples of mesopredator release). Because top predators often suppress the abundance and impact of mesopredators, their conservation has been identified as a key management priority to curb the predatory impact that mesopredators have on species occupying lower trophic levels within ecosystems (Ritchie and Johnson, 2009).

An interesting afterthought regarding the mesopredator release hypothesis is that when one top predator is lost from an ecosystem another smaller predator (a mesopredator) will ultimately fulfil this vacant ecological space, even if this species occupies a lower trophic level. For example, coyotes are thought to benefit the abundance of some rodent species in western Texas by suppressing the abundance of smaller mesopredators (Henke and Bryant, 1999). However larger wolves (*Canis lupus*), which have been functionally extinct from Texas for nearly 100 years, likely constrained the abundance of coyote before their extirpation (Ripple et al., 2013). Because of this, our perception of top predators ecological roles within ecosystems must be informed by our definition of what a top predator is and our expectation of how top predators interact with other species within ecosystems.

1.2 The dingo, Australia’s top dog

Genetic evidence suggests that dingoes (12 – 22 kg) immigrated to Australia from East Asia sometime between 3000 to 5000 years before present and are derived from domestic dogs of South-East Asia (Oskarsson et al., 2012). After arrival, the dingo soon became Australia’s largest terrestrial predator following the extinction of the Thylacine (*Thylacinus cynocephalus*) from mainland Australia (Johnson, 2006; Prowse et al., 2013). Dingoes were distributed throughout mainland Australia when Europeans arrived in 1788 (Rolls, 1969). At present, dingoes are widely distributed throughout central, north and western Australia however they are functionally absent from large areas of south-eastern and south-western Australia due to government regulated dingo-control programs; dingoes are defined as pests in many areas of Australia because dingoes kill sheep (Fig. 1.2; Allen and Sparkes, 2001; Letnic et al., 2012). Dingoes have readily hybridised with domestic dogs in southern Australia and dingo / dog hybrids dominate in some areas (Daniels and Corbett, 2003).

Dingoes are thought to play a keystone role within Australian ecosystems (Letnic et al., 2012). By suppressing the abundance of smaller red foxes (*Vulpes vulpes*), dingoes are thought to indirectly benefit the abundance of species such as rodents and small ground-dwelling marsupials which fall within the preferred prey-size range of foxes (Johnson et al., 2007; Letnic et al., 2009a; Letnic et al., 2009b; Colman et al., 2014). Further, by suppressing the abundance of large mammalian herbivores such as kangaroos, dingoes are thought to 1) increase vegetation cover by reducing grazing pressure (Macropus sp.; Letnic et al., 2009b; Colman et al., 2014), and 2) facilitate the abundance of medium-sized grazers, such as rabbits, by reducing competition within herbivore communities (Letnic et al., 2009b).

In spite of the large and ever-growing body of evidence asserting that dingoes play keystone roles in Australian ecosystems, dingoes continue to be persecuted as pests over large areas of Australia (Letnic et al., 2012; Colman et al., 2014). For example, the advent of landscape-scale 1080 poison-baiting programs in the early 1970s has increased the efficiency of dingo-control, with growing numbers of 1080 poison baits continuing to be used throughout Australia (Allen and Sparkes, 2001; Fleming et al., 2001; Northern Territory Parks and Wildlife Service, 2006). State governments also continue to spend millions of dollars each year to maintain Australia's dingo-proof fence which excludes dingoes from sheep growing areas to the south and east of the fence (Fleming et al., 2001; Agforce Queensland, 2009). Because dingoes are thought to initiate 'ecosystem-wide' trophic cascades in many areas of Australia, the persistent exclusion of dingoes from areas where they were once common may have led to an alternate stable state – an new ecosystem state resistant to reverting back to its original state over 'ecological' time scales (Beisner et al., 2003) - whereby trophic interaction within ecosystems are 'controlled' by fox and cat predation (Letnic et al., 2012). Because fox and cat predation has led to the extinction and / or functional extinction of many native species over vast areas of arid and semi-arid Australia where dingoes are now functionally extinct (and have often been so for over a century; Risbey et al., 2000; Noble et al., 2007), it is possible that these systems will never return to their previous state, even if the abundance and predatory impacts of foxes and cats are checked by human intervention. The candidature of ‘dingo free’ ecosystems dominated by fox and cat predation as Alternate Stable States will dependant on the length of time necessary for ecosystems to reach new stable states.

Although dingoes are classed as pest over large areas of Australia, they are afforded protection through state and federal law within national parks in many Australian states (Dickman and Lunney, 2001; Hytten, 2009).

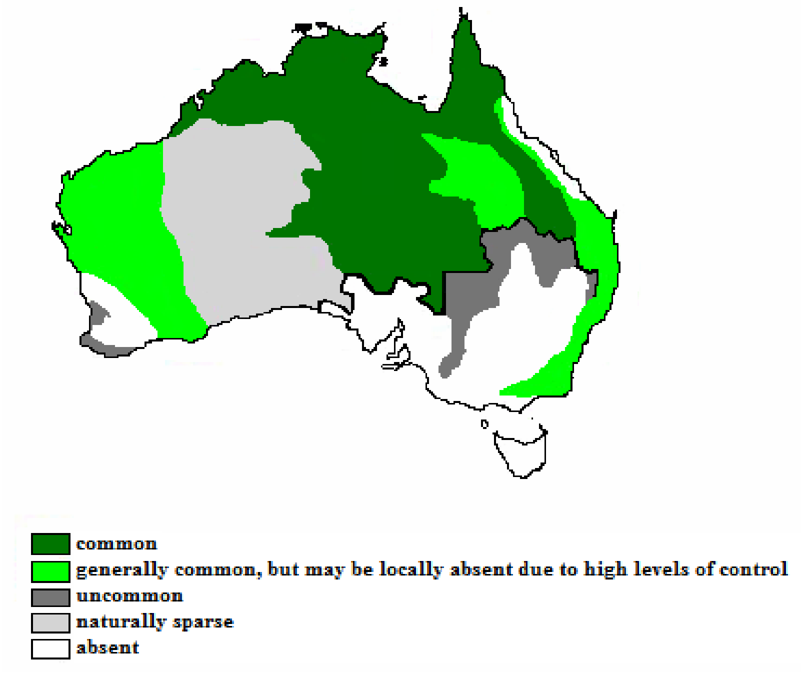

Figure 1.2. Map showing the distribution of the dingo in Australia. The black line represents the dingo-proof fence. The map was sources from Fleming et al (2001).

In relation to this thesis, it is important to note that debate exists within Australia’s scientific community regarding dingoes’ roles as trophic regulators in Australian ecosystems (Letnic et al., 2011; Fleming et al., 2012; Allen et al., 2013; Fleming et al., 2013; Johnson et al., 2014). While strong evidence supports the hypothesis that dingoes initiate trophic cascades within

Australian ecosystems by suppressing the abundance and impact of mesopredators and large herbivores (Brook et al., 2012; Kennedy et al., 2012; Letnic et al., 2012; Letnic et al., 2013; Colman et al., 2014), some researchers have challenged this idea. This group feels that dingoes role as trophic regulators has yet to be proven because: 1) many studies have used pre-existing experimental treatments rather than before-after-treatment-control type experimental treatments (Allen et al., 2013); and 2) predator abundance has typically been sampled using methods which estimate true population densities only (Hayward and Marlow, 2014). Although these authors have provided valuable suggestions which call for increased rigor of experiments used to quantify dingo effects, many of their suggestions are impracticable for the study of ‘ecosystem-wide’ trophic cascades initiated by top predators which operate at large landscape-scales (Oksanen, 2001; Letnic et al., 2011). In lieu of ‘traditional’ experimental design and sampling methods, large landscape-scale studies often rely upon spatially applicable experimental design principles and sampling methods (Oksanen, 2001; Dormann et al., 2007). For example, statistical models are often used to account for spatial and temporal confounding, which often occurs in datasets sampled at large landscape-scales (Dormann et al., 2007).

1.3 Small and medium-sized mammal (< 5 kg) effects on vegetation dynamics

Small to medium-sized mammals (< 5 kg body mass) can influence vegetation dynamics through herbivory, granivory and pollination, their diggings which facilitate increases in productivity, or the bottom-up benefits they provide for predators as prey. For example, through granivory and through their habitat mediating diggings, kangaroo rats (*Dipodomys* sp.) of the Chihuahuan Desert in North America allow for increases in vegetation and rodent diversity (Heske et al., 1993). By providing suitable habitat through their burrow systems, and by indirectly increasing food availability, North American black-tailed prairie dogs

(*Cynomys ludovicianus*) allow for increases in the diversity of smaller mammals (Cully et al., 2010). By providing a limiting food resource, plateau pikas (*Ochotona curzoniae*) of the Tibetan plateau and European rabbits (*Oryctolagus cuniculus*) of southern Europe allow for increased abundances of predatory birds (Lai and Smith, 2003; Delibes-Mateos et al., 2007).

In synergy with top predators, many smaller mammals (< 5 kg), which function as keystone species within ecosystems, have experienced large-scale population declines (Delibes-Mateos et al., 2011). The loss of these species has often altered the way species interact with one another, and in doing so has influenced the way ecosystems are structured (Delibes-Mateos et al., 2011; Davidson et al., 2012).

Australia has the severest mammal extinction record of any continent on Earth. Almost half of the 40 species known to have become extinct globally over the past 200 years have come from Australia (Short and Smith, 1994). The majority of these species have fallen within a 'critical-weight-range' between 35 – 5500 g (Johnson, 2006; Johnson and Isaac, 2009). Predation by invasive foxes and cats is thought to be the primary reason for critical-weight-range mammal declines throughout Australia (Short and Smith, 1994; Johnson, 2006). This assertion is supported by the close associations which have occurred between species extinction and historical fox and cat invasion, as well as the survival of once-abundant mainland species on fox and / or cat free offshore islands including Tasmania (Short and Smith, 1994; Johnson, 2006).

Many smaller mammals which are now extinct on mainland Australia would have once influenced the way ecosystems function through processes such as herbivory and competition, as well as through their digging habits. For example, burrowing bettongs (*Bettongia lesueur*) and Woylies (*Bettongia penicillata*) which are now extinct on the mainland but still exist on predator-free islands or in predator-free fenced areas, increase soil water retention, nutrient cycling and vegetation recruitment through their diggings (Garkaklis et al., 1998; Noble et al., 2007; Eldridge and James, 2009). Similarly, the extinction of numerous rodent species following European settlement (i.e. several species of now extinct hopping mice which likely consumed seed; *Notomys* spp.) is likely to have released plants from granivory and herbivory constraints (Morton, 1985). Because many of Australia's extinct small and medium-sized mammal species would have once constrained or facilitated the abundance of other species within ecosystems, it is conceivable that their functional extinction may be responsible, at least in part, for some of Australia's current day environmental problems (Noble et al., 2007). For example, the extinction of the burrowing bettong is thought to have allowed for increases in the abundance of encroaching woody shrubs **-** which may decrease biodiversity and ecosystem resilience (Sirami et al., 2009) **-** by releasing shrubs from herbivory constraints (Noble et al., 2007).

1.4 Shrub encroachment

Shrub encroachment, bush encroachment or woody shrub thickening is a global phenomenon characterised by an increase in the abundance of generally indigenous, medium-sized woody plants (1 – 4 m) at the expense of grasses (van Auken, 2000; D'Odorico et al., 2012). Shrub encroachment often results in the conversion of once-open grasslands or woodlands to closed woodland ecosystems. Although shrub encroachment typically occurs in arid and semi-arid rangelands, seasonal monsoonal floodplains and mesic savannas of Africa, North America, Australia (Archer et al., 1995; Fensham et al., 2005; Naito and Cairns, 2011), South America (Cabral et al., 2003), and India (Singh and Joshi, 1979), shrub encroachment may also occur in Arctic (Sturm et al., 2001), sub-Alpine (Anthelme et al., 2007) and Mediterranean (Acácio et al., 2009) climates. In Australia, shrub encroachment occurs in the northern savanna of tropical Australia; arid and semi-arid rangelands of western New South Wales, south-western Queensland, central South Australia, the Northern Territory and Western Australia; and more temperate areas of Victoria and Tasmania (Ayers et al., 2001; Fensham and Fairfax, 2002).

A unifying factor influencing shrub encroachment across a variety of ecosystems is historical land-use. This is demonstrated by numerous studies which show that factors such as ‘time since colonisation’, ‘colonial impact’, and ‘degree of land management for conservation and agriculture’ can have profound effects on the degree of shrub encroachment (van Auken, 2000; Throop and Archer, 2007; Naito and Cairns, 2011). These observations lend strong support to the idea that shrub encroachment is linked to human land-use, as does the close associations of shrub encroachment with increases in human populations.

Shrub encroachment is of particular concern because of the economic and conservation issues it poses. Shrub encroachment is of major economic concern to the livestock industry, as encroaching woody species are often unpalatable to domestic livestock, compete with nutrient-rich grass species, and reduce the total area that grasses and hence livestock can occupy (van Auken, 2000; Ayers et al., 2001; Zarovali et al., 2007). In Uganda, East Africa, the economic cost of shrub encroachment to cattle production is estimated to be a halving of cattle value from US $49 to US $23 annual profit per head of cattle in areas affected by shrub encroachment (Mugasi et al., 2000). Because of its prevalence within rangelands globally - 13 million and 220 – 330 million hectares of land was thought to be affected by shrub encroachment in South Africa by the late 1980s and North America by 2008, respectively - the impact of shrub encroachment on the pastoral industry is large (Pacala et al., 2001; Knapp et al., 2008).

As well as economic costs, shrub encroachment may also impose environmental costs on ecosystems. For example, the diversity of African dung beetles, lizards, birds, rodents, mammalian carnivores and arthropods has been shown to decrease with increasing shrub encroachment (Blaum et al., 2007; Sirami et al., 2009). Some ecosystem attributes which influence the species composition of vegetation communities, such as soil carbon and nitrogen, soil pH and grass cover, differ in concentration or abundance between shrub encroached and non-shrub encroached areas (Eldridge et al., 2011). It is also commonly believed that shrub encroachment reduces habitat heterogeneity (Sirami et al., 2009; Naito and Cairns, 2011). Although some examples do exist, comparatively few studies have quantified the ecological consequences of shrub encroachment on species composition and biodiversity when compared with the large number of studies which have focused on understanding processes causing shrub encroachment.

1.4.1 Shrub encroachment – mechanisms

Knowledge of common mechanisms leading to shrub encroachment is crucial for an understanding of how ecosystems threatened or affected by shrub encroachment can be managed for conservation and economic benefit. Although many studies have tried, no single unifying mechanism has been identified as causing shrub encroachment (van Auken, 2000; Kraaij and Ward, 2006; Van Auken, 2009; Naito and Cairns, 2011). Instead, shrub encroachment is thought to be mediated by a number of different controlling factors which operate at a site-specific scale. Below I briefly discuss the three most common processes thought to mediate shrub encroachment: livestock grazing, changes in fire regime and a global increase in atmospheric CO_2 concentrations.

Livestock grazing model for shrub encroachment

The effects of livestock grazing on shrub dynamics has received much attention in the scientific literature owing mainly to the negative effects that shrub encroachment has on pastoral productivity. The livestock grazing model predicts that overgrazing of palatable herbaceous species (grasses and forbs) by livestock releases unpalatable woody shrubs from competition with herbaceous species (Archer et al., 1995; Roques et al., 2001; Riginos, 2009). The result of continual overgrazing is an increase in the density (encroachment) of woody species and the transition of grasslands to shrublands or woodlands (van Auken, 2000; Briggs et al., 2005; Naito and Cairns, 2011).

Globally, the correlation between high stocking densities and shrub encroachment provides strong evidence that overgrazing is a factor that contributes to shrub encroachment (van Auken, 2000; Naito and Cairns, 2011). For example, in south-west USA, the introduction of heavy livestock grazing in the 1860s in semi-arid Utah coincided with a rapid increase in recruitment of ponderosa pine (*Pinus ponderosa*) until the 1930s, when stock levels were relaxed, and subsequently recruitment of woody species declined (Madany and West, 1983).

Fire-mediated model for shrub encroachment

Fire burning regime can influence vegetation succession and shrub encroachment, especially in tropical, mesic, semi-arid and arid grasslands (van Langevelde et al., 2003; Higgins et al., 2007; Lehmann et al., 2008). In areas where many small low intensity fires burn often, grasses often flourish, as ephemeral grasses grow more quickly, and have a higher fecundity than woody species (McPherson, 1995). In areas where fewer high intensity fires burn, woody shrub species may flourish, as long lived perennial species have time to establish and outcompete ephemeral grasses. In areas where the return-rate of high intensity fire is relatively high, faster-growing species dominate (ie. grass, herbs, forbs) as continued burning can kill long-lived woody shrubs (Taylor Jr et al., 2012; Twidwell et al., 2013). In a ‘natural’ state, grasslands are often typified by a mosaic of low intensity high frequency fires which encourages dominance of perennial grasses, but also allows for the establishment of woodlands in areas sheltered from fire (Bond and Keeley, 2005).

A fire-mediated hypothesis explaining shrub encroachment posits that increases in grazing pressure reduce the intensity and frequency of fires by reducing the amount of fuel, and the degree of connectivity between fuel loads (Bond and Keeley, 2005; Van Auken, 2009). Decreased fire frequency then allows for increased shrub abundance by decreasing fire related mortality of shrubs and shrub seedlings. A shift from a regime dominated by a high frequency of low intensity fires to infrequent but high intensity fires has accompanied shrub encroachment in many areas globally (White et al., 2008; Acácio et al., 2009).

Contemporary ideas relating to relationships between grazing, fire regimes and shrub encroachment have stressed the importance of integrated approaches that consider fauna, flora and the physical environment. For example, substrate and soil type often affect burning regimes, with the potential for shrub encroachment dependant on fire regime, which is in turn dependant on environmental soil gradients (Vigilante and Bowman, 2004; Levick and Rogers, 2011). Shrub, tree, and grass succession is highly dependent on the interaction between grazing and fire through a positive feedback loop relating to fuel load (grass biomass) and fire intensity (van Langevelde et al., 2003). Rainfall, and particularly rainfall patchiness (mean annual rainfall is universally low in arid and semi-arid areas however is almost always unevenly distributed throughout the landscape) results in variable soil moisture and nutrient profiles which influence shrub growth in conjunction with grazing and fire effects (Ward, 2005; Wiegand et al., 2005).

Elevated atmospheric CO_2 model for shrub encroachment

Carbon dioxide is needed by all plants in order to capture energy via C_3 or C_4 pathways of photosynthesis. In warm climates most grasses are characterised by C_4 photosynthesis, which confers a competitive advantage over C_3 photosynthesis in dry areas of high sunlight due to the quick sequestering of CO_2 and a reduction in water loss resulting from efficient stomata control (Taiz and Zeiger, 2002). Many of the world's grassland habitats are dominated by dry climate - high sunlight environments and have evolved under relatively low atmospheric CO_2 concentrations when compared to those observed today (Morgan et al., 2007). Because of this, C_4 grasses dominate in many grassland habitats globally.

Numerous authors have suggested that the 40 % increase in atmospheric CO_2 concentration which has occurred between 1750 and present (Stocker et al., 2013) has provided an evolutionary advantage for C_3 plants in many grasslands (Polley et al., 1992; Bond and Midgley, 2000; Morgan et al., 2007). This is because the photosynthetic metabolism of C_3 plants is generally more efficient in enriched CO_2 environments than that of C_4 plants (Polley et al., 1997). Improved water efficiency use (Morgan et al., 2004a) and seedlings recruitment (Morgan et al., 2004b) can also confer adaptive advantages of C_3 over C_4 plants at elevated CO_2 concentrations.

As encroaching shrub species are typically C_3 plants, it has been hypothesised that dominance of woody C_3 species over C_4 grasses is a direct result of increases in atmospheric CO_2 concentrations (Bond and Midgley, 2000; Ward, 2010). The CO_2 enrichment model is supported by correlated increases in atmospheric CO_2 and shrub encroachment over the past 200 years (Archer et al., 1995; Bond and Midgley, 2000; Archer, 2009), paleo-historical evidence of similar shifts from C_4 grass dominant communities to C_3 woody vegetation communities in the past (Cole and Monger, 1994), and manipulative studies which have demonstrated that elevated atmospheric CO_2 concentrations can mediate dominance of C_3 shrubs over C_4 grasses (Morgan et al., 2007).

Although elevated atmospheric CO_2 likely influences shrub abundance, a number of authors have contended that the overall influence that elevated atmospheric CO_2 concentration has on shrub encroachment is probably dependent upon interactions with other controlling factors such as livestock grazing, fire or geology (Archer et al., 1995; van Auken, 2000; Naito and Cairns, 2011). For example, soil type influences the aboveground net primary productivity of C_3 grasses and forbs over a gradient of atmospheric CO_2 concentrations (Fay et al., 2009).

1.5 Thesis objectives

Although top predator extirpation is often linked to human land-use, top predator extinction and resulting ecosystem restructure has yet to be assessed as a mechanism influencing shrub encroachment. In this thesis I will test the hypothesis that the functional extinction of dingoes from large areas of the Strzelecki Desert in Australia initiates an ecosystem wide trophic cascade which indirectly benefits the abundance and recruitment of encroaching shrub species (see Fig 1.3).

I have used a hypothesis testing framework throughout this thesis. Hypotheses have been derived from *a priori* knowledge of interaction pathways thought to occur between test variables based on information obtained from the scientific literature, or in some cases from pilot study research. The relatively large body of research regarding trophic cascades initiated by dingoes, drivers of vegetation recruitment, and herbivore effects on vegetation which exists for arid Australia, and particularly for the immediate study area, warranted the use of such a hypothesis testing framework here. This is not to say that other ‘less supported’ hypotheses may not also influence shrub abundance. It is however, less probable that they do so. For example, although it is possible that shrub cover increases may benefit rabbit abundance by providing suitable habitat, I could find no studies to support this hypothesis for Australian landscapes; indeed rabbits only spread across Australia after pastoralist converted forests and scrub into grazing pasture which favoured rabbits (Rolls, 1969).

The dingo-proof fence was used as a pre-defined experimental treatment throughout my study. Dingoes have been excluded from areas to the south and east of the fence since the early 1900s through baiting, trapping and shooting, whereas dingoes are common in adjoining areas to the north and west of the fence (Letnic and Dworjanyn, 2011). The dingo-proof fence provided an ideal location to test my hypotheses because encroaching shrub species are thought to be more abundant where dingoes are rare ‘inside’ the fence than where dingoes are common ‘outside’ the fence.

In chapter 2 I use aerial photographs (1948 till 1999) to show that shrub cover was twice as dense where dingoes are known to have been historically rare than historically common. I then use field data and structural equation modelling to show that decreases in the abundance and consumptive impact of browsing rabbits and granivorous rodents – resulting from increases in the abundance and predatory impacts of foxes – was the most parsimonious pathway by which dingo extirpation influenced shrub recruitment.

In chapter 3 I test the hypothesis that dingoes indirectly benefit the abundance of a small ground-nesting bird, *Turnix velox* by suppressing the abundance of fox and cat mesopredators. *Turnix velox* and predator abundance estimates, herbivore grazing pressure and ground cover (grass and forb cover) were measured on both sides of the dingo-proof fence to test this hypothesis. My results indicate that the strong positive association which was observed between dingoes and *T. velox* was likely explained by the suppressive effects of dingoes on foxes, and not by the influence of livestock grazing pressure on *T. velox* abundance.

In chapter 4 I test the hypothesis that by suppressing the abundance and predatory impact of fox and cat mesopredators, dingoes create a ‘safer’ foraging environment for a rodent, *Notomys fuscus* to feed less apprehensively from food patches containing post-dispersal shrub seed. Giving up density trials using shrub seeds, predator activity estimates, *N. fuscus* abundance estimates and a manipulative experiment were used to test this hypothesis. My results show that: cat activity was low where dingo activity was high; *N. fuscus* foraged less apprehensively and consumed more shrub seed from food patches when dingo activity was high; and *N. fuscus* foraged more apprehensively and consumed less shrub seed from food patches when cat activity was high.

Rodent granivory is commonly thought to be unimportant in influencing seed fate and vegetation assemblages in Australian deserts when compared with ant granivory or with rodent granivory in other deserts globally. In chapter 5 I test the hypothesis that the low levels of rodent granivory previously recorded in Australian deserts is an artefact of historical rodent declines. To test this hypothesis I quantified rodent abundance over a 7 year period and rodent granivory over a 2 year period, and used manipulative experiments to 1) compare the effects of rodent and ant granivory on shrub seed patches, and 2) to compare the accumulation of the shrub seed in the soil in areas where rodents were excluded and allowed entry. All experiments were conducted in areas where the rodent, *N. fuscus* was known to have been historically common and in areas where they were known to have been functionally rare. My results demonstrate that *N. fuscus* is a functionally important granivore which likely limits shrub recruitment by consuming large numbers of seed.

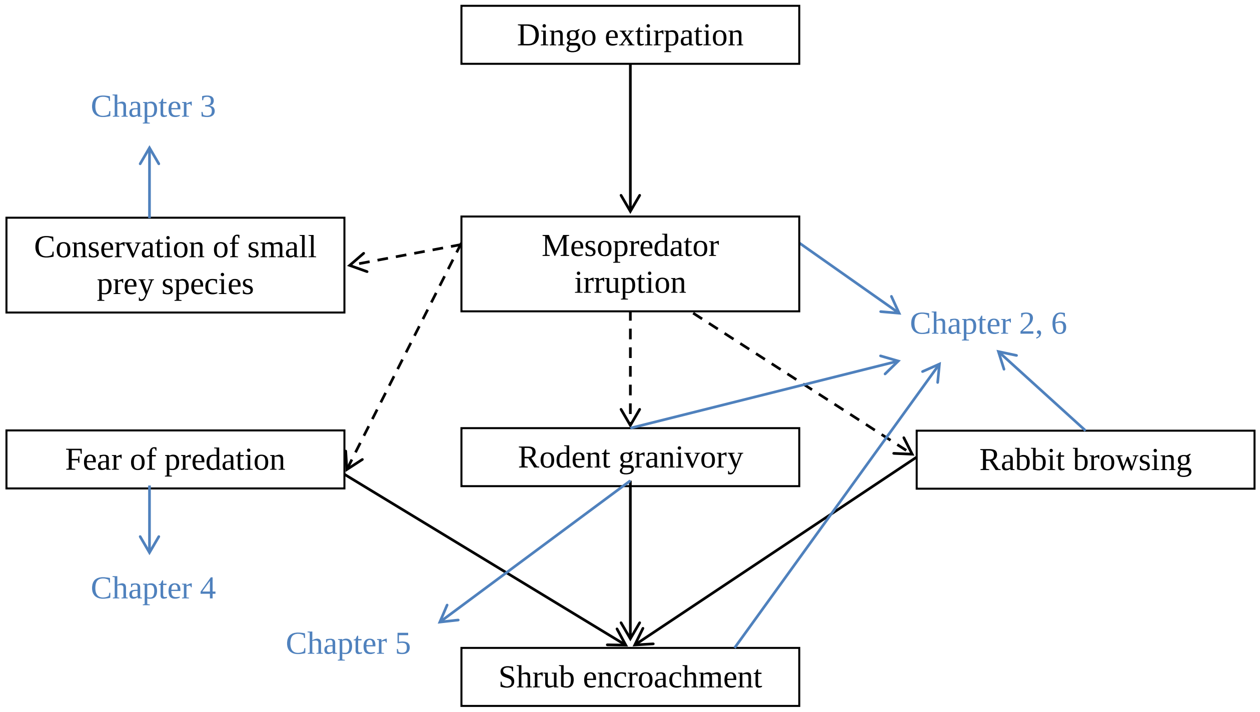

Figure 1.3 Conceptual diagram describing hypothesised interaction pathways between dingo extirpation and shrub encroachment. Black arrows indicate positive (solid lines) and negative (dashed lines) interaction pathways. Blue arrows and text indicate how the conceptual diagram relates to thesis chapters 2 - 6.

In chapter 6 I test the 'mesopredator cascade' hypothesis proposed in chapter two. I do this using abundance and activity estimates for predators, rabbits, *N. fuscus* and a common shrub (hopbush; *Dodonaea viscosa angustissima*) in areas where dingoes are known to have been historically common and historically rare, over a 30 month period. I also assess the survival of hopbush seedlings in areas where rabbits were common and rare, and experimentally manipulated the access that rodents have to hopbush seed. Collectively, my results support the ‘mesopredator cascade’ hypothesis proposed in chapter two.

Finally, in chapter 7 I draw on data collated from chapters 2 – 6 to propose a novel ‘top predator extirpation’ conceptual model which may account for increases in the abundance of shrub encroaching species not only in arid Australia, but also on other continents where shrub encroachment has followed top predator extirpation.

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Chapter 2: Shrub encroachment in an arid landscape is linked to extirpation of a top predator

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A dingo shown in a recently burnt section of the Strzelecki Desert

Chapter 2. Top predator extirpation is linked to shrub encroachment

2.1 Abstract

The abundance of woody shrubs has increased throughout Earth’s arid lands. This ‘shrub encroachment’ has been linked to livestock grazing, fire-suppression and elevated atmospheric CO_2 facilitating shrub recruitment. Extirpation of top predators is linked inextricably to pastoralism, but has not been considered as a driver of shrub encroachment. Here, we ask if trophic cascades triggered by the extirpation of Australia’s largest terrestrial predator, the dingo (*Canis dingo*) could be a driver of shrub encroachment? Using aerial-photographs spanning 51 years we show that suppression of dingoes was associated with increased shrub cover in the Strzelecki Desert, Australia. After quantifying contemporary patterns of shrub, shrub seedling and mammal abundances, and recent fire history we used structural equation modelling to compare ‘herbivore’ and ‘mesopredator’ cascade hypotheses to explain how dingoes could influence shrub recruitment. Our results support the hypothesis that top predator removal facilitates shrub encroachment by relaxing factors that function as recruitment bottlenecks for shrubs via two interaction pathways: 1) predators of shrub seeds and seedlings are suppressed by irrupting populations of mesopredators in the absence of a top predator and 2) fire induced mortality of shrub seedlings is suppressed by higher levels of grazing in the absence of a top predator. We contend that trophic cascades induced by top predator extirpation may be an overlooked driver of shrub encroachment.

Keywords: shrub encroachment, trophic cascade, keystone species, top predator, mesopredator release hypothesis, fire, environmental history

2.2 Introduction

Recent studies show that top predators play a pivotal role in the functioning of ecosystems and their importance in shaping ecological communities has been enormously underestimated (Estes et al., 2011; Ripple et al., 2014). Top predators’ suppressive, typically non-linear effects on populations of herbivores and smaller predators (mesopredators) can have cascading, indirect effects on species at lower trophic levels. The disruption to ecosystems caused by the removal of top predators, such as big cats, canids and sharks can shift ecosystems to alternate states due to over-abundant mesopredators and herbivores regulating trophic pathways (Estes et al., 2011; Ritchie et al., 2012).

Numerous studies have demonstrated the existence of trophic cascades whereby the biomass of plants palatable to herbivores is depleted in areas where top predators are absent due to an increase in herbivore abundance and impact (Terborgh et al., 2001; Beschta and Ripple, 2009). A similar cascade of effects is predicted by the mesopredator release hypothesis (MRH). According to the MRH reduced abundance of top-order predators results in an increase in the abundance and predatory impact of smaller predators (Myers et al., 2007; Ritchie and Johnson, 2009). Consequently, the prey of mesopredators may decline in abundance in the absence of top predators (Myers et al., 2007; Ritchie and Johnson, 2009).

Woody encroachment is a global phenomenon characterised by an increase in cover and density of generally indigenous woody plants at the expense of grasses, particularly in arid and semi-arid grasslands (van Auken, 2000; van Auken, 2009; Eldridge et al., 2011; D'Odorico et al., 2012). Encroachment has increased dramatically over the past century, particularly in areas with a long history of pastoral land use and shrub encroachment is largely thought of as a pastoral problem; few studies have investigated how shrub encroachment impacts biodiversity, ecosystem structuring or ecosystem attributes (Sirami et al., 2009; Eldridge et al., 2011). The drivers of encroachment are not well understood but encroachment is thought to result from complex interactions among grazing, burning, and increased concentrations of atmospheric CO_2 altering the competitive relationships between woody seedlings and grasses (Briggs et al., 2005; Kraaij and Ward, 2006; Knapp et al., 2008).

The overgrazing model for shrub encroachment posits that sustained overgrazing by livestock depletes aboveground grass biomass, reducing competition for resources between grasses and shrub seedlings and hence facilitating the recruitment of shrubs (Roques et al., 2001; Riginos, 2009). Livestock grazing also reduces fuel loads and consequently the frequency and intensity of fires which favour the dominance of grasses over shrubs (Bond and Keeley, 2005; van Auken, 2009). Thus, by suppressing fire, grazing can further promote the recruitment and survival of shrubs (Scholes and Archer, 1997). However fire may also favour shrub dominance if low intensity fire kill grasses however leave shrubs or shrub seedlings relatively untouched (D'Odorico et al., 2012).

According to the CO_2 emissions hypothesis, woody shrubs have increased in abundance because they out-compete grasses in high CO_2 environments. This is hypothesized to occur because the C_3 photosynthetic pathway used by most shrubs is more efficient at sequestering energy in high-CO_2 environments than the C_4 photosynthetic pathway utilized by most grasses in warm-climate environments (Archer et al., 1995; van Auken, 2000; Ward, 2010).

Existing models to explain woody shrub encroachment in arid lands have not considered whether vertebrate predators could play an indirect role in determining shrub abundance through their effects on consumers of shrubs. Extirpation of large mammalian carnivores is a worldwide phenomenon linked to livestock husbandry because people kill predators in order to protect livestock (Woodroffe, 2000). The removal of large carnivores has the potential to influence shrub population dynamics because it frequently results in changes in the abundance and impact of consumers and dispersers of grasses, shrubs and their seeds, such as large herbivores, burrowing herbivores and rodents (Weltzin et al., 1997; Browning and Archer, 2011; Davidson et al., 2012). In this study we ask if trophic cascades, triggered by the removal of large carnivores, could be a driver of woody ‘shrub encroachment’ in arid lands.

Specifically, we examined the effect that extirpation of a large mammalian carnivore (the dingo; *Canis dingo*) has had on woody shrubs by comparing: 1) historical woody shrub cover, and 2) contemporary recruitment of encroaching woody shrub species on either side of the dingo-proof fence in the Strzelecki Desert, Australia. Extending over 5000 km, this fence excludes dingoes from its eastern and southern sides and thus provides a rare, large-scale experiment to examine the effects that top predators have on ecosystems (Letnic et al., 2012).

To investigate the effects that different dingo management regimes on either side of the dingo-proof fence have had on woody plant abundance, we used a sequence of aerial photographs spanning 51 years to quantify historical changes in shrub abundance. Because our analyses of aerial photographs linked dingo suppression to marked increases in historical shrub cover, we then quantified contemporary patterns of mammal and shrub seedling abundance at study areas situated on either side of the dingo-proof fence, and used structural equation modelling (SEM) to compare hypotheses to explain how dingoes might influence shrub recruitment (Box 2.1).

Box 2.1. A priori hypotheses to explain how dingoes may influence the abundance of shrub seedlings.

The mesopredator cascade hypothesis: The suppression of predators of shrub seeds and seedlings by foxes in the absence of dingoes facilitates an increase in shrub density. This can potentially occur because the removal of dingoes results in an increase in fox abundance owing to reduction in direct killing and competition (Moseby et al., 2012). In turn, irrupting foxes suppress the abundances of rabbits and mice (Letnic et al., 2009). Rabbits consume shrub seedlings and mice prey on shrub seeds. Where dingoes have been removed, decreased predation on the seedlings and seeds of shrubs by rabbits and mice facilitates an increase in shrub abundance.

The herbivore cascade hypothesis: Shrub density increases in the absence of dingoes because suppression of grasses by herbivores facilitates an increase shrub density. This can potentially occur because shrub seedlings which are less palatable than grasses are released from competition with grasses owing to herbivores effects on grasses (Tiver and Andrew, 1997). High levels of grazing also suppress fire due to fuel depletion, and fire kills shrubs and shrub seedlings. The removal of dingoes exacerbates herbivores effect on grasses and fire frequency because kangaroos irrupt in the absence of dingoes and pastoralists increase their stocking rates (Letnic et al., 2009; Letnic et al., 2012). Where dingoes have been removed, decreased competition from grasses and decreased mortality of shrubs and shrub seedlings facilitates shrub recruitment.

2.3 Methods

2.3.1 Study area

The study was conducted in the region surrounding the dingo-proof fence in the Strzelecki Desert (Fig. 2.1). The dingo (15-22 kg) is Australia's largest terrestrial predator and preys primarily on mammals (Letnic et al., 2012). To prevent immigration of dingoes into New South Wales (NSW) and thus reduce their attacks on sheep (*Ovis aries*), the NSW state government constructed an approximately 2 m tall dingo-proof fence along the NSW / South Australia (SA) border and NSW / Queensland (Qld) border between 1914 and 1917 (Fig. 2.1; Letnic and Dworjanyn, 2011). The boundaries of NSW with Qld and SA were established along the meridians 29° S and 141° E, respectively (Geoscience Australia). Thus the borders are arbitrary administrative boundaries and do not reflect geographical features that may be expected to influence shrub or mammal abundance.

Dingoes are rare on the NSW (henceforth 'inside') side of the fence where intensive control using poison-baiting, trapping, and shooting have been carried out since domestic livestock grazing commenced in the second half of the 19th century (Fleming et al., 2001). Dingoes are common on the SA and Qld (henceforth 'outside') sides of the fence where they are controlled only sporadically (Letnic et al., 2009). The suppression of dingoes in western NSW has induced a trophic cascade evidenced by a marked difference in mammal assemblages across the fence. Kangaroos (*Macropus* spp.) and red foxes (*Vulpes vulpes*) are more abundant inside the fence where dingoes are rare, while rabbits (*Oryctolagus cuniculus*), rodents and grasses are more abundant outside the fence where dingoes are common (Letnic et al., 2009).

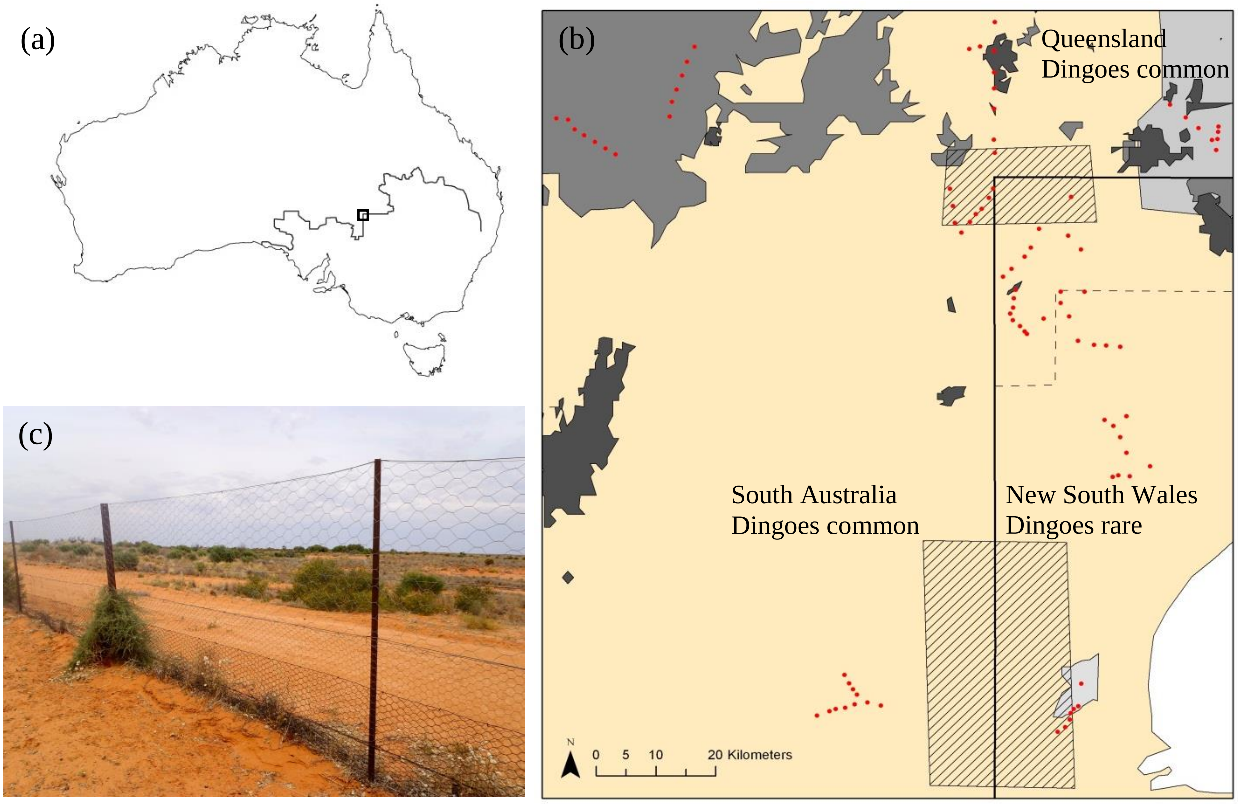

Figure 2.1. (a) Map showing the location of the dingo-proof fence (black line) and study area (square) in Australia. (b) Locations of the study areas in the Strzelecki Desert showing sites where historic shrub cover was assessed (diagonal lines within polygons; Fort Gray in the north, Hawker Gate in the south), sites where the contemporary patterns of hopbush seedling and consumer abundance were measured (red circles), and fire history for the study area was determined (light grey polygons: 1972 fires, middle light grey polygons: 1974 / 75 fires, middle dark grey polygons: 2011 fires, dark grey polygons: 2012 fires). Black lines represent the dingo-proof fence. Dashed lines represent the southern boundary of Sturt National Park which extends north to the dingo-proof fence. Shaded orange backing shows the extent of Simpson Strzelecki

Dunefields bioregion within the study region. (c) A photograph showing a section of the dingo-proof fence.

The dominant landforms in the Strzelecki Desert are longitudinal, west-east trending sand dunes reaching 8 m in height. Mean annual rainfall in the study site decreases from north to south and ranges from 188 to 227 mm (Australian Bureau of Meteorology). Vegetation on sand dunes is dominated by the perennial shrubs *Acacia ligulata*, *Acacia aneura* and *Dodonaea viscosa*, and the annual shrubs *Crotalaria eremaea* and *Crotalaria cunninghamii*. Inter-dunal swales are dominated by grasses of the genera *Aristida* and *Eragrostis*, and forbs of the genera *Sclerolaena* and *Atriplex*.

Sheep were grazed throughout the study area during the late 19th century when dingo-control was undertaken primarily by trapping and poisoning with strychnine. Following this initial period of high grazing pressure, cattle and sheep were grazed at lower densities until the erection of the dingo-proof fence between 1914 and 1917 (Letnic and Dworjanyn, 2011). Since the erection of the dingo-proof fence, and because sheep are frequently killed by dingoes, sheep grazing is now restricted to areas inside the fence, where both sheep and cattle are grazed commercially (Letnic et al., 2009). Cattle are also grazed outside the fence. A large area not subject to commercial livestock grazing, Sturt National Park, occurs inside the fence (Fig. 2.1). The park has not been grazed by livestock since 1972. Dingoes are routinely killed in and around the park and are therefore rare.

2.3.2 Historical shrub cover

We compared changes in woody shrub cover through time (hence-forth ‘shrub cover’) for areas where dingoes were historically rare (inside dingo-proof fence) and common (outside dingo-proof fence) at two separate locations, Hawker Gate to the south of the study area (2770 sample units; pastoral land) and Fort Gray to the north of the study area (2018 sample units; pastoral land outside the dingo-proof fence, conservation land inside the dingo-proof fence; Fig. 2.1). Unfortunately, no conservation reserves were located outside the dingo-proof fence within the immediate study area. Thus we were unable to quantify shrub cover in areas not subject to pastoral grazing outside the dingo-proof fence. Changes in woody shrub cover were assessed using monochromatic aerial photographs taken in 1948, 1972, 1983 and 1999 (United Photo and Graphics; see Table S2.1). Aerial photographs were digitized at 800 dpi, homogenised to a 1:50, 000 scale, and geo-referenced through a 1st order rectification in ArcGIS (version 9.3; ESRI, Redlands, CA).

To estimate shrub cover, circular sample units (100 m diameter; see Table S2.1 for replication) were overlaid onto aerial photographs at 500 m intervals (from the central point of each sample unit) in ArcGIS (see Table S2.1 for replication). We scored shrub cover as the number of shrubs visible within each sample unit. Because woody vegetation generally occurs on and around sand dunes, and to ensure that replicate points were sampled from similar habitat types, we limited our sampling to sand dune areas (> 30% coverage). Woody shrubs were recognisable from understory cover in aerial photographs (Fig. S2.1). To minimise confounding effects resulting from environmental variation, the sample units within each year were always situated within 15 km of the dingo-proof fence and within 5 km of other sample units on the same side of the dingo-proof fence.

For each sampling unit we scored the following attributes hypothesised to influence shrub abundance for inclusion as predictor variables in generalized linear models (Table S2.2): year of the photograph; distance to dingo-proof fence; distance to closest artificial watering point (AWP; a proxy for historic grazing activity); geographic coordinates; average annual rainfall in the previous 20 years; and the occurrence of fire within the last 20 years at the centroid of each sampling unit. Because historical information indicated that the intensity and efficiency of dingo-control has increased over time (Allen and Sparkes, 2001; Fleming et al., 2001) we included an interaction term between dingo-proof fence and year of photograph in our models (Table S2.2).

Maps of the distribution of AWP were created using information gleaned from historical maps held at the National Library of Australia (Canberra, Australia). Average annual rainfall within the previous 20 years was assessed using annual gridded rainfall data obtained from the Australia Bureau of Meteorology (Australian Bureau of Meteorology, 2013). Fire history maps were created for the entire sample period using aerial photographs (1948 – 1999), satellite imagery (1975 – 2012), achieve maps (State Library of New South Wales, Sydney, Australia) and on-line fire-mapping resources (www.firenorth.org.au /nafi2/).

2.3.3 Statistical analysis of historical shrub cover

Continuous predictor variables were standardized to have a mean of 0 and a standard deviation of 1. Spearman’s rank correlation was used to assess collinearity between predictor variables. If the correlation coefficient between variables exceeded 0.7, then the two variables were considered proxies and one variable was removed from analysis (Zuur, 2009). Generalized linear modelling (GLM) with a Poisson log-link function was used to assess the effects of predictor variables on shrub cover throughout the entire study area. We tested all combinations of predictor variables and ranked the fit of models based on Akaike's Information Criteria (AIC; Burnham and Anderson, 2002). Scaled coefficient strength and associated standard errors from the GLMs were used to infer predictor variable influence within the best model.

To account for spatial autocorrelation within our data set, we used autocovariate models, which estimated the degree to which the response variable at any one site reflected the response variables at surrounding sites (Dormann et al., 2007). All of our GLMs included a distance-weighted spatial autocorrelation term. The GLM models were conducted in the program R (R Development Core Team, 2013), and the spatial autocorrelation coefficient was generated using the package 'spdep' (spatial dependence; Bivand, 2011).

2.3.4 Contemporary patterns in shrub seedling and mammal abundance

We quantified the abundances of woody shrub seedlings, grasses, and mammals, and the cover of woody shrubs between May 2012 and June 2013 at 91 study sites spread on either side of the dingo-proof fence. The 1 hectare study sites were located on sand dunes and each encompassed the bottom, middle and top of the dunes. Our sampling occurred after a prolonged period of high rainfall associated with the La Niña phase of the El Niño Southern Oscillation. Previous studies have shown that shrub recruitment in arid Australia is associated with the wet climatic conditions that prevail during La Niña periods (Nicholls, 1991).

Because we were interested in identifying the effects that dingoes may have had on shrub recruitment through 'mesopredator' and 'herbivore' cascade pathways (Box 2.1), we sampled sites subject to a range of contemporary grazing and dingo-control regimes. These included sites with: sheep and cattle grazing where dingoes were rare; cattle grazing where dingoes were common; no livestock grazing where dingoes were rare; and no livestock grazing where dingoes were common (Fig. 2.1).

The density of shrub seedlings (< 30 cm height) at each site was quantified by scoring the number of seedlings on three 2 m x 100 m belt transects. The density of seedlings was calculated at each site as the number of seedlings per hectare. The canopy cover of mature shrubs (> 1 m height) was assessed at each site using a Bitterlich gauge (Friedel and Chewings, 1988). This technique produces a shrub cover estimate (within an infinite circular radius) which is proportional to shrub canopy size. Shrub cover was averaged among six evenly spaced points at each site using a Bitterlich gauge of 75 cm length, and with a 7.5 cm cross bar. *Dodonaea viscosa*, *Acacia ligulata*, *A. aneura, A. tetragonophylla*, *Hakea leucoptera*, *Casuarina pauper*, *Senna artemisioides spp.* and *S. pleurocarpa* were the dominant woody shrubs and shrub seedlings included in counts.

The abundance of grasses was quantified using a step-point method (Landsberg et al., 2003). On each site grass cover was scored on three 100 m transects at 1 m intervals, resulting in a total of 300 points per site. The grass cover of each site was calculated as the percentage of points where grass was recorded.

Indices of dingo, fox and feral cat (*Felis catus*) activity were recorded at each site using a 40 m tracking plot located on single-lane dirt roads adjacent to each site. The track plots were swept daily. The presence of dingo, fox and cat tracks was recorded for two to three consecutive nights, and an index of the activity of each predator species was calculated as the percentage of nights that each predator was recorded.

The grazing activity of kangaroos (*Macropus* spp.), rabbits (*Oryctolagus cuniculus*), and livestock (cattle, sheep and horses) at each site was quantified by scoring the presence of fresh dung (dung with a black patina) on three 2 m x 100 m belt transects. An index of grazing activity for each species was calculated as the total number of dung groups per hectare (Letnic et al., 2009). We chose dung counts over other estimators of grazing activity (ie. livestock stocking rates) as our measurement of grazing activity on our sites at the time of the study because they can be used to index recent grazing activity at the scale of our 1 hectare study sites. Although stocking rates are a precise measure of the number of livestock at the property scale, they do not provide as useful a measurement of grazing activity at the scale of our sites because grazing activity within properties is influenced by factors such as the location of AWP and natural wetlands, the uneven allocation of stock to paddocks within properties, location of fences, prevailing wind direction and location of recent fires (Landsberg et al., 2003; Letnic, 2004).

Previous studies suggest that grazing activity can influence fire regimes by depleting fuel loads, and thereby influence the survival and recruitment of shrubs (Scholes and Archer, 1997). Because our study was undertaken in 2011 and 2012 we could not use dung counts to determine if grazing activity was linked to fires which occurred prior to our study, between 2010 and 2011. Instead we used property-scale records of livestock numbers, obtained from land-managers, divided by the area of each property as an index of livestock grazing activity (sheep and cattle per km^2) for the 2010 financial year (before the 2011 and 2012 fires). Prior to analysis stocking records were converted to Dry Sheep Equivalents (DSE) to account for differences in the *per capita* consumption of fodder by sheep and cattle. We calculated one sheep as equalling one DSE and one cow as equalling six DSE (www.dpi.nsw.gov.au). The livestock grazing 2010 index used in our SEM model was calculated as the sum of sheep and cattle DSE values per km^2 for each study property.

We used live-trapping to index the abundance of granivorious mice (*Notomys fuscus*, *Pseudomys hermannsburgensis* and *P. desertor*). Trapping was conducted at each site using 20 box traps baited with peanut butter, oats and golden syrup. Traps were placed in four rows spaced 20 m apart with the traps in each row spaced 20 m apart. Sites were trapped for two or three consecutive nights. Bait was replenished daily. To prevent double counting, trapped mice were given a unique mark with a marker pen. Total mouse abundance was calculated as the number of unique individuals captured per 100 trap nights.

We used foraging trays to experimentally test if mice readily consumed seed of the dominant encroaching shrub species within the study area, *Dodonaea viscosa angustissima*. Five plastic bowls (15 cm diameter, 5 cm depth) filled with sand were buried flush with the ground on dune tops at 76 of the 91 study sites. Forty *D. viscosa angustissima* seeds (2 mm diameter) were then mixed through the sand matrix. The number of seeds eaten from each tray was recorded each night for two or three consecutive nights. Seed in the trays was replenished daily. To identify which mouse species were consuming the seeds, we placed a portable trail camera (ScoutGuard, SG560-8M) on 26 of the 76 sites. Cameras were placed on 20 cm high platforms at a distance of 3 m from foraging trays. Feeding rodents were identified using 30 s film fragments.

Previous studies have linked episodes of shrub recruitment to sustained periods of high rainfall associated with the La Niña phase of ENSO (Nicholls, 1991). Our study was conducted following a sustained period of high rainfall associated with the La Niña event of 2010 / 2011 (Australian Bureau of Meteorology, 2012). We calculated an index of the rainfall received at each study site during the recent La Niña event by summing the estimated amount of rainfall received between January 2010 and the month during which each experimental site was sampled, using the Australian Bureau of Meteorology’s monthly gridded database (5 x 5 km grid resolution; Australian Bureau of Meteorology, 2013).

The presence of fire since 2010 and the occurrence of historical fires were quantified using historic fire maps (*Historic shrub cover* section; Fig. 2.1). Information regarding dingo-control at each site was obtained from landholders. The intensity of dingo-control was treated as an ordinal variable where: areas inside the dingo-proof fence subject to poisoning, exclusion by the dingo-proof fence and shooting were allocated a value of 3; areas outside dingo-proof fence where dingo baiting and shooting occurred were allocated a value of 2; and areas outside the dingo-proof fence where no dingo baiting occurred were allocated a value of 1.

2.3.5 Statistical analysis of contemporary patterns in shrub seedling and mammal abundance

Piecewise structural equation modelling (SEM; Grace et al., 2012) was used to test hypotheses explaining how dingoes might influence shrub recruitment (Box 2.1, Fig. 2.2). SEM uses correlative data and *a priori* knowledge of biologically relevant interactions to infer causal relationships between test variables. As opposed to classical SEM approaches which use a co-variance matrix to determine a global estimator, piecewise SEM uses localised estimators allows the use of different statistical tests throughout the SEM (Grace et al., 2012). Piecewise SEM approaches are particularly relevant for data which pose problems for classical SEM analyses. For example, count data which are not easily normalised or data which incorporate spatial dependency into local estimators (Pasanen-Mortensen et al., 2013).

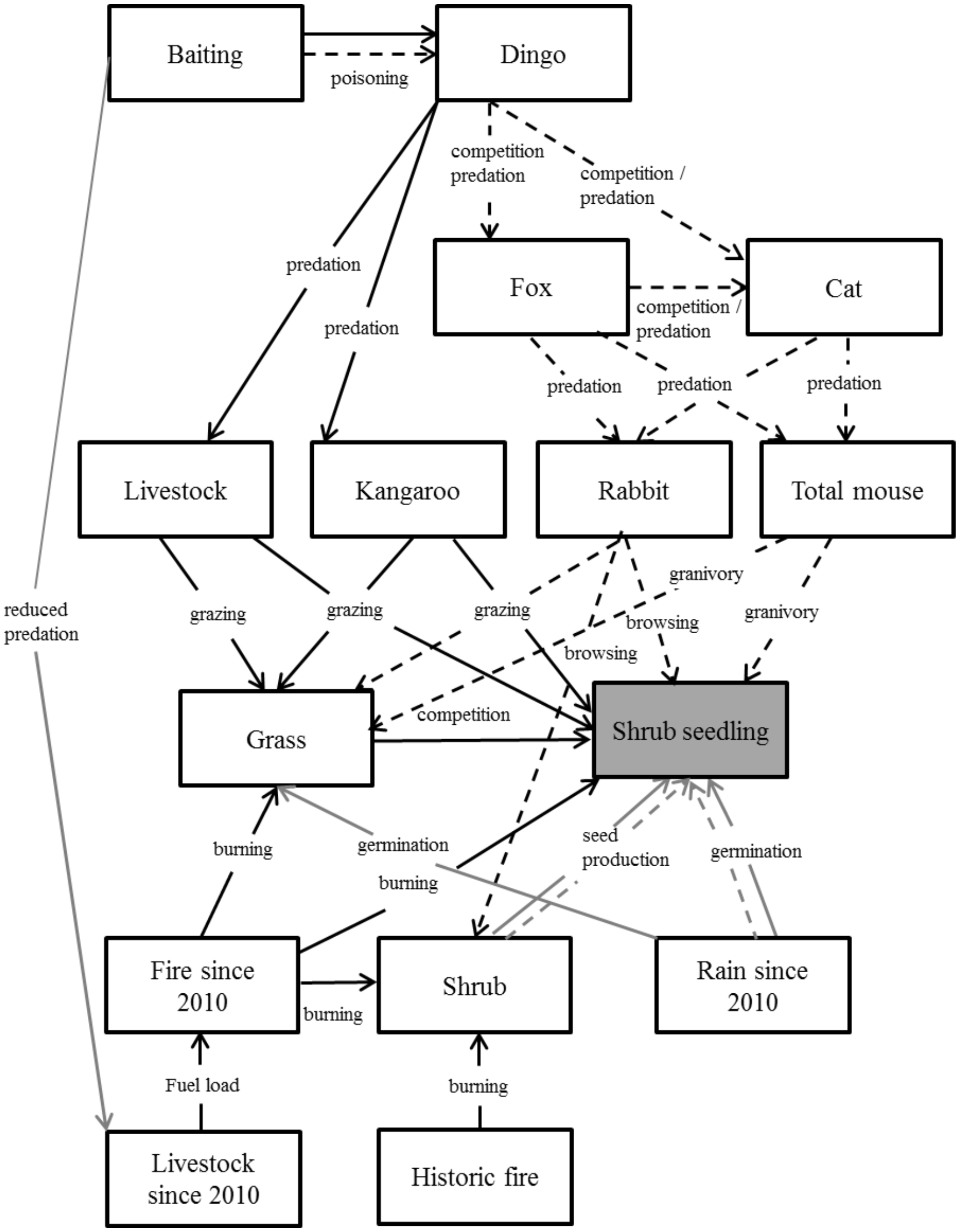

Figure 2.2. The a priori structural equation model describing interaction pathways through which dingoes were predicted to influence shrub seedling recruitment. Dashed lines represent the mesopredator cascade hypothesis and solid lines represent the herbivore cascade hypothesis, respectively (as described in Box 2.1). Text bisecting or lying below arrows describe

hypothesised causal effects. Black lines represent predicted negative effects, grey lines represent predicted positive effects.

We created an *a priori* SEM model (Fig. 2.2) describing the expected relationships between test variables based on previous research in the area, and on our mesopredator cascade and herbivore cascade hypotheses (Box 2.1). In addition to pathways described in Box 2.1, rabbits and rodent were predicted to negatively affect the abundance of grasses due to granivory and grazing effects; adult shrubs were predicted to positively affect the recruitment of shrub seedlings due to nursery effects (Cunningham et al., 1992); fire since 2010 was expected to negatively affect shrubs and shrub seedlings due to burning; historic fire was expected to negatively affect adult shrubs due to burning; and rain since 2010 was expected to positively affect shrub seedlings because seedlings often recruit after episodic periods of high rainfall (Nicholls, 1991). Because livestock and kangaroos may episodically graze some shrub seedlings or may kill seedlings through trampling, livestock and kangaroos were expected to negatively affect shrub seedlings. We did not construct causal pathways between dingoes and rabbits and dingoes and mice because previous studies and preliminary analyses revealed strong positive correlations between these variables (Letnic et al., 2009). Similarly, we did not construct positive effects pathways between shrubs and rodents and shrubs and rabbits as we could find no studies which suggested that shrubs positively influence rabbit and rodent abundances by providing shelter and habitat. Contemporary grazing regime (ie. pastoral area or conservation reserve) was not included as a fixed factor in our SEM analysis.

Quasi-Poisson and negative binomial (log link function) generalized linear models (GLM) were used to calculate local estimators within our SEM analysis. A number of test variables showed almost mutually exclusive relationships with one another, and because of this, quasi-Poisson and negative binomial models did not adequately detect relationships between test variables (i.e. variation within one test variable only occurred at sites where the other was absent). For example, kangaroos were present but rarely observed where dingoes were present and their abundance shows a strong non-linear relationship with dingo activity (here and Letnic and Crowther, 2013). In these cases binomial presence / absence GLM's were used. We used backward step-wise model reduction to simplify models, where non-significant explanatory variables were sequentially excluded from analysis until all variables in an analysis were significant (Grace, 2006; Pasanen-Mortensen et al., 2013). Standardised path coefficient estimates and deviance explained (d.e) were then calculated for variables in the most parsimonious models (Grace et al., 2012; Pasanen-Mortensen et al., 2013).

2.4 Results

2.4.1 Historical shrub cover

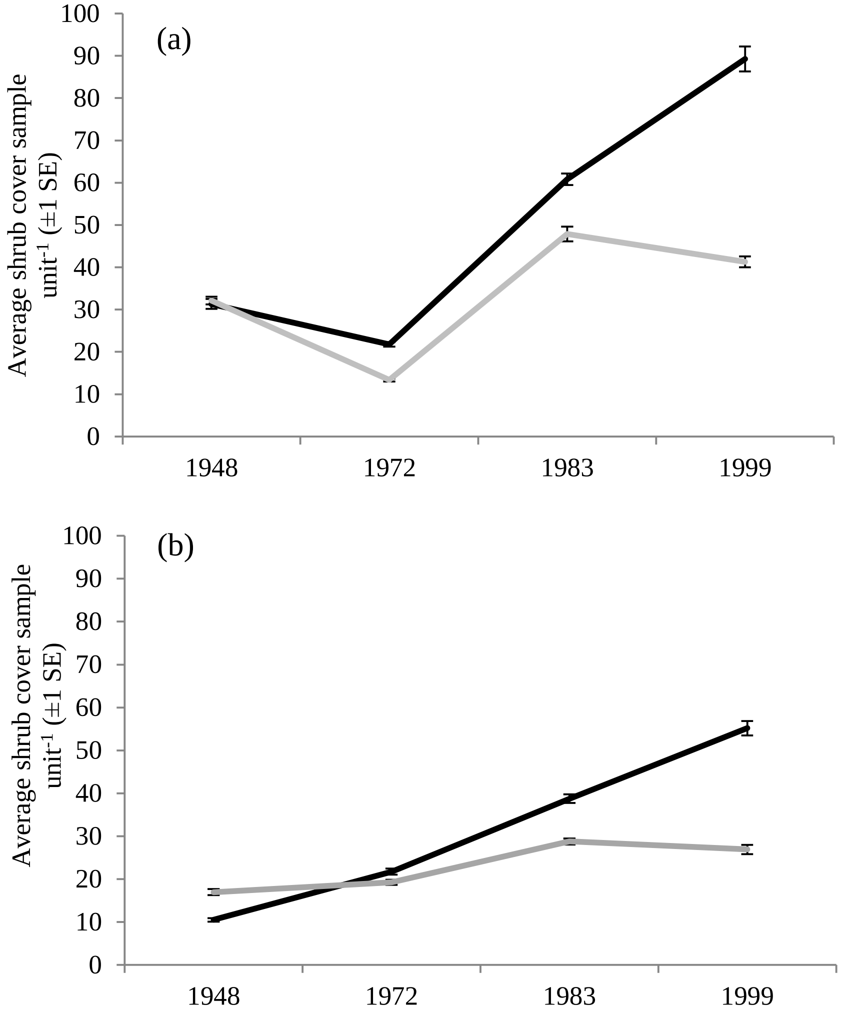

Figure 2.3. Average shrub cover (± SE) within 100 m diameter sample units at (a) Fort Gray and (b) Hawker Gate during 1948, 1972, 1983, 1999. Black lines indicate areas with low dingo abundance located inside the dingo-proof fence, grey lines indicate area with high dingo abundance areas located outside the dingo-proof fence. Shrub cover was quantified at sites used

for pastoral grazing and as conservation reserves inside the dingo proof fence but only pastoral grazing outside the dingo proof fence.

Shrub cover increased from 1948 to 1999 on both sides of the dingo-proof fence, but after 1972 the rate of increase was greater in areas without dingoes (Fig. 2.3). On average, shrub cover increased by 33 % on pastoral sites inside the dingo-proof fence, by 7 % on pastoral sites outside the dingo-proof fence in the southern Hawker Gate region, by 89 % on conservation reserve sites inside the dingo-proof fence and by 41 % on pastoral sites outside the dingo-proof fence at the northern Fort Gray region. Shrub cover was consistently higher at the more northern Fort Gray region than the southern Hawker Gate region (Fig. 2.3).

The GLM which best explained shrub cover (w_i= 0.574; Fig. 2.4 & Table S2.3) contained all predictor variables excluding fire in the previous 20 years. Year was the most important determinant of shrub cover followed by the interaction between year and dingo abundance, the spatial autocorrelation term, latitude and rainfall, respectively (Fig. 2.4). The effect of distance to water, a correlate of grazing activity by livestock (Landsberg et al., 2003), was smaller than that of all other predictor variables except for distance to fence.

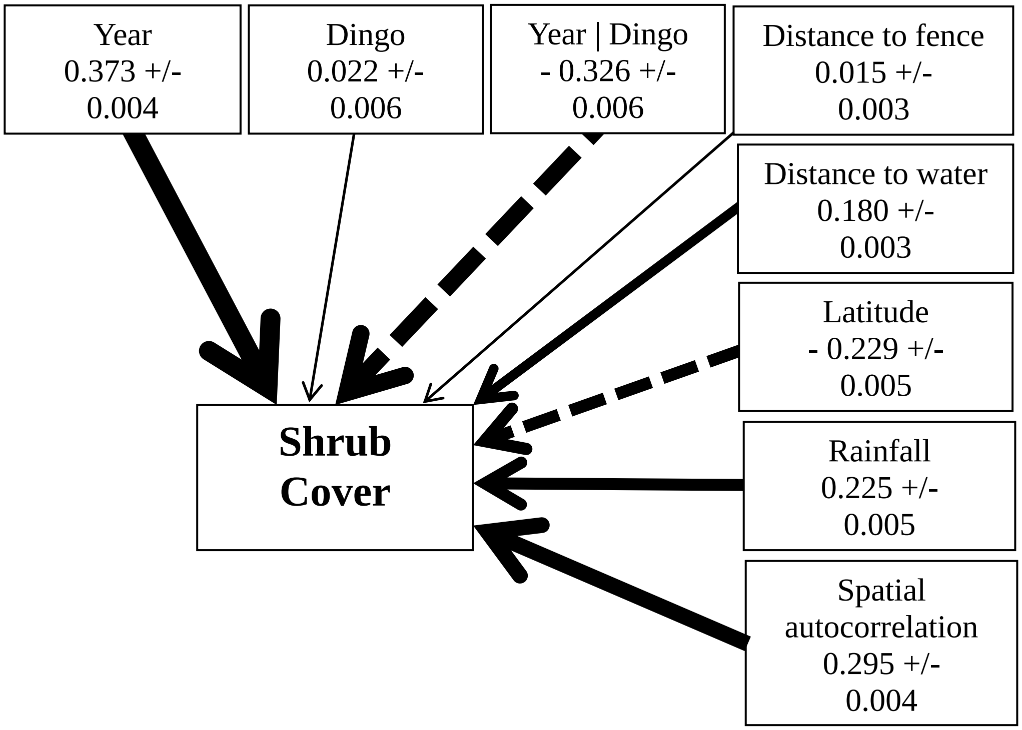

Figure 2.4. Path diagram showing parameter estimates (± SE) for standardized predictor variables included in the most parsimonious generalized linear model based on AIC value. Solid lines indicate positive effects on shrub cover, dashed lines indicate negative effects on shrub cover. Line width is weighted by the magnitude of the coefficient estimate.

2.4.2 Contemporary patterns in shrub seedling and mammal abundance

The mesopredator cascade hypothesis (Box 2.1) best explained shrub seedling abundance (Fig. 2.5). This is because rabbits (correlation coefficient: -0.13), rodents (correlation coefficient: -0.12) and shrubs (correlation coefficient: 0.35) mediated through foxes cumulatively explained more of the variance in shrub seedling abundance than fire (correlation coefficient: -0.15) mediated through livestock grazing. Plots of untransformed data revealed non-linear, negative relationships between the variable-pairs that comprised the mesopredator cascade hypothesis pathway (Fig. 2.6).

In accordance with the mesopredator cascade hypothesis, the SEM model revealed that dingo baiting was correlated negatively with dingo activity, and that dingo activity was correlated negatively with fox and cat activity. Thus, high levels of dingo baiting had an indirect positive effect on the activity of foxes and cats. In turn, fox activity was correlated negatively with rabbit grazing pressure and mouse abundance. Rabbit grazing pressure and mouse abundance were correlated negatively with shrub seedling density. Rabbit grazing pressure was correlated negatively with shrub abundance shrub cover. Thus, fox activity had an indirect positive effect on shrub seedling abundance. Further, because dingo activity was correlated negatively with fox activity, dingoes had an indirect negative effect on shrub seedling abundance.

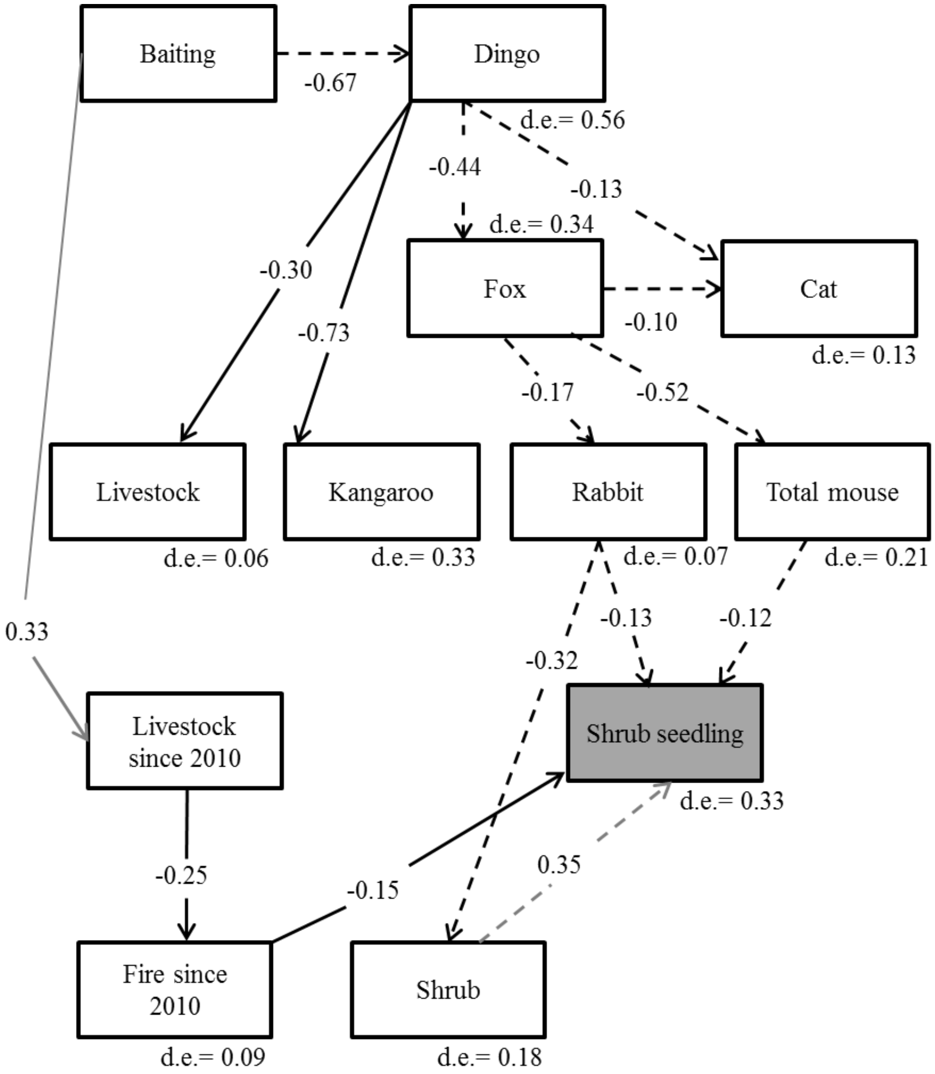

Figure 2.5. The most parsimonious structural equation model to explain the abundance of shrub seedlings. Numbers bisecting or lying below arrows show standardized path coefficient estimates and deviance explained (d.e.) is shown above or below endogenous variables.

Although the herbivore cascade hypothesis (Box 2.1) was not as well supported as the mesopredator release pathway in our most parsimonious SEM, significant effects of fire on shrub seedlings arising from human control of dingoes through baiting and dingoes suppressive effects on herbivores were supported by the model (Figs. 2.5 and 2.6). Dingo-control was correlated negatively with dingo activity. Dingo activity was correlated negatively with livestock grazing and kangaroo grazing activity. The intensity of dingo-control was correlated positively with livestock activity in 2010. In turn, livestock grazing activity in 2010 was correlated negatively with the occurrence of fire since 2010, and fire since 2010 was correlated negatively with shrub seedling abundance (Figs. 2.5 and 2.6). Thus dingo-control had an indirect positive effect on shrub seedling abundance mediated by livestock grazing activity 2010 and fire occurrence.

2.4.3 Seed trays

Mouse abundance was positively correlated with the number of seeds taken from foraging trays (linear regression: $y = 0.027\ x + 7.772$, r^2: 0.445, $F_{1,73} = 58.48$, $P < 0.001$; Fig. S2.2). Trail cameras showed that *Notomys fuscus* was the only mouse to consume seed from foraging trays and that *N. fuscus* readily consumed seed (seed was consumed on 43 of the 53 sampling nights).

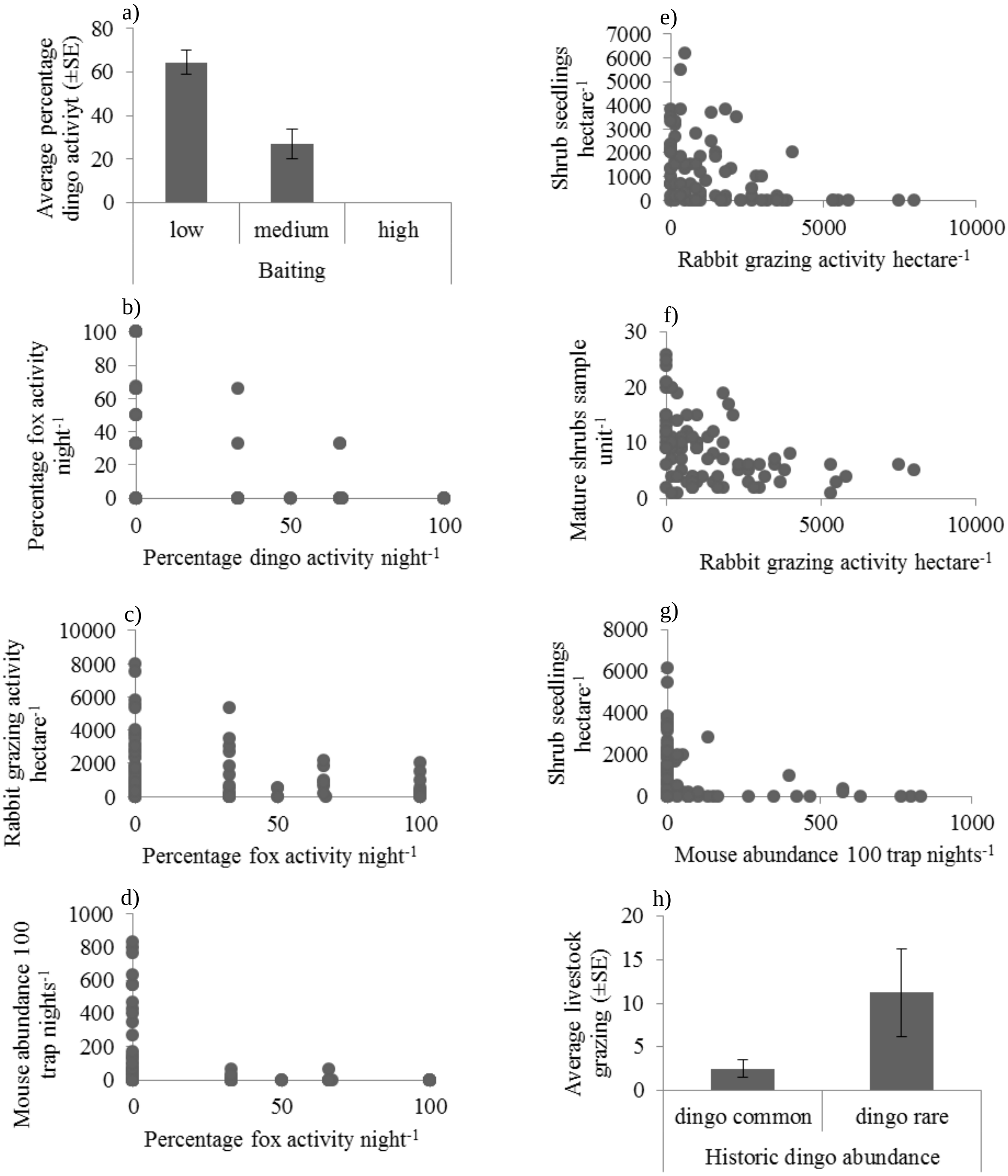

Figure 2.6. Graphs (untransformed data) showing important interactions identified in the most parsimonious structural equation model (Fig. 2.5). Bi-plots are shown for (b) dingo activity vs red fox activity, (c) red fox activity vs rabbit grazing activity, (d) red fox activity vs mouse

abundance, (e) rabbit grazing activity vs shrub seedling density, (f) rabbit grazing activity vs shrub abundance, and (g) mouse abundance vs shrub seedling density. Column graphs (± SE) are shown for (a) average dingo activity for sites at low medium and high levels of baiting, and (h) average livestock grazing activity (dry sheep equivalence) during 2010 for sites where dingoes were common and rare.

2.5 Discussion

Our results provide evidence linking the suppression of a top predator to the historical encroachment of woody shrubs (Figs. 2.3 and 2.4). Although there was a general increase in shrub abundance over time on both sides of the dingo-proof fence, the increase in shrub cover was greater at locations where dingoes were rare. Our analysis of contemporary patterns of consumer abundances and vegetation revealed strong non-linear relationships between the abundances of dingoes, foxes, predators of shrubs, seeds and shrub seedlings that accord with our mesopredator cascade hypothesis (Figs. 2.5 and 2.6). Our results also lend support for the hypothesis that dingo suppression, by facilitating increases in livestock grazing, has positive effects on shrub seedling density by suppressing the occurrence of fire. Viewed collectively, our results are consistent with the hypothesis that shrub encroachment within our study area results from trophic cascades induced by the suppression of a top predator.

2.5.1 General changes in historic shrub cover through time

The general increase in shrub cover, both in areas where dingoes were common (outside fence) and rare (inside fence), is consistent with the CO_2-enrichment hypothesis for shrub encroachment

(Briggs et al., 2005). However, the CO_2-enrichment hypothesis cannot explain the divergent trends in shrub abundance between areas where dingoes were common and rare. This is because CO_2 levels would have been similar on each side of the dingo-proof fence through time.

Another plausible explanation for the general increase in shrub abundance through time on both sides of the dingo-proof fence is the reduced impact of rabbits as regulators of shrub recruitment following the introduction of the biological control agent myxomatosis in the early 1950s. Studies conducted since the introduction of myxomatosis have demonstrated that rabbits can suppress the regeneration of shrubs and trees by browsing on seedlings (Auld, 1995; Booth et al., 1996). Following the release of myxomatosis rabbit numbers crashed throughout Australia (Ratcliffe et al., 1952) and their influence on shrub and tree recruitment is thought to have been diminished (Crisp and Lange, 1976). The effect of rabbits on shrub recruitment in the Strzelecki Desert may have been greater, both now and in the past, in areas where there are dingoes because dingoes facilitate higher numbers of rabbits (Newsome et al., 2001; Letnic et al., 2009).

2.5.2 A mesopredator release cascade hypothesis for shrub encroachment in arid Australia

According to our structural equation modelling, the most parsimonious explanation for the observed pattern of shrub seedling abundance at the time of our study is that in the presence of dingoes, browsing of shrubs by rabbits, and predation of shrub seedlings and shrub seeds by rabbits and rodents imposes a recruitment bottleneck on shrubs. Conversely, in the absence of dingoes this recruitment bottleneck no longer exists because rabbit and rodent abundances are suppressed by high numbers of foxes, owing to the release of foxes from direct killing and competition with dingoes.

While caution is required when interpreting correlative data, our mesopredator cascade hypothesis for shrub encroachment is well supported by previous studies and data collected in this study which demonstrate: 1) that rabbits, which are consistently more abundant in the presence of dingoes (Newsome et al., 2001; Letnic et al., 2009) can suppress the recruitment of shrubs and trees in arid Australia by eating seedlings (Auld, 1995; Booth et al., 1996) and 2) that mice (including *Notomys fuscus*) which are consistently more abundant in the presence of dingoes during periods of both wet and dry climatic conditions (Letnic and Dworjanyn, 2011), are important consumers of shrub seeds. Moreover, our field sampling for consumer, shrub seedling and shrub abundance occurred following one of the strongest La Niña events recorded in Australia during the last 100 years, and thus, represented an optimal recruitment period for shrubs (Nicholls, 1991). Rodent and rabbit populations typically irrupt following La Niña driven rainfall events in arid Australia (Letnic et al., 2005). Thus we propose that high levels of browsing and granivory by rabbits and rodents, facilitated by the presence of dingoes, could limit shrub recruitment in the wake of periodic La Niña events.

Although the dingo-proof fence was constructed between 1914 and 1917, the cover of shrubs on either side of the fence measured from aerial photographs was not markedly different in 1948 or 1972, but began to diverge after 1972. Because government and local pastoral records showed that sheep and cattle were similarly abundant between 1940 and 1980 both inside and outside the dingo-proof fence (Fig. S2.3), it is unlikely that these divergent trends were caused by increases in livestock grazing. The divergent trends in historic shrub cover either side of the dingo-proof fence could be due to increased efficiency of dingo-control in NSW resulting from the introduction of the poison sodium fluoroacetate (“1080”) in the late 1960s, coupled with improvements in the effectiveness of the dingo-proof fence resulting in fewer incursions of dingoes into western NSW (Fleming et al., 2001). Dingo-control, primarily using meat baits impregnated with 1080, is conducted extensively in western NSW but less intensively in adjoining areas in Queensland and South Australia, where dingoes remain relatively common. Prior to the use of 1080, dingoes occurred at higher numbers than they do now in western NSW (Fleming et al., 2001), and although controlled by trapping, shooting, poisoning and exclusion by the dingo-proof fence, they may have been sufficiently abundant to suppress fox populations.

Improvements in the efficiency of dingo-control through time is evidenced in the study region and elsewhere in Australia by the reduction in dingo bounty payments paid following the introduction of 1080 (Allen and Sparkes, 2001). Although bounty payments are not a particularly sensitive index of dingo abundance, the sharp decrease in bounties paid following the introduction of 1080 across Australia is thought to reflect a dramatic decrease in dingo abundance (Allen and Sparkes, 2001). Thus, if our hypothesis is correct, a reduction in the influence of dingoes on mammalian assemblages and therefore increases in shrub populations in western NSW (inside the fence) could be expected following the introduction of 1080.

Prior to the introduction of rabbits, similarly sized herbivorous marsupials such as the burrowing bettong (*Bettongia lesueur*), hare-wallabies (*Lagorchestes spp.*) and nail-tail wallabies (*Onychogalea spp.*) likely fulfilled a similar ecological function (Noble et al., 2007). Marsupials within this size range have disappeared from most of arid mainland Australia, including the study area, owing to predation by introduced predators, particularly foxes (Johnson et al., 2007). The effects of foxes on these species have been exacerbated by the suppression of dingoes (Johnson et al., 2007). Similarly, native rodents are rare or extinct in the semi-arid lands of Australia where dingoes have been extirpated (Letnic et al., 2009). Consistent with our trophic cascade hypothesis for shrub encroachment, shrub encroachment in arid Australia has been reported to occur primarily in regions where dingoes have been extirpated (Noble 1998) and has coincided with the irruption of foxes and loss of medium-sized marsupials and native rodents (Noble, 1998; Letnic et al., 2012). These concordant macro-ecological patterns lend support to the argument that small marsupial herbivores and rodents may once have played an important role in suppressing shrub abundance in arid Australia and that the loss of these species has facilitated shrub encroachment (Noble *et al.* 2007).

Unfortunately we were unable to determine if grassland / woodland mosaic or woodland ecosystems dominated the Strzelecki desert dune fields before the arrival of European settlers and non-native rabbits, foxes, cats and livestock in the late early 19th century. However, diverse assemblages of browsing medium-sized marsupials and seed consuming rodents were present before European settlement. Thus, it is highly likely that these native browsing and granivorous species would have once placed constraints on shrub recruitment in a similar way as current day rabbits and rodents.

2.5.3 A herbivore cascade hypothesis for shrub encroachment in arid Australia.

Our results provide mixed support for the hypothesis that livestock grazing and fire are drivers of shrub encroachment within our study area. The marked increase in historic shrub cover between 1972 and 1983 at sites where dingoes exist at low densities (inside the fence) occurred irrespective of whether sites were used for livestock grazing (Hawker Gate) or as conservation reserve (Fort Gray; Fig. 2.3). In addition, distance to closest watering point, a proxy for livestock grazing intensity (Landsberg et al., 2003) and fires had weak and negligible correlations with historic shrub cover in our analysis, respectively. However, our modelling of contemporary patterns of consumer and hopbush seedling abundance suggested that dingo suppression by facilitating livestock grazing has positive effects on shrub seedling abundance by suppressing the occurrence of fire.

Previous studies have highlighted how the trophic effects from dingoes extend to the human economy by influencing the type of livestock grazed (Letnic et al., 2012). In our study the correlations evident in the SEM model, between the intensity of dingo-control and density of livestock and intensity of dingo-control and dingo activity, also suggest that dingo activity - mediated through human dingo-control - influences stocking rates with higher stocking rates occurring in areas where dingoes are rare, presumably because the risk of livestock being killed by dingoes is less. In turn, areas with higher stocking rates, both inside and outside the dingo-proof fence were less likely to have been burnt in recent fires. The link between livestock density and fire evident in the SEM likely stems from the suppressive effects that livestock can have on grasses (Landsberg et al., 2003; Letnic, 2004) and hence fuel loads and is consistent with previous studies that have linked shrub encroachment to livestock grazing and fire suppression (Scholes and Archer, 1997). Although a limitation of our study is that we were unable to quantify grass cover prior to the fires. In addition, kangaroo abundances, although not included in our SEM as a driver of fire occurrence in 2010 owing to the absence of data for this period, are consistently higher at sites where dingoes are rare (Letnic et al., 2012) and thus may also be expected to have contributed to reductions in fuel loads by reducing grass cover (Letnic et al., 2009).

While our SEM provides some support for the hypothesis that fire occurrence, mediated by livestock stocking densities and the intensity of dingo-control, suppresses the abundance of shrub seedlings, it is important to note that fires did not occur at all of the sites located outside the dingo-proof fence (Fig. 2.1). Shrub seedling abundance was generally low also at unburnt sites outside the dingo-proof fence (a mean of 0.006 ± SE 0.001 seedlings per m^2 in unburnt areas outside the dingo-proof fence compared with a mean of 0.02 ± SE 0.002 seedlings per m^2 inside the dingo-proof fence) where, however, activity levels of rabbits and rodents were high. Indeed rabbit and / or rodent activity at all sites located outside the fence was high in comparison to sites located inside the fence. Thus we suggest that both predation by rabbits and rodents and the occurrence of fire were factors limiting shrub seedling abundance and hence recruitment at sites where dingoes were common. It is likely that these two models interact with one another to influence the abundance of shrubs and shrub seedlings both spatially and temporally. For example, increased livestock grazing and decreased fire frequency may facilitate decreases in the abundance and consumptive effects of rabbits and rodents on shrub seedlings and seeds by altering habitat structure on dunes used by rabbits and rodents. Further experimental studies are required to test these hypotheses.

2.5.4 Could extirpation of top predators be a global driver of shrub encroachment?

Suppression of large predators by humans is a global phenomenon, owing to their depredations on livestock and, in some regions, the direct threat that predators pose to people (Woodroffe, 2000; Ripple et al., 2014). The irruption of mesopredators that follows removal of top predators is also a global phenomenon which has been linked in turn to the suppression of mammalian predators of shrubs such as lagomorphs and rodents (Ritchie and Johnson, 2009; Ripple et al., 2013). Could trophic cascades and the loss of ecosystem function induced by large predator removal, similar to that we have proposed in the Strzelecki Desert of Australia, be driver of shrub encroachment in many areas of the Earth where top predators were once common but are now rare?

Because of human persecution of mammalian predators there are few arid regions on Earth where sufficient numbers of top predators remain to allow evaluation of the mesopredator cascade hypothesis for shrub encroachment that we propose here. However, given evidence that widespread top predator decline and concurrent mesopredator irruption has resulted in the suppression of lagomorphs and / or rodents (Henke and Bryant, 1999; Ripple et al., 2013), it is plausible that the diminished ecological function of these herbivores and granivores has facilitated shrub encroachment elsewhere (Davidson et al., 2012). For example, in the south-western USA, there is evidence of changes in ecosystem structure at multiple trophic levels analogous to those we have used to link top predator extirpation to shrub encroachment in arid Australia. In this region encroachment of shrubs has coincided with the decline of wolves, expansion of livestock grazing, reduced fire frequency (van Auken, 2000), irruption of mesopredators and wild herbivores, and decline of burrowing, herbivorous mammals that consume shrubs such as rodents and lagomorphs (Weltzin et al., 1997; Roth et al., 2009; Davidson et al., 2012). While we do not discount that livestock grazing, fire frequency and increases in atmospheric CO_2 emissions (as well as other drivers such as rainfall) may still be influential proximal drivers of shrub encroachment, we contend that trophic cascades stemming from the decline of top predators, irruption of mesopredators and associated decline of mammalian consumers of shrubs may be an overlooked driver of shrub encroachment. Although an exciting idea, we stress that trophic cascades stemming from top predator extirpation will likely influence seed recruitment and shrub encroachment differently in different areas of the Earth. These differences will likely result from context-dependant factors such as the nature of pairwise species interactions across trophic levels, the length of food chains, and shrub seed ecology.

2.6 Acknowledgements

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2.8 Supplementary Information

Table S2.1. Total number of sample units used to assess historic shrub cover estimates from aerial photographs. Shrub cover was estimated at two sites (Fort Gray, Hawker Gate) over four years (1948, 1972, 1983, 1999) in areas of high and low dingo abundance inside and outside the dingo-proof fence.

	Fort Gray		Hawker Gate	
	Dingo high abundance	Dingo low abundance	Dingo high abundance	Dingo low abundance
1948	207	136	203	369
1972	544	385	409	229
1983	187	228	557	583
1999	199	132	219	201
Total	1137	881	1388	1382

Table S2.2. Predictor variables measured and entered into generalized linear models and their hypothesized effect on the historical cover of woody shrubs in the Strzelecki Desert.

Variable	Predicted response of *shrub* cover	Description
Year	Positive due to global increase in $C0_2$	Year of photograph
Dingo	Negative because unpublished date suggested shrub cover was greater where dingoes were controlled	Side of dingo-proof fence (dingoes common, dingoes rare)
Distance to fence	Little effect on shrub abundance because the fence was constructed along lines of latitude and longitude that represented the administrative boundaries of British colonies and do not represent ecosystem boundaries or environmental gradients.	Distance (m) to dingo-proof fence calculated in GIS.
Distance to water	Negative because previous study has shown shrub abundance to increase with distance from water (Tiver and Andrew, 1997) and livestock grazing pressure increases with proximity to water	Distance (m) to nearest waterpoint calculated from historical photographs and maps for each individual sampling year
Latitude	Negative because unpublished date suggested that shrub abundance increased with latitude.	Geographic coordinate in utm
Geographic coordinates	Shrub cover is autocorrelated and will increase with proximity to other shrubs.	Geographic coordinates in utm
Annual average rainfall in previous 20 years	Positive because successful shrub recruitment often occurs after episodic periods of high rainfall (Nicholls, 1991).	Average annual rainfall (mm) over the previous 20 years calculated from the Australian Bureau of Meteorology's gridded rainfall data (Australian

		Bureau of Meteorology, 2013).
Variable	Predicted response of *shrub* cover	Description
Fire within previous 20 years	Negative because shrub cover is predicted to increases as fire frequency decreases	Presence of fire scars in the 20 years preceding sampling. Assessed using aerial photographs (1948 - 1999), satellite imagery (1977 – 2012), achieve maps and on-line resources.
Year : dingo	Divergent trajectory of shrub abundance expected through time owing to different dynamics of mammalian herbivores and granivores where dingoes were common and rare.	Interaction term between year and dingo

Table S2.3. Comparisons of the best five candidate Generalised Linear Models used to describe temporal trends in historic shrub cover in the Strzelecki Desert between 1948 and 1999. TSF represents time since fire, D represents dingo treatment, SAC represents the spatial auto-correlation term, D2F represents distance to the dingo-proof fence, D2W represents distance to the closest artificial water source, R represents the average annual rainfall in the previous 20 years, L represents latitude, Y represents year of sampling, SF:Y represents the interaction between year of sampling and side of dingo fence.

Model	AIC	ΔAIC	w_i
D + AC + D2F + D2W + R + L + Y + D:Y	63677	0	0.574
TSF + D + AC + D2F + D2W + R + L + Y + D:Y	63677	0.603	0.425
D + AC + D2W + R + L + Y + D:Y	63695	17.745	< 0.001
TSF + D + AC + D2W + R + L + Y + D:Y	63696	19.530	< 0.001
D + AC + D2F + D2W + L + Y + DY	65887	2210.444	0

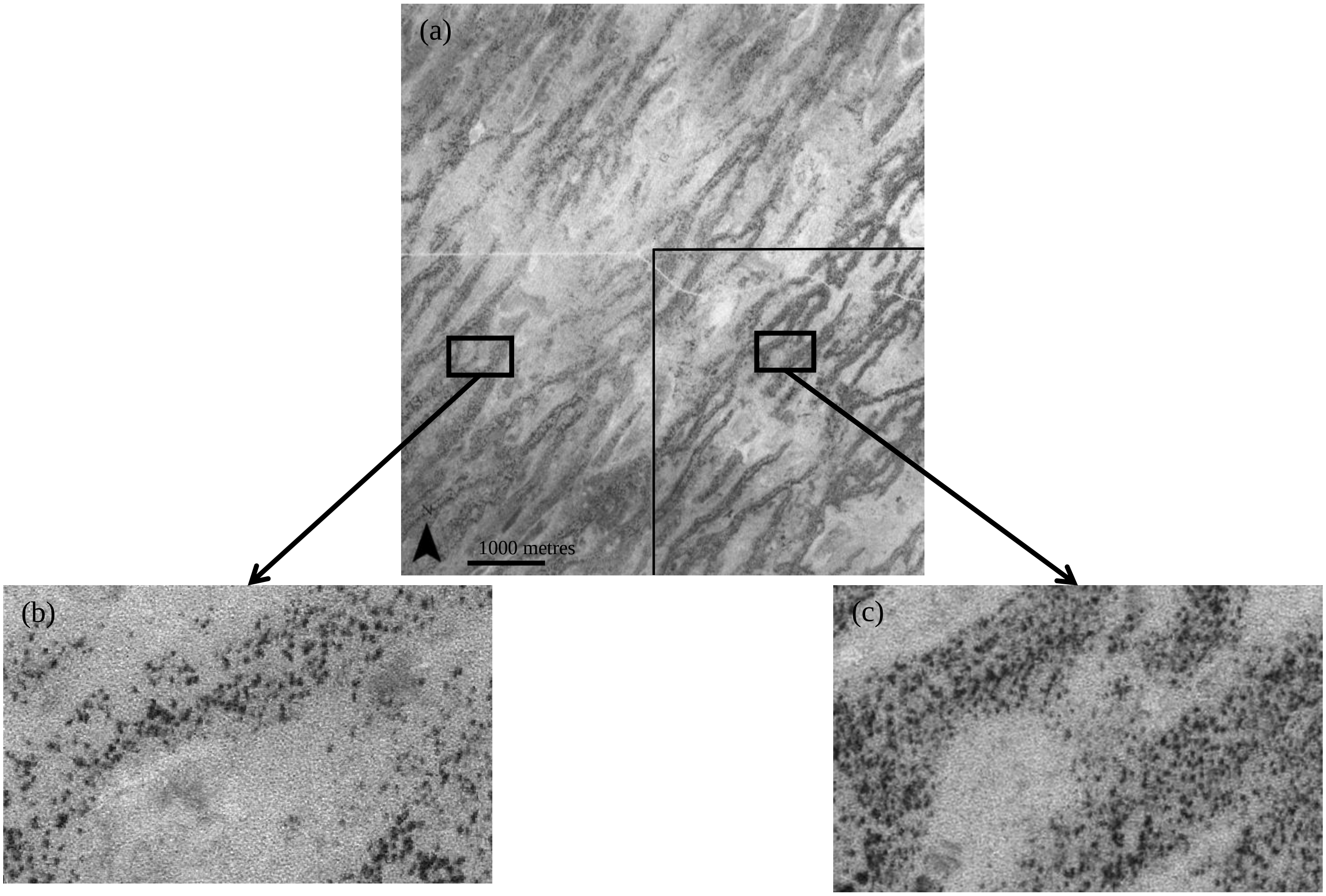

Figure S2.1. An example of an aerial photograph (a) showing shrub cover on south west-north east trending sand dunes where dingoes are rare (b) and common (c) on either side of the dingo-proof fence. The photograph shows a section of the northern study area (Fort Gray) during 1999. Shrubs are seen as noticeably darker areas on sand dunes and the dingo-proof fence is shown as a thin black line in (a).

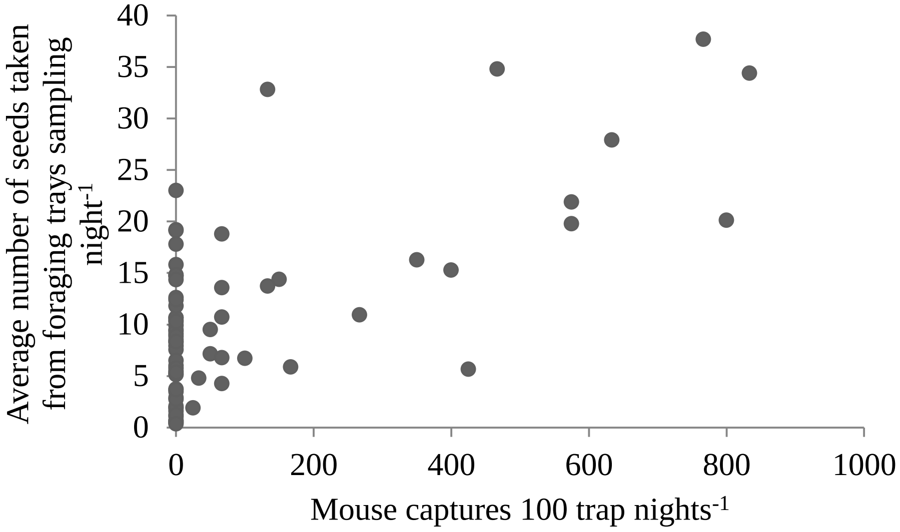

Figure S2.2. Scatterplot showing average number of Dodonaea viscosa angustissima seeds removed from foraging trays versus mouse abundance (Linear regression: Avg seed take = 0.027 mouse + 7.772, r^2: 0.445, P: <0.001).

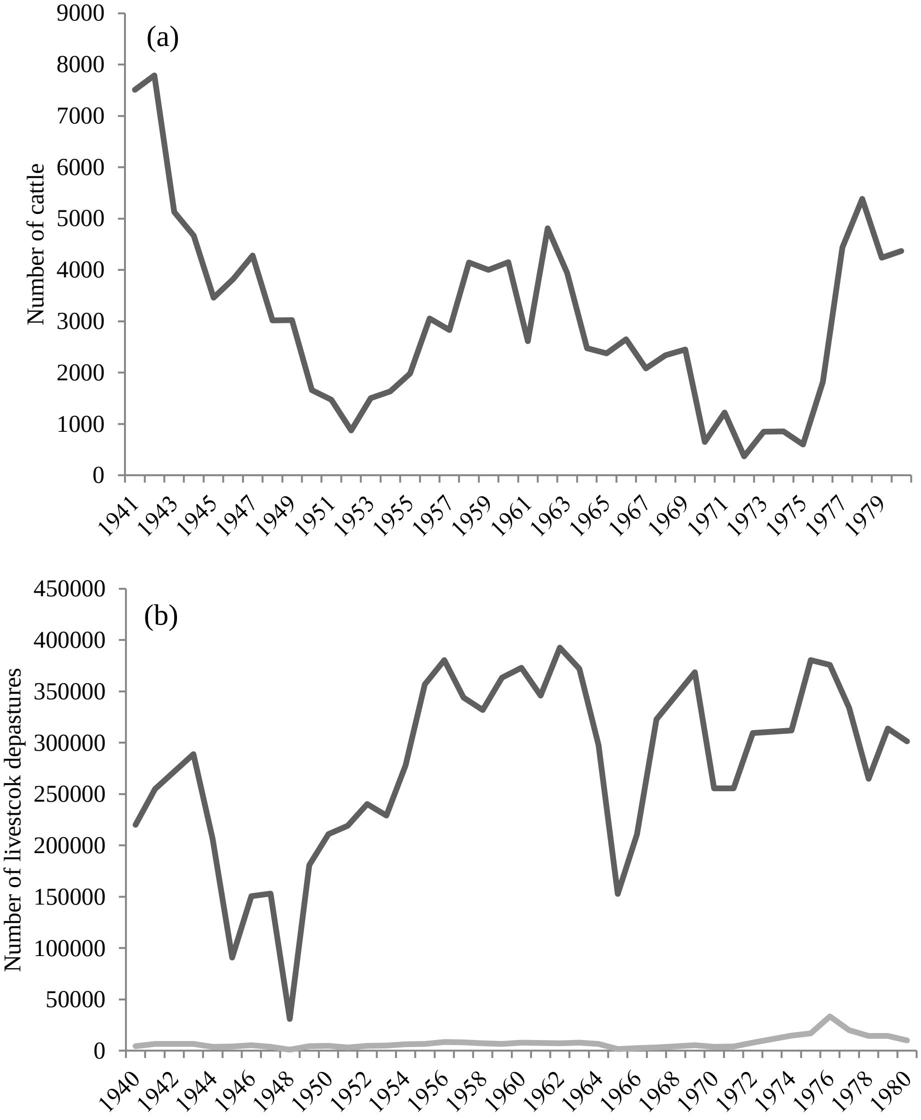

Figure S2.3. (a) Total number of cattle (1941 – 1980) reported from a large cattle station outside the dingo-proof fence which occurred within our study area (station area: 12, 000 km^2). (b) Total number of sheep (dark grey line) and cattle (light grey line) depastured from the western Division of New South Wales (division area: 325000 km^2) between 1940 and 1980. Annual livestock totals were obtained from landholders outside the dingo-proof fence and gleaned from

New South Wales Government reports (Annual Reports of the Western Lands Commission) inside the dingo-proof fence.

Chapter 3: Evidence that a top predator benefits a ground-nesting bird by suppressing the abundance of an invasive mesopredator

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Statement of Authorship: CG, ML and BM designed the study, CG conducted field work, CG wrote the manuscript, all authors edited the manuscript.

Two dingoes drinking from a dam outside the dingo-proof fence. Photo provided by Ben Moore.

Chapter 3. Evidence that dingoes benefit a ground-nesting bird

3.1 Abstract

The irruption of mesopredators and large herbivores that often follows the removal of top predators is a key factor contributing to losses of biodiversity from Earth's ecosystems. Here we test the hypotheses that 1) a top predator, the dingo (*Canis dingo*), benefits a small ground-nesting bird, the little button-quail (*Turnix velox*), by reducing the abundance of red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) mesopredators, and 2) herbivore grazing negatively affects little button-quail abundance by reducing ground cover. We compared little button-quail and predator abundance indices, herbivore grazing activity, ground cover and predator diets across a 10,000 km^2 area of the Strzelecki Desert in arid Australia within which dingoes were subject to varying levels of lethal control. Little button-quails were 38 times more frequently observed where dingoes were common than rare. Ground cover and herbivore grazing activity were poor correlates of little button-quail abundance. Birds occurred less frequently in dingo (7.4%) than mesopredator (14.6% of fox, 21.7% of cat) scats. Our results support the hypothesis that suppression of foxes by dingoes can benefit a small ground-nesting bird at a landscape scale. Our results suggest that the mesopredator-suppressive effects of top predators could be incorporated into ecosystem-scale biodiversity conservation programmes to check the predatory impact of mesopredators.

Keywords: trophic interaction, top-down, dingo, fox, *Turnix velox*, top predator re-introduction

3.2 Introduction

Recent studies suggest that top predators can have a profound influence on the structure of ecosystems through their top-down effects (Estes et al., 2011). The magnitude of top predators effects are particularly evident when mammalian predators with high metabolic demands are removed from ecosystems (Ripple et al., 2014). The disruption to ecosystem organisation caused by the irruption of both herbivores and smaller predators (mesopredators) following the removal of top predators can shift ecosystems to alternative states, and has been identified as a major factor contributing to the loss of biodiversity globally (Estes et al., 2011; Ripple et al., 2014). Consequently, restoring and maintaining populations of top predators has been identified as a critical imperative for the conservation of biodiversity (Ritchie et al., 2012).

The mesopredator release hypothesis (MRH) predicts that reduced abundance of top predators results in an increase in the abundance and predatory impact of mesopredators (Crooks and Soule, 1999; Ritchie and Johnson, 2009). The MRH also predicts that the abundances of small species that are the preferred prey of mesopredators may decline in the absence of top predators (Prugh et al., 2009; Ritchie and Johnson, 2009). The predictions of the MRH are borne out in the southern regions of Australia where an inverse relationship exists between the abundance of dingoes (*Canis dingo*; body-weight 15-22 kg) and invasive red foxes (*Vulpes vulpes*: body-weight 5-7 kg), and a positive relationship exists between the persistence and abundance of dingoes and of ground-dwelling mammals weighing less than 5500 g (Johnson et al., 2007; Letnic et al., 2009b). These patterns suggest that dingoes' fox-suppressive effects could be harnessed in conservation programs to mitigate the predatory impacts of foxes on native fauna (Letnic et al., 2012).

The relationship between the abundance of dingoes and the other invasive mesopredator in Australia, the feral cat (*Felis catus*: body weight 3-6 kg) is less clear (Letnic, Ritchie & Dickman 2012). Dingoes kill cats (Moseby et al. 2012) and cats avoid dingoes (Brook, Johnson & Ritchie 2012). However, at the population level, positive, neutral and negative effects of dingoes on cat activity have been reported (Letnic *et al.* 2009; Brook, Johnson & Ritchie 2012; Kennedy *et al.* 2012).

Because ground-nesting birds (hence forth GNBs) roost and reproduce on the ground, adult birds and their fledglings and eggs are particularly susceptible to failure or death resulting from flooding, fire, trampling or predation by terrestrial vertebrates (Reid and Fleming, 1992; Askins, 1995). In arid regions of Australia, GNBs have become rare or locally extinct across large areas since the introduction of invasive fox and cat mesopredators, and the advent of pastoral settlement in the mid to late 19th century (Reid and Fleming, 1992; Davies et al., 2010). Predation by foxes and cats has been identified as a key driver of GNB declines (Reid and Fleming, 1992; Priddel et al., 2007). Predator impacts on GNBs are thought to be exacerbated by livestock grazing which depletes the ground-cover vegetation often used by GNB for cover and nesting (Davies et al., 2010), Consequently, there has been speculation that dingoes, by modulating mesopredator abundance and behaviour, could provide conservation benefits for GNBs (Garnett, 2012).

One way to examine the impacts of large predators is to evaluate large-scale ‘artificial experiments’ in which the abundance of top predators varies in time or space across otherwise similar landscapes (Terborgh et al., 2001; Elmhagen et al., 2010). Such studies can provide valuable insights into ecological processes at spatial and temporal scales that cannot be achieved through small-scale experimentation (Oksanen, 2001). In the arid regions of Australia, the dingo-proof fence provides an unparalleled opportunity to investigate the complexity of top predators effects on ecosystems and the role they play in sustaining biodiversity (Letnic et al., 2012). Because dingoes are common on one side of the fence and comparatively rare on the other, the dingo-proof fence allowed us to conduct a large-scale study to test the predictions of the MRH by measuring abundance indices of dingoes, mesopredators and a GNB, the little button-quail (*Turnix velox*) across a 10, 000 km^2 area surrounding the fence in the Strzelecki Desert. The little button-quail is a small (60 g) nomadic GNB that is distributed throughout arid Australia and experiences population ‘booms’ following high rainfall periods. Although the little button-quail is considered an IUCN species of least concern (www.iucnredlist.org), it is thought to be experiencing population declines throughout its range (del Hoyo et al., 1996).

Applying the MRH, we predicted that 1) indices of mesopredator abundance should be lower in the presence of dingoes; 2) little button-quail abundance should be greater in the presence of dingoes owing to release from predation by mesopredators and 3) smaller foxes and cats should be more likely than larger dingoes to consume birds (Table 3.1). Because little button-quail abundance may also be influenced by herbivore grazing activity and ground cover, we also predicted that 4) little button-quail abundance should be negatively correlated with herbivore grazing and positively correlated with herbaceous ground cover owing to the negative effects that herbivore grazing activity has on ground cover (Table 3.1). Because grazing pressure is known to vary in response to land-use and dingo removal (Letnic et al., 2012) we conducted our study across lands used for livestock grazing and for conservation reserves where livestock is excluded, on both sides of the dingo-proof fence.

3.3 Methods

3.3.1 Study area

The study was conducted in the region surrounding the dingo-proof fence in the Strzelecki Desert (Fig. 3.1). The dominant landforms in the Strzelecki Desert are longitudinal, west-east trending sand dunes (8 m height). Vegetation on sand dunes is dominated by perennial and annual shrubs and inter-dune swales are dominated by grasses, herbs and forbs. Average annual rainfall in the study site decreases from north to south and east to west and ranges from 188 mm (Milparinka, 30.14° S 141.73° E) to 227 mm (Tibooburra Post Office, 29.43° S 142.01° E; Australia Bureau of Meteorology, 2014). The study was conducted during a ‘boom’ period of high productivity associated with a La Niña phase of the El Niño Southern Oscillation. Rainfall was extremely high in the two years preceding sampling, especially during 2010 when annual rainfall exceeded the 95th percentile of the historic rainfall distribution (since 1886; Tibooburra Post Office). The predominant land-use in the region is livestock grazing. A large area not subject to commercial livestock grazing, Sturt National Park, occurs in the Australia state of New South Wales (NSW; Fig. 3.1). Dingoes are routinely killed in and around Sturt National Park and are therefore rare. A similarly large conservation reserve not subject to livestock grazing, Strzelecki Regional Reserve exists in South Australia (SA; Fig. 3.1). Dingo populations are not subject to control within Strzelecki Regional Reserve.

To prevent immigration of dingoes into NSW and thus prevent attacks on sheep (*Ovis aries*), the NSW State Government constructed an approximately 2 m tall dingo-proof fence along parts of the NSW / SA and NSW / Queensland (Qld) borders between 1914 and 1917 (Fig. 3.1; Letnic and Dworjanyn, 2011). The boundaries of NSW with Qld and SA were established by government decree along the meridians 29° S and 141° E and thus represent arbitrary administrative boundaries and not natural geographic boundaries.

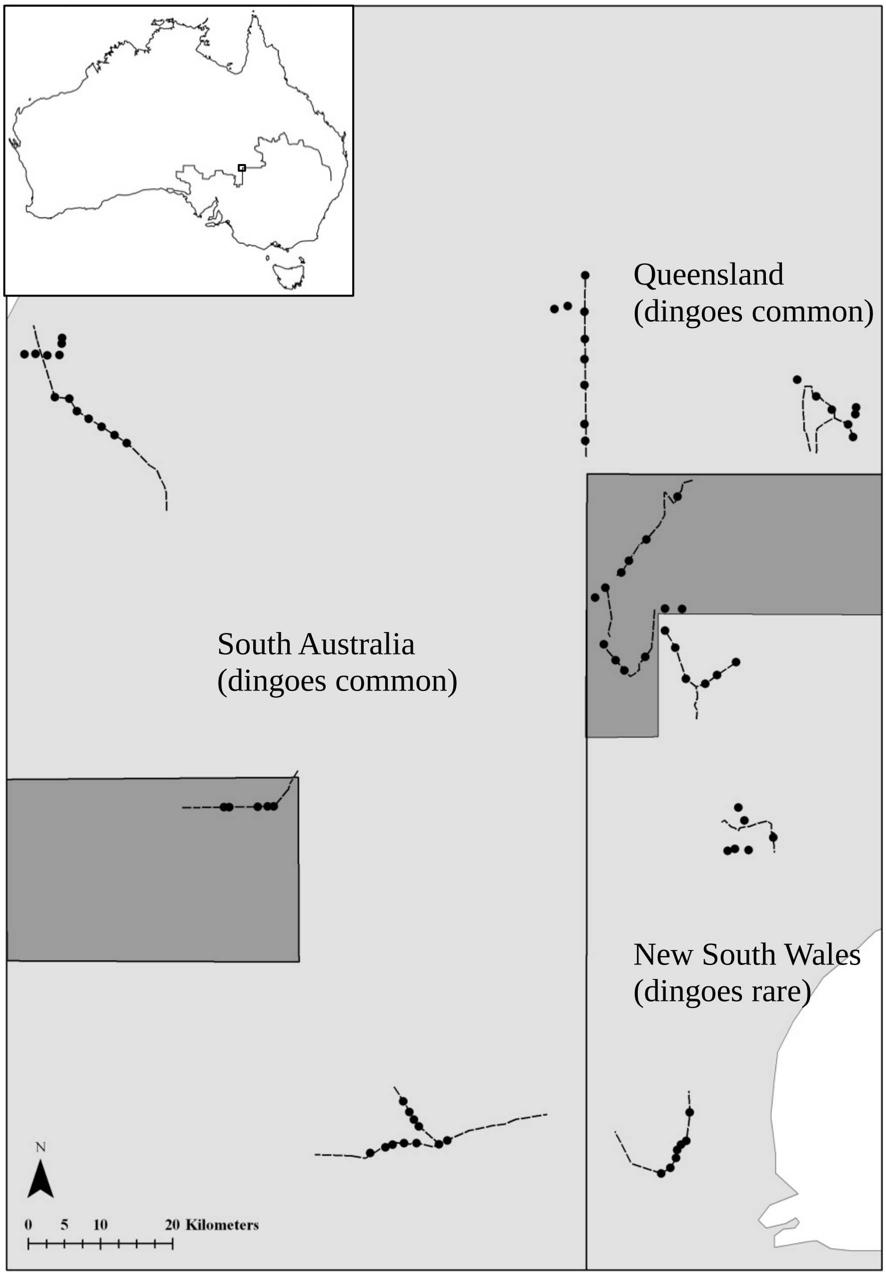

Figure 3.1. Map showing the study area in the Strzelecki Desert. Black dashed lines represent spotlight transects used to measure little button-quail, predator, kangaroo and rabbit abundance indices. Black lines represent the dingo-proof fence, dark grey areas

represent reserve areas (Sturt National Park to the east, Strzelecki Regional Reserve to the west) and light grey areas represent the extent of the Simpson-Strzelecki Desert dunefield. Black circles represent plots where ground cover was assessed. The inset shows the location of the dingo-proof fence (black line) and sample area (rectangle) in Australia.

Dingoes are rare to the south and east of the fence (‘inside’ the dingo-proof fence) where dingoes are baited, trapped and shot. Dingoes are common to the north and west of the fence where dingo-control occurs sporadically (‘outside’ the dingo-proof fence). Previous studies provide evidence that dingo-control in the region has initiated a trophic cascade among mammal species and influenced the stocking practices of pastoralists. In accordance with the MRH, foxes are common inside the fence (Newsome et al., 2001a; Letnic and Koch, 2010). Kangaroo populations are suppressed by dingoes. Consequently kangaroos occur at much higher population densities in areas where dingo populations are controlled, especially inside the dingo-proof fence (Letnic et al., 2012). Invasive rabbits are present throughout the study area, but generally occur at higher abundances outside the dingo-proof fence (Newsome et al., 2001a; Letnic and Koch, 2010). Pastoralists stock both sheep and cattle (*Bos primigenius*) inside the dingo-proof fence. However, only cattle are grazed outside the dingo-proof fence (Newsome et al., 2001a; Letnic and Koch, 2010).

3.3.2 Indexed abundance of ground-nesting birds and predators

Spotlight surveys have been used in previous studies of GNBs and carnivores in the Australian arid zone (Baker-Gabb et al., 1990; Letnic and Dworjanyn, 2011), and are suitable for constructing indices of predator and little button-quail abundance in the Strzelecki Desert because the sparse vegetation allows for long lines of sight. The little button-quail was chosen as a study species because its largely nocturnal behaviour makes it easily observed

Table 3.1. Predicted responses of test variables on either side of the dingo barrier fence. Dingoes have been historically rare inside the dingo-proof fence (DF) and historically common outside the dingo-proof fence.

Variable	Predicted response	Description	Units
Dingo	Greater abundance outside the DF due to decrease in human persecution	Index of abundance from nocturnal spotlight surveys	Dingo/km
Red fox	Greater abundance inside the DF due to release from dingo suppression	Index of abundance from nocturnal spotlight surveys	Fox/km
Feral cat	Greater abundance inside the DF due to release from dingo suppression	Index of abundance from nocturnal spotlight surveys	Cat/km
Herbivore grazing activity	Greater activity inside the DF due to decreases in predation by dingoes	Cumulative dry sheep equivalence of sheep, cattle, kangaroos and rabbits	DSE/km^2
Ground cover	Greater cover outside the DF due to decreases in grazing pressure	% cover of live or dead grasses and forbs	% cover
Little button-quail	Greater abundance outside the DF due to dingo suppression of fox and cat predation and increases in ground cover used for cover	Index of abundance from nocturnal spotlight surveys	LBQ/km

during spotlight surveys, and it is active during similar periods as largely nocturnal dingoes, foxes and cats.

Between May and November 2012 we conducted 20 spotlight transects along a total of 263.7 kilometres of single-lane dirt track (inside dingo-proof fence: 101.9 km, outside dingo-proof fence: 161.8 km). Each spotlight transect was undertaken on a different section of dirt track and consequently, each transect was treated as a separate replicate. The spotlight transects varied in length from 10 - 20 km and were conducted on lands used for sheep and cattle grazing inside the dingo-proof fence, cattle grazing outside the dingo-proof fence, and ungrazed areas inside and outside the dingo-proof fence.

Spotlight transects commenced at dusk. During spotlight surveys, dingoes, foxes, cats and little button-quails were counted by an observer using a 50 W spotlight while sitting on the roof (2.3 m above ground level) of a 4-wheel-drive vehicle moving at 10 - 15 km h^{-1}. Little button-quails were observed at night when disturbed by the car and spotlight. To ensure road size or road condition did not bias our results, we only surveyed small ungraded tracks. Little button-quails were identifiable because of their small size, colouration, and distinctive flight pattern. Indices of little button-quail, dingo, fox and cat abundance were calculated as the number of individuals observed during a spotlight transect divided by the length of each transect.

Detection functions were not included in our abundance estimates for predators and little button-quails because 1) our predator abundance indices derived from spotlight transects showed similar results to predator activity index values derived from track plots measured during a concurrent study within the same sample area and period (Fig. S3.1); 2) predators and button-quails were detected at similar distances from the vehicle either side of the dingo-proof fence (Fig. S3.2); 3) detection functions are not always necessary when making population comparisons between structurally similar landscapes (Welsh et al., 2013); and 4) due to low detection rates, detection probabilities could not be calculated for dingoes or button-quails inside the dingo-proof fence. Conversely, due to low detection rates, detection probabilities could not be calculated for foxes or cats outside the dingo-proof fence.

3.3.3 Herbivore grazing activity and ground cover

The numbers of cattle and sheep on each of the pastoral stations for the 2012 final year were obtained from landholders. Sheep and cattle abundances were converted to dry sheep equivalents (DSE; Russell and Orchard, 2010; Smith et al., 2012), summed and then divided by the size of each property to yield a DSE km^2 estimate. Kangaroo and rabbit abundances were indexed using the previously described spotlight surveys. As kangaroos and rabbits were frequently observed up to 80 and 60 m perpendicular distance from the vehicle, respectively (Fig. S3.3), we estimated kangaroo and rabbit abundance per km^2 by dividing the total number of kangaroos or rabbits observed during spotlight surveys by the length of each survey when multiplied by 160 and 120 m (80 and 60 m perpendicular distance on either side of the surveyed road) respectively. Kangaroo and rabbit abundance indices were then converted to DSE. Total DSE was calculated by summing sheep, cattle, kangaroo and rabbit DSE values. We estimated total grazing pressure of sheep, cattle, kangaroos and rabbits by first indexing herbivore abundance, then standardising these abundance to dry sheep equivalents (DSE) where: 1 sheep = 1 DSE, 1 cow = 6 DSE, 1 kangaroo = 0.625 DSE and 1 rabbit = 0.125 DSE (Russell and Orchard, 2010; Smith et al., 2012).

Ground cover vegetation was measured on 76 plots (inside fence: 31, outside fence: 45) using a point-step method (Fig. 3.1; Landsberg et al., 2003). Plots were spaced at least 2 km apart and were situated in areas immediately adjacent to the spotlight transects. In each plot an observer noted the presence or absence of grasses and forbs (live or dead < 40 cm height) at one metre point intervals along three 100 m survey transects. The percentage of ground cover was then calculated for each plot.

3.3.4 Predator scat analysis

Predator scats were collected during the daytime by walking along the tracks used for spotlight transects and during active searches around livestock watering points (Letnic and Dworjanyn, 2011). Scats were collected in paper bags, dried, and stored for laboratory analysis. In the laboratory, scats were dried at 100 °C, placed in nylon bags, and washed using a dishwashing machine (Letnic and Dworjanyn, 2011). Scat contents were then sorted and bird remnants identified from bones and feather fragments. Because bird remains could not be identified to species levels, all bird remains were grouped for analysis.

3.3.5 Statistical analysis

We compared little button-quail, dingo, fox, and cat abundance indices, the grazing pressure of kangaroos, rabbits and total herbivore grazing pressure (DSE), and ground cover either side of the dingo-proof fence using generalised linear mixed-effects models (GLMM; Poisson log-link function). GLMMs we conducted on raw count data offset by the length of each replicate spotlight (the Poisson distribution requires unstandardized count data for dependant variables). A linear mixed-effects model (LME) was used to compare ground cover either side of the dingo-proof fence. Because sheep and cattle grazing pressure were estimated at a property scale, no statistical tests were conducted for these variables. α values were Bonferroni corrected for multiple comparisons. To account for inter-annual and seasonal variation in little button-quail abundance, sample period was included as a random effect in all analyses. Low samples sizes prevented statistical comparisons between conservation and pastoral areas inside and outside the dingo-proof fence.

Spatial autocorrelation exists if the value of a variable at one location is influenced by the values of neighbouring variables, indicating that observations are not independent. To test whether our data exhibited such underlying spatial clustering, we tested for spatial autocorrelation in the Pearson's residuals of GLMM and LME models, using a Moran I test in the 'ape' package (Paradis et al., 2004) in R (R Development Core Team, 2008). Spatial autocorrelation occurs if the Moran I value tends towards 1 or -1, and the associated P value is significant when $P < 0.05$. Moran I tests were conducted on raw count data for variables where GLMMs could not be conducted. Contingency tables were used to compare the frequency of bird remains in dingo, fox and cat scats inside and outside the dingo-proof fence.

3.4 Results

3.4.1 Abundance of little button-quail and predators, herbivore grazing pressure and ground cover

Little button-quails were more frequently observed outside the dingo-proof fence where dingoes were common than inside the dingo-proof fence where dingoes were rare (Table 3.2). Little button-quails were similarly scarce in conservation (0 observations / km) and pastoral areas (0.02 observations / km) inside the dingo-proof fence and similarly abundant between conservation (0.21 observations / km) and pastoral areas (0.18 observations / km) outside the dingo-proof fence. Dingoes were common outside the dingo and rare inside the dingo-proof fence (Table 3.2). Conversely, foxes were common inside the dingo-proof fence and rare outside the dingo-proof fence (Table 3.2). The abundance of cats did not differ between sides of the dingo-proof fence (Table 3.2).

Total herbivore grazing pressure (DSE) was higher inside the dingo-proof fence than outside the dingo-proof fence (Table 3.2). Total herbivore grazing pressure was greater in conservation (508 ±SE 142) than pastoral areas (280 ±SE 105) inside the dingo-proof fence. This was probably because kangaroos were much more abundant in conservation areas where livestock were excluded than pastoral areas where livestock were present (personal observation, CG and ML). Total herbivore grazing pressure was similar between conservation (21 ±SE 6) and pastoral areas (32 ±SE 8) outside the dingo-proof fence. Sheep and kangaroo DSE values were higher inside the dingo-proof fence, rabbit DSE values were higher outside the dingo-proof fence, and cattle DSE values did not differ between sides of the dingo-proof fence (Table 3.2).

Ground cover was high throughout the study area (Table 3.2). Ground cover did not differ between conservation reserves (0.52 ±SE 0.01) and pastoral areas (0.50 ±SE 0.06) inside the dingo-proof fence, but was greater for pastoral areas (0.59 ±SE 0.01) than conservation areas (0.34 ±SE 0.06) outside the dingo-proof fence. Spatial autocorrelation was not evident in the residuals of our models (Table 3.3).

3.4.2 Predator scat analysis

Three hundred and seventy eight predator scats were collected from across the study area (Table S3.1); 171 from areas inside the dingo-proof fence (dingo: 40, fox: 117, cat: 14), and 207 from areas outside the dingo-proof fence (dingo: 164, fox: 34, cat: 9). Pairwise comparisons revealed that bird remains were more likely to occur in fox than dingo scats ($\chi^2 = 4.841$, df = 1, $P = 0.028$; Fig. 3.2) and cat than dingo scats ($\chi^2 = 3.684$, df = 1, $P = 0.050$), but were similarly likely to occur in fox and cat scats ($\chi^2 = 0.237$, df = 1, $P = 0.627$; Fig. 3.2).

3.5 Discussion

The results provide general support for our predictions made according to the mesopredator release hypothesis. In accordance with prediction 1, foxes were not detected where dingoes were common. However, there was no difference in the index of abundance of cats between sides of the dingo-proof fence. In accordance with prediction 2, the abundance of little button-quails was positively associated with dingoes and negatively associated with foxes, but there was only a weak association between little button-quails and cats. In accordance with prediction 3, bird remains were more often found in fox and cat scats than in dingo scats. Collectively, these findings lend support to the notion that dingoes' beneficial effects for species vulnerable to predation by foxes may not be limited to mammals, but may extend to other taxa within the preferred prey-size range of foxes.

Contrary to prediction 2, our results provided no support for the hypothesis that dingoes suppressed cat abundance. Cat abundance indices were low throughout the study area and cats were a poor predictor of little button-quail abundance. Because cats are substantially smaller than both dingoes and foxes, it is possible that the abundance and / or behaviour of cats may be suppressed or altered by the presence of both dingoes and foxes (Letnic et al., 2012). If this is the case, the low numbers of cats observed throughout our study area may be due to suppression by dingoes outside the dingo-proof fence, and suppression by foxes inside the dingo-proof fence. Support for this explanation comes from a study showing that dingoes limit the activity of cats in northern Australia where foxes are absent (Kennedy et al., 2012),

Table 3.2. Average values (± SE) for the indices of little button-quail and predator abundance, herbivore grazing activity (dry stock equivalents; DSE), and ground cover for areas where dingoes have been historically rare (inside dingo-proof fence, n = 8 transects) and common (outside dingo-proof fence, n = 12 transects). Results of linear and generalised linear mixed-effects models are also shown.

Variable	Site		Model output		
	Low dingo abundance (inside the dingo-proof fence)	High dingo abundance (outside the dingo-proof fence)	Coefficient estimate	*z* score	*P*
Little button-quail (spotlight transect / km)	0.006 ± 0.023	0.229 ± 0.089	3.31 ± 1.03	3.19	0.035
Dingo (spotlight transect / km)	0	0.12 ± 0.05	n/a	n/a	n/a
Red fox (spotlight transect / km)	0.21 ± 0.06	0	n/a	n/a	n/a
Feral cat (spotlight transect / km)	0.08 ± 0.03	0.07 ± 0.03	-0.28 ± 0.49	-0.57	0.57
Sheep DSE (km^2)	8.44 ± 2.50	0	n/a	n/a	n/a
Cattle DSE (km^2)	4.56 ± 1.33	5.71 ± 2.43	n/a	n/a	n/a
Kangaroo DSE (km^2)	348.68 ± 93.62	4.58 ± 4.58	-8.61 ± 1.26	-6.18	<0.0001
Rabbit DSE (km^2)	4.51 ± 2.47	19.85 ± 5.08	1.68 ± 0.19	8.73	<0.0001

Variable	Site		Model output		
	Low dingo abundance (inside the dingo-proof fence)	High dingo abundance (outside the dingo-proof fence)	Coefficient estimate	*z* score	*P*
Total DSE (km^2)	366.18 ± 92.90	30.14 ± 22.21	-2.61 ± 0.07	-35.35	<0.0001
Ground cover (% cover)	48.39 ± 1.80	56.62 ± 2.29	0.07 ± 0.03	2.66	0.05

and another showing that foxes can limit cat populations where dingoes are absent (Risbey et al., 2000).

Table 3.3. Moran's I statistic, indicating spatial autocorrelation within a) Pearsons residuals from linear and generalized linear mixed-models and b) raw data for test variables.

Model	Observed score	Expected score	SD	*P*
a) tests on persons residuals				
Little button-quail	0.062	-0.053	0.087	0.187
Feral cat	-0.153	-0.053	0.090	0.265
Kangaroo DSE	-0.012	-0.053	0.091	0.656
Rabbit DSE	-0.115	-0.053	0.087	0.472
Total DSE	-0.066	-0.056	0.091	0.883
Ground cover	-0.207	-0.053	0.089	0.082
b) test on raw data				
Dingo	0.012	-0.053	0.084	0.445
Red fox	0.021	-0.053	0.081	0.367

Many small GNBs require ground cover for nesting and predator avoidance (Fondell and Ball, 2004). The reduction of ground cover that frequently accompanies intensive grazing can cause declines in the abundance of GNBs and reduce nesting success (Söderström et al., 2001; Fondell and Ball, 2004). Although our herbivore grazing pressure metric was greater inside than outside the dingo-proof fence, ground cover vegetation was similar on both sides of the dingo-proof fence and was a poor correlate of little button-quail abundance. Furthermore, ground cover did not differ markedly between conservation and pastoral areas inside the dingo-proof fence even though herbivore grazing pressure was greater in conservation areas. Given the weak relationships which exist between herbivore grazing pressure, ground cover and little button-quail abundance (Table 3.2), our results indicate that grazing was not an important factor influencing little button-quail abundance at the time of our study. Formal statistical tests which characterise grazing effects and ground cover between pastoral and conservation areas are required to identify finer scale trends between herbivore grazing, ground cover and little button-quail abundance.

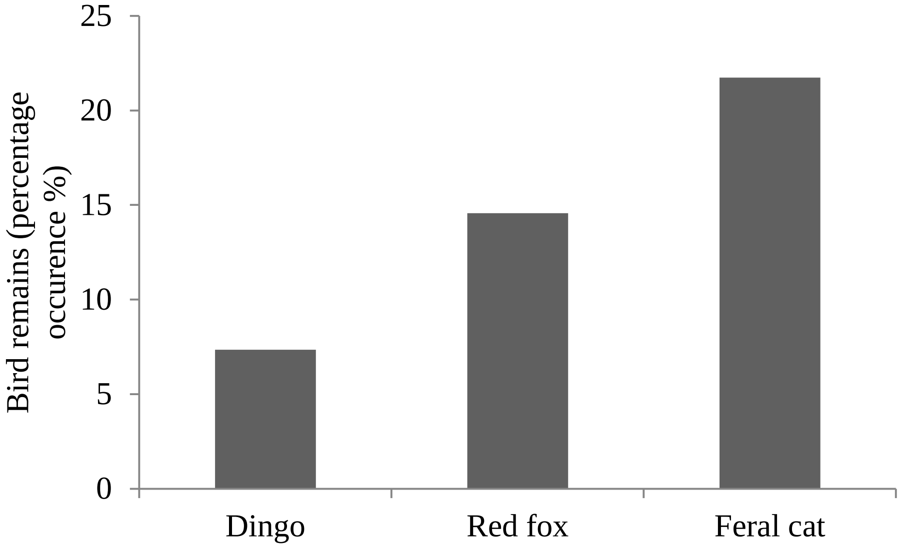

Figure 3.2. The percentage of dingo (n = 204 scats), red fox (n = 151 scats) and feral cat (n = 23 scats) scats containing bird remains when scat data for each species were pooled from areas inside and outside the dingo-proof fence.

Although our study supports the MRH, we caution that because our results derive from an ‘experimental manipulation’ which was applied ~ 100 years ago, replicated controlled experiments that manipulate predator abundance or the exposure of little button-quails and their nests to predators are required to confirm or refute the patterns observed here. Another caveat is that our study was a ‘snapshot’ survey that was conducted soon after an unusually wet period of climatic conditions associated with the La Niña phase of the El Niño Southern Oscillation. Thus the abundance and distribution of little button-quails, predators, ground cover and herbivore grazing activity may differ during dry conditions that typically prevail in the region. For example, little button-quail abundance and ground cover were much higher during the current study than during previous periods (ML unpublished data). However, the magnitude and direction of the correlations that we report between the indices of abundance of dingoes and foxes were consistent with those reported from the region during drier periods (Newsome et al., 2001b; Letnic et al., 2009a; Letnic and Dworjanyn, 2011). This result suggests that dingoes consistently suppress fox abundance during periods of both wet and dry climatic conditions.

3.5.1 Using dingoes to benefit small prey

If, as proposed here and elsewhere, dingoes provide broad-scale benefits for ground dwelling animals vulnerable to predation by foxes such as the little button-quails, native rodents and marsupials weighing less than 5500 g (Johnson et al., 2007; Letnic et al., 2012), maintaining dingo populations or restoring them in areas where dingoes have previously been extirpated or suppressed has potential to be used as a strategy to mitigate the predatory impact of foxes. Such strategies are most likely to be successful in remote, relatively undisturbed landscapes such as the deserts and forests of inland and eastern Australia respectively, where poison-baiting campaigns are unlikely to be effective and conflict between dingoes and livestock producers is less likely. We caution however, that while capable of alleviating the impact of foxes on wildlife, dingoes will not entirely remove foxes. Indeed, the mass extinction of mammals from the Australian deserts that has occurred in the last 100 years, despite the presence of dingoes (Johnson 2006), demonstrates that dingoes are not a ‘silver bullet’ for biodiversity conservation. This highlights the need also for the development of control measures that are specific for foxes.

3.6 Acknowledgments

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3.8 Supporting Information

Table S3.1. Total number of scats collected from areas inside and outside the dingo-proof fence during May, July, August and November 2012.

		Inside dingo-proof fence	Outside dingo-proof fence
Dingo	May 2012	1	26
	July 2012	8	33
	August 2012	15	53
	November 2012	16	52
Red fox	May 2012	36	2
	July 2012	26	9
	August 2012	22	17
	November 2012	33	6
Feral Cat	May 2012	3	2
	July 2012	3	3
	August 2012	4	2
	November 2012	4	2

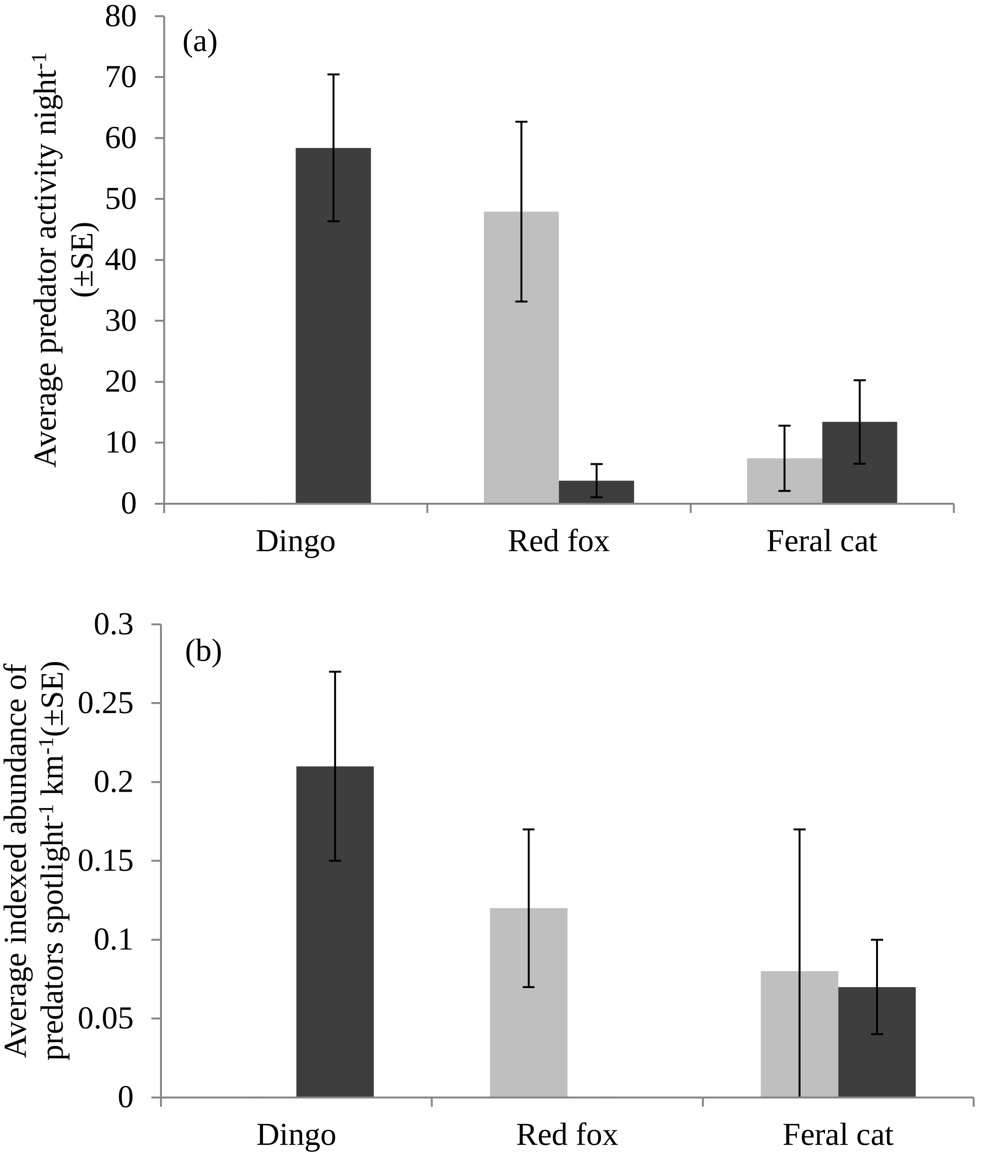

Figure S3.1. Average (± SE) dingo, red fox and feral cat (a) activity per sampling night from predator-tracking plots (inside fence: 31 plots, outside fence: 45 plots)*, and (b) indexed abundance per sample spotlight per km from spotlight surveys (inside fence: 8 spotlight transects, outside fence: 12 spotlight transects). Dark bars represent areas outside the dingo-proof fence where dingoes have been historically common and light grey bars represent areas inside the dingo-proof fence where dingoes have been historically rare.

* Track plot surveys measuring predator activity were compared with spotlight surveys to validate the reliability of spotlight survey in estimating predator abundance. Twenty meter long tracking plots were spaced at 1 – 3 km intervals along roads used for spotlight surveys and were located at all sites used to assess ground cover (see main text, Fig. 3.1). Predator tracks were noted each morning for two to three consecutive mornings and tracking plots were swept daily. Each tracking plot was associated with the closest spotlight transect (5 – 9 tracking plots / spotlight transect) and activity was averaged between tracking plots for these sites. An index of predator activity was calculated as the percentage of nights predator tracks were observed on tracking plots.

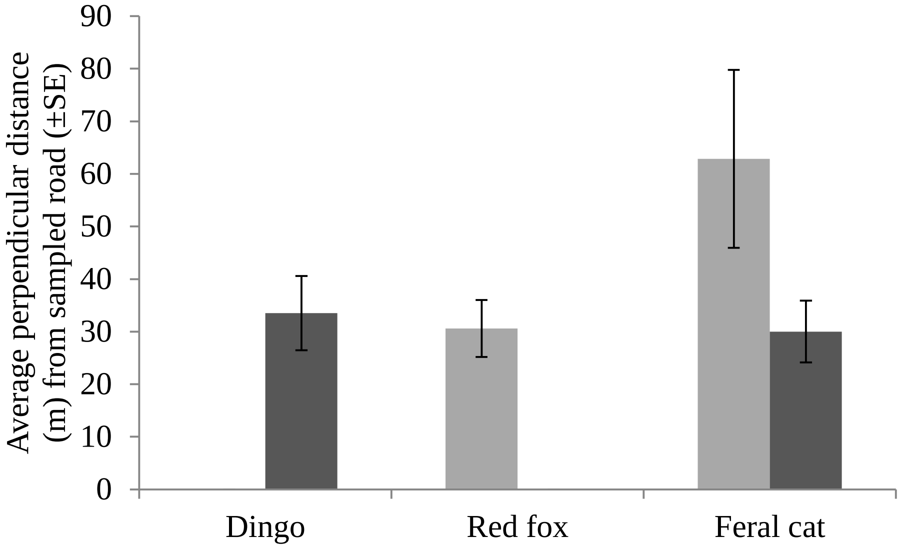

Figure S3.2. Average (± SE) perpendicular distance that dingoes, red foxes and feral cats were observed from sampled roads during spotlight transects (inside the dingo-proof fence: n= 8 transects, outside the ding fence: n= 12 transects) used to calculate predator abundance indices. Dark bars represent areas outside the dingo-proof fence where dingoes have been historically common and light grey bars represent areas inside the dingo-proof fence where dingoes have been historically rare.

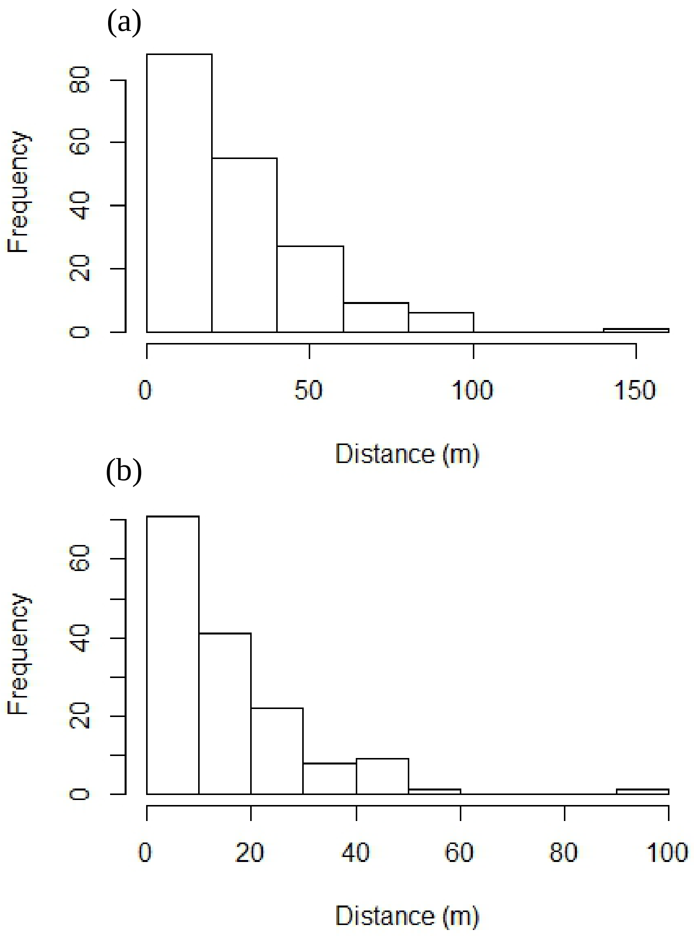

Figure S3.3. Frequency histograms showing the perpendicular distance that (a) kangaroos and (b) rabbits were observed from sampling roads during spotlight surveys.

Chapter 4: Mesopredator suppression by a top predator can alleviate the risk of predation perceived by small prey

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Statement of Authorship: CG and ML designed the study; CG, AF and JG collected data; CG wrote the manuscript; all authors edited the manuscript.

A photo of *Notomys fuscus*, the Dusky Hopping Mouse. Photo provided by Ben Moore.

4.1 Abstract

Predators can impact their prey via consumptive effects that occur through direct killing and via non-consumptive effects that arise when prey phenotypes shift in response to the risk of predation. Although predators' consumptive effects can have cascading population level-effects on species at lower trophic levels there is less evidence that predators' non-consumptive effects propagate through ecosystems. Here we provide evidence that suppression of mesopredator abundance by a top predator has positive effects on both abundance and foraging efficiency of a desert rodent. Then by manipulating predators' access to food patches we further the idea that top predators provide small prey with refuge from predation by showing that rodents increased their habitat breadth and use of "risky" food patches where a top predator was common but mesopredators were rare. Our study suggests that top predators' suppressive effects on mesopredators extend to alleviating consumptive and non-consumptive effects on the prey of mesopredators.

Keywords: non-lethal effect, non-consumptive effect, dingo, *Notomys fuscus*, giving up density, fear, mesopredator, top predator

4. 2 Introduction

Predators can impact their prey and smaller predators (mesopredators) via 2 mechanisms: consumptive (i.e lethal) effects that occur through direct killing; and non-consumptive (i.e. non-lethal) effects that become manifest as prey and competitors shift their phenotype in response to risks associated with predation (Lima, 1998; Schmitz, 2008). The consumptive effects of predators, by moderating the consumptive effects that herbivores and smaller predators have on their prey, can induce trophic cascades whereby predators' effects propagate through ecosystems and have alternating positive and negative population level effects on species at lower trophic levels (Estes et al., 2011).

Most studies investigating the non-consumptive impacts of predators have investigated their effects on the behavioural, physiological, morphological and life history traits of their prey and competitors (Werner and Peacor, 2003; Schmitz et al., 2004; Creel and Christianson, 2008; Spencer et al., 2014). Such studies typically show that prey and competitors at risk of being killed by a predator shift their behaviour to reduce predation risk and undergo associated shifts in metabolism and the quality and quantity of food ingested (Creel and Christianson, 2008). These non-lethal effects of predators can be translated to the demography of herbivores and mesopredators if they impair the reproduction and longevity of individuals (Creel et al., 2007).

If predators consumptive effects can propagate cascades of population level effects and induce non-lethal effects in their prey, it follows then that they should also be capable of propagating cascades of non-consumptive effects (Ripple and Beschta, 2004). Such cascades of non-consumptive effects may arise if top predators moderate the risk posed by smaller predators and herbivores to their prey, and thus may be expected to alternate with trophic level in a manner analogous to the consumptive effects of predators.

The mesopredator release hypothesis (MRH) proposes a trophic pathway through which top predator removal can dramatically alter community structure (Crooks and Soule, 1999; Ritchie and Johnson, 2009). This hypothesis posits that the absence of top predators ‘releases’ smaller mesopredators from predation and / or competition constraints once placed on them by top predators, and in doing so facilitates increased mesopredator abundance (Prugh et al., 2009). Hyper-abundant mesopredators may then prey heavily on, and suppress the abundances of animal species which fall below the weight range normally preyed on by top predators (Crooks and Soule, 1999; Johnson et al., 2007; Letnic et al., 2009).

Mesopredator release pathways have classically been described using lethal effects models, whereby the frequency of fatal encounters between mesopredators and prey, and hence population level impacts of mesopredators, is reduced in the presence of a top predator. However, it is conceivable also that lower encounter rates between mesopredators and prey in the presence of a top predator should reduce the risk of predation perceived by small prey species (Frid et al., 2008). Such a refuge effect might be expected to become manifest as prey species reducing their vigilance and allocating more time to foraging in environments where top predators are common and mesopredators rare (Letnic and Dworjanyn, 2011).

Giving up density (GUD) trials use enriched food patches to titrate the relative influence that food and “safety” have in determining foraging animals’ allocation of time, taking the amount of food left uneaten in foraged food patches as a proxy for ‘fear’ (Brown, 1988; Brown and Kotler, 2004). Foraging theory predicts that a foraging animal will cease to forage in a food patch when the perceived benefit of continuing to exploit the patch is outweighed by the perceived risk (Brown and Kotler 2004). Thus low GUD values (a low density of food remaining in patches) are expected in low risk areas where animals forage more efficiently by foraging food patches more thoroughly (Brown 1998). Conversely, high GUD values are expected in high risk areas where diminishing rates of return become outweighed by the risks associated with continuing to forage. When replicated spatially, GUDs can be used to map ‘landscapes of fear’ which seek to explain how animals exploit food and habitat resources across heterogeneous foraging environments (Laundré et al., 2001).

In this paper we investigate how foraging behaviour (food patch using: GUD) and habitat use in a desert rodent, *Notomys fuscus*, are influenced by the activity levels of an top predator, the dingo (*Canis dingo*), two mesopredators, the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*), and conspecific abundance. We conducted our study in the Strzelecki Desert, Australia. In this region, dingoes benefit *Notomys fuscus* populations by suppressing the abundance of foxes (Letnic et al., 2009; Letnic and Dworjanyn, 2011). There is evidence also, that direct killing by dingoes can suppress the abundance of the other invasive mesopredator in the region, the feral cat (Read et al., 2001; Moseby et al., 2012).

Applying the mesopredator release hypothesis and our *a priori* knowledge of interactions thought to occur between dingoes, mesopredators and *N. fuscus*, we tested two hypotheses concerning how dingoes may influence food patch and habitat use of *N. fuscus*. First, because predation risk is expected to reduce the amount of time individuals allocate to foraging, we predicted that the GUD of *N. fuscus* will be lower in areas where dingoes are common because the risk of predation is lower owing to dingoes' suppressive effects on mesopredators. Second, because risk of predation can reduce foraging animals' use of "risky" habitats (Orrock and Fletcher, 2014) we predicted that the breadth of habitat used by *N. fuscus* should be greater in areas where dingoes are common because the risk of predation is lower (Hernández and Laundré, 2005). In addition to the above hypotheses, because con-specific density dependence can potentially increase animals' allocation of time to foraging and increase the range of habitats exploited owing to intra-specific competition and / or "safety" in numbers' effects (China et al., 2008; Searle et al., 2008), we also predicted that the GUD of *N. fuscus* should be lower and the breadth of habitat use greater in areas with higher *N. fuscus* population densities.

We conducted two experiments to test our predictions. We conducted a landscape-scale GUD trial and used structural equation modelling, in conjunction with activity and abundance estimates for predators and *N. fuscus*, to explore if variation in the activity levels of a top predator influenced the GUD of *N. fuscus*. To further parse out the effects that predators and conspecifics had on the foraging efficiency of *N. fuscus* we then conducted a manipulative cover experiment to compare how *N. fuscus* exploited “risky” and “safe” food patches in response to variation in the activity levels of a top predator, mesopredators and con-specifics.

4.3 Methods

4.3.1 Study site

The study was conducted on rangeland properties that are used for grazing cattle at low densities (< 0.1 – 2.85 cattle / km^2; Fig. 4.1). The predominant landforms in the Strzelecki Desert are east west trending longitudinal sand dunes. Mean annual rainfall in the study area ranges from 188 – 227 mm (Australia Bureau of Meteorology, 2013). Vegetation on sand dunes is dominated by an understory of ephemeral grasses, forbs and herbs (< 40 cm) and a relatively spares overstory of ephemeral and perennial shrubs.

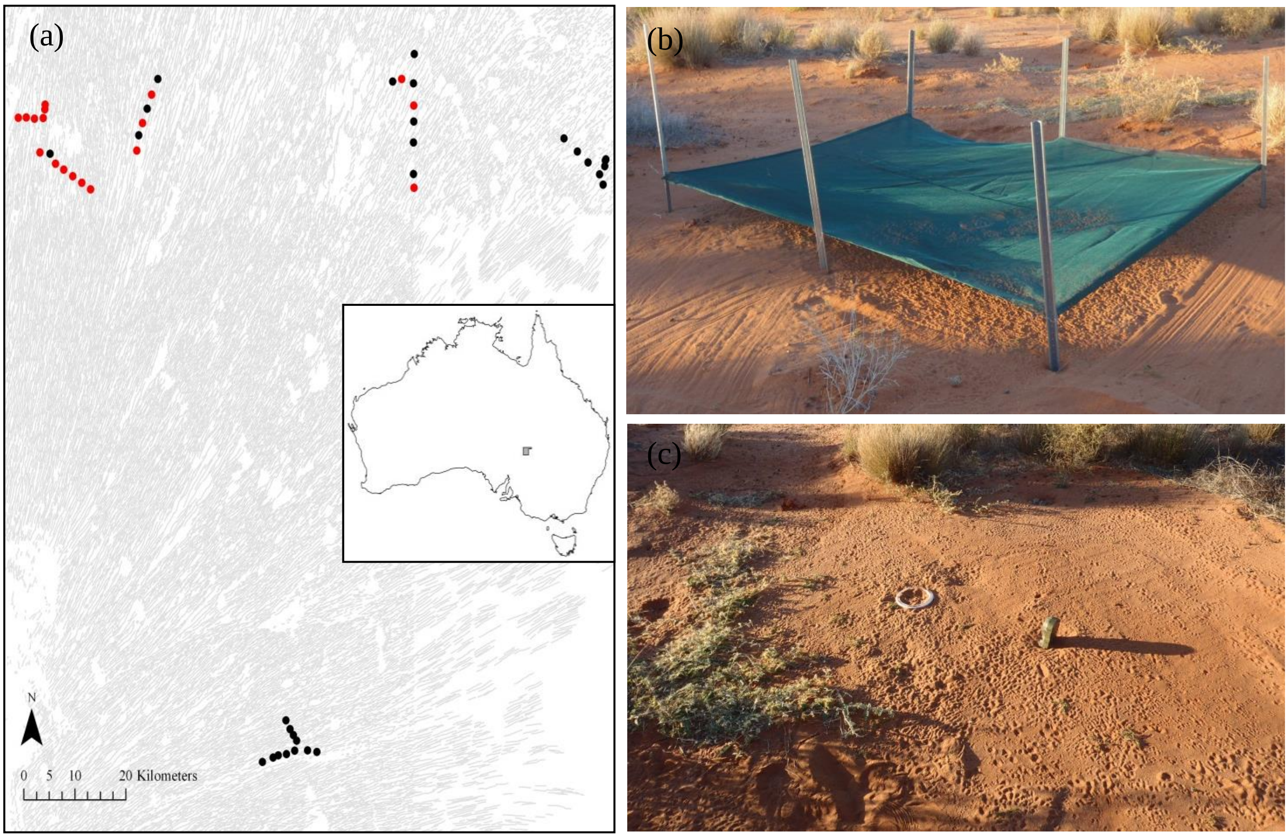

Figure 4.1. (a) Map showing the study area in the Strzelecki Desert of central Australia. Black and red circles represent sites used in Experiment 1. Red circles represent areas used in the Experiment 2. Underlying grey lines represent longitudinal sand dunes. (b) A photograph of the covered, "safe" treatment areas used in Experiment 2. (c) A photograph of the open, "risky" treatment areas used in Experiment 2.

The study was conducted in the states of South Australia and Queensland. Dingoes are relatively common in the region (Newsome et al., 2001; Letnic et al., 2009; Letnic and Dworjanyn, 2011). Because dingoes may kill cattle, some landholders control dingo populations using meat baits impregnated with the poison 1080 (sodium monofluoroacetate) and shooting. However in other parts of the study area no dingo-control is undertaken. Fox and cat populations typically increase in areas where dingo populations are suppressed because they are released from direct killing and inter-specific competition by dingoes (Letnic et al., 2012). The variation in dingo abundance resulting from the different levels of dingo-control employed in our study region, provided a natural experiment to evaluate the effects that dingoes, and in turn mesopredators, had on the foraging behaviour of *N. fuscus*.

Our study followed a prolonged period of high rainfall associated with a La Niña phase of the Southern Oscillation, and rainfall was within the 95th percentile of historic rainfall (since 1886) during 2010 (Tibooburra post office; Australia Bureau of Meteorology, 2013).

4.3.2 Experiment 1: The effects of predators and conspecific abundance on the GUD of Notomys fuscus

We undertook a landscape-scale study to determine how the GUD of *N. fuscus* varied in response to variation in dingo, fox and cat activity and the abundance of *N. fuscus*. We did this by conducting giving up density trials using enriched patches of narrow-leaved hopbush (*Dodonaea viscosa angustissima*; henceforth ‘hopbush’) seed at 47 sites subject to differing levels of predator control between May and October 2012 (Fig. 4.1). Before conducting our experiment, we constructed an *a priori* structural equation model (SEM) derived from interaction pathways theorized to occur between dingoes, foxes, cats, *N. fuscus* and moon phase (Fig. 4.2). Dingo activity was predicted to negatively affect both fox and cat activity through direct killing and interference competition (see Letnic et al., 2012). In turn, dingo activity was predicted to be correlated negatively with the GUD of *N. fuscus* by decreasing the risk of *N. fuscus* individuals being killed by a cat or fox (Letnic and Dworjanyn, 2011). Cat and fox activity was predicted to negatively affect *N. fuscus* abundance through predation (Letnic et al., 2009). In turn, fox and cat activity were predicted to have a positive correlation with the GUD of *N. fuscus* because the risk of *N. fuscus* individuals being killed by a predator should increase with increasing mesopredator abundance (Letnic and Dworjanyn, 2011). *Notomys fuscus* abundance was expected to negatively affect *N. fuscus* GUD because con-specific density dependence can potentially increase animals' allocation of time to foraging and increase the range of habitats exploited owing to intra-specific competition and / or 'safety in numbers' effects (China et al., 2008; Searle et al., 2008). Moon phase at the time of the study was expected to positively affect the GUD of *N. fuscus* because previous studies show that rodents perceive a greater risk of predation with increasing moonlight (Daly et al., 1992).

Hopbush is the dominant shrub within the study area and *N. fuscus* is known to consume hopbush seed. At each site, five plastic bowls (15 cm diameter, 5 cm depth) were filled with a matrix of sand and placed at 20 m intervals along a transect extending from dune bottom to dune top areas. Forty hopbush seeds (~ 2 mm diameter) were added to each seed tray and mixed through the sand before dusk, and seeds were recounted and replenished daily for two to three consecutive days. Sampling over three nights was not always possible due to logistical constraints imposed by climatic conditions and mechanical breakdowns. To confirm that *N. fuscus* was consuming seeds from the foraging trays the sand surrounding trays was swept daily. Foraging by *N. fuscus* was determined by the presence of their distinctive tracks. Only seed trays foraged by *N. fuscus* were included in analysis. GUD values were calculated for each site as the mean of values recorded across all five trays on the last two sampling nights. The first night of sampling was used to habituate mice to experimental seed trays and was excluded from analysis.

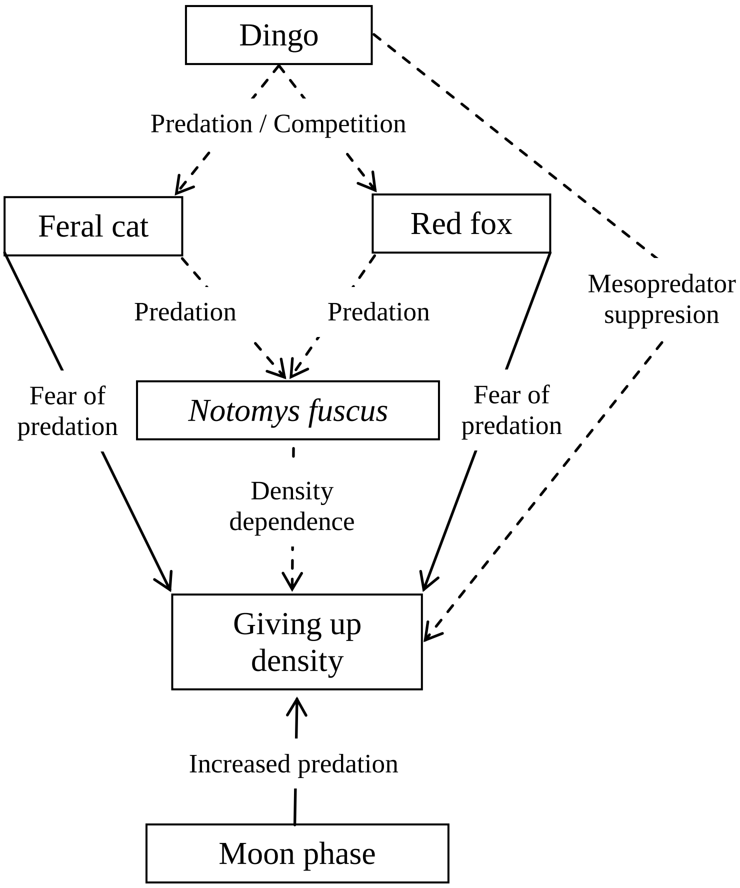

Figure 4.2. The a priori structural equation model showing the hypothesised affects that dingo, fox and cat activity, Notomys fuscus abundance and moon phase were expected to have on the giving up density of N. fuscus in Experiment 1. Solid lines represent positive pathways and dashed lines represent negative pathways. Text dissecting arrows show predicted responses of one variable on another.

Notomys fuscus abundance was indexed by live trapping mice using metal box traps (H.B.Sherman traps, Tallahassee, FL, USA) baited with a mixture of peanut butter, oats and golden syrup. Traps were placed at 20 m intervals within a 4 x 5 grid area and animals were trapped for two to three consecutive nights. Captured animals were given a unique mark and re-captured animals were excluded from analyses. Bait was replenished daily. An index of *N.*

fuscus abundance was calculated at each site as the total number of unique individuals captured per trapping night.

Predator activity was indexed at each site using 40 m long track plots located on single lane dirt roads at the bases of sand dunes. Track plots were swept daily, and the occurrence of dingo, fox and cat tracks was monitored for two to three consecutive days. An index of predator activity was then calculated as the proportion of nights that tracks of each predator was observed at each site. Moon phase data were obtained from the Australian Bureau of Meteorology and expressed as a percentage (0 indicated a new moon and 100 indicated a full moon).

We used structural equation modelling to evaluate support for hypothesised direct and indirect factors influencing the GUD of *N. fuscus* (Fig. 4.2; Bollen, 1989; Grace, 2006). SEMs use path diagrams and correlative data to infer causal relationships between test variables based on knowledge of biologically relevant interaction between species. Because SEMs calculate a covariance matrix between test variables, indirect path coefficients can be estimated and model reduction techniques can be used for model simplification.

We constructed an *a priori* SEM (see above section for model justification) and used an accelerated bootstrap method to test our predictions (Fig. 4.2; Grace, 2006). Accelerated bootstrap methods are appropriate for SEMs with relatively low sample sizes or with non-normal data (Grace, 2006). The Bollen-Stine (BS) test statistic was used to assess how well the final SEM fit the bootstrapped covariance matrix (ie. how well the model reproduces the data; Grace, 2006). Non-significant Bollin-Stine *P* values (α 0.05) indicated consistency between the replicated bootstrapped distribution and the data and are required for the interpolation of causal pathways within SEMs (Grace, 2006).

We used backward step-wise model reduction to simplify our model (Elmhagen et al., 2010). Non-significant pathways were sequentially deleted from the *a priori* model until all coefficient estimates were significant. The significance of direct path coefficients within this ‘most parsimonious’ SEM was then assessed by comparing estimated values against bootstrapped distributions, and indirect path coefficients were calculated by multiplying all direct path coefficients along indirect pathways (Grace, 2006). Analyses were conducted in the computer program IBM SPSS AMOS (Armonk, NY, USA).

Because spatial dependence is a problem within many landscape scale studies (Dormann et al., 2007), we tested for spatial autocorrelation of our dependent variable (the GUD of *N. fuscus*) using a Moran I test on the residuals of a generalized linear model (Poisson log-link function) which contained all variables used in our full SEM model. Data is not spatially auto-correlated if the Moran I statistic tends towards 0 and the associated *P* value is non-significant (α 0.05)

4.3.3 Experiment 2: The effects of predator activity and con-specific abundance on habitat use by foraging Notomys fuscus

Because the results of a pilot study and preliminary findings from Experiment 1 suggested that both predator activity and con-specific abundance influenced the GUD of *N. fuscus* (see results below), we conducted a manipulative experiment to parse out their effects by comparing the exploitation of food patches by *N. fuscus* in adjacent “risky” and “safe” habitats. The rationale for this experiment was that where *N. fuscus* perceived greater risk of predation, they should forage more from “safe” sheltered habitats than “risky” open habitats (Brown and Kotler, 2004; Orrock and Fletcher, 2014). To conduct our experiment we established 18 pairs of “risky” and “safe” food patches across a gradient of predator activity and measured the difference in the GUD between “risky” and “safe” pairs, as well as the activity of predators and abundance of *N. fuscus*. We used the difference in the GUD between “risky” and “safe” sites within each pair, measured as the log response ratio (LnRR; Hedges et al., 1999), as our response variable. By using the LnRR, a standardized metric of effect size, we were able to measure the relative allocation of foraging effort by *N. fuscus* in “safe” versus “risky” food patches while controlling for the effects that con-specific abundance and predator activity had on the GUDs that were evident in the results of Experiment 1. If dingoes provided *N. fuscus* with refuge from predation by mesopredators we predicted that the difference in the GUD between “risky” and “safe” patches should be similar in areas of relatively low predation risk where dingoes are common and mesopredators rare. Conversely we expected that *N. fuscus* should forage more from “safe” patches, and thus the difference in the GUD of “risky” and “safe” patches should be greater, in areas of high predation risk where dingoes are rare and mesopredators common. If con-specific abundance was an important determinant of the GUD of *N. fuscus,* we predicted the difference in the GUD between “risky” and “safe” patches should decrease with increasing population density.

Paired “safe” and “risky” food patches were established in open areas on dune tops at 18 of the 47 replicate sites (6 sites sampled during July 2012, 12 sites sampled during August 2012) used in *Experiment 1*. “Safe” patches were constructed by suspending a 2 x 2 m shade cloth (Coolaroo shade cloth, www.coolaroousa.com) 20 cm above the ground using wire and metal fence posts (Fig. 4.1). “Risky” patches were placed in open areas devoid of vegetation spaced 5 m from “safe” patches and consisted of 4 metal fence posts marking a similar 2 x 2 m area (Fig. 4.1). Experimental treatment blocks were constructed at least three days before experiments were conducted. One seed tray containing 50 hopbush seeds was placed at the centre of each “safe” and “risky” patch at each site. The GUD of *N. fuscus* was then assessed for three consecutive nights (for methods see the *Experiment 1*).

Dingo, fox and cat activity was assessed using the same 40 m predator-tracking plots used in the *Experiment 1*. To increase the detection rate of predators, an addition 40 m tracking plot was located on dune top areas surrounding experimental blocks. An index of dingo, fox and cat activity was calculated as the total activity between dune top and bottom areas per sampling night. Live trapping data from the *Experiment 1* were used to estimate *N. fuscus* abundance at each replicate site.

The risk perceived by foraging *N. fuscus* was assessed by calculating the difference in the GUD of paired “safe” and “risky” food patches using the LnRR, with “safe” food patches as the numerator and “risky” patches as the denominator (Hedges et al., 1999). If a positive LnRR values were recorded, *N. fuscus* consumed more seed from “risky” patches than “safe” patches (i.e. GUD higher at “safe” treatments than “risky” treatments). If negative LnRR values were recorded, *N. fuscus* consumed more seed from ‘“safe”’ patches than ‘“risky”’ patches (i.e GUD higher at “risky” patches than “safe” patches).

We used a linear mixed-effects model to assess the relative importance that dingo, fox and cat activity, and *N.fuscus* abundance (henceforth ‘predictor variables’) had on the LnRR of *N. fuscus* GUDs when sample period was treated as a random factor. All predictor variables were standardised to have a mean of 0 and a standard deviation of 1 prior to model fitting. We tested for spatial autocorrelation within our response variable using a Moran’s I test on the residuals of the linear mixed-effects model. Linear mixed-effects models were conducted in the computer program R (R Development Core Team, 2013) using the nlme (Pinheiro et al., 2013) library.

4.4 Results

4.4.1 Experiment 1: The effects of predators and con-specific abundance on the GUD of Notomys fuscus

Dingoes (range: 0 – 1 plots disturbed / night; average: 0.53 ± 0.05 SE plots disturbed / night) were the most active predators during the study period, followed by cats (range: 0 – 0.66 plot disturbed / night; average: 0.14 ± 0.03 plots disturbed / night) and foxes (range: 0 – 1 plot disturbed / night; average: 0.04 ± 0.03 SE plots disturbed / night). *Notomys fuscus* abundance varied considerably between sites (range: 8.33 – 0 captures / night; average: 1.78 ± 0.35 SE captures / night). The most parsimonious SEM explaining the GUD of *N. fuscus* contained all variables except moon phase (Fig. 4.3). Dingo activity was correlated negatively with cat activity (path coefficient: -0.50), and fox (path coefficient: -0.18) and cat (path coefficient: -0.39) activity were correlated negatively with *N. fuscus* abundance (Fig. 4.3). Because dingoes had a negative effect on cat activity and cat activity had a negative effect on *N. fuscus* abundance, dingo activity had an indirect positive effect on *N. fuscus* abundance (-0.50 x -0.39 = 0.20; Fig. 4.3).

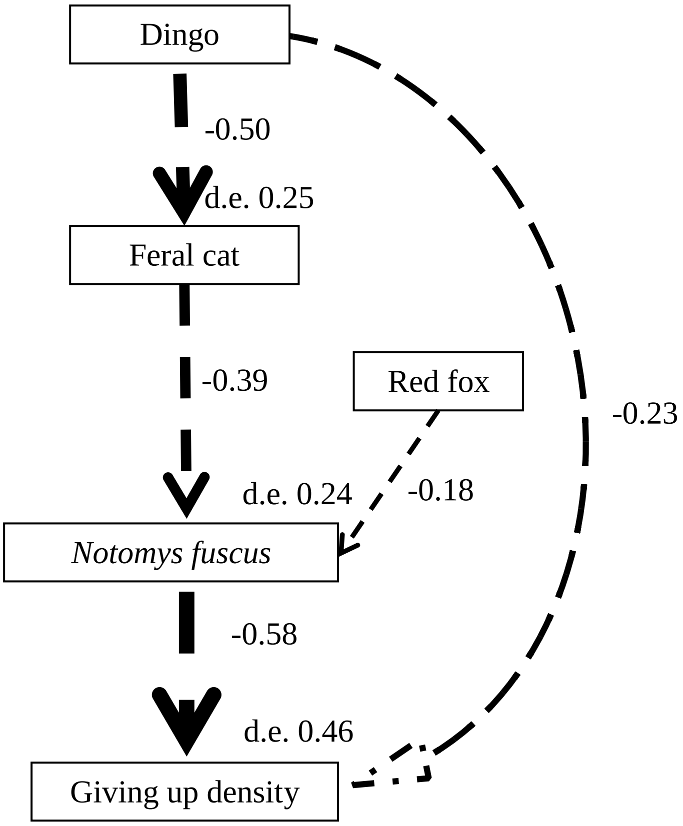

Figure 4.3. The most parsimonious structural equation model explaining the giving up density of Notomys fuscus in Experiment 1. Dashed arrows represent negative pathways and are weighted by standardised path coefficient estimates. d.e. shows the deviance explained by each variable.

Dingo activity (path coefficient: -0.23) and *N. fuscus* abundance (path coefficient: -0.58) were correlated negatively with the GUD of *N. fuscus* (Figs. 4.3 and S4.1). Thus increases in dingo activity and *N. fuscus* abundance resulted in decreased ‘fear’ responses of *N. fuscus*. Fox and cat activity had no direct effect on the GUD of *N. fuscus* however cats had an indirect positive effect on the GUD of *N. fuscus* because cat activity had a negative effect on *N. fuscus* abundance (-0.39 x -0.58 = 0.23; Figs. 4.3 and S4.1); increases in cat activity and associated decreases in *N. fuscus* abundance resulted in increased ‘fear’ responses of *N. fuscus*. Dingoes had an indirect negative effect on the GUD of *N. fuscus* because dingo activity had a negative effect on cat activity, and cat activity had a negative effect on *N. fuscus* abundance (-0.50 x -0.39 x -0.58 = -0.11; Fig. 4.3). No spatial autocorrelation occurred within the residuals of the response variable used in our SEM (Moran I statistic = 0.006, *P* = 0.638).

4.4.2 Experiment 2: The effects of predator activity and con-specific abundance on habitat use by foraging Notomys fuscus

As for Experiment 1, dingoes (range: 0 – 1 plot disturbed / night; average: 0.83 ± 0.02 SE site / night) were the most active predators at sampled sites, followed by cats (range: 0 – 0.83 plot disturbed / night; average: 0.21 ± 0.02 SE site / night) and foxes (range: 0 – 0.66 plot disturbed / night; average: 0.11 ± 0.01 SE site / night). *N. fuscus* abundances were similar to those recorded in Experiment 1 (range 4.33 – 0 captures / night; average: 1.37 ± 0.08 SE site / night). Collinearity was low between all predictor variables prior to model fitting (Table S4.1).

The linear mixed-effects model revealed that *N. fuscus* consumed more seed from '"safe"' patches than '"risky"' patches where cat activity was high, but took similar amounts of seed from "safe" and "risky" patches where dingo activity was high (Table 4.1, Fig. S4.2). This was because dingoes had a strong positive effect (coefficient estimate: 0.646) on the LnRR of *N. fuscus* GUDs and cats had a strong negative effect (coefficient estimate: -0.391) on the LnRR of *N. fuscus* GUDs (Table 4.1, Fig. S4.2). These results suggest that *N. fuscus* altered its behaviour to minimise encounters with cat but not dingoes. *Notomys fuscus* abundance was not present within the most parsimonious linear mixed-effects model (Table 4.1), and thus had a negligible influence on patch use by *N. fuscus*. No spatial autocorrelation occurred within the response variable used in our linear mixed-effects model (Moran I statistic = 0.019, $P = 0.399$).

Table 4.1. Results of a linear mixed-effects model comparing the effects that dingo, fox and cat activity and Notomys fuscus abundance had on the log response ratio (LnRR) of giving up densities of N. fuscus in "safe" and "risky" foraging patches measured in Experiment 2. The LnRR represents the proportional difference in GUD values between covered and opened experimental treatments. Negative LnRR values indicate a preference for sheltered habitats and positive LnRR values indicate a preference for open habitats.

Predictor variable	Coefficient estimate	F statistic	*P*
Dingo	0.646 ± 0.113	32.56	< 0.001
Red Fox	0.232 ± 0.132	< 0.001	0.992
Feral Cat	-0.391 ± 0.109	7.572	0.020
Notomys fuscus	0.170 ± 0.149	2.967	0.135

4.5 Discussion

Our study provides evidence that mesopredator suppression by a top predator can alleviate the risk of predation perceived by a small prey species. This refuge effect was evidenced by results showing that 1) where dingoes were common, cats were rare, 2) *N. fuscus* were more abundant where dingoes were common and cats were rare; 3) *N. fuscus* foraged less apprehensively where dingoes were common and cats were rare and 4) *N. fuscus* foraged more apprehensively in open versus shelter habitats where dingoes were rare and cats common, but showed similar levels of apprehension between shelter and open habitats where dingoes were common and cats were rare. Viewed collectively our results provide evidence that a top predators' suppressive effects on a mesopredators propagate to both population level and phenotypic effects on the prey of mesopredators.

Contrary to our first prediction and a wealth of literature suggesting that dingoes suppress fox activity throughout much of arid and semi-arid Australia (see Letnic et al., 2012), dingoes appeared to have a negligible effect on fox activity in our study. The absence of a correlation between dingo and fox activity in this study may have been due to the relatively high abundances of dingoes, and hence high suppressive effects of foxes by dingoes, throughout the study area. This interpretation is supported by previous studies showing consistently high dingo activity, and consistently low fox activity within the immediate study area between 2007 - 2012 (Letnic et al., 2012, Letnic & Dworjanyn 2011; ML unpublished data).

Consistent with the mesopredator release hypothesis, dingo activity was correlated negatively with cat activity. Previous studies have suggested that dingoes, even though they kill and sometimes eat cats (Moseby et al., 2012) do not always have a strong negative correlation with cat abundance (Letnic et al., 2012). In northern regions of the continent, where foxes are absent, dingoes appear to suppress the abundance and activity of cats (Kennedy et al., 2012). However, dingo and cat abundance show negative, neutral and even positive associations in central and southern areas where foxes are common (Risbey et al., 2000; Brook et al., 2012). Some authors have suggested that this variability in the numerical relationships between dingo and cat abundance may be due to both dingoes and foxes suppressing cat populations (Risbey et al., 2000; Kennedy et al., 2012). This is supported by studies in North America which have shown complex inter-predator relationships between wolves (*Canis lupus*), coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*; Levi and Wilmers, 2011). If this was the case, the rarity of foxes within our study area may have released cats from suppression by foxes, allowing cat activity to increase to a level where dingoes' suppressive effects on them could be detected.

In accord with the mesopredator release hypothesis our results revealed a positive correlation between dingo activity and *N. fuscus* abundance and negative correlations between *N. fuscus* abundance and the activity of cats and foxes (Letnic & Dworjanyn 2011; Letnic *et al.* 2012). Previous studies suggest that this refuge effect exists because the rate of per-capita predation on *N. fuscus* is reduced in the presence of dingoes (Letnic & Dworjanyn 2011). This effect may arise because where dingoes are not controlled they tend to occur at lower population densities than foxes and cats do in areas where dingoes have been removed. Additionally, dingoes are less likely to prey upon small mammals than are foxes or cats (Letnic et al. 2012).

Our GUD experiments are consistent with the idea that a top predator can shape the 'landscape of fear' for small prey by reducing the risk of predation. In our landscape-scale GUD trial (*Experiment 1*), the GUD of *N. fuscus* was positively correlated with cat activity but negatively correlated with dingo activity. This result suggests that *N. fuscus* dedicated more time to anti-predator behaviours than feeding behaviours where cat activity was high and dingo activity was low. This presumably occurred because dingoes suppressed cat activity, and in doing so reduced the predatory risk that cats posed to *N. fuscus*. However, hopping mouse abundance was also correlated negatively with the GUDs suggesting that density dependent factors also influenced the foraging behaviour of *N. fuscus* (see below). Our manipulative cover experiment (*Experiment 2*), which compared rodents' allocation of foraging effort to adjacent "risky" and "safe" food patches furthers the idea that dingoes provide *N. fuscus* with refuge from predation by showing that *N. fuscus* increased their habitat breadth and made relatively more use of "risky" food patches in areas where dingoes were common but cats rare. Taken together, these findings provide evidence that the refuge effects of top predators' can 1) increase the effort that prey species allocate to foraging, and 2) increase the breadth of habitats in which prey species choose to forage. Such alleviation of mesopredators' non-consumptive effects could potentially extend to the demography of *N. fuscus* and contribute to increased abundances, if greater foraging efficiency in the presence of dingoes translates to increased survival and reproductive success.

GUD experiments typically focus on predation risk as being the primary factor influencing foraging behaviour. However a suite of other factors may also place constraints on foraging such as resource variability, the energy state of foragers and intra-specific competition (Morris, 1997; Wasserberg et al., 2007; China et al., 2008; Searle et al., 2008). We predicted that, in addition to predation risk, con-specific abundance would influence food patch and habitat use of *N. fuscus* because individuals should allocate more effort to foraging as population density increases owing to intra-specific competition and / or a 'safety in numbers' effects (China et al., 2008; Searle et al., 2008). Our landscape scale GUD trials provided support for the idea that *N. fuscus* feed less apprehensively when occurring at high population densities. However, our manipulative cover experiment showed that *N. fuscus* abundance did not influence food patch use between "safe" and "risky" habitats when *N. fuscus* density was adjusted for in the analyses. Collectively, these results suggest that although *N. fuscus* abundance was positively correlated with foraging behaviour, food patch use by *N. fuscus* was primarily a response to the risk of predation perceived by foraging individuals.

4.6 Acknowledgements

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4.7 References

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4.8 Supplementary Information

*Table S4.1. Spearman's correlation matrix for predictor variables used in our Generalized Linear Models explaining the log response ratio of N. fuscus GUD. * significance at P < 0.05*

	Notomys fuscus	Dingo	Red fox	Feral cat
Notomys fuscus	1.000			
Dingo	-.122	1.000		
Red fox	-.529*	-.358	1.000	
Feral cat	.185	.292	-.395	1.000

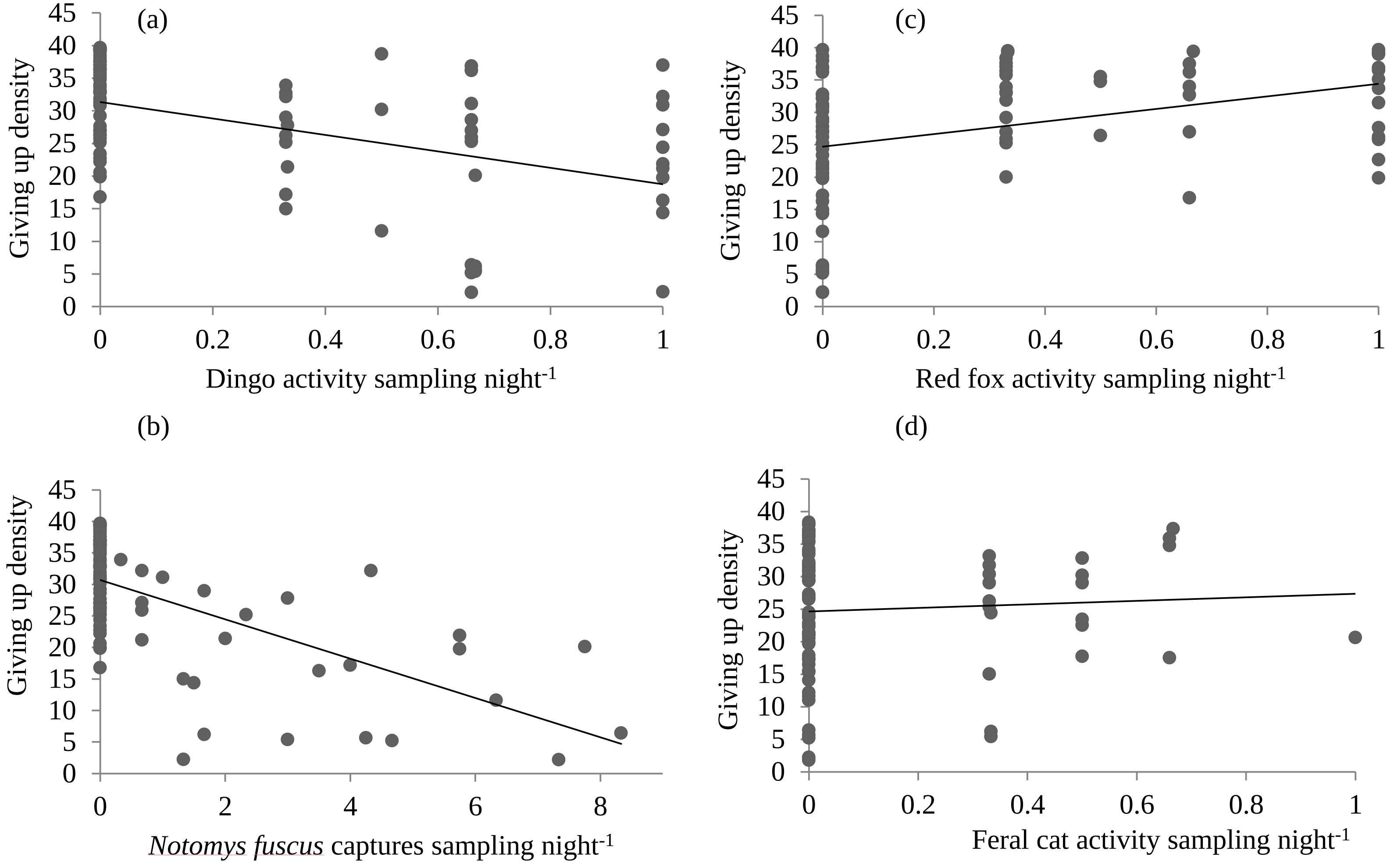

(a)
Giving up density
45
40
35
30
25
20
15
10
5
0
0
0.2
0.4
0.6
0.8
1
Dingo activity sampling night-1
(c)
Giving up density
Red fox activity sampling night-1
(b)
Giving up density
0
2
4
6
8
Notomys fuscus captures sampling night-1
(d)
Giving up density
Feral cat activity sampling night-1

Figure S4.1. Scatter plots showing the Giving Up Density (GUD) of Notomys fuscus plotted against a) dingo activity sampling night^{-1}*, b) feral cat activity sampling night*$^{-1}$*, c) red fox activity sampling night*$^{-1}$*, and d) Notomys fuscus captures sampling night*$^{-1}$*. Data were used in structural equation models for the Experiment 1 of the article. Linear trend lines are shown in black.*

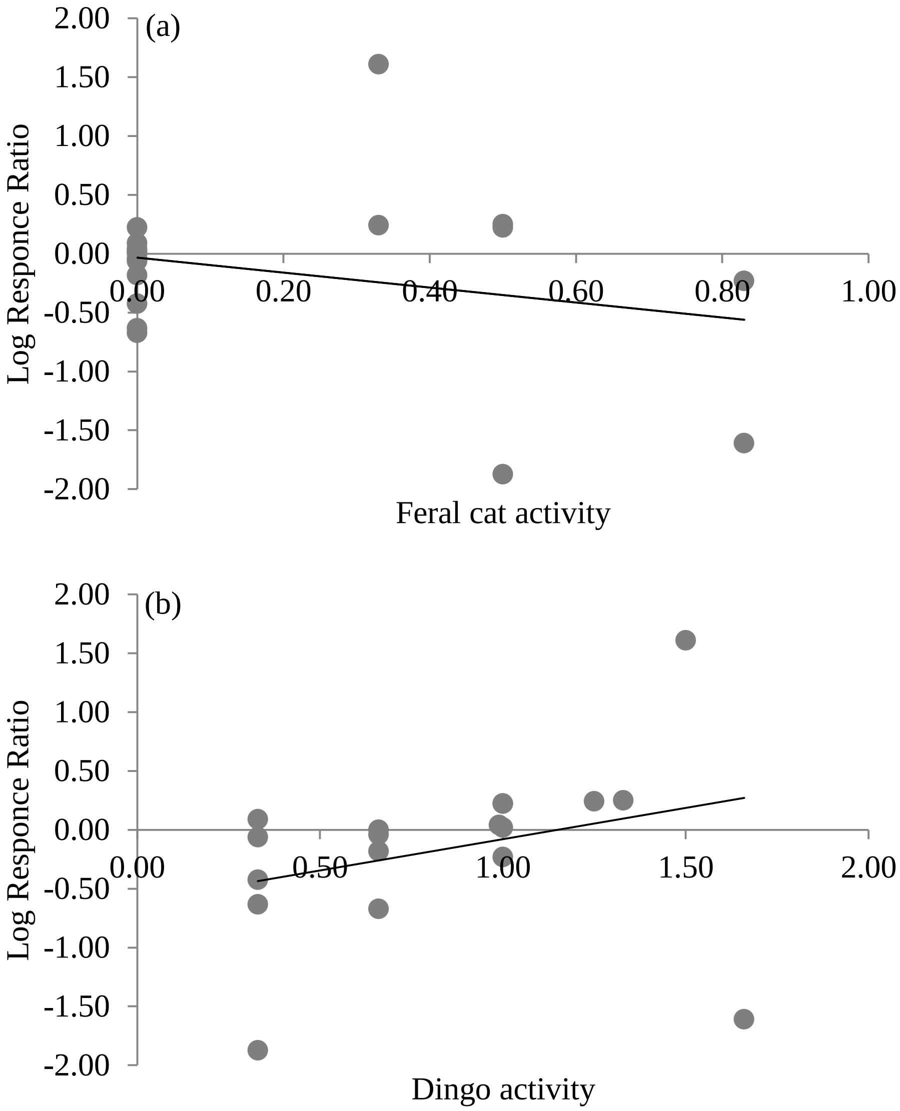
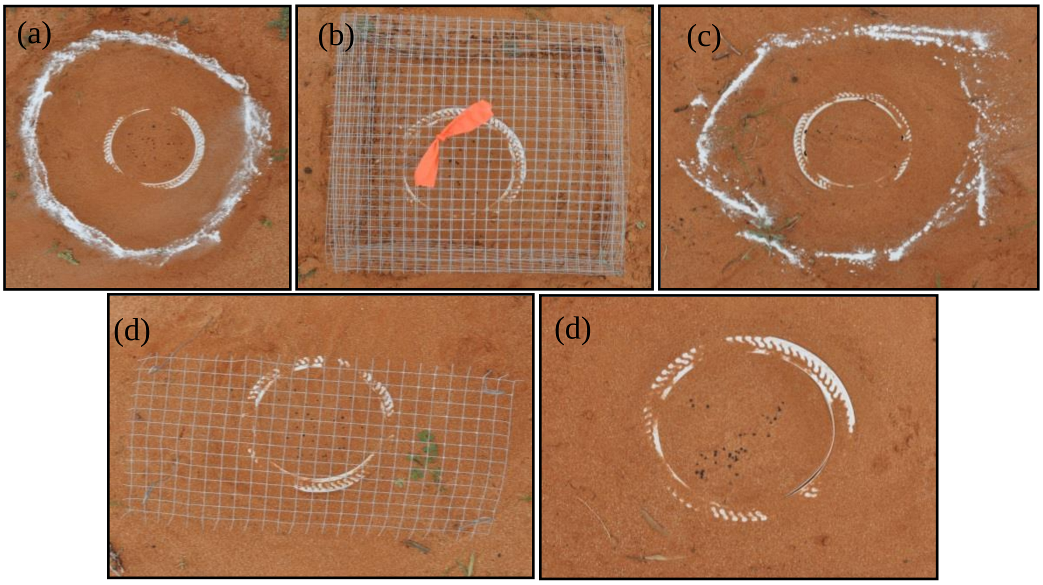


Figure S4.2. Scatter plots showing the Log Response Ration of the Giving Up Density of Notomys fuscus using in plotted against a) dingo activity sampling night^{-1}, and b) feral cat activity sampling night^{-1}. Data were used in generalised linear models for Experiment 2 of the article. Linear trend lines are shown in black.

Chapter 5: Functional extinction of desert rodents: implications for seed fate and vegetation dynamics

Gordon, C. E. & Letnic, M.

Statement of Authorship: CG and ML designed the study; CG collected data; CG wrote the manuscript: CG and ML edited the manuscript.



The five experimental treatments used in the *Rodent versus ant seed removal experiment*. (a) Shows the ant exclusion treatment, (b) shows the rodent exclusion treatment, (c) shows the ant exclusion procedural control treatment, (d) shows the rodent exclusion procedural control treatment, (e) shows the rodent and ant access treatment. Photos provided by Ben Moore.

Chapter 5. Functional extinction of desert rodents

5.1 Abstract

Population declines of once-abundant species have often preceded understanding of their roles within ecosystems. Although rodents can alter vegetation community composition through granivory, rodents have experienced large-scale species extinctions throughout the Earth. Australia's desert rodents have been thought to have little numerical impact on seed fate and ultimately on vegetation recruitment when compared with ants or with desert rodents on other continents. However most research on granivory by Australia's desert rodents has occurred in areas where rodents were rare or functionally extinct. Here we ask if the paradigm that rodents are relatively unimportant granivores in Australian deserts is an artefact of their historical decline. We used foraging trays to compare rates of seed removal (*Dodonaea viscosa angustissima* shrub seed; hopbush) between areas where a rodent, *Notomys fuscus*, and hopbush shrubs were rare and common and found that seed removal was consistently higher where rodents were common and hopbush were rare. By excluding ants and rodents from foraging trays we show that ants removed more seed than rodents where rodents were rare but rodents removed far more seeds than ants where rodents were common. By manipulating the access that rodents had to the soil seed bank we showed that hopbush seed accumulated in greater numbers where rodents were excluded than where they were allowed to enter. Our results suggest that granivory by rodents may once have been a far more important process influencing the fate of seeds and shaping plant communities in areas of arid Australia where rodents are now rare.

Keywords: granivore, rodent, functional extinction, *Notomys fuscus*, ant, arid, Australia

5.2 Introduction

Disruption to species interaction networks caused by the decline of species which have strong interactions with other species, such as predators or pollinators, can have far-reaching effects that result in the reorganization of ecosystems (Jordán, 2009; Delibes-Mateos et al., 2011). However, in many cases population declines of once abundant species have preceded understanding of their roles within ecosystems (Jackson et al., 2001). Consequently, important drivers of environmental change may remain undiagnosed because we simply do not know how species that are now rare or extinct shaped ecosystems through their inter-specific interactions in the past.

In many regions of the Earth, rodents influence the way ecosystems function through the engineering activities associated with constructing their shelter sites or by directly limiting plant recruitment via herbivory and granivory (Howe and Brown, 2000; Herrera and Pellmyr, 2002; Kauffman and Maron, 2006; Noble et al., 2007). However, because many species of rodents have undergone population declines their significance as ecosystem engineers and ecosystem architects is declining in some regions (Delibes-Mateos et al., 2011; Davidson et al., 2012).

The post-dispersal predation of seeds by granivores can be an important factor influencing plant recruitment and ultimately vegetation community composition in desert ecosystems where granivorous rodents, birds and ants tend to be conspicuous elements of the fauna (Morton, 1985a; Kelt et al., 1996). In the deserts of North America, the Middle East, Africa and South America predation and dispersal of seeds by rodents is a relatively important process shaping the seed bank and in turn vegetation communities (Morton, 1985a; Kelt et al., 1996; Kelt et al., 2004). In Australian deserts on the other hand, predation and dispersal of seeds by rodents is thought to have little influence on seed fate and plant community dynamics in comparison to ants (Morton, 1985a; Morton, 1985b; Kelt et al., 1996).

Explanations put forward to explain the weak influence that rodents have as seed predators in Australian desert ecosystems are 1) that because most species are omnivores and not facultative granivores their effects on seed populations are negligible and 2) that rodents have little predatory impact because they typically occur at very low population densities (Morton, 1985a; Murray and Dickman, 1994; Predavec, 1997). Indeed, the Australian rodent fauna has experienced large-scale population declines following the introduction of placental predators, the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*; Smith and Quin, 1996). Many Australian desert rodents are now extinct or so rare that they may be considered functionally extinct, except for brief periods following major rainfall events when high reproductive success of rodents can release them from top-down control (Letnic et al., 2011). Hence it is plausible that rodents were once much more important predators of seeds in arid Australia than they are now and that their decline has contributed to shifts in vegetation composition.

Here we ask if the paradigm that rodents are unimportant granivores in Australian deserts is an artefact of their historical decline and hence functional extinction. To conduct our study we performed a series of measurative and manipulative experiments to quantify the predatory effect that a desert rodent, *Notomys fuscus*, has on the seeds of a common shrub, *Dodonaea viscosa angustissima* (henceforth hopbush), in the Strzelecki Desert, Australia. Hopbush is one of a number of ‘shrub encroaching’ species which have increased in abundance in the study region over the past century (Noble, 1998). Our specific aims were 1) to compare hopbush cover and hopbush seed abundance in areas were *N. fuscus* were common and rare; 2) compare the rate of hopbush seed removal in areas where rodents were common and rare; 3) to experimentally compare rates of hopbush seed removal by *N. fuscus* and ants; and 4) compare the rate of hopbush seed accumulation between areas where rodents were excluded and allowed access.

5.3 Methods

5.3.1 Study area and Notomys fuscus

The study was conducted in adjacent areas on either side of the dingo-proof fence in the Strzelecki Desert, Australia (mean annual rainfall 188 - 227 mm; Tibooburra Post Office; Fig. 5.1; Australia Bureau of Meteorology, 2014). The dingo-proof fence was constructed along the New South Wales (NSW) / South Australia border between 1914 – 1917 to reduce dingo attacks on sheep in NSW (Letnic and Dworjanyn, 2011).

The dominant landforms in the study area are east – west trending sand dunes. Vegetation on dunes is dominated by an understory of grasses and forbs and an overstory of annual and perennial shrubs. The study was conducted before, during and after a period of wet climatic conditions that prevailed between 2010 and 2012 (annual rainfall between 592 - 317 mm; Tibooburra Post Office).

Our comparisons between areas with high and low abundance of *N. fuscus* were possible because sustained suppression of fox populations by abundant dingoes (*Canis dingo*; Australia’s largest terrestrial predator) on one side of the dingo-proof fence releases *N. fuscus* from top-down population control by foxes (Letnic and Dworjanyn, 2011). Consequently, where dingoes are common the populations of *N. fuscus* fluctuate in response to rainfall driven resource pulses but their abundance tends to remain consistently high through both high and low rainfall phases when compared to desert rodent populations in other regions of

Australia (Letnic et al., 2009a; Letnic et al., 2011). Conversely, where dingoes are suppressed by humans, fox populations irrupt and suppress *N. fuscus* abundances to very low levels except for brief periods following high rainfall events, which is typical of the dynamics of rodents in other regions of Australia (Letnic and Dworjanyn, 2011).

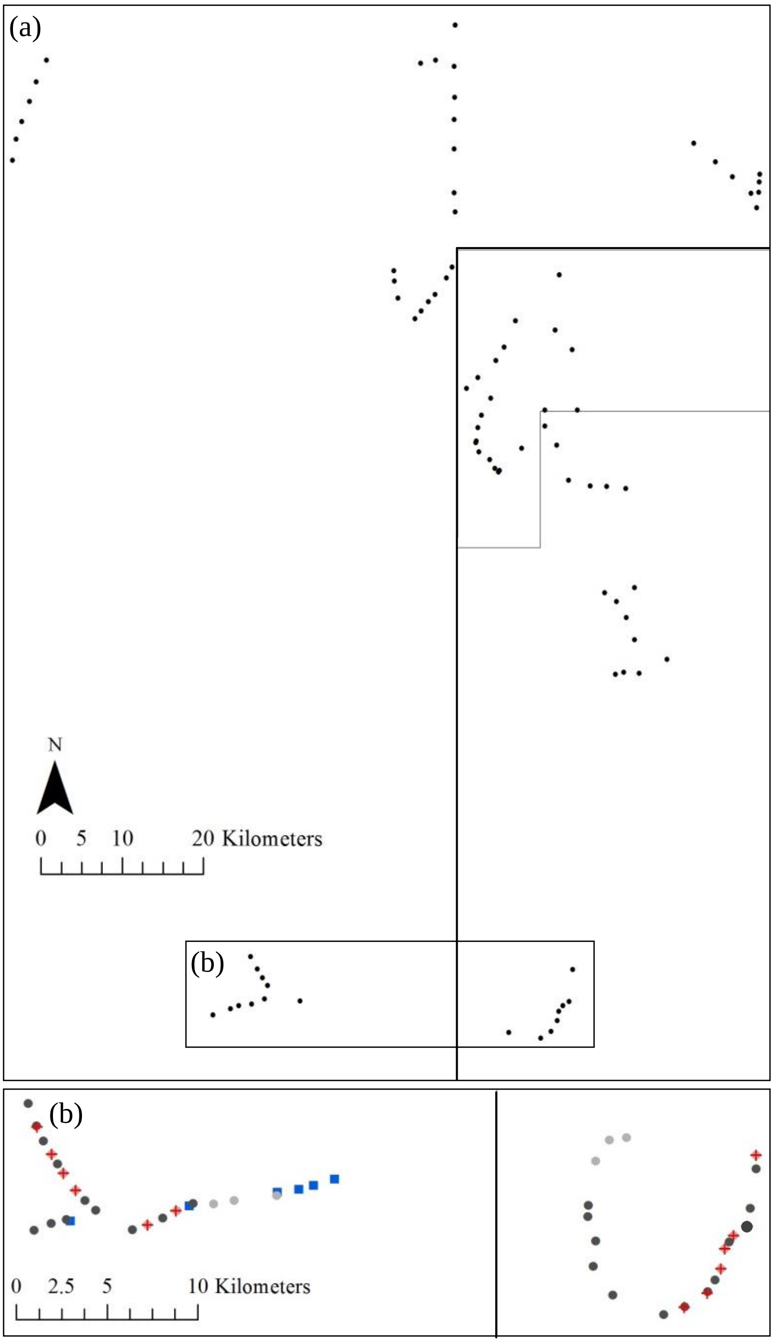


Figure 5.1. (a) Map showing the location of the dingo-proof fence (black line), the south boundary of Sturt National Park (grey line) and sites used to quantify hopbush cover (black circles). The insert (b) shows the location of sites used to 1) quantify temporal trends of hopbush seed removal and hopbush seed bank accumulation (red crosses), 2) conduct the rodent versus ant seed removal experiment during May 2012 (light and dark grey circles)

and March 2013 (dark grey circles), and 3) conduct the rodent exclusion and seed bank accumulation experiment (blue squares).

5.3.2 Hopbush cover, rodent abundance, hopbush seed removal and hopbush seed bank accumulation

Hopbush cover (> 100 cm height) was estimated at 86 sites (~ 1 ha) spread over an area of 5600 km^2. Sites were located on sand dunes, were spaced > 1 km from one another, and were always > 1 km (but typically > 2 km) from artificial water sources. Sites were located on pastoral properties (22 sites) and a conservation reserve (Sturt National Park; 21 sites) situated to the east of the dingo-proof fence (henceforth ‘inside’ the dingo-proof fence) where rodents were known to be rare, and pastoral properties (43 sites) situated to the west of the dingo-proof fence (henceforth ‘outside’ the dingo-proof fence) where previous studies have indicated that rodents are common (Fig. 5.1; Letnic et al., 2009a; Letnic and Dworjanyn, 2011). The Bitterlich gauge method was used to estimate hopbush cover (Friedel and Chewings, 1988). This method produces a shrub cover estimate (within an infinite radius) which is proportional to shrub abundance (Friedel and Chewings, 1988). A Bitterlich gauge was constructed (75 cm length, 7.5 cm cross bar) and shrub cover estimated at three points on the top of dunes and three points at the base of dunes (50 m interval between points). All sites were sampled between May 2012 and June 2013. An index of hopbush cover was calculated at each site as the average number of hopbush shrubs counted between the six sampling points.

We indexed *N. fuscus* abundance by counting the number of individuals within a 20 m belt transect during nocturnal spotlight surveys conducted from the top of a four-wheel drive vehicle moving at 10 – 15 km per hour using a 50 W spotlight (Letnic and Dworjanyn, 2011).

Three or four (10 – 20 km length) surveys were conducted on either side of the dingo-proof fence on nine occasions between September 2007 and March 2014. An index of *N. fuscus* abundance (*N. fuscus* sighted per km^2) was calculated on either side of the dingo-proof fence during each sample period by dividing the number of individuals counted by the area surveyed.

Foraging trays, 15 cm diameter, 5 cm depth filled with a matrix of sand, containing 40 hopbush seeds were used to compare the rate of seed removal at six sites on each side of the dingo-proof fence where rodents were rare and common on five occasions between June 2011 and March 2013 (Fig. 5.1). Sites were situated on dunes and were spaced 1 km apart but never closer than 10 km or further than 30 km from the dingo-proof fence. Within sites, five foraging trays were spaced 20 m apart along a transect which extended from the base to the top of dunes. Seed removal was measured for three consecutive nights and seeds replenished daily. An index of seed removal was calculated for each site as the average number of seeds removed from the five foraging trays during the last two nights of sampling. The first night of sampling was used to habituate granivores to foraging trays (Morris, 1997).

Soil samples (20 x 20 cm width, 4 cm depth) were used to compare the abundance of hopbush seeds in the soil at five to six sites on each side of the dingo-proof fence during June 2011 (five sites), October 2011 (six sites) and March 2012 (six sites; Fig.5.1). Soil samples were collected from three points at the base of dunes and three points at the top of dunes. All sampling points were spaced at 20 m intervals and soil samples were dried and stored in plastic bags for laboratory analysis. In the laboratory, samples were sieved using a 0.05 cm gauge sieve and all unblemished hopbush seeds (glossy black coating, no signs of breakage or seed predation, seeds did not break when a small force was applied using forceps) were counted using a binocular microscope. An index of hopbush seed abundance was calculated at each site during each sample period as the total number of hopbush seeds counted between the six soil samples.

A one factor analysis of variance test was used to compare hopbush cover (log + 1 transformed) between pastoral and conservation sites inside the dingo-proof fence and pastoral sites outside the dingo-proof fence. A linear mixed-effects model was used to compare how sampling period and dingo-proof fence treatment affected temporal trends in hopbush seed removal (log + 1 transformed). A generalised linear mixed-effects model (Poisson log-link function) was used to compare how sampling period and dingo-proof fence treatment affected temporal trends in hopbush seed bank accumulation. Sample site was treated as a random factor for mixed-effects models. Tukey tests were used to undertake *post hoc* pairwise comparisons. Mixed-effects models were conducted in the statistical program R (R Development Core Team, 2013) using the ‘lme4’ (Bates et al., 2014) and ‘car’ (Fox et al., 2009) packages. *P* values were used to infer statistical significance.

5.3.3 Rodent versus ant seed removal

We compared rates of seed removal by ants and *N. fuscus* on either side of the dingo-proof fence by manipulating the access that rodents and ants had to foraging trays. Five trays, each representing a different treatment, were placed at 20 m intervals along the tops of sand dunes at 20 and 12 sites on each side of the dingo-proof fence during May 2012 and March 2013, respectively (Fig. 5.1). Thirty hopbush seeds were placed in foraging trays in May 2012 and 40 in November 2012. Seed removal was assessed for three consecutive nights as described above.

The treatments were; 1) rodent access and ant exclusion (30 cm diameter ring of Coopex Insecticide Dust around foraging trays; Bayer Chemicals, Leuerkusen); 2) ant access and rodent exclusion (30 cm width, 30 cm height, 0.65 cm gauge wire cages, placed over foraging trays); 3) ant and rodent access ; 4) rodent access and ant exclusion procedural control (30 cm diameter circle of sodium bicarbonate around foraging trays allowing rodent and ant access); 5) ant access and rodent exclusion procedural control (30 cm width, 30 cm height, 0.65 cm gauge un-walled wire cages placed over foraging trays allowing rodent and ant access).

Notomys fuscus foraging was identified through the presence of their tracks surrounding foraging trays. Ants were assumed to be the major foragers of seeds at sites where rodent tracks were absent (Harrington and Driver, 1995); ants were observed pilfering seeds from trays. Bird tracks were never observed at foraging trays (Morton and Davies, 1983).

A linear mixed-effects model was used to compare how sampling period, dingo-proof fence treatment and experimental treatment affected hopbush seed removal (log + 1 transformed). An offset was added to the model to account for the different number of hopbush seeds used between sampling trips. Sample site was treated as a random factor. Tukey tests were used to undertake *post hoc* pairwise comparisons.

5.3.4 Rodent exclusion and seed bank accumulation

Rodent granivory of post-dispersal hopbush seed was quantified by experimentally manipulating the access that rodents had to the soil seed bank. Three experimental treatments were constructed around mature hopbush shrubs (276 cm ± SE 0.14 average height) at six sites outside the dingo-proof fence during September 2012 (Fig. 5.1). The three experimental treatments were; 1) rodent exclusion (700 cm by 700 cm width, 100 cm height, 30 cm depth exclusion cages constructed using 0.65 cm gauge wire mesh) 2) rodent access (four metal fence posted marking a 700 by 700 cm width area); 3) rodent exclusion procedural control (700 cm by 700 cm width, 100 cm height, 30 cm depth exclusion cages constructed using 0.65 cm gauge wire mesh and containing twelve 60 cm height, 100 cm width windows which allowed for rodent access). Within each site, experimental treatments were spaced at 20 m intervals and were located at the base of dunes.

After construction, experimental treatments were left until January 2014 at which time four 20 cm x 20 cm width, 4 cm depth soil samples were randomly collected from within each treatment and stored for laboratory analysis; hopbush seed annually between September and November (Cunningham et al., 1992). In the laboratory, samples were sieved using a 0.05 cm gauge sieve and all unblemished hopbush seeds were counted using a binocular microscope (as previously described). An index of hopbush seed abundance was calculated for each experimental treatment at each site as the total number of hopbush seed counted between the four soil samples.

A generalised linear mixed-effects models (Negative Binomial link function) was used to compare how rodent exclusion affected hopbush seed bank abundance. Sample site was treated as a random factor for all mixed-effects analyses. Tukey tests were used to undertake *post hoc* pairwise comparisons.

5.4 Results

5.4.1 Hopbush cover, rodent abundance, hopbush seed removal and hopbush seed bank accumulation

Hopbush cover was greater inside than outside the dingo-proof fence (*F* statistic = 37.78, df = 2, $P < 0.0001$) and was similarly high between conservation and pastoral areas inside the dingo-proof fence (Fig. 5.2a, Table 5.S1). *Notomys fuscus* was more abundant outside than inside the dingo-proof fence on all sampling occasions except June 2011 (Fig. 5.2b). Similarly, hopbush seed removal was greater outside than inside the dingo-proof fence on all sampling occasions except June and October 2011 (Fig. 5.2c; Tables 5.1 and 5.S1). Hopbush seed was present at greater numbers within soil samples collected inside rather than outside the dingo-proof fence (Fig. 5.2d; Tables 5.1 and 5.S1).

5.4.2 Rodent versus ant seed removal

Seed removal was higher outside than inside the dingo-proof fence for all experimental treatment comparisons excluding the ant access treatment (Fig. 5.3; Tables 5.1 and 5.S2); *N. fuscus* exclusion resulted in similarly low levels of seed removal by ants throughout the study area.

When experimental treatment groups were compared with the control treatment (*N. fuscus* and ant access) on either side of the dingo-proof fence, seed removal was only higher for the ant access treatment outside the dingo-proof fence, and the rodent access treatment inside the dingo-proof fence (Fig. 5.3, Table 5.S2).

5.4.3 Rodent exclusion and seed bank accumulation

Hopbush seed accumulated in greater numbers where rodents were excluded than in the control or procedural control treatments where *N. fuscus* were allowed entry ($\chi^2 = 7.653$, df = 2, $P = 0.0218$; Fig. 5.4, Table 5.S3). Hopbush seeds were equally abundant in the rodent access and procedural control treatments (Fig. 5.4, Table 5.S3).

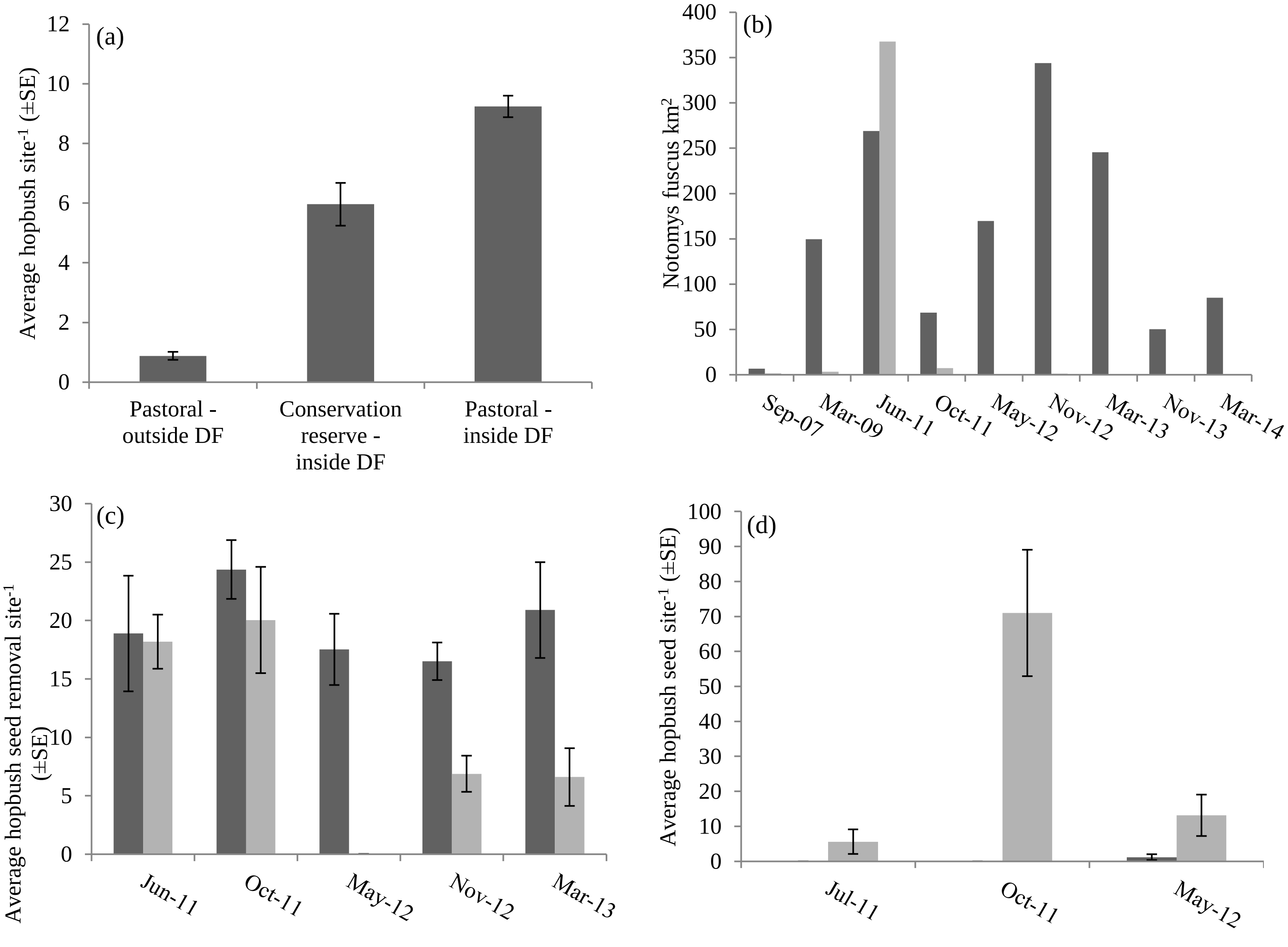


Figure 5.2. (a) Average number of hopbush shrubs observed (± SE) on pastoral sites inside and outside the dingo-proof fence and conservation sites inside the dingo-proof fence. DF

represents dingo-proof fence. (b) Notomys fuscus abundance on nine sampling occasions. (c) Average number of hopbush seeds taken from foraging trays (± SE) on five sampling occasions. (d) Average number of hopbush seeds found in soil seed bank samples on three sampling occasions. For (b), (c) and (d) light bars represent inside the dingo-proof fence, dark bars represent outside the dingo-proof fence.

Table 5.1. Results of linear mixed-effects models comparing (a) hopbush seed removal on either side of the dingo-proof fence during five sample periods, and (b) hopbush seed removal from experimental treatment on either side of the dingo-proof fence during two sample periods for the Rodent versus ant seed removal experiment. (c) Results of a generalised linear mixed-effects model comparing hopbush seed bank accumulation on either side of the dingo-proof fence during three sample periods.

	df	χ^2 statistic	*P*
a) Temporal trends in hopbush seed removal			
Sample period	4	235.28	< 0.0001
Dingo-proof fence treatment	1	107.50	< 0.0001
Sample period : dingo-proof fence treatment	4	197.07	< 0.0001
b) Rodent versus ant seed removal			
Sample period	1	2.37	0.124
Dingo-proof fence treatment	1	70.08	< 0.0001
Experiment treatment	4	91.38	< 0.0001
Sample period : dingo-proof fence treatment	1	5.27	0.022
Sample period : experimental treatment	4	7.19	0.126
Dingo-proof fence treatment : experimental treatment	4	100.65	< 0.0001

	df	χ^2 statistic	*P*
Sample period : dingo-proof fence treatment : experimental treatment	4	1.54	0.819
c) Temporal trends in hopbush seed bank accumulation			
Sample period	2	296.37	< 0.0001
Dingo-proof fence treatment	1	16.67	< 0.0001
Sample period : dingo-proof fence treatment	2	10.08	0.0064

5.5 Discussion

5.5.1 Rodent extinction and granivory

Our results provide evidence that granivory by rodents may once have been a far more important process influencing the fate of seeds and shaping plant communities in areas of arid Australia where rodents are now rare. On average, the rate of seed removal by *N. fuscus* was 1.8 times higher in areas where they were abundant than where they were rare. Our experimental comparison of seed removal by ants and rodents confirmed the results of our seed removal study and showed that ants were the most important seed predators where *N. fuscus* was rare. Our experimental comparison of hopbush seed accumulation showed that hopbush seed was more abundant in areas where rodents were excluded than allowed access. Collectively, our findings suggest that seed predation by rodents is likely to be an important factor influencing the fate of seeds in areas of arid Australia where abundant populations of rodents persist. Our results imply that both the dominance of ants as granivores in arid Australia and the relatively low levels of overall granivory previously reported for Australian deserts (Morton, 1985a; Murray and Dickman, 1994; Kelt et al., 1996; Predavec, 1997) may be an artefact of the decline and hence functional extinction of rodents.

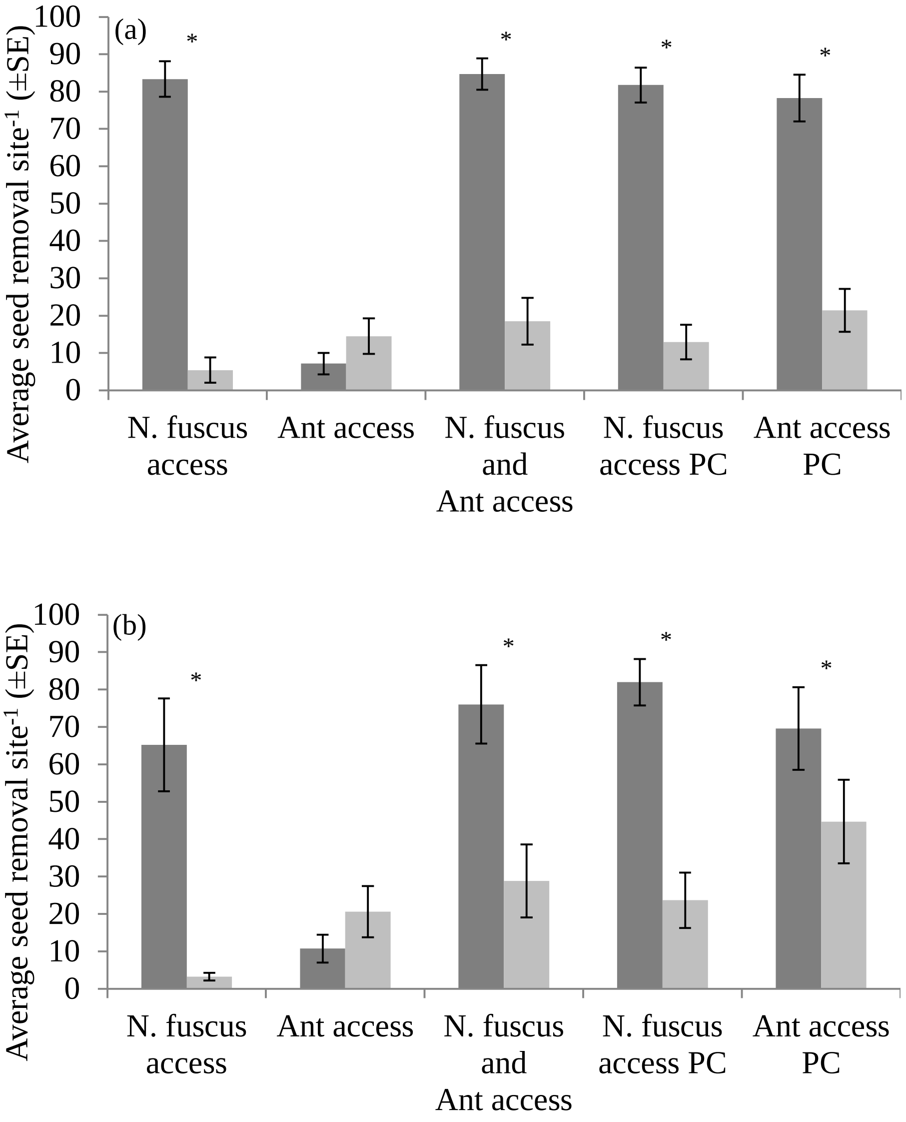


Figure 5.3. Average number of hopbush seeds removed from areas inside (light bars) and outside (dark bars) the dingo-proof fence (± SE) for the Rodent versus ant seed removal experiment during (a) May 2012 and (b) March 2013. Asterisks indicate significant ($P < 0.05$) cross dingo-proof fence comparisons. PC represents procedural control.

In accordance with previous studies (Morton, 1985a; Murray and Dickman, 1994; Kelt et al., 2004), our results show that ants were the most important seed predators where *N. fuscus* was rare. However *N. fuscus* removed far more seed than ants in areas when high population abundances persisted. Studies that have previously reported low levels of granivory by desert rodents in Australia when compared with deserts on other continents have largely occurred in places and at times where rodents were rare (Morton, 1985a; Murray and Dickman, 1994; Predavec, 1997; Kelt et al., 2004). Throughout much of arid Australia where dingoes were once common but are now rare, desert rodents have undergone dramatic declines in abundance, owing primarily to predation by invasive foxes and cats (Smith and Quin, 1996). In these areas, most rodent species are usually rare, except for relatively brief periods following high-rainfall events when a surfeit of food resources allows their populations to escape top-down regulation by invasive predators (Letnic et al., 2011; Greenville et al., 2012). While previous studies have hypothesised that rodents may be important predators of seeds during their population irruptions (Murray and Dickman, 1994), few attempts have been made to assess their seed consumption during periods of high rodent abundance. One reason for this paucity of studies may be that most rodent irruptions are short-lived, as occurred at our study sites inside the dingo-proof fence during June 2011, owing to the onset again of top-down predation by predators coupled with the dwindling of food resources that inevitably occurs following resource pulses (Letnic et al., 2011).

Our Strzelecki Desert site located outside the dingo-proof fence is unusual when compared to areas of arid Australia where introduced predators are abundant because rodent populations were consistently high during both periods of wet and dry climatic conditions (Letnic et al., 2009a; Letnic and Dworjanyn, 2011). The high populations of rodents that occur at this site and other locations where invasive predators are excluded by predator-proof fencing (for example, areas of central South Australia where dingoes are common and foxes and cats rare; Moseby et al., 2009) may provide an indication of what rodent populations and in turn rates of granivory were like prior to the introduction of red foxes and feral cats. Indeed, numbers of *N. fuscus* we observed were consistent with the account of Charles Sturt, who remarked upon their abundance when he explored the region in 1844, prior to the establishment of foxes and cats (qualitative observations made in Charles Sturts diary; Sturt, 1984).

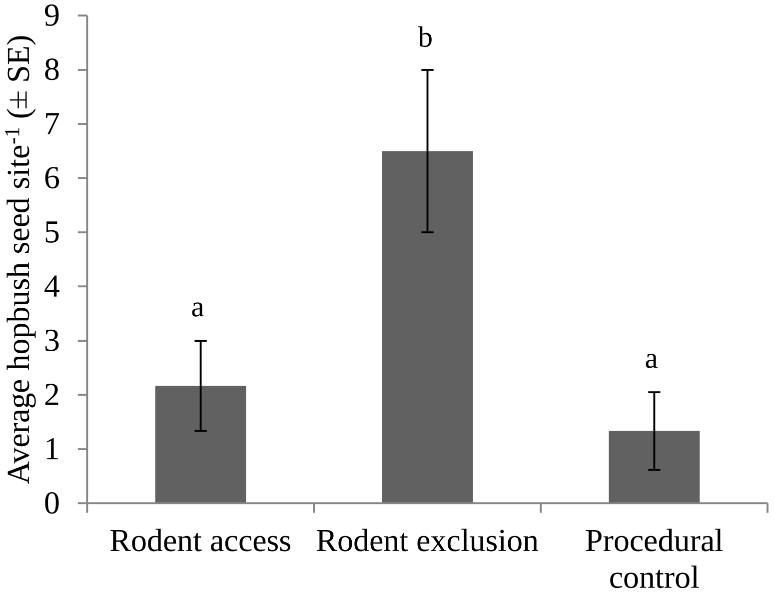


Figure 5.4. Average (±SE) number of hopbush seeds found in soil seed bank samples collected from rodent exclusion, rodent access and procedural control treatments for the Rodent exclusion and seed bank accumulation experiment. a and b represent statistically similar and different pairwise comparisons P < 0.05.

5.5.2 Rodent extinction and vegetation dynamics

The recruitment of plants is often dependent upon the positive and / or negative effects that pollinators, frugivores, granivores or herbivores place on the production and survival of seeds

(Olff and Ritchie, 1998; Valone and Schutzenhofer, 2007; Anderson et al., 2011; Wotton and Kelly, 2011). Previous research has shown that historic declines of functionally important frugivores and pollinators can alter vegetation community structure by limiting plant recruitment through their effects on seed production and dispersal (Anderson et al., 2011; Wotton and Kelly, 2011). Experimental studies have demonstrated that rodents often limit plant recruitment through granivory and in doing so can also influence vegetation community composition (Heske et al., 1993; Kauffman and Maron, 2006; Valone and Schutzenhofer, 2007).

Unlike ants, which typically do not destroy hopbush seeds but consume the elaiosme only and in doing so often facilitate seed growth and dispersal (Harrington and Driver, 1995), *N. fuscus* consumed seeds at foraging trays (broken seeds were observed at all trays foraged by *N. fuscus*). In addition, results of our exclusion experiment which showed that *N. fuscus* can suppress the rate of accumulation of hopbush seed in the seedbank, suggest that predation by *N. fuscus* can suppress the rate of hopbush seed accumulation in the soil. Thus it is plausible that the functional extinction of *N. fuscus* could be a factor contributing to the greater abundance of hopbush seed that we observed in areas where *N. fuscus* were rare (Fig. 5.2d). Moreover, diminished seed predation by *N. fuscus* could conceivably be a factor driving the disparity in hopbush cover on either side of the dingo-proof fence (Fig. 5.2a), if the abundance of viable seed is a factor that limits hopbush recruitment (Semple and Koen, 1997); the longevity of the hopbush seed bank is relatively short (0 - 20 % of seeds present in the seed bank often 1 year; Harrington and Driver, 1995) and seed survival is negatively affected by desiccation, ant burial and fire related mortality (Hodgkinson and Harrington, 1985; Harrington, 1991; Harrington and Driver, 1995).

Hopbush is one of a number of native woody shrub species which have increased in abundance in arid regions of Australia in the last 150 years (Noble, 1998; Fensham and Fairfax, 2002). This phenomenon referred to as shrub encroachment has occurred in arid regions throughout the Earth, and can result in the conversion of once opened grassland or mixed grassland / woodland mosaic ecosystems to close woodland communities (Van Auken, 2000). Shrub encroachment is hypothesized to result from complex interactions among grazing, burning, and elevated atmospheric $C0_2$ concentrations facilitating the recruitment of shrubs, however, the drivers of encroachment are not well understood (Briggs et al., 2005). Diminished seed predation by rodents has been overlooked as a driver of shrub encroachment, even though rodents have undergone dramatic declines in abundance in many regions of the Earth where encroachment has occurred, including Australia’s arid lands (Smith and Quin, 1996; Noble, 1998; Letnic et al., 2009b; Davidson et al., 2012). In light of the results presented here, we propose that the functional extinction of rodent granivores may be an overlooked driver of shrub encroachment and vegetation dynamics more generally in arid Australia, and possibly other regions where declines of rodents have occurred.

5.5.3 Conclusion

We contend that seed predation by native rodents may once have been a much more important process limiting seed fate and vegetation dynamics in Australian deserts than at present. Further, because rodents have undergone dramatic species extinction and range restrictions in many areas of the Earth where vegetation changes are known to have previously occurred, we propose that the functional extinction of rodents may be an under-appreciated driver of vegetation change.

5.6 Acknowledgments

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5.8 Supplementary Information

Table 5.S1: Pairwise post hoc comparisons (Tukey test) comparing a) hopbush cover between pastoral sites inside and outside the dingo-proof fence and conservation reserve sites inside the dingo-proof fence, b) hopbush seed removal on either side of the dingo-proof fence during each sampling period and c) hopbush seed bank accumulation on either side of the dingo-proof fence during each sampling period. DF represents dingo-proof fence.

	Estimate	*z* / *t* value	*P*
a) Hopbush cover			
Pastoral inside DF– Pastoral outside DF	1.393	7.687	< 0.0001
Conservation reserve inside DF – Pastoral outside DF	1.176	6.387	< 0.0001
Pastoral inside DF – Conservation reserve inside DF	0.218	1.031	0.558
b) Hopbush seed removal			
June 2011	-0.078	-0.514	0.976
October 2011	0.135	0.891	0.947
May 2012	1.212	8.361	< 0.001
November 2012	0.427	2.932	0.017
March 2013	0.545	3.739	< 0.001
c) Hopbush seed bank accumulation			
June 2011	-3.302	-2.162	0.088
October 2011	-6.691	-4.432	< 0.0001
May 2012	-2.607	-2.695	0.021

Table 5.S2. Pairwise post hoc comparisons (Tukey test) for the Rodent versus ant seed removal experiment. Comparisons are shown between a) experimental treatment groups and the control treatment group (N. fuscus and ant access) outside the dingo-proof fence, b) experimental treatment groups and the control treatment group (N. fuscus and ant access) inside dingo-proof fence, and c) experimental treatment groups on either side of the dingo-proof fence. Data from the May 2012 and March 2013 sampling periods were grouped for analyses; no interaction occurred between sample period and experimental treatment groups within the linear mixed-effects model. PC = procedural control.

	Estimate	*z* value	*P*
a) Within experimental treatment group comparisons – outside the dingo-proof fence			
Ant access - *N. fuscus* and ant access	-1.008	-10.274	<0.01
Ant access PC - *N. fuscus* and ant access	-0.097	-0.990	0.992
N. fuscus access - *N. fuscus* and ant access	-0.090	-0.922	0.995
N. fuscus access PC - *N. fuscus* and ant access	0.041	0.422	1
b) Within experimental treatment group comparisons – inside the dingo-proof fence			
Ant access - *N. fuscus* and ant access	-0.0693	-0.706	0.999
Ant access PC - *N. fuscus* and ant access	0.092	0.939	0.995
N. fuscus access - *N. fuscus* and ant access	-0.427	-4.351	<0.01
N. fuscus access PC - *N. fuscus* and ant access	-0.105	-1.069	0.987
c) Experimental treatment group comparisons on either side of the dingo-proof fence			
Ant access	-0.219	-1.854	0.688
N. fuscus access	1.056	8.925	<0.01
N. fuscus and ant access	0.720	6.081	<0.01
Ant access PC	0.530	4.482	<0.01

N. fuscus access PC	0.866	7.317	<0.01

Table 5.S3: Pairwise post hoc comparisons (Tukey test) comparing hopbush seed bank accumulation between rodent exclusion, rodent access and procedural control treatments used in the Rodent exclusion and seed bank accumulation experiment.

	Estimate	*z* value	*P*
Rodent exclusion – Rodent access	1.100	3.414	0.002
Procedural control – Rodent access	-0.486	-1.078	0.497
Rodent exclusion – Procedural control	-1.585	-2.633	0.020

Chapter 6: Dingo (*Canis dingo*) extirpation initiates a trophic cascade ultimately leading to shrub encroachment

Gordon, C. E., Moore, B. D., Feit, A. & Letnic, M.

Statement of Authorship: CG and ML designed the study; CG and AF collected data; CG wrote the manuscript; all authors edited the manuscript.

An example of dingo tracks walking along a road in the Strzelecki Desert. Photo provided by Ben Moore.

Chapter 6. Evidence that dingo extirpation facilitates shrub encroachment

6.1 Abstract

Shrub encroachment is a world-wide phenomenon that describes an increase in the abundance of woody shrub species at the expense of grasses. Top predators, by suppressing the abundance of large herbivores and mesopredators, can initiate trophic cascades which influence the abundance of organisms at lower trophic levels. Although top predator extirpation and shrub encroachment are both common throughout Earth’s rangelands, no studies have tested whether top predator extirpation can drive shrub encroachment. Here we test the hypothesis that the functional extinction of Australia’s largest terrestrial predator, the dingo (*Canis dingo*) indirectly benefits the recruitment of an encroaching shrub species, hopbush (*Dodonaea viscosa angustissima*). This is predicted to occur because dingo extirpation allows irrupting populations of two mesopredators, the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*), to suppress the abundance and impact of browsing rabbits (*Oryctolagus cuniculus*) and a granivorous rodent, *Notomys fuscus* on hopbush seedlings and seed, respectively. By comparing mammal and shrub activity and abundance indices and predator diets on either side of the dingo-proof fence in the Strzelecki Desert over a 30 month period, we show that where dingo activity was high, fox activity, hopbush cover and hopbush seedling density were low, whereas rabbit and *N. fuscus* abundance were high. We designed manipulative experiments that demonstrated that 1) hopbush seedlings survived in greater numbers where rabbits and rodents were common than rare, and 2) hopbush seed accumulated in greater numbers where rodents were excluded than allowed entry. Collectively, our results are consistent with the hypothesis that dingo extirpation initiates a trophic cascade which indirectly benefits shrub recruitment and ultimately shrub encroachment.

6.2 Introduction

Through their predatory impacts on prey including smaller predators, top predators can initiate cascading effect pathways which influence the abundance of species occurring at multiple trophic levels (Estes et al., 2011; Ripple et al., 2014). Although top predators are often highly interactive and functionally important species within ecosystems, owing to conflicts with pastoralists they have been extirpated from vast areas of the Earth (Ripple et al., 2014). The removal of top predators from many areas has been identified as a key process leading to losses of biodiversity and ecosystem restructuring (Terborgh et al., 2001).

Trophic cascade theory postulates that ecosystems are often structured by the predatory or consumptive impacts of species acting across multiple trophic levels (Schmitz et al., 2000). The mesopredator release hypothesis is an extension of trophic cascade theory that predicts that smaller mesopredators will increase in abundance following top predator extinction due to release from competition and predation (Crooks and Soule, 1999; Ritchie and Johnson, 2009). Newly abundant mesopredators may then suppress the abundance of smaller prey species which are seldom consumed by larger predators (Ritchie and Johnson, 2009). Further propagation of the effects of top predator extinction may then extend to influence the abundance of species occurring at even lower trophic levels. This is especially so if species that are negatively impacted by irrupting mesopredators themselves interact strongly with other species. For example, arid Australian rodents and rabbits are negatively impacted by fox predation yet may constrain plant recruitment through granivory and / or herbivory (Morton, 1985; Auld, 1995; Booth et al., 1996; Letnic and Koch, 2010; Chapter 5 of this thesis).

Shrub encroachment is characterised by increases in the abundance of woody shrubs (1 – 3 m height) at the expense of grasslands, savannas, sparsely wooded woodland, or grassland / woodland mosaic ecosystems (van Auken, 2000; van Auken, 2009; Eldridge et al., 2011; D'Odorico et al., 2012). Shrub encroachment is widespread across the Earth, particularly in arid and semi-arid grasslands or savannas which have experienced long histories of pastoral land-use (van Auken, 2000; Naito and Cairns, 2011; D'Odorico et al., 2012). An interplay of livestock grazing, alterations to historical fire regimes and global increases in atmospheric CO_2 concentrations which favour the C_3 photosynthetic pathway used by shrubs over the C_4 pathway used by warm-climate grasses, are all thought to contribute to shrub encroachment (van Auken, 2000; Briggs et al., 2005; Kraaij and Ward, 2006; Knapp et al., 2008; Ward, 2010).

Globally, there is a strong association between human population increases and historical pastoral land-use and shrub encroachment (van Auken, 2000). Because of these close associations, many authors have concluded that livestock grazing is the most important process causing shrub encroachment (Scholes and Archer, 1997; van Auken, 2000; Roques et al., 2001). The livestock grazing hypothesis predicts that livestock preference for palatable grasses over un-palatable shrubs reduces competition from grasses, allowing for shrubs to dominate (Roques et al., 2001). High grazing pressure may also reduce the frequency and intensity of fires by reducing fuel loads, making fires less damaging to shrubs and further promoting shrub dominance (Scholes and Archer, 1997).

Although like shrub encroachment, top predator extirpation is often linked to human activity, particularly pastoral land-use (Woodroffe, 2000), the reorganisation of ecosystems associated with top predator extirpation has yet to be tested as a mechanism influencing shrub encroachment. Gordon *et al.* (Chapter 2 of this thesis) were the first authors to propose this hypothesis to explain strong positive associations between the suppression of dingoes (*Canis dingo*) in the Strzelecki Desert, Australia and increases in shrub cover over a 51 year period. Their analyses of correlative field data collected during an optimal period for shrub recruitment supported a ‘mesopredator cascade’ hypothesis to facilitate shrub recruitment and hence mediate shrub encroachment. This ‘mesopredator cascade’ hypothesis predicted that dingo extirpation allowed for population increases of fox mesopredators which subsequently reduced the abundance and consumptive impact of browsing rabbits and granivorous rodents on shrub seedlings and seed (see Chapter 2 of this thesis for further explanation of the model).

Here we use manipulative experiments to test the ‘mesopredator cascade’ hypothesis proposed by Gordon *et al* (Chapter 2 of this thesis). To quantify the impact of rabbit browsing of shrub seedlings, we tracked the survival of seedlings (< 30 cm height) of a common ‘shrub encroaching’ species, *Dodonaea viscosa angustissima* (henceforth hopbush) between areas where rabbits were common and rare. To quantify the impact that rodent granivory had on shrub seed accumulation, we measured the accumulation of hopbush seed between areas where rodents were excluded and allowed entry. Finally, to identify if the correlations observed in chapter two of this thesis between predators, herbivores and shrubs were consistent through time, we compared indices of the activity and abundance of dingoes, foxes, cats, rabbits, a small seed-eating rodent, *Notomys fuscus*, hopbush seedlings and mature plants, and the collective impacts of predators on rabbit and *N. fuscus* abundance between areas where dingoes have been and remain historically common and rare over a 30 month period.

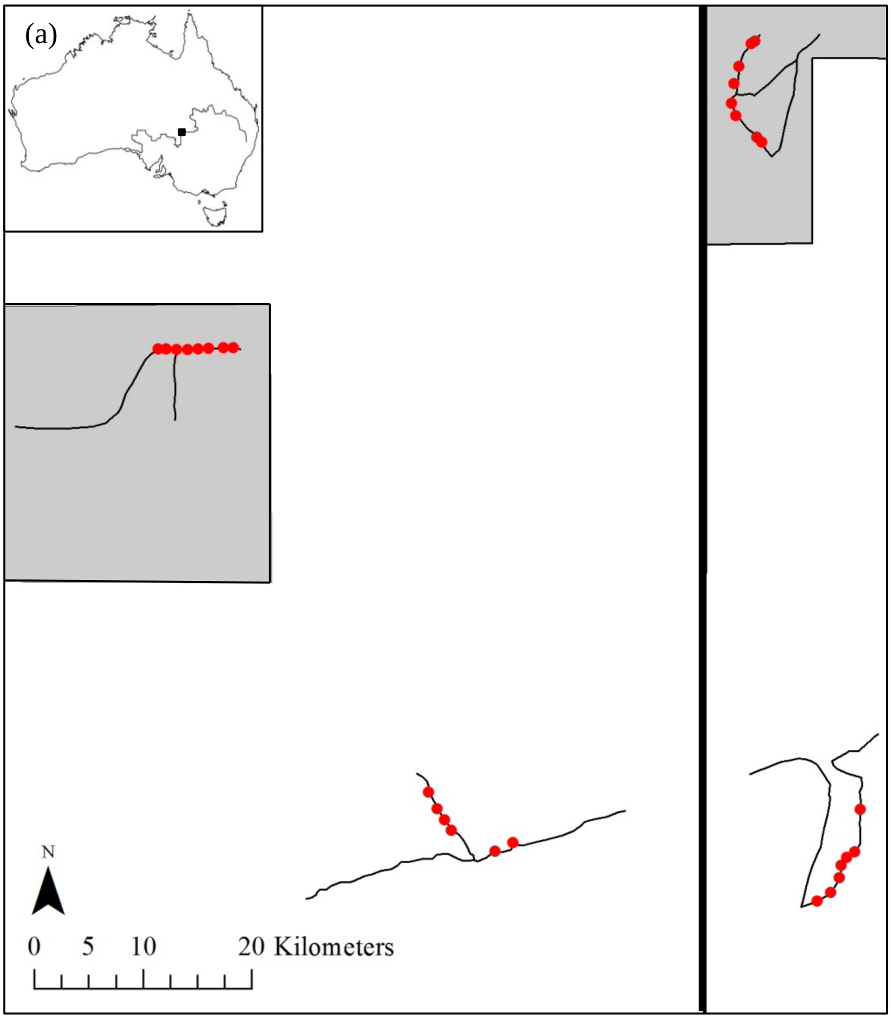

Figure 6.1. Map showing the location of trapping grids used to index Notomys fuscus abundance, hopbush cover and hopbush seedling density (red circles), and roads used to index rabbit abundance and predator activity (thin black lines) in the Strzelecki Desert, Australia. The thick black line represents the dingo-proof fence. The shaded grey polygons represent Sturt National Park to the east and Strzelecki Regional Reserve to the west. The insert (a) shows the location of the dingo-proof fence in Australia (black line) and the location of the study area (black polygon)

6.3 Methods

6.3.1 Study site

The study was conducted on adjoining pastoral properties and conservation reserves on both sides of Australia’s dingo-proof fence in the Strzelecki Desert, Australia (Fig. 6.1). The dingo-proof fence extends for over 5000 km and effectively excludes dingoes from sheep (*Ovis aries*) grazing areas to the south and east of the fence. Used in conjunction with the fence are poison baiting, trapping and shooting (Fleming et al., 2001). As a consequence of these measures, dingoes have been and remain historically rare to the south and east of the fence (henceforth ‘inside’ the dingo-proof fence; Fig. 6.1). Dingoes have remained common to the north and west of the fence where dingo-control occurs only sporadically (henceforth 'outside' the dingo-proof fence; Newsome et al., 2001; Letnic et al., 2009; Letnic and Dworjanyn, 2011).The section of the dingo-proof fence which runs along the border separating the Australian states of New South Wales and South Australia - along which our study occurred - was completed between 1914 and 1917 (Letnic and Dworjanyn, 2011).

Herbivore assemblages differ markedly between sides of the dingo-proof fence. Sheep were grazed at relatively high densities throughout the study area in the late 1800s and early 1900s (Fleming et al., 2001). For example, 15 million head of sheep were grazed throughout the Western Division of New South Wales (a legal division roughly encompassing the western third of the state, 3.2 million ha in area) between 1887 and 1897 (Fanning, 1999). Since the end of the Second World War, both sheep and cattle (*Bos primigenius*) have been grazed inside the fence and cattle have been grazed outside the fence. Sturt National Park (3106 km^2 area) is a conservation reserve inside the dingo-proof fence which has experienced no livestock grazing since 1972. Strzelecki Regional Reserve (11,702 km^2 area) is a conservation reserve outside the dingo-proof fence which has experienced no livestock grazing since the early 1990s. Owing to release from dingo predation, kangaroos (*Macropus rufus, M. fuliginosus, M. giganteus, M. robustus*) are relatively common inside the dingo-proof fence (e.g. 17.1 red kangaroos per km2 in the Tibooburra kangaroo harvest zone, within which our study occured during 2012; NSW Kangaroo Management Program, 2013) but relatively rare outside the dingo-proof fence where their populations are checked by dingo predation (Letnic and Crowther, 2013). Rabbits are present throughout the study area, but are generally more abundant outside than inside the dingo-proof fence (Newsome et al., 2001; Letnic et al., 2009). Although herbivore assemblages differed between pastoral and conservation sites sampled on either side of the dingo-proof fence here, the impact that herbivore grazing had on the abundance of mammalian species and shrubs was not a focus of this study.

The Strzelecki Desert is dominated by longitudinal east – west trending sand dunes (8 m height) and experiences low annual rainfall (188 – 227 mm), hot summer maxima (> 50 °C) and low winter minima temperatures (< 0 °C; Tibooburra Post Office; Australia Bureau of Meteorology, 2014). Vegetation in inter-dune areas is dominated by herbaceous growth (grasses, herbs and forbs). Dune vegetation is dominated by grasses and annual and perennial shrubs (1 – 3 m). Our study occurred during a prolonged period of high rainfall associated with a La Niña phase of the El Niño Southern Oscillation (Australian Bureau of Meteorology, 2012), and rainfall was within the 95th percentile of historic rainfall during 2010 (1886 till present; Tibooburra Post Office; Australian Bureau of Meteorology, 2014).

6.3.2 Activity and abundance indices

Dingo, fox and cat activity were indexed at one pastoral and one conservation site both inside and outside the dingo-proof fence (Fig. 6.1) using 25 tracking plots spaced at 1 km intervals along small ungraded tracks (Table 6.1). Plots (100 cm length, width of road) were swept daily and predator tracks were noted the following morning for three to four consecutive nights. To ensure that wind and / or rain did not obscure tracks, a distinctive mark was left at each plot each night. Indices of dingo, fox and cat activity were calculated as the average percentage plot nights that predator tracks were observed on plots at pastoral and conservation sites.

An index of rabbit abundance was recorded at all four sites using two to four nocturnal spotlight transects (Table 6.1; Letnic and Dworjanyn, 2011; see Chapter 3 of this thesis for further description of the spotlight method). Spotlight transects (25 – 40 km total length) were conducted on small ungraded tracks and commenced at dusk. During spotlight surveys, all rabbits were counted by an observer on the top of a four-wheel drive vehicle (230 cm above ground level) travelling at 10 - 15 km per hour using a 50 W spotlight. The average number of rabbits observed per km of road at pastoral and conservation sites was used as an index of rabbit abundance.

The abundance of a seed-eating rodent, *Notomys fuscus*, was estimated by live trapping mice on trapping grids located within the pastoral (inside the ding-proof fence: 7 trapping grids, outside the dingo-proof fence: 6 trapping grids) and conservation sites (inside and outside the dingo-proof fence: 8 trapping grids; Table 6.1). Logistical constraints imposed by weather events, mechanical breakdowns, and the sheer number of animals captures at sites outside the dingo-proof fence resulted in unequal replication of trapping grids between sites. Trapping grids (1 hectare area) were spaced at 1 – 3 km intervals and each included the dune bottom, middle and top. *Notomys fuscus* was selected as a focal species because it was the most abundant rodent at the study sites during the study period (between 60 – 92 % of captured rodents) and because *N. fuscus* is known to consume shrub seeds (Chapters 2 and 5 of this thesis). Each trapping grid comprised 20 metal box traps (H. B. Sherman traps, Tallahassee, FL, USA) spaced at regular 20 m intervals within a 4 × 5 row matrix and six pitfall traps (60 cm depth, 15 cm diameter) installed with a 10 m drift fence (10 cm height) spaced at 30 m intervals within a 3 × 2 row matrix. Sherman traps were baited with a mixture of oats, peanut butter and honey. Pitfall traps were not baited. Each trapping grid was sampled for three to four consecutive nights and bait was replenished daily. To prevent double counting, captured individuals within a trapping session were given a unique mark (nail polish on tail) and re-captured animals were excluded from analysis. The number of unique *Notomys fuscus* captures per trapping night per trapping grid was used as an index of abundance.

The density cover of a common shrub species, hopbush (> 1 m height) was recorded on pastoral trapping grids inside and outside the dingo-proof fence using a Bitterlich gauge (Table 6.1; Friedel and Chewings, 1988). The Bitterlich gauge method produces a shrub abundance estimate (within an area of infinite radius) which is proportional to canopy cover (Friedel and Chewings, 1988). A Bitterlich gauge (75 cm length, 7.5 cm cross bar) was constructed and shrub cover estimated at three points 50 m apart along the base of dunes and three points on dune tops. Shrub cover was calculated as the average number of shrubs observed per trapping grid. Hopbush was chosen as a focal species because it is a widely encroaching shrub species (Noble, 1998), it was the dominant shrub in the study area during sampling (50 - 77 % woody shrub cover), and rabbits and rodents were known to consume hopbush seedlings and seeds. Hopbush cover and hopbush seedling density (see below) was not presented for conservation sites here because inclement weather and mechanical failures constrained sampling during some sample periods. However, chapters 2 and 5 of this thesis have demonstrated that hopbush cover and hopbush seedlings density were similarly high between pastoral and conservation sites inside the dingo-proof fence and similarly low between pastoral and conservation sites outside the dingo-proof fence.

The density of hopbush seedlings (< 30 cm height) was recorded on pastoral site trapping grids inside and outside the dingo-proof fence by counting all seedlings occurring within three 100 m x 2 m belt transects located at the bottom, middle and top of sand dunes (Table 6.1). Hopbush seedling density was expressed as seedlings per m^2.

Generalised linear mixed-effects models with a Poisson log-link function were used to compare indices of *N. fuscus* abundance, hopbush cover and hopbush seedling density on both sides of the dingo-proof fence between sample periods. Repeated surveys of trapping grids were included as a random factor in models. Tukey tests were used for *post hoc* pairwise comparisons. All statistical analyses were performed in the computer program R version 3.0.3 (R Development Core Team, 2013) using the lme4 (Bates et al., 2012), car (Fox et al., 2009) and multcomp (Hothorn et al., 2008) packages.

6.3.3 Dingo, fox and cat predation of rabbits and Notomys fuscus

Predator scats were used to gauge the predatory impacts of dingoes, foxes and cats on rabbits and *N. fuscus* at pastoral sites inside and outside the dingo-proof fence (Table 6.1). Predator scat samples were collected during active searches along roads and around livestock watering points. In the laboratory, scats samples were dried at 100 °C, placed in individual nylon bags, and washed using a dish-washing machine. Rabbit and *N. fuscus* remains were then identified from bone fragments and hair using a binocular microscope; N. *fuscus* has disproportionally long legs (femur, fibula bones) and a distinctive skull morphology when compared with other rodent species present at the field site (Menkhorst and Knight, 2010). The total proportions of predator scats containing rabbit and *N. fuscus* remains were then calculated on either side of the dingo-proof fence during each sample period.

Table 6.1. Sample effort used to index the activity of predators and the abundance of rabbits and Notomys fuscus, and estimate the cumulative consumptive effects of dingoes, foxes and cats on rabbits and N. fuscus (through scat analysis and by calculating Predator Impact Index scores) at pastoral and conservation sites inside and outside the dingo-proof fence.

Factor	Sample area	Sample period	Sample occasions	Sample method	Units
Dingo, Red Fox, Feral Cat activity	Pastoral	June 2011 – November 2013	6	Tracking plots	activity / night
	Conservation	May 2012 – November 2013	4	Tracking plots	activity / night
Rabbit abundance	Pastoral	June 2011 – November 2013	6	Spotlight surveys	count / km
	Conservation	May 2012 – November 2013	4	Spotlight surveys	count / km
Notomys fuscus abundance	Pastoral	June 2011 – November 2013	6	Live-trapping	capture / night
	Conservation	November 2012 –	3	Live-trapping	capture / night

Factor	Sample area	Sample period	Sample occasions	Sample method	Units
		November 2013			
Hopbush cover	Pastoral	October 2011 – November 2013	5	Bitterlich gauge	count / sample point
Hopbush seedling density	Pastoral	June 2011 – November 2013	6	Band transect	count / m^2
Predator scat analysis	Pastoral	June 2011 – November 2013	6	Scat analysis	count
Predator Activity Index (PII)	Pastoral	June 2011 – November 2013	6	PII equation (see methods)	PII values

We calculated indices of the cumulative predatory impact (Predator Impact Index; PII; Table 6.1) of dingoes, foxes and cats upon rabbits and *N. fuscus*, both inside and outside the dingo-proof fence using the equation:

$$PII_{prey} = occurence\ in\ scats_{prey} \times \frac{1}{abundance_{prey}} \times\ activity_{predator}$$

Our PII equation represents an index based measure only which was used to compare PII values between treatment areas inside and outside the dingo-proof fence; PII $_{\text{rabbit}}$ values and PII $_{\textit{N. fuscus}}$ values were not comparable because rabbits and *N. fuscus* were sampled using different methods. *Notomys fuscus* trapping data and rabbit spotlight data were used as indices of prey abundance. The sum of activity index scores for dingoes, foxes and cats were used to estimate predator abundance. The frequency of occurrence of rabbits and *N. fuscus* in dingo, fox and cat scats was calculated using predator scat data. If zero values were recorded for any variable during any sample period (for example, *N. fuscus* was not captured inside the dingo-proof fence during June 2012, March 2013 and November 2013) the equivalent of one detection or capture per sample period was substituted into the PII equation for this study period to avoid division by zero. This was justified because we know that all species were present throughout the study period, even if they were not detected (Letnic et al., 2009; Letnic and Koch, 2010; Letnic and Dworjanyn, 2011).

6.3.4 Rabbit impacts on hopbush seedlings

To compare the survival of hopbush seedlings between pastoral sites inside the dingo-proof fence where kangaroos and sheep were common and rabbits were rare, and outside the dingo-proof fence where rabbits were common, kangaroos were rare and sheep were excluded, we initiated a seedling survival study. Small metal tags were attached to the bases of seven hopbush seedlings (21.54 ±SE 0.92 cm average seedling height inside the dingo-proof fence, 22.86 ±SE 0.77 cm average seedling height outside the dingo-proof fence) at 15 sites on either side of the dingo-proof fence during November 2012. Sites were separated by 1 – 2 km intervals and were located at the bottom of dunes. Seedling survival was then assessed in March 2013, September 2013 and January 2014. Seedling death was identified by the absence of seedlings, or the presence of desiccated seedlings that were brittle to touch. In addition to survival, any signs of mammalian browsing were also noted during each visit. Mammalian browsing was identified as either leaf browsing (large rip marks on leaves) or bark browsing (large rip marks on bark of stems).

The survival of hopbush seedlings on either side of the dingo-proof fence was compared using Kaplan-Meier survival curves associated with Wilcoxon tests for statistical significance (Therneau and Lumley, 2009). A generalised linear mixed-effects model with a binomial logit-link function was used to compare the occurrence of browsing of surviving hopbush seedlings between sides of the dingo-proof fence, sample periods, and the interaction between the two. Repeated surveys of trapping grids were included as a random factor in this model.

6.3.5 Rodent exclusion and hopbush seed accumulation

Consumption by rodents of hopbush seed post-seedfall was quantified by experimentally manipulating rodent access to seed. Three experimental treatments were applied around mature hopbush shrubs (276 cm ±SE 0.14 average height) at six experimental sites outside the dingo-proof fence (pastoral sites only) during September 2012. Rodents were rarely observed inside the dingo-proof fence and thus experimental sites were sampled outside the dingo-proof fence only. The three experimental treatments were: 1) rodent exclusion

(exclusion cages: 700 cm x 700 cm width, 100 cm height, 30 cm depth, 0.65 cm gauge mesh size); 2) full rodent access (control: four metal posts marking a 700 cm x 70 cm width area), and 3) sham rodent exclusion (procedural control: exclusion cages; 700 cm x 700 cm width, 100 cm height, 30 cm depth, 0.65 cm gauge mesh size with regular 60 cm height, 100 cm width openings allowing rodent access).

Four seed trays (30 cm × 30 cm width, 5 cm height) intended to catch falling hopbush seed were buried flush with the ground in each experimental plot in September 2013. Seed trays were left until January 2014 to collect seed (hopbush seed annually in spring), after which time all material found in seed trays was collected and stored for laboratory analysis. In the laboratory, all intact hopbush seeds (glossy black exterior, un-damaged, resistant to breaking when force was applied) were counted under a binocular microscope.

A generalised linear mixed-effects model with a negative binomial link function was used to model the effect of rodent exclusion treatments on the final abundance of hopbush seed. Site was included as a random factor. Tukey tests were used for *post hoc* pairwise comparisons.

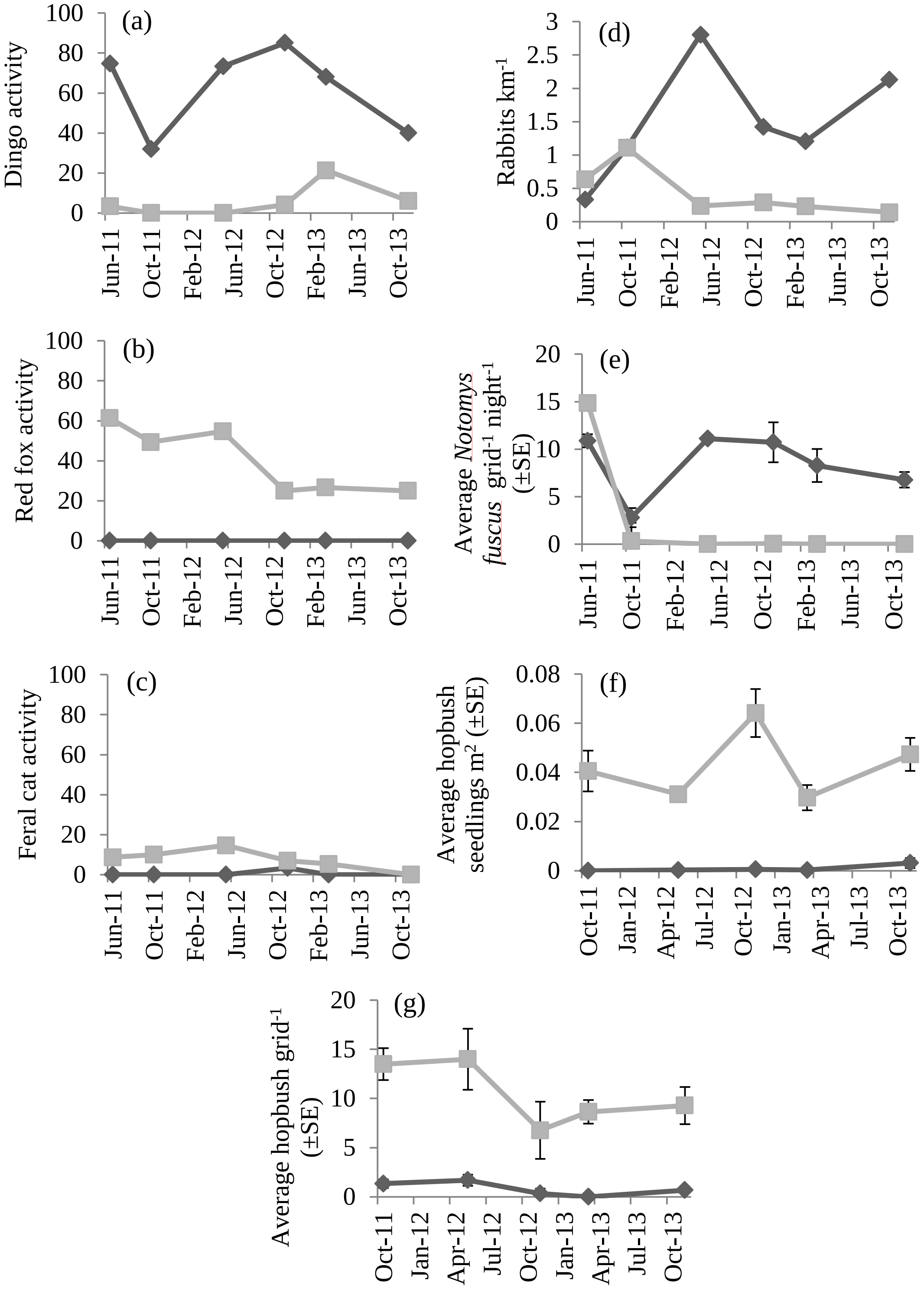

Figure 6.2. Line graphs showing activity indices for (a) dingoes, (b) red foxes, and (c) feral cats; abundance indices for, (d) rabbits and (e) Notomys fuscus; (f) hopbush seedling density, and (g) hopbush cover inside (light grey lines) and outside (dark grey lines) the dingo-proof

fence. Dingo, fox and cat activity indices and rabbit and N. fuscus abundance indices are shown for pastoral sites before November 2012 and averaged between pastoral and conservation sites after November 2012. Hopbush cover and hopbush seedling density was measured at pastoral sites throughout the study period.

6.4 Results

6.4.1 Activity and abundance indices

Dingo activity was greater outside the dingo-proof fence than inside the dingo-proof fence on all sampling occasions (Fig. 6.2a). Conversely, fox activity was greater inside the dingo-proof fence than outside the dingo-proof fence on all sampling occasions (Fig. 6.2b). Fox activity decreased throughout the study whereas dingo activity remained high (Fig. 6.2a,b). Cat activity did not differ on either side of the dingo-proof fence and was low in comparison with dingoes and foxes (Fig. 6.2a,b,c).

Rabbits were typically more common outside the dingo-proof fence, where abundance indices were consistently high, than inside the dingo-proof fence, where abundance indices decreased throughout the study (excluding 2011; Fig. 6.2d). *Notomys fuscus* abundance indices were higher outside than inside the dingo-proof fence for all sampling periods except June 2011, when abundance indices were equally high on both sides side of the dingo-proof fence (Fig. 6.2e, Tables 6.2 & 6.S1). Hopbush cover and hopbush seedling density were always greater outside the dingo-proof fence than inside the dingo-proof fence (Fig. 6.2f,g, Tables 6.2 & 6.S1).

6.4.2 Dingo, fox and cat predation of rabbits and Notomys fuscus

Dingo scats accounted for a greater percentage of scats collected outside the dingo-proof fence (92 % scats) than inside the fence (22 % scats; Table 6.3). Conversely, fox scats accounted for a greater percentage of scats collected inside the dingo-proof fence (72 %) than outside the fence (5 %). Cat scats represented a similarly small percentage of scats collected inside (6 % scats) and outside the dingo-proof fence (3 % scats; Table 6.3).

N. fuscus remains were frequently found in predator scats throughout the study period and were found in scats more often inside the dingo-proof fence (on average 28 % of scats) where *N. fuscus* remains were typically found in fox scats, than outside (on average 20 % of scats) the dingo-proof fence where *N. fuscus* remains were typically found in dingo scats (Table 6.3). *Notomys fuscus* remains were more commonly found in dingo and fox scats collected during 2011 than either 2012 or 2013 (Table 6.3).

Dingoes, foxes and cats produced greater $\text{PII}_{\textit{N. fuscus}}$ scores inside the dingo-proof fence where abundant foxes were the dominant predator and *N. fuscus* was usually rare, than outside the dingo-proof fence where abundant dingoes were the dominant predator and *N. fuscus* was typically common (Table 6.3, Fig. 6.3a). The high $\text{PII}_{\textit{N. fuscus}}$ values recorded inside the dingo-proof fence occurred because a high proportion of *N. fuscus* remains were found in fox scats inside the dingo-proof fence, even though *N. fuscus* abundance was low. Conversely, $\text{PII}_{\textit{N. fuscus}}$ values were low outside the dingo-proof fence because dingoes consumed *N. fuscus* in areas where *N. fuscus* abundance was consistently high.

*Table 6.2. Results of generalised linear mixed-effects models comparing the a) Notomys fuscus abundance index, b) hopbush cover, and c) hopbush seedling density, between both sides of the dingo-proof fence during the sample period. * represents interaction models.*

Model	df	χ^2 statistic	*P*
a) Notomys fuscus abundance index			
Dingo-proof fence	1	1.52	0.217
Sample period	5	59.29	< 0.001
Dingo-proof fence * sample period	5	12.38	0.030
b) Hopbush cover			
Dingo-proof fence	1	154.83	< 0.001
Sample period	4	23.17	0.0001
Dingo-proof fence * sample period	4	0.84	0.932
c) Hopbush seedling density			
Dingo-proof fence	1	160.96	< 0.001
Sample period	4	21.01	< 0.001
Dingo-proof fence * sample period	4	13.18	0.010

Rabbit remains were frequently found in predator scats throughout the study period and were found in scats more often outside than inside the dingo-proof fence (Table 6.3). The frequency of occurrence of rabbit remains in dingo scats was always higher than that of *N. fuscus*, excluding October 2011 inside the dingo-proof fence (Table 6.3). The frequency of occurrence of rabbits in fox scats was always lower than that of *N. fuscus*, excluding March 2013 inside the dingo-proof fence.

Dingoes, foxes and cats had a similar $\text{PII}_{\text{rabbit}}$ inside and outside the dingo-proof fence throughout the study period, except in June 2011 when $\text{PII}_{\text{rabbit}}$ values were higher outside than inside the dingo-proof fence (Fig. 6.3b). This was because dingoes consumed many rabbits outside the dingo-proof fence in areas where rabbit abundance was typically high, whereas foxes consumed few rabbits inside the dingo-proof fence in areas where rabbit abundance was typically low.

6.4.3 Rabbit impacts on hopbush seedlings

Hopbush seedlings showed higher survival rates inside the dingo-proof fence (83 % survival) than outside the dingo-proof fence (72 % survival; Fig. 6.4a; $\chi^2 = 4.81$, df = 1, $P = 0.0278$). Surviving hopbush seedlings experienced similar rates of browsing by mammals on either side of the dingo-proof fence (Fig. 6.4b; Table 6.4). Mammalian browsing of surviving hopbush seedlings increased throughout the sample period irrespective of side of fence treatment (Fig. 6.4b; Table 6.4).

T*able 6.3. Total number of dingo, fox, cat scat collected during the sample period and the percentage of dingo fox and cat scats containing Notomys fuscus and rabbit remains a) inside the dingo-proof fence where dingoes are rare and b) outside the dingo-proof fence where dingoes are common.*

Sample	Dingo			Red Fox			Feral cat			Grand %	Grand %
Period	Number scats	*N.fuscus*	Rabbit	Number scats	*N.fuscus*	Rabbit	Number scats	*N.fuscus*	Rabbit	*N.fuscus*	Rabbit
a) Inside the dingo-proof fence - dingoes rare											
Jun-11	8	25	75	6	83	17	5	0	60	37	53
Oct-11	16	69	25	14	57	7	0	0	0	63	17
May-12	0	0	0		19	8	3	0	0	18	8
Nov-12	2	0	50	12	17	8	0	0	0	14	14
Mar-13	2	0	50	20	15	20	0	0	0	14	23
Nov-13	1	0	0	8	25	0	0	0	0	22	0
Grand %	29	45	41	96	28	10	8	0	38		
b) Outside the dingo-proof fence - dingoes common											
Jun-11	30	47	67	1	100	0	3	0	33	44	62

Sample	Dingo			Red Fox			Feral cat			Grand %	Grand %
Period	Number scats	*N.fuscus*	Rabbit	Number scats	*N.fuscus*	Rabbit	Number scats	*N.fuscus*	Rabbit	*N.fuscus*	Rabbit
Oct-11	27	48	59	1	0	0	0	0	0	46	57
May-12	26	8	69	2	0	0	2	0	0	7	60
Nov-12	26	12	92	2	0	50	1	100	0	14	86
Mar-13	35	9	89	0	0	0	2	0	50	8	86
Nov-13	10	20	80	0	0	0	0	0	0	20	80
Grand %	154	24	76	6	17	17	8	13	25		

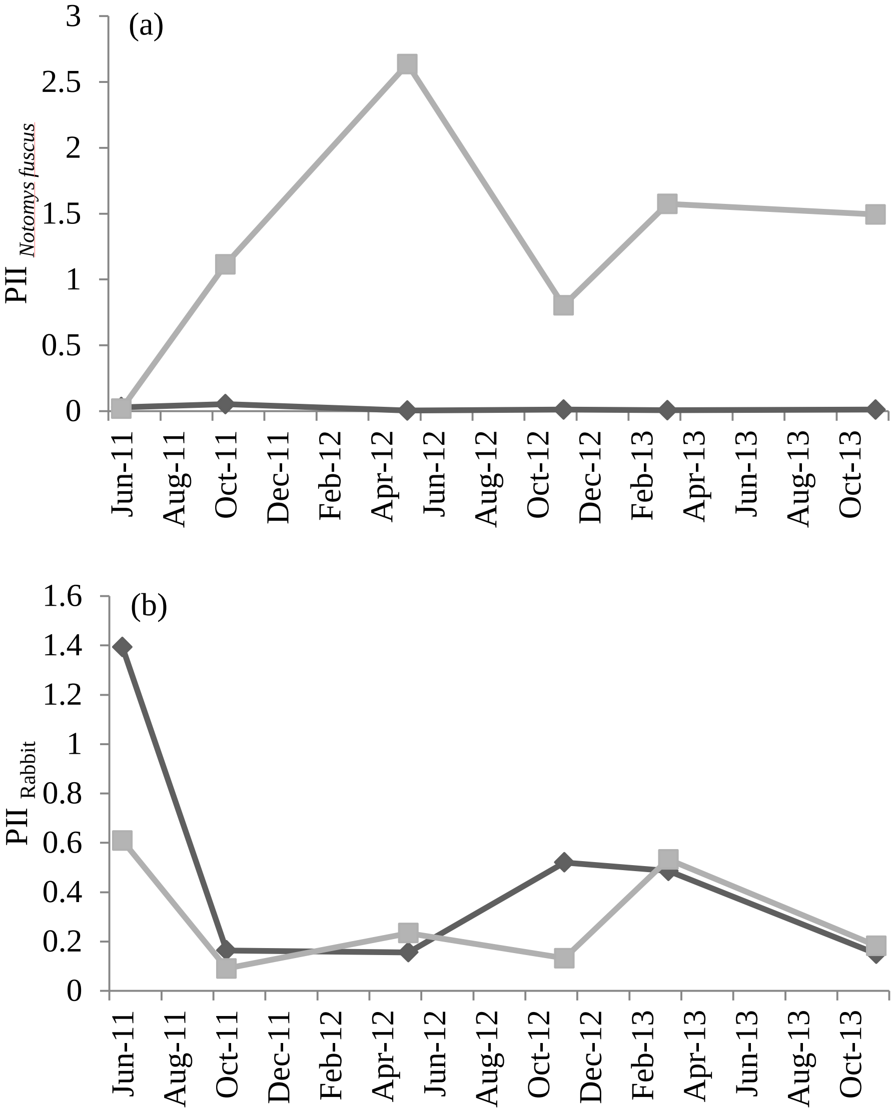

Figure 6.3. Predator Impact Index (PII) scores representing the impacts of dingoes, foxes and cats on (a) Notomys fuscus and (b) rabbit abundance indices at pastoral sites inside (light grey) and outside (dark grey) the dingo-proof fence between June 2011 and November 2013.

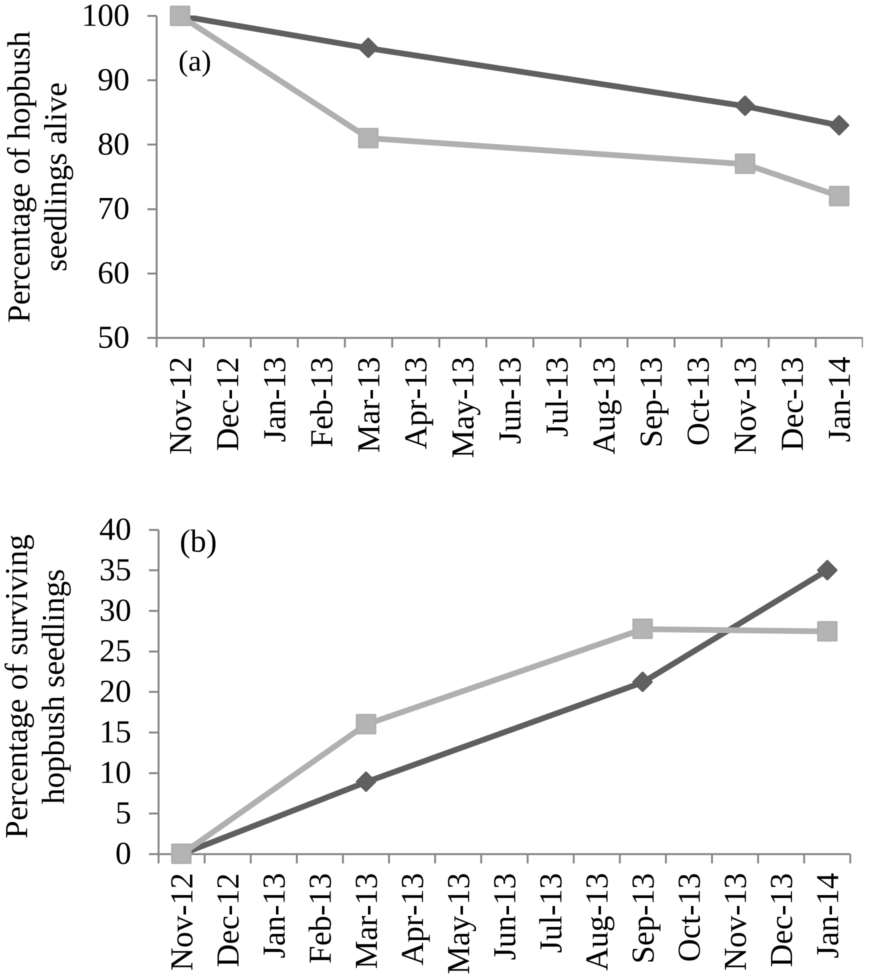

Figure 6.4. (a) Percentage survival of the 105 hopbush seedlings located at both the ‘inside’ (light grey line) and ‘outside’ (dark grey lines) the dingo-proof fence study sites. (b) Percentage of surviving hopbush seedlings showing signs of mammalian browsing at the ‘inside’ (light grey line) and ‘outside’ (dark grey line) the dingo-proof fence study sites.

*Table 6.4. Results of a generalised linear mixed-effects model comparing the incidence of mammalian browsing of surviving hopbush seedlings on both sides of the dingo-proof fence during the sample periods. * represents interaction models.*

	df	χ^2 statistic	*P*
Dingo-proof fence	1	0.41	0.522
Sample period	1	22.01	<0.0001
Dingo-proof fence * sample period	2	5.55	0.062

6.4.4 Rodent exclusion and hopbush seed accumulation

Hopbush seed accumulated in greater numbers where rodents were excluded than where they were allowed entry (χ^2 = 9.182, df = 2 , *P* = 0.010; *post hoc* comparisons, rodent exclusion vs rodent access: *z* score = 4.267, *P* = <0.001, rodent exclusion vs procedural control: *z* score = 2.825, *P* = 0.013, rodent access vs procedural control: *z* score = 0.573, *P* = 0.833; Fig. 6.5).

6.5 Discussion

Trophic cascade theory predicts that top predators will have alternating positive and negative effects on the population abundance of species occurring at sequentially lower trophic levels. Here, using a combination of population monitoring and manipulative experiments, we marshal support for a four-level terrestrial trophic cascade; trophic cascades have most commonly been described across only three trophic-levels in terrestrial habitats (Schmitz et al., 2000). Collectively, our results support the hypothesis that by suppressing foxes, dingoes release rabbit and rodent populations from fox predation, leading to increased browsing and granivory, which in turn limits shrub recruitment and ultimately shrub encroachment.

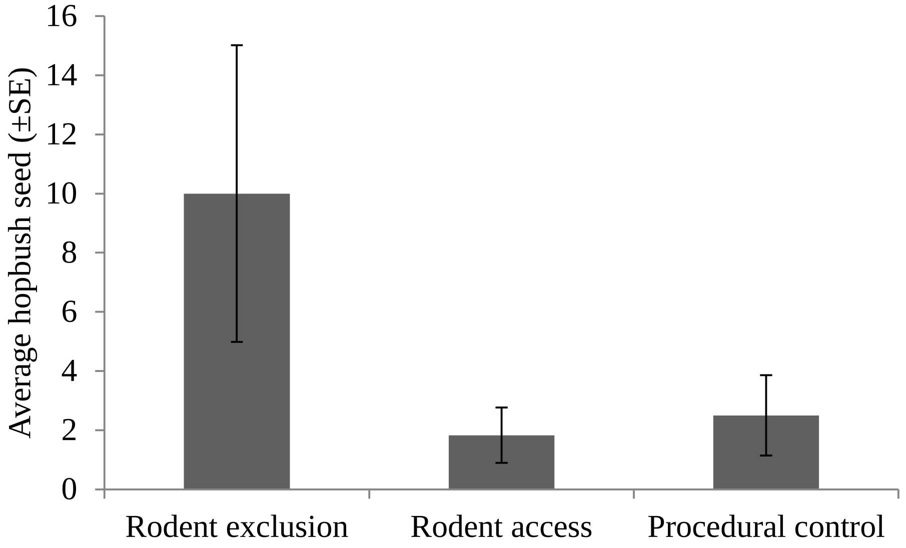

Figure 6.5. Average number of hopbush seeds accumulated in rodent access, rodent exclusion and procedural control experimental treatments.

6.5.1 Mesopredator suppression

Our study builds on previous work conducted at the same study sites (pastoral sites) inside and outside the dingo-proof fence using the same sampling methods as those used here, but during low rainfall periods in 2007 and 2009 (Letnic et al., 2009; Letnic and Koch, 2010; Letnic and Dworjanyn, 2011). In accordance with previous studies which have identified that productivity in arid Australia is primarily dependant on rainfall (Nicholls, 1991; Letnic et al., 2005), the activity and abundance of mammalian species observed here were much higher than those recorded in 2007 or 2009. However, the numeric associations observed between dingoes, foxes, rabbits and rodents were similar during both sampling periods: negative associations were observed between the abundance and / or activity of dingoes and foxes, foxes and rodents, and foxes and rabbits; positive associations were observed between the abundance and / or activity of dingoes and rabbits, and dingoes and rodents; and *N. fuscus* occurred in more fox scats than dingo scats. Considered alongside studies that have shown similar associations between dingoes, foxes, rodents, rabbits and ground-dwelling marsupials at sites throughout arid Australia (Johnson et al., 2007; Letnic et al., 2009) and coastal eastern Australia (Colman et al., 2014), our results suggest that dingoes had a net positive effect on the abundance of rodents (and possibly rabbits, discussed below) by suppressing the abundance of foxes in our study area.

In our study, cats were detected rarely when compared to dingoes or foxes. Because negative, neutral and positive associations have been previously shown to occur between dingoes and cats over a range of dingo, fox and cat activities, other authors have hypothesised that cat abundance is largely determined by complex three-way interactions between dingoes, foxes and cats whereby smaller cats are suppressed by both larger dingoes and foxes (Brook et al., 2012; Kennedy et al., 2012; Letnic et al., 2012). This hypothesis may explain the low cat activity scores recorded both inside the dingo-proof fence, where abundant foxes may have suppressed cats, and outside the dingo-proof fence, where abundant dingoes may have suppressed cats. Alternatively, cat activity may have been underestimated using our sampling technique because cats may have avoided walking along roads in areas where dingoes and foxes were abundant (Brook et al., 2012; Kennedy et al., 2012). Further research is required to determine processes influencing, and methods used to assess cat abundance throughout arid Australia.

The predator impact index (PII) presented here provides further support that dingo suppression of foxes benefits the abundance of small ground-dwelling species such as *N. fuscus*. $\text{PII}_{\textit{N. fuscus}}$ values were consistently low outside the dingo-proof fence where dingoes were common, and foxes and *N. fuscus* were rare. Conversely, $\text{PII}_{\textit{N. fusucs}}$ values were consistently high inside the dingo-proof fence (except for June 2011) where foxes were abundant and dingoes and *N. fuscus* were rare. When viewed collectively with dingo and fox scat data, our results suggest that although dingoes consumed *N. fuscus,* they had little impact on *N. fuscus* populations outside the dingo-proof fence where they were the dominant predator (foxes were rare) because dingoes were largely persisting on rabbits. Conversely, our results also suggest that foxes significantly impacted *N. fuscus* abundance inside the dingo-proof fence because foxes, which were the dominant predator (dingoes were rare), consistently consumed relatively large numbers of *N. fuscus*, even at low *N. fuscus* population densities.

Interestingly, $\text{PII}_{\text{rabbit}}$ values were generally similar on both sides of the dingo-proof fence throughout the sample period, excluding June 2011. This presumably occurred because abundant dingoes frequently preyed on abundant rabbits outside the dingo-proof fence, whereas abundant foxes preyed less frequently on rabbits which were relatively rare inside the fence; the occurrence of rabbit remains in dingo and fox scats was proportional to rabbit abundance. Given that $\text{PII}_{\text{rabbit}}$ values were similar on both sides of the dingo-proof fence, it is likely that some other process facilitated the higher rabbit abundances observed outside rather than inside the dingo-proof fence. For example, dingo predation of large herbivore grazers such as kangaroos and sheep may have released rabbits from competition with these large herbivores outside the dingo-proof fence where dingoes were common, but not inside the dingo-proof fence where dingoes were rare. Support for this hypothesis comes from a number of studies which have indicated that dingoes indirectly benefit vegetation cover by reducing the abundance and grazing impacts of large herbivores such as kangaroos and livestock (Letnic et al., 2009; Colman et al., 2014). Support for this hypothesis also comes from a study which supports that competition between red kangaroo (*Macropus rufus*), sheep and rabbit herbivores influences vegetation dynamics in arid areas of western New South Wales, Australia (Dawson and Ellis, 1994).

A final note regarding our PI index was that it was indeed an index only, and did not quantify the actual predatory impact that dingoes, foxes and cats had on rabbit and *N. fuscus* abundance. Although our results support the hypothesis that predation limited the abundance of *N. fuscus* inside the dingo-proof fence but had little impact on rabbit abundance, it is still unknown if the differences or similarities in PII scores observed here between sides of the dingo-proof fence represent levels of predation which may have suppressed rabbit or *N. fuscus* abundance. A per capita predator impact measure, such as that used by Wootton (1997) is required to quantify the actual impact that predators have on rabbits and *N. fuscus* abundance.

6.5.2 A mesopredator release model to explain shrub encroachment

Our results provide support for the hypothesis that rabbit browsing and rodent granivory, which is primarily dependant on dingo suppression of foxes, limits the accumulation of hopbush seed and the survival of hopbush seedlings. In doing so, rabbit browsing and rodent granivory may limit shrub recruitment and thus constrain shrub encroachment. This is because hopbush seedlings survived in greater numbers where rabbits were relatively rare; hopbush seed accumulated in greater numbers where rodents were excluded; and rabbit and *N. fuscus* abundances were negatively correlated with hopbush cover and hopbush seedling density. This hypothesis is supported by studies which have shown that: rabbits negatively influence the survival of arid Australian shrubs and shrub seedlings - including hopbush - through browsing (Auld, 1995; Booth et al., 1996); *N. fuscus* consumes large numbers of hopbush seeds where it occurs at high population densities (Chapter 5 of this thesis);

historical observations showing that rabbit and house mouse (*Mus musculus*) plagues dramatically reduce the abundance of vegetation through browsing and granivory (Caughley et al., 1994; Coman, 2010); and a study which has hypothesised that low levels of granivory in Australian deserts may have resulted from the widespread decline of rodents which has followed European settlement (Morton, 1985).

Although rabbits are an introduced species in Australia, they likely fill a similar ecological niche as a suite of medium-sized marsupials such as Bettongs (*Bettongia sp.*) and Nail-tailed wallabies (*Onychogalea sp.*) which are now extinct from mainland Australia (Read et al., 2008). This is because rabbits are a similar size and fulfil similar browsing and digging ecological roles as this now extinct cohort of marsupials (Noble et al., 2007; Read et al., 2008). Many of these marsupials would have once played important roles in limiting vegetation recruitment through browsing. For example, *Bettongia* species (*B. lesueur, B. penicillata*) which were once widespread throughout arid Australia but are now restricted to predator free fenced areas, browse heavily on perennial shrubs and seedlings and also consume shrub seeds (Noble et al., 2007; Bice and Moseby, 2008). Because of this, the functional extinction of species such as *B. lesueur* and *B. penicillata* has been proposed as an explanation for shrub encroachment (Noble et al., 2007). Although the niche of the rabbit may not completely overlap with that of marsupial species which are now extinct on the mainland (James and Eldridge, 2007), our results suggest that rabbits somewhat compensate for the loss of these species. Indeed, rabbit browsing has been demonstrated to limit the survival of several shrub species including *Acacia carneorum, Alectryon oleifolius* and *Casuarina pauper* in arid areas of western New South Wales where browsing marsupials were once common but are now extinct (Denham and Auld, 2004).

Our study occurred during the second-highest recorded rainfall period in the Strzelecki Desert (1886 till present; Tibooburra Post Office; Australian Bureau of Meteorology, 2012). Although our study showed differences in seedling survival between areas inside and outside the dingo-proof fence, the magnitude of these differences was probably reduced by the fact that diverse and abundant fodder was available to rabbits, kangaroos and sheep throughout much of the study period. As aridity increases, food availability decreases following high-rainfall periods in arid Australia (Holmgren et al., 2006). Because of this, it is likely that rabbits will have a proportionally greater impact on hopbush seedling survival as the desert ‘dries-up’ follow the high rainfall period which occurred during this study. For example, 40 % of the hopbush seedlings affected by mammalian browsing outside the dingo-proof fence in January 2014 had bark chewed from large sections of stem, and thus are likely to perish in the coming year. This was a period following an extremely low-rainfall year in 2013 (150 mm annual rainfall; Australia Bureau of Meteorology, 2014; Tibooburra Post Office) which corresponded with marked decreases in forb and grass cover (Fig. 6.S1). Although a high proportion (27 %) of seedlings were also browsed inside the dingo-proof fence during this period, these seedlings were typically leaf (88 %) and not stem browsed (12 %), and because of this, may show higher tolerance and survival than heavily-browsed seedlings outside the dingo-proof fence.

Australian desert rodents have been thought to have little impact on post-dispersal seedbank survival, and vegetation recruitment when compared to rodent assemblages in North and South American, Israeli and South African deserts (Morton, 1985; Kelt et al., 2004). However, many studies which have quantified rodent granivory in arid Australia have done so in places and during times when rodents were rare (Morton, 1985; Murray and Dickman, 1994; Predavec, 1997). Indeed our assessment of *N. fuscus* abundance on either side of the dingo-proof fence highlights how spatially and temporally variable rodent abundance can be in arid Australia. In chapter 5 of this thesis, we show strong associations between *N. fuscus* abundance and hopbush seed fate, providing evidence to support the hypothesis that the functional extinction of *N. fuscus* has released hopbush seed from granivory constraints inside the dingo-proof fence. By demonstrating strong negative associations between *N. fuscus* and hopbush seedling density, and demonstrating that rodent exclusion results in increased hopbush seed accumulation, we found further evidence that where they are present rodents can dramatically affect seed fate, and shrub encroachment more broadly if seed abundance affects shrub recruitment.

6.5.3 An explanation for shrub encroachment in the Strzelecki Desert

Although our results support a ‘mesopredator cascade’ hypothesis in limiting shrub recruitment in the Strzelecki Desert, it is likely that dingo extirpation also interacts with other mechanisms in suppressing shrub recruitment and ultimately shrub encroachment. For example, by allowing increases in the abundance of kangaroos and livestock, dingo extirpation likely decreases competition between grasses and shrub seedlings through selective grazing (a 'herbivore cascade' hypothesis; Chapter 2 of this thesis, van Auken, 2000). The establishment of encroaching shrub communities through either ‘mesopredator’ or ‘herbivore cascade’ pathways may suppress the frequency and intensity of fires which kill shrubs (Chapter 2 of this thesis; Roques et al., 2001). Increased shrub abundance, by providing shelter and habitat, may facilitate increased rabbit and / or rodent abundance via a feedback mechanism untested here. Further research is required to understand how dingo and top predator extinction more generally interacts with other mechanisms thought to influence shrub encroachment.

6.6 Acknowledgements

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6.8 Supplementary information

Table 6.S1. Post hoc pairwise comparisons (Tukey test) comparing a) the Notomys fuscus abundance index, b) hopbush cover, and c) hopbush seedling abundance between trapping grids inside and outside the dingo fence during each sample periods. Pairwise comparisons could not be made for the N. fuscus abundance index after May 2012 because no mice were captured inside the dingo fence during these periods.

	Estimate	*z* value	*P*
a) Notomys fuscus abundance index			
June 2011	-0.256	-1.296	0.352
October 2011	2.40	3.170	0.003
May 2012	n/a	n/a	n/a
November 2012	n/a	n/a	n/a
March 2013	n/a	n/a	n/a
November 2013	n/a	n/a	n/a
b) Hopbush cover			
October 2011	-2.355	-6.383	<0.0001
May 2012	-2.192	-6.592	<0.0001
November 2012	-2.646	-4.432	<0.0001
March 2013	-2.367	-5.073	<0.0001
November 2013	-2.673	-5.177	<0.0001
c) Hopbush seedling abundance			
October 2011	-4.989	-4.891	<0.0001
May 2012	-4.660	-4.485	<0.0001

	Estimate	*z* value	*P*
November 2012	-4.744	-6.483	<0.0001
March 2013	-4.670	-4.591	<0.0001
November 2013	-2.711	-7.397	<0.0001

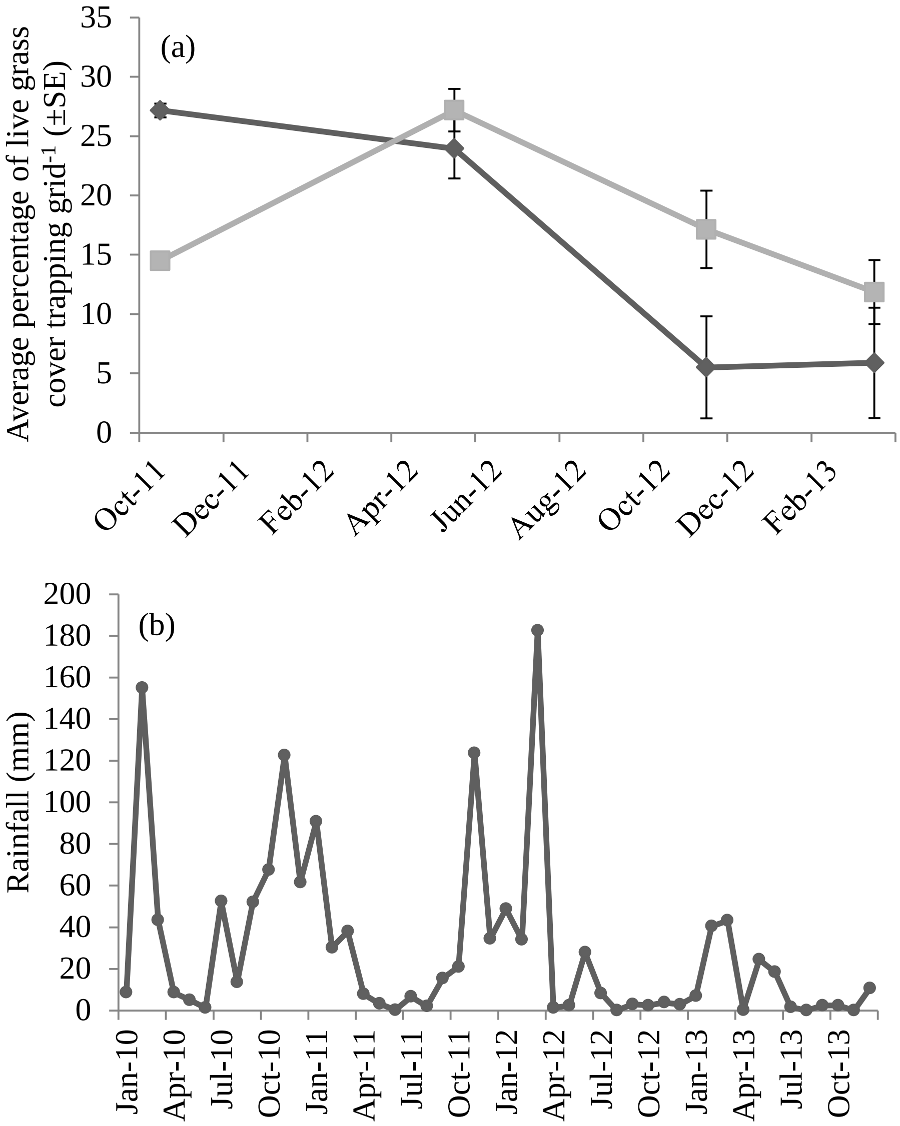


Figure 6. S1. (a) Average percentage cover of live grass (±SE: see Chapter 2 and 3 of this thesis for description of sample protocol) observed at trapping grids inside (light grey line) and outside (dark grey line) the dingo-proof fence between June 2011 and March 2013. Note that a fire burnt a number of trapping grids outside the dingo-proof fence in November 2012. (b) Monthly rainfall totals between January 2010 and December 2013 from the closest weather station to the study area, Tibooburra Post Office (Australian Bureau of Meteorology, 2012)

Chapter 7: General Discussion

Gordon, Christopher E.

An inter-dune swale located outside the dingo-proof fence in the Strzelecki Desert.

Chapter 7. General discussion

The objective of this thesis was to investigate whether Australia’s largest terrestrial top predator, the dingo (*Canis dingo*) initiates an ecosystem-wide trophic cascade which suppresses the recruitment and abundance of encroaching shrub species. In this general discussion I briefly summarise my results. I then propose a top predator extirpation model which may account for shrub encroachment not only in arid Australia, but also in other areas of the Earth where shrub encroachment has followed top predator extirpation. Finally, I discuss the implications of my thesis research for conservation and ecosystem management, and identify and discuss some of the problems that I encountered during my thesis research and how they were resolved.

7.1 Dingoes initiate ecosystem-wide trophic cascades in arid Australia

Below, I briefly review and discuss the major research findings of this thesis.

Thesis outcome 1: Correlative evidence supports the hypothesis that larger dingoes suppressed the abundance of smaller red fox (Vulpes vulpes) and feral cat (Felis catus) mesopredators.

In chapters 2, 4 and 6 I used track plot surveys, and in chapter 3 I used spotlight line transect surveys to show that where dingo activity and abundance indices were high fox activity and abundance indices were low. Conversely, where dingo activity and abundance indices were low, fox activity and abundance indices were high. These relationships were shown to occur over a 13, 200 km^2 area (Chapter 2) and over an extended 30 month period (Chapter 6).

Cats were rarely detected throughout the study when compared with dingoes and foxes using both tracking plot (Chapters 2, 4 and 6) and spotlight line transect surveys (Chapter 3).

Although cats were rarely detected, cat activity was typically lower where dingo activity was high and fox activity was low than where dingo activity was low and fox activity was high (Chapters 4 and 6). The rarity of cats in the study area may have resulted from complex three-way interactions occurring between larger dingoes (15 - 22 kg) and foxes (4 - 9 kg) and smaller cats (3 - 6 kg), whereby dingoes suppressed cat abundance ‘outside’ the dingo-proof fence where dingoes were abundant, and foxes suppressed cat abundance ‘inside’ the dingo-proof fence where foxes were abundant.

Thesis outcome 2: Correlative evidence supports the hypothesis that dingoes indirectly benefited the abundance of rodents and a small ground-nesting bird, Turnix velox, by suppressing the abundance and predatory impact of foxes and cats.

In chapters 2, 3, 4 and 6 I showed that where dingo activity and abundance indices were high and fox activity and abundance indices were low, the indexed abundance of rodents and a ground-nesting bird (*Turnix velox*) were high. However, where dingo activity and abundance indices were low and fox activity and abundance indices were high, the indexed abundance of rodents and *T. velox* were low. These relationships were shown to occur over a 13,200 km^2 area (Chapters 2, 3 and 4) and over an extended 30 month period (Chapter 6).

In chapter 6, I provided evidence that foxes had a high predatory impact on a rodent, *Notomys fuscus* because *N. fuscus* remains were found in a high proportion of fox scats, even when *N. fuscus* occurred at low abundances. Conversely, I provided evidence that dingoes had a low predatory impact on *N. fuscus*, because dingoes consumed *N. fuscus* in areas where *N. fuscus* abundances were consistently high.

Cats were rarely detected during the study (Chapters 2, 3 and 6). Thus, it is likely that the overall effect that cat predation had on the abundance of rodents and *T. velox* was low. However, because negative associations were observed between cat activity and *N. fuscus* abundance in areas where dingoes and foxes were rare (Chapter 4), cat predation may have influences rodent and *T. velox* abundance in some areas. Further, our sampling methods may have under-estimated cat abundance.

Thesis outcome 3: Evidence from correlative data and a manipulative experiment supporting the hypothesis that dingoes indirectly benefited the foraging behaviour of N. fuscus by suppressing the abundance and impact of cats.

In chapter 4 I showed that *N. fuscus* foraged less apprehensively from “risky” habitats when dingo activity was high and cat activity was low. Whereas *N. fuscus* foraged more apprehensively from “risky” habitats when dingo activity was low and cat activity was high. Foxes were rarely detected in areas used to quantify the foraging behaviour of *N. fuscus*. This presumably occurred because dingo abundances were high enough to have almost completely excluded foxes from the study area used in chapter 4.

Thesis outcome 4: Correlative evidence supports the hypothesis that dingoes indirectly benefited the abundance of rabbits by 1) suppressing the abundance of competing large herbivores such as kangaroos and livestock or 2) suppressing the abundance and impact of foxes and cats.

In chapters 2 and 6 I showed that rabbit abundance indices were consistently higher where dingoes were common and foxes were rare than where dingoes were rare and foxes were common. In chapter 3 I showed that total grazing pressure was lower outside the dingo-proof fence where rabbits were common and livestock and kangaroos were rare, than inside the dingo-proof fence where rabbits were rare and livestock and kangaroos were common. In chapter 6 I provide evidence which supports the hypothesis that dingo and fox consumption of rabbits was proportional to rabbit abundance indices. This suggests that neither dingoes nor foxes limited the abundance of rabbits through predation in this study.

My results provide greater support for the hypothesis that dingoes benefited rabbit abundance by releasing rabbits from competition with large herbivores, than by suppressing the abundance and impact of mesopredators. However future research which measures grazing responses of rabbits and larger mammalian herbivores over a range of rabbit and large mammalian herbivore densities is needed to further quantify this claim.

Thesis outcome 5: Evidence from correlative data and manipulative experiments supporting the hypothesis that rabbit browsing and rodent granivory limited the recruitment and hence abundance of an encroaching shrub species, Dodonaea viscosa angustissima (hopbush).

In chapters 2 and 6 I showed that hopbush cover, hopbush seedling density and hopbush soil seed bank acclamation were consistently greater inside the dingo-proof fence where rabbits and rodents where typically rare, than outside the dingo-proof fence where rabbits and rodents were common. In chapter 6 I demonstrated that hopbush seedlings survived in greater numbers where rabbits were typically rare than where they were common. In chapters 5 and 6 I demonstrated that hopbush seed accumulated in greater numbers where rodents were excluded than where rodents were allowed entry. In chapter 5 I showed that hopbush seed removal by rodents was consistently higher in areas where *N. fuscus* were common than in areas where they were rare.

Thesis outcome 6: Correlative evidence supports the hypothesis that dingoes did not facilitate increases in the recruitment and abundance of encroaching shrub species by suppressing the abundance and consumptive impacts of livestock during the study period.

Control of dingo populations by humans allowed sheep (*Ovis aries*) grazing to occur inside the dingo-proof fence where total livestock grazing pressure was high, but not outside the dingo-proof fence, where total livestock grazing pressure was low (Chapter 3). In chapters 2 and 3 I showed that herbaceous plant cover (grasses, herbs and forbs) was high throughout the study area used in this thesis, and did not differ between areas inside the dingo-proof fence where shrub and shrub seedlings were abundant and outside the dingo-proof fence where shrub and shrub seedlings were rare. In chapters 2 and 3 I provide evidence supporting the hypothesis that competition between herbaceous plants and shrub seedlings was high throughout the study.

Because my study occurred during a high rainfall high productivity period, I contend that livestock grazing - which is primarily dependant on dingo-control by humans - may still influence shrub recruitment during drier periods. This is because the growth of herbaceous plants is constrained by desiccation during low rainfall periods.

Thesis outcome 7: Correlative evidence supports the hypothesis that high incidence of total grazing pressure negatively affected shrub recruitment by reducing the frequency, extent and impact of fire on shrub seedlings.

In chapter 2 I showed that historical wild-fire events were rare within the study area and were observed in 1931, 1972 - 1976 and 2011 - 2012. The 2011 - 2012 fires largely occurred outside the dingo-proof fence where total grazing pressure was low rather than inside the dingo-proof fence where total grazing pressure was high (Chapters 2 and 3). Shrub seedlings were less abundant in recently burnt areas outside the dingo-proof fence than in neighbouring unburnt areas (Chapter 2). Mature shrub cover was similarly low between burnt and unburnt areas outside the dingo-proof fence (Chapter 2).

Although the 2011 - 2012 fires typically occurred outside the dingo-proof fence where total grazing pressure was low, I could not demonstrate a causal link between grazing pressure, fuel loads (herbaceous plant cover) and fire. This is because I did not measure total grazing pressure and fuel loads before the 2011 - 2012 fire event.

7.2 A top predator extirpation model to account for shrub encroachment

Trophic cascades initiated by top predators have typically been described through simple interaction-pathway cascades between three trophic levels (Schmitz et al., 2000). For example, numerous studies have demonstrated that top predators benefit the abundance of vegetation by suppressing the abundance and consumptive impacts of grazing herbivores (Terborgh et al., 2001; Beschta and Ripple, 2009). However, top predator effects may further propagate to influence the abundance of species occupying even lower trophic levels (Polis et al., 2000; Schmitz et al., 2000). This is especially so if these ‘lower trophic level’ species (e.g. plants, rodents) interact strongly with other species through consumptive effects, competition, or by facilitation effects.

Although theory suggests that the effects of top predators may propagate to species occupying sequentially lower trophic levels in ecosystems, few studies have shown this in practice. Possibly the best example of an ‘ecosystem-wide’ trophic cascade initiated by a top predator comes from the greater Yellowstone region of North America where wolf top predators (*Canis lupus*) are thought to 1) indirectly benefit the abundance of forest trees by supressing the abundance, behaviour and consumptive impacts of large grazing herbivores, and 2) indirectly benefit the abundance of small mammals by supressing the abundance, behaviour and consumptive impact of coyote mesopredators (Fig. 7.1; see Ripple et al., 2014 for a full description of the trophic cascde). By facilitating the growth of forests, wolves are also thought to 1) indirectly benefit the abundance of many forest-dwelling species (Baril et al., 2011), and 2) facilitate the recovery of wetland habitats by stabilising river channels, which in turn benefits the abundance of many species which depend on (and in the case of beavers further modifying) wetland habitats (Beschta and Ripple, 2012).

In arid Australia, compelling evidence supports the hypothesis that dingoes initiate ecosystem-wide trophic cascades analogous to those described above (this thesis; Letnic et al., 2012). Here I outline a novel conceptual model through which dingo extirpation, by relaxing or eliminating ecosystem-wide trophic cascades initiated by dingoes, may result in an increase in the recruitment and abundance of encroaching shrub species in arid Australia (Fig. 7.2). To introduce the model I will briefly describe the extent of dingo extirpation and shrub encroachment throughout arid Australia. I will then describe each of the factors input into the top predator extirpation model. Finally, I will briefly discuss the relevance of the model to explain shrub encroachment in other areas of the Earth.

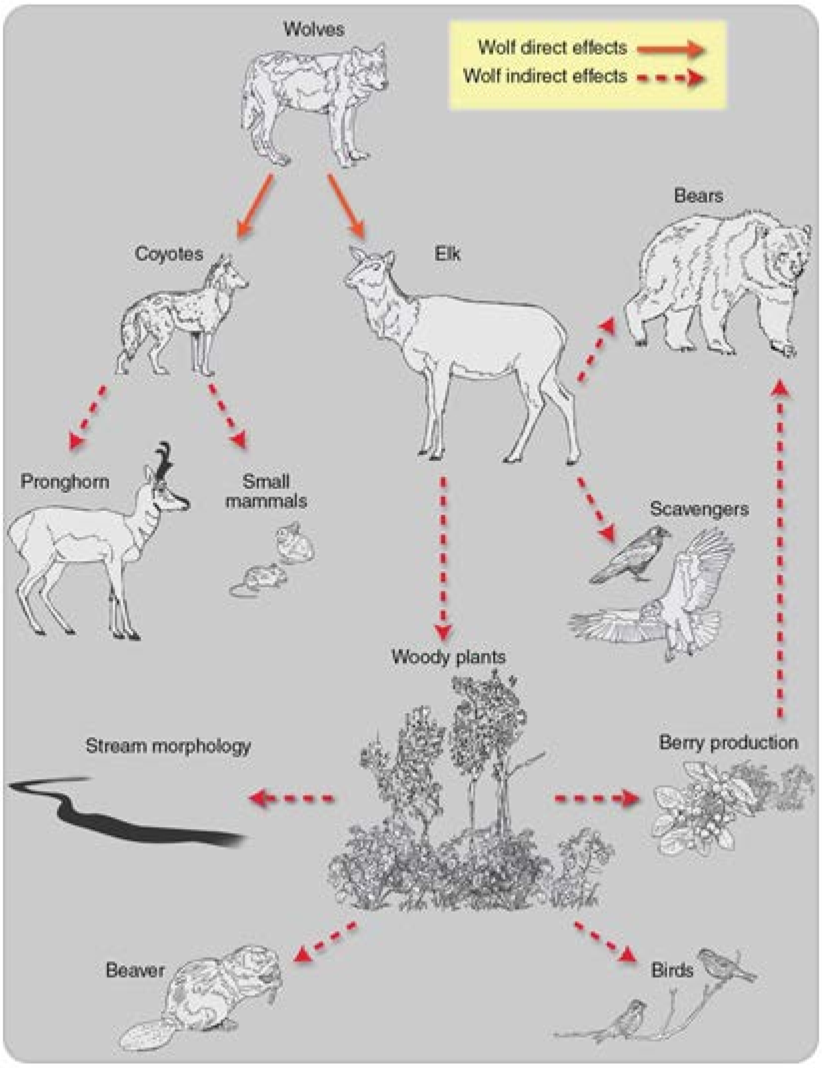


Figure 7.1. An ecosystem-wide trophic cascade initiated by a top predator, the wolf (Canis lupus) in the greater Yellowstone area of North America. The figure was obtained from Ripple et al. (2014).

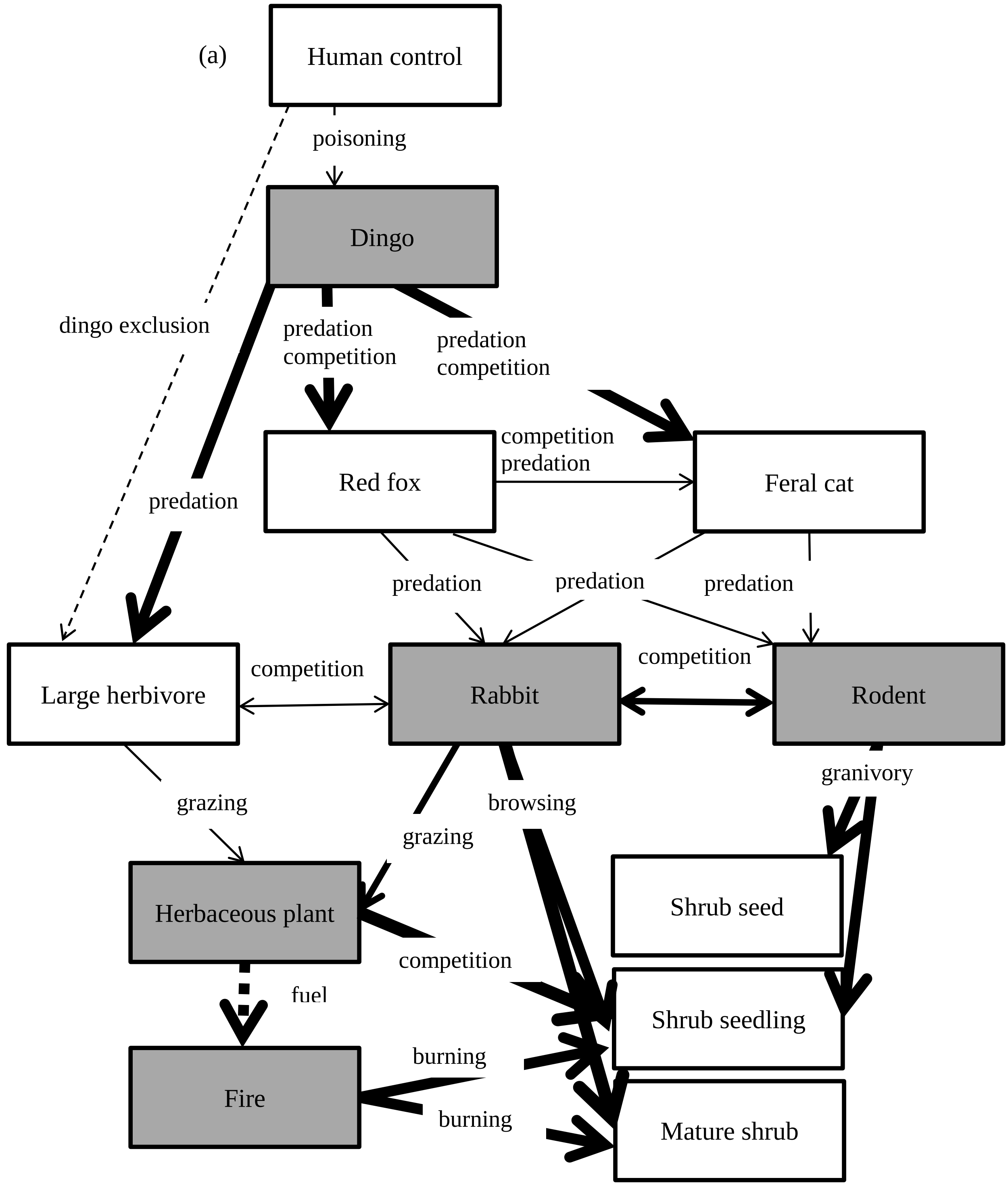
7.2.1 Dingo extirpation and shrub encroachment in arid Australia

The dingo is Australia’s largest terrestrial predator. Because dingoes may kill sheep and young cattle (*Bos primigenius*), humans have eliminated dingoes from large areas of south-eastern and south-western Australia through poisoning, trapping, shooting and physical exclusion (see Fig 1.2 in Chapter 1; Fleming et al., 2001; Letnic et al., 2012). In arid and semi-arid Australia, dingoes are subjected to particularly high levels of control in sheep growing areas to the south and east of Australia's dingo-proof fence (henceforth 'inside' the dingo-proof fence). Dingoes are consequently rare inside the dingo-proof fence (and have been for almost 100 years), but are common in adjoining areas to the north and west of the fence (henceforth 'outside' the dingo-proof fence) where dingo-control occurs sporadically (Letnic and Dworjanyn, 2011).

Shrub encroachment occurs in semi-arid and arid rangelands and tropical savannas in Australia (Noble, 1998; Fensham and Fairfax, 2002). Shrub encroachment typically occurs in areas which have experienced a long history of pastoral land-use (van Auken, 2000; Van Auken, 2009). In arid and semi-arid Australia, shrub encroachment is particularly apparent inside the dingo-proof fence where sheep grazing occurs and dingoes are rare (Noble, 1998; Chapters 2 and 3). Shrub cover is relatively low outside the dingo-proof fence where cattle are grazed and dingoes are common when compared with areas inside the dingo-proof fence (Chapters 2 and 3). The close association between dingo extirpation and shrub encroachment throughout arid Australia, and especially in areas inside the dingo-proof fence, lends support to the hypothesis that shrub encroachment is somehow linked to dingo extirpation.

7.2.2 The conceptual model

Factor 1: Dingo extirpation facilitates decreases in the abundance of browsing and granivorous mammals and increases in the abundance of large mammalian grazers.


(a)
Human control
poisoning
dingo exclusion
Dingo
predation
competition
predation
competition
Red fox
competition
predation
Feral cat
predation
predation
predation
predation
Large herbivore
competition
Rabbit
competition
Rodent
grazing
grazing
browsing
granivory
Herbaceous plant
Shrub seed
competition
Shrub seedling
fuel
burning
Fire
burning
Mature shrub

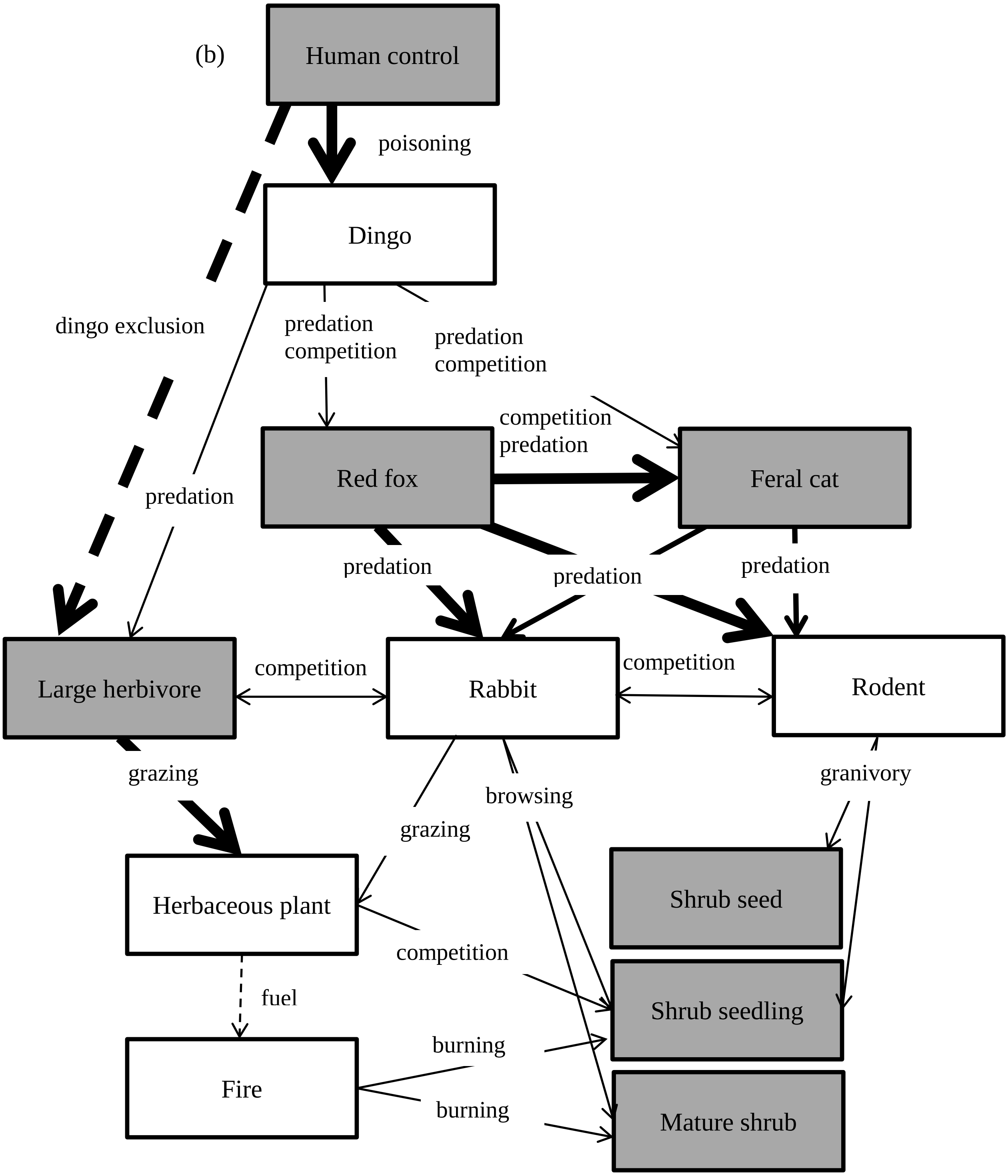


Figure 7.2. A conceptual diagram illustrating how a 'top predator extirpation' model could facilitate shrub encroachment in areas of arid Australia where (a) dingo abundance is not controlled by humans, and (b) dingo abundance is controlled by humans. The interactions

shown in panels (a) and (b) are primarily dependant on rainfall and productivity. The solid lines represent negative interactions and the dashed lines represent positive interactions. Line width is weighted by the hypothesised interaction strength between species. Grey filled boxes represent species which reside at high densities, and white filled boxes represent species which reside at low densities. Text bisecting arrows show the hypothesised effect that one species has on another.

Strong evidence supports the hypothesis that dingoes suppress the abundance and activity of smaller fox and cat mesopredators through direct killing or competitive exclusion (Brook et al., 2012; Kennedy et al., 2012; Letnic et al., 2012). Foxes and cats have a dietary preference for ‘smaller prey species’ (< 4 kg body weight; Johnson et al., 2007; Letnic et al., 2012), and predation by foxes and cats can limit the abundance and species diversity of rodent granivores, small ground-dwelling marsupials such as dunnarts (*Sminthopsis* sp.), and a ground-nesting bird, *Turnix velox* (Smith and Quin, 1996; Letnic et al., 2009; Chapters 2, 3, 5 and 6 of this thesis). By suppressing the abundance of foxes (and possibly cats), dingoes are thought to facilitate increases in the abundance and diversity of many ‘smaller prey species’ (Johnson et al., 2007; Letnic et al., 2009; Chapters 2, 3, 4 and 6). Conversely, dingo extirpation is thought to facilitate decreases in the abundance and diversity of ‘smaller prey species’, such as rodent granivores, by releasing foxes and cats from predation and competition constraints once placed on them by dingoes (Letnic et al., 2009).

Dingoes have a dietary preference for ‘larger prey species’ such as kangaroos (Macropodidae family), feral pigs (*Sus scrofa*), feral goats (*Capra hircus*) and sheep (> 10 kg body weight; Letnic et al., 2009; Letnic et al., 2012; Letnic and Crowther, 2013), and predation by dingoes can limit the abundance of these ‘larger prey species’ (or in the case of sheep, can increase the risk of predation perceived by pastoralists; Letnic et al., 2012). Large mammalian herbivores can limit the abundance of plants through herbivory (Tiver and Andrew, 1997; Letnic, 2004). By limiting the abundance and consumptive impacts of large mammalian herbivores, dingoes are thought to indirectly benefit the abundance of herbaceous plants including grasses (Letnic et al., 2012). Conversely, dingo extirpation is thought to facilitate decreases in the abundance of herbaceous plants by releasing large mammalian herbivores from predation constraints once placed on them by dingoes (Letnic et al., 2009; Letnic et al., 2012).

Although rabbits are a non-native species in Australia, they likely occupy a similar browsing niche as that of a cohort of similarly sized browsing marsupials such as bettongs (*Bettongia* sp.), hare-wallabies (*Lagorchestes* sp.) and nail-tail wallabies (*Onychogalea* sp.) which are now extinct on mainland Australia (Short and Smith, 1994; Johnson, 2006). Rabbits are a primary prey-species for dingoes, foxes and cats in many areas of arid Australia (Letnic et al., 2009; Allen and Leung, 2012). However, in areas adjoining the dingo-proof fence, rabbit abundance is generally greater in areas where dingoes are common and foxes and cats are rare, than in areas where dingoes are rare and foxes and cats are common (Newsome et al., 2001; Letnic et al., 2009; Letnic et al., 2012; Chapters 2 and 6 of this thesis). The positive associations observed between dingoes and rabbits on either side of the dingo-proof fence are thought to have resulted due to 1) dingoes suppressing the abundance and predatory impacts of foxes and cats, and / or 2) dingoes suppressing the abundance of large mammalian herbivores, which in turn release rabbits from inter-specific competition (Newsome et al., 2001; Letnic et al., 2009). By allowing for increases in the abundance of foxes, cats and large mammalian herbivores, dingo extirpation is thought to facilitate decreases in the abundance of rabbits, although it is likely that rabbit populations are also controlled by the pathogens myxomatosis and calicivirus (Saunders et al., 2010a).

Due to a legacy of sustained dingo-control, dingoes have been excluded from many areas of Australia (Fleming et al., 2001; Letnic et al., 2012). Where dingoes have been extirpated, foxes and cats have become top predators regulating trophic interactions within ecosystems (Letnic et al., 2012). Thus, the suppressive effects that dingoes have on the abundance of mesopredators and large mammalian herbivores, as well as trophic cascades initiated by dingoes, are primarily dependant on dingo-control by humans in many areas of arid Australia.

Factor 2: Rodent granivory limits the accumulation of shrub seed in the soil seed bank. Rabbit browsing limits the survival of shrub seedlings. The functional extinction of granivorous rodents and browsing rabbits facilitates shrub encroachment.

Although granivorous rodents have experienced dramatic range restrictions throughout arid Australia (Morton, 1985b; Smith and Quin, 1996), where they still occur they can dramatically impact the fate of plant seeds which rely on a post-dispersal seed bank for recruitment (Chapters 2, 5 and 6). Many encroaching shrub species such as *Dodonaea* sp., *Senna* sp. and *Eremophilla* sp. produce large numbers of seed annually, have a post-dispersal seed bank, lack a hard seed case which guards against rodent granivory, and are consumed by rodents (Booth et al., 1996; Noble, 1998; Chapter 5 of this thesis). High rates of rodent granivory on encroaching shrub species can limit the number of shrub seeds residing in the soil seed bank (Chapters 5 and 6 of this thesis). By reducing seed bank accumulation, rodent granivory is hypothesised to limit the abundance of encroaching shrub species and reduce the extent and impact of shrub encroachment (Chapter 5 and 6).

Ants and birds are the dominant granivores of post-dispersal seed in areas of arid Australia where rodent abundance is low (Morton, 1985a). Although ants harvest large quantities of shrub seed, their overall effects in limiting post-dispersal seed bank survival of encroaching shrub species (including hopbush which was a focal species used throughout this thesis) may be small in comparison to that of rodents. This is because 1) ants typically consume the elaiosome of shrub seeds only and do not kill seeds (Harrington and Driver, 1995), and 2) ants can facilitate shrub seed survival and germination by storing seeds below-ground in their nests away from other granivores and fire (Harrington and Driver, 1995). However, ants may still limit the survival of shrub seeds if seeds are stored deep below-ground in their nests. In this case, shrub recruitment is muted because germinating seeds die before they reach the soil surface (Harrington and Driver, 1995). Although bird granivores potentially consume large quantities of seed (Morton, 1985a), I could find no studies to verify the hypothesis that bird granivory limits the post-dispersal seed bank of arid Australian shrubs, or vegetation more generally. Because rodent granivores consume large quantities of seed and are probably the dominant granivores in areas where they are abundant, the functional extinction of rodents may be an important process facilitating shrub encroachment in arid Australia (Chapters 5 and 6 of this thesis).

Rabbit browsing can limit the recruitment of Australian desert plants, including encroaching shrub species such as hopbush, through browsing of mature plants and seedlings (Auld, 1995; Booth et al., 1996; Chapters 2 and 6 of this thesis). The abundance of encroaching shrub species and their seedlings is higher in areas of the Strzelecki Desert where rabbits are typically rare than common (Chapters 2 and 6 of this thesis). Rabbits occupy a similar browsing niche as that of a cohort of similarly sized browsing marsupials which are now extinct on the mainland Australia (Short and Smith, 1994; Johnson, 2006; Noble et al., 2007). Browsing by many of these marsupials would have likely limited the survival and recruitment of encroaching shrub species in the past. For example, the extinction of burrowing bettongs (*Bettongia lesueur*) from semi-arid areas of south-eastern Australia is thought to have contributed to shrub encroachment by, in part, releasing shrubs from browsing constraints (Noble et al., 2007). Because of their functionally similar browsing habits, current day rabbit populations (when occurring at high densities) may constrain the recruitment and abundance of encroaching shrub species in arid Australia in a similar way as did this now locally extinct cohort of browsing marsupials.

Factor 3: Where large mammalian herbivores are abundant, increased grazing of palatable herbaceous plants (grasses and forbs) over unpalatable shrubs facilitates shrub encroachment. By reducing the abundance of herbaceous plants, large mammalian herbivores reduce the frequency of fires which kills shrubs and shrub seedlings.

Herbivory by large mammals such as sheep, cattle, kangaroos, and feral goats can suppress the abundance of herbaceous plants and vegetation more generally in arid Australia (Noble, 1998; Fensham and Fairfax, 2002). This is especially so in areas and during times when herbivores reside at high population densities (Landsberg et al., 2003). Large mammalian herbivore communities of arid Australia are dominated by grazing species (Harrington, 1978; Dawson and Ellis, 1994; Dawson and Ellis, 1996). However, goats often browse on shrubs, and sheep and cattle may infrequently browse on shrubs during dry periods when productivity is low (Dawson and Ellis, 1994; Dawson and Ellis, 1996). The influence that goat, sheep and cattle browsing has on shrub abundance is likely dependant on species-specific traits which influence the ‘palatability’ of individual shrub species (e.g. plant secondary metabolites; Wittstock and Gershenzon, 2002).

Where livestock (sheep and cattle) are abundant, preferential grazing of palatable herbaceous plants over unpalatable shrubs can facilitate shrub encroachment (Noble, 1998; van Auken, 2000; Chapters 2 and 3 of this thesis). Kangaroos frequently graze on herbaceous plants and rarely browse on shrubs (Dawson and Ellis, 1994). Thus preferential grazing of herbaceous plants by abundant kangaroos may also contribute to shrub encroachment; however this hypothesis has yet to be tested. Because goats browse on shrubs, preferential grazing of herbaceous plants by goats may have a negligible impact on shrub encroachment; however this hypothesis is also yet to be tested.

Productivity likely influences the interaction between grazing by large mammalian herbivores and shrub encroachment. Australian desert plants exhibit dramatic population increases following ephemeral periods of high rainfall (Nicholls, 1991). Grazing by large mammalian herbivores often limits vegetation cover during prolonged dry periods when productivity is low, but not during ephemeral wet periods when productivity is high (Nicholls, 1991; Letnic et al., 2009; and Chapter 3 of this thesis). Livestock grazing (and possibly grazing by other large mammalian herbivores) is hypothesised to promote shrub recruitment during low rainfall periods when plant growth is constrained by desiccation and selective grazing by herbivores releases shrubs from inter-specific competition (Noble, 1998; Fensham and Fairfax, 2002; Chapter 2 of this thesis). However selective grazing by livestock (and possibly other large mammalian herbivores) is hypothesised to have little effect on shrub recruitment during high rainfall periods when plant growth is not constrained by desiccation, herbivore grazing cannot limit plant abundance, and inter-specific competition between shrub seedlings and herbaceous plants is high (Fensham et al., 2005; Chapter 2 of this thesis).

Grazing by large mammalian herbivores can reduce the frequency and intensity of fire by reducing fuel loads (Scholes and Archer, 1997; Letnic, 2004). Reduced fire frequency can facilitate shrub encroachment by reducing fire-related mortality of shrubs and shrub seedlings (Roques et al., 2001; Chapter 2 of this thesis). Fire-related mortality of mature shrubs greatly reduces the reproductive output of shrub populations in the years that follow a fire

(Harrington and Driver, 1995). Established shrubland communities can retard the frequency of fires by further reducing the abundance of combustible fuel (herbaceous plants including grasses; van Auken, 2000; Roques et al., 2001). Thus, increased grazing pressure by abundant large mammalian herbivores can facilitate decreases in shrub recruitment by suppressing fire related morality of shrubs and shrub seedlings.

Factor 4: La Niña phases of Southern Oscillation promote the recruitment of shrub seedlings, but also promote the abundance and impact of mammalian granivores and browsers, and the frequency of fires which constrain shrub recruitment. La Niña phases of Southern Oscillation facilitate increased shrub encroachment in areas where mammalian granivores and browsers are rare, but large mammalian herbivores are common.

Productivity in arid Australian ecosystems is primarily dependant on rainfall and the El Niño Sothern Oscillation (Nicholls, 1991; Letnic et al., 2005). During ephemeral and relatively short-lived La Niña phases on Southern Oscillation high rainfall releases vegetation from physiological constraints placed on plants by desiccation and allows for population increases; vegetation can because extremely abundant during La Niña periods (Nicholls, 1991). In response to increased productivity during La Niña phases of Southern Oscillation, mammalian granivores, browsers and grazers can become extremely abundant because food is not limited at any trophic level (Hunter, 1992; Letnic et al., 2005; Chapters 3 and 6 of this thesis). In contrast to La Niña phases, low rainfall - low productivity periods associated with dominant El Niño phases of Southern Oscillation constrains the recruitment and persistence of many plant species (Nicholls, 1991), which in turn constrains the abundances of mammalian granivores, browsers and grazers (Letnic et al., 2005; Letnic et al., 2009).

The mass recruitment of encroaching shrub species is often limited to La Niña phases of the Southern Oscillation when consistently high rainfall allows seedlings to reach the below-ground water table before desiccation (Harrington, 1991; Roques et al., 2001; Fensham et al., 2005). This represents a 1 in 20 year event for many encroaching shrub species (Harrington, 1991). Although the mass recruitment of shrubs largely occurs during La Niña phases of Southern Oscillation, shrub recruitment may be constrained during these periods if 1) herbaceous plants are abundant and inter-specific competition is high between herbaceous plants and shrub seedlings (Nicholls, 1991, Chapter 3 of this thesis), 2) abundant herbaceous plants facilitate fires which kill shrubs and shrub seedlings (Letnic et al., 2009; Chapters 2 and 3 of this thesis), and / or 3) abundant mammalian granivores and browsers consume large numbers of shrub seed and seedlings (Auld, 1995; Booth et al., 1996; Chapters 2, 5 and 6 of this thesis).

Although encroaching shrub species may produce seed during El Niño phases of Southern Oscillation - many encroaching shrub species seed annually (Cunningham et al., 1992) - the successful mass recruitment of shrub seedlings is ultimately constrained by aridity during El Niño periods (Harrington, 1991).

7.2.3 Could top predator extirpation promote shrub encroachment in other areas of the Earth?

Suppression of large predators by humans is a global phenomenon, owing to their depredations on livestock and, in some regions, the real or perceived threat that predators pose to people (Woodroffe, 2000; Ripple et al., 2014). Increases in the abundance of mesopredators and large herbivore grazers that follow the removal of top predators are also global phenomena (Roemer et al., 2009; Ripple et al., 2014), which have been linked in turn to 1) reduced abundances of mammalian predators of shrubs such lagomorphs and rodents (Ritchie and Johnson, 2009), and 2) increases in the abundance of livestock which preferentially graze palatable herbaceous plants over unpalatable shrubs (van Auken, 2000; Naito and Cairns, 2011). Given these widespread associations, it is possible that trophic cascades and the loss of top predators could also account for shrub encroachment in other areas of the Earth.

South-western United States of America (USA): an application of the 'top predator extirpation' model

In semi-arid areas of the south-west of the USA (USA states of Texas, Arizona, New Mexico) the historical decline of wolf top predators is thought to have altered ecosystem structure at multiple trophic levels equivalent to those we have used to link dingo extirpation to shrub encroachment in arid Australia. Because of this, the south-west of the USA provides an ideal location to test the top predator extirpation model proposed here.

Shrub encroachment is widespread through semi-arid grasslands of south-western USA where mesquite (*Prosopis* sp.), creosotebush (*Larrea tridentate*) and Juniper (*Juniperus* sp.) are the dominant encroaching shrub species (Dick-Peddie, 1999; van Auken, 2000; Romme et al., 2009). Increases in the abundance of encroaching shrub species in the south-western USA have been linked to the expansion of livestock grazing, reduced fire frequency in the region (van Auken, 2000; D'Odorico et al., 2012) and the decline of burrowing, herbivorous mammals such as rodents and lagomorphs that are known to consume shrubs (Weltzin et al., 1997; Roth et al., 2009; Davidson et al., 2012). The shift in the herbivory and fire regimes in the south-west USA coincided with the decline of wolves which became extinct in the region in the early 20th century (Ripple et al., 2013). Coyote abundance has increased following the extirpation of wolves; coyotes function as mesopredators in areas where they co-occur with wolves (Ripple et al., 2013). In turn, high densities of coyotes have been linked to the suppression, and in some cases endangerment of lagomorph and rodent populations (Henke and Bryant, 1999; Fedriani et al., 2000), a process that could conceivably release shrubs from herbivory and granivory by these taxa (Roth et al., 2009). Increased livestock grazing pressure which has occurred throughout the region following wolf extirpation (Ripple et al., 2013) has been linked to decreased grass cover (van Auken, 2000). Decreases in grass cover are thought to have facilitated increases in shrub recruitment by 1) releasing shrubs from inter-specific competition with grass, and 2) decreasing the frequency of fires which kill shrubs by reducing combustible fuel loads (van Auken, 2000; Knapp et al., 2008).

7.3 Implications of my thesis research

This thesis supports the hypothesis that top predator dingoes initiate an ecosystem-wide trophic cascade which directly and indirectly influences the abundance of many species within arid Australian ecosystems. The results of this thesis have particular relevance for conservation of Australia’s arid land ecosystems. Below I discuss how maintaining or restoring dingo populations could be used as a management strategy to conserve arid Australian ecosystems.

7.3.1 Dingo conservation suppresses the impact of mesopredators

My thesis research suggests that maintaining dingo populations or restoring them in areas where dingoes have previously been extirpated or suppressed has great potential as a strategy to mitigate the consumptive impacts of foxes and cats. It is likely that such dingo conservation programs will more broadly influence the productivity, structure and functioning of arid Australian ecosystems.

Current fox and cat management strategies typically rely upon distribution of baits impregnated with poisons such as 1080 (sodium flouroacetate; Burrows et al., 2003; Saunders et al., 2010b). Poison-baiting programs conducted at small spatial scales (< 12, 000 hectares) along roads can effectively suppress foxes and cats and reduce their impacts (Kinnear et al., 2002). However, ground-baiting campaigns are expensive and labour intensive, and are often ineffective in suppressing fox, and especially cat (cats generally require fresh poison baits distributed at high densities for effective control) populations over large areas owing to the absence of roads required to distribute baits, immigration of foxes and cats from surrounding areas, and the sheer number and cost of baits needed (Burrows et al., 2003; Gentle et al., 2007; Walsh et al., 2012). Because poison-baiting campaigns targeted at foxes and cats also tend to result in the suppression of dingo populations (Burrows et al., 2003), they may also be counter-productive from a biodiversity-conservation perspective if they reduce the top-down effects that dingoes have on fox and cat populations.

In contrast to cost and labour-intensive 1080 baiting programs, maintaining or restoring dingo populations may provide an economically viable ‘natural’ management strategy to control fox populations (Ritchie et al., 2012). Such a strategy would likely to be most successful in remote largely undisturbed landscapes such as the deserts and forests of inland and eastern Australia, respectively, where poison-baiting campaigns are unlikely to be effective and conflict between dingoes and livestock producers is less likely.

7.3.2 Dingo conservation suppresses the impact of native and non-native herbivores

Native kangaroos and non-native feral pigs and goats can reach extremely high densities in areas where dingoes are rare (Caughley et al., 1987; Letnic et al., 2012; Letnic et al., 2013). For example, density estimates of 17.1 red kangaroos (*Macropus rufus*) per km^2 were recorded for the Tibooburra district of western New South Wales during 2012 (NSW Kangaroo Management Program, 2013). Abundant kangaroos, pigs and goats, in combination with livestock, can dramatically impact the abundance, diversity and composition of vegetation communities through herbivory, as well as reducing pastoral productivity by reducing the abundance of fodder for livestock (Tiver and Andrew, 1997). Indeed, many cattle farms forgo dingo-control because dingo predation of kangaroos benefits cattle productivity (Letnic et al., 2012; plus commentaries such as www.abc.net.au/radionational/programs/bushtelegraph/dingoes/5269382).

Governments expend large sums of money to control the abundance of non-native pigs and goats, often to no avail (Reddiex et al., 2004). Although the kangaroo meat industry may somewhat constrain kangaroo abundance (NSW Kangaroo Management Program, 2013), governments and pastoralists expend little effort in controlling the abundance of kangaroos. Reintroducing dingo populations would greatly reduce the abundance of native and non-native large herbivore grazers. Such dingo reintroductions would likely benefit the abundance and diversity of vegetation communities by reducing herbivore grazing pressure, as well as benefiting pastoralists by producing more fodder for livestock. However dingo reinstalment would dramatically limit the area of sheep grazing land available for pastoralists (see 7.3.4 for further discussion regarding dingo – pastoralist conflict).

The control of feral pigs and goats for ‘ecosystem benefits’ is championed by most environmentalists and ecologists. However some authors have raised concerns about the relevance of population control programs which aim to reduce the abundance of ‘native’ kangaroos (Olsen et al., 2000). Because we simply do not know what kangaroo densities were like before European settlement, our management of kangaroo populations must be informed by an understanding of how kangaroos interact with other species within current day ecosystems. In light of this, kangaroo population control programs are probably warranted during times when abundant kangaroos limit the mass recruitment of vegetation through grazing.

7.3.3 Dingo conservation suppresses shrub encroachment

Burning of shrub-encroached lands is currently the most common method used by pastoralists to kill invasive woody shrubs and limit the effects of shrub encroachment (Hodgkinson and Harrington, 1985; Date, 1987; Noble, 1998; Roques et al., 2001). Burning over multiple years and during the correct season can reduce shrub encroachment by killing mature shrubs (Hodgkinson and Harrington, 1985; Harrington and Driver, 1995; Taylor Jr et al., 2012; Twidwell et al., 2013). In doing so, burning constrains shrub recruitment by reducing the gross reproductive output of shrub individuals (Harrington and Driver, 1995; Taylor Jr et al., 2012). As well as shrubs, burning reduces the abundance of herbaceous plants. During high rainfall and productivity periods, the seed of herbaceous plants quickly germinates and plants which are not killed by fires quickly re-sprout following fire (Bradstock, 2010). However, during low rainfall periods, shortage of water for germinating seeds or resprouting plants often constrains growth (Bradstock, 2010). Thus, continued prescribed burning to manage encroaching shrub species must be focused during high rainfall periods to allow for the persistence of herbaceous vegetation.

My thesis results and the top predator extirpation model proposed here to explain shrub encroachment assert that dingo reintroduction in areas where dingoes were once common but are now rare may be used as a management action to curb the impacts of shrub encroachment. A dingo reintroduction strategy such as this would represent a long-term solution which aims to ‘cure’ the root causes of shrub encroachment rather than the ‘prevention’ of shrub encroachment in the short term. Although an exciting idea, future research is required to further evaluate if and / or how dingo reinstalment may initiate trophic cascades which limit shrub encroachment in different land systems types (e.g. arid grasslands, semi-arid woodlands, tropical savanna of northern Australia) and during different climatic conditions. Long term experiments which quantify ecosystem responses to dingoes over a range of dingo densities would produce such results. However such experiments may be logistically difficult to conduct due to the long time frames required to track the fate of shrub seed from germination to death (up to 70 years for hopbush).

7.3.4 Implementing dingo conservation and reinstalment management strategies

Maintaining or restoring dingo populations for conservation purposes poses particular problems for pastoral productivity. Dingoes kill sheep and in doing so cost graziers (mainly sheep growers) millions of dollars each year (Fleming et al., 2001). Because of this, conservation programs which aim to maintain or restore dingo populations must incorporate actions which mitigate the predatory impacts of dingoes on livestock. Such mitigation could include 1) the use of guardian animals such as Maremma shepherding dogs, donkeys or alpacas which defend livestock from dingoes through olfactory, auditory, visual cues and physical defences (van Bommel, 2013), 2) the development of ‘mosaic’ type poison bating and exclusion fencing programs which exclude dingoes from some areas but not others in a way which spreads the ecosystem benefits initiated by dingoes across landscapes (Knowlton et al., 1999), and 3) the transition of pastoral land-use practices away from sheep growing and towards cattle growing. Government subsidy programs which compensate pastoralists for dingo related stock losses could also be used to minimise the economic impact of dingoes on the pastoral industry. Although such strategies may mitigate stock losses caused by dingo predation, it is important to note that ‘precautionary management’ principles maintain that further knowledge is required regarding how dingoes interact within arid Australian ecosystems before such ‘dingo reintroduction’ programs could be implemented.

7.4 Limitations and problems encountered during my thesis research

7.4.1 Natural and pre-defined experiment

The study of large mammalian carnivores and trophic networks poses a number of logistical problems owing to the large spatial and temporal scales necessary to conduct *in situ* experiments (Oksanen, 2001). One way to examine the role of large predators is to evaluate ‘natural experiments’ or ‘predefined experiments’ wherein the abundance of top-predators varies in space or time in otherwise similar landscapes (Terborgh et al., 2001; Elmhagen et al., 2010). My thesis utilised Australia’s dingo-proof fence as a predefined experimental treatment. Sample sites on either side of the dingo-proof fence were matched based on information regarding land-use history obtained from archive documents and consultation with local landholders. All sites experienced sheep grazing during the late 1800s and early 1900s ; were paired for habitat type and distance from natural water source; occurred in areas where fire has been historically rare; were spatially clustered in relatively close proximity to the dingo-proof fence; and were similarly distanced from artificial watering points (at least 1 – 3 km; distance to artificial watering points is a proxy for livestock grazing pressure; James et al., 1999). By closely matching sites inside and outside the dingo-proof fence I have ensured that my results are comparable and do not simply identify underlying differences in land-use history or geography.

Although I tried to match sites on both sides of the dingo-proof fence as closely as possible, some differences were still evident. The most obvious of these differences was that sheep and cattle were grazed inside the dingo-proof fence and only cattle were grazed outside the dingo-proof fence. Sheep and cattle graze and browse differently and thus can differently affect vegetation composition (Holechek et al., 2010). I employed a number of approaches to account for differences in livestock grazing on either side of the dingo-proof fence in this thesis. First, I compared abundance indices of mammals and vegetation cover between pastoral areas where livestock were grazed and conservation areas where livestock were excluded (Strzelecki Regional Reserve and Sturt National Park) both inside and outside the dingo-proof fence. Second, I sampled sites along transects which were spaced 1 - 3 km from artificial watering points. Third, I used dry sheep equivalents to express total grazing pressure. Fourth, I used statistical models to compare the strength of influence that livestock grazing had on ecosystem processes when compared with the influence of other variables (i.e. predator abundance).

7.4.2 Spatial and temporal confounding

Experiments which replicate across space and through time are needed to understand processes and patterns occurring in ecological communities (Quinn and Keough, 2002). A major issue facing experiments which replicate at large spatial (1000 km^2, 10000 km^2, 100000 km^2) and temporal (years, decades, centuries) scales is that logistical constraints imposed on sampling can result in low replication, or independence issues which arise when replicate units are not sampled at the correct scale (Oksanen, 2001).

My thesis research asked a question which required replication at large spatial and temporal scales; do dingoes initiate ecosystem-wide trophic cascades within arid Australia? Although my thesis experiments were replicated at a large spatial scale (~ 13,000 km^2) and were conducted over an extended 30 month period, a number of potentially confounding factors may have influenced my results. The most obvious of these was that I sampled within a relatively (in relation to the size of Australia) small section of the Strzelecki Desert during and after a rare high rainfall event. It was beyond the reach of this thesis to replicate in other desert areas of Australia or during drier ‘drought’ periods. However because other studies have also shown that dingoes initiate ecosystem-wide trophic cascades which influence the abundances of many species within arid Australian ecosystems (Johnson et al., 2007; Letnic et al., 2009; Letnic and Dworjanyn, 2011; Letnic and Crowther, 2013), it is likely that many of my results reflect broad patterns which operate at larger spatial scales. This said, the strength or weakness of dingo effects within ecosystems are likely dependant on a number of exogenous variables such as rainfall, latitude, predator and / or prey abundance and diversity, or soil productivity. Because of this, it is likely that the dingo effects in arid Australia ecosystems show considerable variation in space and through time in ways not previously reported within the scientific literature.

In chapters 3 and 4 of this thesis logistical constraints meant that some sites were sampled during different time periods than others. Productivity was high between sampling periods (as shown through high grass, herb and forb cover; Chapters 2 and 3) owing to high rainfall conditions which dominated during sampling. Because of this it is likely that ecosystem processes did not show considerable variation between sampling periods. Although this may be true, I incorporated random factors within generalized and linear mixed-effects models to ensure that if temporal variability in sampling period did influence my results, this variability was accounted for in my statistical models.

Another potentially confounding factor which may have affected my sampling was spatial autocorrelation. Spatial autocorrelation occurs when the value of a variable at one location is influenced by the values of neighbouring variables (Dormann et al., 2007). Spatial autocorrelation indicates that observations are not independent and is a common issue affecting the interpretation of datasets which are replicated at large-spatial scales. I tested for spatial autocorrelation (using the Moran I test statistic) in the residuals of all the linear and generalized linear models and mixed-effects models used in this thesis to identify if the relationships between independent variables influenced the abundance of dependant variables within models. Statistical significant levels of spatial autocorrelation were not detected within the residuals of my models, excluding the residuals of the shrub cover estimates produced in chapter 2 (see Chapter 2 for a description of methods used to incorporate spatial autocorrelation in models). By testing for and incorporating spatial dependency within the statistical models used in this thesis I have ensured that my conclusions are not due to spatial autocorrelation.

7.4.3 Abundance estimates

Many ecological monitoring programs ultimately aim to quantify the actual population densities of animals occurring in any one area (Borchers et al., 2002). Although an ideal, it is practically impossible to quantify actual population densities in many cases because it is unlikely that every animal within a vast landscape will be counted. Because of this, sampling techniques which produce suitable correlates of actual population abundance are often used to estimate population abundance (Wilson and Delahay, 2001; Borchers et al., 2002).

Two methods frequently used to estimate population abundances of animals are mark-recapture surveys (White and Burnham, 1999), and line and point transect surveys which incorporate detection functions (MacKenzie and Kendall, 2002). Unfortunately, constraints imposed on my data which resulted from 1) the sample methods used, and 2) the markedly different animal abundances observed on either side of the dingo-proof fence and between high and low rainfall periods, negated the use of these methods here. For example, mark re-capture surveys were not used to estimate population densities of rodents because re-capture rates between trips were very low. Detection functions were not included in my spotlight surveys because low detection of dingoes and rabbits inside the dingo-proof fence and low detection of foxes, cats and kangaroos outside the dingo-proof fence meant that detection probabilities could not be calculated independently for these areas.

In lieu of quantifying actual population abundance or incorporating mark-recapture studies or detection function estimates, I have used a number of ‘tried and tested’ sampling methods to estimate animal abundance and activity in this thesis. These techniques included live trapping to estimate rodent abundance (Moseby and Read, 2001; Tasker and Dickman 2001); spotlight line transects to estimate predator, rabbit, rodent, and little button-quail abundance (Fletcher et al., 1999; Sharp et al., 2001; Letnic and Dworjanyn, 2011); and predator-tracking plots to estimate predator activity (Funston et al., 2010; Letnic et al., 2012). Although these techniques approximate abundance only, the use of the same methods between treatment areas inside and outside the dingo-proof fence has ensured that my results are comparable between sites. The consistent trends which were observed between sampling techniques used within this thesis further validated their use. For example, rodent abundance estimates were similar using live trapping and spotlight survey methods (Chapters 2, 4, 5 and 6). Predator activity estimates were similar using tracking plot and spotlight survey methods (Chapter 2, 3, 4 and 6).

Although the abundance estimates used here were appropriate, it is important to note that further research is needed to develop sight specific methods which efficiently estimate animal abundances within a cost and time efficient framework. Indeed there are few scientific papers which do this in arid Australian environments.

7.5 Avenues for future research

Natural or pre-defined experimental treatments such as the dingo-proof fence provide valuable insight into processes occurring at spatial and temporal scales which are logistically difficult to manipulate using traditional before-after-control-treatment experiments. The development of such before-after-control-treatment type experiments which manipulate the density of dingoes and control for differences in livestock grazing would further promote the hypothesis that dingoes act as trophic regulators in arid Australia. Although such experiments are logistically difficult to conduct at large spatial and temporal scales, given the weight of evidence that is continuing to support the assertion that dingoes benefit arid Australian ecosystems by suppressing mesopredators and large herbivores, I (and many others) feel that funding for such before-after-control-treatment type experiments is warranted. Given the opportunity, these would both experimentally test the assertion that dingoes are important top predators in arid Australia, as well as provide valuable information regarding how dingoes may do this. For example, do dingoes similarly influence ecosystems at high and low population densities; during dry and wet climatic conditions; in different habitat types; at different population densities of prey and / or mesopredators? The results of such experiments would be extremely informative in the development of land management strategies which aim to conserve biodiversity and functionality not only in Australian deserts, but also globally in areas where top predators are thought to play ‘keystone’ roles within ecosystems.

7.6 References

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